







RESEARCH ARTICLE

Using 3D-digital photogrammetry to examine scaling of the body axis in burrowing skinks

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Funding information

Cameron Siler, Grant/Award Number: 1353683; Duncan Irschick, Grant/Award Number: 1353743; Gunter Wagner, Grant/Award Number: 1353691; Philip Bergmann, Grant/Award Number: 1353703

Abstract

Three-dimensional (3D) modeling techniques have been increasingly utilized across disciplines for the visualization and analysis of complex structures. We employ 3D-digital photogrammetry for understanding the scaling of the body axis of 12 species of scincid lizards in the genus *Brachymeles*. These skinks represent a diverse radiation which shows tremendous variation in body size and degree of axial elongation. Because of the complex nature of the body axis, 3D-methods are important for understanding how the body axis evolves. 3D-digital photogrammetry presents a flexible, inexpensive, and portable system for the reconstruction of biological forms. As body size increased among species, the cross-sectional area and circumference of the head and other portions of the body axis increased isometrically, which indicates that species of differing sizes possess proportionally similar head and body shapes. These results suggest that there are no substantial head and body shape changes with body size among the sampled species, but further comparative studies with larger sample sizes and functional studies of size and morphology effects on burrowing or above-ground locomotion are needed.

KEYWORDS

3D-body forms, 3D-modeling, morphology, morphospace, reptiles, visualization

1 | INTRODUCTION

Understanding the scaling of the body axis is an important topic for understanding the evolution of body form (Koob & Long Jr., 2015). Evolutionary changes in the scaling of different body parts, including the body axis, lead to diversification of form in teleost fishes, reptilian sauropsids, and other vertebrates (Bergmann, Meyers, & Irschick, 2009; Brandley, Huelsenbeck, & Wiens, 2008; Cernansky, 2016; Claverie & Wainwright, 2014). For example, the evolution of snakes in large part resulted from the elongation of the body axis with a commensurate evolutionary shrinkage and loss of limbs (Sanger & Gibson-Brown, 2007). This evolutionary process contributed to the radiation of the vertebrate clade into a diverse suite of ecological niches (e.g., fossorial, arboreal, riparian, marine; Sites, Reeder, & Wiens, 2011). Within squamate reptiles, skinks represent

one of the most interesting evolutionary examples of how changes in the body axis and body size may be closely tied to evolutionary diversification (Bergmann & Moringa, 2019; Brandley et al., 2008; Siler & Brown, 2011; Siler, Diesmos, Alcala, & Brown, 2011). Such changes in both lizards in general, and skinks in particular, are tied closely to the evolution of locomotor capacity (Bergmann & Irschick, 2010). For example, in the lizard genus *Niveoscincus*, species in open microhabitats are characterized by an overall larger body, longer legs, and faster sprinting abilities than species that are located in closed microhabitats (Melville & Swain, 2000). Furthermore, research in two clades of lizards, subfamily Phrynosomatinae and genus *Lerista*, has shown that these groups evolved body and limb shapes that were advantageous to particular kinds of locomotion (Bergmann & Irschick, 2010). Some members of Phrynosomatinae have evolved shorter, broader bodies with shorter limbs, and some *Lerista* have evolved longer, slimmer

bodies with shorter limbs. Both phenotypes are correlated with changes in locomotor kinematics (Bergmann & Irschick, 2010).

Within skinks, the genus *Brachymeles* presents a particularly interesting case for investigating the evolution of the body axis, as members of the clade display a spectrum of body sizes and degree of elongation, as well as reduction of limbs and limb anatomical elements (Siler & Brown, 2011). This group of 41 species is largely endemic to the Philippines and shows notable variation in size, with a more than four-fold difference in body length among species (Uetz, Freed, & Hošek, 2019; Wagner et al., 2018). Previous research on *Brachymeles* has revealed that species with reduced or absent limbs tend to have longer, slimmer bodies with more presacral vertebrae, while species with longer limbs have shorter, fatter bodies with fewer presacral vertebrae (Bergmann & Moringa, 2019; Greer, Caputo, Lanza, & Palmieri, 1998; Siler & Brown, 2011). However, measures of “slimness” were taken with standard morphometric techniques such as linear measurements on specimens. The complex nature of the body axis suggests that a more holistic 3D-modeling approach would allow consideration of how cross-sectional areas and circumference scale with size. We focus on the body axis, and not on the degree of limb development, which was addressed in Siler and Brown (2011) and Wagner et al. (2018).

We apply digital 3D-photogrammetry for reconstructing the body axis of 12 species of *Brachymeles*. Over the last 20 years, scientists have increasingly used three-dimensional (3D) data visualization and imaging as a means of understanding complex morphological forms, body shape, and testing hypotheses of evolutionary diversification (Falkingham, 2012; Herzlinger, Goren-Inbar, & Grosman, 2017; Lawing & Polly, 2010). The increased availability of various 3D-methods, including computed tomography (CT) scanning, magnetic resonance imaging (MRI), laser scanning, and photogrammetry, provides biologists with a toolkit to visualize formerly unquantifiable complexity (Laforsch, Imhof, Robert, Settles, & Heb, 2012). These 3D-geometries are then used in downstream shape analyses, including 3D-geometric morphometrics (Adams, Rohlf, & Slice, 2004) and 3D-elliptical Fourier analysis (Shen, Farid, & McPeck, 2009).

The practice of 3D-photogrammetry is described widely in the literature, and has been used in a variety of systems, including the estimation of body mass for mammals, the analysis of soft tissues of the human face, and quantification of craniofacial morphology in domestic dogs (Deli et al., 2013; Evin et al., 2016; Falkingham, 2012; Postma et al., 2015). Much of the focus of 3D-photogrammetry has been on the reconstruction of 3D-models of bones and fossils, and there has been less exploration of the technique for accurate reconstruction and analysis of soft-bodied preserved organisms (but see Ferreira Amado, Moreno Pinto, & Olalla-Tárraga, 2019).

We used 3D-digital photogrammetry to create 3D-models of the primary body axis of 12 species of *Brachymeles* that differ notably in size and shape (Siler & Brown, 2011). We first confirmed model accuracy by comparing standard morphometric measurements taken on the preserved specimens with the same measurements taken on the 3D-models. We then studied the scaling of the circumference and

cross-sectional area of at various points along the anterior–posterior axis of the body among species.

We used our 3D-models to test the hypothesis that scaling of the cross-sectional area and circumference of the body axis will deviate from isometry and show allometric relationships. Testing this hypothesis may provide insights about relationships between body size, ecology, and locomotor performance in lizards of the genus *Brachymeles*, and more generally squamates. For example, allometry of circumference and cross-sectional area should be correlated with scaling of muscle mass along the body axis, which would be a closer proxy for scaling of locomotor performance than more traditional morphometric variables. Since many elongate skink species are semi-fossorial, positive allometry of body cross-sectional area or circumference associated with larger muscle mass may allow animals to move through denser or more packed substrates (Albert et al., 2001; Ducey, Formanowicz, Boyet, Mailloux, & Nussbaum, 1993).

2 | MATERIALS AND METHODS

2.1 | Sampling

We selected 12 vouchered museum specimens representing 12 distinct species of *Brachymeles* available from the collections at the Sam Noble Oklahoma Museum of Natural History, University of Kansas Biodiversity Institute, and the California Academy of Sciences (Table S1). The number of taxa and specific focal species were selected as a manageable sample size to test our photogrammetry protocol, ensuring that significant variation in body size (SVL: ~63 to ~120 mm) and limb morphology (limbless to pentadactyl) was represented. Given that the primary variation in skinks is related to the length and width of the body axis, as well as in size (Bergmann & Irschick, 2012), we chose species that vary in these features. As our goal was not to reconstruct the limbs and toes, which were variable among this group of species (e.g., six species are pentadactyl, five species are non-pentadactyl with variable digits, and one species are limbless [Davis, Feller, Brown, & Siler, 2014; Siler & Brown, 2011]), we did not use our photogrammetry methods to resolve these features. Morphological measurements were collected on both museum specimens and 3D-digital specimens.

2.2 | Image acquisition

We photo-captured both dorsal and ventral sides of each specimen in separate photo sets and created independent 3D-models for each side. Images of each specimen were taken using a Canon Powershot G16 camera, which was mounted on a tripod and equipped with a wireless trigger. The tripod was placed in front of a rotating stool. LED lights on tripods were distributed equally around the stool. An LED light panel was placed underneath each specimen to eliminate shadows and to provide further illumination. On top of this 3D-panel a speckled piece of paper was placed that aids in 3D-reconstruction

of the specimen by acting as additional landmarks for the 3D-photogrammetry software to recognize. A white poster board was placed behind the stool as a backdrop. Each specimen was placed ventral side down on the rotating stool and was propped up using clay in a desired orientation (Figure S1). The stool was manually rotated slightly between photographs so that we obtained 60–80 photographs after a full 360° rotation. After the specimen was placed with its dorsal side down and the process was repeated. A total of 50 photos were ultimately used per each full rotation, as we only used photos that were clearly in-focus, which required elimination of some photos. Given the shallow depth of field, and the small subjects, we used the highest aperture setting for a G16 (F8). The size of the images used in the photo reconstruction (once compressed from the RAW files) were typically on the order of 4 K × 3 K pixels. Photo acquisition took on average 40 min for one complete specimen.

2.3 | Image post-processing

Once all the photos were obtained, each JPEG file was loaded into Adobe Photoshop (Adobe Photoshop CS, Berkeley, California, 2004) as a batch. Photogrammetry is most effective when there is consistency among photos in terms of parameters such as white balance temperature, sharpness, and radius, which we adjusted during different shoots to conform to one another. We did not make the same set of adjustments for every shoot, as lighting conditions were slightly different on different days, even though we used the same LED lighting Scheme.

2.4 | 3D-model rendering and combining dorsal and ventral sides

After image post-processing was completed, the photos for the dorsal side for a specimen were loaded into Reality Capture software (Capturing Reality, Bratislava, Slovakia, 2018). Reality Capture uses standard photogrammetry algorithms which aligns 2D-images and then converts the xy-system to xyz. After a 3D-model for the dorsal side was rendered, the post-processed photos of the ventral side of the same specimen were loaded into the software. This process was repeated for each specimen. The Reality Capture software took on average 10 min for one side of the specimen but was dependent on the number of photos, photo quality, and processor speed. Once a 3D-model was created for the dorsal and ventral sides of each specimen, they were exported as OBJ-files and imported into Meshmixer 3.3 (Autodesk, San Rafael, California). In Meshmixer, the dorsal and ventral sides of each specimen were uniformly sized using the “Measure” tool set in millimeters. For some of the models, the dorsal and ventral sides were combined using GeoMagic Studio 2014.1.0 (3D-Systems, Rock Hill, South Carolina, 2014; RRID:SCR_016978). GeoMagic Studio has a more robust set of tools to manipulate 3D-models and is more intuitive than Meshmixer. The sides were pieced together using the “Transform” tool. The “Combine” tool finished this

process once the two pieces were combined. All models were transported into GeoMagic Studio 2014.1.0. and the seam on each of the models that was an artifact of joining the dorsal and ventral pieces was smoothed out using the “Sandpaper” tool.

2.5 | Morphology

Eight morphological measurements were taken from museum specimens using digital calipers to the nearest 0.01 mm (Table S1). Measurements taken include: SVL (snout–vent length), tail length, head height, midbody height, mid-tail height, head width, midbody width, and mid-tail width. SVL was measured from the anterior tip of the snout to the opening of the cloaca. Tail length was measured from the opening of the cloaca to the posterior tip of the tail. Head height was measured from the dorsal portion of the head (frontal) to the ventral edge of the head (dentary) using the eye as a reference point. Head width was measured from the lateral to medial portion of the head from eye to eye. Midbody height measured the height of the body at half SVL length. Midbody width measured from the left lateral to right lateral edge at half SVL length. Mid-tail height measured the height of the tail at half its length. Mid-tail width was measured from the left lateral to right lateral edge of the tail at half the tail length. SVL measurements on digital specimens were taken using the “Measure” tool in Autodesk Meshmixer 3.3 (Autodesk Inc., San Rafael, A, 2017; RRID: SCR_015736) and the remaining measurements were taken using the “Distance” tool in GeoMagic Studio (Table S1).

2.6 | Accuracy

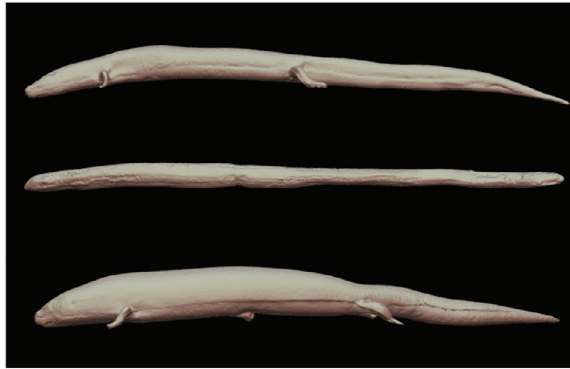
To determine the accuracy of our 3D-models we log transformed the digital (X axis) and physical (Y axis) specimen measurements (Table S1). Then we performed ordinary least squared regressions (Table S2) using the `lm` function in the base R package (R Core Team, 2018).

2.7 | Area and circumference data acquisition and comparative analyses

We also calculated the circumference and cross-sectional surface area from the 3D-models. In Geomagic Studio, each 3D-model was sliced in cross section at three locations: immediately posterior to the head, at midbody and at mid-tail (Figure 1; Figure S2). At each point, the Geomagic “Feature” tool was used to automatically generate an oval feature that most closely approximated the outline of each cross section. From these ovals both circumference and area data were calculated.

Phylogenetic generalized least squares (PGLS) regressions were performed to test for a scaling relationship (isometry or positive or negative allometry) between axis morphology (circumference and cross-sectional area) and SVL independent of phylogenetic similarity.

Workflow for acquisition of 3D model axis morphology and analysis



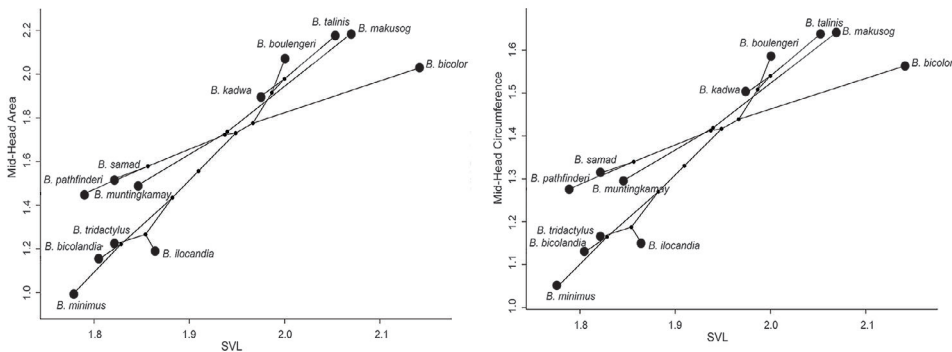
Import 3D models into GeoMagic Studio



Use GeoMagic Studio to acquire circumference and area data



Performed PGLS analysis to examine scaling relationship between SVL and axis morphology (mid-head, midbody, mid-tail) independent of phylogenetic similarity



PGLS analyses for Mid-Head Area and Circumference for 12 *Brachymeles* species

FIGURE 1 Workflow for acquisition of 3D-model axis morphology and analysis

All of these analyses were performed in R (R Core Team, 2018). Using the “ape” package (Paradis, Claude, & Strimmer, 2004), we pruned a time-calibrated maximum-likelihood estimated phylogeny (Siler & Brown, 2011) to the 12 species in our 3D-dataset. We used the “caper” package (Orme, Freckleton, Thomas, Petzoldt, & Fritz, 2012) to conduct PGLS regressions of head, mid-dorsal, and tail circumference and cross-sectional area measurements on SVL of all species, using Pagel’s lambda to estimate the amount of phylogenetic signal in the regression residuals (Pagel, 1999). Under this framework, when lambda is equal to 1 the traits evolved in a manner one would expect under Brownian motion. When lambda is equal to 0 the traits evolved independently of branch length. We used the package “phytools” to generate phylogenospaces that illustrate body axis measurements across species

(Revell, 2012). Because the default significance test of slope used by the *pgls* function in the “caper” package tests whether or not the slope is equal to zero, we performed additional *t* tests for each PGLS analysis to test whether the estimated slope was different from the expected slope under isometry for that measurement. To calculate the *p* values accounting for isometry for circumference, we calculated the *t* value using: $t = (\text{slope} - 1)/\text{SE}$. The slope and slope standard errors were used from our original *pgls* analysis. Using the calculated *t*-value and degrees of freedom (10) we calculated the *p* value using a standard *t* statistic formula. This process was repeated for the cross-sectional areas using two instead of one when calculating *t* values. Thus, reported *p* values <.05 represent deviations from isometric slopes (slope of one for circumference; slope of two for cross-sectional area).

3 | RESULTS

3.1 | Accuracy

The range of R^2 values for OLS regressions of all digital body axis measurements on the same physical specimen measurements was 0.938–0.996 (Table S2), indicating the accuracy of our 3D-models was suitable for investigating the scaling of the body axis.

3.2 | Sample 3D-models

Lateral views of the completed 3D-models are displayed in Figure 2. The older museum specimen of *Brachymeles vermis* was more distorted than other specimens examined, resulting in a 3D-model that

reflected that shape. All 3D-models we used for our analysis can be viewed at <https://sketchfab.com/irschicklab>.

3.3 | Cross-sectional area and circumference

We performed a PGLS regression of three different circumference measurements on SVL (Figure 3, top panel). The expected slope for circumference in relation to body length under isometry is 1. The mid-head circumference scaled isometrically with SVL ($R^2 = 0.77$, slope = 1.27 ± 0.20 , $t = 1.35$, $p = .21$). Similarly, the midbody circumference scaled isometrically with SVL ($R^2 = 0.63$, slope = 1.08 ± 0.24 , $t = 0.33$, $p = .24$). The mid-tail circumference also scaled isometrically with SVL ($R^2 = 0.49$, slope = 0.94 ± 0.28 , $t = -0.21$, $p = .83$).

We likewise performed a PGLS regression of three different cross-sectional area measurements on SVL (Figure 3, bottom panel).

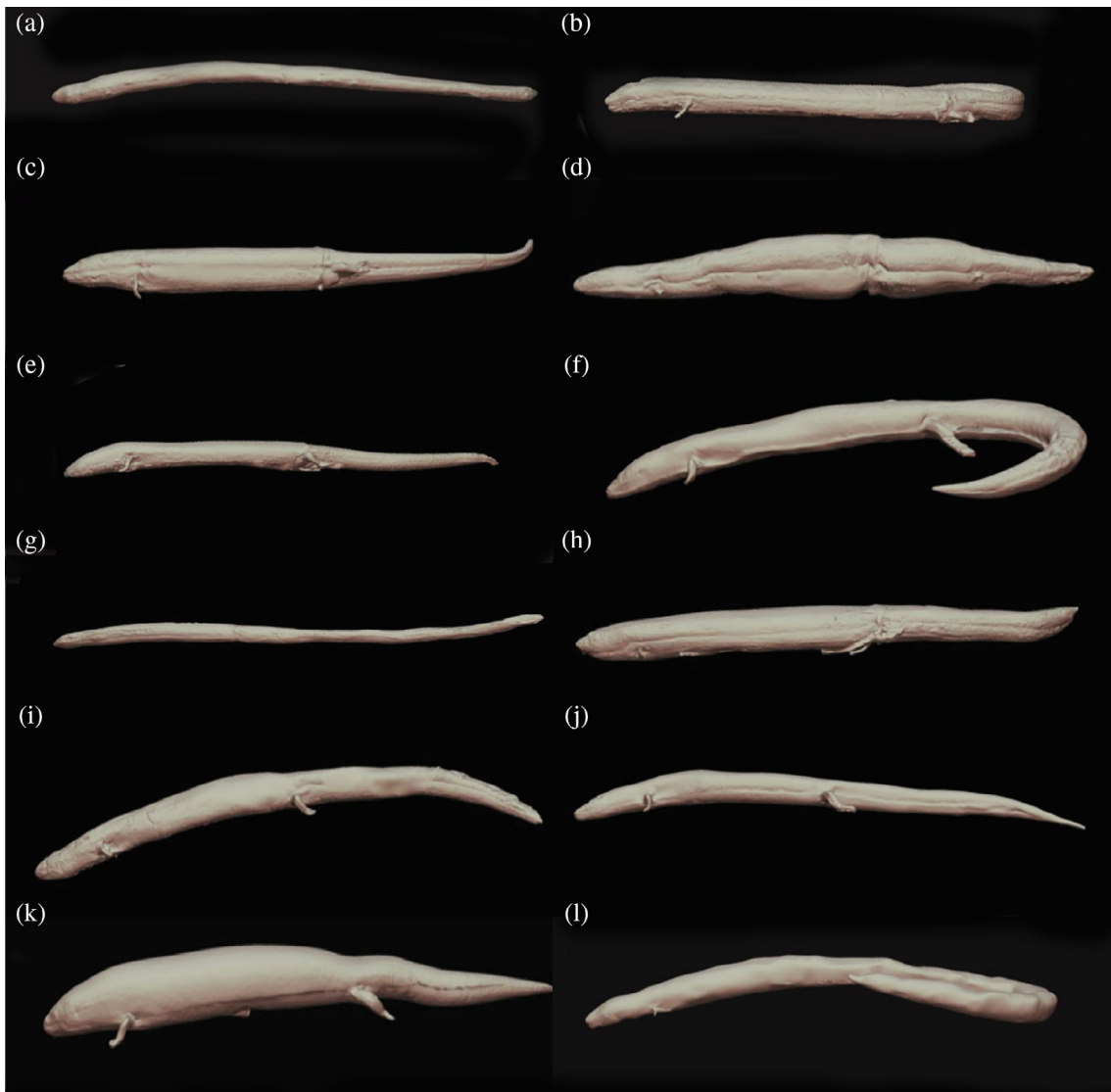


FIGURE 2 Lateral views of completed 3D-models: (a) *Brachymeles bicolorandia*; (b) *B. bicolor*; (c) *B. boulengeri*; (d) *B. ilocandia*; (e) *B. kadwa*; (f) *B. makusog*; (g) *B. minimus*; (h) *B. muntingkamay*; (i) *B. pathfinderi*; (j) *B. samad*; (k) *B. talinis*; (l) *B. tridactylus*

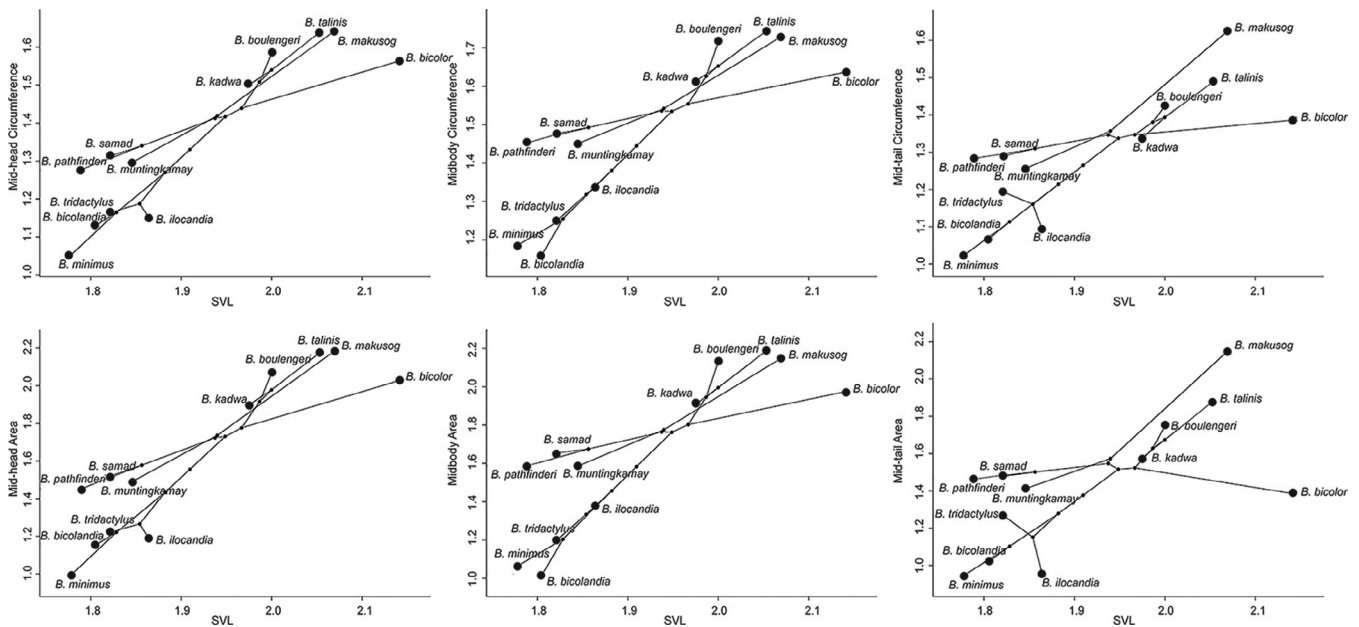


FIGURE 3 The top panel shows phylogenetic generalized least squares regressions of mid-head, midbody and mid-tail circumferences. The bottom panel shows phylogenetic generalized least squares regressions for the same measurements (head, body, and tail) cross-sectional areas. There were no deviations from isometry

The expected slope of an area under isometry is 2. All cross-sectional area measurements scaled isometrically with SVL (mid-head cross sectional area: $R^2 = 0.77$, slope = 2.55 ± 0.41 , $t = 1.34$, $p = .21$.; midbody cross sectional area: $R^2 = 0.64$, slope = 2.20 ± 0.49 , $t = 0.41$, $p = .69$; mid-tail cross sectional area: $R^2 = 0.19$, slope = 1.37 ± 0.73 , $t = -0.86$, $p = .41$). Lambda estimates are included in the supplemental materials for both circumference and cross-sectional area measurements ~SVL.

4 | DISCUSSION

We used 3D-digital photogrammetry to create 3D-models of 12 species of *Brachymeles* skins, and then examined patterns of scaling of the circumference and cross-sectional area at different points along the body. Our paper adds to the body of photogrammetry literature in demonstrating how this method can be used to effectively reconstruct and analyze fluid-preserved and soft-bodied specimens (Ferreira et al., 2019; Laforsch et al., 2012). As noted previously, evolution of the body axis represents a key aspect of morphological diversification among vertebrates, especially among lizards and snakes, and our paper represents another effort to understand how such shape changes occur. We found that, in *Brachymeles*, the cross-sectional area and circumference of the body axis scaled isometrically with body length in all the body regions.

The ecological, behavioral, and functional consequences of isometry or allometry have been widely discussed (Carrier, 1996; Gould, 1966; Slater & Van Valkenburgh, 2009). Prior studies in lizards have shown that lizards display a variety of deviations from typical scaling, depending on the taxa, and whether the comparisons are intraspecific or interspecific. For example, within some *Anolis* lizard

species, head dimensions tend to scale at, or close to isometry with body size (Herrel & O'Reilly, 2006), whereas within *Podarcis* species, one sees both positive and negative allometry (Kaliontzopoulou, Carretero, & Llorente, 2008). In other groups, there is evidence for positive allometry of head shape (Varanus, Openshaw & Keogh, 2014) and head weaponry (*Phrynosoma*, Bergmann & Berk, 2012). Thus, there are a range of patterns observed within and among lizard species, but among species, there seems to be more evidence for positive allometry. Against this background, *Brachymeles* presents a different pattern, although more species should be studied to assess what more typical patterns will look like. Departures from isometry in other studies have typically been interpreted as impacting function and ecology. For example, departures from isometry may impact locomotor performance (jackrabbits; Carrier, 1996), or bite force (lizards; Meyers, Herrel, & Birch, 2002), with relative increases or decreases in body dimensions impacting leverage, and therefore mechanics. However, it is also important to note that depending on the system, isometry can impact function. If the morphology is isometric, then this may result in bones that are actually relatively less stiff because force increases as a square of size and mass as a cube of size.

For the species examined here, one of the interesting functional implications of this finding is that the cross-sectional areas of smaller species are, therefore, proportionately smaller than for larger species. Since cross-sectional area should be proportional to force (Jones, Bishop, Woods, & Green, 2008) generated by muscles of the body axis, this would suggest that all species can generate about the same amount of force relative to their body size. A prediction of this might be that all the species would be able to bury into the substrate with the same performance, all else being equal. In the absence of

functional data, this remains a hypothesis for further testing, one that would require gathering burrowing data on species of different sizes.

In general, effective burrowers often have more streamlined heads (Vanhooydonck, Boistel, Fernandez, & Herrel, 2011). A bulky head, such as observed in the larger pentadactyl species of *Brachymeles*, suggests that they may not be highly effective burrowers. Previous work has shown that wider objects have a more difficult time getting through substrate due to drag (Albert et al., 2001), unless there are mechanical adaptations to help overcome this issue, as seen in Atlantic razor clams. They use a unique combination of valve and foot motions that reduces burrowing drag and energy consumption (Winter, Deits, Dorsch, Slocum, & Hosoi, 2014). Indeed, head shape diversification has been previously shown to be correlated with diet, habitat use, and locomotion in various lizard species (Barros, Herrel, & Kohlsdorf, 2011; Openshaw & Keogh, 2014; Vanhooydonck & Van Damme, 1999). The fact that skinks of different sizes do not differ dramatically in head circumference is intriguing in light of the fact that smaller *Brachymeles* appear to be more obligately fossorial than larger *Brachymeles*. In general, one would expect that a more gracile body may facilitate burrowing, although more functional and biomechanical data would be valuable for testing this possibility. Although we did not investigate limb morphology, previous research has shown that *Brachymeles* with robust bodies also tend to have well-developed limbs, whereas species with reduced or absent limbs have longer, slimmer, and overall smaller bodies (Greer et al., 1998; Greer & Wadsworth, 2003; Siler & Brown, 2011; Bergmann & Moringa, 2019).

Three-dimensional photogrammetry has been widely used for reconstruction of hard biological structures (e.g., bones), but few studies have employed this technique for reconstruction of soft-bodied preserved structures. Therefore, an additional value of our work is a workflow for accurate reconstruction of body forms using an inexpensive, portable, user-friendly, and widely accessible method. Accuracy and repeatability of 3D-photogrammetry has also been demonstrated in various other studies (Aldridge, Boyadjiev, Capone, DeLeon, & Richtsmeier, 2005; Chiari, Wang, Rushmeier, & Caccone, 2008), and our data are consistent with these studies. Measurements of our 12 3D-models had R^2 values of 0.94 or higher when comparing morphological measurements of the physical, preserved specimens (Table S1). One of the key value propositions of 3D-photogrammetry is the relatively small investment in equipment required for modeling. We only needed a camera, wireless trigger, tripod, rotating stool, and basic 3D-photogrammetry and post processing software. Although neither of the software packages we used (Geomagic and Reality Capture) is free, all of the work described herein can also be done using open-source software solutions, such as in Blender (Blender.org) and Meshroom 3D-photogrammetry software (Alicevision.com). Establishing this method allows researchers anywhere to use 3D-photogrammetry to create 3D-visualizations of biological specimens that can be analyzed and shared with the public. Sharing

these 3D-models allows others to verify findings and affords digital access to specimens that are otherwise rarely physically accessible due to remoteness of specimens, scarcity, or expense. These 3D-models can then be used to study a range of morphological questions, in this case the evolution of the body axis in *Brachymeles* skinks.

5 | CONCLUSIONS

We demonstrate that 3D-photogrammetry can be used to accurately investigate body axis evolution and morphology in *Brachymeles* skinks. Our analysis of the 3D-models showed an interesting trend in body shape given that as body size increased among species, the cross-sectional area and circumference of the head, body, and tail did not show evidence for deviation from isometry. This may suggest that all species can generate the same amount of force compared to their body size. Further functional and anatomical studies must be performed to further investigate these findings.

ACKNOWLEDGMENTS

We thank Daniel Daye, who assisted with construction of several of the 3D-models. We thank the following institutions for access to specimens: the Sam Noble Oklahoma Museum of Natural History (J. Watters), the Biodiversity Institute of The University of Kansas (R. Brown), and the California Academy of Science (J. Vindum & L. Scheinberg). This research was supported by the following NSF grants: IOS-1353683, 1353743, 1353691, and 1353703.

CONFLICT OF INTEREST

The authors declare no competing or financial interests.

DATA AVAILABILITY

The 3D-models are available at sketchfab.com/irschicklab. Supplementary information is available online at https://osf.io/2z4db/?view_only=b6f8a9f2bbc0404da455fcad2d4ed641 upon acceptance of manuscript.

AUTHOR CONTRIBUTIONS

Conceptualization: Duncan J. Irschick; Methodology: Duncan J. Irschick, Leah DeLorenzo; Investigation and visualization: Leah DeLorenzo; Analysis: Leah DeLorenzo, Abby Vander Linden, Duncan J. Irschick; Writing—original draft: Leah DeLorenzo, Duncan J. Irschick; Writing—revising and editing: Leah DeLorenzo, Abby Vander Linden, Duncan J. Irschick, Philip J. Bergmann, Gunter P. Wagner, Cameron D. Siler; Supervision: Duncan J. Irschick; Funding acquisition: Duncan J. Irschick, Philip J. Bergmann, Gunter P. Wagner, Cameron D. Siler.

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How to cite this article: DeLorenzo L, Vander Linden A, Bergmann PJ, Wagner GP, Siler CD, Irschick DJ. Using 3D-digital photogrammetry to examine scaling of the body axis in burrowing skinks. *Journal of Morphology*. 2020;1–9. <https://doi.org/10.1002/jmor.21253>