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1 **Fossorial ánd durophagous: implications of molluscivory for head size and bite**  
2 **capacity in a fossorial worm lizard**

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15 *Short title:* Fossoriality and durophagy in a worm lizard

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24 **Abstract**

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

49 *Keywords:* Amphisbaenia — Bite performance — Diet — Ecomorphology —  
50 Feeding strategy — *Trogonophis wiegmanni*

51

## 52 **Introduction**

53 Animals often use the same features to carry out different tasks. If these tasks are  
54 optimized by conflicting designs, a functional trade-off emerges that will result in the  
55 evolution of a compromise phenotype (Maynard Smith *et al.*, 1985; Arnold, 1992;  
56 Van Damme *et al.*, 2002, 2003). The cranial system of vertebrates is responsible for a  
57 variety of functions, such as chemoreception, defence, drinking and feeding (e.g.  
58 Bels, Goosse & Kardong, 1993; Schwenk, 1993, 2000; Alfaro & Herrel, 2001; Aerts  
59 *et al.*, 2002, Huyghe *et al.*, 2005). Because these tasks require different, sometimes  
60 conflicting head morphologies, functional and ecological trade-offs occur that may  
61 constrain head morphology evolution (e.g. Herrel, O'Reilly & Richmond, 2002,  
62 Herrel *et al.*, 2004b, 2007, 2009; Van Wassenbergh *et al.*, 2010; Barros, Herrel &  
63 Kohlsdorf, 2011; Vanhooydonck *et al.*, 2011)

64 In lepidosaurians, head shape and size are critical determinants of bite  
65 performance (Herrel *et al.*, 1999; Herrel, De Grauw & Lemos-Espinal, 2001a; Herrel  
66 *et al.*, 2005 a , b , 2006; Verwaijen, Van Damme & Herrel, 2002; Huyghe *et al.*, 2009;  
67 Schaerlaeken *et al.*, 2012). The bite capacity of an animal strongly affects its dietary  
68 spectrum, because an animal can only 'crush' and process food items with a  
69 'hardness' below its maximal bite force (Herrel, Van Damme & De Vree, 1996,  
70 Herrel *et al.*, 1999, 2001 b, 2004 a; 2008; McBrayer & Corbin, 2007; Huyghe *et al.*,  
71 2007; Anderson, McBrayer & Herrel, 2008; Measey *et al.*, 2011; Kaliontzopoulou *et*  
72 *al.*, 2012; Edwards *et al.*, 2013; De León *et al.*, 2014; Des Roches *et al.*, 2014;  
73 Sagonas *et al.*, 2014). Animals that feed upon hard-shelled prey (known as

74 ‘durophagous’), such as molluscs, typically display a specialized cranial morphology  
75 with more massive cranial muscles (Dalrymple, 1979; Rieppel & Labhardt, 1979;  
76 Herrel & Holanova, 2008), and greater bite forces (Schaerlaeken *et al.*, 2012).

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

83 In fossorial limbless animals, the evolution of body shape is constrained due to  
84 limitations imposed by body diameter while burrowing, as the energetic cost required  
85 to compress soil increases exponentially with body diameter (Navas *et al.*, 2004). In  
86 ‘head-first’ diggers, head diameter is believed to be most constrained (Gans, 1969;  
87 López, Martín & Barbosa, 1997; Teodicki *et al.*, 1998; Measey & Herrel, 2006;  
88 Barros *et al.*, 2011). For instance, Vanhooydonck *et al.* (2011) showed that in  
89 burrowing skinks (*Acontias percivali*) narrow-headed specimens were able to dig into  
90 the substrate faster than broader-headed individuals. At the same time, bite  
91 performance increased with head size in this species. The burrow/bite trade-off is also  
92 hypothesized to prevent large sexual dimorphism in head shape of limbless burrowers  
93 (Teodicki *et al.*, 1998; Heideman *et al.*, 2008). While the ability to burrow fast most  
94 likely allows fossorial animals to escape predators rapidly and to lower their  
95 locomotory energy expenditure (Martín, López & Barbosa, 2000; Wu *et al.*, 2015),  
96 their compact cranial system might constrain their dietary ecology (Andrews *et al.*,  
97 1987; Webb *et al.*, 2000; Barros *et al.*, 2011). For these reasons, and despite the  
98 Sarlacc, combining a fossorial lifestyle with durophagy seems extremely difficult.

100 Limbless worm lizards (Amphisbaenia) are an overlooked group within Squamata,  
101 with no information available on their bite capacity and only little on their feeding  
102 and foraging biology. Most amphisbaenians are believed to be dietary generalists  
103 (Cabrera & Merlini, 1990; Cusumano & Powell, 1991; White *et al.*, 1992; Colli &  
104 Zamboni, 1999; Kearney, 2003; Bernardo-Silva *et al.*, 2006; Gomes *et al.*, 2009;  
105 Balestrin & Cappellari, 2011), although the narrow dietary spectrum of some species  
106 (mostly limited to specific small-sized arthropods) suggest a more selective foraging  
107 system (López, Martín & Salvador, 1991; Cruz-Neto & Abe, 1993; Gil, Guerrero &  
108 Pérez-Mellado, 1993; Web *et al.*, 2000; Vega, 2001; Bernardo-Silva *et al.*, 2006).  
109 *Blanus cinereus*, for instance, is a selective forager, as it prefers large insect larvae  
110 and avoids particular ant species (López *et al.*, 1991). A diet study by Martín *et al.*  
111 (2013 a), evaluating both prey availability and prey consumption in the  
112 amphisbaenian *Trogonophis wiegmanni*, surprisingly established shelled-gastropods  
113 as one of the most abundant prey items in the faecal pellets of the species (23% of the  
114 total prey item composition). In addition, *T. wiegmanni* individuals do not seem to  
115 prey at random, but avoid ants and isopods while positively selecting for snails  
116 (Martín *et al.*, 2013 a). This finding is remarkable, because snails are a highly unusual  
117 food item in the diet of other amphisbaenian and lizard species (Pregill, 1984; Pérez-  
118 Mellado & Corti, 1993; Vitt & Pianka, 2005).

119 Molluscivory is rare in squamates, likely due to the hard and brittle nature of  
120 snail shells (Greene, 1982). Putative adaptations to molluscivory in squamates include  
121 blunt and rounded teeth (reducing the risk of tooth breakage and increasing area in  
122 contact with the shell) and increased bite force (Gans, 1978; Dalrymple, 1979;  
123 Rieppel & Labhardt, 1979; Herrel & Holanova, 2008). However, an alternative

124 strategy to feeding on gastropods is by entering the snail's shell via the opening (=  
125 shell aperture) and by eating the soft tissue from inside (Hoso, Asami & Hori, 2007),  
126 which has been frequently observed in *T. wiegmanni* in the field (pers. obs.). In sharp  
127 contrast to the 'shell-crushing' strategy, a 'shell-entering' strategy requires a slim  
128 head to fit into the aperture, suggesting a trade-off between two feeding strategies.  
129 Still, because shell remnants are common in *T. wiegmanni* faeces from both sexes  
130 (Martín *et al.*, 2013 a), we can expect that all adult amphisbaenians of this species are  
131 equipped with the required cranial characteristics to handle (at least some of) the  
132 available gastropods in their surroundings.

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

144

145 The present study was designed to provide more insight into the relationships between  
146 head morphology, bite force and diet in molluscivorous fossorial limbless animals,  
147 with the amphisbaenian *T. wiegmanni* as study species. The first goal of the study was  
148 to investigate whether head shape and size predict bite force in amphisbaenians, and

149 to establish potential intersexual difference in bite capacity. As for lizards of the sister  
150 clade Lacertidae (Gauthier *et al.*, 2012; Pyron, Burbrink & Wiens, 2013), we  
151 predicted that amphisbaenian head size is strongly correlated with maximal bite  
152 capacity. Additionally, we expected males to have higher relative bite forces than  
153 females, based on the results of a previous study showing sexual dimorphism in *T.*  
154 *wiegmanni* relative head size (Martín *et al.*, 2012). The second aim was to examine  
155 the relationship among head dimensions, bite force capacities, and potential gastropod  
156 diet of *T. wiegmanni*. We expected that the force needed to crush gastropod shells  
157 falls within the range of bite forces observed in *T. wiegmanni*. Also, we predicted that  
158 greater head size, and consequently bite force, increases the number and variation of  
159 gastropod prey items that can be consumed by ‘shell-crushing’, but reduces the  
160 number of prey items that can be consumed by ‘shell-entering’, and *vice versa*. The  
161 final goal of this study was to compare head size and bite force of *T. wiegmanni* with  
162 those of other lizard species in a phylogenetic context, to determine the impact of  
163 fossoriality and molluscivory on the direction of evolution in head size and bite force.

164

## 165 **Material and methods**

### 166 *Worm lizards*

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

172 A sample of 25 adult *T. wiegmanni* individuals (10 females; 15 males) was  
173 used to document external head morphology and to quantify bite performance. All

174 animals were hand-caught under rocks on the Chafarinas Islands (Spain) in March  
175 2012. This small archipelago is located in the Mediterranean Sea (35°11'N, 2°25'W),  
176 4.6 km off the northern Moroccan coast (Ras el Ma) and 43 km to the east of Melilla,  
177 Spain. The islands have a dry, warm, Mediterranean climate, and vegetation is  
178 dominated by plants adapted to salinity and drought, such as bushes of the genera  
179 *Salsola*, *Lycium*, *Atriplex* and *Suaeda* (Civantos *et al.*, 2003; Martín *et al.*, 2013 b)

180         The amphisbaenians were carefully transported to “El Ventorrillo” Field  
181 Station (Navacerrada, Madrid, Spain) and housed indoors. Animals were kept in pairs  
182 (male/female) in plastic terraria (40 x 30 x 30 cm) containing a layer of loose  
183 coconut-fibre substrate approximately 5 cm thick. We placed a flat tile (20 x 20 cm)  
184 on the fibre substrate that served as a shelter. Below the terraria, we placed a heating  
185 cable, connected to a thermostat, which resulted in a soil temperature gradient ranging  
186 23 °C – 27 °C. The preferred body temperature of *T. wiegmanni* is around 25 °C  
187 (Gatten & McClung, 1981; López, Civantos & Martín, 2002). The photoperiod was  
188 natural (approximately 13h light / 11h dark), and the terraria received direct sunlight  
189 through two large windows. The animals were fed twice a week (*Tenebrio* sp. larvae  
190 and *Acheta domesticus*, dusted with multivitamin powder), and the substrate was  
191 sprayed with water three times a week.

192

### 193 ***Bite forces***

194 Bite forces were measured *in vivo* using an isometric force transducer (type 9203,  
195 range ± 500 N; Kistler, Switzerland) mounted on a custom-built holder and connected  
196 to a charge amplifier (type 5058 A, Kistler; for a more detailed description of the  
197 experimental set-up see Herrel *et al.*, 1999). *Trogonophis wiegmanni* readily and  
198 repeatedly bit onto the two metal plates positioned at the free end of the holder. To

199 standardize gape angle, we increased the distance between the bite plates for larger  
200 animals (as suggested by Anderson *et al.*, 2008). We were able to perform three trials  
201 for each individual, and the hardest bite was considered an individual's maximal bite  
202 force. Because bite force is affected by body temperature (Anderson *et al.*, 2008),  
203 prior to each test, animals were placed in individual cloth bags and kept for at least 45  
204 minutes in an incubator set at 25 °C. This procedure ensured that all measures were  
205 taken near the selected and optimal body temperature of this species.

206

### 207 ***Worm lizard morphometrics***

208 For each individual amphisbaenian, we recorded: body mass, snout-vent length  
209 (SVL), head length, head width and head height. Head length was measured from the  
210 posterior extremity of the parietal scale to the tip of the snout. Head width was the  
211 largest distance measured between the temporal scales, and head height was the  
212 maximum distance measured between the base of the mandible and the parietal  
213 surface. All head variables were measured using digital callipers (Mitutoyo, CD-  
214 15CPX, precision = 0.01 mm). SVL was measured by stretching the animals along a  
215 ribbon rule (precision = 1 mm). Body mass was assessed on a microbalance  
216 (Adventurer, Ohaus Corp., precision = 0.01 g).

217

### 218 ***Prey characteristics***

219 Snails are one of the most abundant prey items found in *T. wiegmanni* faecal samples,  
220 and assumed to be a preferred food item in their diet (Martín *et al.*, 2013 a). By  
221 randomly lifting stones — under which the amphisbaenians were also often found —  
222 we collected specimens of the four most abundant gastropod species on the island (de  
223 Lozoya, 2006): *Cochlicella acuta* (7), *Dupotetia arabica* (29), *Rumina decollata* (21),

224 and *Theba pisana* (32) (Fig. 2). For every individual animal, we measured: shell  
225 width, shell height, shell mass (incl. snail itself), and shell opening size (i.e. aperture  
226 diameter). See Supplementary Material (Fig. S1) for a visualisation of the shell  
227 morphometrics and measurements recorded.

228 To assess the force needed to crush shell items consumed by *T. wiegmanni*  
229 and to estimate the effect of bite force on the potential prey spectrum, we compared  
230 the mean and maximal bite force of *T. wiegmanni* with the force (or load) required to  
231 break the shell of the different gastropod species. Shell breaking load (N) was  
232 measured by pushing the flattened top (2 mm<sup>2</sup>) of a screw (as in e.g. Aguirre *et al.*,  
233 2003; Broeckhoven & Mouton, 2014), mounted on a force transducer (type 9302;  
234 Kistler), onto the prey until the gastropod shell showed mechanical failure (for a  
235 detailed description of the set-up see Fig. S2 and Herrel *et al.*, 2001 b). Snail shells  
236 were positioned aperture down, and the point on which external forces were applied  
237 to standardized (Fig. S2). The force required to crush the shell was considered the  
238 shell's breaking load. Although 'shell breaking load' is theoretically not identical to  
239 'shell strength' or 'shell hardness' (Denney, 2015), latter terms are used  
240 interchangeably throughout the text, referring to load.

241

### 242 ***Phylogenetic comparison***

243 To put *Trogonophis wiegmanni*'s head size and bite force into an interspecific  
244 comparative context, we searched the literature for data on body size, head width and  
245 bite force of lizards. Since species cannot be treated as independent data points, we  
246 used phylogenetic generalised least square regression (pGLS) analyses (functions  
247 'pgls' and 'phyl.resid' and packages 'caper' and 'phytools', Freckleton, Harvey &  
248 Pagel, 2002; Revell, 2009). The phylogenetic tree presented by Pyron *et al.* (2013),

249 was assumed to represent the evolutionary relationships among the species in our  
250 phylogenetic analysis. We obtained our point estimate of the phylogeny by pruning  
251 Pyron's tree to comprise only the species (including *T. wiegmanni*) of this study (n =  
252 83 species).

253

#### 254 ***Data analyses***

255 Prior to analysis, all data were  $\log_{10}$ -transformed to meet the assumptions of  
256 normality. We used reduced major axis regressions (RMA) to explore allometric  
257 relationships among head and body dimensions (which are expected to scale  
258 isometrically), and bite force (expected to scale proportional to length to the second  
259 power; Herrel & O'Reilly, 2006). The relative contribution of morphological  
260 variables (SVL, mass, head length, head width, head height) to the variation in bite  
261 performance was assessed through multiple regression analyses (backward stepwise  
262 elimination). Analyses of variance (ANOVA) were conducted to test for differences  
263 in SVL, body condition, body mass, head morphometrics and bite force.

264 A proxy for body condition was calculated using the residual values obtained  
265 by the regression of  $\log_{10}$  body mass over  $\log_{10}$  SVL. The three head variables (head  
266 length, head width and head height) were strongly intercorrelated (all  $r > 0.60$ , all  $P <$   
267  $0.001$ ). Principal component analysis on  $\log_{10}$ -transformed head measures yielded one  
268 composite variable (individual scores for PC1 are hereafter referred to as 'head size'),  
269 which accounted for 76% of the total variation and showed high positive loadings for  
270 all original variables (all loadings  $> 0.85$ ).

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

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

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

282

## 283 **Results**

### 284 *Worm lizard morphometrics and sexual dimorphism*

285 A summary of the morphological measurements of the *T. wiegmanni* amphisbaenians  
286 used in this study is given in Table 1. The sexes did not differ in SVL, and no  
287 evidence for sexual dimorphism in head dimensions, overall head size, body mass,  
288 body condition and relative bite force was found (Table 1). Consequently, data on all  
289 individuals were pooled and no distinction between sexes was made in further  
290 analyses. Martín *et al.* (2012) reported for the same species similar body sizes for  
291 both sexes, but conversely, established males having larger heads than females of the  
292 same size. Although the researchers described only minor intersexual differences,  
293 their results were based on a sample size ten times the size of this study (Martín *et al.*  
294 2012: 139 females and 131 males vs. this study: 10 females and 15 males), most  
295 likely explaining the discrepant results amongst both studies (Cox, Skelly & John-  
296 Alder, 2003).

297

298 ***Determinants of bite force***

299 Individual maximal bite force in *T. wiegmanni* varied between 3.30 and 8.00 N (mean  
300  $\pm$  SE = 5.15  $\pm$  0.23 N). Overall, a strong and positive relationship was found between  
301 all head and body measures (Table 2; Figure 3a). In line, bite force related positively  
302 to all head variables (Figure 3b). The multiple regression analysis resulted in a  
303 significant model ( $r^2 = 0.52$ ,  $F_{1,23} = 24.88$ ,  $P < 0.001$ ) selecting head width as the  
304 main variable explaining variation in bite force: animals with relatively wider heads  
305 managed to bite harder (ordinary least square regression coefficient  $B \pm$  SE = 1.53  $\pm$   
306 0.31). Our data indicated bite force to increase with the second power relative to head  
307 width (intercept= -0.70, slope = 2.13 with CI 1.58 — 2.86), while bite force scaled  
308 with strong positive allometry to body size (intercept=-6.80, slope = 3.42 with CI 2.83  
309 — 4.92). Body size is often considered a more irrelevant independent variable when  
310 examining scaling of performance traits (Gardner *et al.*, 2001; Herrel & O'Reilly,  
311 2002).

312

313 ***Prey characteristics***

314 The four gastropod species differed significantly in the hardness of their shell  
315 (ANOVA,  $F_{3,85} = 172.70$ ,  $P < 0.001$ ), and size of their shell opening (ANOVA,  $F_{3,85} =$   
316 199.20,  $P < 0.001$ ). Overall, the larger species (*Dupotetia* and *Rumina*) were equipped  
317 with the hardest shells and widest shell opening, while the small gastropods  
318 (*Cochlicella* and *Theba*) had weaker shells and narrower shell openings (Table 3; Fig.  
319 4). More specifically, shells of *Dupotetia* were stronger than shells of *Rumina*  
320 (Tukey's HSD test: difference = 35.32 N,  $P < 0.001$ ). Shell hardness did not differ  
321 significantly between *Cochlicella* and *Theba* (Tukey's HSD test: difference = 2.18 N,  
322  $P = 0.556$ ).

323 The average size of the shell opening of *Rumina* was significantly larger than  
324 that of *Dupotetia* (Tukey's HSD test: difference = 1.53 mm,  $P < 0.001$ ). Also, the  
325 shell opening of *Theba* was slightly, but significantly, larger than the average opening  
326 of *Cochlicella* (Tukey's HSD test: difference = 0.82 mm,  $P < 0.001$ ).

327

### 328 ***Potential dietary spectrum***

329 The proportion of individual snails that (in theory) can be eaten by *T.*  
330 *wiegmanni* varies among gastropod species and depends on the feeding strategy.  
331 From figure 4 and 5; all *Rumina* snails measured could be entered by all *T. wiegmanni*  
332 (as their aperture was larger than the widest amphisbaenian head) but none of them  
333 could be crushed (as their hardness was above the amphisbaenians' maximal bite  
334 force). Similarly, most *Dupotetia* could be entered, but none of them could be  
335 crushed. In contrast, all *Cochlicella* were too small to enter, but most could be  
336 crushed by all *T. wiegmanni*. Finally, only small amphisbaenians could enter *Theba*  
337 shells, and the smaller — but not the larger — snails could be crushed by *T.*  
338 *wiegmanni*.

339

### 340 ***Phylogenetic comparison***

341 Our search of the literature returned data on SVL, head width and bite force of 82  
342 species of lizards (Appendix 1). Overall head width co-evolved tightly with SVL ( $\lambda =$   
343 0.96,  $F_{1,81} = 277.4$ ,  $P < 0.001$ ; pGLS regression with slope = 1.06, intercept = -0.91),  
344 but the two burrowing species in the data set (the skink *Acontias percivali* and  
345 amphisbaenian *Trogonophis wiegmanni*) clearly stood out with much narrower heads  
346 than expected for their body size (Fig. 6a). In the same interspecific dataset, bite force  
347 was strongly correlated with head width ( $\lambda = 0.97$ ,  $F_{1,81} = 421.7$ ,  $P < 0.001$ ; pGLS

348 regression with slope = 2.23, intercept = -1.42), but there *T. wiegmanni* stood out for  
349 having a high bite relative to its head width (Fig. 6b). The absolute bite force of *T.*  
350 *wiegmanni*, however, appeared much lower in comparison to (partly) molluscivorous  
351 lizard species, such as *Dracaena guianensis* (383.3 N), *Tupinambis merianae* (334.8  
352 N), *Tiliqua rugosa* (161.6 N) and *Varanus exanthematicus* (86.6 N).

353

## 354 **Discussion**

### 355 *The burrow/crush dilemma*

356 As in many other species of lizards (Herrel, Aerts & De Vree, 1998; Herrel *et*  
357 *al.*, 1999, 2001 a, b), bite force in *T. wiegmanni* was highly dependent on head size.  
358 Our findings indicate head width as the best predictor of bite capacity in this species:  
359 animals with a (relative) wider head bite harder. Given that ectothermic vertebrates  
360 typically grow nearly geometrically (O'Reilly, Lindstedt & Nishikawa, 1993; Richard  
361 & Wainwright, 1995; Robinson & Motta, 2002), we predicted that bite force in *T.*  
362 *wiegmanni* should increase with head width to the second power (Hill, 1950), which  
363 our results confirm. This strong relationship between head size and bite force presents  
364 *T. wiegmanni* with a probable trade-off. Selection for burrowing capacity would result  
365 in small heads and, consequently, low bite forces (Vanhooydonck *et al.*, 2011).  
366 Indeed, head size of burrowing species appears very small in comparison to the  
367 species' body size (Fig. 6a). Still, the small head of *T. wiegmanni* is capable of  
368 producing remarkable high bite forces (Fig. 6b). On the basis of our interspecific  
369 analyses, lizards with heads the size of *T. wiegmanni* should bite merely 1.41 N. In  
370 reality, an average *T. wiegmanni* bites 3.7 times as hard. Yet, it is unclear how *T.*  
371 *wiegmanni* succeeds in combining a small head with a relative high bite force.  
372 Caecilians, for example, have evolved a unique dual jaw-closing mechanism that

373 allows them to bite hard while maintaining a narrow head for burrowing (Nussbaum,  
374 1983; Kleinteich, Haas & Summers, 2008). It would be most interesting to investigate  
375 whether *Trogonophis wiegmanni* differs in aspect of its muscle masses, muscle  
376 architecture (e.g. proportion of pennate muscles, muscle fibre orientation) or muscle  
377 physiology (as in e.g. Gans, de Vree & Carrier, 1985, Herrel *et al.*, 1998, 1999;  
378 Huyghe *et al.*, 2010).

379         An important ecological driver of bite force evolution in *T. wiegmanni* may be  
380 its reliance on gastropod prey. Molluscivory has evolved several times in squamates  
381 species, such as in *Dracanaena guianensis*, *Tupinambis meranae*, *Tiliqua rugosa*,  
382 *Varanus exanthematicus*, which have all been reported to consume shelled snails  
383 regularly (Dalrymple, 1979; Rieppel & Labhardt, 1979; Pregill, 1984; Herrel *et al.*,  
384 2002). However, in these cases, the high bite forces required for durophagy are  
385 simply the isometric outcome of larger body sizes and heads (Fig. 6). In sharp  
386 contrast, *T. wiegmanni* combines a relatively small body and a (disproportionally)  
387 small head with relatively high bite capacities. Specialized dentitional and cranial  
388 adaptations may allow this remarkable ‘head size / bite force’ relationship, and may  
389 also explain *T. wiegmanni*’s success as a durophagous species. First of all,  
390 trogonophids differ from other amphisbaenians by their acrodont dentition, which  
391 constitutes a possible mechanism to avoid tooth breakage and to increase contact with  
392 shelled prey items (Gans, 1960; 1968; 1978). Regarding cranial morphology, two  
393 main traits are present. First, the presence of a marked parietal crest might allow for  
394 the attachment of jaw adductor muscles, as it is found in the snail-eating lizard  
395 *Chameoleolis chamaeleonides* to increase bite performance (Herrel & Holanova,  
396 2008). Second, the posterior maxillary processes are outwardly projected (Gans,  
397 1960), making the skull wider than at the occipital lobes, offering ample space for an

398 enlarged jaw musculature, as it is inferred from the highly elongated skull (Martín *et*  
399 *al.*, 2013 a).

400

401 ***Implications of feeding strategy on the potential dietary spectrum***

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

411 Besides the burrow/crush dilemma, the conflicting body size requirements for  
412 the two alternative feeding strategies pose a second dilemma: either to stay small  
413 enough to be able to penetrate the shell opening, or to grow large enough to be able to  
414 crush snail shells. Our comparison of bite forces and shell hardness on the one hand,  
415 and head size and aperture size on the other hand, suggest that the 25% strongest  
416 biters are able to crush all tested *Cochlicella* shells and 88% of the *Theba* shells.  
417 However, due to the width of their heads, these individuals are unable to enter any  
418 *Theba* shell opening and only 55% of the *Dupotetia* shells. In comparison, the 25%  
419 weakest biters may merely crush 71% of the tested *Cochlicella* shells and 47% of the  
420 *Theba* shells, but are able to enter up to 16% of the *Theba* shells and 100% of the  
421 *Dupotetia* shells. These findings confirm our prediction that head size, and  
422 consequently bite force, increases the number and variation of gastropod prey items

423 that can be consumed by ‘shell-crushing’, but reduces the number and variation of  
424 prey items that can be consumed by ‘shell-entering’, and *vice versa* (e.g. Fig. 7). Of  
425 course, the abundance of the different snail species in the field, and *T. wiegmanni*’s  
426 gastropod preferences, might influence the direction of head morphology evolution in  
427 *T. wiegmanni*.

428 Evidently, more extensive research is required to determine the actual  
429 existence of a body size-dependent feeding strategy in *T. wiegmanni*. Behavioural  
430 observations and feeding experiments may shed light on the relative (natural)  
431 incidence of both feeding behaviours and the effect of prey-gastropod species and size  
432 on feeding preference and strategy, and on prey handling time. Information on  
433 maximal gape angles, which are known to affect bite performance (Dumont & Herrel,  
434 2003; Anderson *et al.*, 2008; Williams, Pfeiffer & Ford, 2009), may also aid in  
435 estimating the dietary spectrum of *T. wiegmanni*. Nevertheless, flexibility in feeding  
436 behaviour may also compensate for morphological constraint of fossoriality (López,  
437 Martín & Salvador, 2013).

438

#### 439 ***Conclusion***

440 Head size is conventionally believed to be constrained in limbless fossorial animals,  
441 due to the limitations imposed while burrowing, therefore selecting for small heads  
442 and, consequently, low bite forces. However, in the burrowing amphisbaenian  
443 *Trogonophis wiegmanni*, we establish small head sizes with remarkably high relative  
444 bite capacities in comparison to other lizard species. Such biting may be important for  
445 their molluscivorous diet, since they manage to crush a wide variety of the most  
446 abundant gastropod shells in their environment. However, the wide head necessary to  
447 bite hard imposes a limitation towards an alternative snail-feeding strategy: entering

448 the snail's shell via the shell opening and eating the flesh from inside. Our results  
449 shows that head size, and consequently bite force, increases the number and variety of  
450 gastropods that can be consumed by 'shell-crushing', but reduces the number and  
451 variety of prey items that can be consumed by 'shell-entering', and *vice versa*. This  
452 study implies that the cranial design of (molluscivorous) limbless burrowers may  
453 therefore not only evolve under constraints for efficient soil penetration, but also  
454 through selection for diet.

455

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469

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