Fossorial and durophagous: implications of molluscivory for head size and bite capacity in a burrowing worm lizard

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Abstract

Limbless animals that burrow head-first are often considered to be evolutionarily constrained in the development of a large head, due to limitations imposed while penetrating the soil. Whilst animals with a small head experience less resistance when digging, they are believed to have a weak bite, hence restricting their potential dietary spectrum to soft prey. Yet, recent findings established molluscivory in the fossorial worm lizard Trogonophis wiegmanni (Amphisbaenia), suggesting a high bite capacity for this burrowing species necessary to crush snail shells. To tackle this burrow/crush dilemma, we examined the relationship between head morphology, bite force and gastropod diet in T. wiegmanni males and females. In vivo bite force analyses and shell hardness measurements were used to assess the potential dietary spectrum of the amphisbaenians. In addition, phylogenetic analyses were performed to put T. wiegmanni's head size and bite force into an interspecific comparative context. Our results show a strong positive relation between head size and bite force, and we found no evidence for sexual dimorphism. In sharp contrast to other durophagous lizards, T. wiegmanni combines a relatively small body and a (disproportionally) small head with relatively high biting forces. In fact, T. wiegmanni is able to crush a wide array of the most abundant gastropod shells in their environment. However, the head size of the strongest biters imposes a limitation towards a common alternative snail-feeding strategy: entering the opening of the gastropod shell. This study shows that head size, and consequently bite force, increases the number and variety of gastropods that can be consumed by 'shell-crushing', but reduces the number and variety of snails that can be consumed by 'shell-entering', and vice versa. The cranial design of (durophagous) limbless burrowers may therefore not only evolve under constraints for efficient soil penetration, but also through selection for diet.

Introduction

Animals often use the same features to carry out different tasks. If these tasks are optimized by conflicting designs, a functional trade-off emerges that will result in the evolution of a compromise phenotype (Maynard Smith et al., 1985; Arnold, 1992; Van Damme et al., 2002, 2003). The cranial system of vertebrates is responsible for a variety of functions, such as chemoreception, defence, drinking and feeding (e.g. Bels, Goosse & Kardong, 1993; Schwenk, 1993, 2000; Alfaro & Herrel, 2001; Aerts et al., 2002; Huyghe et al., 2005). Because these tasks require different, sometimes conflicting head morphologies, functional and ecological trade-offs occur that may constrain head morphology evolution (e.g. Herrel, O'Reilly & Richmond, 2002; Herrel, Vanhooydonck & Van Damme, 2004b; Herrel et al., 2007, 2009; Van Wassenbergh et al.,

2010; Barros, Herrel & Kohlsdorf, 2011; Vanhooydonck et al., 2011).

In lepidosaurians, head shape and size are critical determinants of bite performance (Herrel et al., 1999, 2005a,b; Herrel, De Grauw & Lemos-Espinal, 2001a; Verwaijen, Van Damme & Herrel, 2002; Herrel & O'Reilly, 2006; Huyghe et al., 2009; Schaerlaeken et al., 2012). The bite capacity of an animal strongly affects its dietary spectrum, because an animal can only 'crush' and process food items with a 'hardness' below its maximal bite force (Herrel, Van Damme & De Vree, 1996; Herrel et al., 1999, 2001a, 2004a, 2008; Huyghe et al., 2007; McBrayer & Corbin, 2007; Anderson, McBrayer & Herrel, 2008; Measey et al., 2011; Kaliontzopoulou et al., 2012; Edwards et al., 2013; De León et al., 2014; Des Roches et al., 2014; Sagonas et al., 2014). Animals that feed upon hard-shelled prey (known as 'durophagous'), such as molluscs,

typically display a specialized cranial morphology with more massive cranial muscles (Dalrymple, 1979; Rieppel & Labhardt, 1979; Herrel & Holanova, 2008), and greater bite forces (Schaerlaeken *et al.*, 2012).

Habitat use, however, may provide a selective pressure for an alternative head morphology. For example in rock-dwelling lizards, the use of crevices appears to select for flat heads (Herrel *et al.*, 2001a; Lappin, Hamilton & Sullivan, 2006; Revell *et al.*, 2007; Broeckhoven & Mouton, 2014). Similarly, a large head may hamper climbing performance by shifting the lizard's centre of mass away from the substrate (Vanhooydonck & Van Damme, 1999; Vanhooydonck, Herrel & Van Damme, 2007).

In fossorial limbless animals, the evolution of body shape is constrained due to limitations imposed by body diameter while burrowing, as the energetic cost required to compress soil increases exponentially with body diameter (Navas *et al.*, 2004). In 'head-first' diggers, head diameter is believed to be most constrained (Gans, 1969; López, Martín & Barbosa, 1997; Teodecki *et al.*, 1998; Measey & Herrel, 2006; Barros *et al.*, 2011). For instance Vanhooydonck *et al.* (2011) showed that in burrowing skinks *Acontias percivali* narrow-headed specimens were able to dig into the substrate faster than broader-headed individuals. At the same time, bite performance increased with head size in this species. The burrow/bite trade-off is also hypothesized to prevent large sexual dimorphism in head shape of limbless burrowers (Teodecki *et al.*, 1998; Heideman *et al.*, 2008). While the ability to burrow fast most likely allows fossorial animals to escape predators rapidly and to lower their locomotory energy expenditure (Martín, López & Barbosa, 2000; Wu *et al.*, 2015), their compact cranial system might constrain their dietary ecology (Andrews *et al.*, 1987; Webb *et al.*, 2000; Barros *et al.*, 2011). For these reasons, and despite the Sarlacc, combining a fossorial lifestyle with durophagy seems extremely difficult.

Limbless worm lizards (Amphisbaenia) are an overlooked group within Squamata, with no information available on their bite capacity and only little on their feeding and foraging biology. Most amphisbaenians are believed to be dietary generalists (Cabrera & Merlini, 1990; Cusumano & Powell, 1991; White *et al.*, 1992; Colli & Zamboni, 1999; Kearney, 2003; Bernardo-Silva *et al.*, 2006; Gomes *et al.*, 2009; Balestrin & Cappellari, 2011), although the narrow dietary spectrum of some species (mostly limited to specific small-sized arthropods) suggest a more selective foraging system (López, Martín & Salvador, 1991; Cruz-Neto & Abe, 1993; Gil, Guerrero & Pérez-Mellado, 1993; Webb *et al.*, 2000; Vega, 2001; Bernardo-Silva *et al.*, 2006). *Blanus cinereus*, for instance, is a selective forager, as it prefers large insect larvae and avoids particular ant species (López *et al.*, 1991). A diet study by Martín *et al.* (2013a), evaluating both prey availability and prey consumption in the amphisbaenian *Trogonophis wiegmanni*, surprisingly established shelled-gastropods as one of the most abundant prey items in the faecal pellets of the species (23% of the total prey item composition). In addition, *T. wiegmanni* individuals do not seem to prey at random, but avoid ants and isopods while positively selecting for snails (Martín *et al.*, 2013a). This finding is remarkable, because

snails are a highly unusual food item in the diet of other amphisbaenian and lizard species (Pregill, 1984; Pérez-Mellado & Corti, 1993; Vitt & Pianka, 2005).

Molluscivory is rare in squamates, likely due to the hard and brittle nature of snail shells (Greene, 1982). Putative adaptations to molluscivory in squamates include blunt and rounded teeth (reducing the risk of tooth breakage and increasing area in contact with the shell) and increased bite force (Gans, 1978; Dalrymple, 1979; Rieppel & Labhardt, 1979; Herrel & Holanova, 2008). However, an alternative strategy to feed on gastropods is by entering the snail's shell via the opening (= shell aperture) and by eating the soft tissue from inside (Hoso, Asami & Hori, 2007), which has been frequently observed in *T. wiegmanni* in the field J. Martín (pers. obs.). In sharp contrast to the 'shell-crushing' strategy, a 'shell-entering' strategy requires a slim head to fit into the aperture, suggesting a trade-off between two feeding strategies. Still, because shell remnants are common in *T. wiegmanni* faeces from both sexes (Martín *et al.*, 2013a), we can expect that all adult amphisbaenians of this species are equipped with the required cranial characteristics to handle (at least some of) the available gastropods in their surroundings.

Based on a large-scale population study on *T. wiegmanni*, Martín *et al.* (2012) observed a minor, but significant, sexual dimorphism in relative head size, with male amphisbaenians having larger heads than females of a similar size. If the head size of amphisbaenians is strongly correlated with bite capacity, one could expect intersexual diet differences in *T. wiegmanni*. In such a scenario males would have the opportunity to feed on harder prey than females, and/or females the ability to insert their heads in the narrow shell opening. However, the diet of adult male and female *T. wiegmanni* appears to be similar, with snails being one of the main prey types in both sexes (Martín *et al.*, 2013a). Still, males and females could differ in their reliance on strategies to feed on gastropods ('shell crushing' vs. 'shell entering'), or differ in the size of snails they prey upon.

This study was designed to provide more insight into the relationships between head morphology, bite force and diet in molluscivorous fossorial limbless animals, with the amphisbaenian *T. wiegmanni* as study species. The first goal of the study was to investigate whether head shape and size predict bite force in amphisbaenians, and to establish potential intersexual difference in bite capacity. As for lizards of the sister clade Lacertidae (Gauthier *et al.*, 2012; Pyron, Burbrink & Wiens, 2013), we predicted that amphisbaenian head size is strongly correlated with maximal bite capacity. In addition, we expected males to have higher relative bite forces than females, based on the results of a previous study showing sexual dimorphism in *T. wiegmanni* relative head size (Martín *et al.*, 2012). The second aim was to examine the relationship among head dimensions, bite force capacities and potential gastropod diet of *T. wiegmanni*. We expected that the force needed to crush gastropod shells falls within the range of bite forces observed in *T. wiegmanni*. Also, we predicted that greater head size, and consequently bite force, increases the number and variation of gastropod prey items that can be consumed by 'shell-crushing', but reduces the number of prey items that can be

consumed by 'shell-entering', and *vice versa*. The final goal of this study was to compare head size and bite force of *T. wiegmanni* with those of other lizard species in a phylogenetic context, to determine the impact of fossoriality and molluscivory on the direction of evolution in head size and bite force.

Materials and methods

Worm lizards

The checkerboard worm lizard *Trogonophis wiegmanni* Kaup 1830; (Fig. 1 and S3) is a burrowing species of the amphisbaenian family Trogonophidae endemic to the Maghreb (southwest Morocco to northeast Tunisia). The species prefers sandy soils with a high abundance of leaf litter (Civantos, Martín & López, 2003; Martín, López & García, 2013b).

A sample of 25 adult *T. wiegmanni* individuals (10 females; 15 males) was used to document external head morphology and to quantify bite performance. All animals were hand-caught under rocks on the Chafarinas Islands (Spain) in March 2012. This small archipelago is located in the Mediterranean Sea (35°11'N, 2°25'W), 4.6 km off the northern Moroccan coast (Ras el Ma) and 43 km to the east of Melilla, Spain. The islands have a dry, warm, Mediterranean climate and vegetation is dominated by plants adapted to salinity and drought, such as bushes of the genera *Salsola*, *Lycium*, *Atriplex* and *Suaeda* (Civantos *et al.*, 2003; Martín *et al.*, 2013b).

The amphisbaenians were carefully transported to 'El Ventorrillo' Field Station (Navacerrada, Madrid, Spain) and housed indoors. Animals were kept in pairs (male/female) in plastic terraria (40 × 30 × 30 cm) containing a layer of loose coconut-fibre substrate approximately 5 cm thick. We placed a flat tile (20 × 20 cm) on the fibre substrate that served as a shelter. Below the terraria, we placed a heating cable, connected to a thermostat, which resulted in a soil temperature gradient ranging 23–27°C. The preferred body temperature of *T. wiegmanni* is around 25°C (Gatten & McClung, 1981; López, Civantos & Martín, 2002). The photoperiod was natural (approximately 13 h light/11 h dark), and the terraria received

Figure 1 A photograph of an adult *Trogonophis wiegmanni* amphisbaenian.

direct sunlight through two large windows. The animals were fed twice a week (*Tenebrio* sp. larvae and *Acheta domesticus*, dusted with multivitamin powder), and the substrate was sprayed with water three times a week.

Bite forces

Bite forces were measured *in vivo* using an isometric force transducer (type 9203, range ± 500 N; Kistler, Switzerland) mounted on a custom-built holder and connected to a charge amplifier (type 5058 A, Kistler; for a more detailed description of the experimental set-up see Herrel *et al.*, 1999). *Trogonophis wiegmanni* readily and repeatedly bit onto the two metal plates positioned at the free end of the holder. To standardize gape angle, we increased the distance between the bite plates for larger animals (as suggested by Anderson *et al.*, 2008). We were able to perform three trials for each individual, and the hardest bite was considered an individual's maximal bite force. Because bite force is affected by body temperature (Anderson *et al.*, 2008), prior to each test, animals were placed in individual cloth bags and kept for at least 45 min in an incubator set at 25°C. This procedure ensured that all measures were taken near the selected and optimal body temperature of this species.

Worm lizard morphometrics

For each individual amphisbaenian, we recorded: body mass, snout-vent length (SVL), head length, head width and head height. Head length was measured from the posterior extremity of the parietal scale to the tip of the snout. Head width was the largest distance measured between the temporal scales, and head height was the maximum distance measured between the base of the mandible and the parietal surface. All head variables were measured using digital callipers (Mitutoyo, CD-15CPX, precision = 0.01 mm). SVL was measured by stretching the animals along a ribbon rule (precision = 1 mm). Body mass was assessed on a microbalance (Adventurer, Ohaus Corp., precision = 0.01 g).

Prey characteristics

Snails are one of the most abundant prey items found in *T. wiegmanni* faecal samples, and assumed to be a preferred food item in their diet (Martín *et al.*, 2013a). By randomly lifting stones – under which the amphisbaenians were also often found – we collected specimens of the four most abundant gastropod species on the island (de Lozoya, 2006): *Cochlicella acuta* (7), *Dupotetia arabica* (29), *Rumina decollata* (21) and *Theba pisana* (32) (Fig. 2). For every individual animal, we measured: shell width, shell height, shell mass (incl. snail itself) and shell opening size (i.e. aperture diameter). See Supplementary Material (Fig. S1) for a visualization of the shell morphometrics and measurements recorded.

To assess the force needed to crush shell items consumed by *T. wiegmanni* and to estimate the effect of bite force on the potential prey spectrum, we compared the mean and maximal bite force of *T. wiegmanni* with the force (or load) required to

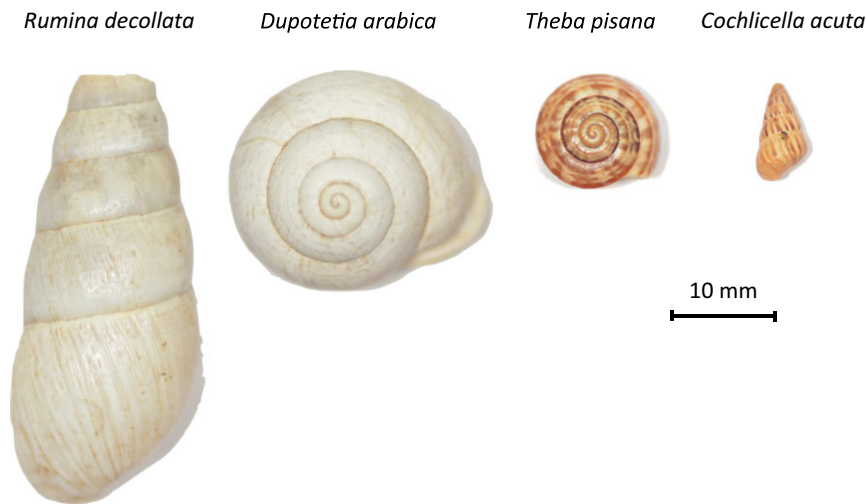*Rumina decollata*   *Dupotetia arabica*   *Theba pisana*   *Cochlicella acuta*

10 mm

Figure 2 Overview of the four prey gastropod species under study.

break the shell of the different gastropod species. Shell breaking load (N) was measured by pushing the flattened top (2 mm^2) of a screw (as in e.g. Aguirre *et al.*, 2003; Broeckhoven & Mouton, 2014), mounted on a force transducer (type 9302; Kistler), onto the prey until the gastropod shell showed mechanical failure (for a detailed description of the set-up see Fig. S2 and Herrel *et al.*, 2001b). Snail shells were positioned aperture down, and the point on which external forces were applied to standardized (Fig. S2). The force required to crush the shell was considered the shell's breaking load. Although 'shell breaking load' is theoretically not identical to 'shell strength' or 'shell hardness' (Denney, 2015), latter terms are used interchangeably throughout the text, referring to load.

Phylogenetic comparison

To put *T. wiegmanni*'s head size and bite force into an interspecific comparative context, we searched the literature for data on body size, head width and bite force of lizards. Since species cannot be treated as independent data points, we used phylogenetic generalized least square regression (pGLS) analyses (function 'pgls' and packages 'caper' and 'phytools', Freckleton, Harvey & Pagel, 2002; Revell, 2009). The phylogenetic tree presented by Pyron *et al.* (2013), was assumed to represent the evolutionary relationships among the species in our phylogenetic analysis. We obtained our point estimate of the phylogeny by pruning Pyron's tree to comprise only the species (including *T. wiegmanni*) of this study (*n* = 83 species).

Data analyses

Prior to analysis, all data were log$_{10}$-transformed to meet the assumptions of normality. We used reduced major axis regressions (RMA) to explore allometric relationships among head and body dimensions (which are expected to scale isometrically), and bite force (expected to scale proportional to length to the second power; Herrel & O'Reilly, 2006). The relative contribution of morphological variables (SVL, mass, head

length, head width, head height) to the variation in bite performance was assessed through multiple regression analyses (backward stepwise elimination). Analyses of variance (ANOVA) were conducted to test for differences in SVL, body condition, body mass, head morphometrics and bite force.

A proxy for body condition was calculated using the residual values obtained by the regression of log$_{10}$ body mass over log$_{10}$ SVL. The three head variables (head length, head width and head height) were strongly intercorrelated (all $r > 0.60$, all $P < 0.001$). Principal component analysis on log$_{10}$-transformed head measures yielded one composite variable (individual scores for PC1 are hereafter referred to as 'head size'), which accounted for 76% of the total variation and showed high positive loadings for all original variables (all loadings >0.85).

Differences in shell hardness and aperture size among the four gastropod species were tested by ANOVAs and multiple comparisons (Tukey's HSD test).

To evaluate the theoretical dietary spectrum of *T. wiegmanni* individuals, we compared maximal amphisbaenian bite capacities with the hardness of the gastropod shells, and head widths with shell opening diameters. Comparisons are based on the assumptions that amphisbaenians are able to crush gastropod shells with a hardness below their maximal bite force, and enter shells with an opening larger than the width of their head.

Statistical analyses were conducted in R STUDIO, version 0.97.248 (R Core Team, 2012; R Studio, 2012) and SPSS v. 23.0 (Chicago, IL, USA). Probabilities (*P*) lower than 0.05 were considered statistically significant.

Results

Worm lizard morphometrics and sexual dimorphism

A summary of the morphological measurements of the *T. wiegmanni* amphisbaenians used in this study is given in Table 1. The sexes did not differ in SVL, and no evidence for

sexual dimorphism in head dimensions, overall head size, body mass, body condition and relative bite force was found (Table 1). Consequently, data on all individuals were pooled and no distinction between sexes was made in further analyses. Martín *et al.* (2012) reported for the same species similar body sizes for both sexes, but conversely, established males having larger heads than females of the same size. Although the researchers described only minor intersexual differences, their results were based on a sample size ten times the size of this study (Martín *et al.*, 2012: 139 females and 131 males vs. this study: 10 females and 15 males), most likely explaining the discrepant results among both studies (Cox, Skelly & John-Alder, 2003).

Determinants of bite force

Individual maximal bite force in *T. wiegmanni* varied between 3.30 and 8.00 N (mean $\pm$ SE = 5.15 $\pm$ 0.23 N). Overall, a strong and positive relationship was found between all head and body measures (Table 2; Fig. 3a). In line, bite force related positively to all head variables (Fig. 3b). The multiple regression analysis resulted in a significant model ($r^2 = 0.52$,

$F_{1,23} = 24.88$, $P < 0.001$) selecting head width as the main variable explaining variation in bite force: animals with relatively wider heads managed to bite harder (ordinary least square regression coefficient $B \pm$ SE = 1.53 $\pm$ 0.31). Our data indicated bite force to increase with the second power relative to head width (intercept = -0.70, slope = 2.13 with CI 1.58–2.86), whereas bite force scaled with strong positive allometry to body size (intercept = -6.80, slope = 3.42 with CI 2.83–4.92). Body size is often considered a more irrelevant independent variable when examining scaling of performance traits (Gardner *et al.*, 2001; Herrel *et al.*, 2002).

Prey characteristics

The four gastropod species differed significantly in the hardness of their shell (ANOVA, $F_{3,85} = 172.70$, $P < 0.001$), and size of their shell opening (ANOVA, $F_{3,85} = 199.20$, $P < 0.001$). Overall, the larger species (*Dupotetia* and *Rumina*) were equipped with the hardest shells and widest shell opening, whereas the small gastropods (*Cochlicella* and *Theba*) had weaker shells and narrower shell openings (Table 3; Fig. 4). More specifically, shells of *Dupotetia* were stronger than shells of *Rumina* (Tukey's

Table 1 Morphometrics and *in vivo* bite forces (mean $\pm$ standard errors) of *Trogonophis wiegmanni*, with results of the analyses of variance (ANOVA) testing for sexual dimorphism

Variable	Females	Males	Total	Sexual dimorphism	
N	10	15	25	$F_{1,23}$	P
SVL (mm)	153.20 $\pm$ 3.32	158.47 $\pm$ 2.48	156.36 $\pm$ 2.02	1.73	0.200
Body mass (g)	6.73 $\pm$ 0.53	6.83 $\pm$ 0.42	6.79 $\pm$ 0.32	0.03	0.862
Body condition	0.02 $\pm$ 0.02	-0.01 ± 0.02	–	1.16	0.292
Head length (mm)	6.69 $\pm$ 0.13	6.96 $\pm$ 0.14	6.85 $\pm$ 0.10	1.79	0.194
Head width (mm)	5.00 $\pm$ 0.14	5.09 $\pm$ 0.15	5.05 $\pm$ 0.10	0.15	0.706
Head height (mm)	4.00 $\pm$ 0.14	4.07 $\pm$ 0.14	4.04 $\pm$ 0.09	0.87	0.770
'Head size'[a]	$- 0.29 \pm 0.40$	0.19 $\pm$ 0.44	–	0.16	0.689
Bite force (N)	5.08 $\pm$ 0.32	5.20 $\pm$ 0.32	5.15 $\pm$ 0.23	0.31	0.862

[a]'Head size' is a composite variable obtained through the principal component analyses on the three head variables (head length, head width and head height) – see Data analyses.

Table 2 Allometries of (1) morphometrics and bite force versus snout-vent length (SVL), and (2) morphometrics versus bite force, obtained through reduced major axis regressions (RMA)

Allometries Variables	Intercept	2.5% CI	97.5% CI	Slope	2.5% CI	97.5% CI	r	r^2
With SVL as independent								
Mass	-6.75	-9.37	-4.81	3.45	2.57	4.64	0.72	0.51
Head length	-1.62	-2.62	-0.92	1.12	0.80	1.58	0.60	0.36
Head width	-2.83	-4.04	-1.92	1.61	1.20	2.16	0.72	0.52
Head height	-3.65	-5.11	-2.55	1.94	1.44	2.61	0.72	0.51
Bite force	-6.80	-10.08	-4.52	3.42	2.83	4.92	0.51	0.26
With bite force as dependent								
Mass	-0.11	-0.44	0.12	0.99	0.71	1.39	0.61	0.37
Head length	-1.84	-2.99	-1.05	3.04	2.09	4.43	0.46	0.21
Head width	-0.79	-1.30	-0.41	2.13	1.58	2.86	0.72	0.52
Head height	-0.36	-0.86	-0.02	1.77	1.19	2.61	0.36	0.13

Slopes and intercepts of the confidence intervals (95%) are also presented. Note that expected slopes are 1 for linear dimensions and 2 for forces when regressed against a linear dimension, such as, for example head width.
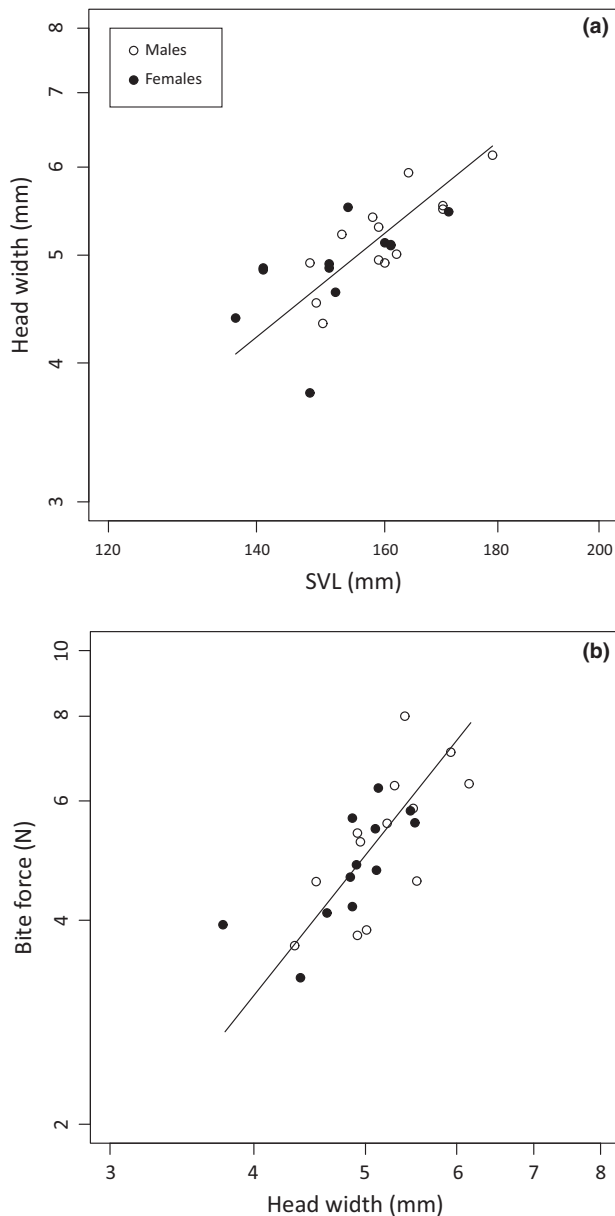
Figure 3 Relationship between snout-vent length (SVL) and head width (a), and between head width and bite force (b) in the amphisbaenian *Trogonophis wiegmanni*. Note the logarithmic scale on both axes.
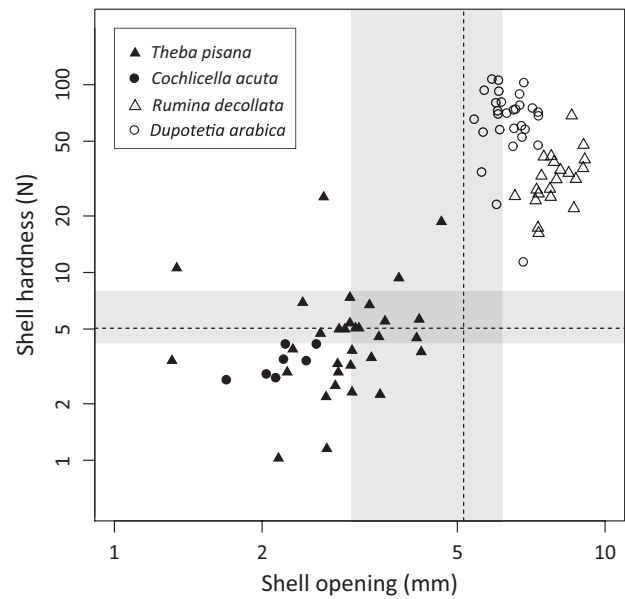

Figure 4 Scatterplot illustrating the relationship between shell opening diameter and shell hardness in four prey gastropod species. Dotted lines represent mean bite force (horizontal) and mean head width (vertical) of *Trogonophis wiegmanni*. Grey zones extent from minima to maxima. Note the logarithmic scale on both axes.

HSD test: difference = 35.32 N, *P* < 0.001). Shell hardness did not differ significantly between *Cochlicella* and *Theba* (Tukey's HSD test: difference = 2.18 N, *P* = 0.556).

The average size of the shell opening of *Rumina* was significantly larger than that of *Dupotetia* (Tukey's HSD test: difference = 1.53 mm, *P* < 0.001). Also, the shell opening of *Theba* was slightly, but significantly, larger than the average opening of *Cochlicella* (Tukey's HSD test: difference = 0. 82 mm, *P* < 0.001).

Potential dietary spectrum

The proportion of individual snails that (in theory) can be eaten by *T. wiegmanni* varies among gastropod species and depends on the feeding strategy. From Figs 4 and 5; all *Rumina* snails measured could be entered by all *T. wiegmanni* (as their aperture was larger than the widest amphisbaenian

Table 3 Morphometrics and shell hardness (mean ± standard errors) of the four gastropod species under study.

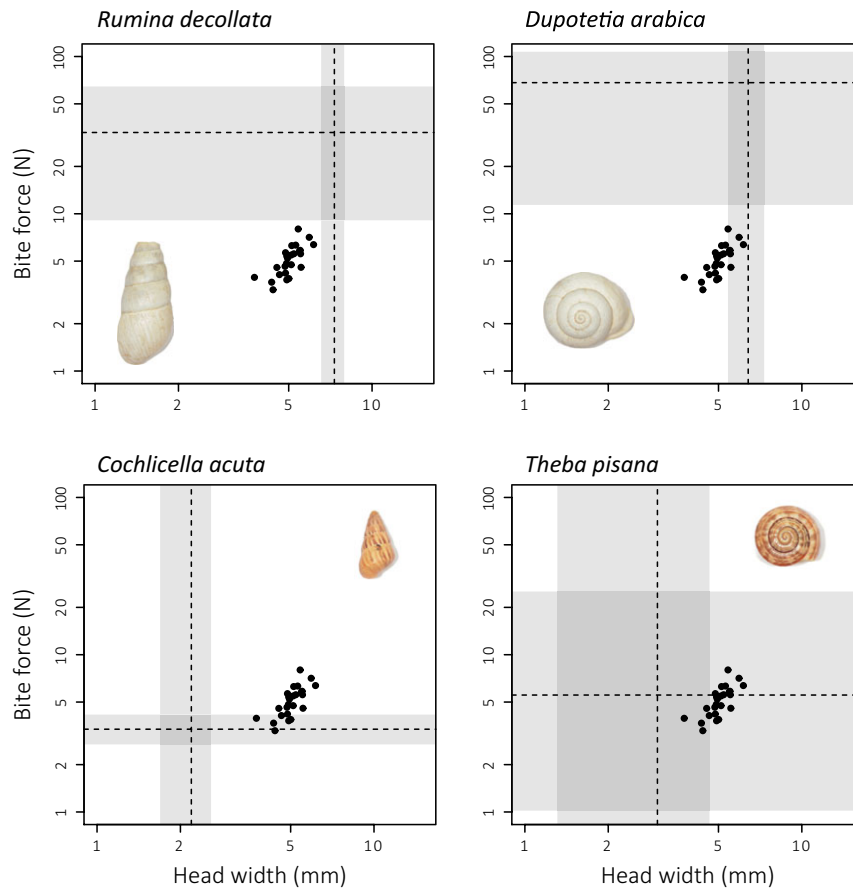| Gastropod species	N	Mass (mg)	Shell width (mm)	Shell height (mm)	Aperture diameter (mm)	Shell hardness (N)
Cochlicella acuta	7	58.14 ± 9.06	4.23 ± 0.11	8.46 ± 0.39	2.19 ± 0.11	3.36 ± 0.24
Dupotetia arabica	29	2427 ± 97	35.94 ± 0.73	19.88 ± 0.16	6.4 ± 0.1	68.19 ± 4.21
Rumina decollata	21	2434 ± 155	58.19 ± 4.89	15.57 ± 0.25	7.93 ± 0.16	32.87 ± 2.52
Theba pisana	32	208 ± 27	10.76 ± 0.66	4.66 ± 0.24	3.01 ± 0.13	5.54 ± 0.86

Figure 5 Scatterplots illustrating the relationship between head width and bite force in *Trogonophis wiegmanni* in comparison with the shell characteristics of the four most abundant gastropod species in their environment. Dotted lines represent mean shell hardness (horizontal) and mean shell opening (vertical) of the gastropod. Grey zones extent from minima to maxima. Note the logarithmic scale on both axes.

head) but none of them could be crushed (as their hardness was above the amphisbaenians' maximal bite force). Similarly, most *Dupotetia* could be entered, but none of them could be crushed. In contrast, all *Cochlicella* were too small to enter, but most could be crushed by all *T. wiegmanni*. Finally, only small amphisbaenians could enter *Theba* shells, and the smaller – but not the larger – snails could be crushed by *T. wiegmanni*.

Phylogenetic comparison

Our search of the literature returned data on SVL, head width and bite force of 82 species of lizards (Table S1). Overall head width co-evolved tightly with SVL ($\lambda = 0.96$, $F_{1,81} = 277.4$, $P < 0.001$; pGLS regression with slope = 1.06, intercept = -0.91), but the two burrowing species in the dataset (the skink *A. percivali* and amphisbaenian *T. wiegmanni*) clearly stood out with much narrower heads than expected for their body size (Fig. 6a). In the same interspecific dataset, bite force was strongly correlated with head width ($\lambda = 0.97$, $F_{1,81} = 421.7$, $P < 0.001$; pGLS regression with slope = 2.23, intercept = -1.42), but there *T. wiegmanni* stood out for

having a high bite relative to its head width (Fig. 6b). The absolute bite force of *T. wiegmanni*, however, appeared much lower in comparison to (partly) molluscivorous lizard species, such as *Dracaena guianensis* (383.3 N), *Tupinambis merianae* (334.8 N), *Tiliqua rugosa* (161.6 N) *and Varanus exanthematicus* (86.6 N).

Discussion

The burrow/crush dilemma

As in many other species of lizards (Herrel, Aerts & De Vree, 1998; Herrel *et al.*, 1999, 2001a,b; Herrel 2007), bite force in *T. wiegmanni* was highly dependent on head size. Our findings indicate head width as the best predictor of bite capacity in this species: animals with a (relative) wider head bite harder. Given that ectothermic vertebrates typically grow nearly geometrically (O'Reilly, Lindstedt & Nishikawa, 1993; Richard & Wainwright, 1995; Robinson & Motta, 2002), we predicted that bite force in *T. wiegmanni* should increase with head width to the second power (Hill, 1950), which our results confirm. This strong relationship between head size and bite force
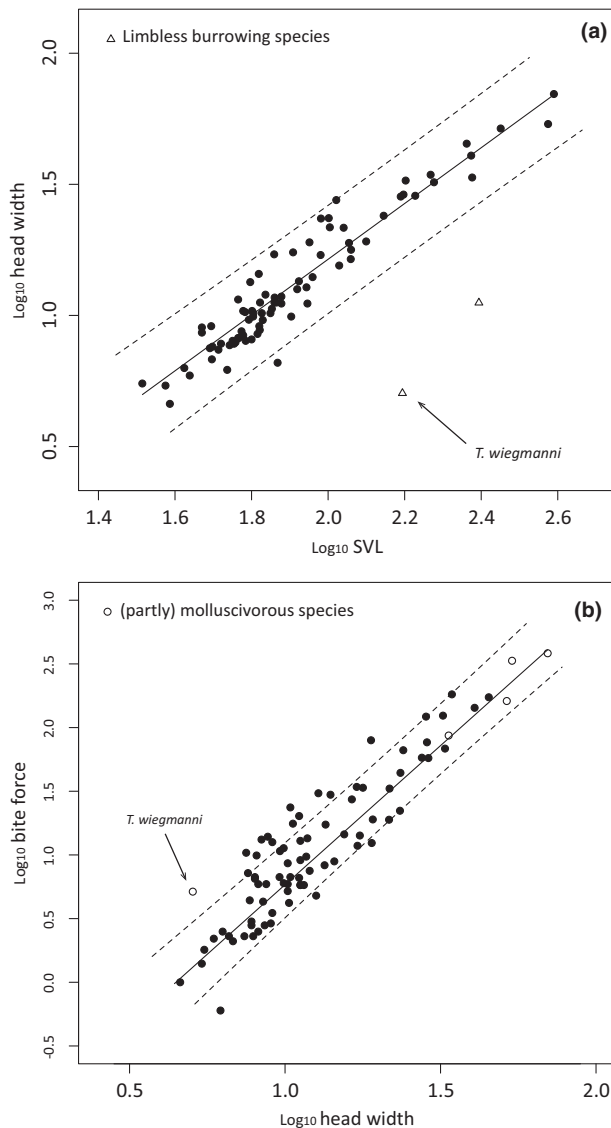
Figure 7 Visualization of the feeding strategy dilemma in *Trogonophis wiegmanni*: a large head, thus high bite force, enables *T. wiegmanni* to crush hard *Theba* shells, but inhibits them to enter the aperture of small *Dupotetia* shells. Quadratic regression models computed the polygonal lines.

Figure 6 Interspecific relationship between (a) snout-vent length (SVL) and head width, and (b) head width and bite capacity among lizard species – including the amphisbaenian *Trogonophis wiegmanni*. Phylogenetic generalized least square regression analyses computed the solid regression lines (function 'pgls'; Freckleton *et al.*, 2002). Confidence intervals (95%) are presented as dashed lines (function 'gls.ci'; Smaers, 2014; Smaers & Rohlf, 2016).

presents *T. wiegmanni* with a probable trade-off. Selection for burrowing capacity would result in small heads and, consequently, low bite forces (Vanhooydonck *et al.*, 2011). Indeed, head size of burrowing species appears very small in comparison to the species' body size (Fig. 6a). Still, the small head of *T. wiegmanni* is capable of producing remarkable high bite forces (Fig. 6b). On the basis of our interspecific analyses, lizards with heads the size of *T. wiegmanni* should bite merely 1.41 N. In reality, an average *T. wiegmanni* bites 3.7 times as hard. Yet, it is unclear how *T. wiegmanni* succeeds in
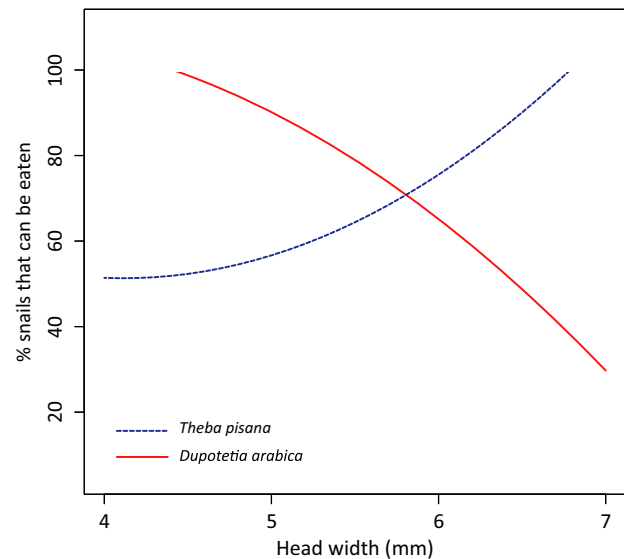
combining a small head with a relative high bite force. Caecilians, for example have evolved a unique dual jaw-closing mechanism that allows them to bite hard while maintaining a narrow head for burrowing (Nussbaum, 1983; Kleinteich, Haas & Summers, 2008). It would be most interesting to investigate whether *T. wiegmanni* differs in aspect of its muscle masses, muscle architecture (e.g. proportion of pennate muscles, muscle fibre orientation) or muscle physiology (as in e.g. Gans, De Vree & Carrier, 1985; Herrel *et al.*, 1998, 1999; Huyghe *et al.*, 2010).

An important ecological driver of bite force evolution in *T. wiegmanni* may be its reliance on gastropod prey. Molluscivory has evolved several times in squamates species, such as in *Dracanaena guianensis*, *Tupinambis meranae*, *Tiliqua rugosa*, *Varanus exanthematicus,* which have all been reported to consume shelled snails regularly (Dalrymple, 1979; Rieppel & Labhardt, 1979; Pregill, 1984; Herrel *et al.*, 2002). However, in these cases, the high bite forces required for durophagy are simply the isometric outcome of larger body sizes and heads (Fig. 6). In sharp contrast, *T. wiegmanni* combines a relatively small body and a (disproportionally) small head with relatively high bite capacities. Specialized dentitional and cranial adaptations may allow this remarkable 'head size/bite force' relationship, and may also explain *T. wiegmanni*'s success as a durophagous species. First of all, trogonophids differ from other amphisbaenians by their acrodont dentition, which constitutes a possible mechanism to avoid tooth breakage and to increase contact with shelled prey items (Gans, 1960, 1968, 1978). Regarding cranial morphology, two main traits are present. First, the presence of a marked parietal crest might allow for the attachment of jaw adductor muscles, as it is found in

the snail-eating lizard *Chameoleolis chamaeleonides* to increase bite performance (Herrel & Holanova, 2008). Second, the posterior maxillary processes are outwardly projected (Gans, 1960), making the skull wider than at the occipital lobes, offering ample space for an enlarged jaw musculature, as it is inferred from the highly elongated skull (Martín *et al.*, 2013a).

Implications of feeding strategy on the potential dietary spectrum

Shelled gastropods, one of the dominant prey items consumed by *T. wiegmanni* in the field, can be eaten in two ways: by crushing the shell, or by entering the shell through the aperture (Martín *et al.*, 2013a; J. Martín, Unpublished data). High bite forces are expected to be essential to crush hard shells, whereas small head sizes (hence, low bite forces) are necessary to enter shells with a narrow opening. Since our results reveal large intra- and interspecific variation in the hardness of the gastropod shell and the size of the shell opening, the bite capacity and head size of *T. wiegmanni* can be considered ecologically relevant variables affecting their potential dietary spectrum and feeding strategy.

Besides the burrow/crush dilemma, the conflicting body size requirements for the two alternative feeding strategies pose a second dilemma: either to stay small enough to be able to penetrate the shell opening, or to grow large enough to be able to crush snail shells. Our comparison of bite forces and shell hardness on the one hand, and head size and aperture size on the other hand, suggest that the 25% strongest biters are able to crush all tested *Cochlicella* shells and 88% of the *Theba* shells. However, due to the width of their heads, these individuals are unable to enter any *Theba* shell opening and only 55% of the *Dupotetia* shells. In comparison, the 25% weakest biters may merely crush 71% of the tested *Cochlicella* shells and 47% of the *Theba* shells, but are able to enter up to 16% of the *Theba* shells and 100% of the *Dupotetia* shells. These findings confirm our prediction that head size, and consequently bite force, increases the number and variation in gastropod prey items that can be consumed by 'shell-crushing', but reduces the number and variation in prey items that can be consumed by 'shell-entering', and *vice versa* (e.g. Fig. 7). Of course, the abundance of the different snail species in the field, and *T. wiegmanni*'s gastropod preferences, might influence the direction of head morphology evolution in *T. wiegmanni*.

Evidently, more extensive research is required to determine the actual existence of a body size-dependent feeding strategy in *T. wiegmanni*. Behavioural observations and feeding experiments may shed light on the relative (natural) incidence of both feeding behaviours and the effect of prey-gastropod species and size on feeding preference and strategy, and on prey handling time. Information on maximal gape angles, which are known to affect bite performance (Dumont & Herrel, 2003; Anderson *et al.*, 2008; Williams, Peiffer & Ford, 2009), may also aid in estimating the dietary spectrum of *T. wiegmanni*. Nevertheless, flexibility in feeding behaviour may also compensate for morphological constraint of fossoriality (López, Martín & Salvador, 2013).

Conclusion

Head size is conventionally believed to be constrained in limbless fossorial animals, due to the limitations imposed while burrowing, therefore selecting for small heads and, consequently, low bite forces. However, in the burrowing amphisbaenian *T. wiegmanni*, we establish small head sizes with remarkably high relative bite capacities in comparison to other lizard species. Such biting may be important for their molluscivorous diet, since they manage to crush a wide variety of the most abundant gastropod shells in their environment. However, the wide head necessary to bite hard imposes a limitation towards an alternative snail-feeding strategy: entering the snail's shell via the shell opening and eating the flesh from inside. Our results shows that head size, and consequently bite force, increases the number and variety of gastropods that can be consumed by 'shell-crushing', but reduces the number and variety of prey items that can be consumed by 'shell-entering', and *vice versa*. This study implies that the cranial design of (molluscivorous) limbless burrowers may therefore not only evolve under constraints for efficient soil penetration, but also through selection for diet.

Acknowledgements

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Figure S1. Visual representation (not to scale) of the morphological measurements taken on the gastropod shells. AD, aperture diameter; SH, shell height; SW, shell width.

Figure S2. Experimental setup designed to determine shell breaking load (N), or 'shell hardness'. The red dots on the shell visualize the position on which external forces were applied. A more detailed description of the procedure and equipment can be found in Herrel *et al.* 2001b.

Figure S3. (a) A picture of *Trogonophis wiegmanni* in its natural habitat, and (b) a close-up photo.

Table S1. Bite force, and head and body size data of various lizard species, extracted from the literature. Species sorted by bite force (low to high).