

# Ventral scale width in snakes depends on habitat but not hunting strategy

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Environment and lifestyle induce substantial variation in the mechanisms of locomotion in vertebrates. A spectrum of adaptations related to locomotion is also present in limbless taxa, especially snakes, which have radiated successfully into a wide range of habitats. The majority of studies concerning habitat-driven variation in locomotor mechanisms of snakes have focused on the musculoskeletal system. Far less recognized is the variation in the morphology of ventral scales, which are another pivotal component of the locomotor system in snakes. Here, we investigated patterns of interspecific variation in the width of ventral scales in terms of lifestyle (hunting mode) and habitat occupied in 55 species of snakes belonging to eight families. We found that increasing terrestriality was associated with enlarged ventral scales. Reduction instead of maintenance of the width of ventral scales was observed in aquatic species, suggesting that wide ventral scales set constraints on aquatic locomotion. In terrestrial species, no significant differences were observed in terms of arboreality or hunting mode, which suggests overall optimization in the size of ventral scales towards terrestrial locomotion. Association between the width of ventral scales and locomotion can result in a habitat-dependent costs of abnormalities in ventral scale morphology, commonly observed in snakes.

ADDITIONAL KEYWORDS: environment – foraging – locomotion – movement – scales – snakes.

## INTRODUCTION

The spectrum of morphological adaptations associated with locomotion is extreme among vertebrates and even includes legless taxa despite the fact that legless body plans might appear to limit the capacity to evolve sophisticated variation (Webb, 1988; Alexander, 1989). In fact, limblessness is an adaptation in itself, and although it does not occur in the majority of vertebrates, it is observed in association with a wide range of life histories and environments (Gans, 1975). The snakes are a clade of limbless vertebrates that are particularly successful, given that its members inhabit a wide spectrum of aquatic and terrestrial habitats, including marine, freshwater, fossorial and arboreal habitats (e.g. Terribile *et al.*, 2009). Such diversity also includes variation in movement strategies (Jayne, 1986) and rates (Secor, 1995). Snakes provide an ideal system

for studies investigating adaptations in legless locomotion driven by environment and lifestyle.

Clear variation among different environments in terms of physical constraints, for example those associated with gravitation and friction, must necessitate corresponding adjustments in structures orchestrating the movement of snakes. Indeed, a growing body of data indicates the occurrence of specific adaptations for locomotion related to the environment (e.g. Shine & Shetty, 2001). The majority of attention has focused on the musculoskeletal system (Jayne, 1988) or body form, such as tail length or shape (Aubret & Shine, 2008; Sheehy *et al.*, 2016). However, the pivotal components of the locomotor system in snakes include not only vertebrae and ribs with their associated musculature, but also, tightly connected to them, the ventral scales. Habitat-driven variation in ventral scale properties are studied mainly in terms of their number (e.g. Hampton, 2011), which is generally assumed to result from a tight association with the number of vertebrae (Alexander & Gans, 1966; Lee *et al.*, 2016). Also, the size of ventral scales is likely to

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play an important role in snake locomotion because it defines the body surface area in contact with a substrate and underlies the capacity to cope with friction during movement. Therefore, we predict substantial variation the width of ventral scales in relationship not only to habitat type, but also to the rate of movements. Surprisingly, to date no quantitative support for such variation is and thus there is a considerable knowledge gap concerning limbless locomotion in the most widespread group of legless vertebrates.

Here, we aimed to investigate the patterns of variation in the width of the ventral scales in two ecological contexts. First, we explored how snake habitat type is related to the width of scales by comparing purely aquatic species with semi-aquatic and terrestrial ones. As indicated for marine snakes, we predicted that small size of ventral scales is a general feature of the whole aquatic group of species. We expect that such a tendency towards a reduction in ventral scale size also occurs in semi-aquatic species when compared with terrestrial ones, given the relaxed friction of the amphibious environment. Second, we checked whether foraging mode, that is, ambush vs. active, is associated with a variation in the width of the ventral scales. Given that active hunters have a greater rate of movement and more slender body shape (Secor & Nagy, 1994), we expected that they would express thinner ventral scales compared with sit-and-wait foragers. Since our study covers a wide range of snake taxa, we have additionally controlled for phylogenetic effects.

## MATERIAL AND METHODS

### DATA COLLECTION

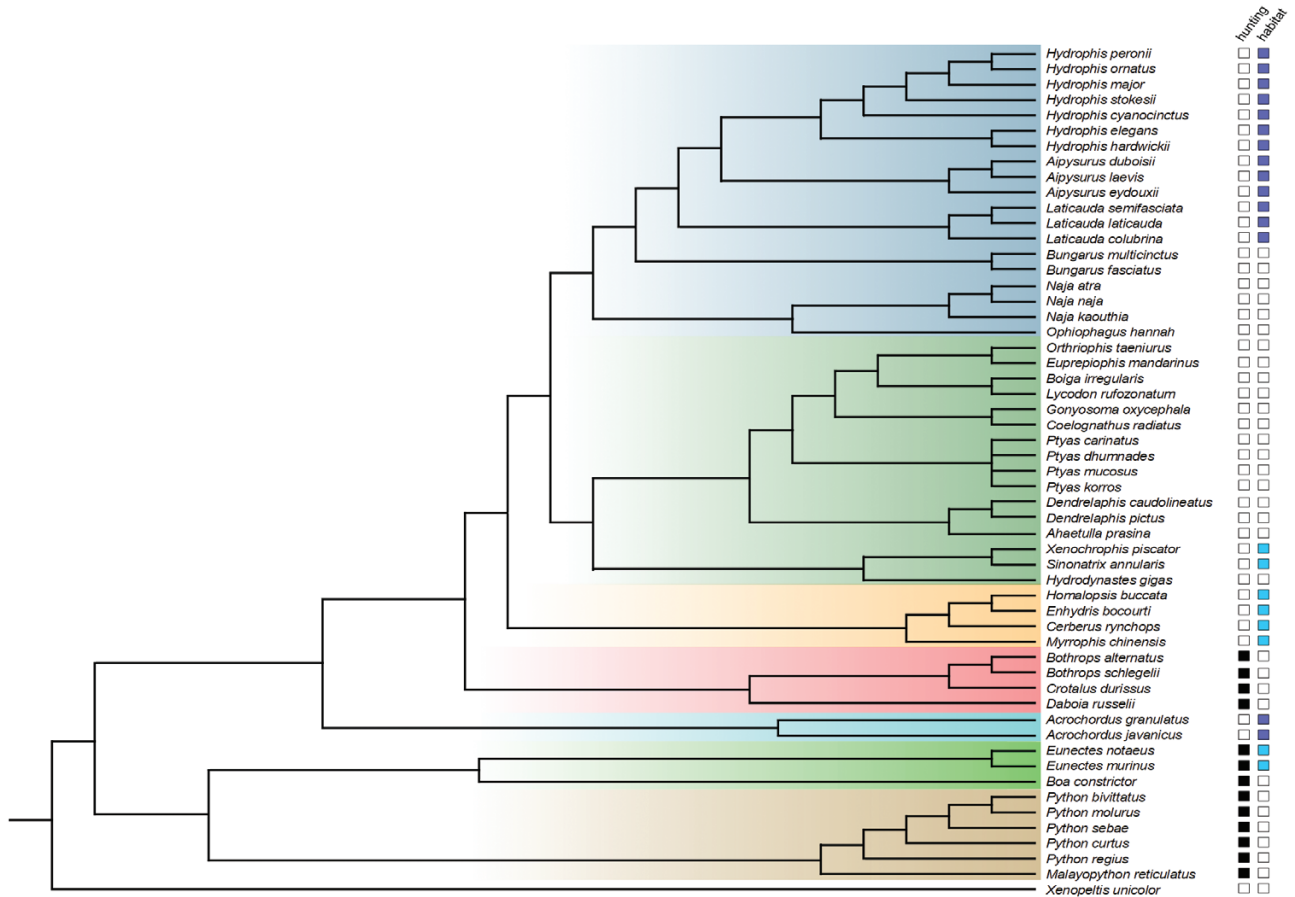
Data on the width of ventral scales from 51 species were collected from Fuchs & Fuchs (2003), which includes the largest dataset on ventral scale size in snakes available. Additionally, we measured the width of ventral scales in four species (*Ahaetulla prasina*, *Dendrelaphis pictus*, *Dendrelaphis caudolineatus* and *Gonyosoma oxycephala*) based on specimens from the collection of the Museum of Natural History, University of Wrocław (Appendix S1). These four species represent the subgroup of terrestrial species that occupy the arboreal habitat. Measurements were made on adult specimens using string and taken to the nearest 1 mm. The total width of the skin (circumference of the specimen, which includes dorsolateral and ventral skin parts) and width of the scales were assessed in the midbody of each individual. The width of the scales was measured as the distance between the most lateral margins of the scales in all species. The relative width of the ventral scales was expressed as a percentage of the total width of the skin including the ventral scales.

The final dataset consisted of 55 snake species belonging to eight families. Classifications of snakes in terms of habitats and hunting modes were based mainly on Brischoux *et al.* (2011) and Lourdaux *et al.* (2014) (Fig. 1). For species that were missing from these publications, we assessed categories based on field guides.

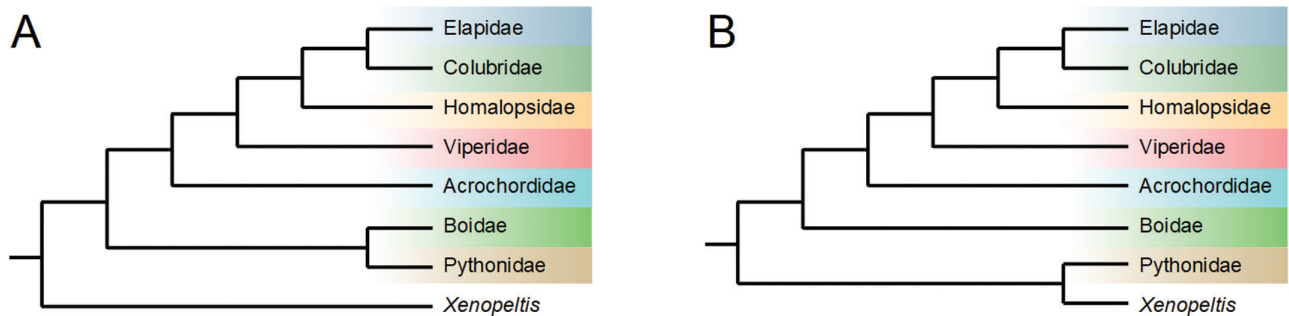
### STATISTICAL ANALYSES

To test whether there was a relationship between foraging strategy (active or ambush, scored as zero and one, respectively) or habitat (terrestrial, semi-aquatic or aquatic, scored as zero, one and two, respectively) and relative width of ventral scales (expressed as a percentage of the width of the skin, i.e. the circumference of the snake in the mid-body), we conducted phylogenetically informed statistical analyses using phylogenetic generalized least squares (PGLS) (Grafen, 1989). The correlation between the foraging strategy and relative width of the ventral scales was also analysed on the sample reduced to only terrestrial species, because this was the only group containing a reliable representation of both foraging modes. For terrestrial snakes, we checked whether there were any differences between the arboreal subgroup and purely terrestrial species, but no significant differences were observed ( $t = -1.117$ , d.f. = 5.186,  $P = 0.313$ ). Therefore, in the final analysis we included the arboreal species within the 'terrestrial' category.

We tested these correlations with two competing phylogenetic hypotheses of snakes: morphological and molecular (Fig. 2). The core topology of the trees was taken from Hsiang *et al.* (2015), whereas the interrelationships of given subclades were taken from other, more specialized analyses: Pythonidae from Barker *et al.* (2015); Viperidae, Homalopsidae and Colubridae from Pyron *et al.* (2011); and Elapidae from Lee *et al.* (2016). Two *Ptyas* species were not included in the study by Pyron *et al.* (2011); therefore, we created a polytomy containing all four *Ptyas* species. This polytomy is located on a very shallow node; therefore, its effect on the analyses was negligible. Although homalopsids were not included in the study by Hsiang *et al.* (2015), we resolved them as sister to the clade containing colubrids and elapids on both topologies based on the results of the combined morphological–molecular analysis of Harrington & Reeder (2017). We calibrated the dendrograms stratigraphically, using primarily the calibration points discussed by Head (2015) and Head *et al.* (2016) (all calibration points are given in Supporting Information, Appendix S2). When the fossil record of a given group was unknown, we set the respective branch lengths as three. This also applied to deeper nodes; therefore, the minimal



**Figure 1.** Data about the hunting strategy (white, active; black, ambush) and habitat (white, terrestrial; light blue, semi-aquatic; blue, aquatic) plotted onto the morphological phylogeny of snakes. The colours on the dendrogram are analogous to those in Figure 2.



**Figure 2.** The two main phylogenetic hypotheses of snakes: A, morphological phylogeny; and B, molecular phylogeny. The colours on the dendrogram represent each of the higher-level clades of snakes and are analogous to those in Figure 1.

branch length was three. For example, each of two sister species had a branch length of three, whereas the species sister to this clade had a branch length of six (three plus three). Although this is arbitrary, this approach has been used in several recent studies (e.g. Werneburg & Sánchez-Villagra, 2015; Skawiński

& Borczyk, 2017). In alternative analyses, we set all branch lengths as one.

We also tested whether there was a phylogenetic signal in the relative width of the ventral scales. We calculated the *K* statistic, which quantifies whether the species are more or less similar to

one another than expected on the basis of their phylogenetic relationship (Blomberg *et al.*, 2003). We also calculated Pagel's  $\lambda$  (Pagel, 1999) because this statistic and Blomberg *et al.*'s (2003)  $K$  have different strengths and weaknesses (Münkenmüller *et al.*, 2012). These analyses were also performed on both morphological and molecular phylogenies and using both fossil-calibrated trees and uncalibrated trees. We also tested the localized phylogenetic signal in three snake subclades containing at least six species (i.e. Pythonidae, Colubridae and Elapidae) using the  $K$  statistic, because it performs better than  $\lambda$  when few species are analysed (Münkenmüller *et al.*, 2012). All statistical analyses were conducted in R (R Core Team, 2018) and the add-on packages ape (Paradis *et al.*, 2004), nlme (Pinheiro *et al.*, 2015) and phytools (Revell, 2012), following the instructions of Swenson (2014).

# RESULTS

## PHYLOGENETIC STATISTICAL ANALYSES

In all analyses (i.e. using molecular and morphological phylogenies, calibrated and uncalibrated trees, and  $K$  and  $\lambda$  statistics), a statistically significant phylogenetic signal was detected in the relative width of the ventral scales (Table 1). However, the phylogenetic signal was not uniformly distributed across the tree. There was no statistically significant phylogenetic signal in the Pythonidae (calibrated tree,  $K = 0.6467$ ,  $P = 0.615$ ; uncalibrated tree,  $K = 0.4253$ ,  $P = 0.855$ ); it was weak but statistically significant in the Colubridae (calibrated tree,  $K = 0.67102$ ,  $P = 0.01$ ; uncalibrated tree,  $K = 0.90971$ ,  $P = 0.015$ ) and very strong in the Elapidae (calibrated tree,  $K = 3.518671$ ,  $P = 0.001$ ; uncalibrated tree,  $K = 5.1755$ ,  $P = 0.001$ ). These results indicate that the phylogenetic statistical models fit the data better than the conventional, non-phylogenetic ones.

In our phylogenetically corrected statistical analyses (PGLS), no correlation between the hunting mode (active or ambush) and relative width of the ventral scales was detected when all species were

analysed, nor when only terrestrial species were included ( $P > 0.2336$  in all cases; for details, see Tables 2 and 3). However, there was a statistically significant correlation (in all analyses) between habitat (terrestrial, semi-aquatic or aquatic) and the relative width of the ventral scales. Ventral scales in aquatic species were on average 19–21% narrower than those in terrestrial species, and the semi-aquatic species had intermediate values (Fig. 3; Table 4).

# DISCUSSION

Our study clearly demonstrates that ventral scales exhibit interspecific variation that goes beyond the most commonly invoked ventral count and concerns their size, defined here as width. Most importantly, the association of observed variation with environmental habitat clearly points to its adaptive value. As predicted, the type of habitat occupied affects the width of snake ventral scales in that species tend to exhibit wider scales with increasing terrestriality (Fig. 3). However, contrary to predictions, the width of ventral scales in terrestrial species did not show any clear distinction between the two foraging strategies, ambush and active, despite known differences in locomotor activity between the two hunting modes (Secor, 1995). Habitat-driven differences in the width of scales are most likely to represent adjustments to the physical constraints imposed on locomotion by different environments. The lack of a clear effect of hunting mode suggests that the size of ventral scales remains optimized for terrestrial movement, including variable activity rates. Despite being commonly overlooked, we promote the idea that the morphology of ventral scales is important to consider as ecologically relevant, and future studies on environmental morphology in snakes should include morphology of ventral scales.

The significance of ventral scales in snake locomotion is well established (Alexander & Gans, 1966), but despite this, the shift towards aquatic habitats appears to be associated with reduced relative ventral scale size. Given that semi-aquatic and aquatic lifestyles have evolved secondarily

**Table 1.** The phylogenetic signal in the relative width of the ventral scales

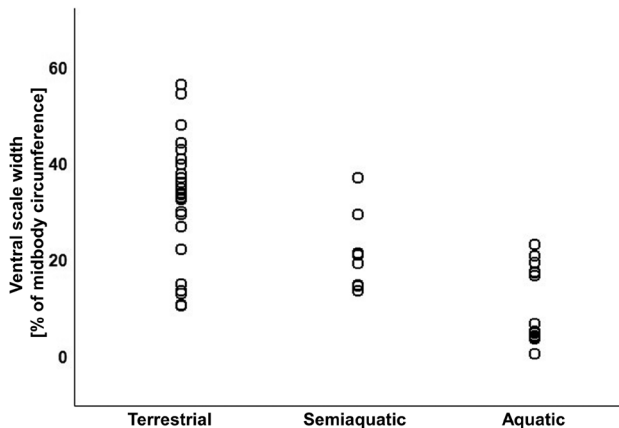
Phylogenetic hypothesis	K statistic		Pagel's $\lambda$	
	K	P-value	$\lambda$	P-value
Morphological calibrated	1.456963	0.001	1.008716	$4.805378 \times 10^{-20}$
Morphological uncalibrated	1.303983	0.001	0.9999339	$3.218102 \times 10^{-18}$
Molecular calibrated	1.515137	0.001	1.008998	$4.016369 \times 10^{-20}$
Molecular uncalibrated	1.585417	0.001	0.9999339	$4.502756 \times 10^{-18}$



**Table 2.** Correlations between the relative width of the ventral scales and hunting mode using phylogenetic generalized least squares

	Slope	AIC	BIC	Log-likelihood	P-value
Morphological calibrated	−3.279852	358.6776	364.5884	−176.3388	0.5200
Morphological uncalibrated	−4.002422	363.8333	369.7441	−178.9166	0.4453
Molecular calibrated	−3.480094	358.2531	364.164	−176.1265	0.4960
Molecular uncalibrated	−4.748418	364.7762	370.6871	−179.3881	0.4152

Abbreviations: AIC, Akaike information criterion; BIC, Bayesian information criterion.



**Figure 3.** Variation in the width of ventral scales of snakes from terrestrial, semi-aquatic and aquatic habitats. Each dot represents a species. Raw data are presented, and the observed pattern remains significant after phylogenetic corrections (see main text for details).

(Proches, 2001; Vidal & Hedges, 2004), the reduction in ventral scales instead of their maintenance indicates that the presence of large ventral scales results in fitness-related costs for aquatic snakes. Such costs are most likely to be attributed to limitations imposed on aquatic locomotion by wider ventral scales. Under the greater gravitational constraints in terrestrial environments, large ventral scales stabilize the body and help in the use of static friction during movement on dry surfaces (Baum *et al.*, 2014), but such functions necessitate a tight connection between ventral scales and the musculoskeletal system (Alexander & Gans, 1966). When combined with the high total surface of the stiff keratinized ventral layer, these factors are likely to limit the capacity for lateral flattening, a prerequisite for optimal swimming performance (Patishall & Cundall, 2008), and might also reduce the overall elasticity of the body. The latter can represent a constraint for aquatic snakes, because aquatic environments are associated with movements in three-dimensional space, in contrast to the planar movements in terrestrial environments. The tendency towards increased body elasticity in aquatic snakes is

supported by the reduction of ventral scale size shown here, but also corroborated by the relaxation of the correlation between the number of ventral scales and vertebrae observed in marine species compared with terrestrial ones (Voris, 1975).

A wider spectrum of movement directions is also advantageous in the arboreal environment; therefore, smaller scales would also be anticipated for arboreal species, but according to our data this is not the case, because arboreal snakes did not exhibit a tendency towards reduced ventral scale size. However, in the arboreal environment the surface available to repulse and move the body is limited to the area of tree branches; therefore, maintenance of wide ventral scales is necessary to use the limited availability of the substrate. Overall, we posit that the width of ventral scales and their association with other components of the locomotor system might reveal opposing consequences for locomotion depending on the environmental context. Benefits and constraints associated with ventral scale size thus represent a promising avenue for further studies as a factor that is likely to underlie performance and costs of locomotion in snakes from different habitats.

The role of variation in ventral scale size in locomotion is considerable in view of fluctuating asymmetry, i.e. deviations from bilateral symmetry, a common phenomenon in snake populations (Shine *et al.*, 2005). Specifically, such asymmetry in snakes often manifests as anomalies in the shape of ventral scales driven by various factors, such as a reduced population gene pool (Gautschi *et al.*, 2002) or disrupted thermal conditions during embryogenesis (Lowenborg *et al.*, 2011). Those anomalies are known to affect locomotor performance (Lowenborg & Hagman, 2016) and survival (Lindell *et al.*, 1993) in snakes, and thus represent a substantial evolutionary cost. Owing to the apparently tight association between ventral scale morphology and habitat-dependent locomotion, we propose that the effect of such anomalies on fitness might exhibit different magnitudes in aquatic, semi-aquatic and terrestrial species. Considering the ongoing worldwide tendency towards population declines (Reading *et al.*, 2010), probably followed by increases

**Table 3.** Correlations between the relative width of the ventral scales and hunting mode using phylogenetic generalized least squares performed on the reduced dataset that included only terrestrial species

	Slope	AIC	BIC	Log-likelihood	P-value
Morphological calibrated	-2.151527	191.767	195.9706	-92.88348	0.6269
Morphological uncalibrated	-3.619724	199.5324	204.736	-96.7662	0.3997
Molecular calibrated	-2.803837	191.6112	191.6112	195.8148	0.5265
Molecular uncalibrated	-6.463114	207.73	211.9336	-100.865	0.2336

Abbreviations: AIC, Akaike information criterion; BIC, Bayesian information criterion.

**Table 4.** Correlations between the relative width of the ventral scales and habitat using phylogenetic generalized least squares

	Slope	AIC	BIC	Log-likelihood	P-value
Morphological calibrated	-10.62637	345.9327	351.8436	-169.9664	$2 \times 10^{-4}$
Morphological uncalibrated	-9.554947	348.402	354.3128	-171.201	<0.001
Molecular calibrated	-10.68546	345.5052	351.4161	-169.7526	$2 \times 10^{-4}$
Molecular uncalibrated	-9.621291	349.8552	355.7661	-171.9276	<0.001

Abbreviations: AIC, Akaike information criterion; BIC, Bayesian information criterion.

in homozygosity and climate instability, we propose that the susceptibility to such scale abnormalities and associated costs might depend on the niche occupied.

## ACKNOWLEDGEMENTS

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## SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article at the publisher's web-site:

- Appendix S1.** The width of ventral scales in snakes (expressed as a % of the snake's circumference) and the ecological data (hunt: 0 – active predator, 1 – ambush predator; habitat: 0 – terrestrial, 1 – semiaquatic, 2 – aquatic).
- Appendix S2.** Calibration points used in time-calibrated phylogenetic statistical analyses.