Body Shape and Food Habits of South American Goo-Eater Snakes of the Genus *Sibynomorphus*

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Abstract. Snakes of the tribe Dipsadini feed mostly on annelids, slugs, and snails. Some species that feed exclusively on snails are able to de-shell their prey prior ingestion. On the basis of dissection of preserved specimens from museums, we report the dietary habits of three species of *Sibynomorphus* from Brazil. Eighteen to 26% of the snakes had stomach contents, varying from 1–8 items, and the number of prey was not correlated with snake size. Prey mass was positively correlated with snake mass, but relative prey mass decreased with increasing snake size. Prey mass represented less than 5% of the predator mass for all species. *Sibynomorphus neuwiedi* and *S. mikanii* only had Veronicellidae slugs in their digestive tract, whereas *S. ventrimaculatus* also included snails in their diet. *Sibynomorphus mikanii* ingested most prey rear-first, but there was no difference in direction of prey ingestion by the other two species. Snake morphology differed among species and provided insights into habitat use and feeding habits. *Sibynomorphus neuwiedi* was the largest species and had the longest tail. Its eyes were also larger than those of *S. mikanii,* which, together with tail size, suggests more arboreal habits. *Sibynomorphus ventrimaculatus* had the largest head relatie to the body, which might facilitate ingestion of snails. In summary, the three species of *Sibynomporphus* are slug specialists. Like other goo-eaters, these snakes feed on very small and low caloric prey, which might require them to feed frequently. This hypothesis is supported by the larger number of prey ingested by these snakes compared to non-goo-eater species of Dipsadini.

Keywords. Diet; Feeding habits; Morphology; Slug; Snail.

Resumen. Culebras de la tribu Dipsadini se alimentan de anélidos, caracoles y babosas. Algunas especies se alimentan solamente de caracoles que sacan de sus conchas antes de ingerílos. Basado en la disección de espécimen preservadas en museos, nosotros reportamos los hábitos alimentarios de tres especies de *Sibynomorphus* de Brasil. Dieciocho a 26% de las culebras tenían algún contenido estomacal, variando de una a ocho presas, y el número de presas no estaba correlacionado con el tamaño de las culebras. La masa corporal de las presas estaba positivamente correlacionada con la masa corporal de las culebras, pero la masa relativa de la presa disminuía con lo incremento del tamaño de la culebra. La masa de la presa representaba menos de 5% de la masa del predador en todas las especies. *Sibynomorphus neuwiedi* y *S. mikanii* se alimentan solamente de babosas Veronicellidae, mientras *S. ventrimaculatus* tanbien incluye caracoles en su dieta. Las culebras ingerían las presas por la cabeza o por la parte posterior del cuerpo, excepto la *S. mikanii,* que frecuentemente ingería las presas por la parte posterior. La morfología se diferencia en cada especie y nos sugere una idea del uso de hábitat y hábitos alimenticios. *Sibynomorphus neuwiedi* es la mayor especie y tiene la cola más larga. Sus ojos son también mayores que los ojos de la *S. mikanii.* Estas características sumadas a la larga cola sugieren hábitos más arbóreos. *Sibynomorphus ventrimaculatus* tiene la cabeza más grande en proporción al cuerpo, y esto podría facilitar la ingestión de caracoles. En resumen, las tres especies de *Sibynomporphus* son primariamente especialistas en babosas. Como otras culebras que comen caracoles, babosas y anélidos, las *Sibynomporphus* se alimentan de presas muy pequeñas y de baja calorías, y por eso tienen que comer con más frecuencia. Este facto és apoyado por el alto número de presas ingeridas por cada individuo cuando comparado a otros Dipsadini que comen otros tipos de presas.

INTRODUCTION

The 12 species of snakes in the genus *Sibynormorphus* Fitzinger, 1843 are restricted to South America and 5 species occur in Brazil (Cadle, 2007). Together with *Dipsas* Laurenti, 1768, *Sibon* Fitzinger, 1826, *Plesiodipsas* Harvey et al, 2008, and *Tropidodipsas* Günther, 1858, the genera likely form a monophyletic group in the tribe Dipsadini Bonaparte, 1838 (Zaher, 1999; Harvey et al., 2008), species of which feed mostly on soft and viscous invertebrates such as annelids, slugs, and snails (Stuart, 1948; Martin, 1958; Peters, 1960). In reviewing the anatomy and tax-

onomy of dipsadine snakes, Dunn (1951) suggested the inward direction of the teeth towards the maxilla could help these snakes to extract the snail's body from its shell. About 10 years later, Peters (1960) reported that only slugs and de-shelled snails were found in the 100 stomach contents he analysed (species not reported). He concluded that most species of the tribe are monophagous and that cranial morphology and dentition in Dipsadini are associated with malacophagy (Peters, 1960).

Further field-based evidence on the snail-eating habits of *Dipsas* and *Sibon* species are available (Martins and Oliveira, 1999; Ray et al., 2012). De-shelling behavior

was described for *Dipsas indica* Laurenti, 1768 (Sazima, 1989), and captive *Sibon nebulatus* Linnaeus, 1758, *Tropidodipsas philippii* (Jan, 1863), and *T. annulifera* Boulenger, 1894 (Sheehy III, 2012). Although most *Tropidodipas* and *Sibon* are commonly referred to as snail eaters, quantitative studies of their diet are absent. Similarly, the only evidence for snail eating in a *Sibynomorphus* species (*S. neuwiedi* Ihering, 1911 derives from a captive-based study (Laporta-Ferreira et al., 1986), with all other records of prey being slugs (Palmuti et al., 2009; Maia-Carneiro et al., 2012).

Skull and muscle anatomy can be directly related to the evolution of food habits of snakes (Savitzky, 1981; Gans, 1983; Scanlon and Shine, 1988; Rodríguez-Robles et al., 1999a; Cundall et al., 2000). Thus, differences in body shape among (Shine et al., 2014) and within species (Shine, 1991; Luiselli and Angelici, 1998; Aubret et al., 2004) can reflect dietary differences, not only in snakes but also in lizards (Sagonas et al., 2014). Differences in head size might reflect divergences in the diet and foraging mode between *Dipsas variegata* (Duméril et al., 1854) and *D. trinitatis* Parker, 1926 (Murphy and Rutherford, 2014), but this kind of relationships remain unstudied in the tribe. Skull differences between *Sibynomorphus mikanii* Schlegel, 1837 and *S. newiedi* were also associated with the ability of the latter to eat snails (Laporta-Ferreira et al., 1986).

In the present work we used large samples of preserved museum specimens to investigate the diet of three species of sleep snakes from Brazil: *Sibynomorphus mikanii, S. neuwiedi,* and *S. ventrimaculatus* (Boulenger, 1885) to test the hypothesis that, like other Dipsadini, *Sibynomorphus* snakes feed on both snails and slugs. We also investigated differences in body shape and possible relationships of body shape and habitat use in the three species.

MATERIALS AND METHODS

Studied species

Sibynomorphus mikanii occurs in the Atlantic Forest Domain and Brazilian Savannah (Cerrado) bordering the wet coastal areas in the east side, Pinewood (*Araucaria*) forest in the south, and the Pantanal wetland in the west (Franco, 1994). *Sibynomorphus neuwiedi* is restricted to the coastal Atlantic Forest in Brazil. *Sibynomorphus ventrimaculatus* occurs in the Pinewood forest of south Brazil, the Atlantic Forest Domain, and the Cerrado, ranging from Rio Grande do Sul to Mato Grosso do Sul, São Paulo, and Minas Gerais states (Franco, 1994). Phylogenetically, *S. ventrimaculatus* is more closely related to *S. neuwiedi* and certain *Dipsas,* while *S. mikanii* is more closely related to *S. turgidus* Cope, 1868 and *Ninia* Baird and Girard, 1853 (Grazziotin et al., 2012).

Methods

We analysed preserved specimens of *Sibynomorphus mikanii* (*n* = 203), *S. neuwiedi* (*n* = 84), and *S. ventrimaculatus* (*n* = 79) belonging to the herpetological collections of Instituto Butantan, São Paulo (IB), Laboratório de Herpetologia do Museu de Ciências e Tecnologia da Pontifícia Universidade Católica do Rio Grande do Sul, Porto Alegre (MCP), Museu de História Natural da Universidade Estadual de Campinas, Campinas (ZUEC), Museu de História Natural do Capão da Imbuía, Curitiba (MHNCI), and Departamento de Zoologia da Universidade Federal de Santa Maria, Santa Maria (ZUFSM), all in Brazil. Collection dates spanned from 1914–2000. To avoid taxonomic problems, we restricted our analyses of *S. mikanii* to specimens from São Paulo state (northern limit: 19°57′S, 50°32′W; southern limit: 25°00′S, 47°55′W; eastern limit: 22°41′S, 44°19′W; western limit: 22°34′S, 53°03′W), *S. neuwiedi* from São Paulo and Paraná states (northern limit: 19°57′S, 50°32′W; southern limit: 26°25′S, 51°18′W; eastern limit: 22°41′S, 44°19′W; western limit: 24°04′S, 54°15′W), and *S. ventrimaculatus* to specimens collected only in Rio Grande do Sul state (northern limit: 27°08′S, 55°24′W; southern limit: 33°45′S, 53°23′W; eastern limit: 29°20′S, 49°43′W; western limit: 30°12′S, 57°33′W).

Each specimen was measured for snout–vent length (SVL), tail length (TL), and head length (HL), dissected by a mid-ventral incision, and inspected for sexual maturity, according to Pizzato et al. (2008). We dissected the stomachs of each snake to check for prey items. When prey was present, we noted the direction of ingestion (head or rear), and removed it from the stomach. If intact or poorly digested, each prey was measured (total length) and blotch dried on paper towel and weighed. Snakes presenting stomach contents had the preserving liquid drained and were also weighed. Prey items were preserved in 70% ethanol and later identified to family. There were four vestiges of prey for *Sibynomorphus mikanii,* eight for *S. neuwiedi,* and six for *S. ventrimaculatus* that could not be identified to any taxonomic level and thus were not included in the prey type analyses. At a later time, we measured HL and the greatest diameter of the left eye (EYE) of *S. mikanii* (20 females, 22 males) and *S. neuwiedii* (20 females, 21 males) from IB. Unfortunately, no *S. ventrimaculatus* were available for measurement in the IB collection.

Analyses

We compared body shape among species using Kruskall-Wallis (SVL), ANOVA (TL, HL), and *t*-test (EYE), and Tukey post hoc tests when appropriate. For these general comparisons sexes were pooled together. Because of allometric relationships, TL and HL were regressed against SVL, and EYE was regressed against HL. Their residuals (i.e., relative

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measurements) were then used in the ANOVAs and *t*-tests. Eye and head size were log-transformed prior to analyses.

We calculated the percentage of snakes that presented stomach contents from the total of individuals dissected to infer about feeding frequency, using only specimens that were not kept captive after collection. We tested if relative prey mass (prey mass/snake body mass) increases proportionally with snake SVL using ANCOVA, with species as covariate. The number of each different prey types present in the stomach of a species was compared by χ^2 test. The average number of prey ingested per snake was compared among the species using Kruskall-Wallis test and post hoc Tukey. Snake SVL was linear regressed by the number of prey ingested to test the hypothesis that larger snakes would ingest more prey. Statistical analyses were done using the software Statistica version 5.5 (Statsoft, 1999) and JMP version 13.0 (SAS Institute, 2016). Averages are followed by standard deviation and range.

RESULTS

Sibynomorphus neuwiedi had a significantly larger SVL (423.5 ± 117.7 mm, 254–660 mm, *n* = 126) than *S. mikanii* (352.9 ± 100.0 mm, 280–580 mm, *n* = 144) and *S. ventrimaculatus* (335.3 ± 105.9 mm, 240–577 mm, *n* = 111; $H_{535.2}$ = 75.55, *P* < 0.001; Fig. 1A). Relative TL differed between all pairs of species ($F_{387.2}$ = 163.82, *P* < 0.001); *S. neuwiedi* had the largest relative TL and *S. mikanii* the shortest (Fig. 1B). All pairs of species also differed from each other in terms of relative HL ($F_{346.2}$ = 32.81, *P* < 0.001): *S. ventrimaculatus* was the species with the largest relative HL, and *S. mikanii* had the smallest relative HL (Fig. 1C). Eye size differed between species, with *S. neuwiedi* presenting proportionally larger eye than *S. mikanii* (*t* = 10.04, df = 81, *P* < 0.0001; Fig. 1D).

The percentage of snakes that had stomach contents was 26.1% for *Sibynomorphus mikanii,* 18.5% for *S. neuwiedi,* and 25% for *S. ventrimaculatus.* All identifiable prey of *S. mikanii* (*n* = 85 recovered from 53 snakes) and *S. neuwiedi* (*n* = 39 from 32 snakes) were veronicellid slugs. Unlike the other species, *S. ventrimaculatus* had both veronicellid slugs and snails as stomach contents (from a total of 41 snakes), with slugs (*n* = 59, 84.3%) being significantly more abundant than snails (*n* = 11, 15.7%; χ^2 = 28.45; df = 1; *P* < 0.001). We could not identify to family level the snails ingested by *S. ventrimaculatus.*
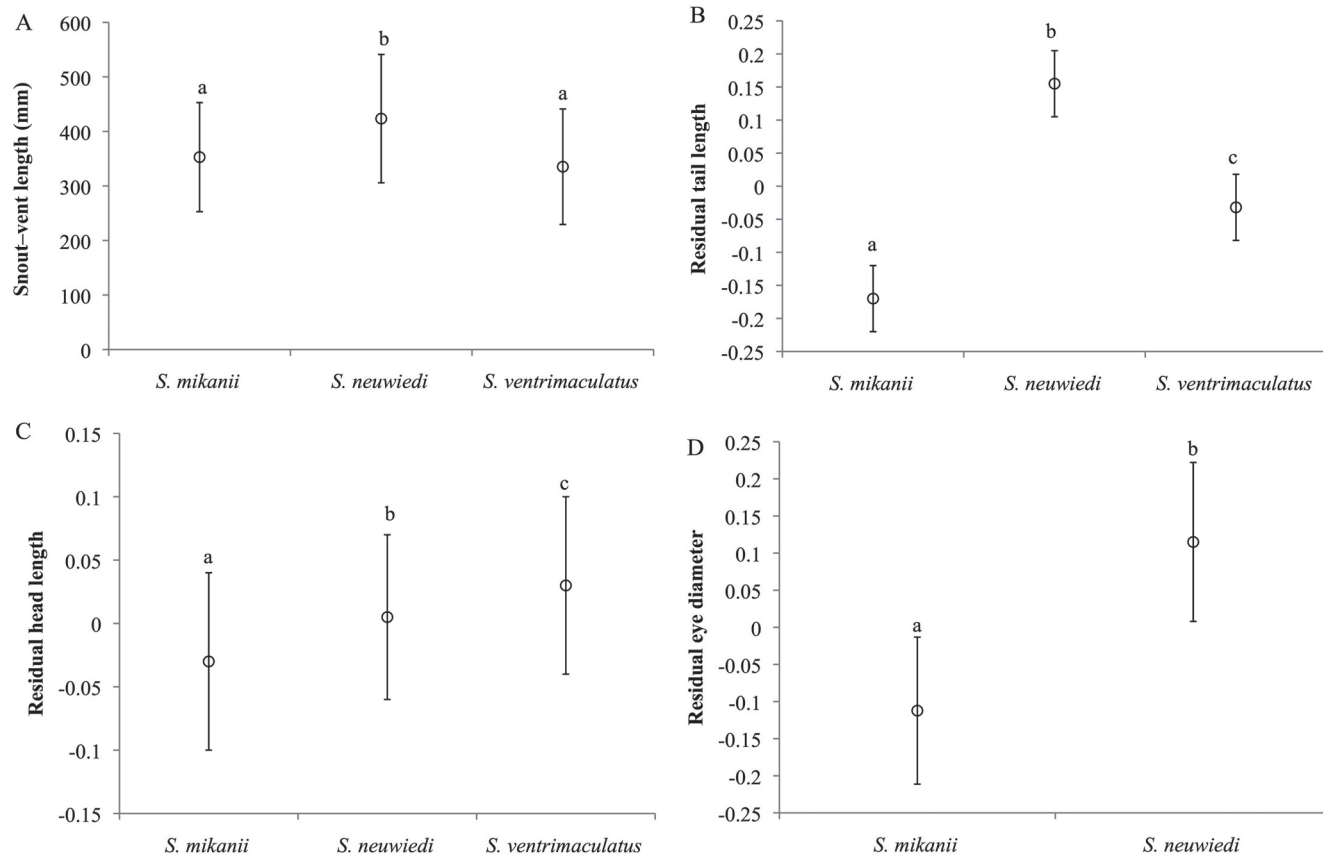

Figure 1. Snout–vent length **(A)**, residual tail length **(B)**, residual head length **(C)**, and residual eye size **(D)** of *Sibynomorphus* species from Brazil. Circles are averages and whiskers are standard deviations. Letters above the whiskers represent statistical difference according to Tukey post hoc test.

The number of prey ingested per snake varied from 1–8 (1.70 ± 1.74) in *Sibynomorphus mikanii,* 1–4 (1.56 ± 0.92) in *S. neuwiedi,* and 1–5 (1.9 ± 1.2) in *S. ventrimaculatus,* but these differences were not significant ($H_{2,110}$ = 3.68, P = 0.159). Snake SVL was not correlated with number of prey ingested in any of the species (*S. mikanii,* R^2 = 0.03, t = 1.26, P = 0.215; *S. neuwiedi,* R^2 = 0.04, t = 0.84, P = 0.414; *S. ventrimaculatus,* R^2 = 9.4 × 10^{-6}, t = -0.02, P = 0.987).

The relative mass of each prey was similar and < 5% of the snake body mass for all species (*Sibynomorphus mikanii,* 0.04 ± 0.054, n = 41; *S. neuwiedi,* 0.035 ± 0.029, n = 16; *S. ventrimaculatus,* 0.039 ± 0.035, n = 29). Larger snakes tended to eat larger prey (*S. mikanii,* R = 0.35, P = 0.003, n = 67; *S. neuwiedi,* R = 0.60, P = 0.004, n = 21; *S. ventrimaculatus,* R = 0.53, P = 0.001, n = 34), but relative prey mass decreased with snake SVL ($F_{1,69}$ = 12.19, P = 0.0009) independently of the species ($F_{2,69}$ = 0.13, P = 0.873; Fig. 2).

In *Sibynomorphus neuwiedi* and *S. ventrimaculatus* the number of prey ingested head-first was not significantly higher than rear-first (χ^2 = 2.66, df = 1, P = 0.102, n = 24; and χ^2 = 0.36, df = 1, P = 0.549, n = 25, respectively). However, *S. mikanii* usually ingested prey rear-first (χ^2 = 18.3,
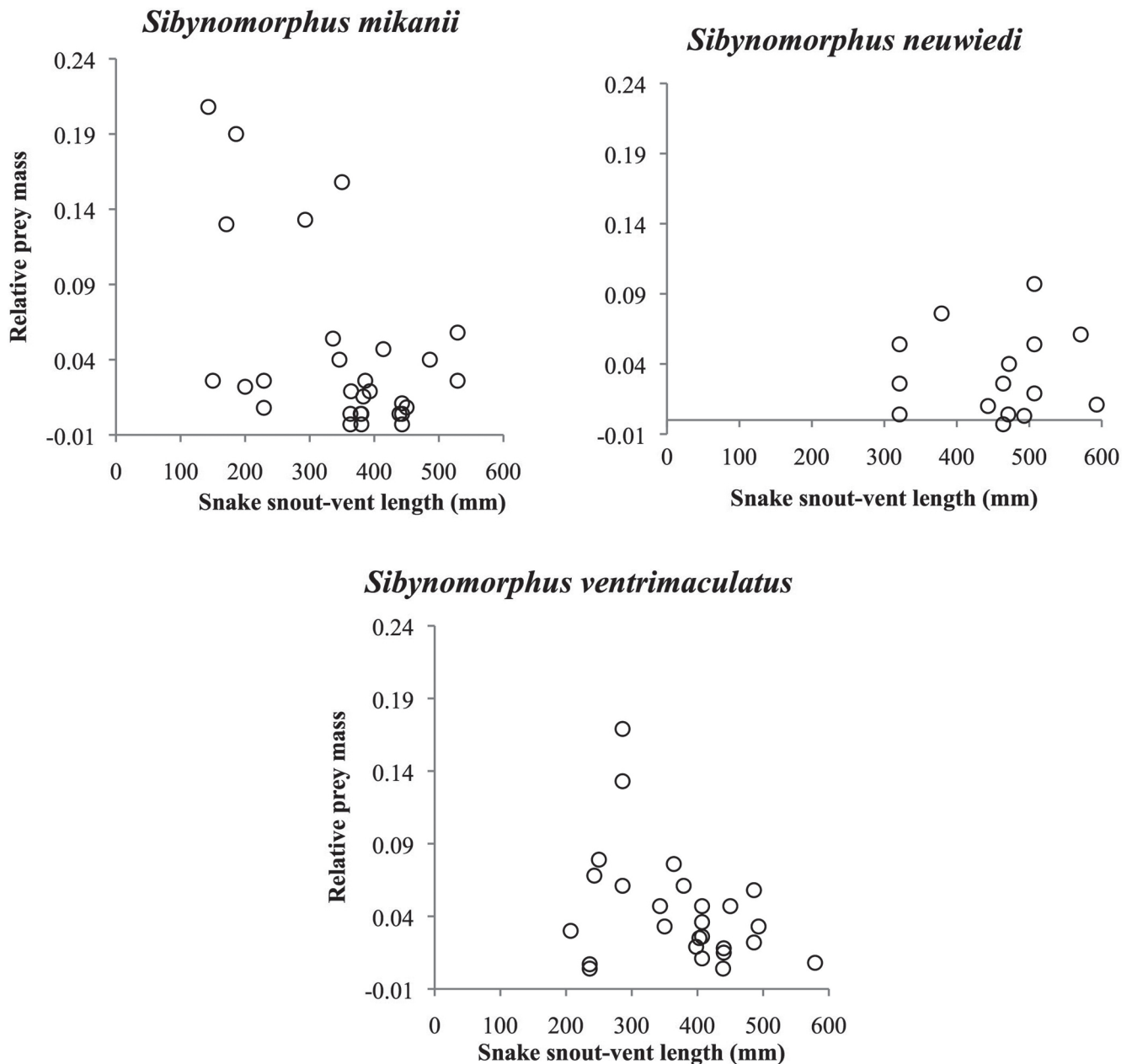

Figure 2. Relationships between relative prey mass and snake snout–vent length in three species of *Sibynomorphus.*

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df = 1, *P* < 0.001, *n* = 56) and two individuals ingested by the middle of the body (prey were folded inside the stomach).

DISCUSSION

Lateral compression of the body, elongation of the body and tail, abrupt narrowing of the neck, large, protruding eyes, and widening of the scales of the vertebral row are traits commonly reported in several lineages of arboreal snakes (Peters, 1960; Lillywhite and Henderson, 1993), including many Dipsadini (Peters, 1960; Kofron, 1985). Additionally, even when phylogenetic relationships are taken into account, lateral compression of the body and long tails are recurrent traits in arboreal pythonids and boids (Pizzatto et al., 2007). *Sibynormorphus neuwiedi* is at least partially arboreal, whereas *S. mikanii* and *S. ventrimaculatus* are terrestrial (Marques et al., 2004, 2015; Marques and Sazima, 2004). In agreement with the arboreality traits suggested by Peters (1960), *S. neuwiedi* has larger body size and the longest relative tail length compared to the other two studied species. The larger eyes of *S. neuwiedi* than *S. mikanii* also reinforce more arboreal habits in the former. Moreover, the eyes of *S. neuwiedi* are clearly more protrusive than those of the other two species (cf. Marques et al., 2004, 2015). Nevertheless, larger eyes might also be involved in vision-mediated prey recognition, as in the snail-eating *Pareas carinatus* (Boie, 1828) (Danaisawadi et al., 2016).

The three studied species of *Sibynomorphus* are slug specialists, and all slugs preyed on belonged to the family Veronicellidae, the most diverse group of slugs in Brazil. However, *S. ventrimaculatus* also include snails in its diet. A large number of snakes in Dipsadini are known as goo-eaters, specialized in eating almost exclusively molluscs (Greene, 1997), but with some species of *Dipsas* and *Sibon* also eating earthworms (Ray et al., 2012) and some *Sibon* preying on frog eggs (Ryan and Lips, 2004; Montgomery et al., 2007; Ray et al., 2011, 2012). Diet specialisation is often reflected in particular morphology (Savitzky, 1981, 1983; Hoso et al., 2007; Cundall et al., 2000). Laporta-Ferreira and Salomão (2004) suggests that the larger quadratum of *S. neuwiedi,* when compared to *S. mikanii,* would facilitate capture and ingestion of snails, as recorded in captivity. Geometric morphometrics confirmed large quadratum in *S. neuwiedi* when compared to slug specialist *S. mikanii* (Santos et al., 2017). Despite our results showing *S. neuwiedi* has a larger head than *S. mikanii,* only veronicellid slugs were consumed by these species, as also shown for *S. neuwiedi* in other areas in Brazil (Palmuti et al., 2009; Maia-Carneiro et al., 2012). *Sibynomorphus ventrimaculatus* was the only species we studied to also include snails in its diet, and it was the species with the largest head of all three. Given the phylogenically closeness of *S. ventrimaculatus* and *S. neuwiedi* (Grazziotin et al.,

2012) head size could be a conservative trait. However, snail-eating *S. turgidus* also have larger quadratum than its closely related slug specialist *S. mikanii,* and non goo-eater Dipsadini *Leptodeira annulata* Linnaeus, 1758 (Santos et al., 2017).

In *Pareas* Wagler, 1830, a genus not closely related to *Sibynomorphus,* jaw and teeth asymmetry in some species facilitates consumption of dextral snails (Hoso et al., 2007). Whereas the little asymmetry in *P. carinatus,* prey handedness recognition and change in capture behavior enable predation of both dextral and sinistral snails (Danaisawadi et al., 2015, 2016). Jaw and teeth asymmetry, suggesting snail-eating capabilities, has also been recorded in *S. neuwiedi* and *S. tugidus,* but not in *S. mikanii* or *Leptodeira annulata* (Santos et al., 2017). In this context, asymmetry is also expected in *S. ventrimaculatus.*

In general, ca. 25% of the specimens of each *Sibynomorphus* species had stomach contents. In vertebrate-eating dipsadines, the reported frequencies of specimens with prey items are more variable: 33% in *Imantodes cenchoa* Linnaeus, 1758 from the Amazon (Sousa et al., 2014) and 12% in *Hypsiglena torquata* (Günther, 1860) in the arid areas of California, USA (Rodríguez-Robles et al., 1999b). However, feeding frequency can be largely related to type of prey consumed. The vertebrate-eating dipsadines usually had only one prey in their stomach (Rodríguez-Robles et al., 1999b; Sousa et al., 2014) indicating a lower feeding frequency compared to goo-eaters. *Sibynomorphus* ingested on average almost two prey. This suggests similar feeding frequency and prey number as in another dipsadine, *Atractus reticulatus* (Boulenger, 1885) from the savannahs and grasslands of southern Brazil, that feeds on earthworms and leeches (Balestrin et al., 2007). Slugs and annelids have much lower energetic contents than vertebrate prey, such as fish and mammals (Cummins and Wuycheck, 1971; Arnold, 1993). Thus, to compensate for the low energy intake per unit of prey, snakes cosuming low-energy prey should feed more frequently than species consuming high-energy prey. Accordingly, a high frequency of individuals with prey in the gut was found for arthropod specialists *Leptotyphlops* spp. (Punzo, 1974) and earthworm specialist *Thamnophis scaliger* (Jan, 1963), which also consumes multiple prey per feeding event, and females continue to feed while gravid (Reguera et al., 2011). In *S. mikanii,* the high frequency of road-kills (Marques and Sazima, 2004) and of individuals collected by lay people and taken to Instituto Butantan also strongly supports the hypothesis of high foraging activity in these snakes. However, the percentage of snakes with stomach contents in our samples was not particularly high compared to other dipsadines that feed on more caloric vertebrate prey. This lack of difference might be due the fact that snails are more easily digested than prey containing bones, scales, or an exoskeleton and, therefore, might remain in the snake stomach for a short time.

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The number of prey ingested can depend on predator size and/or prey size (Voris and Moffett, 1981; Godley et al., 1984). Number of prey was not related to snake SVL in *Sibynomorphus,* likely because slugs are digested quickly, leading to underestimation of prey numbers. Similarly, no relationship between snake SVL and number of prey was found for *Tantilla gracilis* Baird and Girard, 1853, which feeds on small invertebrates (Cobb, 2004). However, our results suggest a relationship between prey size and number among snake species: *Sibynormorphus* species often had more than one prey in the stomach and on average prey accounted for only 5% of the snake body mass. In contrast, *Imantodes cenchoa* and *Hypsiglena torquatus* that eat larger items (mostly > 10% and 24% of snake mass, respectively) mostly ingest only one prey per feeding event, except for *H. torquatus* specimens containing squamate eggs (Rodríguez-Robles et al., 1999b; Sousa et al., 2014). Other snake species that feed on very small prey (e.g., *Tantilla gracilis* and *Leptotyphlops* spp.) also ingest multiple prey per feeding event (Punzo, 1974; Webb et al., 2000; Cobb, 2004).

Relative prey mass decreased with snake size, showing that small snakes eat relatively large prey and larger snakes do not exclude small prey from their diet. This pattern, although unusual among snakes (Arnold, 1993), has also been detected in other snakes (Shine, 1977, 1987; Slip and Shine, 1988; Arnold, 1993; Cobb, 2004). For example, large Australian elapids continue to consume small prey, likely because Australian ecosystems lack large potential prey. These snakes are diet generalists and active foragers, capture and ingestion costs are small in relation to energy content of the prey, and envenomation of prey eliminates risks (Shine, 1977, 1987). In contrast, *Sibynormorphus* snakes are highly specialized on one type of very low calorie prey and have no venom. So why do these snakes not exclude small prey as they grow? A possible explanation is that capture and ingestion costs might be minimal and large prey may not be abundant. Most of the Neotropical Veronicellidae Gray, 1840 slugs are small (4–6 cm; Thomé, 1972) and large species seem to be rare in Brazil (Agudo-Padrón, 2009). Most exotic species are also small (Agudo-Padrón, 2009; Gomes et al., 2011), except for *Limax maximus* Linnaeus, 1758 (CABI, 2016). Combined with the low energy content of the slugs, *Sibynomorphus* snakes might need to consume as many prey as they can find and might not afford, energetically, to refuse any prey.

Most snakes, and some lizards, that feed on large items ingest prey head-first, which might facilitate ingestion of the limbs (Diefenbach and Emslie, 1971; Loop and Bailey, 1972; Greene, 1976). However, direction of ingestion should not be important for species that feed on elongate, malleable, or easy to swallow prey (de Queiroz and de Queiroz, 1987). This is supported by our results in which *Sibynomorphus neuwiedi* and *S. ventrimaculatus*

ingested prey head- or rear- first equally. However, *S. mikanii* preyed mostly from the rear, which differs from the 'head-first' preference found in *Sibon* and *Tropidodipsas* (Sheehy III, 2012). Accordingly, only 32% of prey was ingested by the head in the goo-eater *Atractus reticulatus,* as opposed to 71.96% in vertebrate-eaters *Imantodes cenchoa* and 88% in *Hypsiglena torquata* (Rodríguez-Robles et al., 1999b; Sousa et al., 2014).

In conclusion, the three studied *Sibynomorphus* species are mollusc specialists feeding mostly on small slugs, and only one species also prey on snails. They tend to ingest multiple prey per feeding event and do not exclude small items from their diet as they grow. Differences in head size might be related to the ability to ingest snails and differences in relative tail length suggests different degrees of arboreality among the species.

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