



Contents lists available at ScienceDirect

Zoology

journal homepage: www.elsevier.com/locate/zool

ZOOLOGY

Cranial adaptations for feeding on snails in species of *Sibynomorphus* (Dipsadidae: Dipsadinae)

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ARTICLE INFO

Article history:

Received 29 September 2015

Received in revised form 31 July 2016

Accepted 27 September 2016

Available online xxx

Keywords:

Convergence

Geometric morphometrics

Malacophagy

Dipsadinae

Sibynomorphus

ABSTRACT

Neotropical “goo-eating” dipsadine snakes display a set of morphological and histo-chemical adaptations linked to the capture of their soft-bodied, viscous invertebrate prey. Within this group, species from the genus *Sibynomorphus* feed chiefly on snails and slugs. Here, we analyzed a series of skull and mandible characters in *S. mikanii*, *S. neuwiedi* and *S. turgidus* using geometric morphometrics, with the aim of assessing morphological adaptations related to slug- and snail-feeding in that genus. We further compared the results with *Leptodeira annulata*, a species that feeds on vertebrates. To evaluate shape differences of the skull and mandible between species we performed a multivariate analysis of variance and a linear discriminant analysis. Our results show that the narrow, elongate skull in *S. mikanii* may help with slug ingestion, while asymmetry in teeth number and mandibular shape in *S. neuwiedi* and *S. turgidus* are likely related to snail feeding.

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1. Introduction

The joint adaptation of various traits seems to be fairly consistent along the phylogeny of snakes (e.g., Shine, 1980; Hibbitts and Fitzgerald, 2005; Herrel et al., 2008), leading to common cases of phenotypic convergence in the group. For example, adaptations for durophagy, piscivory, fossoriality and arboreality appeared independently in numerous clades during the evolution of snakes (Peters, 1960; Savitzky, 1983).

One of the most remarkable cases is associated with the acquisition and consumption of gastropods and soft-bodied animals, a behavior known as “goo-eating” (*sensu* Cadle and Greene, 1993), which has evolved in a number of distinct lineages, such as the Asiatic Pareatidae, the natricid genus *Storeria*, the dipsadid tribes Dipsadini and some species of Tachymenini (*Tomodon dorsatus*, *Tomodon ocellatus* and *Calamodontophis paucidens*) (Gallardo, 1972; Rossman and Myer, 1990; Hoso et al., 2007; Zaher et al., 2014). Some of the morphological adaptations to malacophagy include asymmetry in the number of mandibular teeth in snakes of the genus *Pareas* (Hoso et al., 2007), slender and flexible jaws to extract the

snail from the shell in some species of *Storeria* (Rossman and Myer, 1990), and the presence of a complex protein-secreting delivery system in Dipsadini (Zaher et al., 2014).

Within Dipsadinae, a speciose group of Neotropical snakes with ample morphological diversity, this strategy seems to be restricted to a monophyletic group that contains the genera *Adelphicos*, *Atractus*, *Geophis*, *Ninia*, *Dipsas*, *Sibon*, *Tropidodipsas* and *Sibynomorphus* (Zaher et al., 2009, 2014; Grazziotin et al., 2012). This group is defined by a set of morphological and histo-chemical characters related to “goo-eating” (Peters, 1960; Laporta-Ferreira et al., 1986, 1988; Sazima, 1989; Cadle and Greene, 1993; Oliveira et al., 2008; Zaher et al., 2014). *Adelphicos*, *Atractus*, and *Geophis* feed mainly on earthworms (Landy et al., 1966; Campbell et al., 1983; Cunha and Nascimento, 1983; Seib, 1985; Martins and Oliveira, 1993; Cisnero-Heredia, 2005; Zaher et al., 2014), whereas *Ninia*, *Dipsas*, *Sibynomorphus*, *Sibon*, and *Tropidodipsas* are molluscivorous specialists that feed mainly on slugs and snails (Mertens, 1952; Greene, 1975; Kofron, 1985, 1987, 1988; Laporta-Ferreira et al., 1986; Sazima, 1989; Ray et al., 2012; Zaher et al., 2014).

Here, we investigate the ecomorphological differences associated with different kinds of malacophagy within the genus *Sibynomorphus*. We specifically aimed to test the ecomorphological association between snail-feeding and differences in the shape (Rossman and Myer, 1990) and asymmetry (Hoso et al., 2007) of

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the feeding apparatus. In order to do that, we employed geometric morphometric methods to investigate differences in the skull and mandible shape between species, and to investigate directional asymmetry of the mandible that could be associated with feeding ecology and behavior. We also tested for the presence of significant directional asymmetry in tooth counts between species. For both shape and tooth count asymmetry we focused on testing the presence of directional asymmetry for the species as a whole, given that we lack any specific information about prey availability or preference for individual populations of the analyzed species. In any case, even if asymmetry in different directions was present, this would hide any signal of directional asymmetry in the sample. Thus, we view the test of directional asymmetry as a conservative first approach to the issue.

We analyzed the only exclusive slug feeders of the group *S. mikanii* and compared it with its snail-feeding sister species *S. turgidus* (Laporta-Ferreira et al., 1986, 1988; Melgarejo, 1980) as well as the more distantly related snail feeder *S. neuwiedi* (Laporta-Ferreira et al., 1986, 1988). The rationale is that, given that *S. mikanii* and *S. turgidus* are closely related, any convergence between *S. turgidus* and *S. neuwiedi* could be a product of functional demands on snail-eating. Similarly, differences between *S. mikanii* and the other two species could be associated with either the relaxation of mechanical demands for snail-feeding, or adaptations to slug-feeding. To further clarify this issue, we also introduced *Leptodeira annulata* as a model for a generalized non goo-eating dipsadine snake (Zaher et al., 2009).

We chose to focus on the analysis of interspecific variation to evaluate if morphological variation between species is discrete and can be used as a source of information for ecomorphological comparative analyses.

2. Materials and methods

2.1. Material examined

We analyzed a total of 76 skulls from adults belonging to four species: *S. mikanii* (skulls=28; left mandibles=22; right mandibles=19), *S. neuwiedi* (skulls=15; left mandibles=15; right mandibles=13), *S. turgidus* (skulls=25; left mandibles=25; right mandibles=25), and *Leptodeira annulata* (skulls=8; left mandibles=6; right mandibles=8). For *S. mikanii* and *S. neuwiedi* we classified individuals as adults when the snout–vent length was >300 mm (Oliveira, 2001). For *S. turgidus*, specimens were identified as adults or sexually mature through inspection of the gonads in the laboratory. For *L. annulata*, individuals were considered adults or sexually mature females with snout–vent lengths >490 mm and males with snout–vent lengths >431 mm (Vitt, 1996).

This is the largest skull series with regard to intraspecific variation of the genus *Sibynomorphus* that we are aware of. Specimens have been deposited in various Brazilian scientific collections as specified Appendix A.

2.2. Preparation of skulls and digitalization of landmarks

Skulls were manually prepared using hot water and photographs were taken under a Leica M80 stereomicroscope. Photographs were taken in dorsal view of the skull, and in lateral view of left and right mandibles. Landmarks were chosen so as to correspond mainly to cranial sutures and extremes of structures following Zelditch et al. (2004). This produced a total of 14 landmarks for the dorsal view of the skull and 7 for the lateral view of mandible and quadrate (Fig. 1). Each image included a scale, and landmarks were digitized using the software TPSUtil 1.56 (Rohlf, 2013a) and TPSDig2 2.17 (Rohlf, 2013b). The images were digitized

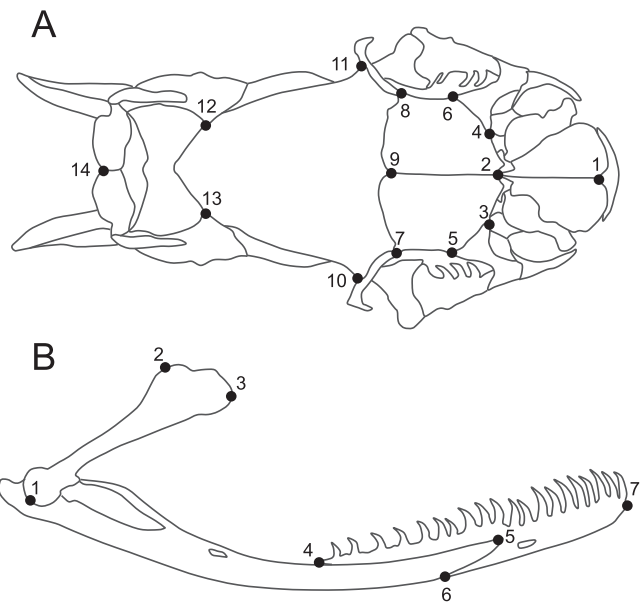


Fig. 1. Anatomical landmarks used in the present study. Duplicates refer to symmetrical points. (A) Cranium. 1, suture between pre-maxillae and nasals; 2, suture between nasals and frontal; 3 and 4, anterior-most points of the suture between pre-frontal and frontal; 5 and 6, posterior-most points of the suture between pre-frontal and frontal; 7 and 8, lateral-most points of the suture between frontal and parietal; 9, median point of the suture between frontals and parietal; 10 and 11, lateral-most points of the suture between post-orbital and parietal; 12 and 13, lateral-most points between parietals and prootic; 14, posterior-most sagittal point of the exoccipital. (B) Mandible. 1, quadrate-mandibular articulation; 2, posterior-most point of the quadrate; 3, anterior-most point of the quadrate; 4, superior extremity of the dentary; 5, anterior-most point of the suture between the compound and the dentary; 6, inferior extremity of the dentary; 7, posterior tip of the dentary.

twice to assess the precision in landmark positioning. After digitalization we conducted a repeatability analysis in order to evaluate the percentage of digitalization error at each anatomical landmark. The error was measured through a two-way analysis of variance (ANOVA) using individuals and picture as factors, and the percentage of variation explained by “picture” factor was taken as the amount of digitalization error. This was done univariately (for each landmark dimension) and multivariately (for the full structure). In both cases the error was not greater than 10% and was not considered significant. Additionally, mandibular teeth were counted on both sides.

2.3. Shape analysis

To remove effects arising from an arbitrary positioning of the articulation between the quadrate and compound bones of the mandible, we used the method of fixed angles according to Adams (1999). According to this method, a subset of landmarks is rotated around a fixed point in order to set the angle between two baselines (one for each structure) to a fixed value, in this case, the average of the angles measured on the sample. In the present analysis, the subset of landmarks contained in the quadrate (landmarks 2 and 3) were rotated around the landmark in the articulation (1) in order to fix the angle formed by the lines 1–2 and 1–7. We chose to fix the angle at the sample average because mandibles were photographed in order to minimize angle variation between these structures.

Landmark configurations from the skull and mandible were subjected to a generalized Procrustes analysis (GPA) to remove effects from position, orientation and size (Rohlf and Slice, 1990; Rohlf, 1999). In conventional geometric morphometrics analysis the number of variables can far exceed the number of specimens. This happens because the data dimensionality is a function of the

Table 1

Proportion of correct reclassification of specimens belonging to the four species analyzed based on linear discriminant analysis for the skull and mandible.

Species	Skull				Mandible			
	<i>L. annulata</i>	<i>S. mikanii</i>	<i>S. neuwiedi</i>	<i>S. turgidus</i>	<i>L. annulata</i>	<i>S. mikanii</i>	<i>S. neuwiedi</i>	<i>S. turgidus</i>
<i>L. annulata</i>	100	0	0	0	100	0	0	0
<i>S. mikanii</i>	0	100	0	0	0	94.44	0	5.56
<i>S. neuwiedi</i>	0	0	100	0	0	6.67	86.67	6.67
<i>S. turgidus</i>	0	3.57	7.14	89.29	0	4.17	0	95.83

number of landmarks and of dimensions under investigation. This is particularly problematic in discriminant analysis (see below) where a low specimen/variable ratio can lead to a spurious increase in the discrimination of groups (see [Strauss, 2010](#); [Mitteroecker and Bookstein, 2011](#)). For this reason, we here performed principal components analyses (PCAs) on the GPA residuals as a dimension reduction technique. The resulting PCAs can be interpreted as new shape variables that explain sequentially decreasing amounts of variation on the sample. Thus, the selection of the first principal components can help not only in the reduction of the number of variables, but also in the removal of noise, which is an intrinsic feature of multidimensional data ([Marroig et al., 2012](#)). For those reasons, we selected the first 10 PCs for each analysis because they explained more than 95% of the variation and they produced an adequate specimen/variable ratio for the *Sibynomorphus* species. PCAs were performed on the skull and mandible for interspecific variation, and also on the mandible of each species separately for the analysis of asymmetry. The selected principal components were used for all subsequent analyses.

To evaluate shape differences between species for the skull and mandible we performed a multivariate analysis of variance (MANOVA) and a linear discriminant analysis (LDA) using species as factors. While the MANOVA tests for significant differences in the centroids of the multivariate data, LDA allows for the evaluation of the relative superposition of groups (e.g., [Machado and Hingst-Zaher, 2009](#); [Nascimento, 2014](#)). This happens because if an individual from a group is closer in terms of Mahalanobis distance to the centroid of another group, then that individual will be misclassified, even though the multivariate centroids of both groups are different (cf. Fig. 2A in [Mitteroecker and Bookstein, 2011](#)). For this reason we used LDA as a means to investigate the degree of morphometric overlap between species. Differences explained by the LDA were visualized by regressing the Procrustes residuals on the linear discriminant analysis scores for the first two axes (e.g., [Rohlf et al., 1996](#)). This analysis was conducted for both mandibles, but since the results were very similar, we only report the results for the right side.

The above-mentioned analyses of the skull were performed on the full configuration, on only one side of the skull and on the full configuration after the removal of the effects of asymmetry (following [Klingenberg et al., 2002](#)). Since the results were nearly identical for all analyses, we only show the results for the full configuration after the removal of asymmetry. For that same reason, asymmetry analysis was only evaluated on the mandible.

To explore shape asymmetry in mandibles we first performed GPAs on the left and right mandible sets for each species and employed PCAs to reduce dimensionality. For the asymmetry analyses, we retained 4 PCs that explained more than 85% of the variation. We used nested MANOVAs for each species, using “individuals” and “side” as factors, with the latter nested within the former. This was done as a way of controlling the variation between individuals before testing for the effect of side, thus ensuring that the asymmetric differences were in the same multivariate direction. To inspect shape differences between sides we performed a

LDA and regressed shape variables on the resulting discriminant function in order to visualize shape differences between both sides.

2.4. Analysis of asymmetry in the number of mandibular teeth

We investigated the asymmetry in the number of mandibular teeth by calculating differences between right and left tooth counts and tested if they were significantly different from zero with a one-sample *t*-test. This analysis was performed separately for each species.

All analyses were performed in the R programming environment ([R Core Team, 2014](#)), using the *shapes* ([Dryden, 2013](#)) and *geomorph* ([Adams and Otárola-Castillo, 2013](#)) packages for geometric morphometric analyses.

3. Results

3.1. Shape variation in skull and mandible

In the principal component analyses of the skull and mandible, the first 10 components explained more than 97% of the observed variations. For the intraspecific analysis of the mandible asymmetry, the first 5 components for each species explained more than 85% of the variation, and thus, these components were used to quantify the shape variation in all posterior analyses.

In the following statistical results, abbreviations are as follows: d.f., degrees of freedom; num.d.f., degrees of freedom numerator; den.d.f., degrees of freedom denominator; *p* – probability of the null hypothesis. The MANOVA results indicate significant differences between species in both skull (d.f. = 3, Wilks' lambda = 0.010, num.d.f. = 30, den.d.f. = 185.59, *p* < 0.001) and mandible (d.f. = 3, Wilks' lambda = 0.018, num.d.f. = 30, den.d.f. = 153.31, *p* < 0.001) shapes. The results for the LDA analyses both indicate an almost complete separation between species, except for a noticeable superposition of *S. turgidus* and *S. neuwiedi* for both structures ([Figs. 2 and 3](#)). For the mandible, the morphology of the mandible shows a degree of overlap between all *Sibynomorphus* species. Despite this, the proportion of correct group reclassification for these species is very high ([Table 1](#)).

The first axis of the skull LDA accounts for more than 80% of interspecific variation and summarizes the differences between *L. annulata* and all *Sibynomorphus* species ([Fig. 2](#)). Along this axis, taller and more robust skulls characterize *L. annulata*, with a larger orbit in contrast to *Sibynomorphus* species, which display straighter, longer skulls with reduced orbits. The second axis of the LDA explains 12% of the interspecific variance and mainly separates *L. annulata* and *S. mikanii* from *S. neuwiedi* and *S. turgidus*, with the former two species showing a laterally compressed skull ([Fig. 2](#)).

The first axis of the LDA analysis of the mandible accounts for 72% of the interspecific variation and depicts a difference between *L. annulata* and *Sibynomorphus* species ([Fig. 3](#)). The warp-grids indicate that this axis is mainly related to the robustness of the quadrate and the dentary bones in *Sibynomorphus* species. The second axis explains 20% of the variation, mainly differentiating *S. mikanii* from

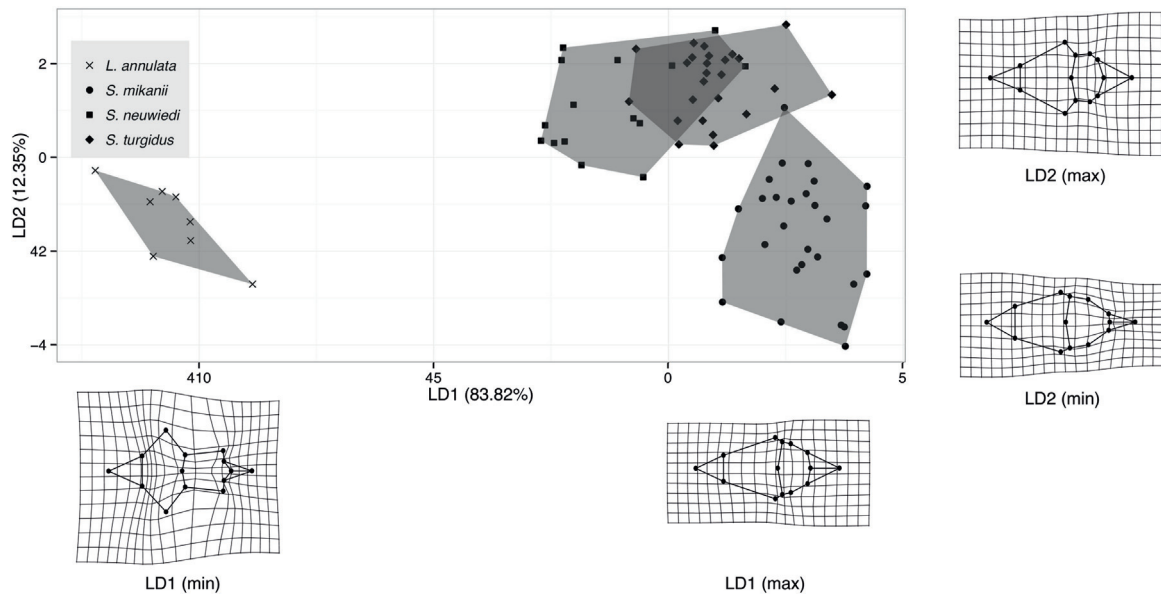


Fig. 2. Linear discriminant analysis performed on the skull landmark coordinates of the studied *Sibynomorphus* and *Leptodeira* species. Values between parentheses are percentages of between-group variation explained by the first and second discriminant axis (LD1 and LD2, respectively). Polygons are convex hulls containing all specimens for a given species. The splines represent the shape variation associated with extreme values of each axis.

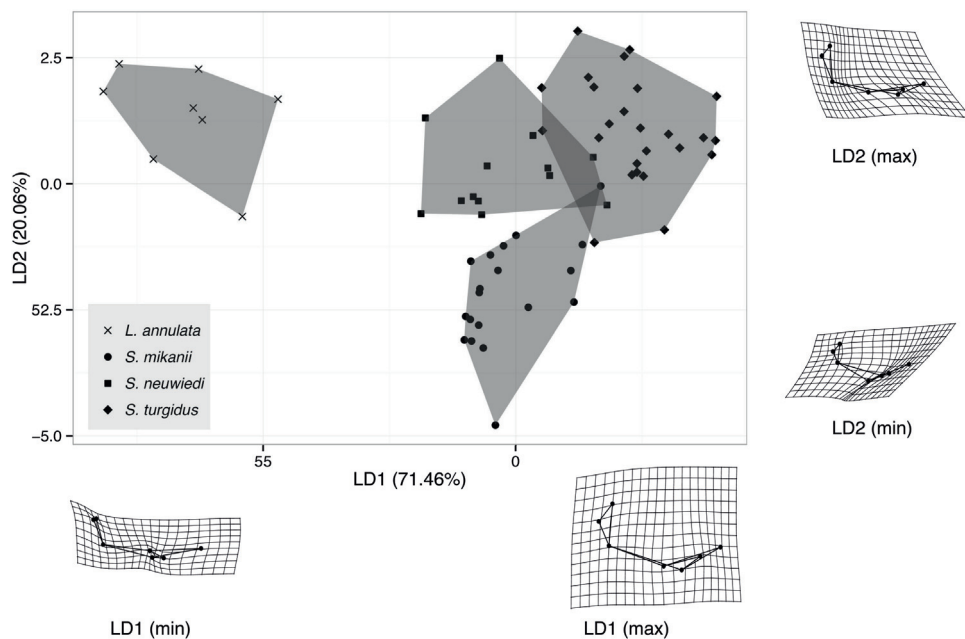


Fig. 3. Linear discriminant analysis performed on the mandible landmark coordinates of the studied *Sibynomorphus* and *Leptodeira* species. Values between parentheses are percentages of between-group variation explained by the first and second discriminant axis (LD1 and LD2, respectively). Polygons are convex hulls containing all specimens for a given species. The splines represent the shape variation associated with extreme values of each axis.

all the other species, with the former displaying a shorter quadrate and smaller dentary (Fig. 3).

3.2. Asymmetry in tooth number and mandibular shape

Sibynomorphus have a conserved number of teeth, with the right side having more teeth on average than the left side (Table 2). The *t*-tests for asymmetry indicate the existence of asymmetry in the number of mandibular teeth in *S. neuwiedi* ($t = 2.562$, d.f. = 14, $p = 0.021$) and *S. turgidus* ($t = 2.694$, d.f. = 21, $p = 0.014$), with a greater number of teeth on the right side of the mandible in both cases (Fig. 4 and Table 2).

Table 2

Average tooth counts of each side and average differences between tooth counts for both sides.

	Right side	Left side	Difference
<i>Leptodeira annulata</i>	23.5 ± 3.0	23.4 ± 2.5	0.1 ± 3.9
<i>Sibynomorphus mikanii</i>	22.4 ± 1.8	21.6 ± 1.8	0.9 ± 2.2
<i>Sibynomorphus neuwiedi</i>	20.9 ± 2.0	19.9 ± 2.8	1.0 ± 1.5
<i>Sibynomorphus turgidus</i>	22.5 ± 1.5	21.2 ± 2.1	1.2 ± 2.1

Furthermore, the MANOVA analysis also showed asymmetry in mandibular shape in *S. turgidus* (d.f. = 1, Wilks' lambda = 0.311, num.d.f. = 4, den.d.f. = 21, $p < 0.001$) and *S. neuwiedi* (d.f. = 1, Wilks'

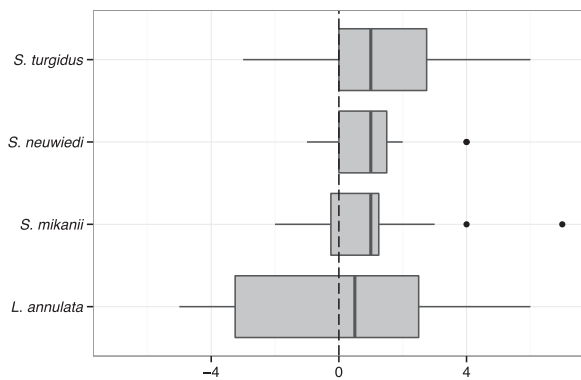


Fig. 4. Asymmetry in the number of mandibular teeth in *Sibynomorphus mikanii*, *S. neuwiedi*, *S. turgidus* and *Leptodeira annulata*. Values are the differences between right and left tooth counts. The dashed line represents the absence of any differences between the two sides (zero).

$\lambda = 0.170$, num.d.f. = 4, den.d.f. = 9, $p = 0.002$), but not in *S. mikanii* (d.f. = 1, Wilks' $\lambda = 0.517$, num.d.f. = 4, den.d.f. = 13, $p = 0.057$) or *L. annulata* (d.f. = 1, Wilks' $\lambda = 0.590$, num.d.f. = 4, den.d.f. = 7.583, $p = 0.832$). The visualization of shape differences between both sides (Fig. 5) indicates that all bones in the right mandible of *S. neuwiedi* are more delicate than those on the left side; particularly, the quadrate and compound bones are more slender and more elongate and the dentary bone is smaller and also more slender in the right mandible than in the left.

Variations similar to those seen in *S. neuwiedi* were found in *S. turgidus*, with the right mandible being more slender than the left, although not as markedly as in *S. neuwiedi*. In this latter species, the quadrate bone is more slender and more elongate, the dentary bone is smaller and the compound bone is more elongate in the right mandible.

4. Discussion

Our results indicate significant cranial and mandibular differences between the two snail-feeding species (*S. turgidus* and *S. neuwiedi*) and the only known exclusively slug-feeding species of the genus *Sibynomorphus* (*S. mikanii*), besides the classically known morphological specializations regarded as adaptations for soft and viscous prey ingestion (e.g., inward-turned jaw and maxillary teeth,

short snout, free posterior end of the pterygoid; Peters, 1960; Laporta-Ferreira et al., 1986, 1988; Laporta-Ferreira and Salomão, 1991). Since *S. turgidus* has been retrieved as the sister species of *S. mikanii* in recent phylogenetic studies of the group (Grazziotin et al., 2012; Zaher et al., 2014), morphological similarities between the former and *S. neuwiedi* are more likely to be convergences improving the performance for snail extraction, especially when considering the mandibular components in both species.

According to Dwyer and Kaiser (1997), elongated bones such as quadrate, supratemporal and jaw are loosely connected to each other to increase the cranial kinesis and mouth opening for larger prey ingestion and swallowing. Vincent et al. (2009) suggested, according to experimental data, that the presence of a larger quadrate bone in snakes allows better adjustment between the cephalic shape of the snake and the body shape of their prey during swallowing. Thus, the larger quadrate length observed in *S. turgidus* and *S. neuwiedi* probably allows a larger gape, favoring the ingestion of larger prey. Elongation of the quadrate in *S. neuwiedi* was indicated by Laporta-Ferreira et al. (1986, 1988) as being one of the characters responsible for removing snails from shells (along with other skull characters, e.g. long and slender mandibles and increased number of dentary, maxillary, pterygoid and mandibular teeth). Sazima (1989) observed that during snail-feeding the mandibles of *Dipsas indica* move in excursions similar to those observed in slug-eating, although the degree of displacement of the quadrate and compound bones is higher in snail-eating taxa.

It is not clear how the difference in robustness of the dentary bone between *Sibynomorphus* species affect prey ingestion. The overall delicate mandible and extremely thin dentary bone in *S. mikanii* could provide greater mandibular excursions during transport of the highly viscous prey. Greater mandibular excursions could affect prey handling time, allowing for a quicker ingestion of viscous prey items as proposed by Sazima (1989) for *D. indica*.

Scartozzoni (2009) observed that some hydrosine snakes have relatively small and gracile heads, supposedly associated with the ingestion of elongated prey. If this ecomorphological association also holds for *Sibynomorphus* species, then a laterally compressed cranium, as observed for *S. mikanii*, could facilitate the ingestion of elongated prey items such as the Veronicellidae slugs predated by this snake (Thomé et al., 2001).

Asymmetry in the mandibular shape and number of mandibular teeth as seen in *S. neuwiedi* and *S. turgidus* may also be suggestive of morphological specializations for snail consumption.

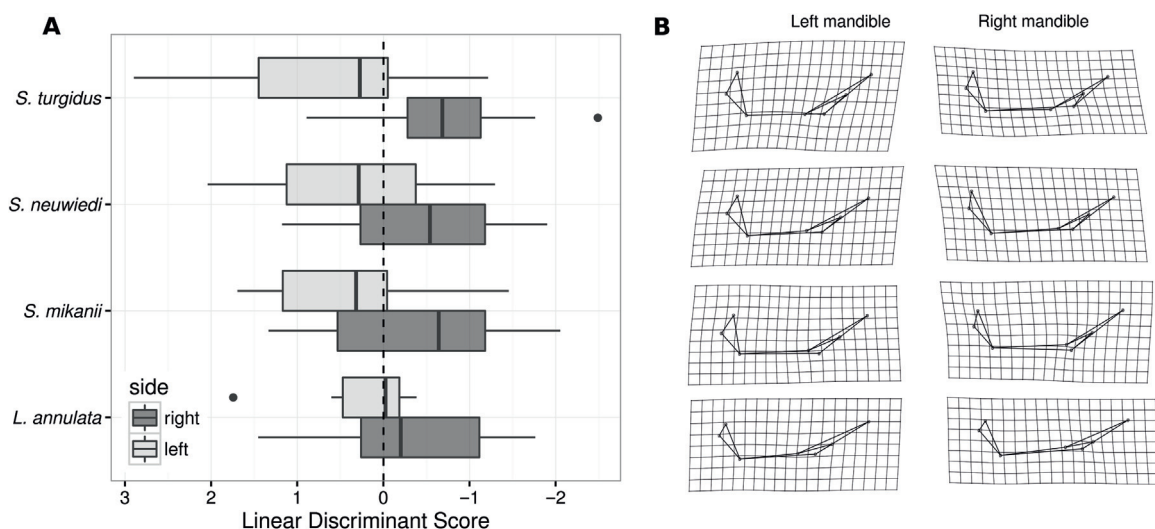


Fig. 5. (A) Linear discriminant score of the discriminant function between the right and left sides of the jaw for each species. (B) Mandibular shape of the right and left side for each species.

In snail-eating snakes of the family Pareatidae, the degree of tooth asymmetry is related to dextral prey predation performance even in cases when morphological asymmetry is not so evident (Danaisawadi et al., 2015, 2016). The degree of asymmetry can be directly correlated with the degree of specialization on snails with the same twist direction of their shells or the relative abundance of snails with different twist directions in the snake's environment (Hoso et al., 2007; Danaisawadi et al., 2015, 2016). Here, we suggest that, similarly to Pareatidae, osteological specializations such as greater robustness of the dentary bone, mandibular shape and tooth number asymmetries are primarily responsible for the mechanical extraction of soft-bodied mollusks during feeding activities, contributing to a greater efficiency and performance in snail extraction. Given that the degree of asymmetry identified here is mild, as exemplified by the small degree of tooth count asymmetry (Fig. 4 and Table 2) and the large superposition between sides on the discriminant analysis (Fig. 5), we would expect that these species are not strict specialists, being able to consume prey with shells with both twist directions but being more efficient in predating one kind of snail (Danaisawadi et al., 2016).

The present work aimed to describe and present patterns of morphological variation in a small group of *Sibynomorphus* species and to speculate on their probable functional correlates. We fully acknowledge that these associations are tentative and should be taken with caution, and that further behavioral and ecological data are essential to test these hypotheses. Additionally, further comparative analyses of the skull morphology of Dipsadinae snakes could help establish the degree of morphological variation and its connection to feeding ecology.

Acknowledgements

We wish to thank Gláucia Maria Funk Pontes (MCT-PUCRS), Guarino Colli (CHUNB), Júlio Cesar de Moura-Leite (MHNCI), Marcos André de Carvalho (UFMT), Oscar Shibatta (MZUEL), Rejane Lira (UFBA), and Vanda Lúcia Ferreira (CEUCH) for the loan of specimens. We are grateful to Thiago Macek for reviewing the manuscript and for the comments from two anonymous reviewers that helped to improve the manuscript. F.A.M. was supported by a PhD fellowship from the Fundação de Amparo à Pesquisa do Estado de São Paulo (FAPESP; process 2011/21674-4). M.M.S. and F.M.S. are supported by fellowships from the Conselho Nacional de Desenvolvimento Científico e Tecnológico (CNPq) and Coordenação de Aperfeiçoamento de Pessoal de Nível Superior (CAPES), respectively. A.L.C.P. was supported by grants from the Conselho Nacional de Desenvolvimento Científico e Tecnológico (CNPq; processes 308950/2011-9, 305475/2014-2, PROTAXA 44.0413/2015-0). This research was supported by grants from the Fundação de Amparo à Pesquisa do Estado de São Paulo (BIOTA/FAPESP; process 11/50206-9) and Conselho Nacional de Desenvolvimento Científico e Tecnológico (CNPq; processes 565046/2010-1 and 303545/2010-0) to H.Z.

Appendix A.

Specimens used in the present study have been deposited in the following Brazilian scientific collections (acronyms in parentheses): Coleção Herpetológica da Universidade de Brasília (CHUNB), Distrito Federal; Museu Paraense Emílio Goeldi (MPEG), Pará; Museu de Zoologia da Universidade Federal da Bahia (UFBA), Bahia; Museu de História Natural Capão da Imbuia (MHNCI), Paraná; Pontifícia Universidade Católica do Rio Grande do Sul (MCT-PUCRS), Porto Alegre; Universidade Estadual de Londrina (MZUEL), Paraná; Universidade Federal de Mato Grosso (UFMT), Mato Grosso; Universidade Federal de Corumbá (CEUCH), Mato Grosso do Sul.

List of specimens with collection numbers

Leptodeira annulata

Brazil: Amazonas: Coari (MPEG 22229); Presidente Figueiredo (MPEG 17542). **Pará:** Almeirim (MPEG 23716); Marabá (MPEG 23795); Melgaço (MPEG 20016); Santarém (MPEG 19077). **Piauí:** Castelo do Piauí (MPEG 22781). **Rondônia:** Guajará-Mirim (MPEG 19480).

Sibynomorphus mikanii

Brazil: Bahia: Barreiras (UFBA 2126, UFBA 2131); Goiás: Goiânia (MPEG 24946, MPEG 24947). **Distrito Federal:** Brasília (CHUNB24014, CHUNB 29403, CHUNB 29922). **Mato Grosso:** Chapada dos Guimarães (UFMT 1967); Tangará da Serra (UFMT 6310). **Maranhão:** Estreito (MPEG 23129); Urbano Santos (MPEG 20556, MPEG 21521). **Minas Gerais:** Unaí (CHUNB 24451). **Paraná:** Apucarana (MHNCI 6886); Cornélio Procopio (MHNCI 2425); Fênix (MHNCI 11190); Ibiporã (MZUEL 153, MZUEL 1320); Ivaiporã (MHNCI 4761, MHNCI 9438); Londrina (MZUEL 60, MZUEL 157, MZUEL 615, MZUEL 620); Toledo (MHNCI 4637). **São Paulo:** Assis (MPEG 10403); Charqueada (MPEG 19232). **Tocantins:** Xambioá (MPEG 19855).

Sibynomorphus neuwiedi

Brazil: Bahia: Cachoeira (UFBA 1790); Caetité (UFBA 2147); Catú (UFBA 548, UFBA 2239); Jacobina (UFBA 902). **Minas Gerais:** Juiz de Fora (UFBA 330). **Paraná:** Balsa Nova (MHNCI 6376); Campina Grande do Sul (MHNCI 2181, MHNCI 7253); Morretes (MHNCI 12161); Quatro Barras (MHNCI 289); Paranaguá (MHNCI 4597); Piraquara (MHNCI 9954). **Santa Catarina:** Garuva (MHNCI 12069). **São Paulo:** Iguapé (MPEG 19234).

Sibynomorphus turgidus

Brazil: Mato Grosso: Cuiabá (UFMT 1974); Jauru (UFMT 6055); Vale de São Domingos (PUC-RS 14071); Vila Bela da Santíssima Trindade (UFMT 8876). **Mato Grosso do Sul:** Aquidauana (CEUCH 1504). Corumbá. (CEUCH 221, CEUCH 277, CEUCH 315, CEUCH 581, CEUCH 1099, CEUCH 1722, CEUCH 1836, CEUCH 1837, CEUCH 1972, CEUCH 1985, CEUCH 1986, CEUCH 3559, UFMT 1401, UFMT 1406, UFMT 1411, UFMT 1413, UFMT 1421, UFMT 1438, UFMT 1440). **Rio Grande do Sul:** São Francisco de Assis (PUC-RS 18735).

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