

## Sexual dimorphism and allometry in malacophagus snakes (Dipsadidae: Dipsadinae)

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### ABSTRACT

Sexual dimorphism in snakes is generally described in association with body or tail size and scale counts, with relatively few studies addressing intrasexual divergence in the skull. Here, we analyzed sexual dimorphism in the size and shape of skull and body in three malacophagous dipsadine snakes, *Dipsas mikanii*, *Dipsas newwiedi* and *Dipsas turgida*, as well as allometric effect on these components. We used linear and geometric analysis to assess: (1) if there is sexual dimorphism in cranial components; (2) if there are differences between the sexes regarding body and tail size, number of ventral and subcaudal scales; (3) whether there is covariation between cranial components and body size; (4) if there are changes in cranial shape associated with increased size; and (5) whether there is an allometric relationship between body and tail size. Our results showed that all three species are dimorphic in cranial shape and size (except *D. turgida* for cranial size), with females having longer and thinner skulls than males. In the three species, the female skull was negatively allometric, whereas the male skull was isometric. Allometry related to cranial shape was significant only in males of *D. turgida*, which showed greater snout robustness and eye size associated with enlargement of the skull. Females of *D. mikanii* and *D. newwiedi* were significantly larger than males. Only males of *D. newwiedi* showed positive allometry for the tail, while dimorphism related to scale counts followed the pattern found in most snakes, with females having a greater number of ventrals and males subcaudals (except *D. newwiedi* in the latter case). Based on our results, we hypothesize that patterns of sexual dimorphism and skull allometry in malacophagous snakes may be explained both by aspects related to diet and reproduction. Meanwhile, patterns associated with body size reflect advantages related to fecundity favoring greater reproductive success of females.

### 1. Introduction

Sexual dimorphism in snakes may be related to body mass and size, tail length, coloration, number of scales, the position of organs or glands, as well as the size and shape of the head and skull (Andjelković et al., 2016; Keogh and Wallach, 1999; Kissner et al., 1998; Shine, 1994). The evolution of sexual dimorphism, especially regarding body size in snakes, has been explained mainly by three hypotheses: fertility-related advantage, sexual selection, and intraspecific niche divergence (Darwin, 1871; Camilleri and Shine, 1990; Shine, 1989).

The hypothesis of sexual dimorphism in body size for fertility-related advantages suggests that females will be larger to ensure more space to accommodate a more significant number of embryos (Darwin, 1871). The dimorphism hypothesis resulting from sexual selection predicts that

males with large body sizes may have evolved through intraspecific interactions in ritual combat, increasing their reproductive success (Shine, 1978; King et al., 1999). The niche divergence hypothesis predicts that ecological factors may influence the evolution of body size in each sex through competition for resources or simply due to differences related to reproductive biology (Shine, 1989). Unlike sexual dimorphism in body size, divergences in head size may be related to visual stimuli in intraspecific interactions, predator defense, or sexual selection (Shine, 1989; Camilleri and Shine, 1990). Intraspecific divergences can be attributed to sexual selection when the head is used in sexual interactions, such as display, partner choice, or ritual combat (Darwin, 1859, 1871).

Nevertheless, the most prevalent hypothesis explaining sexual dimorphism in the head among snakes refers to dietary divergence.

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Variation in shape and size of the head may evolve to allow intrasexual niche partitioning. As a result, the two sexes feed prey of different sizes and types (Shine, 1986; Camilleri and Shine, 1990). Furthermore, the dietary divergence hypothesis predicts that differences in sexually dimorphic species will be more evident in components directly associated with feeding. For example, the trophic apparatus will be disproportionately more prominent in the sex with the larger heads. Several snake's species that prey on vertebrates display sexual dimorphism in head size and shape (Vincent et al., 2004; Meik et al., 2012; Sousa et al., 2014).

Presence of sexual dimorphism in the head size of snakes that specialists in consuming invertebrates or small prey were hypothesized to be less likely due to homogeneity in the diet, cryptic habits, and dependence on small prey (Marques et al., 2006; Braz et al., 2019; Abegg et al., 2020). However, recent studies have described sexual dimorphism in the size and shape of the head of some snakes that feed on small prey, related to the mating system, jaw strength, or other components of feeding behavior (Loebens et al., 2019; Shine and Goiran, 2021).

Dipsadini tribe (subfamily Dipsadinae) is a South American group of snakes specialized in mollusks consumption that exhibits several morphocranial and histochemical adaptations for mollusk ingestion (Peters, 1960; Vidal et al., 2007; Pyron et al., 2010; Grazziotin et al., 2012; Arteaga et al., 2018). However, despite being extensively studied, analyses of skull-related sexual dimorphism are still missing (Peters, 1960; Sazima, 1989; Zaher et al., 2014; Santos et al., 2016).

Here, we compared and described the intraspecific variation between sexes in three Dipsadini species: *Dipsas mikanii*, *D. neuwiedi*, and *D. turgida*. We analyzed cranial size and shape, body size, and ventral e subcaudal scales' number. *Dipsas mikanii* preys exclusively on slugs of the Veronicelidae family. While its sister species *D. turgida*, and the more distantly related *D. neuwiedi*, feed mainly on slugs and less frequently on snails (Peters, 1960; Pizzatto et al., 2018; Zaher et al., 2019; Pilate et al., 2020). *Dipsas mikanii* and *D. turgida* shown terrestrial habits and share several morphological similarities. On the other hand, *D. neuwiedi* has semi-arboreal, and present females with longer body lengths than males, while males have longer tails, pattern also described for *D. mikanii*. For *D. turgida* no available information about sexual dimorphism.

Our objective was to test whether these three goo-eater species will present or have no sexual dimorphism in cranial shape and size since they show some degree of feeding variation. In addition, we hypothesized that, as reported for another closely related dipsadine (*Atractus reticulatus*), feeding homogeneity and dependence on small prey will result in the absence of sexual dimorphism in the cranial components in the analyzed species.

On the other hand, we hypothesized that the females of all three species would show longer bodies and a more significant number of ventral scales while males would have greater caudal length and a larger number of subcaudals (Darwin, 1871; Cadle, 2007). Moreover, we would like to describe and compare female and male cranial and body size allometric trajectories.

## 2. Materials and methods

### 2.1. Material analyzed

We analyzed a total of 167 adult specimens, 68 of *Dipsas mikanii* (30 males and 38 females), 37 of *D. neuwiedi* (15 males and 22 females), and 62 of *D. turgida* (37 males and 25 females). From this total, we prepared 67 skulls, 27 of *D. mikanii* (14 males and 13 females), 15 of *D. neuwiedi* (6 males and 9 females) and 25 of *D. turgida* (13 males and 12 females) (Appendix). The analyzed specimens are from: Museu Paraense Emílio Goeldi (MPEG), Museu de Ciência e Tecnologia da PUCRS (MCT), Museu de História Natural Capão da Imbuia (MHNCI), Museu de Zoologia da Universidade Estadual de Londrina (MZUEL), Universidade de Brasília (CHUNB), Universidade Federal da Bahia (UFBA), Universidade Federal de Mato Grosso (UFMT), and Coleção de Referência de Vertebrados,

Campus de Corumbá, Universidade Federal de Mato Grosso do Sul (CEUCH). We aim to characterize sexual dimorphism for the species in general, not analyzing population differences or differences related to the collected seasonal period. These parameters can be meaningful and affect prey availability and composition. However, dividing our sample into smaller groups would make our statistical analysis unfeasible.

### 2.2. Data acquisition

We determined sex through an incision at the base of the tail to verify the presence or absence of hemipenis. Females of *D. mikanii* and *D. neuwiedi* were classified as adults when the snout-vent length was greater than 339 mm and 415 mm, respectively, and for males when snout-vent length was greater than 280 mm and 254 mm respectively (Pizzatto et al., 2008). For *D. turgida* were considered adults specimens with snout-vent length greater than 254 mm and 236 mm, respectively, for females and males (Santos et al., 2016).

We prepared the skulls by immersing them in hot water, and surgical tweezers were used for total tissue removal. We then obtained images in a dorsal view using a Leica M80 stereomicroscope with an attached camera. We digitized 21 anatomical landmarks in each image using the tpsDig2 program, following the criteria proposed by Zelditch et al. (2004) (Rohlf, 2015) (Fig. 1).

We used eight morphometric and two meristic characters. Among the morphometric data, six were measurements of cranial morphology namely: skull length, maxilla length, palatine length, pterygoid length, dentary length, mandible length, while two referred to external body morphology: snout-vent length (SVL) and tail length (TL). We obtained cranial measurements by analyzing the photographs in the tpsDig2 software, and corporal measurements were obtained with the digital caliper and ruler (1 mm precision). Regarding meristic data, we counted the number of ventral (VE) and subcaudal (SC) scales of each specimen, which were grouped as body components, together with SVL and TL, to describe the results.

### 2.3. Data analysis

To describe shape variation, we analyzed the 21 landmarks, removing the effect of position, size, and orientation of each image by applying the Generalized Procrustes Analysis (GPA) (Rohlf and Slice, 1990; Klingenberg, 2011). GPA analysis extract from the raw

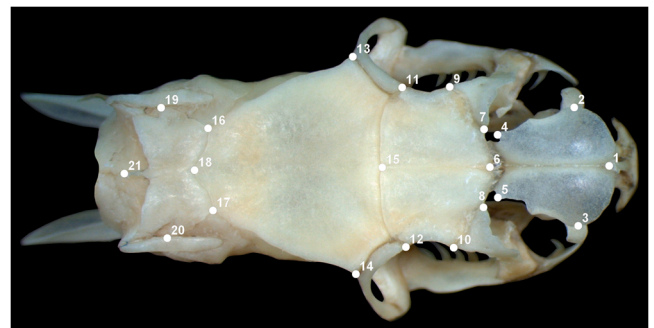


Fig. 1. Landmarks configuration used on the skull of *Dipsas mikanii*, *D. neuwiedi* and *D. turgida* to describe skull shape. 1, suture between pre-maxillae and nasals; 2 and 3, lateral-most point of the nasals; 4 and 5, most posterolateral point of the nasals; 6, suture between nasals and frontals; 7 and 8, anterior-most points of the suture between pre-frontal and frontal; 9 and 10, posterior-most points of the suture between pre-frontal and frontal; 11 and 12, suture between frontal and post-orbital; 13 and 14, suture between post-orbital and parietal; 15, median point of the suture between frontals and parietal; 16 and 17, suture between parietal, supraoccipital and prootic; 18, suture between parietal and supraoccipital; 19 and 20, suture between supraoccipital, prootic and exoccipital; 21, posterior-most point of supraoccipital. Landmarks 1–6 represent the snout, and 9–14 the eyes.

coordinate's information on shape (Procrustes coordinates), and size (centroid size), which is equivalent to the square root of the sum of squared distances between all anatomical landmarks (Zelditch et al., 2004). To test sexual dimorphism in cranial shape and size we performed a Procrustes ANOVA analysis, between shape variables and sex (Klingenberg and McIntyre, 1998). To visualize shape variation between sexes we performed a canonical variate analysis (CVA). All the analyses were applied separately for each species.

We tested the cranial shape allometry for each sex separately using multivariate regression of skull shape variables (Procrustes coordinates) over skull centroid size, with shape variation expressed as the percentage of total shape variation explained by size. We tested the statistical significance over permutations of multivariate regression analyses with 10,000 iterations. All the geometric morphometric analyses were implemented in MorphoJ (Klingenberg and McIntyre, 1998; Klingenberg et al., 2002; Klingenberg and Monteiro, 2005; Klingenberg, 2011).

For linear analysis, we used tests for normality in data distribution and homogeneity of variances. Continuous variables were log-transformed for all analyses. We tested for sexual dimorphism in each of the ten variables using the t-test and Kruskal-Wallis test, and differences were visualized using a boxplot. We tested for sex differences related to tail length by analysis of covariance (ANCOVA), with the snout-vent length as a covariate.

By evaluating allometric effects, it is possible to test whether shape variations are correlated with size variations imposed by developmental processes, or whether they correspond to evolutionary adaptations (Strauss, 1985). Allometric analysis can be performed at different conceptual levels including: ontogenetic allometry, which considers the different ontogenetic stages as a source of morphological variation in species; evolutionary allometry, which considers the covariation of characteristics along phylogenetic branches at a given ontogenetic stage; and static allometry, which compares the covariation of characteristics between individuals of a species at a particular ontogenetic stage within the same population (Cock, 1966; Klingenberg, 1998). Static allometry is relevant in cross-species analyses, as observed patterns of variation can be linked to ecological adaptations (Tamagnini et al., 2018).

We tested whether the measured traits showed allometric relationships with body size by estimating the allometric slope ( $b$ ) from the slope of a linear regression between each log-transformed morphometric variable and the log-transformed snout-vent length. We analyzed the variables for each sex separately to determine whether the allometric slope ( $b$ ), based on the equation,  $Y = aX^b$ , where  $Y$  and  $X$  are indices of trait size and body size, was statistically different from isometry (when  $b=1$ ), using the slope test function on Smatr R software package (where  $p > 0.05$  indicates isometry) (Warton et al., 2012; R Core Team, 2021). The analysis of the allometric slope ( $b$ ) describes the proportional growth of a structure in relation to body size, allowing the recognition of different growth patterns. In this way, a structure can present an isometric growth pattern—that is, when the relative size of the structure grows in the same proportion as body size ( $b=1$ )—or else a positive or negative allometric pattern, depending on whether a given structure grows at a higher ( $b>1$ ) or lower ( $b<1$ ) rate in relation to body size (Bonduriansky, 2007).

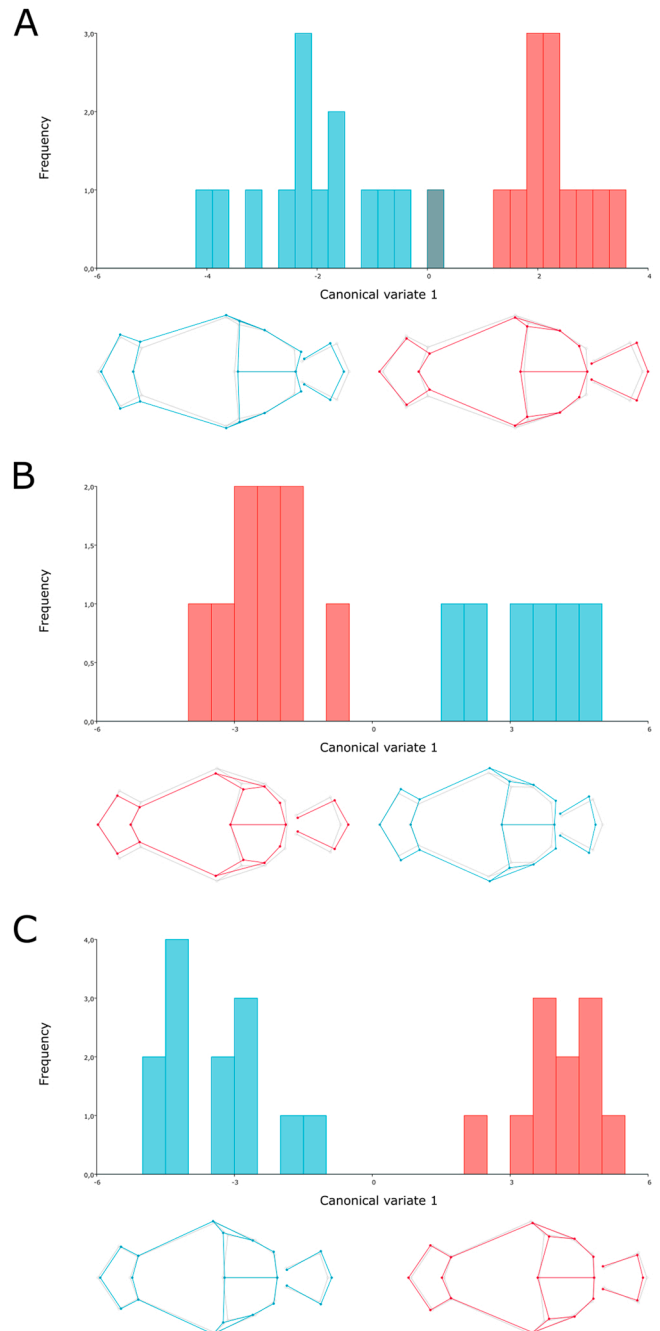
To test for differences between allometric trajectories between males and females, we compare allometric slopes and intercept (which reflects the difference in size of a structure) of each species under an analysis of covariance (ANCOVA) with snout-vent length as a covariate. All statistical analyses were performed in the Car package v. 3.0–11 of R software (Fox and Weisberg, 2019; R Core Team, 2021).

### 3. Results

#### 3.1. Sexual dimorphism and allometry in cranial components

The geometric morphometric analysis reveals significant sexual

dimorphism in cranial shape in all three species. *Dipsas mikanii* showed significant differences between males and females ( $F=2.68$ ,  $p < 0.001$ ); the CVA analysis showed significant Mahalanobis ( $p < 0.001$ ) and Procrustes ( $p = 0.001$ ) distances. Females at the positive of CV1 have slightly elongated snout, slender parietal bones, and larger eyes than males (represented at negative of CV1, Fig. 2A). *D. neuwiedi* males and females have significant different cranial shapes ( $F=2.67$ ,  $p < 0.001$ ), CVA showed significant Mahalanobis ( $p < 0.001$ ) and Procrustes ( $p = 0.01$ ), and females showed, at negative values of CV1, longer snout and slender skull (Fig. 2B). Finally, in *D. turgida* ( $F=2.79$ ,  $p < 0.001$ ) CVA showed significant Mahalanobis ( $p < 0.001$ ) and Procrustes ( $p = 0.009$ ). The differences on skull shape between males and females



**Fig. 2.** Canonical variate analysis of skull shape of males and females of *Dipsas mikanii* (A), *D. neuwiedi* (B) e *D. turgida* (C). The transformation grids demonstrate shape deformations of males (blue) and females (red) relative to the mean (gray) at the positive and negative extremes of the first canonical variate axis.

were subtler, with the females showing a shorter snout, and slightly slender skull (Fig. 2C).

For size (measure by centroid size), there were significant differences between sexes with females having a larger skull, except for *D. turgida* (*D. mikanii* -  $F=11.39$ ,  $p = 0.002$ ; *D. neuwiedi* -  $F=12.01$ ,  $p = 0.004$ ; *D. turgida* -  $F=0.41$ ,  $p = 0.52$ ).

Multivariate regressions over shape and centroid size variables were not significant for *D. mikanii* (male: 12.62%,  $p = 0.05$ ; female: 10.19%,  $p = 0.22$ ) and *D. neuwiedi* (male: 13.29%,  $p = 0.75$ ; female: 15.12%,  $p = 0.27$ ), indicating that variation in the shape of the skull is not related to its size. For *D. turgida* only males showed allometry, suggesting that with increasing skull size changes occur related to greater snout robustness and larger eye size, with just over 15% of the variation in shape explained by skull size (male: 15.77%,  $p = 0.03$ ; female: 13.84%,  $p = 0.13$ ).

Regarding linear analysis, the t-test indicated significant sexual dimorphism in size for all cranial components in *Dipsas mikanii* and *D. neuwiedi*, except for the length of the pterygoid in the latter (Fig. 3; Table 1). *D. turgida* did not show sexual dimorphism associated with size for the analyzed cranial components according to this analysis.

Linear regression of cranial variables over SVL indicated that males of the three species were isometric in all analyzed variables ( $p > 0.05$ ) (Table 2). On the other hand, females showed negative allometry for many cranial variables ( $p < 0.05$ ). This tendency was most pronounced in *Dipsas turgida* females, presenting negative allometry in relation to all cranial components. Females of *D. mikanii* presented negative allometry for cranial and mandibular length, while females of *D. neuwiedi* only in relation to the mandible.

ANCOVA indicated that there were no statistical differences regarding the allometric slope between males and females in all three analyzed species, but for *Dipsas mikanii* and *D. neuwiedi* there were differences in the intercept for some variables (Figs. 4, 5 and 6; Table 3). The absence of differences in relation to allometric slopes indicates parallel allometric patterns, although the slopes for all variables in males were greater than those in females in the three species, except for dentary length in *D. mikanii*. Males and females of *D. mikanii* and *D. neuwiedi* differed statistically in the intercept in relation to the length of the pterygoid and mandible, with females presenting higher values for these variables.

### 3.2. Sexual dimorphism and allometry in body components

Females of *Dipsas mikanii* and *D. neuwiedi* showed greater SVL compared to males (Fig. 7; Table 4). The tail length was significantly longer in females of *D. neuwiedi* and in males of *D. turgida* (Fig. 7). All species were dimorphic in relation to the number of ventral scales, with females showing higher counts (Fig. 7). As for the number of subcaudal scales, there was sexual dimorphism in *D. mikanii* and *D. turgida*, with males presenting a greater number of scales (Fig. 7).

ANCOVA indicated that the tail was significantly longer in males of *D. mikanii* ( $F=55.62$ ;  $p < 0.001$ ) and *D. turgida* ( $F=109.00$ ;  $p < 0.001$ ) (Fig. 8).

Linear regression indicated that only males of *D. neuwiedi* presented allometry for the tail, which was positive ( $b=1.18$ ;  $r^2=0.50$ ;  $p = 0.01$ ). Regarding the slopes of regression lines, males and females of the three species did not differ statistically, suggesting parallel allometric trajectories for the tail.

## 4. Discussion

All three analyzed species presented sexual dimorphism for cranial shape. *Dipsas mikanii* and *D. neuwiedi* showed a similar pattern, with females having a slender skull and slightly elongated snout while females of *D. turgida* have a shorter snout and slightly slimmer skull. Yet, when analyzing cranial size, only *D. mikanii* and *D. neuwiedi* displays significant differences between males and females. Our prediction of the

absence of sexual divergences in cranial shape and size due to the homogeneity diet and small prey size, was not corroborated by shape results and only partially corroborated (for *D. turgida*) for cranial size.

In numerous species of snakes' sexual dimorphism in the head has been explained by differences in diet between females and males (Shine et al., 2002; Vincent et al., 2004; Meik et al., 2012; Silva et al., 2017; Murta-Fonseca et al., 2019). *Atractus reticulatus*, a dipsadine snake specialist in eating earthworms, shows sexual dimorphism in the head shape, and it was suggested that this pattern was related to the ingestion of different sizes of earthworms by females and males (Abegg et al., 2020). For the malacophagous snake *Tomodon dorsatus*, a slug specialist, sexual dimorphism in the head shape was associated with sexual variation in jaw strength, since females have wider heads, allowing more mandibular muscles to be accommodated and greater bite force. However, this hypothesis seems inconsistent for malacophagous species, considering that the preys are largely soft-bodied invertebrates with slow movements, and since greater bite force improves the immobilization capacity in prey actively fighting (Luiselli et al., 2002; Bizerra et al., 2005; Loebens et al., 2019).

The sexual dimorphism of skull size, especially in components directly related to feeding behavior, namely maxilla (swallowing) and dentary (prey capture) in females of *D. mikanii* and *D. neuwiedi*, respectively, are in apparent agreement with the hypothesis of sexual dimorphism by intrasexual niche partitioning (Kardong, 1979, 1980; Shine, 1986; Camilleri and Shine, 1990; Smith, 1993). This hypothesis considers that males and females ingest prey of different sizes or types (Shine, 1991; Houston and Shine, 1993). Regarding the type of prey, studies indicated that *D. mikanii* ingests slugs from the genus *Latipes* and *Sarasinula*, while for *D. neuwiedi* have already been reported slugs of genus *Potamojanuarius*, *Sarasinula*, *Belocaulus* e *Phyllocaulis*, and snails of the genus *Biomphalaria* and *Bradybaena* (Laporta-Ferreira et al., 1986; Laporta-Ferreira and Salomão, 1991; Palmuti et al., 2009; Maia-Carneiro et al., 2012; Pilate et al., 2020). However, there is a lack of information about an intraspecific variation, between females and males, on diet composition for the three analyzed species.

Concerning prey size, small individuals of *D. mikanii* and *D. neuwiedi* ingest relatively large slugs, while larger ones do not exclude small items from their diet (Pizzatto et al., 2018). The ingestion of small prey is an uncommon pattern among snakes, and in the case of malacophagous species, it can be explained by the lower costs of capture and ingestion during feeding, in addition to the fact that large prey can be scarce in the environment (Thomé, 1972; Thomé et al., 2001; Agudo-Padrón, 2009; Pizzatto et al., 2018). In addition, the low energy value of a mollusk-based diet may contribute so that no prey is refused, which is supported by the higher feeding frequency observed in *Dipsas* species (Pizzatto et al., 2018). As described for *Tomodon dorsatus*, the dimorphic differences in head size may be related to predation of slugs of different sizes by *D. mikanii* and *D. neuwiedi* males and females (Bizerra et al., 2005; Loebens et al., 2019).

On the other hand, sexual divergences could be related to reproductive activities that, through natural selection, may impose selective pressures favoring the evolution of an expanded or modified trophic apparatus in one of the sexes (Shine, 1989; Camilleri and Shine, 1990). Observations on reproductive aspects indicate that females of *D. mikanii* nesting communally, such that multiple females share the same cavity for deposition of eggs (Albuquerque and Ferrarezzi, 2004; Braz et al., 2008). Although some snake species dig a hole in the soil to build their nests, this does not seem to be the case for *D. mikanii* (Burger and Zapalorti, 1986; Braz et al., 2008). The cavities where communal nesting of this species have been observed presented highly compacted soil, suggesting that females used pre-existing cavities (Braz et al., 2008). Even if females of *D. mikanii* are unable actively to excavate soil, they probably select existing cavities with optimal thermal conditions and slope, given that nests of *D. mikanii* have been observed to show similar conditions in relation to sunlight exposure and inclination, determining factors for offspring development (Blouin-Demers et al., 2004; Albuquerque and

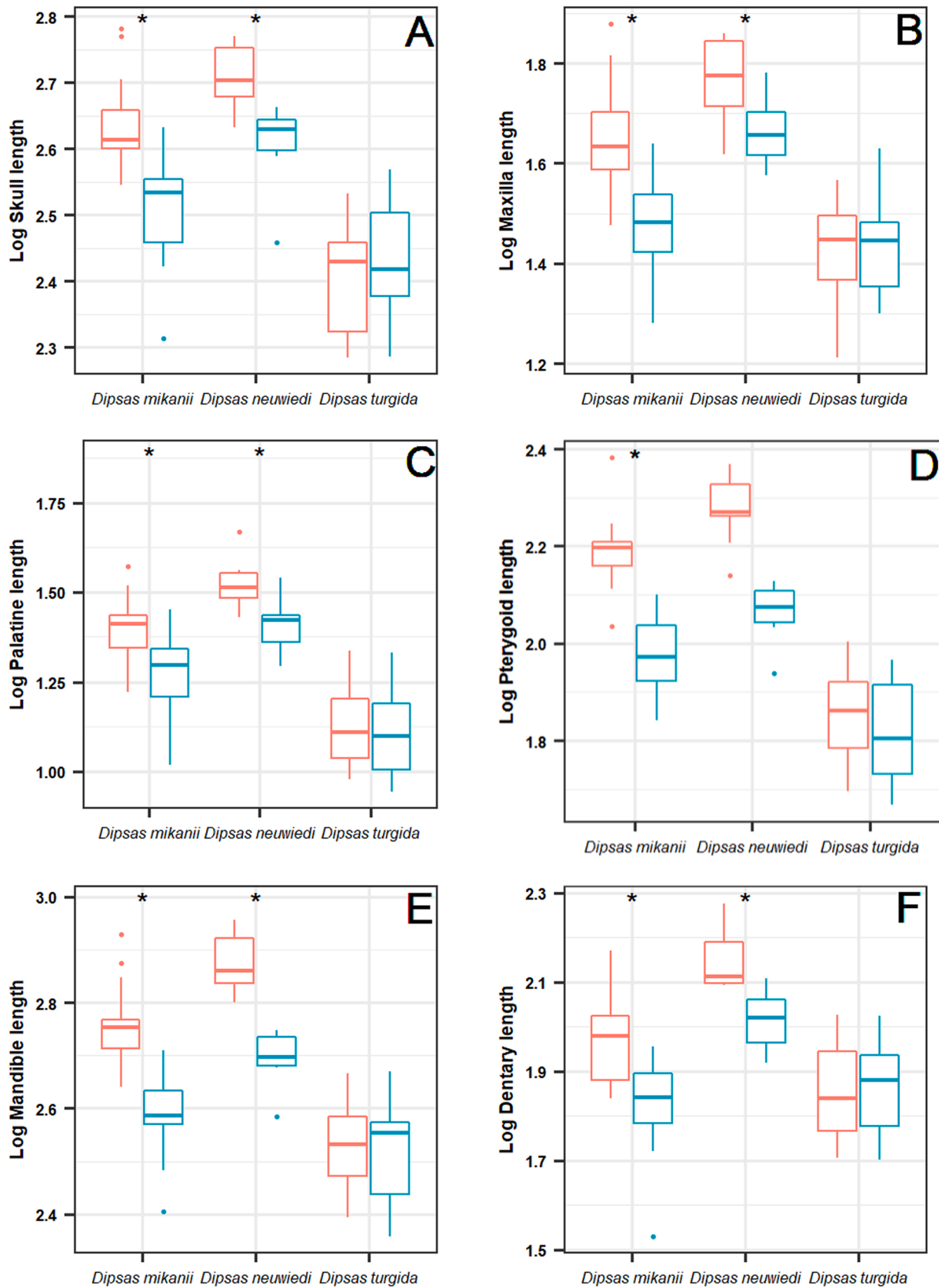


Fig. 3. Boxplot representing variation in skull length (A), maxilla length (B), palatine length (C), pterygoid length (D), mandible length (E), and dentary length (F), for males (blue) and females (red) of each species. Circles represent outliers, asterisk represents statistically significant differences. Middle line represents mean values, boxes show standard deviation, and whiskers represent minimum and maximum values.

**Table 1**

Sexual dimorphism (t-test) and morphometric variation for skull length, maxilla length, palatine length, pterygoid length, mandible length and dentary length between females and males of the species *Dipsas mikanii*, *D. neuwiedi* and *D. turgida*. t: t-test statistic; df: degrees of freedom; p: p statistical significance; mean value ( $\pm$ SD, with intervals and sample size (n) in parentheses). Values in red represent statistically significant variables according to the analysis.

	t	df	p	Mean values $\pm$ SD (intervals and sample size)	
				♀♀	♂♂
<i>Dipsas mikanii</i>					
Skull length	4.18	25.00	< 0.001	14.0 $\pm$ 1.0 (12.7–16.1, n = 13)	12.3 $\pm$ 1.0 (10.1–13.9, n = 14)
Maxilla length	4.29	23.00	< 0.001	5.2 $\pm$ 0.6 (4.3–6.5, n = 13)	4.4 $\pm$ 0.3 (3.6–5.1, n = 14)
Palatine length	2.98	23.00	0.006	4.0 $\pm$ 0.3 (3.4–4.8, n = 13)	3.5 $\pm$ 0.4 (2.7–4.2, n = 14)
Pterygoid length	6.24	23.00	0.002	8.9 $\pm$ 0.7 (7.6–10.8, n = 13)	7.2 $\pm$ 0.5 (6.3–8.1, n = 14)
Mandible length	5.30	25.00	0.01	15.7 $\pm$ 1.3 (14.0–18.7, n = 13)	13.3 $\pm$ 1.0 (11.0–15.0, n = 14)
Dentary length	3.79	25.00	< 0.001	7.2 $\pm$ 0.8 (6.2–8.7, n = 13)	6.2 $\pm$ 0.6 (4.6–7.0, n = 14)
<i>Dipsas neuwiedi</i>					
Skull length	3.37	13.00	0.004	15.0 $\pm$ 0.7 (13.9–15.9, n = 9)	13.5 $\pm$ 0.9 (11.6–14.3, n = 6)
Maxilla length	2.16	13.00	0.05	5.8 $\pm$ 0.5 (5.0–6.4, n = 9)	5.3 $\pm$ 0.4 (4.8–5.9, n = 6)
Palatine length	2.73	13.00	0.01	4.5 $\pm$ 0.3 (4.1–5.3, n = 9)	4.1 $\pm$ 0.3 (3.6–4.6, n = 6)
Pterygoid length	5.74	13.00	0.06	9.7 $\pm$ 0.6 (8.5–10.6, n = 9)	7.8 $\pm$ 0.5 (6.9–8.3, n = 6)
Mandible length	6.06	13.00	0.04	17.8 $\pm$ 1.0 (16.4–19.2, n = 9)	14.7 $\pm$ 0.8 (13.2–15.6, n = 6)
Dentary length	3.60	13.00	0.003	8.5 $\pm$ 0.5 (8.1–9.7, n = 9)	7.5 $\pm$ 0.5 (6.8–8.2, n = 6)
<i>Dipsas turgida</i>					
Skull length	-0.65	23.00	0.51	11.1 $\pm$ 0.9 (9.8–12.5, n = 12)	11.3 $\pm$ 1.0 (9.8–13.0, n = 13)
Maxilla length	-0.10	23.00	0.91	4.1 $\pm$ 0.4 (3.3–4.7, n = 12)	4.2 $\pm$ 0.4 (3.6–5.1, n = 13)
Palatine length	0.22	23.00	0.82	3.1 $\pm$ 0.3 (2.6–3.8, n = 12)	3.0 $\pm$ 0.3 (2.5–3.7, n = 13)
Pterygoid length	0.89	23.00	0.37	6.3 $\pm$ 0.5 (5.4–7.4, n = 12)	6.1 $\pm$ 0.6 (5.3–7.1, n = 13)
Mandible length	0.26	23.00	0.79	12.5 $\pm$ 1.0 (10.9–14.3, n = 12)	12.4 $\pm$ 1.2 (10.5–14.4, n = 13)
Dentary length	0.07	23.00	0.93	6.4 $\pm$ 0.7 (5.5–7.5, n = 12)	6.4 $\pm$ 0.6 (5.4–7.5, n = 13)

Ferrarezzi, 2004; Shine, 2004; Braz et al., 2008). Thus, narrower, and more elongated skulls in adult females of *D. mikanii* could have been favored by natural selection due to reproductive activities, specifically to the selection of cavities for egg deposition, resulting in greater reproductive success in females.

The cranial shape in males showed greater enlargement, with the variation being discrete between males and females of *D. mikanii* and *D. turgida*, but more evident in *D. neuwiedi*. In males, reproductive

**Table 2**

Regressions of log-transformed skull length, maxilla length, palatine length, pterygoid length, mandible length and dentary length vs. log-transformed body size (SVL) in males and females of *Dipsas mikanii*, *D. neuwiedi* and *D. turgida*. b: allometric slope; r<sup>2</sup>: coefficients of determination; p: significance deviation from a slope value of one. Values in red represent statistically significant variables according to the analysis.

	Male allometry			Female allometry		
	b	r <sup>2</sup>	p	b	r <sup>2</sup>	p
<i>Dipsas mikanii</i>						
Skull length	0.59	0.53	0.32	0.35	0.62	< 0.001
Maxilla length	0.70	0.64	0.44	0.59	0.59	0.25
Palatine length	0.77	0.46	0.56	0.42	0.44	0.09
Pterygoid length	0.56	0.50	0.27	0.29	0.27	0.06
Mandible length	0.60	0.64	0.12	0.40	0.57	0.005
Dentary length	0.45	0.18	0.88	0.44	0.42	0.11
<i>Dipsas neuwiedi</i>						
Skull length	0.99	0.64	0.50	0.35	0.61	0.006
Maxilla length	0.92	0.55	0.54	0.59	0.47	0.59
Palatine length	1.06	0.58	0.35	0.39	0.34	0.20
Pterygoid length	1.00	0.77	0.61	0.37	0.31	0.22
Mandible length	0.91	0.84	0.95	0.37	0.51	0.03
Dentary length	0.92	0.60	0.61	0.44	0.52	0.08
<i>Dipsas turgida</i>						
Skull length	0.53	0.54	0.12	0.25	0.37	0.002
Maxilla length	0.44	0.28	0.47	0.29	0.36	0.01
Palatine length	0.65	0.49	0.75	0.32	0.34	0.03
Pterygoid length	0.41	0.23	0.55	0.26	0.35	0.005
Mandible length	0.46	0.36	0.29	0.22	0.30	0.002
Dentary length	0.56	0.43	0.52	0.15	0.08	0.05

activities can also drive divergence in head shape due to vulnerability to predation (Shine, 1989). Males are more active during the mating period searching for females (Almeida-Santos and Salomão, 2002). If one of the sexes is more exposed to predators, selection can favor the expansion of trophic structures to reduce additional risks (Shine, 1989). However, changes in head shape can also occur through behavioral mechanisms. The acquisition of a triangular head shape is the most common and widespread defensive behavior among Dipsadini, representing visual intimidation to prevent predation (Tozetti et al., 2009). This behavior involves the enlargement, or “triangulation” of the head, through lateral expansion of the quadrato-mandibular joint (Greene, 1988; Cadle and Myers, 2003). Thus, in addition to behavioral mechanisms that result in an enlarged head, morphological variations associated with greater skull and snout enlargement in males could reinforce anti-predation mechanisms, minimizing possible predator attacks (Dell’Aglio et al., 2012).

Finally, this dimorphic pattern could be explained by sexual selection. According to this hypothesis, head enlargement in one sex may represent a visual stimulus in intraspecific or defensive displays when choosing partners, or it may reflect the selection of sensory organs or larger brains in one sex (Shine, 1989; Camilleri and Shine, 1990; Tamagnini et al., 2018). Among sexual selection mechanisms, partner choice during mating predicts that larger head size in females would serve as a visual stimulus for males, and that males would choose females with larger heads (Luiselli et al., 2002). However, behavioral observations about the mating system of these species would be necessary to corroborate this hypothesis.

The absence of head size dimorphism in *Dipsas turgida* may reflect homogeneity in diet or semi-fossorial habits (Abegg et al., 2020). In species of the Xenodontinae subfamily, *Apostolepis gaboi* (Elapomorphi), which consumes amphisbaenias and fossorial and semi-fossorial lizards, and *Philodryas agassizii* (Philodryadini), a specialist in spiders, the absence of dimorphism for head size was related to similarities in diet and dependence on small prey in both sexes (Marques et al., 2006; Braz et al., 2019). Among the species studied, *D. turgida* is the least known from an ecological point of view. It is a small terrestrial species, that intake of both slugs and snails has been reported (Melgarejo, 1980). However, information on sexual divergences in relation to the size or

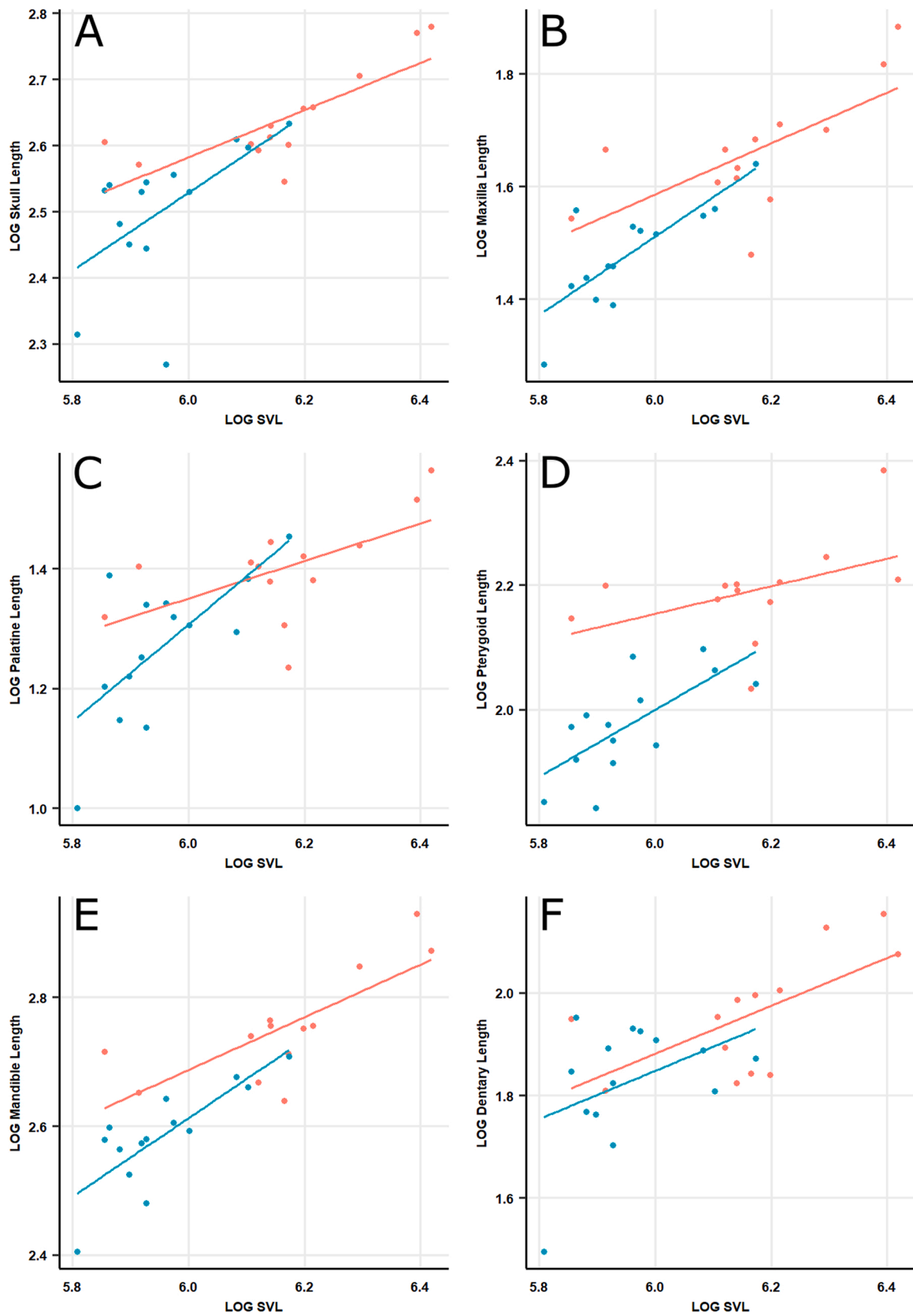


Fig. 4. Regressions of the log-transformed skull length (A), maxilla length (B), palatine length (C), pterygoid length (D), mandible length (E), and dentary length (F) vs. log-transformed body size (SVL) for males (blue) and females (red) of *Dipsas mikanii*.

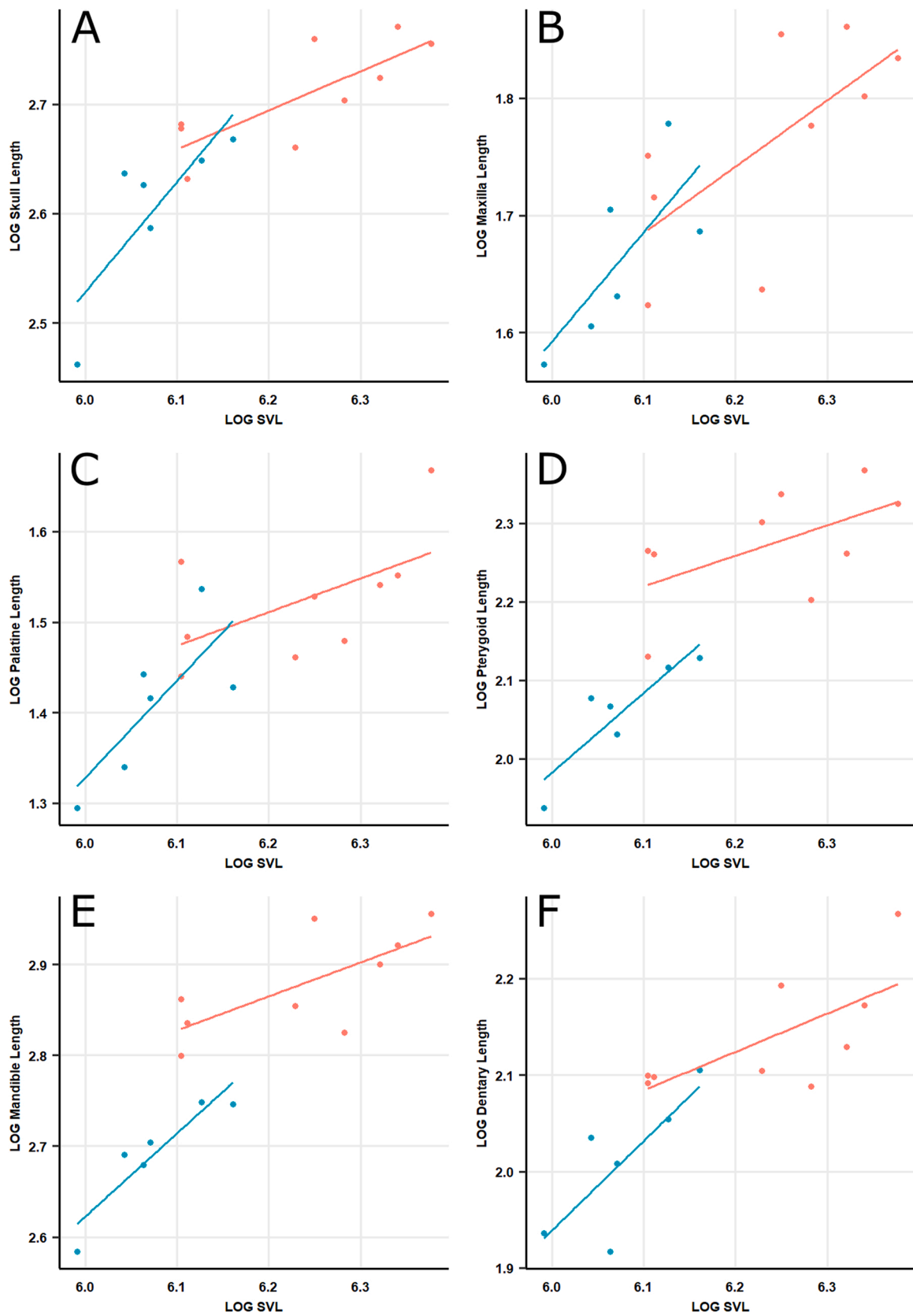


Fig. 5. Regressions of the log-transformed skull length (A), maxilla length (B), palatine length (C), pterygoid length (D), mandible length (E), and dentary length (F) vs. log-transformed body size (SVL) for males (blue) and females (red) of *Dipsas newiedi*.

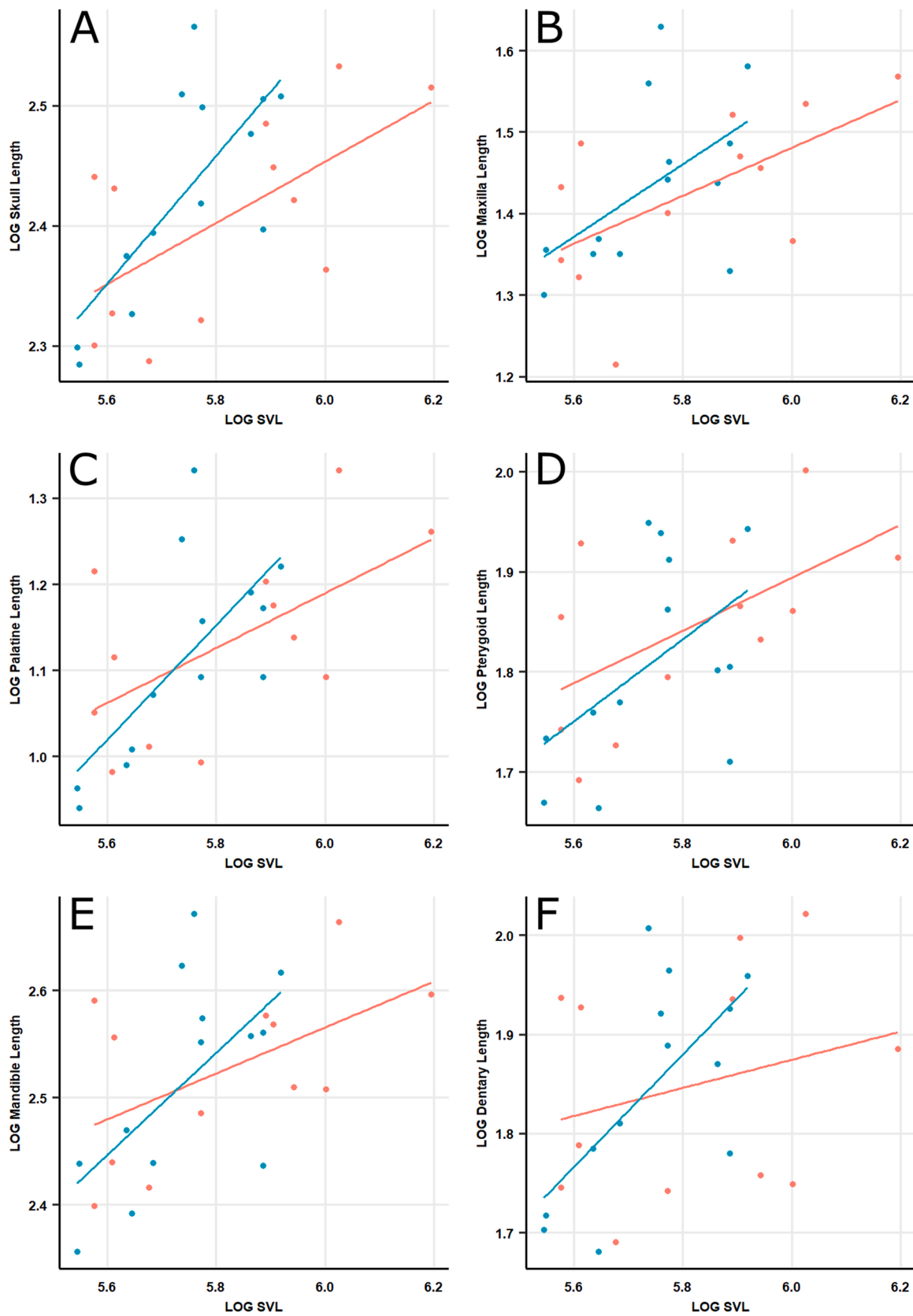


Fig. 6. Regressions of the log-transformed skull length (A), maxilla length (B), palatine length (C), pterygoid length (D), mandible length (E), and dentary length (F) vs. log-transformed body size (SVL) for males (blue) and females (red) of *Dipsas turgida*.

**Table 3**

ANCOVA results for differences in skull length, maxilla length, palatine length, pterygoid length, mandible length and dentary length between sexes. F: statistics F; p: statistical significance. Values in red represent statistically significant variables according to the analysis.

	Slope		Intercept	
	F	p	F	p
<i>Dipsas mikanii</i>				
Skull length	1.81	0.19	1.75	0.19
Maxilla length	0.21	0.64	0.70	0.40
Palatine length	1.54	0.22	0.00	0.95
Pterygoid length	1.34	0.25	9.71	0.005
Mandible length	1.36	0.25	7.05	0.01
Dentary length	0.00	0.98	1.78	0.19
<i>Dipsas newwiedi</i>				
Skull length	4.11	0.06	0.91	0.35
Maxilla length	0.37	0.55	0.02	0.88
Palatine length	1.89	0.19	0.51	0.48
Pterygoid length	2.00	0.18	11.57	0.005
Mandible length	3.19	0.10	15.35	0.002
Dentary length	1.46	0.25	1.89	0.19
<i>Dipsas turgida</i>				
Skull length	2.25	0.14	2.73	0.11
Maxilla length	0.36	0.54	0.62	0.43
Palatine length	1.74	0.20	0.25	0.62
Pterygoid length	0.37	0.54	0.16	0.68
Mandible length	1.43	0.24	0.10	0.74
Dentary length	2.26	0.14	0.16	0.68

type of prey is unknown. For semifossorial snakes the absence of sexual dimorphism was associated with the environment, which would restrict differences in head size due to the digging function (Abegg et al., 2020). The absence of cranial size dimorphism in *D. turgida* could also be explained by the high overlap in relation to the use of the environment, with both sexes not significantly different in relation to the microhabitats used. Despite the record of the use of cavities by individuals of *D. turgida*, the patterns of use of the environment are unknown, and observations of life habits for this species would be necessary to corroborate this hypothesis (Duleba and Ferreira, 2014).

Sexual dimorphism in body size in *Dipsas mikanii* and *D. newwiedi* follows the predominant pattern found in snakes, with females typically larger than males (Shine, 1994; Pizzatto et al., 2008; Parnazio and Vrcibradic, 2018). For these species as well as *D. ventrimaculatus*, body length is significantly related to clutch size, with larger body size conferring selective advantage in females as predicted by the fertility advantage hypothesis (Darwin, 1871; Pizzatto et al., 2008; Parnazio and Vrcibradic, 2018). In contrast, the body size of males and females of *D. turgida* did not differ, which represents an unusual pattern for the genus, since multiple species including *D. albifrons*, *D. catesbyi*, *D. jamespetersi*, *D. neivai*, *D. oligozonata* and *D. oneilli* are all characterized by larger females than males (Hartmann et al., 2002; Alves et al., 2005; Passos et al., 2005; Cadle, 2007; Pizzatto et al., 2008; Parnazio and Vrcibradic, 2018).

Cadle (2007) noted that males of *Dipsas vaga* had greater body size than females but suggested that these observations may have resulted from sampling bias rather than an exception to the usual pattern of sexual dimorphism. Regarding *D. turgida*, our results probably do not suffer from sampling bias, considering that a satisfactory number of males and females were analyzed. According to Shine (1994), ritual combat between males is frequent in species where the male is larger than the female, or where sexual dimorphism in body size is absent. Ritual combat interactions between males have never been described in snakes of the Dipsadini tribe, with reports of this behavior only for *Imantodes cenchoa*, a member of the same subfamily, Dipsadinae (Santos-Costa and Prudente, 2005; Pizzatto et al., 2006, 2008).

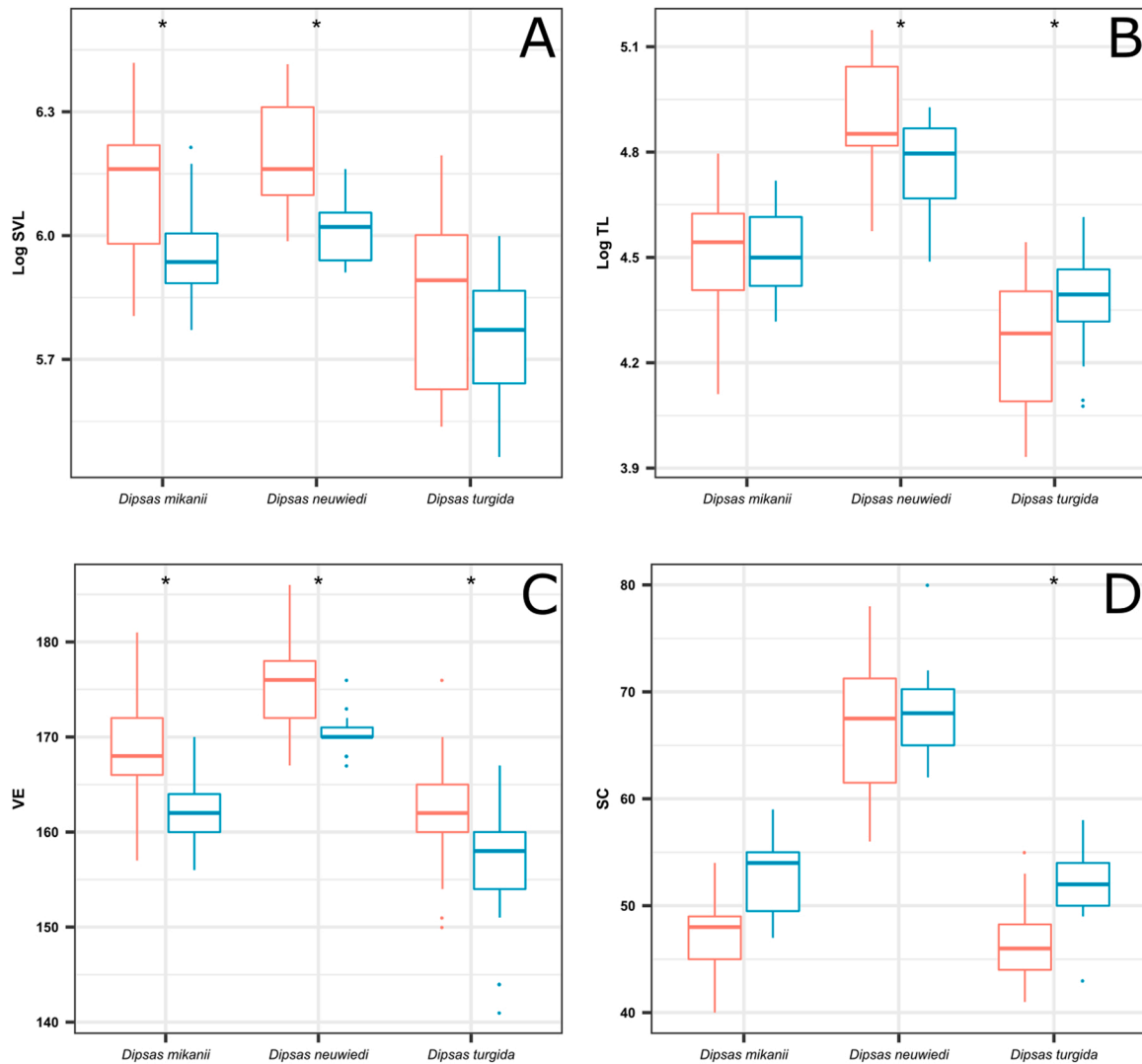
*Dipsas turgida* was sexually dimorphic in relation to tail length, with males having longer tails than females, a pattern consistent with other species of the genus (*D. albifrons*, Hartmann et al., 2002; *D. bucephala*

and *D. peruana*, Harvey and Embert, 2008; *D. catesbyi*, Zug et al., 1979; *D. neivai*, Alves et al., 2005; *D. ventrimaculatus*, Parnazio and Vrcibradic, 2018; *D. jamespetersi*, *D. oligozonata*, *D. oneilli*, *D. vagus*, *D. vagrans* and *D. williamsi*, Cadle, 2007), and other populations of *D. mikanii* and *D. newwiedi* (Pizzatto et al., 2008; Parnazio and Vrcibradic, 2018). According to our statistical analyses *D. newwiedi* showed the opposite pattern (females having longer tails), a result different from that described in previous studies of the same species, which could indicate population variation related to the tail size (Pizzatto et al., 2008; Parnazio and Vrcibradic, 2018). Considering that *D. newwiedi* has a semi-arboreal habit, this pattern could also indicate intraspecific divergence in the use of microhabitats, with females using vegetation more frequently, which would explain their greater tail length (Peters, 1960; Marques and Sazima, 2004; Pizzatto et al., 2008). Tail-related sexual dimorphism is almost always biased towards males, being explained mainly by three hypotheses: 1) the extra space needed to accommodate the hemipenis and retractor muscles; 2) natural selection favoring greater reproductive success in females, resulting in an increase in body size and secondary tail reduction; and 3) the use of the tail in courtship, mating or reproductive aggregation interactions, which would have favored the evolution of larger tails in males (Klauber, 1943; Clark, 1967; Kaufman and Gibbons, 1975; Semlitsch and Gibbons, 1982). During reproductive aggregations, males can use the tail to move other males away during copulation. Thus, in species in which males perform such aggregations, the size of body and tail can be decisive for individual mating success (Madsen and Shine, 1993; Luiselli, 1996). Such interactions have never been described for the species studied here, however, there is information about reproductive aggregations for two other *Dipsas* species, *D. neivai* and *D. alternans*, and even for these species, the use of the tail during such interactions has not been evaluated (Alves et al., 2005; Marinho et al., 2020).

Regarding the number of ventral and subcaudal scales, the three species showed significant differences (except *D. newwiedi* for subcaudal scale counts), following the dominant pattern for most snake species, with females having a greater number of ventral scales, and males having a greater number of subcaudal scales (Shine, 1994). However, for some species of *Dipsas*, a “reverse dimorphism” has been observed in relation to ventral and subcaudal scales, while for others sexual dimorphism for these traits is non-existent (Hartmann et al., 2002; Cadle, 2007; Harvey and Embert, 2008). Cadle (2007) noted that reverse dimorphism for these variables can also occur in species of *Sibon* and *Tropidodipsas*, which could represent a trend among the Dipsadini constituting a synapomorphy for the group (Parnazio and Vrcibradic, 2018). A detailed analysis in a phylogenetic context, expanding the number of analyzed species, could help better understand the patterns of sexual dimorphism in body size in *Dipsas* species, clarifying whether the absence of dimorphism in body size represents an autapomorphy of *D. turgida*, or if it is present in other taxa.

Different definitions of allometry have emerged over time, among which two stand out: the first approach considers allometry as the pattern of covariation between parts, while the second characterizes it as changes in shape correlated to changes in size (Klingenberg, 1998; Hendrikse et al., 2007; Bright et al., 2016; Fabre et al., 2020). In the first case, allometry is described in terms of “allometric slope,” such that the proportional size of a given structure is analyzed in relation to body size. The second approach recognizes shape and size as distinct components and considers that shape changes are associated with increasing size (Klingenberg, 1998).

We detected negative allometry for cranial components in females of the three species. It has been argued that negative allometry is a result of canalization, that is, a reduction in variability, with stabilizing selection being the force responsible for this process due to functional or developmental requirements (Maynard Smith et al., 1985; Wagner et al., 1997; Eberhard et al., 1998, 2009; Flatt, 2005; Buck et al., 2010). The contrasting allometric patterns found between the sexes—with females showing less variation in size cranial, but males showing isometry—may



**Fig. 7.** Boxplot representing variation in snout-vent length (SVL) (A), tail length (TL) (B), number of ventral scales (VE) (C), and number of subcaudals scales (SC) (D) for males (blue) and females (red) of each species. Circles represent outliers, asterisk represents statistically significant differences. Middle line represents mean values, boxes show standard deviation, and whiskers represent minimum and maximum values.

**Table 4**

Sexual dimorphism (t-test/Kruskal-Wallis test\*) and morphometric variation for snout-vent length (SVL), tail length (TL), number of ventral scales (VE) and number of subcaudals scales (SC) between females and males of the species *Dipsas mikanii*, *D. newwiedi* and *D. turgida*. t: t-test statistic; df: degrees of freedom; p: p statistical significance; mean value ( $\pm$ SD, with intervals and sample size (n) in parentheses). Values in red represent statistically significant variables according to the analysis.

	t	df	p	Mean values $\pm$ SD (intervals and sample size)	
				♀♀	♂♂
<i>Dipsas mikanii</i>					
SVL	5.11	61.00	< 0.001	462.7 $\pm$ 75.5 (332–613, n = 38)	387.9 $\pm$ 43.7 (321–500, n = 30)
TL	-0.06	64.00	0.94	92.0 $\pm$ 15.0 (61–121, n = 37)	92.3 $\pm$ 11.5 (75–112, n = 29)
VE	5.73	65.00	< 0.001	168.7 $\pm$ 5.0 (157–181, n = 38)	162.4 $\pm$ 3.6 (156–170, n = 29)
SC	-6.51	62.00	< 0.001	47.2 $\pm$ 3.1 (40–54, n = 37)	52.6 $\pm$ 3.4 (47–59, n = 27)
<i>Dipsas newwiedi</i>					
SVL	5.08	32.40	< 0.001	490.9 $\pm$ 64.7 (398–611, n = 22)	409.0 $\pm$ 31.9 (369–474, n = 15)
TL	2.84	35.00	0.007	135.6 $\pm$ 21.4 (97–172, n = 22)	117.6 $\pm$ 14.6 (89–138, n = 15)
VE	3.55	25.60	0.001	175.2 $\pm$ 4.9 (167–186, n = 18)	170.5 $\pm$ 2.3 (167–176, n = 13)
SC	0.56	28.00	0.57	67.1 $\pm$ 6.5 (56–78, n = 18)	68.4 $\pm$ 4.7 (62–80, n = 12)
<i>Dipsas turgida</i>					
SVL	1.79	38.20	0.08	346.2 $\pm$ 65.4 (254–490, n = 25)	319.3 $\pm$ 43.6 (236–403, n = 37)
TL	-2.85	57.00	0.006	71.7 $\pm$ 12.6 (51–94, n = 25)	80.2 $\pm$ 10.1 (59–101, n = 37)
VE*	13.40	1.00	< 0.001	161.9 $\pm$ 5.6 (150–176, n = 25)	156.6 $\pm$ 5.4 (141–167, n = 37)
SC	-6.30	57.00	< 0.001	46.8 $\pm$ 3.5 (41–55, n = 25)	52.1 $\pm$ 2.8 (43–58, n = 37)

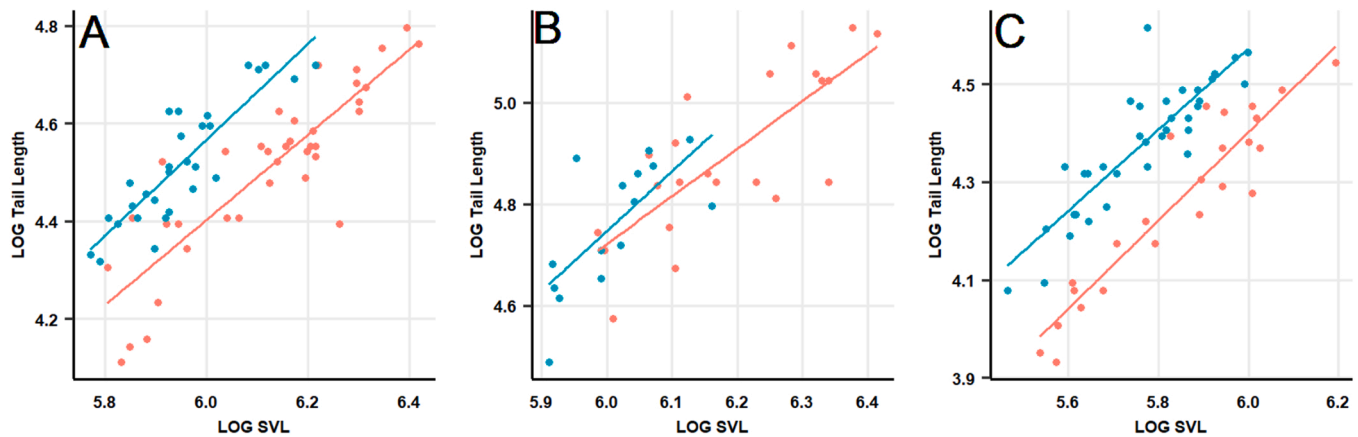


Fig. 8. Regressions of the log-transformed tail length (TL) vs. log-transformed body size (SVL) for males (blue) and females (red) of *Dipsas mikanii* (A), *D. newwiedi* (B) and *Dipsas turgida* (C).

express the need of relatively smaller heads in larger females. Due to functional aspects related to reproduction (the use of cavities for egg deposition, as noted above), the skull in females could be under stabilizing selection to maintain adequate proportions. The smallest variation in skull size was observed in females of both species for which the use of cavities has been reported, *D. mikanii* and *D. turgida*, reinforcing our hypothesis about stabilizing selection for functional aspects. In the amphisbenid *Cynisca leucura*, stabilizing selection was likewise hypothesized to explain reduced variability in cranial shape (Hipsley et al., 2016). In this case, fossorial habit was also thought to exert stabilizing selection that has restricted morphological variability, maintaining cranial proportions suitable for excavation with the head.

Although males and females showed different allometric patterns, the slopes of regression lines indicated parallel allometric trajectories. Similarities in allometric trajectories between males and females may indicate that developmental processes act similarly in each sex, or correspond to evolutionary adaptations through natural selection (Strauss, 1985).

Our allometric analysis indicated that males of *D. newwiedi* show positive allometry for tail length, indicating accelerated growth of the tail in relation to the body, while for females such growth is isometric. Although it is historically assumed that sexual traits exhibit positive allometry, recent studies have shown negative allometry or isometry for reptilian genitalia, which are assumed to be under directional sexual selection (Bertin and Fairbairn, 2007; Klaczko and Stuart, 2015; De-Lima et al., 2019). Positive allometry can also occur in non-sexual traits, being relatively common in structures used for locomotion, such as the tail (Tseng and Rowe, 1999; Hosken et al., 2005; Bonduriansky, 2007). Although the results generated by allometric studies may emphasize adaptive interpretations of the observed patterns, it is important to consider the role of other factors, such as phylogenetic inertia.

This study and those with other South American dipsadine and xenodontine snakes, indicates that the hypothesis of absence of sexual dimorphism in the head as a result of dietary homogeneity and dependence on small prey does not support a simple explanation. In each group or species, other factors may drive head/skull sex differences, including use of the environment, or reproductive activities, as reported here. The patterns of sexual dimorphism and allometry reported here suggest that even in species with numerous cranial adaptations related to food specialization, intraspecific changes in skull morphology may be associated with aspects of life other than diet. However, greater knowledge about behavioral aspects, especially those related to reproduction, are essential to support any inferences about selective processes influencing cranial and body morphology across the sexes. Geometric morphometry proved to be an efficient method for revealing variations

not usually identified by simple linear analysis, thus contributing to a better understanding of intraspecific variations among the studied taxa. The evolution of sexual dimorphism in *Dipsas* will be better understood when approached in a phylogenetic context, while also considering aspects of the group's natural history.

#### Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

#### Data Availability

No data was used for the research described in the article.

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#### Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at [doi:10.1016/j.zool.2022.126026](https://doi.org/10.1016/j.zool.2022.126026).

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