



Diving in head first: trade-offs between phenotypic traits and sand-diving predator escape strategy in *Meroles* desert lizards

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Received 30 March 2016; revised 5 May 2016; accepted for publication 5 May 2016

Survival, in part, depends on an individual's ability to evade predators. In desert regions some lizard species have evolved head-first sand-diving strategies to escape predators. To facilitate this behaviour, a distinctive head morphology that facilitates sand-diving has evolved. This specialised head morphology may, however, come at a cost to other ecologically relevant functions, particularly bite force. Here, we investigated the relationship between morphology and function in a southern African lacertid lizard genus, *Meroles*, which consists of eight species that utilise different escape strategies, including sand-diving and running for cover. It was hypothesized that the specialised head morphology of diving species would negatively affect bite force capacity. We found that species from each escape strategy category differed significantly in head shape, but not bite force performance. A phylogenetic tree of the genus was constructed using two mitochondrial and two nuclear genes, and we conducted phylogenetic comparative analyses. One aspect of the head shape differed between the escape strategies once phylogeny was taken into account. We found that bite force may have co-evolved with head morphology, but that there was no trade-off between biting capacity and escape strategy in *Meroles*. © 2016 The Linnean Society of London, *Biological Journal of the Linnean Society*, 2016, **119**, 919–931.

KEYWORDS: Africa – bite force – Eremiadini – geometric morphometrics – phylogeny.

INTRODUCTION

The ability of an individual to survive within a particular environment is dependent on a number of factors, including having a morphology that allows for optimal utilisation of resources in that environment (Schluter, 2000). Selective pressures within particular habitats have led to the evolution of convergent phenotypes in similar habitats (e.g. arboreal vertebrates: Losos *et al.*, 1998; da Silva & Tolley, 2013;

swimming vertebrates: Chen, DeVries & Cheng, 1997; burrowing lizards: Lee, 1998; rupicolous lizards: Revell *et al.*, 2007; Goodman & Isaac, 2008; sand-dwelling lizards: Edwards *et al.*, 2012; Robinson & Barrows, 2013) and due to similar diets (e.g. ant-eating mammals: Reiss, 2001). In many cases, the phenotypic similarities are associated with habitat use or behavioural variation (or both), independent of ancestry. Indeed, natural selection acts initially upon variants for which performance increases fitness (e.g. better predator avoidance through faster running speeds; Arnold, 1983). A particular

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morphology, however, having evolved in response to environmental selective pressures, may result in poorer performance in other ecologically relevant traits. In many cases, trade-offs evolve when the change in morphology beneficial for a certain behaviour constrains the functionality of another trait. For example, there is a trade-off between sprinting and endurance in lacertid lizards (Vanhooydonck, Van Damme & Aerts, 2001), between song complexity and bite force in finches (Herrel *et al.*, 2009), between running and grasping in chameleons (Losos, Walton & Bennett, 1993; Herrel *et al.*, 2013; da Silva *et al.*, 2014), and between burrowing ability and bite force in fossorial lizards (Vanhooydonck *et al.*, 2011).

The hot-desert environment, which can be characterized as arid, sparsely vegetated and dominated by Aeolian sand-dunes, may place a selection pressure toward a particular morphology in many organisms (e.g. Robinson & Barrows, 2013). In this habitat, shelter is a scarce commodity and many desert-dwelling lizards burrow head first into the sand for shelter. In different hot-desert regions around the world, convergent morphologies and predator evasion behaviour (sand-diving) have evolved in disparate lizard families (e.g. Lacertidae: shovel-snouted lizard *Meroles anchietae*, *Acanthodactylus* spp.; Scincidae: sandfish *Scincus scincus*, wedge-snouted skink *Chalcides sepsoides*; Gerrhosauridae: desert plated lizard *Gerrhosaurus skoogi*; Phrynosomatidae: *Uma* spp.; Arnold, 1994; Robinson & Barrows, 2013). Sand-diving in these lizards occurs by head-first entry into the sand, at which point the lizard will 'swim' through the sandy substrate with side-to-side oscillating movements of the head. Selection for behaviours such as sand-diving, however, may result in other performance traits being affected (such as bite force; e.g. Vanhooydonck *et al.*, 2011). Specifically, changes in head morphology facilitating sand-diving may negatively impact the position of, and the space available for, the jaw adductor muscles and thus lead to a trade-off between sand-diving and biting. Bite force has been linked with diet in lacertid lizards (e.g. Herrel *et al.*, 2001b; Edwards *et al.*, 2013b; Sagonas *et al.*, 2014), as the increased bite force capacity allows lizards to consume harder prey and may increase the range of prey that they are able to process. Bite forces have also been linked with intrasexual competition in lizards (e.g. Herrel, De Grauw & Lemos-Espinal, 2001a; Measey *et al.*, 2011; da Silva *et al.*, 2016). If bite force is reduced, due to selective pressures in particular environments causing a change in head morphology, then this may impact diet and sexual competition. The evolution of the specialised head shape facilitating sand-diving in arid environments, therefore, may limit lizards in

terms of the range of prey that can be processed or may impact inter- and intrasexual interactions.

Here, we investigate the link between predator escape strategy, morphology, and bite force in the genus *Meroles* Gray 1838 because it is comprised of species that run and hide from predators ('runners'), and those that dive into the sandy substrate to escape predation ('divers') (see Branch, 1998). In many other lizards, those with tall, round-snouted heads have higher biting capacities (e.g. Herrel, Vanhooydonck & Van Damme, 2004). Diving *Meroles* have been suggested to have head shapes that facilitate diving (i.e. upper labial scales form a lateral ridge, dorsoventrally flattened snouts, counter-sunk lower jaws, nasal vestibule elongated, and nasal valves present; Arnold, 1994, 1995), although the 'diving' morphotype has not been explicitly investigated in this genus. We expect the specialisation in head shape to sand-diving to negatively affect bite force capacity in sand-diving species. Indeed, in these species the anterior part of the cranium is obviously dorsoventrally flattened, presumably facilitating easier entry into a sandy substrate. As increased head height has been linked with harder bite forces in other lizards (Herrel *et al.*, 2001a), the reduced head height of diving *Meroles* may thus provide less space for the jaw adductor muscles, resulting in lower bite forces. In the present study, we test for a trade-off between sand-diving and bite force capacity within the genus *Meroles*. These phenotypic differences, however, could instead be due to shared ancestry, and so we construct a phylogenetic tree using multiple mitochondrial and nuclear markers for the genus, to investigate the evolutionary history of these species.

MATERIAL AND METHODS

SAMPLING

Meroles are small-bodied, ground-dwelling lizards that inhabit the arid regions of southern Africa (Branch, 1998; Supporting Information, Fig. S1). Whilst all eight species range across the arid western regions of southern Africa to varying degrees, only three are Namib Desert endemics. The eight species of *Meroles* were categorized according to their predator escape strategy (see Branch, 1998) as follows: diving (*M. anchietae*, *M. ctenodactylus*, *M. cuneirostris*, *M. micropholidotus* and *M. reticulatus*), or running (*M. knoxii*, *M. squamulosus* and *M. suborbitalis*). The four species that primarily dive into sand to escape predators all inhabit the Namib Desert region and surroundings (*M. cuneirostris*, *M. ctenodactylus*, *M. micropholidotus* and *M. anchietae*). *Meroles reticulatus*, endemic to Namibia but

found on more hard-packed soils, primarily runs when threatened but, if pursued long enough, will dive into the sand (see Branch, 1998). *Meroles squamulosus* (previously *Ichnotropis squamulosa*; Edwards *et al.*, 2012, 2013a) occurs in the Kalahari sands within the savannah biome (north-east South Africa, Zimbabwe, Botswana, north-east Namibia, and Angola; Supporting Information, Fig. S1), and is parapatric to the other *Meroles* species. *Meroles squamulosus* lives on hard-packed sandy soil, and does not sand dive, a behaviour shared with *M. knoxii* (western South Africa) and *M. suborbitalis* (western and central South Africa and Namibia) (Branch, 1998; Bates *et al.*, 2014; Supporting Information, Fig. S1).

Sampling for the analyses included live specimens obtained during field trips, as well as preserved specimens from the wet collections housed at the Bayworld Museum (Port Elizabeth), the Ditsong Museum (Pretoria), and the Ellerman Collection (Stellenbosch University). Tissue (tail or liver tissue) utilized in the phylogenetic analyses was either obtained during field trips or from previous collections. Sequence data for *M. micropholidotus* from one mitochondrial marker (16S) were obtained from GenBank (<http://www.ncbi.nlm.nih.gov>), as no fresh tissue was available for the genetic analysis. Morphometric analyses were conducted on adults from all eight species obtained from field trips and from the wet collections (Supporting Information, Table S1). Biting performance was measured for live adult specimens (Supporting Information, Table S2). After all measurements were taken, the lizards were released at their site of capture. *Meroles micropholidotus* was not included in the performance analysis as we were not able to capture any live specimens. Sample sizes are listed in the supplementary information (Supporting Information, Tables S1–S3). Unless otherwise specified, all statistical analyses were performed in R Studio v.0.99.878, using R version 3.2.3 (R Core Team, 2015).

PHYLOGENETIC ANALYSES

Genomic DNA was isolated according to standard procedures involving a proteinase K digestion from tail or liver tissue preserved in 99% ethanol, followed by salt-extraction procedures (Bruford *et al.*, 1992). Two mitochondrial (16S and ND4) and two nuclear genes (RAG1 and KIAA-2018) were amplified using standard PCR procedures as in Edwards *et al.* (2012) (Supporting Information, Table S3). PCR products were sequenced at Macrogen Corp. (Seoul, Korea), using the forward primers in all cases. Sequences were aligned using Clustal Omega (Sievers *et al.*, 2011), and the alignment was

viewed in Geneious v.4.8.5 (<http://www.geneious.com>; Kearse *et al.*, 2012). Individuals from sister genera to *Meroles* (*Australolacerta*, *Ichnotropis*, *Pedioplanis* and *Vhembelacerta*) were included as outgroup taxa. To investigate whether there was conflict between the individual markers (16S vs. ND4 and RAG1 vs. KIAA-2018), as well as between the genomes (mitochondrial vs. nuclear), a partition homogeneity test (also called the incongruence length difference (ILD) test; Farris *et al.*, 1994, 1995), implemented in PAUP* v4.0b10 (Swofford, 2002), was used. The two mitochondrial gene trees and the two nuclear gene trees were congruent, as were the mitochondrial and nuclear gene trees, so phylogenetic trees were constructed of the combined total evidence dataset. The third codon position of the ND4 gene was found to be saturated in Dambe v.5.2.65 (Xia *et al.*, 2003), and was partitioned separately from the first two codon positions. Models of evolution for each gene separately were identified in jModelTest v.2.1 (Darriba *et al.*, 2012) (Models used: 16S and ND4: GTR + I + Γ ; RAG1 and KIAA-2018: HKY + Γ). Uncorrected p-distances between and within species (i.e. sequence divergence values) were estimated in MEGA v.6 (Tamura *et al.*, 2013).

Two different algorithms were utilized to obtain phylogenetic trees. Firstly, Bayesian inference (BI) was performed in MrBayes v.3.2.2 (Ronquist *et al.*, 2012), using the CIPRES Science Gateway (http://www.phylo.org/sub_sections/portal/). Priors in MrBayes were set according to the evolutionary models found using jModelTest, and uniform priors were kept for all other parameters. The MCMC were run with two parallel runs for 20 million generations, with trees sampled every 1000 generations. The number of generations to discard as burn-in was determined by examining the number of generations: (1) at which the standard deviation of split frequencies stabilized (at < 0.001), (2) at which the log-likelihood tree scores reached stationarity. The effective sample sizes (ESS) of all parameters, viewed in Tracer v.1.6.0 (Rambaut & Drummond, 2009), were > 200. Thereafter, a 50% majority rule tree was constructed, excluding the burn-in (~10%), using the 'sumt' command in MrBayes, and nodes with ≥ 0.95 posterior probability were considered supported. The second algorithm used was a partitioned maximum likelihood (ML) analysis with the same partitions as the Bayesian analysis, run in RAxML v.7.2.7 (Pfeiffer & Stamatakis, 2010), using the CIPRES Science Gateway. A generalised time-reversible model of evolution with the addition of invariant sites and a gamma distribution of rates (GTR + I + Γ) was utilised, and bootstrapping was halted automatically.

MORPHOMETRIC ANALYSES

Geometric morphometric analyses were used to investigate differences in head shape in all *Meroles* species, using high resolution photographs taken with a digital camera (Fuji Finepix S2000HD: resolution 10.0 MP, and Canon 50D: resolution 10.0 MP and macro lens F18/100). Dorsal (216 individuals, $N \approx 27$ per species) and lateral (223 individuals, $N \approx 28$ per species) views of the heads were photographed on 1 cm square grid paper. Homologous landmarks were digitized in programs from the TPS programs suite (tpsUtil v.1.53, Rohlf, 2004; tpsDig2 v.2.16, Rohlf, 2005) (see landmark numbers in Figure 1 and Supporting Information, Table S4). Further morphometric analyses were conducted using MorphoJ v.1.06a (Klingenberg, 2011). The mean configuration for each species separately was obtained after a full Procrustes analysis was done to project the data to the tangent space by orthogonal projection (Dryden & Mardia, 1998). A new 'tps' file was constructed with only the mean configurations, and a full Procrustes analysis was done on the mean configurations. Principal components analyses (PCAs) were done in MorphoJ on the symmetrical components of the heads to identify which portions showed the most variation, and warped outline diagrams were used to visualize the differences in the head shape. Scores from each principal component (PC) axis were imported into the R program and analyses of variance (ANOVAs) were used to identify whether the two groups of predator escape strategies (divers and runners) differed in the first five PCs (package: 'stats', functions: 'anova' and 'lm'; R Core Team, 2015), as these explained over 95% of the variation (97.7% in the dorsal view analyses and 96.6% in the lateral view analyses).

To account for phylogenetic relationships, phylogenetic analyses of variance (phylANOVAs) were performed on the species means of the first five PCs for both the dorsal and lateral views of the heads to test if there were differences in the morphometric data, using escape strategy as the fixed factor. A phylogeny for the genus was produced (see methods above) and the phylogeny was converted into an ultrametric tree (package: 'ape', function: 'chronos'; R Core Team, 2015). Simulation-based phylANOVAs (Garland *et al.*, 1993) were run with a Bonferroni correction, using 1000 simulations and branch lengths obtained from the genetic phylogeny (package: 'geiger', function: 'aov.phyl', nsim: '1000', p.adj: 'bonferroni'; R Core Team, 2015).

PERFORMANCE ANALYSES

To identify whether the head shapes are linked with performance differences, bite force capacities were

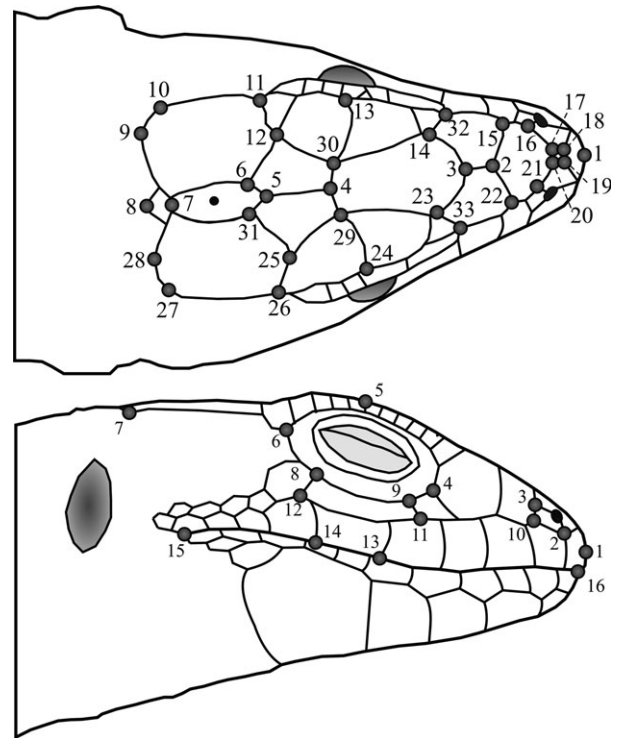


Figure 1. Landmarks used in the geometric morphometric analyses on the dorsal (top) and lateral (bottom) views of the heads of *Meroles*.

determined through five trials of a lizard biting on two metal plates connected to an isometric force transducer and a charge amplifier (see Herrel *et al.*, 1999). Gape angle and the bite point were standardized for all lizards. Live individuals were retained in cloth bags when resting between trials. The maximum bite force values (absolute values) for each individual were retained for analysis and the mean of these values are herein referred to as the mean absolute bite force (package: 'stats', function: 'mean'; R Core Team, 2015).

The mean absolute values were used in ANOVAs to identify whether there were differences in bite force between the species representing the predator escape strategies. To correct for body size, snout-vent lengths (SVL) were used as covariates in analyses of covariance (ANCOVAs; package: 'stats', functions: 'anova' and 'lm'; R Core Team, 2015). PhylAN(C)OVAs were conducted on the mean absolute bite force values for all species, except *M. micropholidotus* (package: 'geiger', function: 'aov.phyl', nsim: '1000', p.adj: 'bonferroni'; R Core Team, 2015).

A potential trade-off between head shape and biting capacity was investigated. Regressions, using a linear model, were performed between the species means from the first three PCs from both views, and

mean absolute, as well as mean residual, bite force values (package: 'stats', functions: 'lm' and 'cor.test', method: 'Pearson'; R Core Team, 2015). The taxa included are related to each other (same genus), thus the data obtained for the phenotypic traits are not independent, resulting in increased type I errors in comparisons between taxa (Felsenstein, 1985). To account for phylogeny, phylogenetic generalised least-squares regressions (PGLS) of the mean absolute and residual bite force and the species means of the first three PCs were conducted using a Brownian motion model (package: 'nlme', function: 'gls', correlation: 'corBrownian'; R Core Team, 2015).

RESULTS

PHYLOGENETIC ANALYSES

The phylogenetic analysis indicated that each species forms a well supported, monophyletic clade (bootstrap values $\geq 75\%$ and posterior probabilities ≥ 0.95) (Fig. 2). *Meroles reticulatus*, a diving species, is well supported as sister to all other *Meroles*. The remainder of the species form three clades: (1) all other divers, (2) a running species *M. squamulosus*, and (3) two running species (*M. suborbitalis* and *M. knoxii*) (Fig. 2). Sequence divergences (uncorrected *p*-distance) between *Meroles* species (16S: $5.07 \pm 1.36\%$, ND4: $15.90 \pm 1.43\%$, RAG1: $2.21 \pm 0.60\%$, KIAA: $1.76 \pm 0.44\%$) were comparable with those found between other lacertid species (Podnar, Pinsker & Mayer, 2009; Edwards *et al.*, 2012, 2013a, b). As the genetic sampling for each species was drawn from across the species' range, there was some variation within species (e.g. *M. suborbitalis*, *M. knoxii* and *M. squamulosus*).

MORPHOMETRIC ANALYSES

Using a principal components analysis, the most variation was found in the shape of the posterior cranium, namely the compression or the elongation of the parietal region, as well as in the head width, head height and snout length, as seen in the deformation grids of the first principal components (PC1) (dorsal PC1 (56.67%): landmarks 5–12, 25–28, 31) [lateral PC1 (49.69%): landmarks 6–7; Fig. 3 and Supporting Information, Fig. S2]. The second largest proportion of the total variation (dorsal and lateral PC2) was found in the shape and length of the snout region and the width of the heads [dorsal PC2 (19.85%): landmarks 1–3, 14–23, 32, 33], and again in the compression of the parietal region [lateral PC2 (25.66%): landmarks 1–4, 10, 16; Fig. 3 and Supporting Information, Fig. S2]. The dorsal PC3 (13.57% of the total variation) contrasted the width of the head

and snout, whilst the lateral PC3 (10.38%) contrasted the height of the posterior cranium (Supporting Information, Fig. S2). The remaining PCs in the dorsal view (PC 4 onwards) and in the lateral view (PC 5 onwards) contributed 5% or less to the variation in the data, and were excluded from the analysis as they are not considered biologically informative.

The head shape of the running species differed significantly from the diving species in PC2 in the dorsal view (ANOVAs: $F_1 = 7.40$, $P = 0.04$) and in the lateral view PC1 (ANOVAs: $F_1 = 21.62$, $P = 0.004$; Table 1). Diving species occupied the negative part of the morphospace along the dorsal PC2 axis and the positive part of the morphospace of the lateral PC1, indicating that diving species had longer snouts and more laterally compressed heads, relative to the running species (Fig. 3). The dorsal view PC1 and the lateral view PC2 contrasted all other species and the most highly psammophilic species, *M. anchietae* (indicated as 'MA' in Fig. 3). This species, relative to the rest, had more posteriorly compressed parietal scales (dorsal landmarks 6–11, 25–28; lateral landmarks 6–7), longer rostral scales (dorsal landmarks 1, 17–20; lateral landmarks 1–3, 16) and overall wider dorsal scales (Fig. 3). The third principal component (PC3) of the dorsal and lateral views also contrasted other aspects of the crania, not related to diving, and the head shapes of the two predator escape strategies were not significantly different in the remaining PCs (Table 1).

Once phylogeny was taken into account, there was a significant difference between the predator escape strategy categories for the lateral view PC1 (which contrasted long snouts and more laterally compressed heads) (phylogenetic $P < 0.05$; Table 1). This indicates that the longer snouts and more dorsoventrally compressed heads of diving species, vs. the higher, more robust heads of the runners, are not merely a result of shared ancestry, but an adaptive trait likely linked to the predator-avoidance behaviour. The differences in the other aspects of the head shapes (the other PCs) between the predator escape strategy categories were not significant once phylogeny was taken into account (Table 1).

PERFORMANCE ANALYSES

There were no significant differences in both the absolute and relative bite force values between diving and running species (absolute values: $F_1 = 0.25$, $P < 0.65$; relative values: $F_1 = 0.03$, $P < 0.9$; Table 2; Fig. 4), nor were there significant differences when phylogeny was accounted for (absolute values: phylogenetic $P < 0.70$; relative values: phylogenetic $P < 0.95$; Table 2). Absolute bite force was

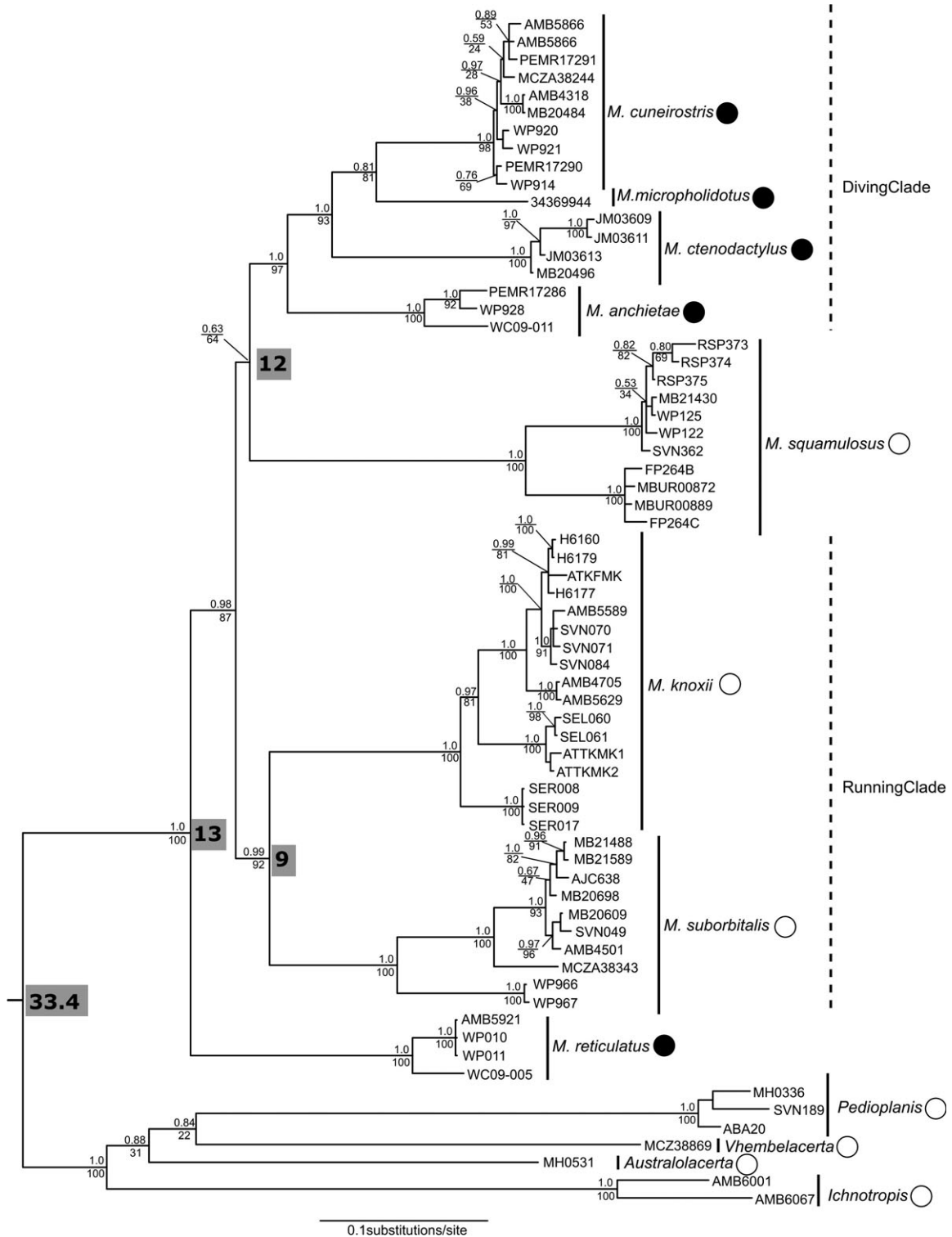


Figure 2. Phylogenetic tree of the genus *Meroles* based on the combined mitochondrial and nuclear datasets and inferred by Bayesian inference (BI) and maximum likelihood analyses (ML) (BI topology shown). Support values from both methods are shown at the nodes (Bayesian posterior probabilities above branch, likelihood bootstrap values below branch). Circles at the terminal tips indicate the predator escape strategy employed by that species: filled circle = diving; open circle = running. Numbers highlighted in grey at the nodes of particular divergences indicate the estimated divergence dates (millions of years), adapted from Hipsley *et al.* (2009).

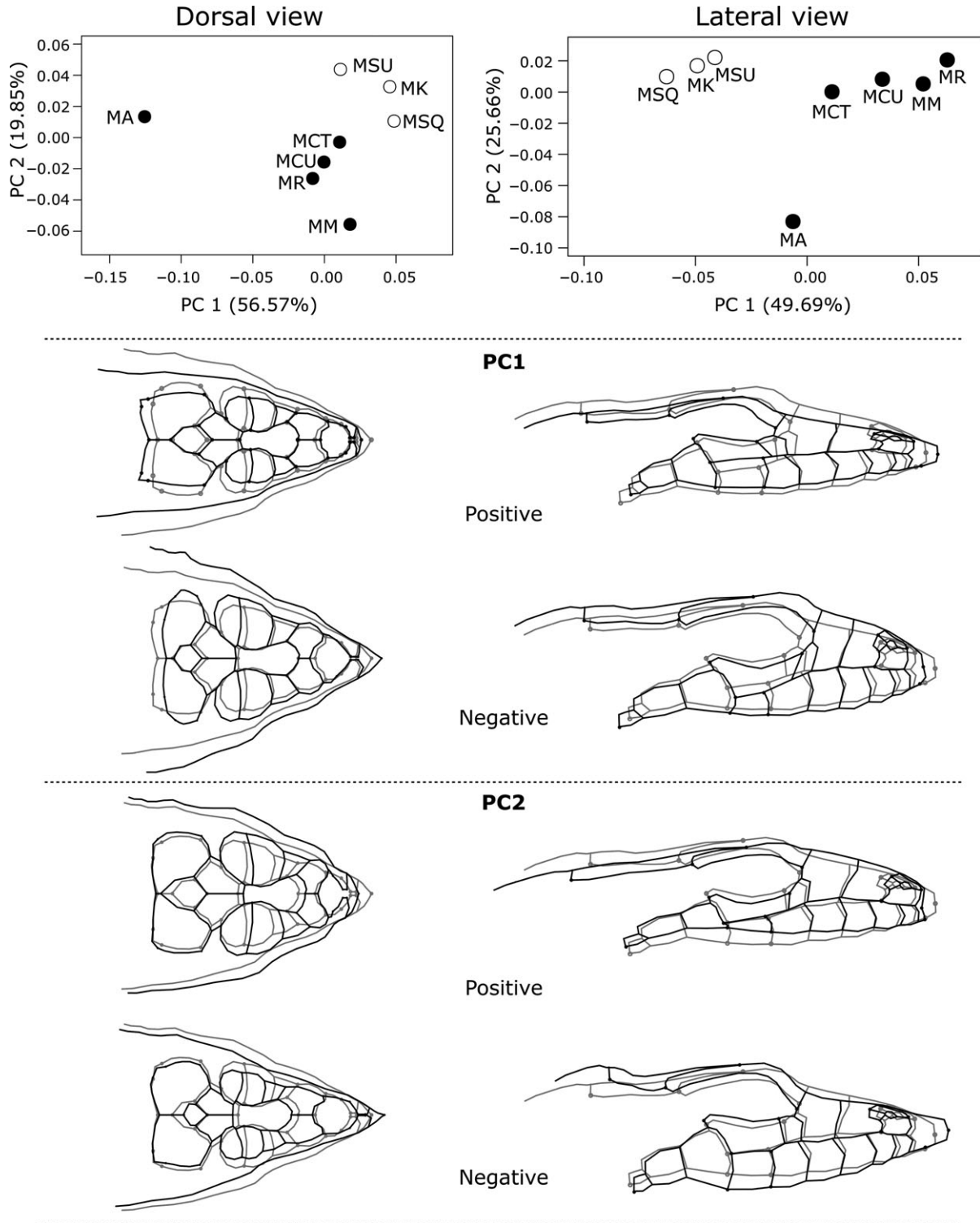


Figure 3. Scatterplots (top) of the first two principal components (PC) for the dorsal view (left) and lateral view (right) of the heads. Symbols for each species indicate diving species (filled circles), or running species (open circles). Warped outline graphs of representatives of the heads showing the deviation from the mean shape (shown in grey) on the positive/negative extremes of the respective components (shown in black). Key to species abbreviations: MA, *Meroles anchietae*; MCT, *M. ctenodactylus*; MCU, *M. cuneirostris*; MK, *M. knoxii*; MM, *M. micropholidotus*; MR, *M. reticulatus*; MSQ, *M. squamulosus*; MSU, *M. suborbitalis*.

Table 1. Results of traditional (trad) and phylogenetic (phyl) analyses of variance (ANOVA) of principal components (PC) of the geometric morphometric head shapes for *Meroles*, investigating the differences between the two predator escape strategies (diving and running)

Components	% Variation	ANOVA			
		d.f.	<i>F</i> (trad)	<i>P</i> (trad)	<i>P</i> (phyl)
Dorsal view					
PC1	56.57	1	2.39	0.17	0.33
PC2	19.85	1	7.40	0.04	0.13
PC3	13.57	1	0.34	0.56	0.70
PC4	4.97	1	0.30	0.60	0.71
PC5	2.73	1	0.07	0.81	0.89
Lateral view					
PC1	49.70	1	21.62	0.004	0.03
PC2	25.66	1	1.09	0.34	0.51
PC3	10.38	1	0.02	0.90	0.93
PC4	7.92	1	0.01	0.93	0.96
PC5	2.95	1	0.23	0.65	0.76

Phylogenetic ANOVAs were performed using a Bonferroni correction. Significance ($P \leq 0.05$) is indicated in bold.

F (trad), *F*-value of traditional ANOVA; *P* (trad), *P*-value of the traditional ANOVA; *P* (phyl), *P*-value of the phylogenetic ANOVA.

Table 2. Results of analyses of variance/covariance (ANOVAs or ANCOVAs) of absolute bite force values for *Meroles*, investigating the differences between the two predator escape strategies (diving and running)

Bite force	d.f.	<i>F</i> (trad)	<i>P</i> (trad)	<i>P</i> (phyl)
ANOVA	1	0.25	0.64	0.69
ANCOVA	2	0.03	0.88	0.91

Phylogenetic AN(C)OVAs were performed using a Bonferroni correction.

F (trad), *F*-value of traditional ANOVA; *P* (trad), *P*-value of the traditional ANOVA; *P* (phyl), *P*-value of the phylogenetic ANOVA.

significantly positively and highly correlated with the dorsal view PC1 (Fig. 4 and Table 3). The residual bite force values were not significantly correlated with the dorsal view PC1. Once phylogeny was accounted for using PGLS, the bite force values were significantly positively correlated with the dorsal view PC1 (*t*-test: $T_5 = 4.12$, $P < 0.02$; Fig. 4 and Table 4) suggesting that the evolution of high bite force has gone hand in hand with the evolution of head shape.

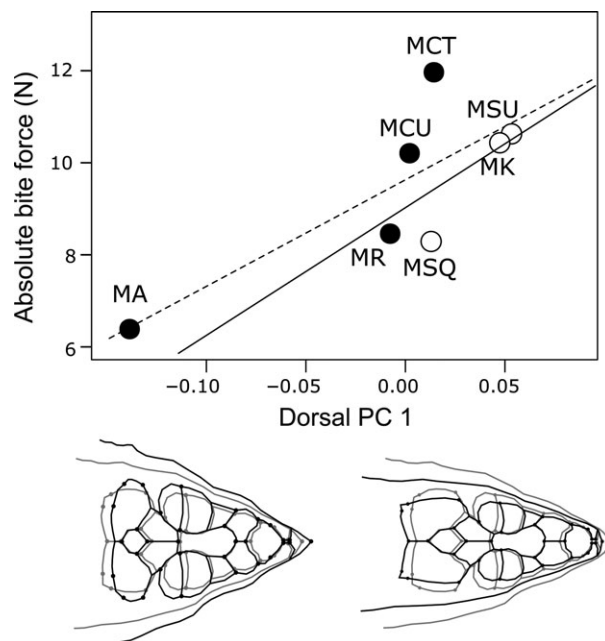


Figure 4. Scatterplot of the first principal component from the dorsal view PCA and the mean absolute bite force values. Symbols for each species indicate whether the species is a diving (filled circle) or a running (open circle) species. Regression lines shown (dotted = traditional regression, solid = phylogenetic generalised least-squares regression). Key to species abbreviations as in Figure 3. Warped outline graphs (below) of representatives of the heads showing the deviation from the mean shape (shown in grey) on the positive/negative extremes of the dorsal PC1 (shown in black).

DISCUSSION

Effective predator escape strategies are crucial to the survival of an individual, and in some instances particular morphologies have evolved to facilitate and enhance a particular escape strategy. In *Meroles*, morphological features (particularly snout length and head width) seem to be linked to escape strategy. Diving species have more dorsoventrally flattened heads with longer snouts, compared to the higher, more robust heads and shorter snouts of the runners; a relationship that remained significant after accounting for phylogeny. Bite force, either absolute or relative, did not differ between the two groups, nor were there any significant differences after accounting for phylogeny. We suggest that head shape is linked with the predator escape strategy, whilst bite force is not. Bite force, however, does appear to have co-evolved with head shape.

Particular head morphologies have been linked to greater biting capacities in lizards, namely higher and/or wider heads (e.g. Herrel *et al.*, 1999, 2001a,

Table 3. Correlations between the first three principal components from the geometric morphometric analyses of both head views and bite force values [absolute and size-corrected (residual) values]

	Absolute bite force						Residual bite force					
	<i>r</i>	d.f.	<i>t</i>	<i>P</i>	Slope	Intercept	<i>r</i>	d.f.	<i>t</i>	<i>P</i>	Slope	Intercept
Dorsal view												
PC1	0.80	5	3.01	0.03	25.51	9.56	0.62	5	1.76	0.14	1.57	0.01
PC2	-0.09	5	-0.20	0.85	-6.62	9.55	-0.15	5	-0.35	0.74	-0.91	0.01
PC3	0.07	5	0.15	0.88	4.41	9.50	-0.01	5	-0.01	0.99	-0.03	0.00
Lateral view												
PC1	-0.18	5	-0.42	0.69	-7.28	9.44	0.07	5	0.16	0.88	0.22	0.00
PC2	0.60	5	1.67	0.16	29.88	9.52	0.52	5	1.37	0.23	2.09	0.00
PC3	0.46	5	1.17	0.29	53.44	9.80	-0.15	5	-0.34	0.75	-1.36	-0.01

Significance ($P \leq 0.05$) is indicated in bold font.

r, Pearson’s correlation coefficient; d.f., degrees of freedom for the *t*-test; *t*, *t*-value obtained from the *t*-test; *P*, *P*-value from the *t*-test; slope, slope of the regression; intercept, intercept on the *x*-axis of the regression.

Table 4. Phylogenetic generalised least-squares regressions and correlations between the first three principal components of both head views and the mean absolute and residual bite force values

	Absolute bite force				Residual bite force			
	d.f.	<i>t</i>	<i>P</i>	Slope	d.f.	<i>t</i>	<i>P</i>	Slope
Dorsal view								
PC1	5	4.12	0.01	31.63	5	2.26	0.07	1.77
PC2	5	-0.77	0.48	-35.30	5	-0.73	0.50	-2.31
PC3	5	1.18	0.29	43.86	5	1.29	0.25	3.26
Lateral view								
PC1	5	0.32	0.76	10.28	5	0.87	0.43	1.81
PC2	5	2.52	0.05	39.93	5	1.93	0.11	2.42
PC3	5	1.84	0.13	110.44	5	0.21	0.84	1.15

Significance ($P \leq 0.05$) is indicated in bold font.

r, Pearson’s correlation coefficient; d.f., degrees of freedom for the *t*-test; *t*, *t*-value obtained from the *t*-test; *P*, *P*-value from the *t*-test; slope, slope of the regression.

2007; Measey, Hopkins & Tolley, 2009). Contrary to our expectations that there would be a trade-off between diving behaviour and bite force capacity, similar to the Tanzanian legless skink (Vanhooydonck *et al.*, 2011). Our results suggest that bite force and head shape have co-evolved, irrespective of diving behaviour exhibited by the lizards. It is therefore likely that regions of the head influenced by diving are different to those affected by biting capacity. The species considered to be the most psammophilic, *Meroles anchietae*, had the lowest absolute bite force and it occupied the extreme negative side of the morphospace along PC1, indicating that the antero-posteriorly compressed parietal region of this species may be negatively affecting biting capacity. Interestingly, *M. anchietae* is one of only a few lizard species that supplements its diet with seeds (Nagy &

Shemanski, 2009). Whether this atypical diet is due to the low availability of arthropod prey in the hyper-arid environment of the Namib Desert or is perhaps influenced by the specialised head morphology relating to the processing of food items remains to be understood. Conversely, species that occupy the positive part of the morphospace along PC1 (*M. knoxii* and *M. suborbitalis*) may have higher bite forces due to the shorter snout and longer parietal regions. A longer neurocranium allows for increased space on the lateral part of the posterior cranium for larger jaw adductor muscles (and hence a more powerful bite through the muscle action) and a shorter snout may provide a shorter outlever for the jaw mechanisms (e.g. Schenk & Wainwright, 2001; Herrel, O’Reilly & Richmond, 2002b; Herrel *et al.*, 2002a). It appears that bite force has co-evolved with

head shape, as the relationship in the PGLS was significantly positively correlated. As diving behaviour does not appear to be linked with biting capacity, other factors, such as diet or intrasexual conflict (e.g. Herrel *et al.*, 2001a; Measey *et al.*, 2011), may be driving the co-evolution between the biting capacity and head morphology in *Meroles*. Investigations into the link between bite force and diet, as well as bite force and intrasexual competition, are needed to elucidate the factors influencing this co-evolution.

The *Meroles* phylogeny estimated in this study differs from previous topologies (Harris, Arnold & Thomas, 1998; Lamb & Bauer, 2003), where *Meroles suborbitalis* (not *M. reticulatus*) was previously found to be sister to all other *Meroles*, although those relationships lacked support (Harris *et al.*, 1998; Lamb & Bauer, 2003). The estimate of the current topology may have been improved by the inclusion of *M. squamulosus*, and the addition of two nuclear gene regions. We found that the diving species and the running species form separate, well supported clades, and that the diving species *M. reticulatus* is sister to all other *Meroles*, a relationship that was previously found using electrophoretic data (Mayer & Berger-Dell'mour, 1988). The evolution of the well supported clades of diving and running *Meroles* is likely linked to the climatic changes, and associated vegetation changes, of the African continent.

The colonization of Africa by lacertid lizards by a European lineage may have occurred as early as 43.2 ± 5.6 Mya based on molecular dating (Hipsley *et al.*, 2009), although initial speculation based on phylogenetic analyses of albumin places this date as recently as 17–19 Mya (Mayer & Benyr, 1994). The southern African genus *Meroles* is estimated to have diverged from other lacertid genera $\sim 33.4 \pm 5.2$ Mya (Hipsley *et al.*, 2009). Species level diversification within *Meroles* is more recent, and ranges from 13 Mya (between *M. reticulatus* and other *Meroles*), to 12 Mya (between runners and the diving clade) and 9 Mya (within runners) (Hipsley *et al.*, 2009; Hipsley, 2012). This dating sequence suggests that the initial divergence between runners and divers was in the mid-Miocene, c. 12 Mya, which coincides well with the development of the Benguela upwelling system off the west coast of Namibia (11–14 Mya; Goudie, 1972; Siesser, 1980; Seely, 1987). This upwelling had two large-scale effects on the region. Firstly, the size of the Namib Desert expanded greatly (Partridge, 1993; Pickford & Senut, 1999; Pickford *et al.*, 2014), and secondly, the upwelling generates a thick fog bank providing a source of moisture and moderate temperatures for desert fauna and flora, and is thought to play an important role in sustaining desert organisms (Goudie, 1972; Siesser, 1980; Seely, 1987). This combination could

have provided ecological opportunity, allowing a radiation of species into the desert biome. In addition, the Namib Sand Sea likely originated via erosion and deposition from the Orange River (Garzanti *et al.*, 2012; Stone, 2013), resulting in a novel habitat that may have been influential in the divergence of some species. At the same time, interior regions of southern Africa, were undergoing changes in vegetation composition (e.g. establishment of savanna biome), presumably facilitating the radiation of 'running' species. The exploration of the evolution of the sand-diving behaviour, in relation to past environmental changes, has provided an understanding of the clumped distribution of the species in the phylogeny of *Meroles*, in that diving species (excluding *M. reticulatus*) are monophyletic and that running species are closely related.

In conclusion, a trade-off was not found between escape strategy and bite force capacity in *Meroles*. We presume that specific aspects of head shape relate directly to biting performance in contrast to diving ability, although bite force appeared to co-evolve with head morphology. We suggest that the evolution of sand-diving corresponds initially with the development of the Benguela System in the mid-Miocene, and later with the deposition of Namib sand seas, and morphological adaptations to sand-diving developed in response to the pressures of the hyper-arid environment.

ACKNOWLEDGEMENTS

We thank the National Research Foundation (NRF) of South Africa (South African Biosystematics Initiative and the Key International Science Capacity Initiative) and the International Foundation of Science (IFS) of Sweden for funding this work. SE was supported by NRF Free-standing and SABI Grant-holder (KAT) linked bursaries, and Erasmus-Mundus (Eurosa programme) scholarship. We thank the City of Cape Town Nature Conservation and Gobabeb Research & Training Station for their assistance and permission to conduct research on their properties. We thank Bayworld (Port Elizabeth) and Ditsong (Pretoria) Museums, and the Ellerman Collection (Stellenbosch University) for access and use of their collections. Many thanks to Ryan Daniels, Zoë Davids, Stephen Doucette-Riise, Thomas Lado, BaAnetse Lesaoana, Buyisile Makhubo, Tracey Nowell, Paula Strauss for field work assistance. This work was conducted under national and provincial research permits: Namibia (1504/2010 & 81305), Northern Cape Province (FAUNA 110/2011, FAUNA 111/2011) and Western Cape Province (AAA004-0322-0035, AAA004-00807-0035, AAA007-00002-

0056). Ethical clearance was obtained from SANBI (permit no. 12 002/10) and University of Stellenbosch (permit no. 11NP_EDW01). Lastly, we thank the three anonymous reviewers for their helpful comments and suggestions, and we believe that the manuscript was greatly improved as a result of their comments.

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SUPPORTING INFORMATION

Additional Supporting Information may be found online in the supporting information tab for this article:

Figure S1. Maps of the geographic distributions of the eight *Meroles* species across southern Africa [adapted from Branch (1998), Bates *et al.* (2014), <http://vmus.adu.org.za/> and <http://www.lacerta.de>].

Figure S2. Warped outline deformation images of the shape change in positive and negative morphospaces of the first four principal components (PC) of the geometric morphometric analyses of head shape in *Meroles*.

Table S1. List of individuals used in the geometric morphometric analyses of head shape.

Table S2. List of individuals used in the biting performance analyses.

Table S3. List of specimens used in the phylogenetic analyses with genus and species names, ID numbers, Museum accession ID numbers and EMBL accession numbers for each gene.

Table S4. Definition of landmarks chosen for the geometric morphometric analyses.