Morphological convergence as a consequence of extreme functional demands: examples from the feeding system of natricine snakes

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Abstract

Despite repeated acquisitions of aquatic or semi-aquatic lifestyles revolving around piscivory, snakes have not evolved suction feeding. Instead, snakes use frontally or laterally directed strikes to capture prey under water. If the aquatic medium constrains strike performance because of its physical properties, we predict morphological and functional convergence in snakes that use similar strike behaviours. Here we use natricine snakes to test for such patterns of convergence in morphology and function. Our data show that frontal strikers have converged on a similar morphology characterized by narrow elongate heads with a reduced projected frontal surface area. Moreover, simple computational fluid dynamics models show that the observed morphological differences are likely biologically relevant as they affect the flow of water around the head. In general, our data suggest that the direction of evolution may be predictable if constraints are strong and evolutionary solutions limited.

Introduction

Convergence has been a prominent theme in evolutionary biology over the past 40 years (MacArthur & Levins, 1967; Frazzetta, 1975; Losos, 1990; see also Schluter & Ricklefs, 1993; Wainwright & Reilly, 1994 and references therein). Classic examples of convergence such as the evolution of a cline in wing length with latitude in *Drosophila* flies (Huey *et al.*, 2000) or the repeated and independent evolution of *Anolis* lizard ecomorphs on the Greater Antilles (Losos *et al.*, 1998) show that evolution can be predictable if environmental constraints are strong. However, recent studies on the evolution of the jaw system in teleost fish (Wainwright *et al.*, 2004; Alfaro *et al.*, 2005; Dean *et al.*, 2007) have shown that in some clades different phenotypes can converge on the same

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area of functional space resulting in so-called many-to-one mapping of morphology and function. This suggests that animals need not necessarily show morphological convergence even when confronted with similar functional or ecological demands.

A key aspect in determining whether any form of convergence is likely to occur is the relationship between resource utilization and whole-organism performance (Arnold, 1983; Irschick & Garland, 2001). If resource use or other environmental factors impose stringent demands on whole-organism performance, functional convergence is expected. However, morphological convergence is only predicted to occur if the design traits needed to realize the level of performance required are intrinsically constrained by the mechanics of the system and/or the Bauplan of the organism; in other words when the morphological solutions to the functional problem are limited. The capture of elusive prey under water by aquatically feeding tetrapods is a behaviour that likely satisfies these criteria because of the strong hydrodynamic demands placed upon the musculoskeletal

system in a dense and viscous medium. Because feeding is critical for survival, strong links among diet, feeding behaviour and morphology are expected (Wainwright & Lauder, 1986; Lauder, 1990; Herrel *et al.*, 2004).

Indeed, for relatively large animals, pressure drag – which is roughly proportional to the surface area exposed to the aquatic medium (see Vogel, 1981) – impedes movement within the aquatic medium and will slow down any movement towards a potential prey item. An additional problem for aquatically feeding animals is the generation of bow waves that tend to push prey away from a rapidly approaching predator. The magnitude of the bow-wave effect has, however, never been measured or modelled for aquatic feeding vertebrates. Consequently, it remains unclear how important bow waves may be in aquatic predator–prey interactions. Based on theoretical reasoning, the magnitude of these bow waves will be a function of the surface area perpendicular to the direction of movement as well as the velocity and shape of the head of the predator (Vogel, 1981). Despite these functional challenges, the majority of aquatically feeding tetrapods appear to have overcome these constraints by evolving a robust hyoid apparatus that allows them to suction feed (Lauder, 1985). Aquatically feeding snakes, however, cannot suction feed as their hyobranchial apparatus is highly reduced (McDowell, 1972). Yet, aquatic snakes regularly capture teleost fish under water.

Aquatic feeding has arisen independently in several groups of snakes (Cundall & Greene, 2000; Alfaro, 2002, 2003; Smith *et al.*, 2002; Hibbits & Fitzgerald, 2005; Bilcke *et al.*, 2006). However, unlike most other aquatic vertebrates, snakes have not evolved suction feeding as the hyobranchial apparatus in snakes is reduced due to specialization of the tongue for chemoreception (McDowell, 1972; Schwenk, 1994). As a result, snakes cannot use suction mechanisms based on hyoid expansion, but instead, must capture aquatic prey in a similar manner as they do terrestrial prey (i.e. by striking at the prey; see Alfaro, 2002, 2003; Smith *et al.*, 2002; Hibbits & Fitzgerald, 2005; Vincent *et al.*, 2005; Bilcke *et al.*, 2006).

Aquatically feeding snakes have evolved at least two drastically different strike behaviours, i.e. lateral side sweeping and frontal striking (see Drummond, 1983 for an overview), which are characterized by different hydrodynamic properties (Young, 1991). Previous work has shown that if the jaws are held open during laterally directed strikes, drag is reduced compared to a situation with the mouth closed (Braun & Cundall, 1995). For frontal strikers, having relatively long heads may improve their hydrodynamic profile and reduce drag as long as the mouth remains closed (Young, 1991; Hibbits & Fitzgerald, 2005). Although this fact leads to the prediction that frontal strikers should keep their mouth closed as long as possible, recent work has shown this is not the case, at least for some aquatic snakes (natricines;

Alfaro, 2002). Thus, we predict that changes in head shape should be present in natricine snakes using frontally directed strikes that enable them to capture prey effectively. Sideways striking, on the other hand, appears less mechanically constrained as long as the elongated and narrow jaws, typical of most snakes, are held open during the strike.

Based on the principle that the drag and bow wave are expected to scale exponentially with the linear element exposed to the direction of flow (Vogel, 1981, 2003), we formulate two testable predictions for how head shape should be designed for both frontal striking species and lateral side sweeping species. We predict that the sum of the dorsal and ventral head surface areas will be smaller in frontal strikers compared to lateral side sweepers, thereby minimizing the total surface area exposed to the direction of flow when the mouth is open (see also Young, 1991). Moreover, we predict a general streamlining of the head in frontal strikers, which should be reflected in a decrease of head width for a given length, again minimizing the surface area exposed to the flow. As lateral strikers are not faced with these constraints on frontal surface area, we expect them to have relatively wider heads as this allows them to eat large prey more effectively (Vincent *et al.*, 2006a).

Here we examine the evolutionary relationships between head shape and prey capture mode in 13 species of natricine snakes in an explicit phylogenetic context. Additionally, we test the biological relevance of the observed differences in head shape using a simple computational fluid dynamics (CFD) model. Natricine snakes are ideally suited for this purpose as both frontal and lateral strike modes have evolved repeatedly and independently in this clade (Alfaro & Arnold, 2001; Alfaro, 2002, 2003; Hibbits & Fitzgerald, 2005; Bilcke *et al.*, 2006).

Materials and methods

Specimens

As sexual dimorphism in body size and head shape, and ontogenetic variation in diet are well-documented phenomena in snakes (e.g. Arnold, 1993; Shine, 1994), we only considered adult males in this study. Sex was determined by the presence or absence of a hemipenis. We measured between 6 and 28 specimens obtained from museum collections (California Academy of Sciences, Florida Museum of Natural History, Louisiana State University Museum of Natural Sciences and the Tulane Museum of Natural History). To avoid geographic differences in head shape, specimens from the same geographic areas were used whenever possible. Moreover, we only used specimens that were minimally distorted during preservation to minimize measurement error.

Head size and shape

The following morphological measurements were taken for each specimen (Fig. 1): snout–vent length (SVL, in mm), head width (at the widest part of the head), head depth (at the tallest part of the head), head length (from
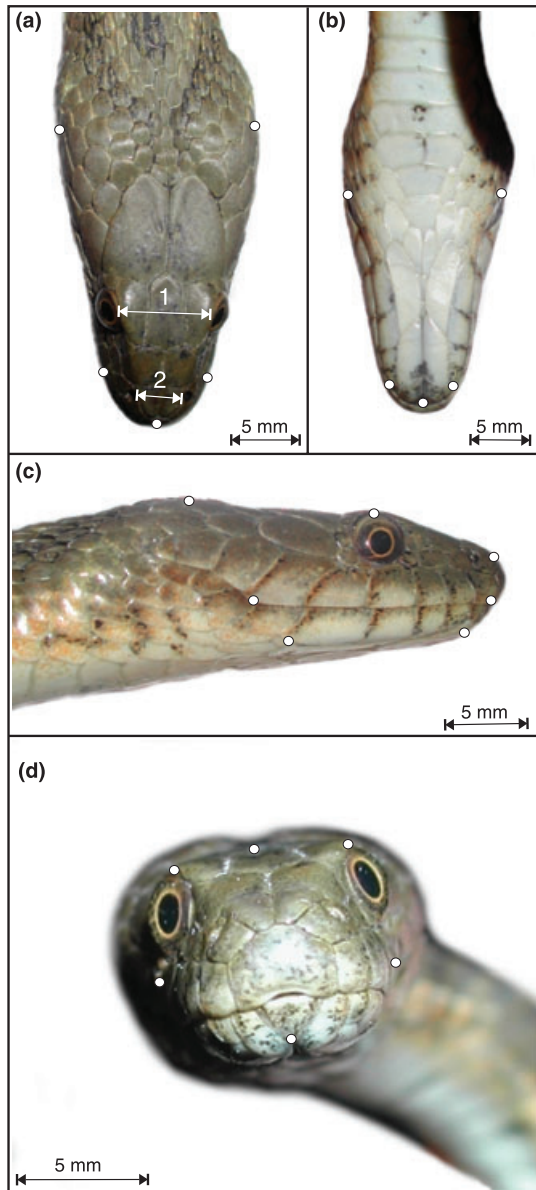

Fig. 1 Morphometric variables used in our analysis. (a) Dorsal view of the head of a *Natrix tesselata* illustrating the landmarks used to quantify dorsal surface area. Also shown are the interocular (1) and internasal (2) distances. (b) Ventral view of the head illustrating the landmarks used to calculate ventral surface area. (c) Lateral view of the head illustrating the markers used to calculate lateral surface area. (d) Frontal view of the head illustrating the markers used to quantify frontal surface area.

the back of the parietal to the tip of the snout), jaw length (from the retro-articular process to the tip of the lower jaw) and the out-lever of the lower jaw (from the articulation of the lower jaw with the quadrate to the tip of the lower jaw). We determined SVL by laying dental floss along the mid-ventral surface of the snake and then measuring the floss using a meter stick. All head measurements were taken using Mitutoyo digital calipers (Mitutoyo (UK) Ltd, Telford, UK) (±0.01 mm). Head volume (mL) was estimated as the amount of water displaced in a graduated cylinder by a snake's submerged head. To ensure that this measurement was comparable among individuals, the posterior-most portion of the back of the jaw was used as a stopping point for submersion.

To quantify aspects of head shape, digital images of the heads were taken in dorsal, lateral, ventral and frontal views using a Nikon COOLPIX S995 digital camera (Nikon Inc., Melville, NY, USA). An object of known size (wire mesh grid, 35×35 mm) was placed in the field of view for scaling purposes. Images were then imported into tpsdig32 (version 1.31; J. Rohlf, SUNY, Stonybrook, NY) and digitized. From these images, we determined the surface area of the head in dorsal, ventral and frontal views. Additionally, we calculated the surface area for the upper jaw (i.e. snout, maxilla and the neurocranium) and lower jaw (i.e. the suspensorial elements of the lower jaw and the mandible) separately in lateral view. The right side of the head was always used for measurements taken in lateral view. In frontal view, we also took two linear measurements: interocular distance (shortest distance between the edges of eyes) and the internasal distance (shortest distance between the edges of the nares). To acquire an estimate of the functionally relevant surface area during frontal striking, we summed the dorsal and ventral areas as forward strikers open their mouths prior to prey contact (Alfaro, 2002; see Fig. 2). Hereafter we refer to this measure as the projected frontal surface area. Although the true area exposed will be smaller than the area calculated here as the jaws are not fully opened during the strike (Alfaro, 2002), it will be proportional to this value as all species open their jaws to a similar degree (70–90°; Alfaro, 2002, pers. obs.).

Strike behaviour

Three to five individuals of the following species: *Nerodia clarkii* (3), *Nerodia fasciata* (5), *Nerodia rhombifer* (4), *Thamnophis couchii* (5), *Thamnophis elegans* (3), *Thamnophis rufipunctatus* (3) and *Natrix tesselata* (5) were filmed using either regular (60 Hz; Sony TVR 900; Sony Corporation, Tokyo, Japan) or high-speed cameras (Redlake motion-cope pci 500; Redlake motionpro 500; Redlake Inc., Tallahassee, FL, USA) set at 250 fps. Sequences were reviewed and strikes were scored as being either frontal or lateral. For the remainder of the species, strike behaviour was based on observations in the field: *Nerodia cyclopion* (A. Herrel), *Nerodia erythrogaster* (M. Alfaro), *Nerodia*
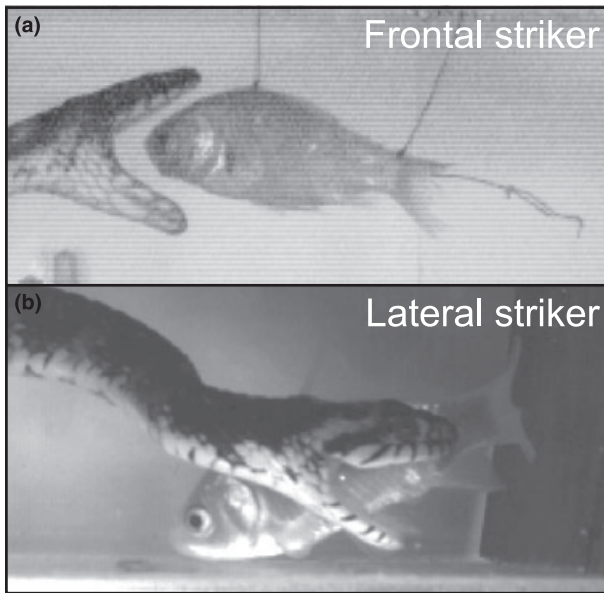
Fig. 2 Images from movies recorded with high-speed cameras illustrating a frontal strike in *Natrix tesselata* (a) and a lateral strike in *Nerodia fasciata* (b). Note how the fish is positioned in front of, vs. to the side of the head in the frontal and lateral strike respectively.

harteri (T. Hibbits), *Nerodia sipedon* (A. Herrel; see also Drummond, 1983), *Thamnophis atratus* (A. Herrel & M. Alfaro) and *Thamnophis hammondii* (S.J. Arnold). Although strike behaviour in natricines is known to vary in response to the abundance of fish, all species use very stereotyped behaviours when confronted with a low abundance of fish in a large body of water (Drummond, 1983, pers. obs.). As none of the strike mode assignments was made based on snakes foraging in drying pools with high fish abundance, our field based observations are a reliable indicator of strike mode in these species.

CFD modelling

CFD simulations were performed to evaluate the hydrodynamic consequences of the relatively small but highly significant differences in head shape in frontal vs. lateral strikers observed here. The jaws were modelled as two semi-elliptical plates (thickness 0.5 mm) at an angle of attack of 40° and −40° respectively (based on high-speed video recordings of frontal strikes in *N. tesselata*; see Movie S1). One-quarter of a cylindrical flow domain (length = 0.488 m, width = 0.2 m, height = 0.2 m) was modelled using sagittal and frontal symmetry planes. The intersection of the modelled jaws (minor semi-ellipse axes; corresponding to the corner of the mouth in a real animal) was placed at 0.1 m from a flow velocity inlet. Depending on the size of the jaws, tetrahedral meshes of 94 to 108×10^3 nodes were created using Gambit 2.3.16 (Fluent Inc., Lebanon, NH, USA). A size function was used to decrease the spacing of the nodes around the jaws.

The meshes were then imported into the commercial CFD solver Fluent (Fluent Inc.). The model was solved for a steady flow of 0.93 m s^{-1} at the velocity inlet (=the average strike speed of *N. tesselata*), while the jaws were held stationary. The pressure-based, 3D solver under laminar flow conditions was used as the Reynolds number (maximum Re = 1.89×10^4) is always safely below the value where transition to turbulent boundary layers occurs (critical Re: approximately 2×10^5). A no-slip shear condition at the modelled jaws (smooth surfaces) was used. The flow equations (the Navier–Stokes equations and the continuity equation) were solved using the SIMPLE pressure–velocity coupling scheme, the standard pressure discretization and a second-order upwind scheme as velocity discretization for at least 500 iterations. First, a simulation was run with the models scaled to a jaw length and width based on the average values for frontal and lateral strikers respectively and corrected for differences in mean SVL. Next, a second simulation was run but this time with the jaws scaled to the same average length for both frontal and lateral strikers, but with a jaw width as dictated by the means of both frontal and lateral strikers and corrected for head length. The values reported for drag in this study equal the sum of both pressure drag and viscous drag. Although we realize that the model is an over simplification of reality (i.e. a snake head does not consist of two flat plates, and the flow will most likely not be steady around the head of the snake during the strike), it allows us to assess whether the relatively small differences in head shape may have effects that could affect the interaction between the predator and the prey.

Phylogenetic analysis

The goal of this analysis was to identify the phylogenetic placement of previously unrecognized forward striking species (*N. tesselata* and *Ne. clarkii*) and so create a framework for comparative analysis of behaviour and morphology. We extracted genomic DNA from *N. tesselata* and *Ne. clarkii* using Chelex following Barber & Bellwood (2005). We used primers and protocols from Alfaro & Arnold (2001) to amplify, and sequenced the entire cytochrome B (cytb) gene for these new species and combined them with previously published data for cytb and ND2 (Alfaro & Arnold, 2001; de Quieroz *et al.*, 2002) to create a matrix with 60 taxa and 2146 characters. We selected a model of sequence evolution from the pool of 203 time-reversible models on the basis of their Akaike Information Criterion score using PAUP* 4.0 b10 (Swofford, 2000) to implement a procedure described in Alfaro & Huelsenbeck (2006). The best model for our data was an unnamed foru-parameter model with index 123143 following the notation of (Huelsenbeck *et al.*, 2004). We used an iterative search strategy to find the maximum likelihood (ML) tree. First we generated a neighbour-joining tree and estimated the parameters of the model (above) on it. Although neighbour-joining
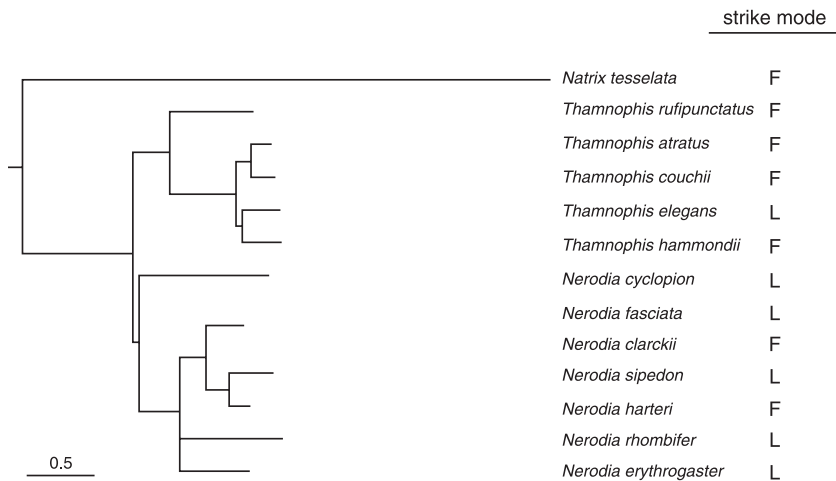
strike mode

Natrix tesselata	F
Thamnophis rufipunctatus	F
Thamnophis atratus	F
Thamnophis couchii	F
Thamnophis elegans	L
Thamnophis hammondii	F
Nerodia cyclopion	L
Nerodia fasciata	L
Nerodia clarckii	F
Nerodia sipedon	L
Nerodia harteri	F
Nerodia rhombifer	L
Nerodia erythrogaster	L

0.5

Fig. 3 Phylogeny showing relationships among species used in this study. Branches are drawn proportional to expected amounts of change based on the molecular data (cytb and ND2). Also indicated is strike mode for each species. F, frontal striker; L, lateral striker.

estimates may be problematic (Marjanovic & Laurin, 2007), in our case the final tree obtained was highly similar in overall structure to those retained using parsimony-guided approaches (Alfaro & Arnold, 2001; de Quieroz *et al.*, 2002). Next we performed a heuristic search using parameter values fixed to those estimated on the neighbour-joining tree. We then re-estimated the parameter values on the ML tree and performed a second round of heuristic searching, this time with five random addition sequence replicates. Four of the five addition sequence replicates found a tree with −LnL = 24710.52484; the fifth tree found was substantially worse (−LnL = 24724.81100). The tree was then pruned to retain those taxa for which strike mode was known. As the genes used in our phylogenetic analysis (cytb and ND2) are not functionally related to the head-shape traits examined in our study, convergence of the genetic markers on the morphological traits is unlikely. Consequently, the tree obtained using these markers can be used to test for patterns of morphological and behavioural coevolution.

Statistical analysis

Prior to comparative analysis, means of all morphological traits were calculated per species and $\log_{10}$ transformed. As species share part of their evolutionary history, they cannot be treated as independent data points. Thus, we conducted these analyses in a phylogenetic framework (Felsenstein, 1985, 1988; Harvey & Pagel, 1991). To do so, we used the pruned ML phylogeny (Fig. 3), once with branch lengths proportional to the amounts of evolutionary change using the molecular data, and once with branch lengths set to unity. We used the PDAP

Table 1 Results of phylogenetic analyses of covariance with snake snout–vent length as covariate, testing for differences in head shape between frontal and lateral strikers.

Variable	F_{phyl}	F_{trad}	P_{trad}	P_{phyl}
Head volume	4.13	15.12	0.003	0.001*
Head length	4.31	5.15	0.047	0.046
Head width	4.62	25.30	0.001	< 0.001*
Head height	4.40	15.31	0.003	< 0.001*
Lower jaw length	4.57	4.88	0.052	0.048
Jaw outlever	4.79	7.42	0.021	0.013*
Internasal distance	4.33	1.08	0.323	0.324
Interocular distance	4.23	12.69	0.005	0.002*
Lateral head surface area	4.20	10.26	0.009	0.003*
Frontal head surface area	4.35	34.62	< 0.001	< 0.001*
Projected frontal surface	4.80	11.29	0.007	0.002*

Bold variables are significantly different between frontal and lateral strikers. Lateral strikers have bigger heads in all dimensions than frontal strikers.
*Significant differences after sequential Bonferroni correction at α = 0.05.

Table 2 Results of phylogenetic analyses of covariance with snake head length as covariate, testing for differences in head shape between frontal and lateral strikers.

Variable	F_{phyl}	$F_{phyl}Ct$	F_{trad}	P_{trad}	P_{phyl}	PCt
Head volume	4.15	5.44	3.17	0.105	0.094	0.111
Head width	4.48	5.78	11.90	0.006	0.003*	0.009
Head height	3.85	5.16	0.57	0.469	0.472	0.496
Lower jaw length	4.65	4.98	0.14	0.908	0.916	0.970
Jaw outlever	4.54	4.69	0.12	0.914	0.908	0.967
Internasal distance	4.13	4.73	0.16	0.695	0.682	0.714
Interocular distance	4.36	5.05	3.12	0.108	0.089	0.110
Lateral head surface area	4.13	4.78	3.45	0.093	0.073	0.089
Frontal head surface area	4.91	4.72	7.68	0.020	0.013	0.013
Projected frontal surface	4.59	5.27	6.30	0.031	0.024	0.035

Bold variables are significantly different between frontal and lateral strikers. $F_{phyl}Ct$ and PCt denote the *F*-value and *P*-value for simulations with constant branch lengths. Lateral strikers have wider heads, greater frontal surface areas and greater projected frontal surface areas than frontal strikers.
*Significant differences after sequential Bonferroni correction at α = 0.05.

package (Garland *et al.*, 1999) for our analysis. To test whether frontal strikers differed from lateral strikers in head-shape variables, simulation analyses were performed using the PDSIMUL and PDANOVA programs (Garland *et al.*, 1993). In the PDSIMUL program, we used Brownian motion as our model for evolutionary change and ran 1000 unbounded simulations to create an empirical null distribution against which the *F*-value from the original data could be compared. In the PDANOVA program, strike mode was entered as dependent, head dimensions were used as independent variables, and SVL or head length were used as covariates. We considered differences among categories significant if the original *F*-value was higher than the *F*95-value derived from the empirical distribution (Tables 1 and 2). Sequential Bonferroni corrections are listed in Tables 1 and 2. However, as we tested specific *a priori* predictions (see below), we interpret significance levels without correction as biologically relevant. The specific hypotheses tested were:

1 for a given body size, frontal strikers have smaller heads in all dimensions compared to lateral strikers;

2 for a given head length, frontal strikers have smaller frontal and projected frontal surface areas compared to lateral strikers and reduce frontal surface area by decreasing head width relative to head length.

Finally, we calculated the phylogenetic signal present in our data using the randomization test described in Blomberg *et al.* (2003) and computed the *K*-statistic (an indicator of phylogenetic signal) for the head-shape variables included in our analysis. This analysis was implemented with MATLAB version 6.1.0 for PC (The MathWorks Inc., Natick, MA, USA) using the module 'PHYSIG' (available by request to Dr T. Garland, University of California at Riverside).

Results

Our phylogenetic ANCOVAS with SVL as covariate show that frontal strikers have smaller heads for a given body size in nearly all dimensions except for the internasal distance (Tables 1 and 3; Figs 4 and 5). Moreover, our analyses show that, for a given head length, frontal strikers have narrower heads that result in a decrease in the frontal surface area as well as in the projected frontal surface area as predicted (Table 2). Head width is approximately 5% smaller relative to body length, and 2% relative to head length in frontal strikers compared to lateral strikers. These results are independent of whether branch lengths are set to unity or relative to expected amounts of evolutionary change (Table 2). Interestingly, the tests for phylogenetic signal as described in Blomberg *et al.* (2003) suggested that only one of the head-shape traits (internasal distance) exhibits significant phylogenetic signal (Table 4). This suggests that closely related species of natricine snakes have similar internasal distances and may explain why this variable was not

Table 3 Head size and shape in the natricines examined in *this study*.

Species (n)	Snout-vent length	Headvol	Width	Length	Height	Intocular	Internasal	Proj front SA	LatSA	FrontSA	Strike mode
Nerodia clarkii (28)	461.56 ± 68.60	1.59 ± 1.38	12.67 ± 1.81	18.84 ± 2.72	9.93 ± 1.49	5.79 ± 0.88	3.44 ± 0.82	636.82 ± 180.71	150.50 ± 48.84	81.58 ± 22.81	Frontal
Nerodia cyclopion (15)	498.73 ± 79.87	4.8 ± 1.57	16.13 ± 2.77	21.75 ± 4.14	11.70 ± 2.13	6.35 ± 0.90	3.51 ± 0.59	1059.93 ± 248.42	224.07 ± 75.36	133.40 ± 35.98	Lateral
Nerodia erythrogaster (14)	522.00 ± 135.21	5.64 ± 4.67	16.81 ± 4.60	24.18 ± 5.32	12.55 ± 4.46	7.48 ± 1.50	4.23 ± 1.15	1078.86 ± 563.45	230.94 ± 92.36	144.00 ± 68.97	Lateral
Nerodia fasciata (10)	430.10 ± 77.86	2.60 ± 1.58	13.79 ± 2.34	19.45 ± 2.29	9.92 ± 1.34	6.57 ± 1.19	3.59 ± 0.72	718.90 ± 183.15	157.86 ± 42.90	98.80 ± 39.31	Frontal
Nerodia harteri (9)	433.44 ± 54.12	1.56 ± 0.53	11.03 ± 1.03	16.72 ± 0.94	8.26 ± 0.77	5.39 ± 0.56	3.17 ± 0.41	485.33 ± 76.55	117.80 ± 21.00	59.89 ± 11.56	Frontal
Nerodia rhombifer (22)	562.91 ± 119.01	7.00 ± 3.82	19.18 ± 5.06	22.81 ± 4.26	13.91 ± 4.03	6.97 ± 1.49	3.72 ± 1.05	1326.10 ± 552.60	235.03 ± 86.27	171.43 ± 77.86	Lateral
Nerodia sipedon (19)	448.21 ± 48.60	3.37 ± 1.01	13.87 ± 1.77	18.87 ± 1.88	10.32 ± 1.44	6.24 ± 0.94	3.37 ± 0.90	744.53 ± 170.82	160.86 ± 32.59	97.51 ± 27.39	Lateral
Thamnophis atratus (10)	407.10 ± 40.44	1.40 ± 0.52	10.17 ± 1.34	15.25 ± 1.61	7.67 ± 0.95	4.78 ± 0.62	2.53 ± 0.53	415.40 ± 72.08	85.37 ± 12.78	54.30 ± 15.64	Frontal
Thamnophis couchii (10)	514.10 ± 70.91	2.70 ± 1.06	12.37 ± 1.44	17.93 ± 1.27	9.82 ± 1.13	5.35 ± 0.51	2.86 ± 0.55	625.30 ± 134.80	129.75 ± 21.72	79.80 ± 13.66	Frontal
Thamnophis elegans (15)	431.40 ± 74.92	1.47 ± 0.99	11.12 ± 2.37	14.85 ± 2.11	8.04 ± 1.30	5.38 ± 0.76	3.12 ± 0.77	463.40 ± 196.21	100.37 ± 45.81	66.07 ± 25.92	Lateral
Thamnophis hammondii (6)	519.00 ± 70.01	2.83 ± 0.98	13.16 ± 2.19	19.11 ± 2.28	10.31 ± 1.57	6.04 ± 0.94	3.85 ± 0.41	698.50 ± 185.03	154.10 ± 36.85	88.83 ± 30.20	Frontal
Thamnophis rufipunctatus (6)	510.33 ± 148.98	3.33 ± 3.44	13.17 ± 4.08	20.38 ± 5.11	10.09 ± 2.91	5.07 ± 0.62	3.15 ± 0.21	791.00 ± 264.46	161.18 ± 90.59	85.50 ± 38.89	Frontal
Natrix tesselata (8)	614.38 ± 81.86	2.63 ± 1.69	13.81 ± 2.19	19.76 ± 1.64	11.50 ± 1.78	6.93 ± 1.09	5.44 ± 0.81	591.25 ± 185.49	174.39 ± 49.42	113.13 ± 35.58	Frontal

Table entries are means ± SDs. Linear dimensions are in millimeter, volume in milliliter and surface areas in square millimeter.
Headvol, head volume; intocular, interocular distance; internasal, internasal distance; Proj front SA, projected frontal surface area; LatSA, lateral surface area; FrontSA, frontal surface area.
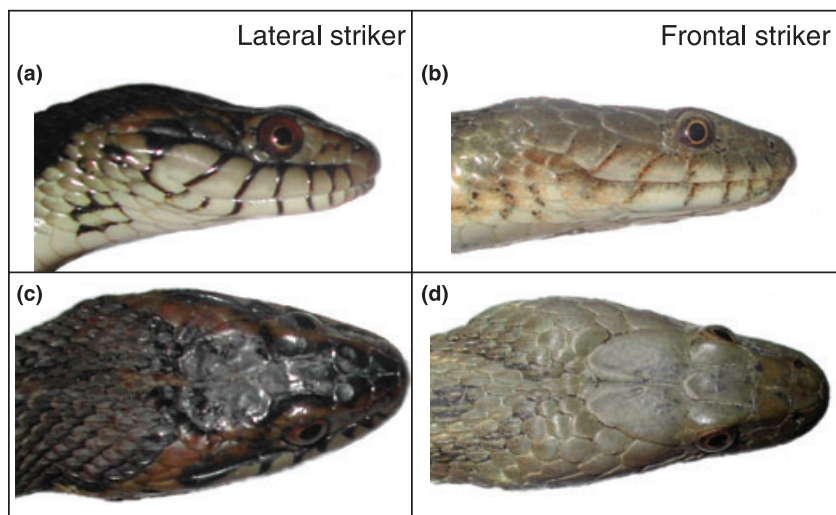
Fig. 4 Pictures of the heads of a *Nerodia fasciata* (a, c) and a *Natrix tesselata* (b, d) illustrating the difference between frontal (*Natrix tesselata*) and lateral (*Nerodia fasciata*) strikers. Note that, whereas heads appear similar in lateral view (compare a with b), they are very different in dorsal view (c and d).

different between frontal and lateral strikers in our phylogenetic ANCOVA with SVL as covariate.

Our CFD models of the snake jaws show the generation of a significant bow wave in front of the mouth regardless of the simulation run (Fig. 6). Thus, frontal striking induces a bow wave (see Movie S1). The effect of the differences in head shape between the frontal and lateral strikers can be quantified by measuring the distance of a given iso-pressure surface from the modelled jaws. For example, the 39.4 Pa iso-pressure surface extends to 19.7 mm in front of the tips of the jaws (measured along the centreline) for the model of the frontal striker scaled to SVL. Compared to this, the same pressure reaches further (and could thus be felt by a potential prey from further way) when using the model of the lateral striker (25.9 mm; 32% increase). A similar result, although less pronounced, is observed for the models scaled to the same head length, with a distance of this iso-pressure surface extending 11% further away from the jaw edge in the lateral striker compared to the frontal striker (21.4 mm compared to 23.7 mm).

Moreover, our CFD models suggest that the observed differences in head width and surface area may have an important impact on the pressure drag experienced by the snake during striking (Table 5). A 5% decrease in head width relative to total length results in a 30% decrease in drag experienced by the snake. Similarly, the 2% difference in width for frontal and lateral strikers of a given head length results in a 12% difference in drag.

Discussion

Our data demonstrate convergence in head shape among species of natricine snakes that employ frontal strikes to capture elusive prey under water. The evolution of frontal striking in natricine snakes has been accompanied
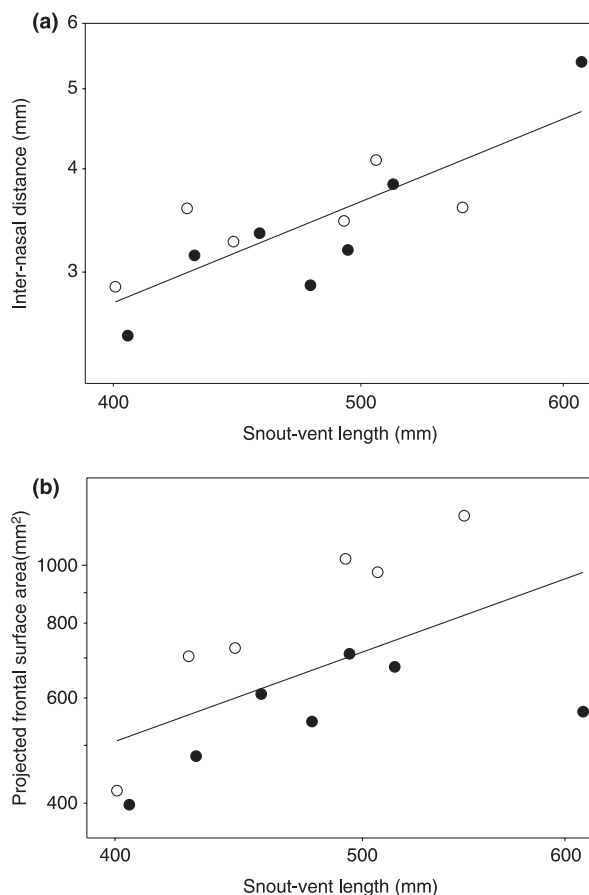

Fig. 5 Graphs illustrating shape differences among lateral and frontal strikers. (a) No differences in internasal distance are present between groups. (b) Frontal strikers have smaller projected frontal surface area for their body size than lateral strikers. Filled symbols: frontal strikers; open symbols: lateral strikers.

Table 4 Summary of an analysis testing for phylogenetic signal (*K*-statistic from Blomberg *et al.*, 2003) in the traits used in the analyses.

Trait	*K*	*P*
Head length	0.537	0.122
Head width	0.525	0.094
Head height	0.478	0.192
Lower jaw length	0.416	0.322
Jaw outlever	0.456	0.223
Internasal distance	0.849	**0.024**
Interocular distance	0.505	0.1
Frontal surface area	0.509	0.147
Lateral surface area	0.532	0.126
Projected frontal surface area	0.499	0.115
Head volume	0.426	0.267

Bold values display a significant amount of phylogenetic signal.

by a decrease in head width, which in turn has resulted in a decrease in the projected surface area perpendicular to the direction of movement. Moreover, our computational fluid dynamics models suggest that a reduction in surface area in our model significantly decreases the pressure drag experienced and reduces the extent of the bow wave considerably. Although our model is a crude simplification of the biological reality of a snake head striking at a prey under water, these results nevertheless suggests that the observed shape differences between frontal and lateral strikers may be biologically relevant

and important. Whereas the observed reduction in drag may give forward strikers a performance advantage over snakes with a less-specialized morphology, thereby enabling them to achieve higher strike velocities (Bilcke *et al.*, 2006), the reduced bow waves may prevent them from pushing the prey away from the axis of the strike. Although much of our current understanding of the evolution of suction feeding in vertebrates is based on the assumption that bow waves are present and biologically relevant to the predator (i.e. potentially affecting the capture success of a predator; see Lauder, 1985), our CFD models provide some of the first quantitative estimates of the magnitude of bow waves in aquatically striking snakes. Future, more complex 3D models or *in vivo* Particle Image Velocimetry based measurements of the flow around the head of a snake attacking a prey under water are crucial to test the validity of our current model.

Our CFD models also suggest a mechanistic framework for the proposed trade-off between the transport of large prey and capturing elusive prey under water (Vincent *et al.*, 2004, 2006a, Vincent & Mori, 2008). Previous work has suggested that increases in head width improve the handling of large and bulky aquatic prey both in laboratory (Savitzky, 1983; Forsman & Lindell, 1993; Vincent *et al.*, 2006b) and field-based settings (Vincent & Mori, 2008). For aquatically feeding snakes, however, a wide head appears to negatively affect the performance of frontally directed strikes because of its effect on the resultant drag and the bow waves generated during
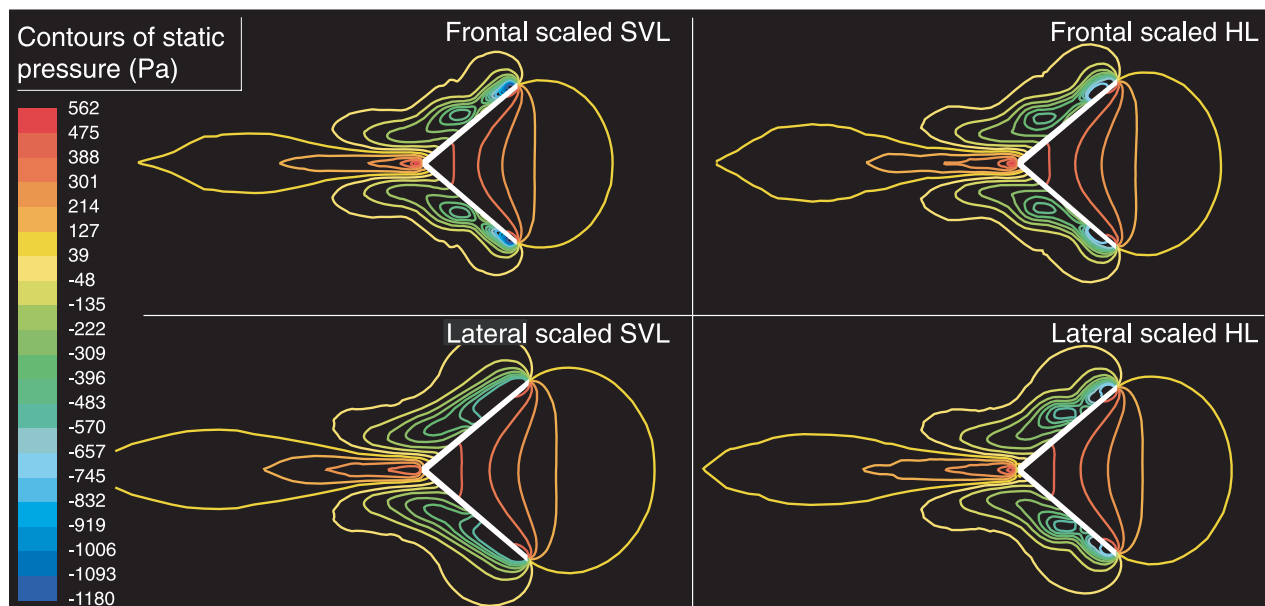

Fig. 6 Pressure profiles in the mid-sagittal plane through the jaws as calculated based on computational fluid dynamics models for the four simulations of frontal strikes. Left: models with the jaws scaled to the average head width of the frontal (top) and lateral (bottom) strikers for a given snout–vent length. Right: models with the jaws scaled to the average head width of frontal (top) and lateral (bottom) strikers for a given head length. Note the presence of a substantial positive pressure inside the mouth that appears more pronounced in lateral strikers than in frontal strikers. HL, head length; SVL, snout–vent length.

Table 5 Drag forces experienced by the snake models exposed to a continuous flow.

Model	Net force (*n*)	% Difference
Frontal striker (scaled to SVL)	0.212	31
Lateral striker (scaled to SVL)	0.307	
Frontal striker (scaled to HL)	0.235	12
Lateral striker (scaled to HL)	0.266	

HL, head length; SVL, snout–vent length.

striking. Thus, snakes specializing on large and bulky prey may be prevented from using frontally directed strikes. One exception is the venomous cottonmouth snake (*Agkistrodon piscivorous*), that has a large and bulky head, yet uses frontally directed strikes when striking at aquatic prey (Vincent *et al.*, 2005). However, the strike success of cottonmouths was markedly lower when striking at prey under water vs. when striking on land (13% compared to 95% respectively). Still, the frontally directed strikes of cottonmouths remain an enigma as laterally directed strikes could reduce the drag experienced considerably even if the lateral profile of this species is far from ideal (see Young, 1991). One explanation for this observation may be that cottonmouths have poor underwater vision, thus constraining them to strike from above the water surface using frontally directed strikes. Indeed, even among semi-aquatic natricines, species that typically do not feed under water have extremely poor underwater vision, which may prevent them from specializing on elusive prey (Schaeffel & de Queiroz, 1990; Schaeffel & Mathis, 1991).

Interestingly, previous data suggest that laterally directed underwater strikes are similar in velocity to frontal strikes in some species (Alfaro, 2003; Bilcke *et al.*, 2006). However, as lateral striking is not limited to the same degree by hydrodynamic constraints (essentially, a lateral strike can be represented by two plates moving in a parallel direction through the water, thus generating minimal drag and negligible bow waves; see Young, 1991), this raises the question why the most specialized species of natricines still use frontally directed strikes. Given the decrease in swallowing performance associated with their narrower heads (Savitzky, 1983; Forsman & Lindell, 1993; Vincent *et al.*, 2006b), this is all the more unexpected. A potential explanation may lie in the lack of visual overlap during lateral striking, which may make estimates of prey distance difficult and may cause lateral striking to be less effective. This possibility accords with the observation that lateral strikers generally strike at prey in higher density (Bilcke *et al.*, 2006). Frontal strikers, on the other hand, have excellent underwater vision (Schaeffel & de Queiroz, 1990; Schaeffel & Mathis, 1991) and some binocular field overlap (Hibbits & Fitzgerald, 2005); frontal strikers should therefore be able to accurately judge distances to teleost fish prey. Whether this explanation is correct needs to be tested, however.

We believe that underwater striking in snakes could be a model system for studying convergence and the role of physical constraints therein. Underwater striking has arisen independently several times in snakes. Many groups such as the aquatic pythons, the acrochordids, the homalopsids and many of the extremely diverse sea snakes remain unexplored today. Our data for underwater prey capture in natricine snakes suggest that the outcome of evolutionary divergence may be predictable in the face of severe physical constraints on performance. Consequently, we would predict that, for example, acrochordids would use laterally directed strikes to capture teleost fish under water given their bulky and wide heads. Analyses of underwater prey capture in acrochordids and other snakes are, however, needed to test the generality of this prediction.

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Supplementary material

The following supplementary material is available for this article:

Movie S1. *Natrix tesselata* striking frontally at a dead goldfish freely suspended from a fine wire. Note how the snake opens its mouth well before reaching the fish and how the fish is pushed away slightly from the approaching predator. The CFD models were based on a frontal strike in *Natrix tesselata* with the jaws opened to 45 degrees.

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