

Burrowing in blindsnakes: A preliminary analysis of burrowing forces and consequences for the evolution of morphology

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Abstract

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

KEYWORDS

anatomy, burrowing, force, snake

1 | 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 (Šumbera, Chitaukali, Elichová, Kubová, & Burda, 2004). However, the underground environment also poses important challenges including low oxygen content (Arieli, 1979; McNab, 1966), and the high energetic cost of creating burrows (Navas et al., 2004; Vleck, 1979). 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, Alton, Clemente, Kearney, & White, 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, Dessauer, & Baic, 1978; Gasc, 1982; O'Reilly, Ritter, & Carrier, 1997; Quillin, 2000; Dorgan, Jumars, Johnson, Boudreau, & Landis, 2005; Dorgan, 2015).

Among limbless tetrapods, snakes occupy a special place as many forms are known to burrow (Davis, 1946; Deufel, 2017; Young & Morain, 2003). 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 & 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 scoleophidians, 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.

Scoleophidians 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 Scoleophidia, but recent molecular phylogenies suggest they might actually be more closely related to Alethinophidians (cfr. Miralles et al., 2018).

Scoleophidians diverged from other snakes (Alethinophidia) about 125–130 Mya in the Early Cretaceous (Schneider Facini et al., 2020; Zheng & Wiens, 2016), 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 alethinophidian snake families diverged beginning in the Eocene into the Oligocene between 40 and 60 Mya (see Pyron & Burbrink, 2012; Zaher et al., 2019; Zheng & Wiens, 2016). Thus, the scoleophidians have long been on a separate evolutionary trajectory from other snakes, but within the group itself the family-level lineages are characterized by long branch lengths and early divergences dating back to the Cretaceous (Adalsteinsson, Branch, Trape, Vitt, & Hedges, 2009; Miralles et al., 2018; Pyron & Burbrink, 2012).

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

Although scoleophidians have a conserved morphology and have therefore been erroneously termed “primitive” or “basal”, they are in fact extremely specialized with a phenotype that is well-adapted to a strictly fossorial life-style (da Silva et al., 2018; Miralles et al., 2018).

They forage underground, primarily on the eggs, larvae, pupae, and adults of ants and termites, and unlike alethinophidians, they consume large numbers of small prey (Shine & Webb, 1990; Webb, Branch, & Shine, 2001; Webb & Shine, 1993). This requires them to move through existing underground passageways (in the case of leptotyphlopids) or to create new underground tunnels (in the case of typhlopids) to invade ant or termite colonies. They use chemoreception to locate their prey, but this does not appear to be restricted to the detection of only a single prey species (Watkins, Gehlbach, & Baldrige, 1967; Webb & Shine, 1992). Leptotyphlopids can avoid detection from ants and termites through chemical crypsis, and this is possibly achieved through sequestration of their prey's defensive compounds with the subsequent release of these compounds through glands (Savitzky et al., 2012; Watkins, Gehlbach, & Kroll, 1969; Webb, Shine, Branch, & Harlow, 2000). Conversely, typhlopids probably withstand attacks by ants or termites through their more heavily armoured body (Webb & Shine, 1993). Thus, while the two superfamilies of scolecophidians have basic similarities in terms of life-history and are superficially similar in morphology, they probably have quite different adaptations allowing them to have a highly specialised ecological niche and different specializations towards burrowing.

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

2 | MATERIALS AND METHODS

2.1 | Animals

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

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

2.2 | Morphometrics

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

2.3 | Force measurements

Measurements of peak push forces were made using a piezoelectric force platform (Kistler Squirrel force plate, ± 0.1 N, Kistler Inc., Switzerland) as described previously (Vanhooydonck, Boistel, Fernandez, & Herrel, 2011; Le Guilloux et al., 2020; Figure 1). In brief, the force platform was positioned on a metal base and connected to a charge amplifier (Kistler Charge Amplifier type 9,865, Kistler Inc.). A Perspex block with 1 cm deep holes of different diameters was mounted on the force plate, level with the front edge. One of the holes was loosely filled with soil. A Perspex tunnel with a diameter approximatively equal to the maximal body diameter of the test animal was mounted on the metal base in front of (but not touching) the force plate, and aligned with the soil-filled hole in the Perspex block. An animal was then introduced into the tunnel and allowed to move through it until reaching the soil-filled chamber. Next, the animal was stimulated to burrow into the soil by touching the end of the tail sticking out of the tunnel, or by prodding the animal inside the tunnel with the blunt end of a thin wooden stick. Forces were recorded during 60 s recording sessions at 500 Hz, and three trials were performed for each individual, with at least 1 hr between trials. Forces

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 ^b
<i>Farancia</i>	<i>abacura</i>	Pet trade	2	11.8 ± 15.7	4.0 ^a	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 ^b
<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

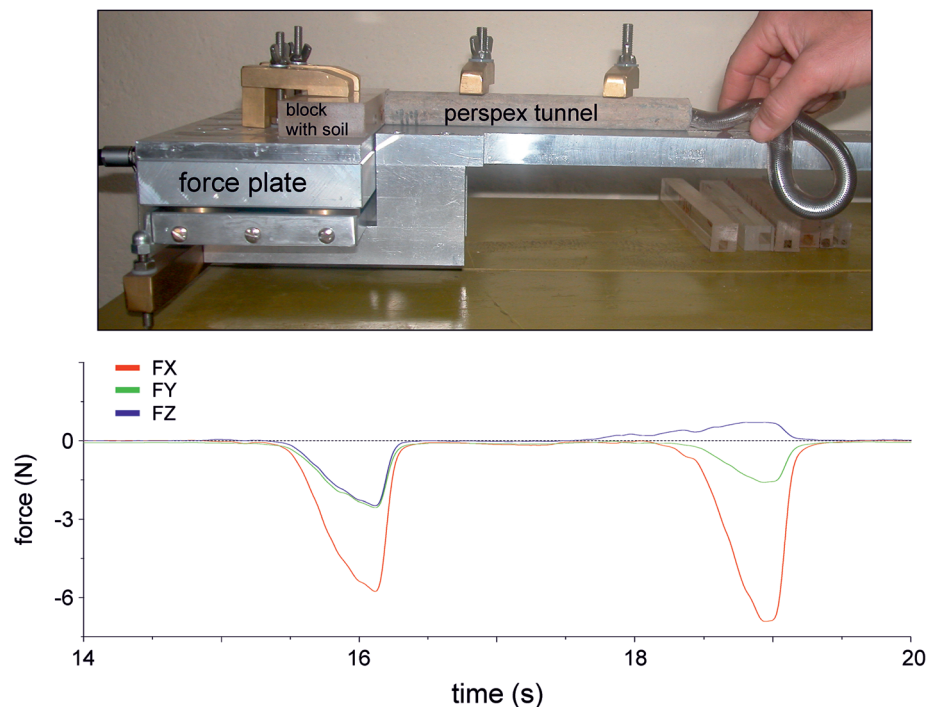
Note: Table entries are means ± SD.

Abbreviations: N, number of individuals sampled; NA: not available; svl, snout-vent length.

^aBody mass data was available only for the smallest specimen.

^bBody diameter was measured for only one of the specimens.

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



were recorded in three dimensions using the Bioware software (Kistler Inc.; Figure 1). For each individual, we then extracted the highest peak resultant force across all trials as an indicator of that animal's maximal push force. A summary of the force data is provided in Table 1.

2.4 | Statistical analyses

All data were Log_{10} -transformed before analyses to ensure normality and homoscedasticity. To explore which traits (snout-vent length, body mass or body

diameter) best explained variation in push force data (resultant force) we ran a stepwise multiple regression across data for all individuals. Next, we tested whether differences between groups (Alethinophidia, Typhlopidae, Leptotyphlopidae, Anomalepididae) were observed in resultant force, using an ANCOVA with snout-vent length as our co-variate. To test which groups differed from one another, we next ran simple regressions on maximal push force (resultant), body diameter, and body mass with snout-vent length as our predictor and extracted unstandardized residuals. We then ran an ANOVA on residual resultant force coupled to Bonferroni post-hoc tests to explore which groups differed from one another. Finally, we ran Pearson correlations between residual data to explore whether body diameter or body mass, independent of the effect of snout-vent length, explained variation in residual maximal resultant force and ran a MANOVA to test whether clades differed in residual body mass and residual body diameter. All analyses were run in IBM SPSS V. 26. Significance was set at $p < .05$.

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

3 | RESULTS

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

A multiple stepwise regression with snout-vent length, body mass and body diameter retained a significant model with only snout-vent length as the predictor ($R^2 = 0.78$; $p < .001$; slope = 1.93 ± 0.20 ,

intercept = -4.40 ± 0.49). Thus, longer snakes were able to produce higher resultant forces (Figure 2a). The ANCOVA detected significant effects of snout-vent length ($F_{1,28} = 62.54$; $p < .001$) and phylogenetic group ($F_{3,28} = 70.70$; $p < 0.001$) on maximal push force, suggesting that individuals from different phylogenetic groups differed in their maximal push force irrespective of variation in snout-vent length. The ANOVA run on residual maximal push force was significant ($F_{3,29} = 8.87$; $p < .001$). Post-hoc tests indicated that Typhlopidae differed from all other groups (all $p < .018$), yet none of the

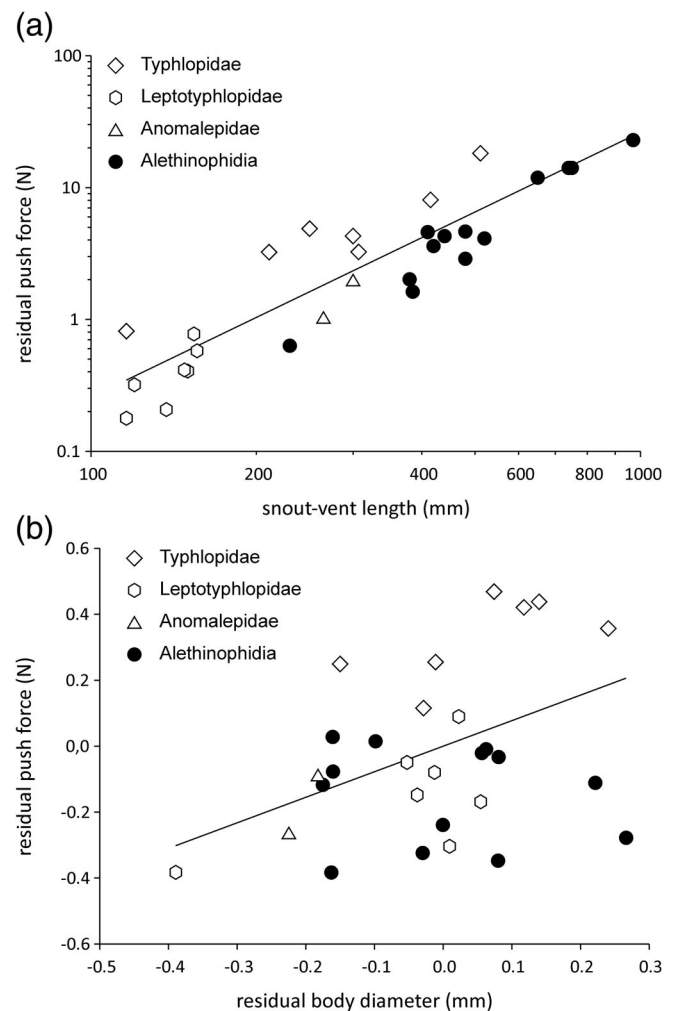


FIGURE 2 (a) Scatterplot showing the relationship between snout-vent length and maximal push force in snakes. Each point is the maximal force recorded for a given individual. On average typhlopids generate higher forces for their snout-vent length than other snakes. Leptotyphlopids and anomalepidids 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 typhloid snakes still generate more force than other snakes

other groups differed. The inspection of the marginal means showed that typhlopids produced higher maximal push forces for a given snout-vent length than other species (marginal means; Typhlopidae: 0.329; Leptotyphlopidae: -0.149 ; Anomalepididae: -0.181 ; Alethinophidia: -0.053). Finally, residual maximal push force was correlated with residual body diameter ($r = 0.44$; $p = .011$) but not residual body mass ($r = 0.33$; $p = .077$), showing that snakes with relatively wider bodies were able to push harder (Figure 2b). Yet, the difference in push force was not explained by the difference in body diameter as a MANOVA on residual body diameter and residual body mass detected no differences between groups (Wilks' lambda = 0.69; $F_{6,48} = 1.67$; $p = .15$; univariate ANOVAs: body diameter: $F_{3,25} = 2.25$; $p = .11$; body mass: $F_{3,25} = 2.49$; $p = .08$).

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

4 | DISCUSSION

The first ever data on maximal push forces in burrowing snakes suggest that significant interspecific differences exist, with typhlopids being able to generate higher forces for a given body length. As typhlopids are considered active burrowers in contrast to leptotyphlopids, which are thought to mostly use existing underground passageways, this observation is in line with our predictions. Alethinophidian snakes also generated relatively low forces for their size which may correspond to the fact that they mostly use the softer top compartment of the soil for burrowing. Interestingly, although snout-vent length and residual body diameter are both correlated to

the force generation capacity in the animals included in our data set, these variables did not explain why typhlopids were able to generate higher forces. Longer snakes can be expected to have more overall muscle mass and an increase in the relative diameter should allow for the packing of muscles with a greater cross-sectional area (Gans, 1974). This is confirmed by our results where longer snakes do indeed have a greater diameter (Pearson correlation: $r = 0.86$; $p < .001$). Whereas this may explain the observed relationships between force, length and diameter, this does not explain differences between the different groups of snakes. It is likely that different burrowing snakes use different mechanisms for burrowing (as suggested for amphisbaenians with different head shapes for example; Gans, 1974), allowing them to recruit the axial muscles differently. This is translated in differences in overall proportions with leptotyphlopids being generally extremely narrow and long in contrast to typhlopids which are much more robust and have a greater diameter for a given snout-vent length (note that exceptions exist with, for example, *Anilius grypus* showing an aspect ratio [total length divided by midbody diameter] of 130).

Although the exact mechanisms used by these snakes to generate burrowing force while in a tunnel remains unknown, the mostly forward-directed forces (very different from what has been described in burrowing scincid lizards, for example; see Vanhooydonck et al., 2011) suggest that they may use a mechanism similar to what has been described for caecilians (Gaymer, 1971; O'Reilly et al., 1997) and hypothesized to exist in uropeltid snakes (Gans et al., 1978): internal concertina. This type of burrowing involves bending followed by an extension of the vertebral column within the skin envelope, allowing animals to recruit most of their body wall muscles to generate forward-directed forces. In contrast, non-specialized snakes will use muscular forces to push laterally against the side of a straight-sided tunnel in a typical concertina movement to traverse smooth tunnels (Gans, 1974; Gray & Lissmann, 1950). X-ray video analysis is needed to be able to understand the movements of the skin and vertebral column and thus to test whether skin-vertebral independence exists in scolecophidian snakes in general and typhlopids more specifically. Unfortunately, our understanding of the axial musculature in burrowing snakes, and especially in scolecophidian snakes, remains extremely fragmentary (Gasc, 1981). The musculature has been suggested to be convergent on that observed in amphisbaenian lizards, another group of very strong burrowers (Gasc, 1982; Hohl et al., 2014; Navas et al., 2004) but with a typical snake bauplan (Gasc, 1981). A remarkable feature of the muscular anatomy in

typhlopids is the absence of the *m. costo-cutanei* resulting in an anatomical independence between the axial and cutaneous muscles (Gasc, 1981). However, these data are based on the dissection of a single specimen of *Afrotyphlops* (*A. punctatus*) and differ from what has been reported by Mosauer (1935), illustrating the

need for further studies on the axial musculature. The small size of many leptotyphlopids and anomalepids has prevented direct dissections of the musculature. However, contrast-enhanced μ CT scans may provide a unique opportunity to better understand the musculature in these extremely small animals (Metscher, 2009).

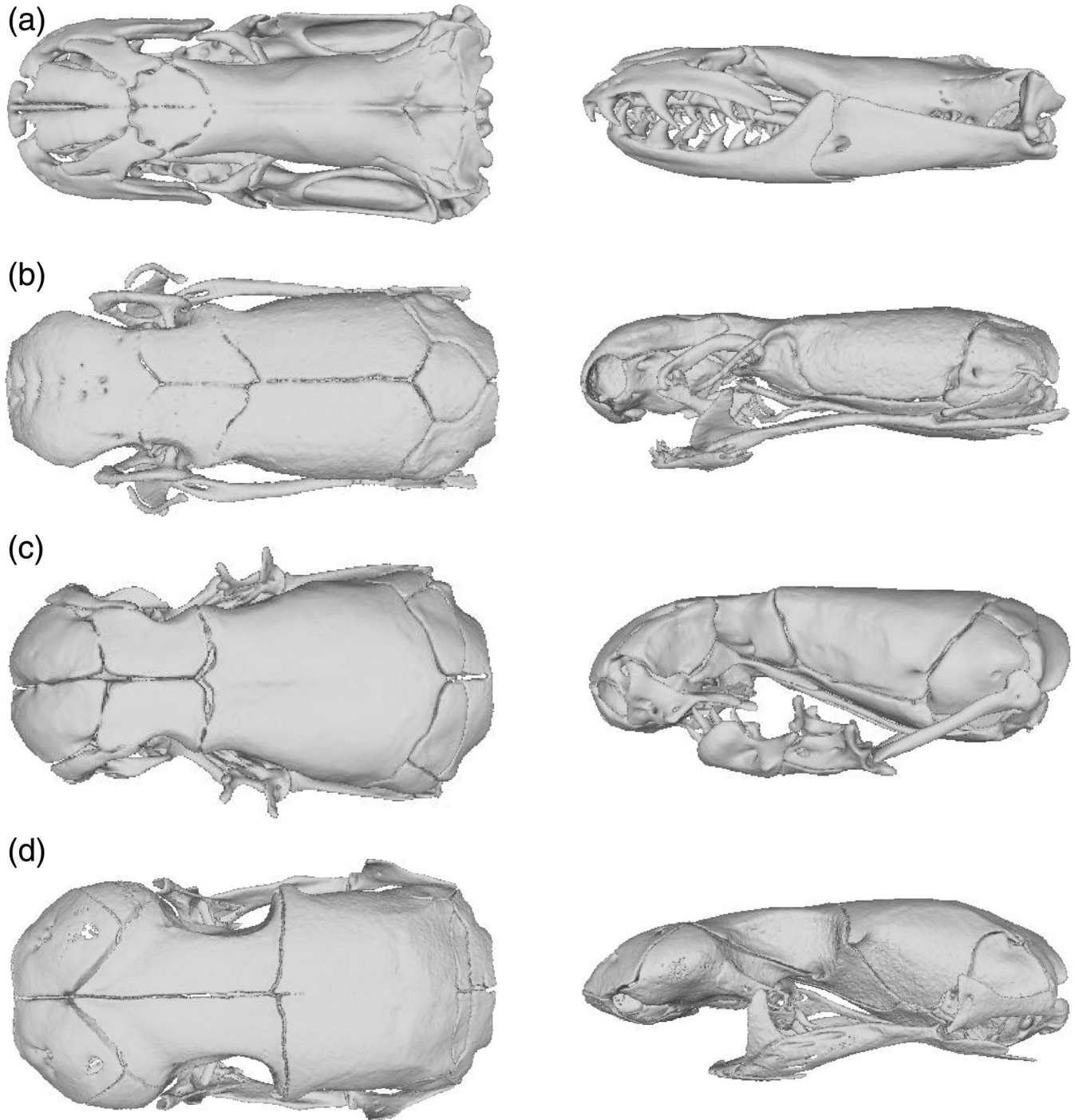


FIGURE 3 Cranial anatomy in burrowing snakes. Computed tomography (CT) scans of skulls in dorsal (left) and left lateral (right) views. (a) *Anilius scytale*: Aniliidae, (b) *Liotyphlops albirostris*: Anomalepidae, (c) *Leptotyphlops nigricans*: Leptotyphlopidae, (d) *Rhinotyphlops lalandei*: Typhlopidae. 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

Our qualitative anatomical comparisons of skull and vertebral morphology suggest that the higher forces generated by typhlopoid snakes may be reflected in the shape of these structures. Whereas all burrowing species had blunt and robust snouts in dorsal view, the shape of the anterior part of the cranium was very different with *Anilius* and *Rhinotyphlops* having more pointed shapes

possibly facilitating substrate penetration. Given the high forces encountered during burrowing it was unexpected to see little or no fusion of the cranial sutures, in contrast to what is observed in, for example, trogonophid amphibiaenians where the cranial sutures are highly interdigitated (Gans, 1974). Elongate and highly interdigitated sutures have been suggested to be a response to torsional

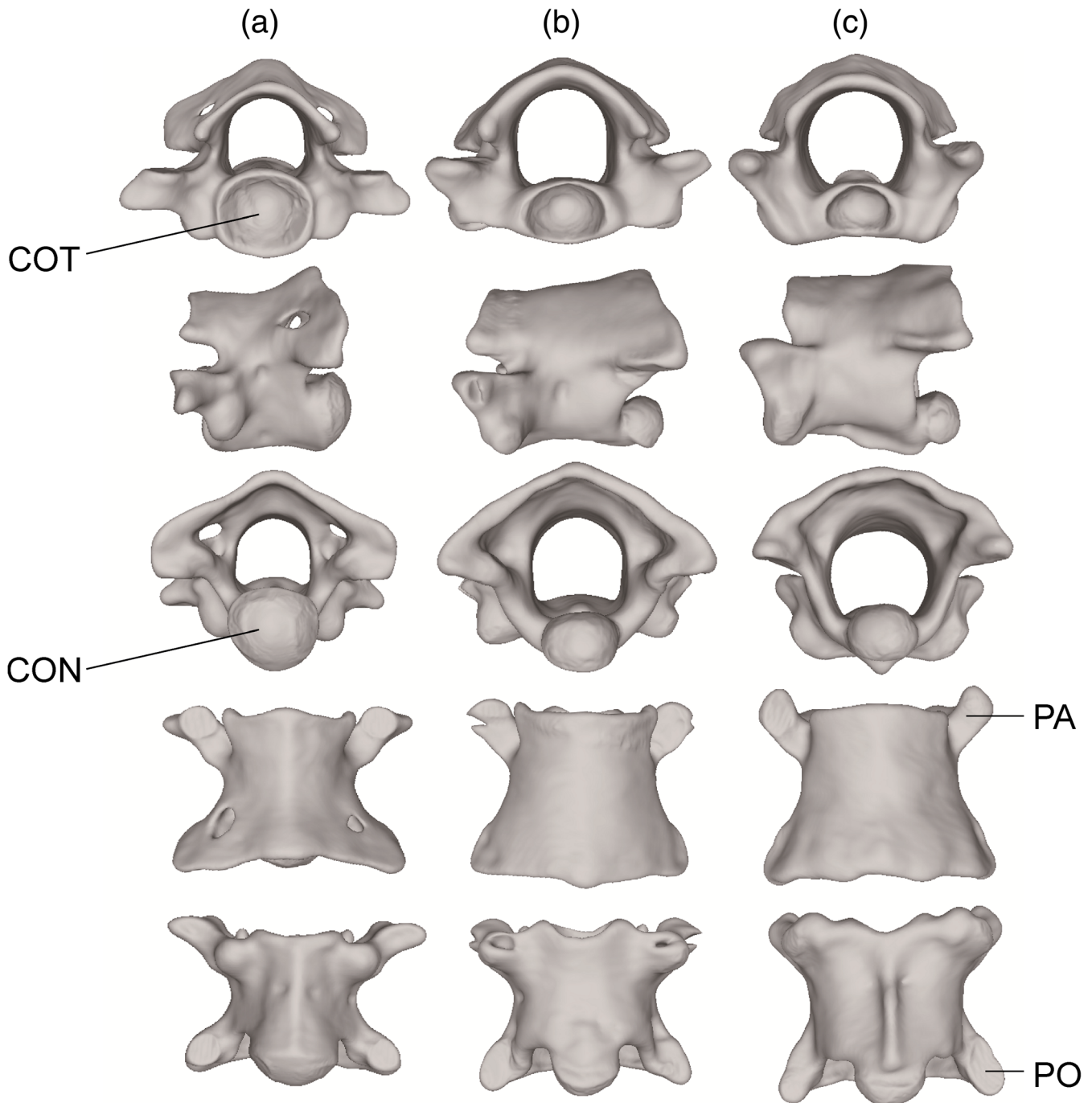


FIGURE 4 Fifth vertebra in cranial, left lateral, caudal, dorsal, and ventral views. Illustrated are vertebrae for (a) *Anilius unguirostris*: Typhlopidae, (b) *Epictia tenella*: Leptotyphlopidae, and (c) *Typhlophis squamosus*: Anomalepidae. Note the robust condyle and corresponding cotyle and pre- and postzygapophyses in *Anilius* compared to the other two species. CON, condyle; COT, cotyle; PA, prezygapophysis; PO, postzygapophysis

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

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

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