Burrowing in blindsnakes: a preliminary analysis of burrowing forces and consequences for the 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.

Introduction

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

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

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

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

6

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 ±

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

7

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 *Anilios* 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 *Anilios* (Fig. 4). Note however, that *Anilios* 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 typhlopid 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 typhlopid 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, *Anilios 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 typhlopid 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 μCT 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 typhlopid 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 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 *Anilios* 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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Figure legends

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

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

Figure 3: Cranial anatomy in burrowing snakes. Computed tomography (CT) scans of skulls in dorsal (left) and left lateral (right) views. A) *Anilius scytale* - Aniliidae, B) *Liotyphlops albirostris* - Anomalepidae, C) *Leptotyphlops nigricans* - Leptotyphlopidae, D) *Rhinotyphlops lalandei* - Typhlopidae. Whereas all three scolecophidian species show robust and blunt crania in dorsal view, the profile in lateral view is rather different with *Rhinotyphlops* having a more 'pointed' snout.
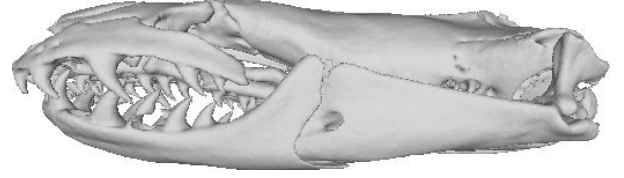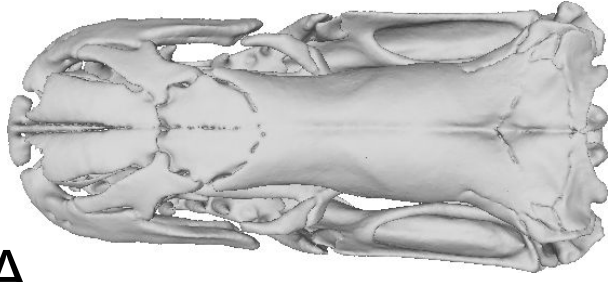
Figure 4: Fifth vertebra in cranial, left lateral, caudal, dorsal, and ventral views. Illustrated are vertebrae for A) *Anilios unguirostris* - Typhlopidae, B) *Epictia tenella* - Leptotyphlopidae, and C) *Typhlophis squamosus* - Anomalepidae. Note the robust condyle and corresponding cotyle and pre- and postzygapophyses in *Anilios* compared to the other two species. CON, condyle; COT, cotyle; PA, prezygapophysis; PO, postzygapophysis.

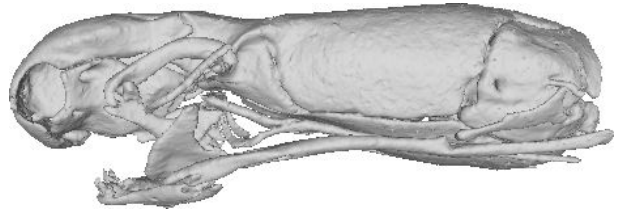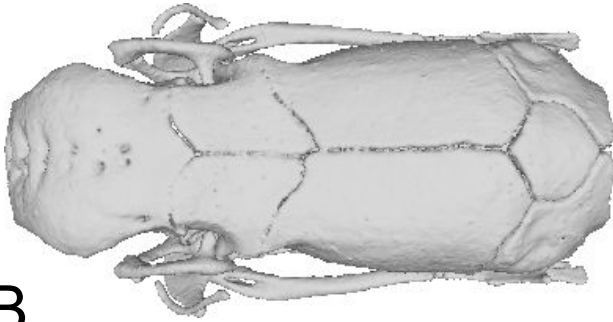**Table 1**: Summary of the morphometric and force data for the species included in this study.

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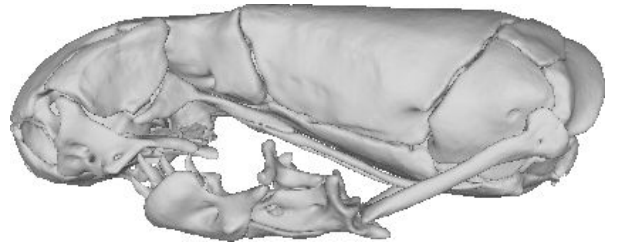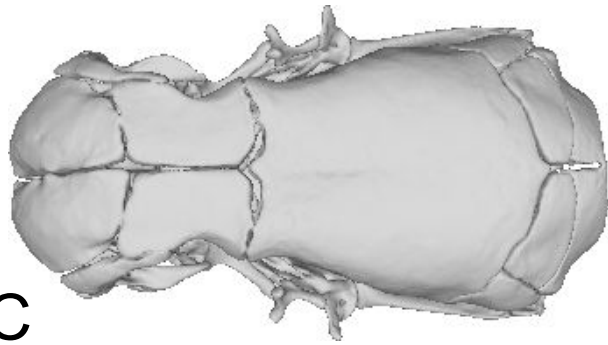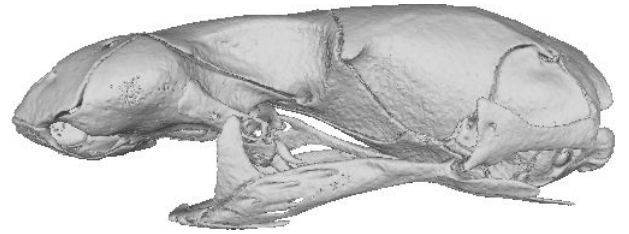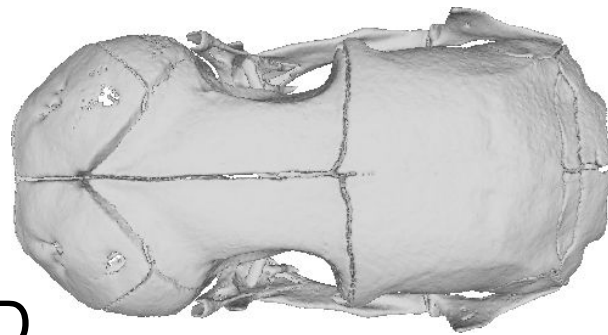
force plate

block with soil

perspex tunnel

A

B

C

D

COT

CON

PA

PO

A

B