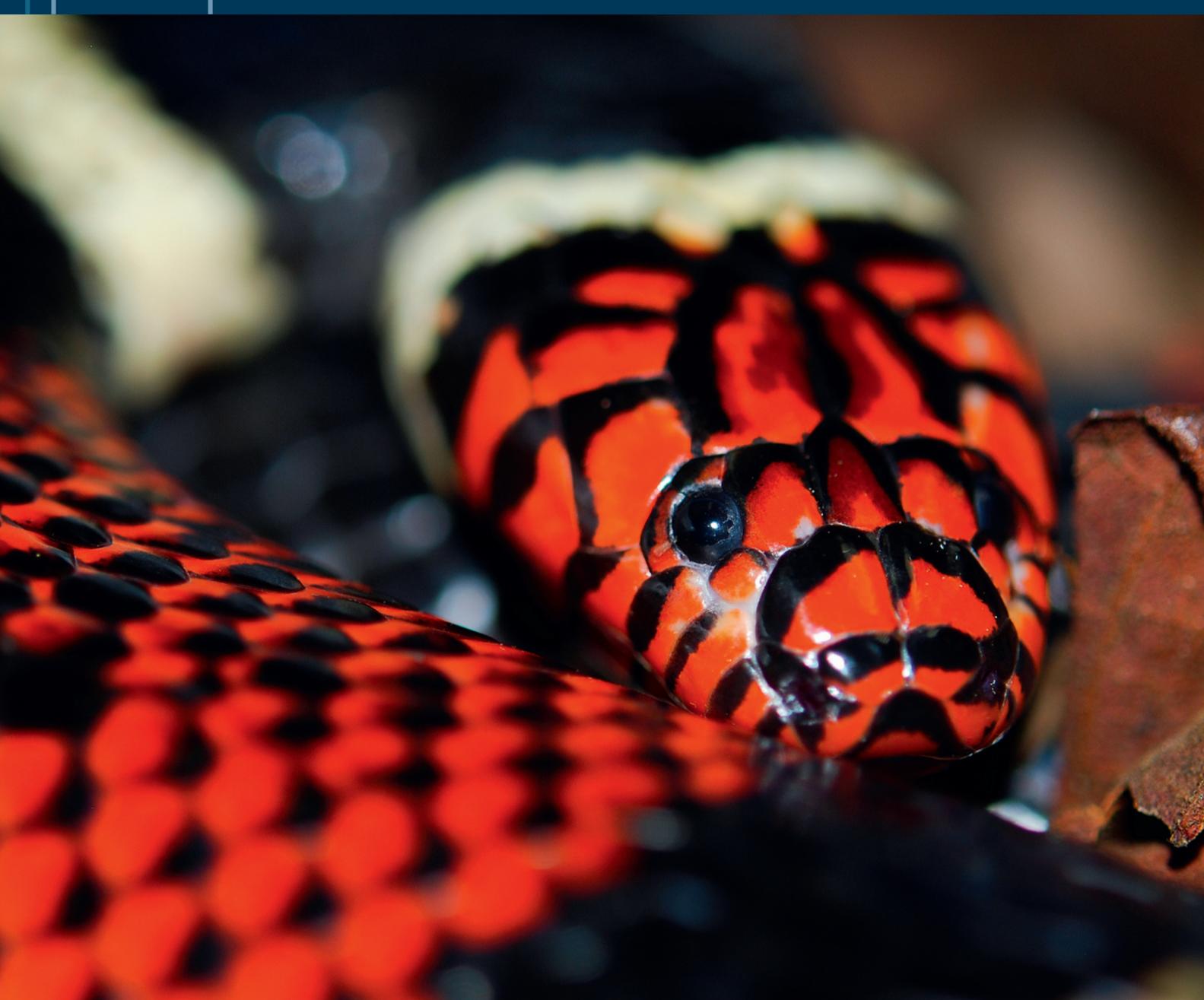


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# Aquatic adaptations in a Neotropical coral snake: A study of morphological convergence

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## Abstract

*Micrurus surinamensis* is an aquatic member of the genus *Micrurus*. This species is known for its highly specialized venom and distinctive diet, mostly made of aquatic vertebrates. Here, we explore both external (head and body) and skull shape morphologies in *M. surinamensis*, comparing it with two terrestrial species of the genus (*M. lemniscatus* and *M. spixii*) and to aquatic and terrestrial species of distantly related groups. We use both traditional and geometric morphometrics to determine whether the presence of similar traits in head shape morphology is rather the result of adaptive convergences between *M. surinamensis* and other aquatic species, or whether it is the product of phylogenetic conservatism within the genus. Results from both traditional and geometric morphometrics show that *M. surinamensis* can be considered convergent with aquatic species, mainly in the skull shape. *Micrurus surinamensis* differs from the two terrestrial species of *Micrurus* by having a wider head, smaller distance between nostrils, and a long tail. Geometric morphometric analysis shows that despite having an extremely conserved skull and mandible shape, *M. surinamensis* shows a longer supratemporal and quadrate bones than in terrestrial *Micrurus*, indicating a larger gape for this species. A more kinetic skull combined with a larger gape would allow *M. surinamensis* to feed on fish, which represent larger and wider prey that contrast with the elongate prey, which compose the main diet of species in the genus *Micrurus*. Our results illustrate the importance of both phylogenetic conservatism and adaptation in shaping species morphology.

## KEY WORDS

aquatic snakes, Elapidae, geometric morphometrics, morphology, skull

## 1 | INTRODUCTION

Snakes represent one of the ecologically and taxonomically most diverse group of tetrapods (Cadle, 1987; Cundall & Irish, 2008; Gans,

1961; Greene, 1997; Hampton, 2011; Rieppel, 1988; Zaher et al., 2009) and are known to occur in a large number of environments, including aquatic habitats (Socha, 2011; Vitt & Cadle, 2009). Several independent lineages of snakes invaded marine and freshwater

environments, including the extinct simoliophiids, palaeophiids, archaeophiids, and the extant acrochordids, elapids, homalopsids, natricids, colubrids, and dipsadids (Graziotin et al., 2012; Rage, 1987; Zaher et al., 2009). Among these, Australasian homalopsids and Neotropical dipsadids of the tribe Hydropsini are predominantly aquatic with morphological adaptations that have been reasonably documented (Greene, 1997; Murphy, 2012; Murphy & Voris, 2014; Zaher, 1999). On the other hand, little is known about the morphology of aquatic snakes that belong to predominantly non-aquatic groups, such is the case of *Micrurus surinamensis*, the single aquatic species from a genus of mostly terrestrial/fossorial animals.

Some of the morphological, physiological, and behavioral attributes necessary to perform in an aquatic habitat are very different from those required for a terrestrial life (Brischoux & Shine, 2011; Segall, Cornette, Fabre, Dodoy-Diana, & Herrel, 2016). Aquatic and semi-aquatic snakes solved in part the problem of locomotion by acquiring a laterally flattened body shape (Greer, 1997; Heatwole, 1999; Pattishall & Cundall, 2008). Some aquatic snakes (e.g., sea snakes) have a laterally compressed tail (paddle-like), which provides an additional thrust against the liquid environment (Brischoux & Shine, 2011; Heatwole, 1999). Moreover, underwater prey capture has been suggested to impose strong constraints on head shape in aquatic snakes (Herrel et al., 2008; Segall et al., 2016; Young, 1991). Ideally, aquatic snakes should have a slender, streamlined, and long head that increases the hydrodynamic efficiency. However, narrower heads are considered less optimal for handling captured prey due to the relatively limited lateral movements of the jaws (Young, 1991). Thus, the "ideal" morphology for an aquatic snake is likely determined by the trade-off between a streamlined head that is functionally capable of swallowing large or bulky prey (Herrel et al., 2008; Segall et al., 2016; Vincent, Brändley, Herrel, & Alfaro, 2009).

*Micrurus* is a distinctly fossorial, terrestrial genus with 79 known species from which *M. surinamensis* is known to exhibit aquatic habits (Campbell & Lamar, 2004; Uetz & Hošek, 2016). Although known species of *Micrurus* feed predominantly on elongated invertebrates and vertebrates (e.g., other snakes, legless lizards, worm lizards, caecilians and freshwater eels; see also Appendix 1), a characteristic likely to be associated with their fossorial condition, the aquatic *M. surinamensis* feeds primarily on fish (Campbell & Lamar, 2004; Cunha & Nascimento, 1993; Martins & Oliveira, 1999; Passos & Fernandes, 2005; Roze, 1996; Silva & Aird, 2001; Slowinski, 1995). Given that members of *Micrurus* are known to have similar diets and habits, we expect morphological traits, such as body and skull shape, to be largely conserved within the genus. Major modifications in the morphology of *Micrurus surinamensis* would therefore reflect adaptations to life in an aquatic environment. To test this hypothesis, we selected and compared two species of *Micrurus* with terrestrial habits (*Micrurus lemniscatus*, which is closely related to *M. surinamensis*, and *Micrurus spixii*), and two aquatic species from the distantly related tribe Hydropsini (*Hydrops martii* and *Helicops hagmanni*). *Hydrops martii* is known to consume elongated fishes of the same taxa as *M. surinamensis*, while *H. hagmanni*

consumes mostly perciform and characiform (Teixeira, Montag, & Santos-Costa, 2017), which are generally wider, thus demanding different adaptations in the snake's morphology to be captured. To have a standard of comparison, we added two terrestrial dipsadids that consume large prey (*Oxyrhopus petolarius*: Costa, Provete, & Feio, 2014; and *Leptodeira annulata*: Santos-Silva et al., 2014) to evaluate whether morphological changes in *M. surinamensis* are associated with habitat transition, or just with the demand of consuming large prey in general. We compared head and body shapes for all species to evaluate whether there is any significant distinction between their morphology. We predict that, as both phylogenetic conservatism and ecological convergence are at play in the determination of morphology, *M. surinamensis* will be largely similar to its congeners, but differences will be in the direction of the aquatic snake models.

## 2 | MATERIAL AND METHODS

### 2.1 | Specimens and data collection

We analyzed a total of 267 adult specimens (male = 145; female = 122), belonging to three aquatic species *Micrurus surinamensis* (Cuvier, 1816), *Helicops hagmanni* Roux, 1910, and *Hydrops martii* (Wagler, 1824), and four terrestrial species, *Micrurus lemniscatus* (Linnaeus, 1758), *M. spixii* Wagler, 1824, *Leptodeira annulata* (Linnaeus, 1758), and *Oxyrhopus petolarius* (Linnaeus, 1758). Specimens were deposited in the following Brazilian scientific collections (acronyms in parentheses): Faculdades Integradas do Tapajós (FIT), Pará; Instituto de Pesquisas Científicas e Tecnológicas do Amapá (IEPA), Amapá; Instituto Nacional de Pesquisa da Amazônia (INPA), Amazonas; Instituto Butantan (IBSP), São Paulo; Museu Paraense Emílio Goeldi (MPEG), Pará; Museu de Zoologia da Universidade de São Paulo (MZUSP), São Paulo; Universidade Federal do Acre (UFAC), Acre; Universidade Federal de Mato Grosso (UFMT), Mato Grosso. The complete list of the analyzed specimens is given in Appendix 2.

### 2.2 | Linear morphometric data

We took eight linear measurements from the head and body of preserved specimens that we considered potentially related to the use of aquatic habitat (Brischoux & Shine, 2011): (i) snout-vent length (SVL)—from the tip of the snout to the cloaca; (ii) tail length (TL)—from the cloaca to the end of the tail; (iii) circumference (Circ)—the average circumference length taken from three different parts of the body: near the head, in the middle of the body and near the cloacae; (iv) head length (HL)—from the tip of the snout to the quadrate-mandibular articulation; (v) head width (HW)—length of the widest part of head; (vi) head height (HH)—maximum distance between the base of the mandible and the parietal surface; (vii) distance between eyes (DE)—maximum distance between the internal border of the orbits in the preocular scale, and (viii) distance between nostrils (DN)—maximum distance between the nostrils. Measurements were taken using a digital caliper with 0.01 mm precision for structures

smaller than 120 mm and a measurement tape with 1 mm precision for structures larger than 120 mm.

### 2.3 | Geometric morphometric data

For the geometric morphometric analysis, we manually cleaned the skulls of 10 specimens from *Micrurus surinamensis*, *M. lemniscatus*, *M. spixii*, *H. hagmanni*, *Hydrops martii*, *L. annulata*, and *O. petolarius*. Specimens were selected for skeletonization based on origin (from well sampled locations) and similarity (how similar they were externally to other individuals from the same location).

Pictures of the skulls in dorsal view, and mandibles and quadrate in lateral view, were taken using a digital camera Nikon D90 (Tokyo, Japan) coupled with a 105-mm macro lens and a tripod. Each image included a scale, and landmarks were digitized by a single investigator (FMS) using the TPSDig2 version 2.18 (Rohlf, 2015). Landmarks were chosen so as to correspond mainly to cranial sutures and extremes of structures—types I and II from Bookstein (1991), respectively—totaling 12 for the skull, five for the mandible, and three for the quadrate (Figure 1).

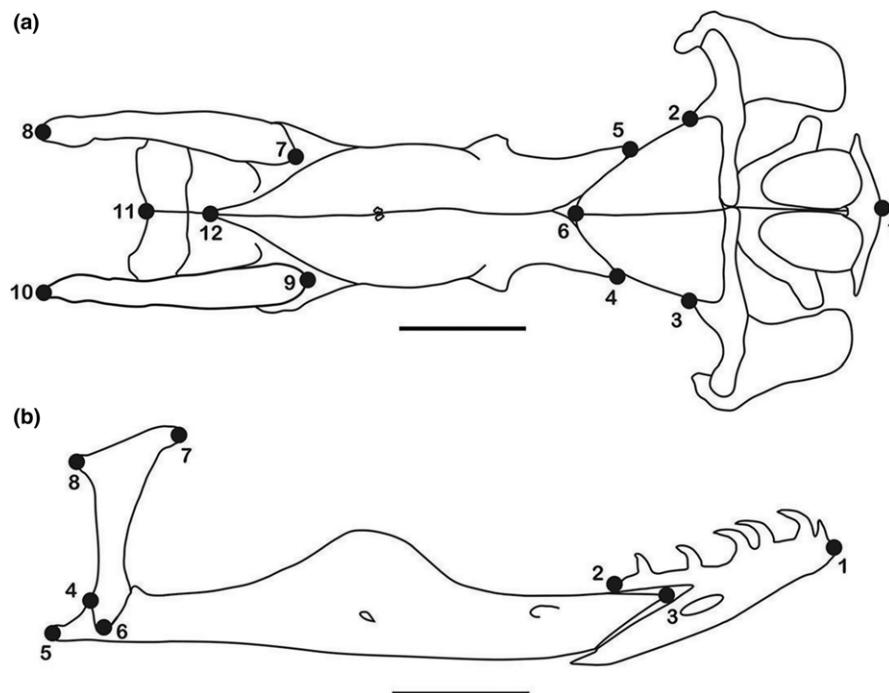
Repeatability was evaluated in a subset of 14 skulls (two for each species) that was photographed twice. Each photograph was digitized two times to access both within- and between-photograph measurement error. Repeatability of the full configuration was

measured using a Procrustes analysis of variance (ANOVA) procedure using individual and photograph as factors. The estimated mean squares were used to calculate photograph, and strict-sense repeatabilities were calculated following the suggestion by Fruciano (2016). The between-photograph repeatability was calculated using the photograph term mean squares, while the strict-sense repeatability (within-photograph, between replicates) was calculated using the residual mean squares.

### 2.4 | Data analyses

Head and body linear variables were log-transformed, and sexual dimorphism was tested through a two-sample Student's *t* test. We performed a principal component analysis (PCA) using the within-group variance–covariance matrix of all linear variables. To control for the effect of size variation between species, we projected the original observations on a plane orthogonal to the first principal component of this analysis, which accounts for the variation attributed to size differences (Bookstein, 1989), producing variables that are size-independent (Burnaby, 1966). To evaluate the differences between species, we conducted a second PCA using the size-corrected, full sample, variance–covariance matrix.

The three landmark configurations (skull, mandible, and quadrate) were subjected to a generalized Procrustes analysis (GPA—Rohlf &



**FIGURE 1** Landmarks used to analyze shape of the skull, mandible, and quadrate of the species with terrestrial and aquatic habits. (a) Dorsal view of the skull. 1—anterior tip of the premaxilla, 2 and 3—lateral extremities of the suture between prefrontal and frontal, 4 and 5—lateral extremities of the suture between frontal and parietal, 6—sagittal point of the suture between frontal and parietal, 7 and 9—anterior tips of the supratemporal bone, 8 and 10—posterior tips of the supratemporal bone, 11—anterior sagittal point between the exoccipital bones, 12—sagittal point of the suture between parietal and supraoccipital bones. (b) Lateral view of the mandible and quadrate. Mandible: 1—anterior tip of the dentary, 2—superior extremity of dentary, 3—anterior tip of the compound bone, 4—posterior extremity between compound and quadrate bones, 5—posterior tip of the compound bone. Quadrate: 6—mandibular articulation, 7—anterior-most point of the quadrate-supratemporal, 8—posterior-most point of the quadrate-supratemporal. Scale bars: 5 mm

Slice, 1990), the residuals of which were used in multivariate principal component analysis (PCA). Deformation grids based on thin plate splines were used to illustrate shape variation. For both the geometric and size-free linear morphometric data, we tested group differences through a two-way multivariate analysis of variance (MANOVA). These analyses were performed on the first two PCs from each dataset using species, sex, and their interaction as factors, using type II sum of squares. If results were significant, a post hoc pairwise MANOVA was conducted to determine what species differ from one another. *p*-Values for repeated comparisons were corrected using Bonferroni correction.

All analyses were performed using R version 3.3.3 (R Core Team 2017) and the R packages shapes (Dryden, 2013), geomorph (Adams & Otárola-Castillo, 2013), and lsmeans (Lenth, 2016).

## 2.5 | Direction of evolution

To test the association between the morphology of *M. surinamensis* and the transition to an aquatic environment, we first calculated the differences between the phenotypic averages of *M. surinamensis* and its closest relative, *M. lemniscatus* (Zaher, Graziotin, Prudente, & Silva, 2016). The vector produced this way is equivalent to the unscaled phylogenetic independent contrast between these species (Felsenstein, 1988) and was used as an estimate of the divergence ( $\Delta z_{\text{sur}}$ ). We then calculated vectors of differences between the reference species *M. lemniscatus* and each individual in the sample. If *M. surinamensis* converged morphologically with other aquatic species (*Hydrops martii* and *H. hagmanni*), we would then expect the vector correlation to be higher for aquatic species than for terrestrial species. We only investigated the alignment of

$\Delta z_{\text{sur}}$  with the divergence of aquatic and terrestrial non-*Micrurus* species.

Vectors of differences were calculated on the size-corrected variables for external morphology (vector size = 8) and on the first two PCs for each skull structure for geometric morphometric (vector size = 6). Vector correlations were calculated as the inner product between normalized vectors, thus ignoring scale differences between them. Because vectors could be more or less aligned by chance, we generated 10,000 random vectors with values drawn from a normal distribution. Each of these vectors was correlated with an arbitrary vector to produce a null distribution of correlation values. Because only positive values were considered favorable to our hypothesis (i.e., *M. surinamensis* should evolve in the direction of the aquatic models, and not away from them), we used the 95% superior quantile of this distribution to evaluate whether correlations are significant. For geometric morphometrics, the inclusion of additional PCs from each structure did not alter the correlation values, but did increase the tests power (i.e., decreased the 95% confidence interval expected by chance). Thus, we chose to retain only two PCs for each structure as a conservative test. Changing the reference species (e.g., *M. spixii*, *M. surinamensis* or the grand mean of terrestrial *Micrurus*) did not alter the overall pattern for either external morphology or geometric morphometric.

## 3 | RESULTS

### 3.1 | External morphology

Our results indicate the existence of sexual dimorphism for some of the external linear measurements of the head and body in all

**TABLE 1** Results of tests for sexual dimorphism between males (♂) and females (♀) in linear morphometric variables for all species included in the analysis.

TAXON	SEX (n)		SVL	TL	Circ	HL	HW	HH	DE	DN
<i>Micrurus surinamensis</i>	♂ (15)	<i>t</i> -value	4.21	-1.38	2.86	3.06	3.13	2.65	3.15	2.24
	♀ (12)	<i>p</i>	.000	.17	.008	.006	.004	.01	.004	.03
<i>Micrurus spixii</i>	♂ (20)	<i>t</i> -value	-2.55	-3.23	-2.64	-2.84	-2.60	-2.47	-3.16	-2.59
	♀ (14)	<i>p</i>	.01	.003	.01	.007	.01	.01	.003	.01
<i>Micrurus lemniscatus</i>	♂ (18)	<i>t</i> -value	0.05	0.24	-0.66	-0.37	-0.28	-0.16	-0.81	-0.03
	♀ (15)	<i>p</i>	.95	.80	.51	.70	.77	.87	.42	.97
<i>Hydrops martii</i>	♂ (20)	<i>t</i> -value	5.92	0.96	7.49	6.95	7.37	7.43	8.94	5.68
	♀ (26)	<i>p</i>	.000	.34	.000	.000	.000	.000	.000	.000
<i>Helicops hagmanni</i>	♂ (21)	<i>t</i> -value	4.76	-1.58	3.38	3.78	4.67	3.21	3.48	3.44
	♀ (7)	<i>p</i>	.001	.14	.01	.006	.001	.01	.006	.01
<i>Oxyrhopus petolarius</i>	♂ (11)	<i>t</i> -value	-0.83	-2.24	-0.46	-1.18	-0.95	-1.43	-1.47	-0.79
	♀ (10)	<i>p</i>	.41	.03	.64	.25	.35	.16	.15	.43
<i>Leptodeira annulata</i>	♂ (15)	<i>t</i> -value	1.42	-2.68	2.61	3.37	4.24	1.53	0.93	1.33
	♀ (15)	<i>p</i>	.16	.01	.01	.002	.000	.13	.36	.19

DE, distance between eyes; DN, distance between nostrils; HH, head height; HL, head length; HW, head width; SVL, snout–vent length; TL, tail length; Circ, circumference.

Significant statistical results are highlighted in bold.

**TABLE 2** Results of the regular (PCA) and size-free (PCA<sub>SF</sub>) PCA on morphological variables, loadings of each variable in the two first axes of each analysis, and percentage of total variance explained by each axis

Variables	PC1	PC2	PC <sub>SF</sub> 1	PC <sub>SF</sub> 2
SVL	-0.359	0.044	0.265	-0.184
TL	-0.269	0.876	-0.858	-0.415
Circ	-0.364	-0.088	-0.000	0.303
HL	-0.378	-0.046	-0.004	0.006
HW	-0.404	-0.306	-0.051	0.249
HH	-0.419	-0.311	0.007	0.352
DE	-0.315	-0.001	0.094	0.083
DN	-0.293	0.178	0.427	-0.714
% var	86.52	4.84	66.98	23.95

% var, proportion of the variance explained; DE, distance between eyes; DN, distance between nostrils; HH, head height; HL, head length; HW, head width; PCA, principal component analysis; SVL, snout-vent length; TL, tail length; Circ, circumference.

analyzed species (Table 1). *Micrurus surinamensis* showed sexual dimorphism for seven of the eight variables analyzed, females being larger than males in all variables except tail length which showed no dimorphism. In *M. spixii*, on the other hand, males were larger than females in all eight variables. Among the Hydropsini, *H. hagmanni* and *Hydrops martii* showed dimorphism in seven variables with females larger than males. Among the terrestrial dipsadids analyzed, *O. petolarius* shows no dimorphism, except in tail length with males having longer tails than females and *L. annulata* presented dimorphism only in a few characters (TL, Circ, HL, and HW) with females being bigger, except for tail length which is longer in males (Table 1).

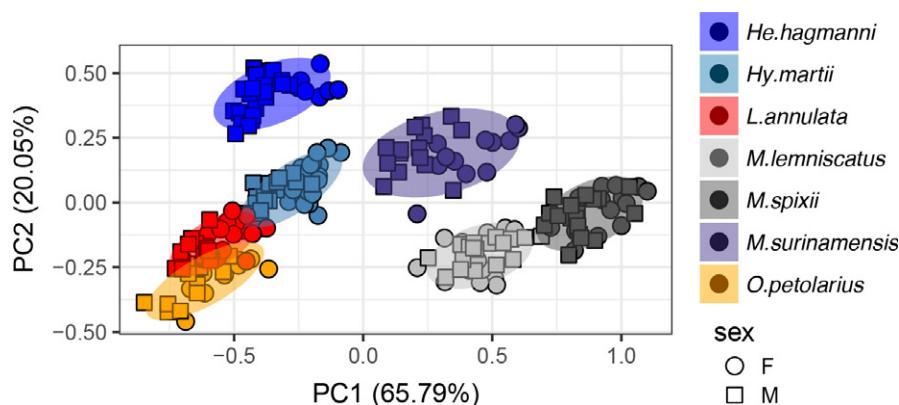
The first principal component of the within-group PCA for the log-transformed linear accounts for 86.52% of all variation showing negative loadings on all variables, thus representing the common allometric trend of the species studied here. The first size-free PCA axis accounts for 66.98% and has high positive loadings for DN and SVL and negative loadings for TL (Table 2). This axis shows the separation between both the aquatic and terrestrial models from the terrestrial *Micrurus*, with *M. surinamensis* assuming intermediate values (Figure 2). The second axis of variation explains 23.95% of the variation and has high positive loadings of HH, Circ, and HW, while

having high negative loadings of DN and TL. This axis mainly explains the contrast between the aquatic and terrestrial models, with *Micrurus* assuming intermediate values. Because the size-correction removes one degree of freedom from the dataset, the two-way MANOVA was performed on the first six PCs of the size-corrected variables. This analysis showed that the effect of sex, species, and interactions between them was significant (Table 3), with the difference between species having a greater effect than both sex and the interaction term (Figure 2, Table 3).

### 3.2 | Shape variation in skull, quadrate, and mandible

Repeatabilities were high for both between (skull = 87.88%; quadrate = 87.15%; mandible = 97.45%)- and within-photograph (>99% for skull and quadrate, and mandible = 84.34%). In all cases, both between-photograph error and within-photograph error were a small fraction of the total sum of squares (Table S1).

The first two components from the PCA analysis for the landmarks in the dorsal view of the skull sum up 86.44% of the sample's total variance, the first principal component (PC1) accounting for 61.81% and the second component (PC2) explaining 24.63% of the total variance. A large part of the variance along the first component is related to the relative size of the supratemporal bones. *Micrurus surinamensis* has lower score values on the first PC, being closer to *Hydrops martii* on this axis than to its congeners (Figure 3a). This PC, as shown in the splines for this axis, reflects mainly differences in the size of the supratemporal bones, with the terrestrial *Micrurus* clustering on the positive side and having small supratemporals, and with *H. hagmanni* on the negative side and having large supratemporals (Figure 3a). Variation in the PC2 is associated with an overall robustness of the skull, with positive values being associated with narrower skulls with larger frontal bones and with negative values being associated with wider skulls with smaller frontals (Figure 3a). The two-way MANOVA for the skull was significant for both the species and sex factor, as well as the interaction between those terms (Table 3). A post hoc pairwise comparisons between species were significant (corrected  $p < .0138$ ) for all comparisons, except for the distinction between *M. lemniscatus* and *M. spixii* (corrected  $p = 1.000$ ).



**FIGURE 2** First two axes of size-free principal component analysis over linear head and body measurements of the aquatic and terrestrial species

**TABLE 3** Two-way MANOVA table results for linear and geometric (skull, quadrate, mandible) morphometrics

	df	Wilks	Approx.F	df num	df den	pr(>F)
<b>Linear</b>						
Species	6	>0.001	135.654	36	881.02	<2.2e-16*
Sex	1	0.574	24.705	6	200.00	<2.2e-16*
Species:Sex	6	0.607	2.951	36	881.02	2.9e-08*
<b>Skull</b>						
Species	6	0.001	269.409	12	100	<2.2e-16*
Sex	1	0.717	9.845	2	50	2.5e-4*
Species:Sex	6	0.571	2.698	12	100	3.4e-3*
<b>Quadrate</b>						
Species	6	0.034	36.710	12	100	<2e-16*
Sex	1	0.999	0.016	2	50	0.984
Species:Sex	6	0.678	1.789	12	100	0.060
<b>Mandible</b>						
Species	6	0.001	226.437	12	100	<2.2e-16*
Sex	1	0.971	0.728	2	50	0.488
Species:Sex	6	0.816	0.892	12	100	0.557

df, degrees of freedom; Wilks, Wilks' Lambda value; Approx.F, approximate multivariate F statistics; df num, numerator degrees of freedom; df den, denominator degrees of freedom; pr(>F), p-value for the multivariate test. Asterisks indicate significant results at  $\alpha = .05$ .

The first two PCs for analysis of the lateral view of the quadrate explain 97.74% of the sample's total variance, the first PC explaining 87.56% while PC2 accounts for 10.18% of the variance. Positive values of PC1 are associated with a shorter, more robust quadrate, while in species with negative scores shows a longer and more slender quadrate (Figure 3b). Even though *Micrurus* tend to have positive values and *Hydropsini* tend to have negative values, specimens are distributed in a continuum along this axis (Figure 3b). PC2 relates to the relative position of landmark 7 of the quadrate in relation to the other two (landmark 6 and 8), with negative values being associated with a more downward position of this landmark and positive values being related to a more upward position. The two-way MANOVA showed a significant difference between species but no significant difference between sexes or sex-species interaction (Table 3). The post hoc pairwise MANOVA comparisons were generally significant (corrected  $p < .003$ ) with the following exceptions: *H. hagmanni*—*H. martii* (corrected  $p = 1.000$ ), *H. martii*—*O. petolorius* (corrected  $p = .071$ ), *L. annulata*—*O. petolorius* (corrected  $p = 1.000$ ), *M. lemniscatus*—*M. spixii* (corrected  $p = .201$ ), *M. lemniscatus*—*M. surinamensis* (corrected  $p = .052$ ), and *M. spixii*—*M. surinamensis* (corrected  $p = 1.000$ ). In summary, we can say that there is no difference within *Micrurus*, but the species of *Micrurus* are different from all the other non-*Micrurus* species.

In respect to the analysis of the lateral view of the mandible, the two first PCs account for 95.3% of total variance, 82.89% of variance explained by the PC1, and 12.41% by the PC2. The first PC axis depicts changes in the relative sizes of both the dentary and the articular, with individuals with negative scores having a relatively

larger dentary and a smaller articular, and individuals with positive scores having a relatively smaller dentary and a relatively longer articular (Figure 3c). *Micrurus* species have positive scores of the first principal component. The second PC axis relates to the angle between the articular and dentary, with smaller scores being associated with a larger angle and larger scores being associated with smaller angles. The two-way MANOVA was significant only for the species factor (Table 3), and the post hoc pairwise comparisons were significant on all accounts, with the exception of the difference between *M. surinamensis* and the other two *Micrurus* species (*M. lemniscatus* corrected  $p = .266$ ; *M. spixii* corrected  $p = 1.000$ ).

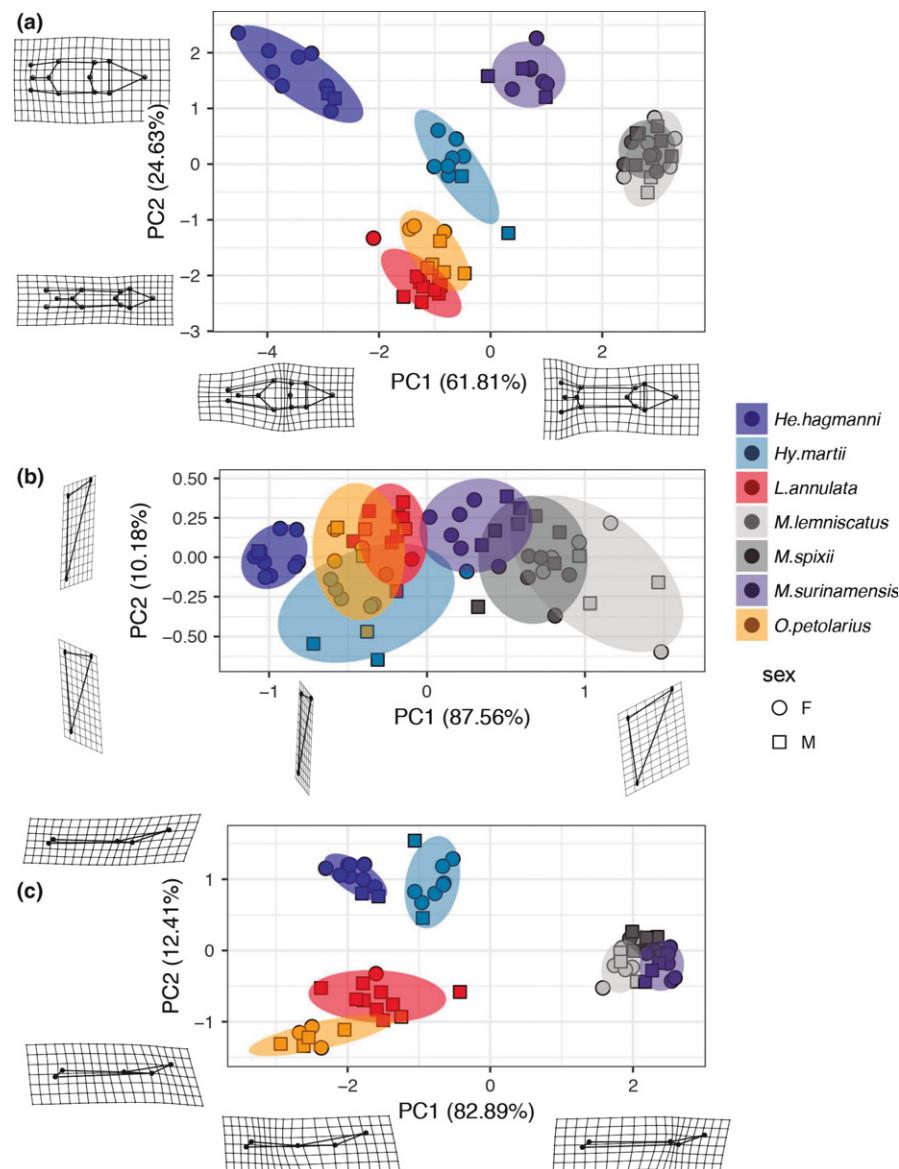
### 3.3 | Direction of evolution

We detected significant interaction of species and sex in the MANOVAs, for both linear and geometric data. For this reason, we estimated both  $\Delta z_{\text{sur}}$  and vectors of divergence between *Micrurus* and other genus for males and females separately. Vector correlation was calculated using vector estimates ( $\Delta z_{\text{sur}}$  and vectors of divergence) for the same sex. Despite the fact that correlation values were different for each sex, the overall pattern among species is similar (Figure 4). Vector correlation shows that, on average, evolution of *M. surinamensis* was more aligned with the direction of the aquatic models than in the direction of the terrestrial models. Vector alignments were greater for external morphology than for geometric morphometrics, with vector alignment between the reference species and *H. hagmanni* being the highest for both datasets, *H. martii* showing intermediate values, followed by *L. annulata* and, lastly, by *O. petolorius* (Figure 4).

If we take the null distribution of vector correlation into account, for external morphology, all species had at least one significant vector, with *H. hagmanni* showing the highest proportion of significant vectors (females = 64.3%, males = 91.4%), again followed by *H. martii* (females = 21.8%, males = 67.0%), *L. annulata* (females = 8.3%, males = 32.4%), and *O. petolorius* (females = 5.8%, males = 14.5%). For geometric morphometric, on the other hand, only *H. hagmanni* showed significant vector correlations with  $\Delta z_{\text{sur}}$  (females = 100%, males = 62.5%).

## 4 | DISCUSSION

Convergence does not refer simply to similarity between taxa, but to the fact that species show similar character transitions despite starting from different points (Stayton, 2015). In the case of species complexes that are morphologically conserved, the existence of a divergent species (i.e., presents a nonzero difference from its sister species) can be used to test the hypothesis of convergence, by evaluating whether that species diverged in the direction of ecologically similar taxa. Here, we have taken this rationale and tested both the morphological conservatism of three species of *Micrurus* in the triad group, and if the divergence of *M. surinamensis*, the only aquatic species of the genus, happened in the direction of other dipsadids with



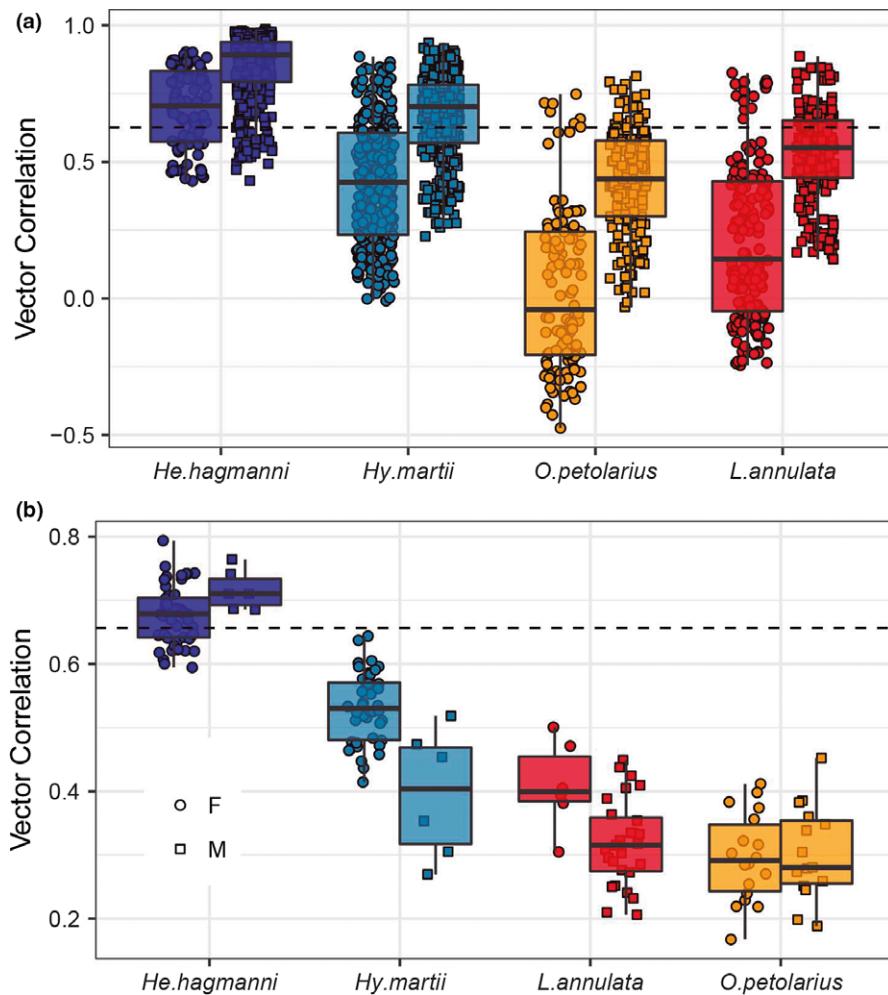
**FIGURE 3** Graph showing the two first axes of the principal component analysis of geometric morphometric variables for dorsal view of the skull (a), lateral view of the quadrate (b), and mandible (c). The splines show the shape changes associated with each axis. Ellipses represent 95% confidence intervals

the same habits. Our results for both external morphology and skull geometric morphometrics show that *Micrurus* was generally morphologically conserved, with the divergence of *M. surinamensis* from its congeners occurring in the direction of *H. hagmanni*, an aquatic dipsadid, and not in the direction of terrestrial species.

The multivariate analyses of variance show that the skull of *Micrurus* was extremely conserved, except for the relative length of the supratemporals. The skull shape divergence of *M. surinamensis* from its congeners occurred in the direction of *H. hagmanni*, an aquatic dipsadid, and not in the direction of terrestrial species. Bones associated with the prey acquisition and ingestion are the main structures involved in this pattern: *M. surinamensis* not only shows supratemporal bones that are relatively longer than in terrestrial *Micrurus* (Figure 3a, Figures S1 and S3), but also possesses a longer, less robust quadrate bone when compared to its congeners (Figure 3b, Figures S2 and S3). Interestingly, if we investigate the relationship between supratemporal and quadrate bones, we observe an

almost perfect superimposition between *M. surinamensis* and *H. hagmanni* (see Figure S4a).

Ecomorphological studies of snakes that consume relatively large and sturdy prey (and particularly piscivorous species: Savitzky, 1983; Dwyer & Kaiser, 1997; Cundall & Greene, 2000) indicate the elongation of bones such as the quadrate and supratemporal, and a mandibular complex that is loosely attached. These specializations are associated with an increase in skull kinesis and gape width that facilitates swallowing and ingestion of larger prey (e.g., Albright & Nelson, 1959; Bolt & Ewer, 1964; Cundall, 1987; Cundall & Gans, 1979; Gans, 1961; Greene, 1983; Kardong, 1974, 1977; Vincent, Herrel, & Irschick, 2004, 2005; Vincent, Moon, Herrel, & Kley, 2007; Vincent et al., 2009). Accordingly, *M. surinamensis* retains elongated supratemporals and quadrates that provides a wider gape, allowing the ingestion of more robust preys in comparison with other species of *Micrurus*. Curiously, while *M. surinamensis* resembles *H. hagmanni* in the relative size of these bones, dietary similarity is greater between *M. surinamensis*



**FIGURE 4** Correlation between evolutionary divergence of *Micrurus surinamensis* ( $\Delta z_{sur}$ ) and the vectors of differences between the reference species *Micrurus lemniscatus* and the aquatic models (*Helicops hagmanni* and *Hydrops martii*) and terrestrial models (*Leptodeira annulata* and *Oxyrhopus petolarius*) for external morphology (a) and skull geometric morphometrics (b). Circles represent vectors for females, and squares represent vectors for males. Dashed line represents the 95% threshold value for the null distribution of random vector correlations

and *Hydrops martii*, as both species consume more elongated fishes (e.g., Gymnotiformes and Siluriformes, *H. martii*: Cunha & Nascimento, 1993; Albuquerque & Camargo, 2004; *M. surinamensis*: Appendix 1) than those consumed by *H. hagmanni* (Teixeira et al., 2017). It is possible that because *Micrurus* in general does not require a wide gap to consume fossorial prey (Deufel & Cundall, 2003), that the extreme sizes of both quadrate and supratemporal in *M. surinamensis* allow the species to produce wider gapes, but not to the same extent than those observed in *H. hagmanni*.

*Micrurus* mandible shape is extremely conserved and shows little evidence of divergence in *M. surinamensis*, as well as no clear convergence with *Hydropsini* groups (Figure 3, Figure S3). Although our analysis of the mandible found a much longer dentary bone in the *Hydropsini* and the other two terrestrial dipsadids, *Micrurus surinamensis* does resemble in having longer and more curved dentary teeth than the other two species of *Micrurus* studied (Figure S2). According to Savitzky (1983), bone elongation and a larger number of teeth may well be linked to skull changes related to the ingestion of more robust prey in piscivorous species. Additionally, Britt, Clark, and Bennet (2009) found similar results when examined morphological variation in tooth structure in four populations of garter snakes (*Thamnophis*) with different feeding habitats (i.e., generalist, malfagous, and piscivorous diets) with the fish specialist *T. couchii*

(Kennicott in Baird, 1859) showing several dentary tooth specializations associated with piscivory, including higher number of narrower and more curved teeth. Longer, more curved dentary teeth may provide a more effective bite to hold the fish against the braincase (Cundall, 1983).

For the external morphology, both conservatism and convergence signals were harder to detect. All species were considered different from each other in body shape. While the evolution of *M. surinamensis* is highly aligned with both terrestrial and aquatic species, the correlation with aquatic species was greater, specifically with *H. hagmanni* (Figure 4). Despite this, the body form of *M. surinamensis* shows a wider variety of traits that are thought to be associated with an aquatic environment. For instance, closer nostrils that are positioned more dorsally in the anterior part of the head are known to be characteristic in marine Elapidae (Greene, 1997; Marx & Rabb, 1972) and other aquatic snake lineages, such as Acrochordidae, Natricidae, and Homalopsidae. Greene (1997) attributes the more dorsal position and approximation of eyes and nostrils as an advantage of these snakes in aquatic environments, because they are less exposed to predators when emerging their head from the water to breathe. Despite not having nostrils as close to each other as those observed in *Hydropsini* (Figure S4b), *M. surinamensis* has a smaller nostril distance than its congeners, as is expected by adaptive convergence. Similarly, the

distance between the eyes is smaller in *M. surinamensis* than in the other members of the genus (Figure S4c).

Similarly, Segall et al. (2016) evaluated the relationship between the shape of the head in snakes and adaptations for an aquatic lifestyle, indicating that aquatic species tend to have a more laterally compressed snout with dorsally positioned eyes and nostrils. In addition, the posterior part of the head tends to be wider when compared to non-aquatic species. They concluded a narrower anterior part of the head will reduce drag, while a wider posterior head allows for a more efficient prey transport. Our results indicate that *M. surinamensis* has a posterior part of the head that is relatively wider head than its congeners, showing a relationship between HL and HW that is similar to the one observed in Hydropsini (Figure S4d).

General aspects of the body shape of *M. surinamensis* also show similarities with the other aquatic species, including sexual dimorphism, whereas in the *Micrurus*' complex either there is no sexual dimorphism (*M. lemniscatus*) or there is a different pattern (*M. spixii*). *Micrurus surinamensis* shows a longer tail than its congeneric terrestrial species (Figure S4e), contradicting Brischoux and Shine (2011). The longer tail observed in Hydropsini and *Micrurus surinamensis* suggests that a greater propulsive surface area would be advantageous during swimming and water displacement on the background of rivers or close to their margins and vegetation. *M. surinamensis* also shows a relatively thicker body (Figure S4f), similarly to that observed for both Hydropsini. According to Brischoux and Shine (2011), marine snakes exhibit specialized morphological adaptations that allow the species to cope with the constraints imposed by the aquatic environment, like lateral body flattening to increase swimming speed. A more robust form as found in our results allows for a lateral flattening of the body during swimming as in the other aquatic taxa. The same authors above also defend that the set of these modifications for an aquatic lifestyle may have been influenced not only by selection on swimming efficiency but also on the advantages of a system that allows for inevitable bodily distension due to other aspects of the animal's ecology (e.g., foraging, reproduction). Another possibility suggested by the authors is that a larger surface area helps to enhance cutaneous underwater gas exchange.

We conclude that *M. surinamensis* shows a set of characters related to an aquatic specialization that could be considered convergent not only with Hydropsini, but also with other aquatic taxa described in the literature (Britt et al., 2009; Cadle & Greene, 1993; Lillywhite, 1987; Segall et al., 2016; Vitt & Vangilder, 1983). Even in cases where traits did not show the same state as aquatic groups, they could be considered as diverging in a similar direction as what would be expected under adaptation to aquatic habitat. The signal of convergence was more evident on geometric morphometric data, suggesting that investigations of shape using this method might be more useful in studies of morphological convergence (e.g., Polly et al., 2016). Nevertheless, some morphological features show different degrees of conservatism suggesting that historical contingency is also an important constraint in morphological evolution in these snakes (Pizzatto, Marques, & Martins, 2007; Vitt & Vangilder, 1983). Thus, the study of both conservatism and divergence is particularly

important in understanding the forces that drive morphological evolution.

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## SUPPORTING INFORMATION

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## APPENDIX 1

Prey items listed in the literature for the species of the genus *Micrurus*. When available, the number of specimens for each species is given in parenthesis.

Species	Prey items	References
<i>Micrurus albicinctus</i>	Snake (1)	Souza, Junqueira, Jakovac, Assunção, and Correia (2011)
<i>Micrurus alleni</i>	Lizards and fish (1)	Roze (1996)
<i>Micrurus altirostris</i>	Amphisbaenians (1) and snakes (3)	Silva and Aird (2001)
<i>Micrurus annellatus</i>	Lizard (1) and snake (1)	Roze (1996)
<i>Micrurus averyi</i>	Lizard (2) and snake (2)	Martins and Oliveira (1999)
<i>Micrurus bernardi</i>	Snake (1)	Roze (1996)
<i>Micrurus bocourti</i>	Caecilians	Roze (1996)
<i>Micrurus brasiliensis</i>	Amphisbaenians (2) and snakes (4)	Silva and Aird (2001)
<i>Micrurus browni</i>	Snakes (4)	Roze (1996)
<i>Micrurus circinalis</i>	Lizard (1) and snake (1)	Roze (1996)
<i>Micrurus corallinus</i>	Amphisbaenians (65), caecilians (9), lizards (12), snakes (8)	Marques and Sazima (1997); Roze (1996)
<i>Micrurus decoratus</i>	Amphisbaenians (2) and caecilians (3)	Marques (2002)
<i>Micrurus diana</i>	Snakes	Roze (1996)
<i>Micrurus diastema</i>	Caecilians, lizards, and snakes (6)	Roze (1996)
<i>Micrurus dissoleucus</i>	Lizard (1)	Roze (1996)
<i>Micrurus distans</i>	Snakes	Roze (1996)
<i>Micrurus elegans</i>	Snakes (3)	Roze (1996)
<i>Micrurus ephippifer</i>	Snakes (2)	Roze (1996)
<i>Micrurus filiformis</i>	Amphisbaenians, snakes, and invertebrates	Cunha and Nascimento (1993); Dixon and Soini (1986)
<i>Micrurus frontalis</i>	Amphisbaenians (12), lizard (1), and snakes (6)	Roze (1996)
<i>Micrurus fulvius</i>	Lizards (5), snakes (21), and occasionally frogs	Roze (1996)
<i>Micrurus hemprichii</i>	Onychophorans (6), Amphisbaenians (4), lizards, and snakes (3)	Bernarde and Abe (2006); Martins and Oliveira (1999); Roze (1996)
<i>Micrurus hippocrepis</i>	Snakes	Roze (1996)
<i>Micrurus ibiboboca</i>	Caecilians (1), amphisbaenians (3), and snakes (5)	Cavalcanti, Santos-Protázio, Albuquerque, Pedro, and Mesquita (2012); Roze (1996)
<i>Micrurus isozonus</i>	Lizards: <i>Bachia</i> sp.; and colubrid snakes	Roze (1996)
<i>Micrurus langsdorffi</i>	Snakes (2)	Roze (1996)
<i>Micrurus latifasciatus</i>	Caecilians (1) and snakes (3)	Roze (1996)
<i>Micrurus lemniscatus</i>	Caecilians (2), amphisbaenians (4), Lizard (2), snakes (11), and fishes (2)	Martins and Oliveira (1999); Roze (1996)
<i>Micrurus limbatus</i>	Colubrid snakes	Roze (1996)
<i>Micrurus medemi</i>	Snake (1)	Roze (1996)
<i>Micrurus mertensi</i>	Snakes (2)	Roze (1996)
<i>Micrurus mipartitus</i>	Lizard (1), amphisbaenian (1), and snakes (2)	Roze (1996)
<i>Micrurus nebularis</i>	Snake (1)	Roze (1996)
<i>Micrurus nigrocinctus</i>	Caecilians, lizards (5), snakes (6), and reptile eggs	Roze (1996)
<i>Micrurus paraensis</i>	Snake (2) and centipedes	Roze (1996); Souza et al. (2011)
<i>Micrurus proximans</i>	Snake (1)	Roze (1996)
<i>Micrurus psyches</i>	Lizard (1), snake (1), and centipedes	Roze (1996)
<i>Micrurus putumayensis</i>	Remains of colubrid snakes	Dixon and Soini (1986); Roze (1996)
<i>Micrurus pyrrhocryptus</i>	Amphisbaenians (1) and snakes (3)	Ávila, Kawashita-Ribeiro, Ferreira, and Strüssmann (2010); Roze (1996); Silva and Aird (2001)

(Continues)

**APPENDIX 1** (Continued)

Species	Prey items	References
<i>Micrurus ruatanus</i>	Lizard (1)	Roze (1996)
<i>Micrurus spixii</i>	Caecilians, lizards (3), amphisbaenians (1), and snakes (12)	Bernarde and Abe (2010); Martins and Oliveira (1999); Roze (1996)
<i>Micrurus surinamensis</i>	Fishes (17) and lizard (1)	Bernarde and Abe (2006); Morais, Ávila, Kawashita-Ribeiro, and Carvalho (2011); Roze (1996)
<i>Micrurus tschudii</i>	Amphisbaenians (1)	Roze (1996)

**APPENDIX 2**

List of analyzed specimens, with collection numbers. Legend: \* = skull prepared; w/n = without number

***Micrurus surinamensis* (43):** IEPA 45; IEPA 311; IEPA TQ185; INPA 16366; INPA 28913; IBSP 43619; MPEG 2552; MPEG 2651; MPEG 2713; MPEG 2855; MPEG 2884; MPEG 3064\*; MPEG 4113; MPEG 4651\*; MPEG 4980; MPEG 5253; MPEG 5594; MPEG 8201; MPEG 10144\*; MPEG 12606; MPEG 12759\*; MPEG 12980\*; MPEG 16556\*; MPEG 18510; MPEG 18751\*; MPEG 20118\*; MPEG 20217; MPEG 20218\*; MPEG 21549; MPEG 22058; MPEG 23115; MPEG 23388; MPEG 24133; MPEG 25634; MZUSP 8716; MZUSP 11453; MZUSP 11467; UFAC 318; UFAC 848; UFAC w/n; UFMT 4041; UFMT 6647; UFMT 6860.

***Micrurus lemniscatus* (54):** MPEG 388; MPEG 2193; MPEG 2390\*; MPEG 3043; MPEG 4319\*; MPEG 5020; MPEG 5382; MPEG 5390; MPEG 5533; MPEG 5551; MPEG 5603; MPEG 8850\*; MPEG 8872; MPEG 8877; MPEG 8878; MPEG 8885; MPEG 8886; MPEG 8887; MPEG 8889; MPEG 11285\*; MPEG 12854; MPEG 12889; MPEG 13001; MPEG 13004; MPEG 15382; MPEG 16313; MPEG 16833\*; MPEG 17260; MPEG 19904; MPEG 22054; MPEG 23146; MPEG 23147; MPEG 23544; MPEG 24063; MPEG 24234; MPEG 24235\*; MPEG 24237; MPEG 24238; MPEG 24536\*; MPEG 25625; MPEG 25626; MPEG 25627; MPEG 25629; MPEG CD058\*; MPEG TM079; MZUSP 8357; MZUSP 9411; MZUSP 17351; MZUSP 17352; MZUSP 18758; UFMT 3876; UFMT 6944; UFMT 8010; UFMT 8011.

***Micrurus spixii* (51):** INPA 313; INPA 10406; INPA 12021; INPA 12092; INPA 12936; LHPA 358; LPHA 1312; LPHA 1332; LPHA 2218; LHPA 2515; LHPA 2649; MPEG 629; MPEG 2551\*; MPEG 3062; MPEG 3970\*; MPEG 4861\*; MPEG 5450\*; MPEG 5497\*; MPEG 5591; MPEG 8447; MPEG 8525\*; MPEG 8882\*; MPEG 10115\*; MPEG 14434; MPEG 14984; MPEG 15709; MPEG 15710; MPEG 16624; MPEG 16656\*; MPEG 17012\*; MPEG 17303; MPEG 21029\*; MPEG CD172; MZUSP 8486; MZUSP 11151; MZUSP 11349; MZUSP 17328; MZUSP 17333; MZUSP 17335; MZUSP 17337; MZUSP 17338; MZUSP 17341; MZUSP 17343; MZUSP 17345; MZUSP 17356; MZUSP 17357; MZUSP 17444; UFMT 911; UFMT 4044; UFMT 4866; UFMT 5165.

***Helicops hagmanni* (40):** MPEG 2140; MPEG 2144; MPEG 2147; MPEG 2468\*; MPEG 2874; MPEG 2879; MPEG 4161; MPEG 4162;

MPEG 4181; MPEG 4941; MPEG 6268; MPEG 8103; MPEG 8746; MPEG 8750; MPEG 8755; MPEG 8791; MPEG 8803; MPEG 10484; MPEG 10485; MPEG 10486\*; MPEG 10487\*; MPEG 10628; MPEG 10632\*; MPEG 10633; MPEG 10929\*; MPEG 11004; MPEG 11006; MPEG 11210; MPEG 11466\*; MPEG 12613; MPEG 12614; MPEG 14480; MPEG 14481\*; MPEG 15513; MPEG 15515; MPEG 16331; MPEG 16941\*; MPEG 21535\*; MPEG 22403; MPEG 24253\*.

***Hydrops martii* (50):** MPEG 970; MPEG 2152\*; MPEG 2699; MPEG 4903\*; MPEG 4908\*; MPEG 4909\*; MPEG 6042; MPEG 8123; MPEG 8124\*; MPEG 8133; MPEG 8137; MPEG 8138; MPEG 8139; MPEG 8141; MPEG 8143; MPEG 8148\*; MPEG 8149; MPEG 8154; MPEG 8618\*; MPEG 8733; MPEG 8734; MPEG 9612; MPEG 9617; MPEG 9676; MPEG 10420; MPEG 10422; MPEG 10424; MPEG 10428; MPEG 10429; MPEG 10434; MPEG 10435; MPEG 10436; MPEG 10437; MPEG 10439; MPEG 10444; MPEG 10445; MPEG 10446; MPEG 10616; MPEG 10620; MPEG 10624; MPEG 10626; MPEG 13049\*; MPEG 21344\*; MPEG CD017\*; MZUSP JA08; MZUSP 5136; MZUSP 6979; MZUSP 15570; MZUSP 18137; MZUSP 18142.

***Leptodeira annulata* (40):** MPEG 17542\*; MPEG 17840\*; MPEG 17853; MPEG 17854; MPEG 17857; MPEG 17859; MPEG 17860; MPEG 17944; MPEG 17945; MPEG 17946; MPEG 17947; MPEG 17950; MPEG 17954; MPEG 17955; MPEG 19005\*; MPEG 19077\*; MPEG 19486\*; MPEG 19796; MPEG 20016\*; MPEG 22153; MPEG 22154; MPEG 22155; MPEG 22229\*; MPEG 22781\*; MPEG 23716\*; MPEG 23765\*; MPEG 23796; MPEG 24917; MPEG 24973; MPEG 24974; MPEG 24976; MPEG 25372; MPEG 25558; MPEG 25559; MPEG 25960; MPEG 25961; MPEG 25963; MPEG 25964; MPEG 25965; MPEG 26241.

***Oxyrhopus petolarius* (29):** MPEG 2680; MPEG 11851; MPEG 14402; MPEG 15265; MPEG 15726; MPEG 16700; MPEG 16914; MPEG 17008; MPEG 17124\*; MPEG 17127\*; MPEG 17237\*; MPEG 17239; MPEG 19377; MPEG 19567\*; MPEG 21020\*; MPEG 22967; MPEG 22970; MPEG 23325; MPEG 23766\*; MPEG 24123\*; MPEG 24599\*; MPEG 24666; MPEG 24987; MPEG 25332; MPEG 25549; MPEG 25833; MPEG 26324; MPEG 26326; MPEG 26340.