

# The evolution of bite force and head morphology in scincid lizards: diet and habitat use as possible drivers

ROBIN SAULNIER MASSON<sup>1,○</sup>, KARIM DAOUES<sup>2</sup>, JOHN MEASEY<sup>3</sup> and ANTHONY HERREL<sup>1,4,5,6\*,○</sup>

<sup>1</sup>UMR 7179 C.N.R.S/M.N.H.N., Département Adaptations du Vivant, Bâtiment d'Anatomie Comparée, 55 rue Buffon, 75005, Paris, France

<sup>2</sup>La Ferme Tropicale, 54 rue Jenner, 75013, Paris, France

<sup>3</sup>Centre for Invasion Biology, Department of Botany & Zoology, Stellenbosch University, Stellenbosch, Private Bag X1, South Africa

<sup>4</sup>Department of Biology, Evolutionary Morphology of Vertebrates, Ghent University, Ghent 9000, Belgium

<sup>5</sup>Department of Biology, University of Antwerp, Wilrijk 2610, Belgium

<sup>6</sup>Naturhistorisches Museum Bern, 3005 Bern, Switzerland

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Diet and habitat use impose mechanical constraints that may impact head morphology and bite force. Skinks (Scincidae) comprise the largest family of lizards with ~1700 species currently described. They also show an important morphological and ecological diversity. Using phylogenetically informed analyses, we studied the interrelationships between ecology (diet, habitat use), head morphology and bite force in these lizards. Our results show a strong link between body size, bite force and diet, with herbivorous species being larger and biting harder than species from other dietary groups. Despite a lack of differences in body size and head morphology, omnivorous species bite harder than insectivorous species, in order to process the fibrous plant material that is part of their diet. Overall, lineages that evolved greater bite forces also showed an increase in relative head height allowing for more vertically oriented jaw muscles. Moreover, we find evidence for correlated evolution between bite force and head length: skinks that bite harder tend to have shorter jaws that likely provide a greater mechanical advantage when biting at the tip of the jaw. Surprisingly, habitat use does not appear to be correlated with morphological traits or bite force, but this needs to be explored further.

ADDITIONAL KEYWORDS: diet – habitat use – head shape – performance – skinks.

## INTRODUCTION

The vertebrate skull is a complex integrated system composed of numerous structural units (Herrel *et al.*, 2007a). These units are forged by different biotic and abiotic interactions and are critical to several functions including defence (e.g. Cooper *et al.*, 1999), locomotion (e.g. Gans, 1975; Teodecki *et al.*, 1998), male-male combat (e.g. Huyghe *et al.*, 2005; Lappin *et al.*, 2006), mating (e.g. Herrel *et al.*, 1999b), drinking (e.g. Bels *et al.*, 1994; Cundall, 2000) and feeding (e.g. Wainwright & Richard, 1995; Cundall & Greene, 2000; Schwenk, 2000). As such the skull plays a key role in many different ecological and behavioural contexts

(Hanken & Hall, 1993). Moreover, the skull houses and protects the brain and the main sensory organs (e.g. eyes, vomeronasal apparatus). As these organs take up space within this integrated system there may be competing demands for space (Barel, 1982) and function (Herrel *et al.*, 2001c) between these different structural units. Thus, the skull is the result of structural integration and functional compromises (Wainwright & Richard, 1995; Vanhooydonck *et al.*, 2011; Corbin *et al.*, 2015; Edwards *et al.*, 2016; Maestri *et al.*, 2016; Watanabe *et al.*, 2019), which renders our understanding of the factors driving variation in cranial morphology complex.

The study of animal performance is important in this context as it allows variation in morphology to be linked to variation in ecology (Wainwright & Reilly,

\*Corresponding author. E-mail: [anthony.herrel@mnhn.fr](mailto:anthony.herrel@mnhn.fr)

1994; Irschick & Higham, 2016). Indeed, selection acts at the level of whole-organism performance rather than on the underlying structural components (Arnold, 1983; Careau & Garland, 2012; Lailvaux & Husak, 2014). Consequently, performance traits reflect both the behaviour and the ecological context of a species (Irschick *et al.*, 2005; Herrel *et al.*, 2007a; Huyghe *et al.*, 2007). One of the most relevant performance traits associated with the cranial system is bite force (Wainwright & Richard, 1995; Schluter, 2000; Anderson *et al.*, 2008). This performance trait is important in the acquisition of resources, in fighting and in defence (Herrel *et al.*, 1998; Erickson *et al.*, 2003). The use of novel resources and the conquest of new ecological niches by an animal are consequently often associated with morphological adaptations of the jaw system resulting in variation in bite force across species (Herrel *et al.*, 2004b; Cattau *et al.*, 2018). Moreover, for some species, bite force has been demonstrated to be heritable (Zablocki-Thomas *et al.*, 2021) and to impact survival in the field (Herrel *et al.*, 2016), making it a key performance trait that is likely under selection.

Previous studies on lizards and other vertebrates have shown that the evolution towards higher bite force often goes hand in hand with the evolution of larger body size (Aguirre *et al.*, 2002; Herrel *et al.*, 2004a, 2010; Chazeau *et al.*, 2013). However, irrespective of variation in body size, the evolution of a bigger head also promotes stronger bites due to the larger absolute jaw muscle volume that can be housed (Herrel *et al.*, 2001a, b, 2006). Bite force has been suggested to determine diet in lizards with an increase in bite force often leading to a greater trophic diversity (Witorski *et al.*, 2016; Taverne *et al.*, 2021). Durophagy and herbivory, for example, are dietary specializations that require high bite force due to the mechanical resistance of hard and fibrous food items (Herrel *et al.*, 1999a, 2004b; Schaerlaeken *et al.*, 2012). It has consequently been suggested that lizards eating such food items should have higher and wider heads with more massive cranial muscles than lizards that eat softer foods (Herrel & Holanova, 2008; Schaerlaeken *et al.*, 2012).

On the other hand, habitat use can also generate mechanical limitations affecting head size and shape and thus indirectly also drive bite force evolution. In fossorial lizards, for example, the time needed to burrow and the energetic cost of burrowing correlate with bite force given that both are determined by head width (e.g. Navas *et al.*, 2004; Barros *et al.*, 2011; Vanhooydonck *et al.*, 2011; Le Guilloux *et al.*, 2020). In addition, crevice dwellers or climbing lizards may show reduced head and body heights to be able to exploit crevices and to avoid toppling backwards during climbing (Herrel *et al.*, 2001b, c; Kohlsdorf *et al.*, 2008). Moreover, tree dwelling lizards typically

have narrow heads allowing more stability when running on narrow branches (Herrel *et al.*, 2001d; Kohlsdorf *et al.*, 2008). Consequently, head size and shape may be the result of trade-offs between feeding, habitat use and locomotion and, as such, affect bite force (Vanhooydonck *et al.*, 2011). Therefore, not only head size but also head shape is likely an important determinant of bite force (Herrel *et al.*, 2007b; Fabre *et al.*, 2014a, b).

In this study, we analyse the proximate determinants of bite force across 56 species of the family Scincidae. This group of lizards was chosen as it is the most species-rich lizard family characterized by an exceptional morphological and ecological diversity (Chapple *et al.*, 2021; Uetz *et al.*, 2022). Skinks show a great diversity in diet ranging from insectivorous to herbivorous and durophagous species. Moreover, they can be found on all continents except Antarctica and exploit a wide variety of habitats ranging from arboreal over fossorial to terrestrial and even semi-aquatic. In addition to this tremendous ecological diversity, scincid lizards are also morphologically diverse, yet remain relatively poorly studied (Greer, 1974; William & Peterson, 1982; Paluh & Bauer, 2017; Foster *et al.*, 2018). Capitalizing on the morphological, ecological and taxonomic diversity of skinks, we examine here the relationship between head morphology and bite force in the sample of skinks and assess whether this differs among lizards with distinct ecologies (diet, habitat use). We specifically predict that bite force will differ between diet groups with herbivorous species biting harder than insectivorous species as shown previously for other lizard groups (Herrel *et al.*, 1999a, 2004b; Vitt *et al.*, 2003; Metzger & Herrel, 2005). We further predict that fossorial species, climbers and saxicolous species will differ in head size and shape, and will have lower bite forces given the constraints on head size and shape in these habitats (Herrel *et al.*, 2001d; Kohlsdorf *et al.*, 2008; Barros *et al.*, 2011; Vanhooydonck *et al.*, 2011; Paluh & Bauer, 2017).

## MATERIAL AND METHODS

### SPECIMENS

The sample consisted of data on head dimensions, body size and bite force for 331 individuals across 56 species of skinks. Seven of these belong to the Acontinae, 16 to the Scincinae and 33 to the Lygosominae. We use binomial nomenclature as provided by the Reptile Database (Uetz *et al.*, 2022). The number of individuals sampled per species (Table 1) varied according to the availability of specimens for morphological and *in vivo* measurements.

**Table 1.** Morphological traits and bite force of the species included in our study. Table entries are means  $\pm$  standard deviations. *N*: number of specimens measured

Species	<i>N</i>	SVL (mm)	Head length (mm)	Head width (mm)	Head height (mm)	Lower jaw length (mm)	Bite force (N)
<i>Ablepharus kitaibelii</i>	13	40.94 $\pm$ 2.43	6.44 $\pm$ 0.45	3.62 $\pm$ 0.28	2.55 $\pm$ 0.22	5.85 $\pm$ 0.57	0.3 $\pm$ 0.14
<i>Acontias kgalagadi</i>	5	116.12 $\pm$ 12.1	7.27 $\pm$ 0.49	3.6 $\pm$ 0.2	3.23 $\pm$ 0.86	5.7 $\pm$ 0.34	1.16 $\pm$ 0.4
<i>Acontias litoralis</i>	42	116.62 $\pm$ 11.72	6.22 $\pm$ 0.86	3.13 $\pm$ 0.24	2.66 $\pm$ 0.18	5.41 $\pm$ 0.62	0.77 $\pm$ 0.19
<i>Acontias meleagris</i>	6	194.24 $\pm$ 16.34	10.43 $\pm$ 1.08	5.81 $\pm$ 0.9	4.56 $\pm$ 0.55	7.67 $\pm$ 1.16	9 $\pm$ 1.77
<i>Acontias percivali</i>	13	224.3 $\pm$ 10.04	14.26 $\pm$ 0.15	8 $\pm$ 0.06	6.98 $\pm$ 0.08	13.25 $\pm$ 0.44	10.08 $\pm$ 2.62
<i>Bellatorias frerei</i>	1	188.36	31.56	22.48	17.9	35.7	81.47
<i>Chalcides ocellatus</i>	13	96.11 $\pm$ 24.98	13.46 $\pm$ 2.84	9.03 $\pm$ 2.24	7.7 $\pm$ 2	14.71 $\pm$ 3.18	8.51 $\pm$ 4.19
<i>Chalcides sepsoides</i>	17	83.41 $\pm$ 5.73	9.9 $\pm$ 0.48	5.93 $\pm$ 0.33	5.05 $\pm$ 0.24	9.97 $\pm$ 0.71	4.12 $\pm$ 0.75
<i>Chalcides sphenopsiformis</i>	1	83	7.99	4.97	4.25	7.51	3.16
<i>Cophoscincopus greeri</i>	4	65.73 $\pm$ 2.09	12.93 $\pm$ 0.55	8.19 $\pm$ 0.66	6.98 $\pm$ 0.56	12.14 $\pm$ 1	7.49 $\pm$ 0.79
<i>Corucia zebrata</i>	2	275 $\pm$ 7.07	50.6 $\pm$ 4.53	48.88 $\pm$ 2.37	36.03 $\pm$ 3.01	57.1 $\pm$ 1.63	206.85 $\pm$ 94.36
<i>Ctenotus uber</i>	3	86.26 $\pm$ 23.66	15.08 $\pm$ 3.61	9.99 $\pm$ 2.41	8.81 $\pm$ 2.54	17.5 $\pm$ 4.19	7.86 $\pm$ 4.19
<i>Cyclodomorphus gerrardii</i>	1	70.92	14.9	10.15	7.34	17.15	16.683
<i>Cyclodomorphus michaeli</i>	2	122.69 $\pm$ 14.11	15.49 $\pm$ 2.12	9.41 $\pm$ 1.07	9.12 $\pm$ 0.04	19.49 $\pm$ 2.7	9.74 $\pm$ 1.15
<i>Eulamprus heatwolei</i>	5	109.17 $\pm$ 23.2	21.37 $\pm$ 3.6	13.7 $\pm$ 2.9	11.24 $\pm$ 2.26	25.96 $\pm$ 5.23	16.66 $\pm$ 7.24
<i>Eumeces schneiderii</i>	3	122.01 $\pm$ 22.8	24.61 $\pm$ 1.57	16.16 $\pm$ 2.98	13.97 $\pm$ 2.53	27.48 $\pm$ 3.02	53.27 $\pm$ 6.25
<i>Isopachys gyldenstolpei</i>	1	180	10.54	6.6	5.82	8.77	5.89
<i>Leptosiphos kilimensis</i>	5	69.81 $\pm$ 14.29	10.26 $\pm$ 1.14	5.63 $\pm$ 0.84	4.18 $\pm$ 0.61	10.5 $\pm$ 1.55	2.36 $\pm$ 1.87
<i>Lerista edwardsae</i>	16	81.03 $\pm$ 7.34	7.99 $\pm$ 0.45	4.91 $\pm$ 0.35	4.18 $\pm$ 0.34	7.4 $\pm$ 0.87	2.51 $\pm$ 0.63
<i>Mochlus fernandi</i>	2	124.75 $\pm$ 11.92	22.09 $\pm$ 1.94	15.96 $\pm$ 2.21	12.19 $\pm$ 2.04	25.36 $\pm$ 3.46	41.07 $\pm$ 0.95
<i>Mochlus sundevallii</i>	15	87.31 $\pm$ 29.36	12.73 $\pm$ 2.84	7.87 $\pm$ 1.87	6.37 $\pm$ 1.73	12.95 $\pm$ 3.08	8.84 $\pm$ 5.06
<i>Morethia butleri</i>	1	45.92	8.34	4.99	3.98	8.92	1.07
<i>Panaspis togoensis</i>	1	35.59	6.89	3.4	2.2	6.95	0.33
<i>Panaspis wahlbergii</i>	1	35.59	6.89	3.4	2.2	6.95	0.33
<i>Plestiodon fasciatus</i>	4	67.72 $\pm$ 1.68	13.8 $\pm$ 1.32	9.31 $\pm$ 0.95	6.33 $\pm$ 0.76	15.72 $\pm$ 1.04	6.58 $\pm$ 1.51
<i>Plestiodon gilberti</i>	1	89.92	16.77	11.32	8.39	18.86	10.19
<i>Plestiodon laticeps</i>	17	99.87 $\pm$ 11.14	19.59 $\pm$ 2.56	15.09 $\pm$ 2.84	9.75 $\pm$ 1.77	22.43 $\pm$ 3.01	17.86 $\pm$ 4.26
<i>Plestiodon tetragrammus</i>	2	58.72 $\pm$ 3.23	9.42 $\pm$ 0.25	6.38 $\pm$ 0.06	5.33 $\pm$ 0.31	11.36 $\pm$ 0.99	1.61 $\pm$ 0.33
<i>Pygomeles braconnieri</i>	1	165	13.31	8.17	6.65	12.33	9.36
<i>Scelotes bipes</i>	9	75.47 $\pm$ 11.8	6.2 $\pm$ 0.62	3.18 $\pm$ 0.61	2.7 $\pm$ 0.32	5.53 $\pm$ 0.62	1.38 $\pm$ 0.71
<i>Scelotes limpopoensis</i>	1	61.07	7.3	3.81	2.81	7.32	0.51

**Table 1.** Continued

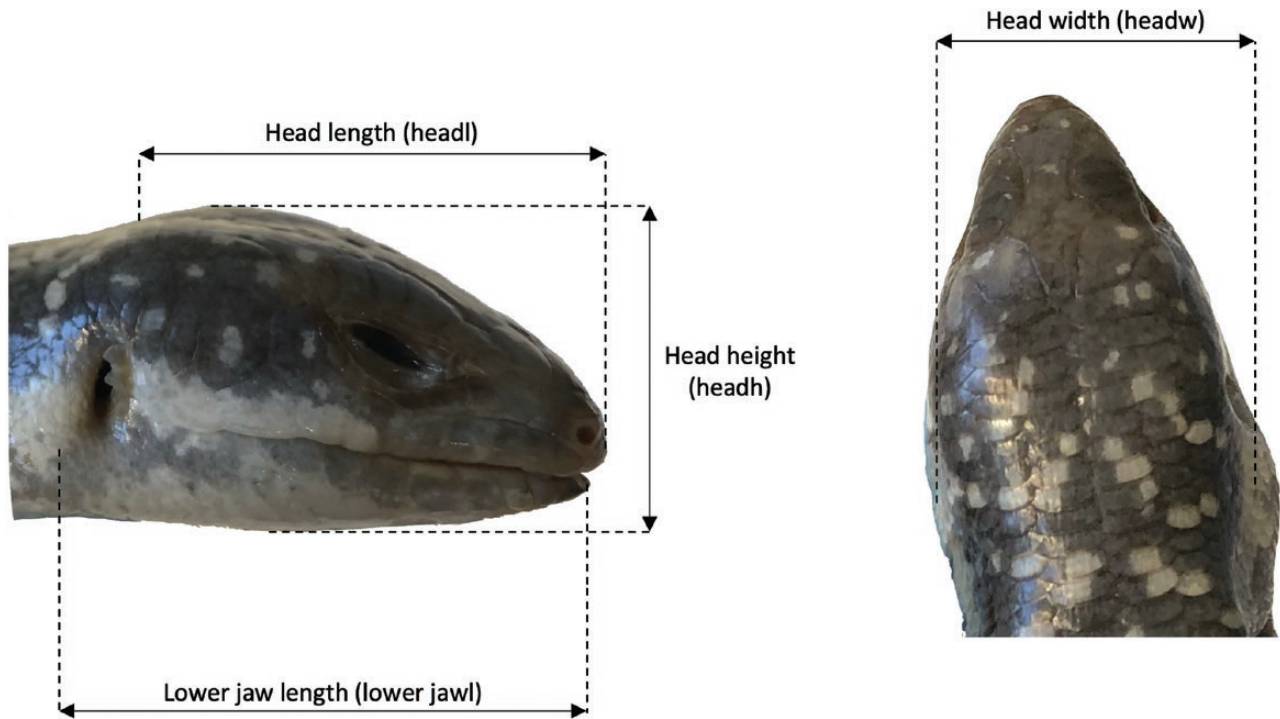
Species	N	SVL (mm)	Head length (mm)	Head width (mm)	Head height (mm)	Lower jaw length (mm)	Bite force (N)
<i>Scelotes montispectus</i>	1	61.58	6.81	3.32	2.83	6.4	1.27
<i>Scelotes sexlineatus</i>	5	80.25 ± 18.98	7.51 ± 1.18	3.81 ± 0.66	3.16 ± 0.54	6.61 ± 1.34	0.54 ± 0.23
<i>Scincella cherriei</i>	1	33.08	7.57	4.26	3.15	7.84	0.37
<i>Scincopus fasciatus</i>	1	154.16	35.71	24.09	18.54	36	29.212
<i>Scincus mitranus</i>	9	90.72 ± 12.14	17.93 ± 2.29	9.99 ± 1.25	9.12 ± 1.13	15.53 ± 2.01	24.87 ± 9.37
<i>Scincus scincus</i>	5	91.02 ± 3.04	18.78 ± 3.96	10.72 ± 0.72	9.82 ± 0.88	17.74 ± 1.47	18.97 ± 3.59
<i>Tiliqua multifasciata</i>	4	181.85 ± 41.77	29.14 ± 4.28	31.8 ± 6.19	21.41 ± 3.06	35.68 ± 7.09	67.23 ± 2.47
<i>Tiliqua occipitalis</i>	1	292.42	58.91	42.32	30.4	49.77	58.89
<i>Tiliqua rugosa</i>	15	281.56 ± 27.79	45.84 ± 4.81	51.41 ± 5.34	32.89 ± 3.61	56.83 ± 7.11	157.11 ± 41.84
<i>Tiliqua scincoides</i>	14	262.09 ± 67.45	48.68 ± 9.63	38.49 ± 8.97	29.57 ± 6.8	52.93 ± 9.18	158.49 ± 38.08
<i>Trachylepis capensis</i>	2	85.72 ± 10.43	15.68 ± 1.07	10.63 ± 0.5	8.78 ± 0.1	17.26 ± 0.34	15.81 ± 1.23
<i>Trachylepis homalocephala</i>	2	62.86 ± 8.22	11.66 ± 0.91	8.02 ± 0.47	5.72 ± 0.93	12.36 ± 0.83	9.97 ± 0.58
<i>Trachylepis punctatissima</i>	1	67.4	13.21	8.3	5.79	13.47	8.07
<i>Trachylepis quinquetaeniata</i>	1	107.9	19.4	10	5.6	17.8	1.05
<i>Trachylepis spilogaster</i>	2	63.68 ± 23.03	13.53 ± 3.26	8.92 ± 3.01	5.78 ± 1.86	13.22 ± 3.15	5.94 ± 4.77
<i>Trachylepis striata</i>	4	89.4 ± 18.96	18.6 ± 4.9	11.31 ± 4.12	7.8 ± 2.73	20.34 ± 6.64	19.7 ± 24.25
<i>Trachylepis sulcata</i>	5	69.82 ± 4.65	14.92 ± 1.07	9.78 ± 0.64	6.3 ± 0.22	16.29 ± 1.06	6.76 ± 2.39
<i>Trachylepis varia</i>	3	72.7 ± 23.48	17.15 ± 5.83	10.53 ± 3.85	5.85 ± 1.34	16.74 ± 5.66	9.04 ± 3.78
<i>Trachylepis variegata</i>	3	48.48 ± 2.73	10.46 ± 0.72	6.24 ± 0.24	4.42 ± 0.31	10.68 ± 0.35	1.37 ± 0.32
<i>Tribolonotus gracilis</i>	3	96.96 ± 9.91	31.1 ± 3.81	23.42 ± 2.49	15.64 ± 1.08	31.29 ± 2.94	55.88 ± 8.15
<i>Tribolonotus novaeguineae</i>	2	90.15 ± 2.69	25.52 ± 1.47	17.51 ± 1.54	12.23 ± 2.37	25.06 ± 0.1	42.41 ± 3.13
<i>Tropidophorus baconi</i>	1	126.17	29.48	20.07	15.41	31.17	43.99
<i>Typhlosaurus caecus</i>	25	186.08 ± 34.42	6.96 ± 0.8	3.59 ± 0.54	2.06 ± 0.27	4.88 ± 0.77	3.53 ± 1.6
<i>Typhlosaurus lomiae</i>	8	109.13 ± 6.75	5.57 ± 0.25	2.63 ± 0.06	2.15 ± 0.05	4.08 ± 0.45	0.45 ± 0.12
<i>Typhlosaurus vermis</i>	5	214.2 ± 48.57	6.93 ± 0.99	3.33 ± 0.37	2.79 ± 0.33	5.46 ± 0.86	1.02 ± 0.25

## MORPHOMETRICS

Five morphological measurements were taken for all specimens (Fig. 1; Table 1). We used the same measurements as described in Herrel & Holanová (2008). Snout-vent length (SVL) was measured from the tip of the snout to the posterior edge of the anal

scale, head length (headl) from the back of the parietal bone to the tip of the upper jaw, head height (headh) at the highest part of the head and posterior to the orbit, head width (headw) at the widest part of the head and at the level of jugal bone, and lower jaw length (lj) was measured from the back of the retroarticular





**Figure 1.** Illustration of The measurements taken on the heads of the lizards, illustrated on a picture of the head of *Eumeces schneiderii*.

process to the tip of lower jaw. The bones used in these measurements were easily identified by palpation. All measurements were taken using digital calipers (Mitutoyo CD-20DC, Kawasaki, Japan; precision: 0.01 mm), and were taken on the right side of the specimens.

#### BITE FORCE

*In vivo* bite forces were taken in captivity or in the field. Only data for adults were used for this study and the number of individuals per species varied (Table 1). Bite force measurements were taken using an isometric Kistler force transducer (type 9203, range  $\pm 500$  N; Kistler, Zurich, Switzerland) mounted on a purpose-built holder and connected to a Kistler charge amplifier (Type 5995 A, Kistler; see Herrel *et al.*, 1999b). When the bite plates were placed between the jaws of the animals, prolonged and repeated biting typically resulted. The place of application of bite forces was standardized for all animals by metal stops that were mounted on the bite plates, thus assuring that animals always bit at the same position along the tooth row. Gape angle was standardized by moving the bite plates away from each other for larger animals resulting in animals biting at a gape angle of  $30^\circ$ . Surgical tape was wrapped around the bite plates to provide grip and to prevent damage to the teeth. Bite forces were measured five times for each animal and only the highest measurement was retained and considered to be the maximal bite force.

The maximal raw bite force recorded from the amplifier was multiplied by 0.67 to correct for the lever arms of the set-up.

#### DIET

Species were classified into one of three dietary categories: herbivory (four species), omnivory (seven species) and insectivory (45 species) (Table 2). Here, herbivorous species are considered to have a diet consisting of at least 70% fibrous plant material (i.e. all plant material except fruits and nectar), omnivorous species have a diet with 10% to 70% of plant material, and insectivorous species are those with less than 10% of plant material (Cooper & Vitt, 2002). As our study included a broad diversity of species, dietary data were not always available for each species. In that case the diet of a sister taxon of the same genus for which data were available was used. Sister taxa were used in only a few instances, and in all cases, diet did not show much variation within the genus. Moreover, we only extrapolated from other species in cases of insectivory to avoid inflating the number of independent origins of the less common diet types.

#### HABITAT USE

Skinks were classified into five habitat groups, in part based on Meiri (2018): arboreal (two species), fossorial (20

**Table 2.** Ecological traits for each species included in the study and references

Species	Family	Diet	Habitat	References
<i>Ablepharus kitaibelii</i>	Lygosominae	Insectivorous	Terrestrial	Meiri, 2018
<i>Acontias kgalagadi</i>	Acontinae	Insectivorous	Fossorial	Meiri, 2018
<i>Acontias litoralis</i>	Acontinae	Insectivorous	Fossorial	Meiri, 2018
<i>Acontias meleagris</i>	Acontinae	Insectivorous	Fossorial	Meiri, 2018
<i>Acontias percivali</i>	Acontinae	Insectivorous	Fossorial	Meiri, 2018
<i>Bellatorias frerei</i>	Lygosominae	Omnivorous	Terrestrial	Meiri, 2018
<i>Chalcides ocellatus</i>	Scincinae	Insectivorous	Fossorial	Andrews <i>et al.</i> , 1987; Carretero <i>et al.</i> , 2010
<i>Chalcides sepsoides</i>	Scincinae	Omnivorous	Fossorial	Meiri, 2018
<i>Chalcides sphenopsiformis</i>	Scincinae	Insectivorous	Fossorial	Andrews & Kenney, 1990; Attum <i>et al.</i> , 2004; Meiri, 2018
<i>Cophoscincopus greeri</i>	Lygosominae	Insectivorous	Semi-aquatic	Meiri, 2018
<i>Corucia zebrata</i>	Lygosominae	Herbivorous	Arboreal	Meiri, 2018
<i>Ctenotus uber</i>	Lygosominae	Omnivorous	Terrestrial	Meiri, 2018
<i>Cyclodomorphus gerrardii</i>	Lygosominae	Insectivorous	Terrestrial	Meiri, 2018
<i>Cyclodomorphus michaeli</i>	Lygosominae	Insectivorous	Terrestrial	Meiri, 2018
<i>Eulamprus heatwolei</i>	Lygosominae	Insectivorous	Semi-aquatic	Meiri, 2018
<i>Eumeces schneiderii</i>	Scincinae	Omnivorous	Terrestrial	Meiri, 2018
<i>Isopachys gyldestolpei</i>	Lygosominae	Insectivorous	Fossorial	Das, 2010; Chan-Ard <i>et al.</i> , 2015; Camaiti <i>et al.</i> , 2022
<i>Leptosiaphos kilimensis</i>	Lygosominae	Insectivorous	Terrestrial	Meiri, 2018
<i>Lerista edwardsae</i>	Lygosominae	Insectivorous	Fossorial	Meiri, 2018
<i>Mochlus fernandi</i>	Lygosominae	Insectivorous	Terrestrial	Meiri, 2018
<i>Mochlus undevallii</i>	Lygosominae	Insectivorous	Terrestrial	Meiri, 2018
<i>Morethia butleri</i>	Lygosominae	Insectivorous	Terrestrial	Meiri, 2018
<i>Panaspis togoensis</i>	Lygosominae	Insectivorous	Terrestrial	Meiri, 2018
<i>Panaspis wahlbergii</i>	Lygosominae	Insectivorous	Terrestrial	Razzetti & Msuya, 2002; Ceriaco <i>et al.</i> , 2018
<i>Plestiodon fasciatus</i>	Scincinae	Insectivorous	Terrestrial	Meiri, 2018
<i>Plestiodon gilberti</i>	Scincinae	Insectivorous	Terrestrial	Meiri, 2018
<i>Plestiodon laticeps</i>	Scincinae	Insectivorous	Terrestrial	Meiri, 2018
<i>Plestiodon tetragrammus</i>	Scincinae	Insectivorous	Terrestrial	Meiri, 2018
<i>Pygomeles braconnieri</i>	Scincinae	Insectivorous	Fossorial	Glaw & Vences, 2007; Meiri, 2018
<i>Scelotes bipes</i>	Scincinae	Insectivorous	Fossorial	Meiri, 2018
<i>Scelotes limpopoensis</i>	Scincinae	Insectivorous	Fossorial	Meiri, 2018
<i>Scelotes montispectus</i>	Scincinae	Insectivorous	Fossorial	Fitzsimons, 1943; Branch & Braack, 1987; Bates <i>et al.</i> , 2014
<i>Scelotes sexlineatus</i>	Scincinae	Insectivorous	Fossorial	Fitzsimons, 1943; Branch & Braack, 1987; Bates <i>et al.</i> , 2014
<i>Scincella cherriei</i>	Lygosominae	Insectivorous	Terrestrial	Meiri, 2018
<i>Scincopus fasciatus</i>	Scincinae	Insectivorous	Fossorial	Meiri, 2018
<i>Scincus mitranus</i>	Scincinae	Omnivorous	Fossorial	Meiri, 2018
<i>Scincus scincus</i>	Scincinae	Omnivorous	Fossorial	Meiri, 2018
<i>Tiliqua multifasciata</i>	Lygosominae	Herbivorous	Terrestrial	Meiri, 2018
<i>Tiliqua occipitalis</i>	Lygosominae	Herbivorous	Terrestrial	Shea, 2006; Swan <i>et al.</i> , 2017
<i>Tiliqua rugosa</i>	Lygosominae	Herbivorous	Terrestrial	Meiri, 2018
<i>Tiliqua scincoides</i>	Lygosominae	Omnivorous	Terrestrial	Meiri, 2018
<i>Trachylepis capensis</i>	Lygosominae	Insectivorous	Terrestrial	Meiri, 2018
<i>Trachylepis homalocephala</i>	Lygosominae	Insectivorous	Saxicolous	Meiri, 2018
<i>Trachylepis punctatissima</i>	Lygosominae	Insectivorous	Terrestrial	Meiri, 2018
<i>Trachylepis quinquetaeniata</i>	Lygosominae	Insectivorous	Saxicolous	Spawls <i>et al.</i> , 2001; Meiri, 2018; Dendi <i>et al.</i> , 2019
<i>Trachylepis spilogaster</i>	Lygosominae	Insectivorous	Arboreal	Meiri, 2018

**Table 2.** Continued

Species	Family	Diet	Habitat	References
<i>Trachylepis striata</i>	Lygosominae	Insectivorous	Terrestrial	Meiri, 2018
<i>Trachylepis sulcata</i>	Lygosominae	Insectivorous	Saxicolous	Meiri, 2018
<i>Trachylepis varia</i>	Lygosominae	Insectivorous	Terrestrial	Meiri, 2018
<i>Trachylepis variegata</i>	Lygosominae	Insectivorous	Terrestrial	Meiri, 2018
<i>Tribolonotus gracilis</i>	Lygosominae	Insectivorous	Terrestrial	Meiri, 2018
<i>Tribolonotus novaeguineae</i>	Lygosominae	Insectivorous	Terrestrial	Meiri, 2018
<i>Tropidophorus baconi</i>	Lygosominae	Insectivorous	Semi-aquatic	Hikida <i>et al.</i> , 2003; Chuaynkern <i>et al.</i> , 2014
<i>Typhlosaurus caecus</i>	Acontinae	Insectivorous	Fossorial	Meiri, 2018
<i>Typhlosaurus lomiae</i>	Acontinae	Insectivorous	Fossorial	Meiri, 2018
<i>Typhlosaurus vermis</i>	Acontinae	Insectivorous	Fossorial	Meiri, 2018

**Table 3.** Results of the phylogenetic ANOVAs. Significant results are in bold

Variable	d.f.	F	P <sub>phylo</sub>
Snout-vent length			
Diet	2, 49	<b>20.14</b>	<b>0.002</b>
Habitat	4, 49	1.47	0.58
Bite force			
Diet	2, 49	<b>36.7</b>	<b>&lt; 0.001</b>
Habitat	4, 49	2.20	0.43
Relative bite force			
Diet	2, 49	<b>6.78</b>	<b>0.0499</b>
Habitat	4, 49	5.32	0.12
Factor: diet			
Head length	2, 53	<b>6.22</b>	<b>0.062</b>
Head height	2, 53	<b>9.39</b>	<b>0.015</b>
Head width	2, 53	<b>8.31</b>	<b>0.02</b>
Lower jaw length	2, 53	4.85	0.102
Factor: habitat			
Head length	4, 51	<b>9.44</b>	<b>0.033</b>
Head height	4, 51	7.11	0.063
Head width	4, 51	<b>10.44</b>	<b>0.028</b>
Lower jaw length	4, 51	<b>11.88</b>	<b>0.014</b>

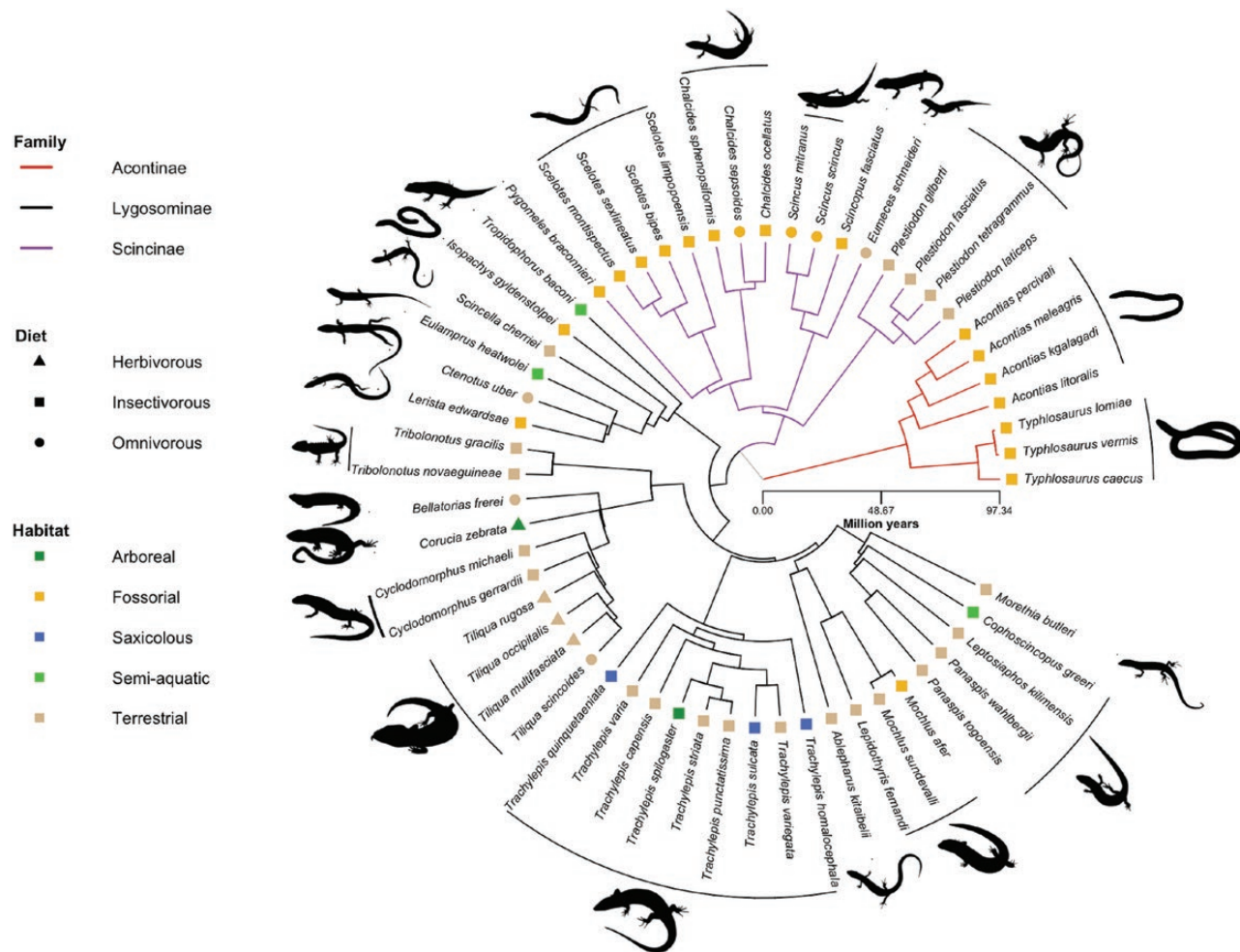
species), saxicolous (three species), semi-aquatic (three species) and terrestrial (28 species) (Table 2). Arboreal species live in the vegetation and are rarely observed on the ground, unlike saxicolous species, which are as comfortable on the ground as in trees or rocks (Ribeiro *et al.*, 2008). Semi-aquatic species spend significant amounts of time in water and are excellent swimmers, contrary to fossorial species which spend most of their time buried in the substrate. All other species were classified as terrestrial.

#### STATISTICAL ANALYSIS

All statistical analyses were run in R (R Development Core Team, 2005). First, we calculated species means

using only adults from the data set. Second, we pruned the time-calibrated phylogeny from Zheng & Wiens (2016) using the R packages ape (Paradis & Schliep, 2019) and geiger (Pennell *et al.*, 2014) to include only the species in our data set (Fig. 2). To account for the non-independence of species due to shared ancestry (Felsenstein, 1985), all statistical analyses were performed in a strict phylogenetic comparative framework.

To explore the effect of diet and habitat on overall body size (SVL), we performed a two-way phylogenetic analysis of variance (PhyANOVA) using a Brownian motion model followed by phylogenetic post hoc tests using the aov.phylo function of geiger (Pennell *et al.*, 2014) and the phyANOVA function of the phytools package (Revell & Revell, 2014).



**Figure 2.** Time-calibrated phylogeny representing the relationships between the species included in this study modified from Zheng & Wiens (2016). The family, diet, habitat and body form of each species are indicated.

To explore morphological differences according to diet and habitat, we performed multivariate phylogenetic analysis of covariance (phylogenetic MANOVA) using residual head dimensions. To do so all morphological variables were logarithmically transformed ( $\log_{10}$ ) to fulfil assumptions of normality and homoscedasticity (Kachigan, 1991; Sokal & Rohlf, 1995). Subsequently, the  $\log_{10}$ -transformed head dimensions were regressed on  $\log_{10}$ -transformed SVL using generalized least squares regressions with phylogenetic size correction (phylogenetic generalized least squares [PGLS]; Mao *et al.*, 2015) and unstandardized residuals were extracted. These were then used as input for a phylogenetic MANOVA to test the effects of diet and habitat irrespective of variation in head size. Subsequently phylogenetic ANOVAs and post hoc tests with the *phylolm* function from the *phylolm* package (Ho *et al.*, 2016) were run to better understand which variables drove the results and which groups differed from one another.

To determine which morphological traits explained variation in bite force, all morphological and bite force measures were  $\log_{10}$ -transformed and used as input for a phylogenetic stepwise multiple regression analysis with bite force as the dependent variable and the morphological traits as the independent variables. To do this, the *phylstep* function of the *phylolm* package (Ho *et al.*, 2016) was used with Brownian motion as the evolutionary model. This evolutionary model was selected by running the *fitContinuous* function from the *geiger* package (Pennell *et al.*, 2014). The best regression model was selected based on the minimal Akaike Information Criterion (AIC) and variables in the model were selected using both forward and backward procedures. A phylogenetic regression was then carried out using the *phylolm* function from the *phylolm* package (Ho *et al.*, 2016) to estimate the relationship between bite force and the morphological traits.



**Table 4.** Bonferroni post hoc results testing for differences between diet categories. Significant results are in bold

	Herbivorous	Insectivorous	Omnivorous
<i>Snout-vent length</i>			
Herbivorous		<b>0.003</b>	<b>0.015</b>
Insectivorous	<b>0.003</b>		0.534
Omnivorous	<b>0.015</b>	0.534	
<i>Bite force</i>			
Herbivorous		<b>0.003</b>	<b>0.003</b>
Insectivorous	<b>0.003</b>		<b>0.021</b>
Omnivorous	<b>0.003</b>	<b>0.021</b>	
<i>Relative bite force</i>			
Herbivorous		0.594	1
Insectivorous	0.594		0.15
Omnivorous	1	0.15	
<i>Head length</i>			
Herbivorous		0.222	1
Insectivorous	0.222		0.282
Omnivorous	1	0.282	
<i>Head height</i>			
Herbivorous		0.075	1
Insectivorous	0.075		0.126
Omnivorous	1	0.126	
<i>Head width</i>			
Herbivorous		<b>0.048</b>	0.528
Insectivorous	<b>0.048</b>		0.396
Omnivorous	0.528	0.396	
<i>Lower jaw length</i>			
Herbivorous		0.33	1
Insectivorous	0.33		0.477
Omnivorous	1	0.477	

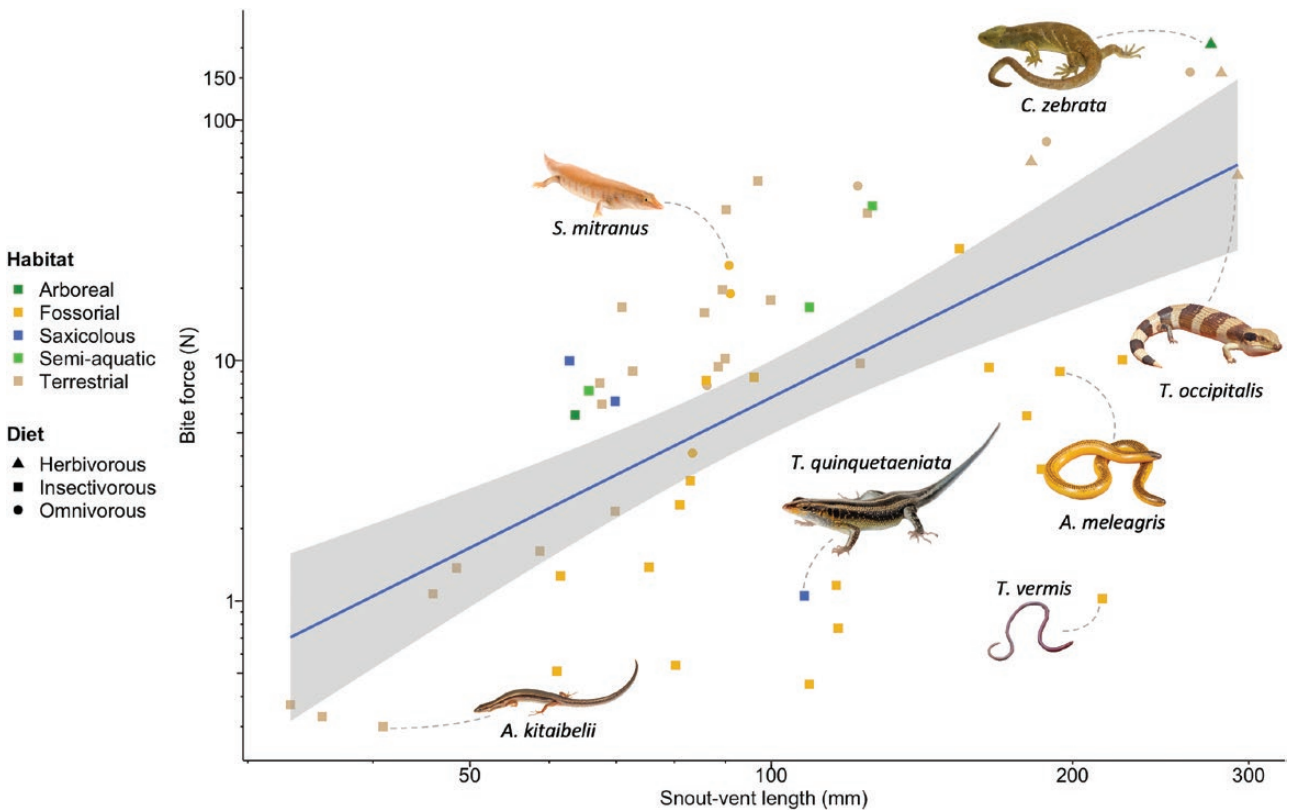
**Table 5.** Results of linear regressions. Significant results are in bold

Variable	Coefficient	SE	R <sup>2</sup>	P
Phylogenetic regression on bite force				
Snout-vent length	<b>1.73</b>	<b>0.217</b>	<b>0.54</b>	<b>&lt; 0.001</b>
Phylogenetic stepwise multiple regression with bite force as factor				
Head height	<b>9.68</b>	<b>0.45</b>	<b>0.7</b>	<b>&lt; 0.001</b>
Head length	<b>-3.02</b>	<b>0.37</b>	<b>0.46</b>	<b>&lt; 0.001</b>

SE; Standard Errors.

To investigate the effect of diet and habitat on bite force, we performed a PhylANOVA with a Brownian motion model and followed by phylogenetic post hoc tests using the *aov.phylo* function of *geiger* (Pennell *et al.*, 2014) and the *phylANOVA* function of the *phytools* package (Revell & Revell, 2014). The post hoc pairwise comparison tests taking phylogeny into account were performed using the Bonferroni method. As bite force is correlated with overall body size, we analysed differences in bite force between diet and habitat groups using phylogenetic analysis of covariance

(PhylANCOVA) with SVL as our co-variate. As no post hoc pairwise comparisons are possible using this approach we extracted the unstandardized residuals from a bite force—SVL phylogenetic regression. These residuals (further referred to as residual bite force in the manuscript) were used as input for a PhylANOVA coupled to phylogenetic post hoc pairwise comparison tests to test for differences between diet and habitat groups. Analyses were run separately for each diet and habitat use as our a priori predictions were different.



**Figure 3.** Scatter plot of species mean bite force against species mean SVL. The diet and the habitat of species are indicated. The species depicted on the graph are: *Corucia zebrata*, *Tiliqua occipitalis*, *Acontias meleagris*, *Typhlosaurus vermis*, *Scincus mitranus*, *Trachylepis quinquetaeniata* and *Ablepharus kitaibelii*. The shaded area represents 95% confidence intervals. Note that the x- and y-axes are on a logarithmic scale.

## RESULTS

The two-way PhylANOVA testing for differences in SVL between species consuming different prey and utilizing different habitats showed significant differences between diet groups ( $F_{2, 49} = 20.14$ ;  $P = 0.002$ ), but not between species occupying different habitats ( $F_{4, 49} = 1.47$ ;  $P = 0.58$ ). The interaction between habitat and diet was also significant ( $F_{2, 47} = 7.11$ ;  $P = 0.003$ ). Phylogenetic post hoc tests indicated that herbivorous species were larger than omnivorous ( $P = 0.015$ ) and insectivorous species ( $P = 0.003$ ).

A phylogenetic MANOVA detected significant differences in head shape between diet groups (Wilks' Lambda = 0.36;  $F_{8, 100} = 8.23$ ;  $P < 0.001$ ). Subsequent univariate PhylANOVAs (Table 3) indicated that species were different for most variables with herbivorous species having relatively wider heads compared to insectivorous species (Table 4). A second phylogenetic MANOVA further indicated significant differences in head shape among species from different habitats (Wilks' Lambda = 0.26;  $F_{16, 147.28} = 5.05$ ;  $P = 0.018$ ). However, the univariate PhylANOVAs

indicated no differences after Bonferroni correction. An inspection of the means suggested that fossorial skinks differed the most from skinks occupying other habitats and had the smallest morphological traits suggesting they have small heads for their body size.

A phylogenetic regression of bite force on SVL was significant ( $P < 0.001$ ; Fig. 3; Table 5) suggesting that larger species have higher bite forces. The phylogenetic stepwise multiple regression analysis with head dimensions as predictors of bite force retained a significant model explaining 78% of the variation of bite force ( $R^2 = 0.78$ ;  $AIC_{(k=2)} = 485$ ). Head height ( $\beta = 9.68$ ) was the best predictor and positively impacted bite force, whereas head length ( $\beta = -3.02$ ) negatively impacted bite force (Table 5).

A PhylANOVA indicated absolute bite force differences between dietary groups ( $F_{2, 49} = 36.7$ ;  $P < 0.001$ ) but not habitat groups ( $F_{4, 49} = 2.20$ ;  $P = 0.43$ ). The interaction between diet and habitat was significant ( $F_{2, 47} = 9.37$ ;  $P = 0.002$ ). Bonferroni phylogenetic post hoc tests indicated that herbivorous species were different from omnivorous and

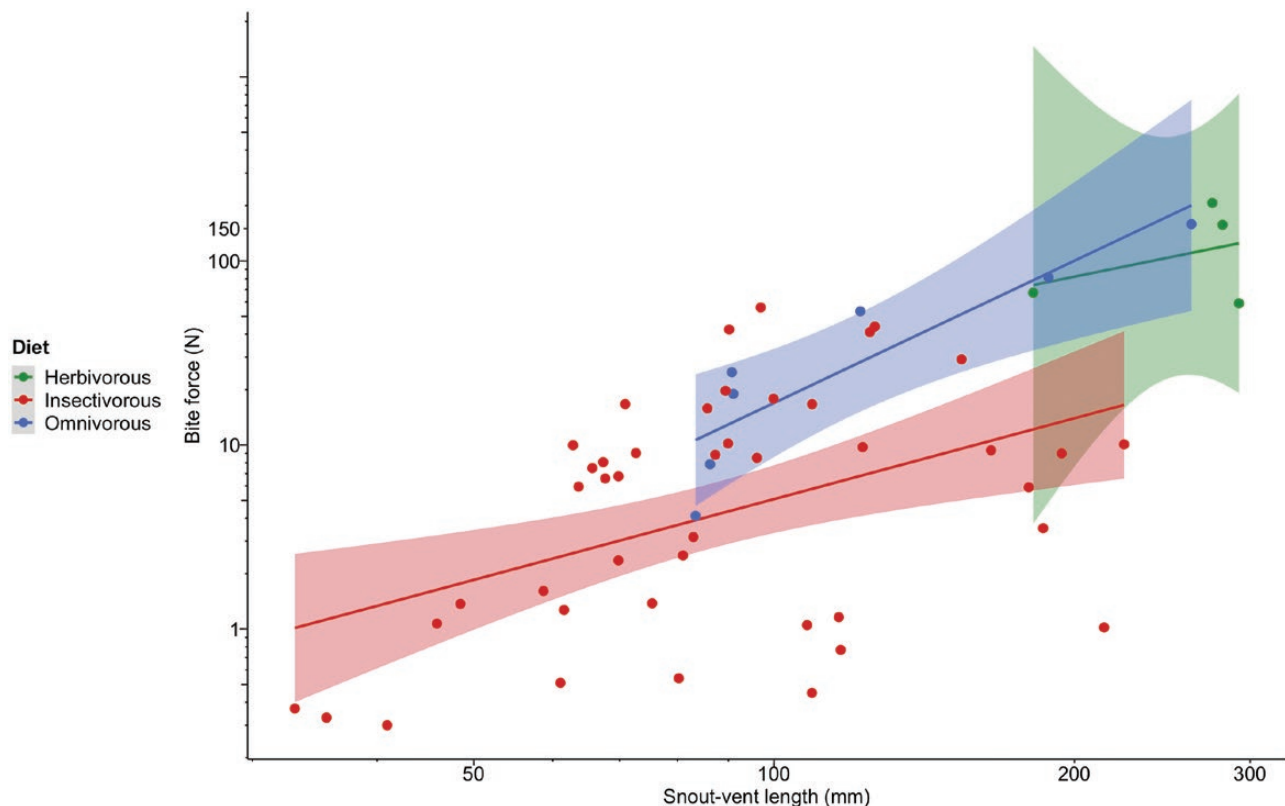
insectivorous species (all  $P < 0.01$ ). Omnivorous species were also different from insectivorous species ( $P = 0.021$ ). An inspection of the means showed that herbivorous species are characterized by higher bite forces followed by omnivorous and insectivorous species (Fig. 4).

A phylogenetic ANCOVA performed on the bite force indicated significant differences ( $F_{2,52} = 11.23$ ;  $P = 0.003$ ) between diet, but not habitats groups ( $F_{4,50} = 6.77$ ;  $P = 0.078$ ) when taking into account differences in SVL. The phylogenetic ANOVA using residual bite forces indicated significant differences between diet groups ( $F_{2,49} = 6.78$ ;  $P = 0.499$ ). The same PhylANOVA on habitat groups indicated, however, no significant differences ( $F_{4,49} = 5.32$ ;  $P = 0.12$ ). Phylogenetic post hoc tests showed that herbivorous species were different from omnivorous species ( $P = 0.036$ ) and insectivorous species ( $P = 0.003$ ) in residual bite force. Insectivorous species were also different from omnivorous species ( $P = 0.039$ ). An inspection of the means showed that herbivorous species have the highest and insectivorous species the lowest relative bite forces.

## DISCUSSION

As the lizard cranial system is implicated in many functions (e.g. [Baeckens et al., 2017](#)) that may require conflicting head morphologies (e.g. [Paluh & Bauer, 2017](#)), trade-offs can occur that constrain its evolution ([Vanhooydonck et al., 2011](#)). Based on data on head morphology and bite force for 56 species of ecologically diverse skinks, we examined the interrelationships between head morphology, bite force and ecology to assess the ecological correlates of cranial design and performance. Phylogenetic comparative analyses showed that cranial morphology and performance were determined by dietary specialization but not habitat use.

Our results show that bite force is dependent on size with larger animals showing greater bite forces as expected based on scaling relationships. Herbivorous species stand out as being larger than insectivorous and omnivorous species, thus providing them with a functional advantage and allowing them to generate larger absolute bite forces ([Herrel et al., 2001b, 2006, 2014](#)). The evolution towards a larger body size in



**Figure 4.** Plot of bite force against SVL. The regression lines for each diet group are represented. Red dots: insectivorous species; blue dots: omnivorous species; green dots: herbivorous species. The shaded areas represent 95% confidence intervals. Note the log-axes.

herbivorous species could also be facilitated by reduced selection on agility which is essential for lizards hunting active prey like insects or small vertebrates (Van Damme, 1999). Moreover, the ubiquitous nature of plants in the environment and a presumably low foraging cost may provide additional advantages promoting large body size in herbivorous lizards (Pough, 1973). Large body size provides several other advantages including a longer intestinal tract, higher thermal inertia and a lower surface to volume ratio, and may thus allow herbivorous lizards to meet their energetic demands (Pough, 1973; Van Damme, 1999). Interestingly, no size difference was observed between omnivorous and insectivorous species. Omnivorous species are considered opportunistically herbivorous with much of their diet being based on arthropods. This may constrain their body size if agility is an important constraint during prey capture (Schwenk, 2000; Herrel, 2007; Hoppe *et al.*, 2021).

Our data further highlight that herbivorous species have relatively wider heads than insectivorous species. A wider head positively affects the maximum allowable muscle volume, and thus the cross-sectional area of the jaw adductors (Bowman, 1961; Herrel *et al.*, 2005). It is tempting to interpret this difference in head morphology as the result of natural selection. Indeed, fibrous plant material requires greater bite forces to be reduced before swallowing and thus a wider head may provide a solution to these physical constraints (Herrel & De Vree, 1999; Herrel *et al.*, 1999c, 2004b). Although omnivorous species did not differ from insectivorous species in overall head shape, they did show a greater bite force. This difference might be explained by the inclusion of fibrous plant material into the diet, as highlighted for other taxa (Herrel *et al.*, 1999b, 2001a; Metzger & Herrel, 2005). Indeed, it can be expected that the most demanding food item is the one driving the upper limit of bite force and as such omnivorous species can be expected to evolve a high enough force to allow them to reduce fibrous and tough plant matter. However, the generalist morphology in omnivorous species may be driven by conflicting demands imposed by dietary diversity (Herrel *et al.*, 2004b). Thus, an increase in bite force but not head size could allow a non-specialist to switch to an omnivorous diet by allowing the inclusion of harder or tougher food items. We might have expected insectivorous species to differ morphologically from omnivorous species with a smaller head and longer snout (Toyama, 2016). This lack of morphological differences suggests that omnivorous species have retained the ancestral morphology of insectivorous species. In a second step, a specialization towards herbivory or a durophagous diet may be allowed by developing a wider, taller head (Herrel & Holanova, 2008; Schaerlaeken *et al.*, 2012; Meyers *et al.*, 2018).

Interestingly, and unlike what has been observed for other taxa (e.g. Barros *et al.*, 2011; Openshaw & Keogh, 2014), no differences in overall body size were observed between species occupying different habitats. This suggests that habitat use may not impose strong constraints on size in skinks. Surprisingly, our results also indicated no differences in head shape and bite force between habitat groups other than a tendency for burrowers to have narrower heads. The tendency for burrowing species to differ in head morphology is not unexpected as a fossorial lifestyle may impose significant energetic constraints on head size (Teodecki *et al.*, 1998; Navas *et al.*, 2004). The lack of strong common morphological and functional specializations in species occupying different habitats is probably the result of functional compromises (e.g. fossorial and durophagous trade-offs; Baeckens *et al.*, 2017) or of independent evolutionary trajectories of different habitat specialists and needs to be investigated further. Moreover, since habitat can impact the width or height of the body as well as limb morphology, further analyses of body shape are needed to better understand the constraints imposed by different habitat types on morphology in skinks (e.g. Pounds, 1988; Goodman *et al.*, 2008; Herrel *et al.*, 2008; Meiri, 2008).

Head height and head length were the primary determinants of bite force in the species of skinks included in our study. A taller head, just like a wider head, likely increases the space available for jaw adductors which may drive the observed increase in bite force (Bowman, 1961; Herrel *et al.*, 2001b, 2006). Moreover, a taller head may also allow for more vertically placed jaw adductors providing them with a greater moment arm and a more efficient conversion ratio of muscle force into bite force (Herrel *et al.*, 2001b). Conversely, head length had a negative effect on bite force (see also Westneat, 2004). An increase in head length involves an increase in the jaw outlever and given that animals were made to bite at the tips of the jaws this can be expected to negatively impact bite force (Herrel *et al.*, 2001b, 2007a). Indeed, the jaws of lizards are in the form of a third-order lever, with the lower jaw being the lever arm (Kerr, 2010; Cox, 2017). Thus, the variation in the length of the head will influence the distance between the input force and the output force of the lever (Wainwright & Richard, 1995; Fabre *et al.*, 2014a). However, to better understand how head length may impact bite force a more in-depth analysis of the jaw in- and outlevers in relation to bite force is needed.

## CONCLUSION

Our data demonstrate a strong link between body size, bite force and diet with herbivorous species being



larger and biting harder in absolute terms. Moreover, in Scincidae the evolution towards more powerful bites goes hand in hand with an increase in head height but a decrease in head length. Habitat use did not appear to be an important driver of head shape or bite force in the species included in our data set, yet this remains to be explored further using a broader and more comprehensive sample of species.

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### DATA AVAILABILITY

All data are available in Table 1 of this manuscript.

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