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1 **Burrowing in blindsnakes: a preliminary analysis of burrowing forces and consequences for the**
2 **evolution of morphology.**

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29

30 **Abstract**

31 Burrowing is a common behavior in vertebrates. An underground life-style offers many advantages
32 but also poses important challenges including the high energetic cost of burrowing. Scolecophidians
33 are a group of morphologically derived subterranean snakes that show great diversity in form and
34 function. Although it has been suggested that leptotyphlopids and anomalepidids mostly use existing
35 underground passageways, typhlopids are thought to create their own burrows. However, the
36 mechanisms used to create burrows and the associated forces that animals may be able to generate
37 remain unknown. Here, we provide the first data on push forces in scolecophidians and compare
38 them with those in some burrowing alethinophidian snakes. Our results show that typhlopids are
39 capable of generating higher forces for a given size than other snakes. The observed differences are
40 not due to variation in body diameter or length, suggesting fundamental differences in the
41 mechanics of burrowing or the way in which axial muscles are used. Qualitative observations of skull
42 and vertebral shape suggest that the higher forces exerted by typhlopids may have impacted the
43 evolution of their anatomy. Our results provide the basis for future studies exploring the diversity of
44 form and function in this fascinating group of animals. Quantitative comparisons of the cranial and
45 vertebral shape in addition to collecting functional and ecological data on a wider array of species
46 would be particularly important to test the patterns described here.

47 **Introduction**

48 Burrowing is a common behavior among vertebrates that dates back at least to the Devonian
49 (Benton, 1988; Kinlaw, 1999). The exploitation of the underground offers many advantages including
50 shelter from predators, novel prey resources and an environment buffered from extreme
51 fluctuations in temperature (Sumbera et al., 2004). However, the underground environment also
52 poses important challenges including low oxygen content (McNabb, 1966; Arieli, 1979), and the high
53 energetic cost of creating burrows (Vleck, 1979; Navas et al., 2004). Tetrapods have radiated into the
54 underground environment many times independently and have developed solutions to the
55 constraints of burrowing and underground locomotion (i.e., substrate density; see Nevo, 1979). As
56 the cost of creating tunnels is directly related to the diameter of the animal (Navas et al., 2004; Wu
57 et al., 2015), it is no surprise that many limbless vertebrates, characterized by a reduced body
58 diameter, have colonised the underground environment including caecilians, lizards and snakes
59 (Gans, 1986). However, the mechanisms used to create, enlarge, or maintain burrows remain
60 relatively poorly understood (but see Gaymer, 1971; Gans et al., 1978; Gasc, 1982; O'Reilly et al.,
61 1997; Quillin, 2000; Dorgan et al., 2005; Dorgan, 2015).

62 Among limbless tetrapods, snakes occupy a special place as many forms are known to
63 burrow (Davis, 1946; Young & Morain, 2003; Deuffel, 2017). Moreover, snakes have been suggested
64 to have gone through a fossorial phase early-on in their evolutionary history (da Silva et al., 2018;
65 Miralles et al., 2018). Despite extensive studies on locomotion in limbless lizards in general, and
66 snakes in particular (e.g., Gans, 1973, 1986; Gasc, 1984; Gasc & Gans, 1990; Hohl et al., 2014;
67 Newman and Jayne, 2018), surprisingly little is known about their burrowing mechanics. Even more
68 surprisingly, not a single study has been devoted to the analysis of burrowing in scolecophidians, an
69 entire 'clade' of burrowing snakes. To date, only a single study has described the anatomy of the
70 muscles of the axial system in any detail (Gasc, 1981), rendering our understanding of how these
71 animals may create burrows nearly inexistent.

72 Scolecophidians are now divided into two superfamilies, the Typhlopoidea (blind snakes) and
73 Leptotyphlopoidea (thread snakes). Based on their anatomy the Anomalepidae have long been
74 regarded as a third group within Scolecophidia, but recent molecular phylogenies suggest they might
75 actually be more closely related to Alethinophidians (cfr. Miralles et al., 2018). Scolecophidians
76 diverged from other snakes (Alethinophidia) about 125 to 130 Mya in the Early Cretaceous (Zheng &
77 Wiens, 2016; Schneider Fachini et al., 2020), and the divergence between Typhlopoidea and
78 Leptotyphlopoidea probably followed soon thereafter, around 120 – 130 Mya (Pyron & Burbrink,
79 2012; Zheng & Wiens, 2016; Miralles et al., 2018; but see Vidal et al., 2010). Comparatively, most

80 alethinophidian snake families diverged beginning in the Eocene into the Oligocene between 40 – 60
81 Mya (see Pyron & Burbrink, 2012; Zheng & Wiens, 2016; Zaher et al., 2019). Thus, the
82 scolecophidians have long been on a separate evolutionary trajectory from other snakes, but within
83 the group itself the family-level lineages are characterized by long branch lengths and early
84 divergences dating back to the Cretaceous (Adalsteinsson et al., 2009; Pyron & Burbrink, 2012;
85 Miralles et al., 2018).

86 Alethinophidian snakes are a species-rich clade (~3,900 species) with at least one clade, the
87 Endoglyptodonta (*sensu* Zaher et al., 2019, or Colubroidea *sensu* Pyron & Burbrink, 2012),
88 contributing to the bulk of the richness. Synapomorphies for this clade are cranial features
89 comprising a venom delivery system, and this key innovation may have allowed them to diversify so
90 suddenly and so widely (Pyron & Burbrink, 2012). The scolecophidians are comparatively species-
91 poor with just 459 species described (see Uetz et al., 2020), although it is very likely that there are
92 numerous cryptic species (Thomas & Hedges, 2007; Busschau et al., 2021). The bulk of these species
93 (60%) resides within one family, the Typhlopidae (Pyron & Wallach, 2014; Uetz et al., 2020). This
94 family has also been noted to have an unusually high net diversification rate (Pyron & Burbrink, 2012)
95 but the mechanisms that drove this elevated diversification rate are obscure. It is possible that the
96 initial advancement of scolecophidians toward specialization was their capitalization on a new
97 trophic niche that arose around 130 Mya; i.e., the divergence of ants from other Hymenoptera (see
98 Brady et al., 2006) and their subsequent dominance of ecosystems, making them a reliable prey
99 source. Furthermore, the increased speciation rate for Typhlopidae beginning around 50 Mya (Pyron
100 & Burbrink, 2012) could have been a response to the increased speciation rate that also occurred
101 around 50 Mya in several New World ant genera (see Moreau & Bell, 2013).

102 Although scolecophidians have a conserved morphology and have therefore been erroneously
103 termed ‘primitive’ or ‘basal’, they are in fact extremely specialized with a phenotype that is well-
104 adapted to a strictly fossorial life-style (da Silva et al., 2018; Miralles et al., 2018). They forage
105 underground, primarily on the eggs, larvae, pupae, and adults of ants and termites, and unlike
106 alethinophidians, they consume large numbers of small prey (Shine & Webb, 1990; Webb & Shine
107 1993; Webb et al., 2001). This requires them to move through existing underground passageways (in
108 the case of leptotyphlopids) or to create new underground tunnels (in the case of typhlopids) to
109 invade ant or termite colonies. They use chemoreception to locate their prey, but this does not
110 appear to be restricted to the detection of only a single prey species (Watkins et al., 1967; Webb &
111 Shine, 1992). Leptotyphlopids can avoid detection from ants and termites through chemical crypsis,
112 and this is possibly achieved through sequestration of their prey’s defensive compounds with the

113 subsequent release of these compounds through glands (Watkins et al., 1969; Webb et al., 2000;
114 Savitzky et al., 2012). Conversely, typhlopids probably withstand attacks by ants or termites through
115 their more heavily armoured body (Webb & Shine, 1993). Thus, while the two superfamilies of
116 scolecophidians have basic similarities in terms of life-history and are superficially similar in
117 morphology, they probably have quite different adaptations allowing them to have a highly
118 specialised ecological niche and different specializations towards burrowing.

119 Here, we provide new data on burrowing performance and cranial and vertebral morphology in
120 scolecophidian snakes and compare them to data for some alethinophidian burrowers. Given that
121 leptotyphlopids are thought to use existing burrows in contrast to typhlopids which construct their
122 own burrows, we predict that typhlopids will be better burrowers for their size. As most
123 alethinophidian burrowers utilize the relatively 'soft' top compartment of the soil we predict them to
124 be more similar to leptotyphlopids and produce less force for a given size.

125 **Materials and methods**

126 *Animals*

127 Burrowing forces were measured in the field in Kenya (*Afrotyphlops angolensis*, *Rhinotyphlops*
128 *unitaeniatus*), or South Africa (*Leptotyphlops scutifrons*, *Rhinotyphlops lalandei*), or in the lab
129 (*Liotyphlops beui*, *Myriopholis algeriensis*). For comparative purposes we also recorded data on
130 alethinophidian snakes in the field (Kenya: *Aparallactus guentheri*; French Guyana: *Anilius scytale*,
131 *Oxyrhopus melanogenys*) and in the lab (*Eryx colubrinus*, *Farancia abacura*, *Loxocemus bicolor*). The
132 number of individuals per species used is summarized in Table 1.

133 To better understand how the measured burrowing forces may impact the anatomy of the head and
134 vertebrae we CT-scanned one specimen each of *Anilius unguirostris* (MNHN 1895.449; voxel size:
135 16.3 μm), *Epictia tenella* (MNHN 2011.319; voxel size: 11.2 μm), and *Typhlophis squamosus* (MNHN
136 1999.8306; voxel size: 8.81 μm) at the AST-RX platform at the Muséum national d'histoire naturelle
137 on a v|tome|x machine. For comparative purposes we also used CT-scans of *Anilius scytale* (KUH
138 125976; voxel size: 23.7 μm), *Leptotyphlops nigricans* (LSUSM Z57237; voxel size: 3.5 μm),
139 *Liotyphlops albirostris* (UMMZ 48173; voxel size: 10.8 μm) and *Rhinotyphlops lalandei* (UMMZ 61525;
140 voxel size: 11.3 μm) that were downloaded from Morphosource.

141 *Morphometrics*

142 Animals captured in the field were weighed using an electronic balance (Ohaus, ± 0.1 g) or a Pesola
143 spring scale (± 0.5 g). Body diameter was measured using a digital calliper (Mitutoyo, ± 0.1 mm). The
144 snout-vent length was measured by stretching the animals along a ruler (± 1 mm). A summary of the
145 morphometric data is provided in Table 1.

146 *Force measurements*

147 Measurements of peak push forces were made using a piezoelectric force platform (Kistler Squirrel
148 force plate, ± 0.1 N, Kistler Inc., Switzerland) as described previously (Vanhooydonck et al., 2011; Le
149 Guilloux et al., 2020; Fig. 1). In brief, the force platform was positioned on a metal base and
150 connected to a charge amplifier (Kistler Charge Amplifier type 9865, Kistler Inc.). A Perspex block
151 with 1 cm-deep holes of different diameters was mounted on the force plate, level with the front
152 edge. One of the holes was loosely filled with soil. A Perspex tunnel with a diameter approximately
153 equal to the maximal body diameter of the test animal was mounted on the metal base in front of
154 (but not touching) the force plate, and aligned with the soil-filled hole in the Perspex block. An
155 animal was then introduced into the tunnel and allowed to move through it until reaching the soil-
156 filled chamber. Next, the animal was stimulated to burrow into the soil by touching the end of the
157 tail sticking out of the tunnel, or by prodding the animal inside the tunnel with the blunt end of a thin
158 wooden stick. Forces were recorded during 60 s recording sessions at 500 Hz, and three trials were
159 performed for each individual, with at least 1 h between trials. Forces were recorded in three
160 dimensions using the Bioware software (Kistler Inc.; Fig. 1). For each individual we then extracted the
161 highest peak resultant force across all trials as an indicator of that animal's maximal push force. A
162 summary of the force data is provided in Table 1.

163 *Statistical analyses*

164 All data were Log_{10} -transformed before analyses to ensure normality and homoscedasticity. To
165 explore which traits (snout-vent length, body mass or body diameter) best explained variation in
166 push force data (resultant force) we ran a stepwise multiple regression across data for all individuals.
167 Next, we tested whether differences between groups (Alethinophidia, Typhlopidae,
168 Leptotyphlopidae, Anomalepididae) were observed in resultant force, using an ANCOVA with snout-
169 vent length as our co-variate. To test which groups differed from one another, we next ran simple
170 regressions on maximal push force (resultant), body diameter, and body mass with snout-vent length
171 as our predictor and extracted unstandardized residuals. We then ran an ANOVA on residual
172 resultant force coupled to Bonferroni post-hoc tests to explore which groups differed from one
173 another. Finally, we ran Pearson correlations between residual data to explore whether body

174 diameter or body mass, independent of the effect of snout-vent length, explained variation in
175 residual maximal resultant force and ran a MANOVA to test whether clades differed in residual body
176 mass and residual body diameter. All analyses were run in IBM SPSS V. 26. Significance was set at $P <$
177 0.05.

178 Although the data set is composed of different species and sometimes contains several individuals
179 within species, we decided not to use phylogenetic comparative methods on species means given the
180 small sample sizes and incomplete taxon sampling. Future analyses on larger and more robust data
181 sets could provide an assessment on whether the patterns described here are born out.

182 **Results**

183 Maximal push forces across the species studied ranged from 0.21 N for *Myriopholis algeriensis*, the
184 smallest species in our data set, to 18.18 N for *Afrotyphlops angolensis*, the largest scolecophidian in
185 our data set (Table 1). In all taxa, forward-directed forces made up between 50 and 65% of the total
186 force, suggesting that all taxa are capable of generating forward-directed forces (Fig. 1). Lateral and
187 dorso-ventral forces contributed roughly equally (between 16 and 25%) to the remainder of the
188 forces generated. No clear differences were observed between groups in how forces were applied,
189 however. Rather individuals within a species sometimes showed different strategies, with one
190 *Rhinotyphlops lalandei* pushing only 34% in the forward direction, whereas in another individual 59%
191 of the force was directed forward.

192 A multiple stepwise regression with snout-vent length, body mass and body diameter retained a
193 significant model with only snout-vent length as the predictor ($R^2 = 0.78$; $P < 0.001$; slope = $1.93 \pm$
194 0.20 , intercept = -4.40 ± 0.49). Thus, longer snakes were able to produce higher resultant forces (Fig.
195 2A). The ANCOVA detected significant effects of snout-vent length ($F_{1,28} = 62.54$; $P < 0.001$) and
196 phylogenetic group ($F_{3,28} = 70.70$; $P < 0.001$) on maximal push force, suggesting that individuals from
197 different phylogenetic groups differed in their maximal push force irrespective of variation in snout-
198 vent length. The ANOVA run on residual maximal push force was significant ($F_{3,29} = 8.87$; $P < 0.001$).
199 Post-hoc tests indicated that Typhlopidae differed from all other groups (all $P < 0.018$), yet none of
200 the other groups differed. The inspection of the marginal means showed that typhlopids produced
201 higher maximal push forces for a given snout-vent length than other species (marginal means;
202 Typhlopidae: 0.329; Leptotyphlopidae: -0.149; Anomalepididae: -0.181; Alethinophidia: -0.053).
203 Finally, residual maximal push force was correlated with residual body diameter ($r = 0.44$; $P = 0.011$)
204 but not residual body mass ($r = 0.33$; $P = 0.077$), showing that snakes with relatively wider bodies
205 were able to push harder (Fig. 2B). Yet, the difference in push force was not explained by the

206 difference in body diameter as a MANOVA on residual body diameter and residual body mass
207 detected no differences between groups (Wilks' lambda = 0.69; $F_{6,48} = 1.67$; $P = 0.15$; uni-variate
208 ANOVAs: body diameter: $F_{3,25} = 2.25$; $P = 0.11$; body mass: $F_{3,25} = 2.49$; $P = 0.08$).

209 Inspection of the CT-scans showed interesting differences in cranial and vertebral anatomy between
210 the different species examined (Fig. 3). Overall, all burrowing species had blunt and robust snouts in
211 dorsal view with surprisingly unfused and rather simple sutures. However, in lateral view differences
212 between species were striking. Aside from differences in the tooth-bearing elements associated with
213 their radically different feeding modes (Kley & Brainerd, 1999; Kley, 2001, 2006; Rieppel et al., 2009;
214 Strong et al., 2021), the shape of the anterior part of the cranium was very different with *Anilius* and
215 *Rhinotyphlops* having more pointed shapes. The vertebral morphology was also rather different with
216 the condyle and cotyle of *Anilius* being wide and tall compared to those in the other species (Fig. 4).
217 Moreover, the facets of the pre- and postzygapophyses appear more laterally positioned and more
218 robust in *Anilius* (Fig. 4). Note however, that *Anilius* was larger than the other species examined and
219 as such that allometry may partly be responsible for the observed differences.

220 **Discussion**

221 The first ever data on maximal push forces in burrowing snakes suggest that significant interspecific
222 differences exist, with typhlopids snakes being able to generate higher forces for a given body length.
223 As typhlopids are considered active burrowers in contrast to leptotyphlopids, which are thought to
224 mostly use existing underground passageways, this observation is in line with our predictions.
225 Alethinophidian snakes also generated relatively low forces for their size which may correspond to
226 the fact that they mostly use the softer top compartment of the soil for burrowing. Interestingly,
227 although snout-vent length and residual body diameter are both correlated to the force generation
228 capacity in the animals included in our data set, these variables did not explain why typhlopids snakes
229 were able to generate higher forces. Longer snakes can be expected to have more overall muscle
230 mass and an increase in the relative diameter should allow for the packing of muscles with a greater
231 cross-sectional area (Gans, 1974). This is confirmed by our results where longer snakes do indeed
232 have a greater diameter (Pearson correlation: $r = 0.86$; $P < 0.001$). Whereas this may explain the
233 observed relationships between force, length and diameter, this does not explain differences
234 between the different groups of snakes. It is likely that different burrowing snakes use different
235 mechanisms for burrowing (as suggested for amphisbaenians with different head shapes for
236 example; Gans, 1974), allowing them to recruit the axial muscles differently. This is translated in
237 differences in overall proportions with leptotyphlopids being generally extremely narrow and long in
238 contrast to typhlopids which are much more robust and have a greater diameter for a given snout-

239 vent length [note that exceptions exist with, for example, *Anilius grypus* showing an aspect ratio
240 (total length divided by midbody diameter) of 130].

241 Although the exact mechanisms used by these snakes to generate burrowing force while in a tunnel
242 remains unknown, the mostly forward-directed forces (very different from what has been described
243 in burrowing scincid lizards, for example; see Vanhooydonck et al., 2011) suggest that they may use a
244 mechanism similar to what has been described for caecilians (Gaymer, 1971; O'Reilly et al., 1997) and
245 hypothesized to exist in uropeltid snakes (Gans et al., 1978): internal concertina. This type of
246 burrowing involves bending followed by an extension of the vertebral column within the skin
247 envelope, allowing animals to recruit most of their body wall muscles to generate forward-directed
248 forces. In contrast, non-specialized snakes will use muscular forces to push laterally against the side
249 of a straight-sided tunnel in a typical concertina movement to traverse smooth tunnels (Gray &
250 Lissmann, 1950; Gans, 1974). X-ray video analysis is needed to be able to understand the movements
251 of the skin and vertebral column and thus to test whether skin-vertebral independence exists in
252 scolecophidian snakes in general and typhlopids snakes more specifically. Unfortunately, our
253 understanding of the axial musculature in burrowing snakes, and especially in scolecophidian snakes,
254 remains extremely fragmentary (Gasc, 1981). The musculature has been suggested to be convergent
255 on that observed in amphisbaenian lizards, another group of very strong burrowers (Gasc, 1982;
256 Navas et al., 2004; Hohl et al., 2014) but with a typical snake bauplan (Gasc, 1981). A remarkable
257 feature of the muscular anatomy in typhlopids is the absence of the *m. costo-cutanei* resulting in an
258 anatomical independence between the axial and cutaneous muscles (Gasc, 1981). However, these
259 data are based on the dissection of a single specimen of *Afrotyphlops* (*A. punctatus*) and differ from
260 what has been reported by Mosauer (1935), illustrating the need for further studies on the axial
261 musculature. The small size of many leptotyphlopids and anomalepids has prevented direct
262 dissections of the musculature. However, contrast-enhanced μ CT scans may provide a unique
263 opportunity to better understand the musculature in these extremely small animals (Metscher,
264 2009).

265 Our qualitative anatomical comparisons of skull and vertebral morphology suggest that the higher
266 forces generated by typhlopids snakes may be reflected in the shape of these structures. Whereas all
267 burrowing species had blunt and robust snouts in dorsal view, the shape of the anterior part of the
268 cranium was very different with *Anilius* and *Rhinotyphlops* having more pointed shapes possibly
269 facilitating substrate penetration. Given the high forces encountered during burrowing it was
270 unexpected to see little or no fusion of the cranial sutures, in contrast to what is observed in, for
271 example, trogonophid amphisbaenians where the cranial sutures are highly interdigitated (Gans,

272 1974). Elongate and highly interdigitated sutures have been suggested to be a response to torsional
273 stresses in the skull induced by oscillatory digging (Gans, 1974). The fact that the recorded forces
274 were mostly directed forward may explain the difference in skull morphology between burrowing
275 snakes and amphisbaenians. However, the snout-complexes in scolecophidian skulls are often
276 characterized by overlapping skull bones and inspection of the CT-scans showed this to be the case in
277 the species included in the present study. Moreover, qualitatively this appeared to be more striking
278 in typhlopids compared to leptotyphlopids and anomalepids, but this needs to be tested quantitatively.
279 If confirmed, this could provide a mechanism by which the snout is reinforced and may allow
280 typhlopids to withstand the higher forces generated during burrowing. The vertebral morphology
281 was also rather different with the condyle and cotyle of the typhlopid *Anilius* being relatively wide
282 and tall. Moreover, the facets of the pre- and postzygapophyses appear more laterally positioned
283 and more robust in this species. Given the higher push forces recorded for typhlopid snakes the
284 larger surface areas in contact with the cranium may permit a better dissipation of the substrate
285 reaction forces during burrowing. Similarly, the more robust pre- and postzygapophyses may help
286 dissipate load in addition to stabilizing the cervical vertebrae when loaded in compression during
287 burrowing. Finite element analyses of the cranium and vertebrae in these animals could be
288 particularly useful to better understand whether the observed morphology is indeed a response to
289 the forces encountered during burrowing. Additionally, exploring variation due to allometry would
290 be important as the animals examined here differed considerably in size.

291 The use of 3D geometric morphometric approaches (e.g., Fabre et al., 2016; Segall et al., 2016) could
292 be of interest to: 1) quantify possible differences in head, cranial and vertebral shape in typhlopids in
293 comparison to other burrowing snakes, and 2) to explore whether cranial and vertebral shape covary
294 with the push forces measured *in vivo*. These studies are ongoing and may provide better insights
295 into the evolution of burrowing and the diversity of form and function in burrowing snakes. Finally,
296 as our study included only a very small part of the diversity of burrowing snakes, scolecophidian or
297 otherwise, future measurements on other species are likely to change our understanding of the
298 evolution of diversity of form and function in burrowing snakes.

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454 **Figure legends**

455 **Figure 1:** Top: set-up illustrating the force plate, tunnel and Perspex block during push force
456 measurements of an *Afrotyphlops angolensis* measured in Kenya. Bottom: example force trace
457 showing two pushes in a *Rhinotyphlops unitaeniatus* measured in South Africa. Note how the
458 forward-directed force (FX, red) is much greater than the lateral (FY, green) or dorso-ventral (FZ,
459 blue) forces, especially during the strongest push.

460 **Figure 2:** A) Scatterplot showing the relationship between snout-vent length and maximal push force
461 in snakes. Each point is the maximal force recorded for a given individual. On average typhlopids
462 generate higher forces for their snout-vent length than other snakes. Leptotyphlopids and
463 anomalepidids do not differ from alethinophidian snakes in the relationship between snout-vent
464 length and push force. B) Scatterplot illustrating the relationship between residual body diameter
465 and residual push force in snakes illustrating that snakes with relatively wider bodies push harder.
466 Interestingly, even for a given residual body diameter typhloid snakes still generate more force than
467 other snakes.

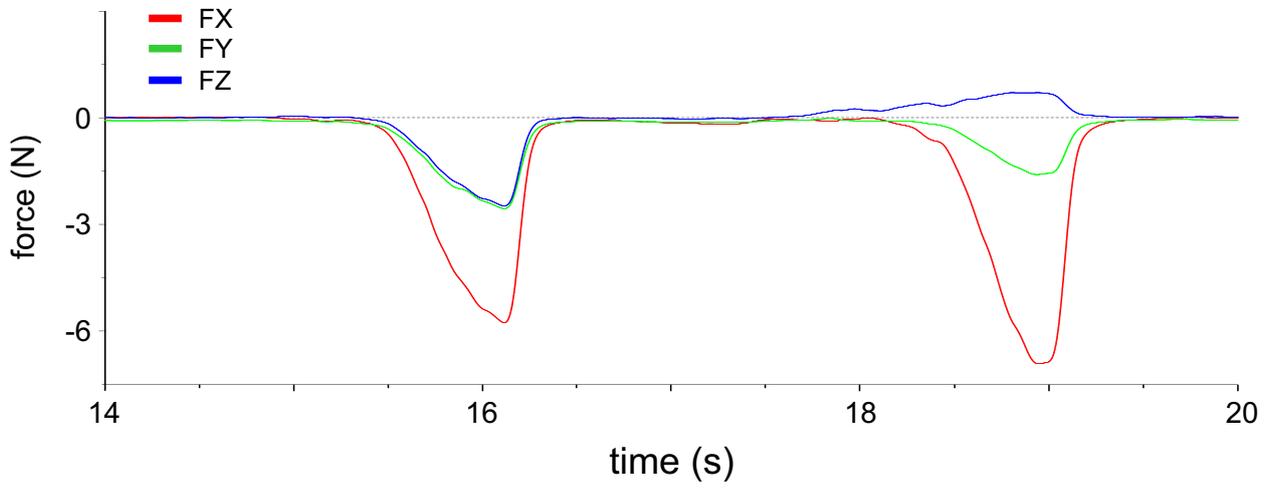
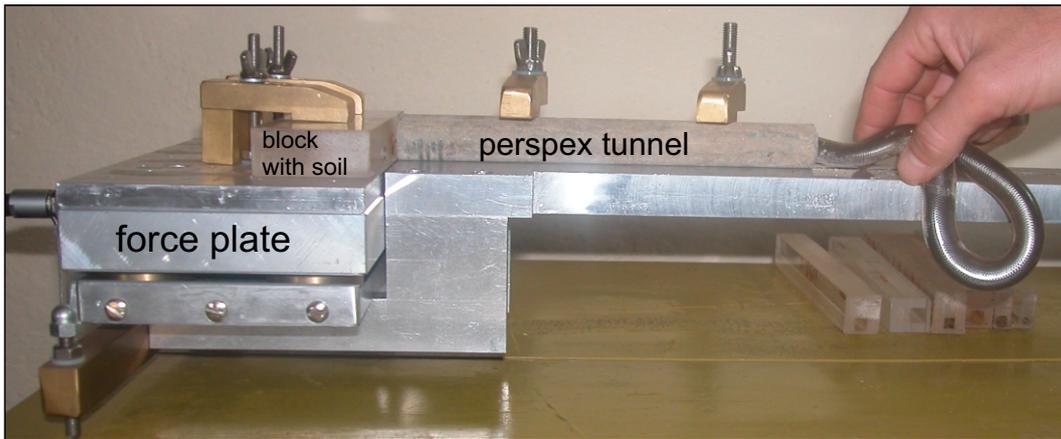
468 **Figure 3:** Cranial anatomy in burrowing snakes. Computed tomography (CT) scans of skulls in dorsal
469 (left) and left lateral (right) views. A) *Anilius scytale* - Aniliidae, B) *Liotyphlops albirostris* -
470 Anomalepididae, C) *Leptotyphlops nigricans* - Leptotyphlopidae, D) *Rhinotyphlops lalandei* -
471 Typhlopidae. Whereas all three scolecophidian species show robust and blunt crania in dorsal view,
472 the profile in lateral view is rather different with *Rhinotyphlops* having a more 'pointed' snout.

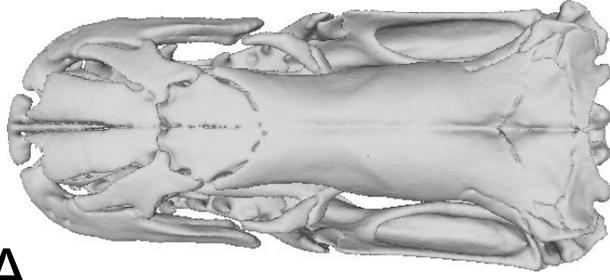
473 **Figure 4:** Fifth vertebra in cranial, left lateral, caudal, dorsal, and ventral views. Illustrated are
474 vertebrae for A) *Anilios unguirostris* - Typhlopidae, B) *Epictia tenella* - Leptotyphlopidae, and C)
475 *Typhlophis squamosus* - Anomalepididae. Note the robust condyle and corresponding cotyle and pre-
476 and postzygapophyses in *Anilios* compared to the other two species. CON, condyle; COT, cotyle; PA,
477 prezygapophysis; PO, postzygapophysis.

Table 1: Summary of the morphometric and force data for the species included in this study.

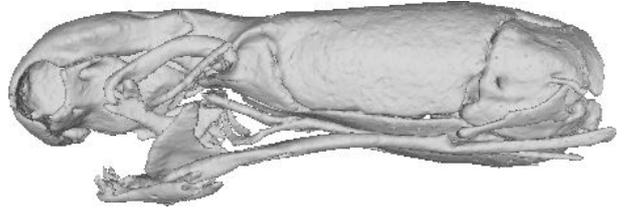
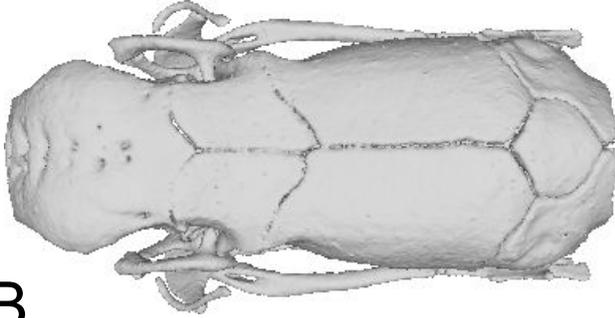
Genus	species	origin	N	force (N)	mass (g)	SVL (mm)	diameter (mm)
Alethinophidia							
<i>Anilius</i>	<i>scytale</i>	French Guyana	5	5.9 ± 3.3	26.3 ± 16.5	500.0 ± 93.5	8.8 ± 2.2
<i>Aparallactus</i>	<i>guentheri</i>	Kenya	1	1.6	5.1	385.0	6.0
<i>Eryx</i>	<i>colubrinus</i>	Pet trade	2	2.8 ± 1.1	77.0 ± 19.8	400.0 ± 28.3	16.0 [†]
<i>Farancia</i>	<i>abacura</i>	Pet trade	2	11.8 ± 15.7	4.0*	600.0 ± 523.3	16.8 ± 15.0
<i>Loxocemus</i>	<i>bicolor</i>	Pet trade	2	14.1 ± 0.0	171.5 ± 2.1	745.0 ± 7.1	19.9 [†]
<i>Oxyrhopus</i>	<i>melanogenys</i>	French Guyana	1	2.9	36.0	480.0	10.3
Typhlopidae							
<i>Afrotyphlops</i>	<i>angolensis</i>	Kenya	1	18.2	48.1	511.5	15.4
<i>Rhinotyphlops</i>	<i>lalandei</i>	South Africa	5	3.3 ± 1.6	6.5 ± 3.2	236.8 ± 78.0	6.1 ± 1.0
<i>Rhinotyphlops</i>	<i>unitaeniatus</i>	Kenya	1	8.1	12.7	415.0	6.7
Leptotyphlopidae							
<i>Leptotyphlops</i>	<i>scutifrons</i>	South Africa	6	0.4 ± 0.2	1.1 ± 0.4	140.7 ± 17.8	3.1 ± 0.5
<i>Myriopholis</i>	<i>algeriensis</i>	Pet trade	1	0.2	NA	137.2	1.2
Anomalepidae							
<i>Liotyphlops</i>	<i>beui</i>	Brazil	2	1.5 ± 0.7	2.9 ± 1.2	282.5 ± 24.8	4.0 ± 0.6

Table entries are means ± standard deviations. * Body mass data was available only for the smallest specimen. † body diameter was measured for only one of the specimens. N, number of individuals sampled; svl, snout-vent length. NA: not available.

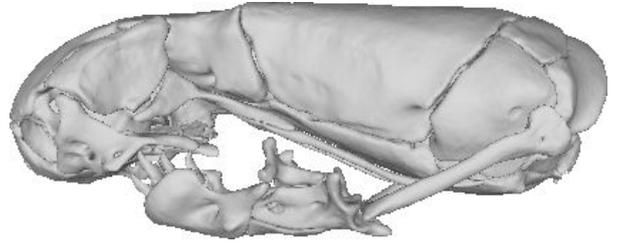
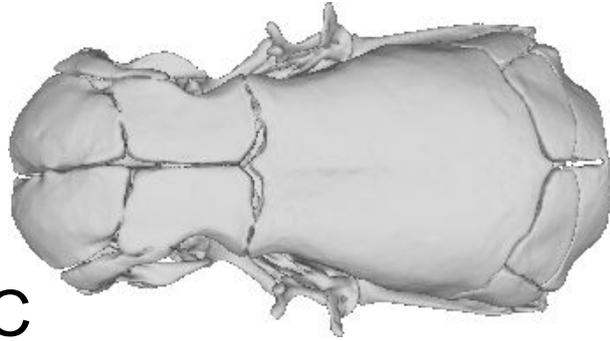




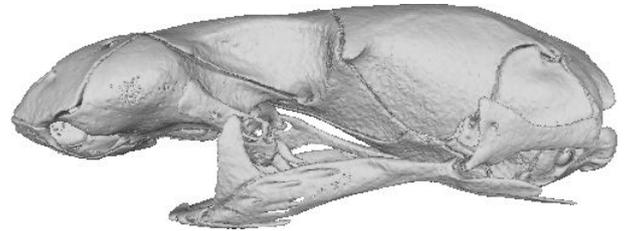
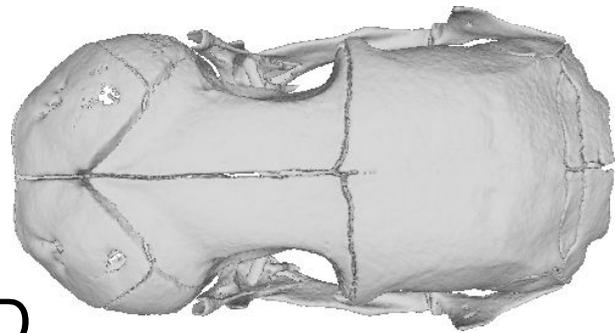
A



B



C



D

