Can all snakes swim? A review of the evidence and testing species across phylogeny and morphological diversity

Guillaume Fosseries [a,*], Anthony Herrel [b,c,d,e], Ramiro Godoy-Diana [f], Philippe Gaucher [g], Margo Traimond [g], Antoine Joris [h], Karim Daoues [i], Antoine Gouygou [j], Olivier Chateau [k], Hugues Gossuin [k], Pierre Banzept [l], Chany Banzept [l], Dimitri Lefebvre [l], Xavier Bonnet [a,*]

[a] *CEBC, Centre d'études Biologiques de Chizé, UMR7372, CNRS, La Rochelle University, France*
[b] *MNHN, National Museum of Natural History, CNRS, Paris, France*
[c] *Department of Biology, Evolutionary Morphology of Vertebrates, Ghent University, Ghent, Belgium*
[d] *Department of Biology, University of Antwerp, Wilrijk, Belgium*
[e] *Naturhistorisches Museum Bern, Bern, Switzerland*
[f] *PMMH, Physique et Mécanique des Milieux Hétérogènes, UMR7636, CNRS, ESPCI Paris-PSL, Sorbonne Université, Université Paris Cité, France*
[g] *Zoo de Guyane, Tonate-Macouria, Guyane française, France*
[h] *Réserve Africaine de Sigean, Sigean, France*
[i] *La Ferme Tropicale, Paris, France*
[j] *Reptiland, Martel, France*
[k] *Aquarium des Lagons, Nouméa, Nouvelle-Calédonie, France*
[l] *La Ferme des Reptiles, La Bastide-de-Sérou, France*

ARTICLE INFO

ABSTRACT

Alternative hypotheses suggest that the reptiles at the origin of snakes were primarily either burrowing, terrestrial or marine. It is possible that the ability to swim varies between the major snake lineages and lifestyles; for example, the highly fossorial blind snakes (Scolecophidia), a lineage that emerged early in snake evolution over 100 My ago, may not be able to swim. However, it is sometimes stated that all snakes can swim suggesting that swimming ability may not be discriminatory. To find out whether this is true, we used a systematic search (PRISMA), including personal communications and information on websites. Of the 3951 species considered, no information was found for 89 % of all snakes. Of the 454 species for which information was found, 382 species were aquatic, only 62 were terrestrial, 6 were arboreal, and only 4 were burrowing. Moreover, almost all belonged to the speciose Colubroides (e.g. 58 % *Colubridae*, 20 % *Elapidae*). No reliable information was available for important early diverging lineages (e.g. Scolecophidia, *Aniliidae*). Faced with this lack of information, we filled in important phylogenetic gaps by testing the swimming capacity of 103 diverse snake species and 13 species of diverse limbed and limbless ectothermic tetrapod vertebrates (Amphisbaenia, Lacertilia, Gymnophiona). All tests were positive. The results show that, 1) all snakes for which information is available (525 species) appear to be able to swim, 2) this is a trait shared by many land vertebrates that undulate laterally. As swimming ability is non-discriminatory, we need to collect detailed measurements on the performance, kinematics and energetic efficiency of swimming snakes. It is also necessary to finely describe the ecology and morphology of the species studied to better understand form~function relationships and the occupation of ecological niches in snakes.

1. Introduction

Estimates based on genomic analyses suggest that snakes diverged from other squamates in the Upper Jurassic, with the main lineages of snakes becoming established in the Cretaceous (Burbrink et al., 2020). However, the ecological context in which the snakes appeared remains debated (Da Silva et al., 2018; Miralles et al., 2018; Strong et al., 2022). There are three main hypotheses: snakes may have had marine, burrowing (fossorial), or terrestrial (living on the ground) ancestors. Debates tend to focus on the marine *versus* burrowing hypotheses and the controversy revolves around cranial features that may indicate the habitat and lifestyle of ancient snakes (Da Silva et al., 2018; Garberoglio et al., 2019; Palci et al., 2017; Yi and Norell, 2015). However, fossils of "proto-serpents" from the Middle Jurassic-Lower Cretaceous are rare and fragmentary, and there are no skulls; these major shortcomings make it impossible to decide definitively between the hypotheses (Caldwell et al., 2015, 2021; Macrì et al., 2023; Zaher et al., 2023).

Therefore, more and more analyses are based on the combination of anatomical and ecological characters, especially those that provide information on the living environment of fossil and extant snakes (Da Silva et al., 2018; Hsiang et al., 2015). Spectacular progress has been made thanks to the assembly of complete genomes (Bradnam et al., 2013; Myers et al., 2000; Peng et al., 2023). Understanding the genetic regulation of embryonic development, morphological traits and physiological function provides a synthetic view of the genes involved in adaptation to different environments (Peng et al., 2023). For example, the ability of snakes to exploit marine environments may have been achieved through the selection of genes involved in osmotic regulation (Rautsaw et al., 2021). Further, important functions that favour aquatic life have been linked to specific genetic processes, in particular those associated with resistance to hypoxia, changes in sensory perception, or immune responses (Ludington et al., 2023). The muscular and tendinous system is clearly different in snakes adapted to aquatic, terrestrial or arboreal life (Jayne, 1982; Mathou et al., 2023; Tingle et al., 2024). However, the relationships between genome evolution and locomotor adaptations, particularly swimming adaptations, remain obscure (Peng et al., 2020). The problem of locomotion, whether in an aquatic, terrestrial or subterranean environment, is central to understanding the type of environment in which snakes evolved. The inability to link snake locomotion to genomics or fossil remains is therefore a major obstacle, and a complex issue.

Swimming with lateral undulations is probably an ancient trait in chordates that predates the appearance of vertebrates (Frolich and Biewener, 1992; Jayne, 1988, 2022; Meinertzhagen et al., 2004; Nishino et al., 2010) Therefore, the ability to swim in modern snakes may simply be a conserved ancestral trait rather than an adaptation derived from terrestrial animals. However, even important traits can be lost rapidly, for example limbs in snakes and other amniotes are no longer expressed due to changes in Hox genes and/or patterning mechanisms (Mann et al., 2022; Roscito et al., 2022). In limbless animals, the actuation pattern underlying undulatory swimming is complex. For lateral undulations to produce effective propulsion in the water, the propulsive forces must exceed (acceleration) or equal (cruise) the drag. Thus, the anteroposterior propagation of muscle activity must exceed the speed of propagation of the alternating lateral curvatures of the body to generate vortices that are themselves moving and on which the body pushes by increasing the amplitude of the undulation backwards (Stin et al., 2023). This movement differs from lateral undulation on land, where the substrate supports are rigid and immobile (Frolich and Biewener, 1992). The underlying neurophysiological mechanisms that control aquatic locomotion are therefore peculiar, complex and precisely tuned; they have not necessarily been conserved during evolution in truly terrestrial snake lineages, such as highly fossorial blind snakes that evolved more than 100 My ago (Fachini et al., 2020). Thus, although knowing that snakes can or cannot swim does not solve the problem of the aquatic or terrestrial origin of snakes, studying this question highlights the impact of specialised lifestyles (e.g. burrowing, arboreal) on the possible maintenance or erosion of an ancestral trait that appeared in fundamentally aquatic animals over 500 My ago.

Independent of these questions about the evolution of snakes, knowing which snake species can swim is important for a better understanding of their ecology. For example, are rivers obstacles that fragment snake habitats, or do they form connective landscape elements? Is the morphology and anatomy of all snakes compatible with swimming or not? In other words, are all species that are strictly arboreal and extremely elongated, or burrowing and extremely stocky, capable of swimming? To what extent does the ingestion of large prey hinder swimming?

Leading experts and several observers have stated that all individuals of all snake species are able to swim (Table S1). If this claim is true, then the criterion "can swim or not" is not discriminatory for evolutionary questions and is not pertinent for ecological or conservation issues. However, little or nothing is known about the swimming ability of many burrowing, arboreal or litter-dwelling species in tropical forests. In addition, most of extant snakes belong to a few lineages that diversified greatly less than 40 My ago (Klein et al., 2021). The other lineages are essentially represented by supposedly fossorial/ litter-dwelling snakes that are almost never observed. This is particularly the case for the hundreds of species in the paraphyletic group Scolecophidia, or for certain groups represented by very few species such as the *Calabaria* (Burbrink et al., 2020; Miralles et al., 2018). The current paucity of actual data on swimming ability somewhat weakens the claim that all snakes can swim.

To address this issue, we first reviewed the available data in both the scientific and grey literature (Mahood et al., 2014). We then tested swimming ability in data-deficient species to fill in some of the critical gaps, both in terms of phylogeny and morphology/ecology.

2. Materials and methods

2.1. Definition of swimming

Swimming, self-propulsion through water, is achieved by coordinated movements of the body, tail, fins, limbs or jet propulsion (or any combination thereof) to generate hydrodynamic thrust that results in directional motion. This excludes uncoordinated movements that may result in uncontrolled displacements. Snakes use eleven types of locomotion; only lateral undulation is used for swimming (Jayne, 2020).

2.2. Review of the evidence

We used the Preferred Reporting Items for Systematic Reviews and Meta-Analyses (PRISMA) method, which combines and compares results from different sources (Mateo, 2020). First, in November 2021, we retrieved a list of 3951 snake species from the Reptile Database (Uetz et al., 2024) (this list does not include the 122 new species described in 2022 and 2023). We then searched for important ecological characteristics of each listed species, in particular habitat and prey type (e.g. aquatic, terrestrial, arboreal, fossorial), which may also indicate whether the species of snake can swim. In fact, by default, we considered all snake species with an aquatic or semi-aquatic lifestyle to be able to swim. In the absence of ecological information, fish-eating snakes were assumed able to swim. Amphibians are also associated with the aquatic environment, but they can be captured out of the water, so the criterion based on the presence of amphibians in the diet was not used. We also included some anecdotal observations from experts. For other snakes whose lifestyle is not clearly associated with aquatic locomotion, we used two approaches.

1) Taxonomy-based search: In Google, we used genera and species of all non-aquatic snake listed as keywords to find articles published in scientific journals or chapters in scientific books (e.g. via

https://www.researchgate.net, websites of research organisations or universities). Articles providing ecological information were retained. For snakes from North America and Europe, most species have been the subject of numerous scientific publications and the information was readily available. For the many species in other parts of the world, where greater diversity and lack of funding makes scientific study more difficult, we supplemented this search by looking beyond scientific articles. In particular, websites dedicated to reptiles but not organised to respond to keyword searches (e.g. Índice taxonómico reptiles Ecuador WWW Document, 2023) and naturalist books (e.g., Branch, 1998; Cogger, 2014; Murphy, 2007; Visser, 2015). The ability of a species to swim (or not) was rarely specified, so we looked for information not only in the text, but also in photos and videos. On Google, we used the genera and species for which we had no information (based on three categories "all", "pictures", "videos") and limited the search to 30 pages. Photos and videos of snakes swimming were used if the species could be identified (species names suggested by observers are often incorrect).

2) Search based on locomotion: In Google Scholar (to make the search more targeted), we used the following keyword pairs in succession "swimming snake" then "swimming reptile". We discarded irrelevant items, such as the many articles on robotics. We limited the search to 30 pages for each keyword pair. We then widened the criteria by using the following keyword pairs "lateral undulation; aquatic locomotion, reptile aquatic lifestyle". Again, the relevant articles were highly redundant, we limited the search to 30 pages, and we did not test other possible relevant keywords such as "fish snakes". In total, out of 1442 positive searches, we retained 42 articles in which swimming was documented or studied, in one or more snake species. To extend the search procedure, we proceeded in the same way as the taxonomy-based search on Google using phots and videos, but using the keywords of locomotion. A snake species was considered to be a swimmer if it could be identified.

We also used scientific articles based on literature reviews (Figueroa, 2016; Harrington et al., 2018; Hartmann et al., 2009; Segall et al., 2016). A large amount of information was available in the appendices, which made it possible to crosscheck with other sources.

After selection, the retained information was classified according to five source categories: scientific articles based on taxonomy (St); scientific articles based on locomotion keywords (Sl); text, photos and videos on websites (W); naturalist books (B); and expert observations (O). Redundancy was common, especially for the most easily observable species (generally the most studied).

2.3. Testing snakes

Several snake species for which information on swimming ability was lacking were tested. We attempted to fill important phylogenetic gaps by testing, for example the genera *Afrotyphlops*, *Typhlophis*, *Anilius* and *Calabaria*. Snakes were obtained from the wild (N=32 sp., metropolitan France, North-Macedonia, New Caledonia, French Guiana) or from captivity (N=71 sp.; various origins, Table S2 provides the list of zoos and other institutions that have loaned individuals and hosted systems used to test the snakes' swimming ability). Individuals were placed in a 4, 6, 9 or 12 m long and 0.5 or 0.6 m wide swimming raceway. The length and the width of the set up varied depending on where the tests were carried-out (laboratory, field or zoo) but the protocol used was the same. Swimming was triggered when the snake was put in the water, trying to escape from the experimenter. Swimming was often observed immediately. However, some individuals floated without attempting to swim, sometimes throwing bluff strikes; a few individuals showed thrashing movements (probably due to panic). These uncooperative or panicking snakes were encouraged to swim by taps on the tail until they began to swim. Swim tests were validated when the snakes covered at least three times their own body length, in most cases

reaching the other end of the raceway. We also tested several terrestrial legless and or legged reptiles belonging to other lineages (e.g. skinks, gecko, amphisbaenians) that were used at outgroups (Table S3).

2.4. Technical caveats for ecological categories

Some species, such as the presumed burrower *Cenaspis aenigma*, have never even been observed alive (Campbell et al., 2018), and their ecology can only be hypothesised using morphological features. Furthermore, information can be unstable. For example, the green water snake *Philothamnus hoplogaster* is terrestrial according to Branch (Branch, 1998), but since it sometimes feeds on fish, it could be considered semi-aquatic, and this species is even arboreal in Harrington et al. (Harrington et al., 2018). In the rare cases of conflict, we chose the most reliable information; for example, *Anilius* is described as terrestrial/fossorial by the field expert F. Starace (2013) but as aquatic in various websites that repeat unverified or vague information (further our own field experience favours terrestrial/burrowing habits). Despite feeding on fish, *Ahaetulla fronticincta* hunts suspended from branches above the water; its diet does not indicate swimming ability.

The categorization was based on the degree of dependence of the species on different environments. For example, the semi-aquatic category includes species that use both aquatic and terrestrial environments, even for short periods in one of the two environments. This category includes species that make brief forays into the water to feed occasionally on aquatic prey (e.g. *Natrix helvetica*, which feeds on amphibians but also regularly consumes small terrestrial mammals; Luiselli et al., 2005) and species that spend much or most of their time in the water such as sea kraits, which feed exclusively on marine prey, or file snakes (Acrochordids), which rarely venture onto land. The "fully-aquatic" category includes species that spend their entire life in the water; it includes only truly marine snakes (Hydrophiinae). Geographical variations in diet, for example, mean that the categories are not always strictly defined (Shine, 1987).

Overall, these complications and the ability of many snakes to move between environments challenge the simplistic classification we have adopted. However, given the results, these difficulties are unlikely to have affected the main conclusions. Nonetheless, snakes were assigned to seven broad lifestyle (ecological) categories: Fully-aquatic (i.e. truly marine snakes), semi-aquatic (amphibious sea snakes, freshwater and brackish water snakes), terrestrial (ground is the main habitat), burrowing (fossorial snakes), semi-burrowing (often found in litter), arboreal, and semi-arboreal (arboreal regularly observed on the ground). For these categories, the prefix "semi" before the primary microhabitat indicates that these species are also commonly found on the ground. In some cases, fully-aquatic and semi-aquatic snakes were grouped as 'aquatic', burrowing with semi-burrowing into 'fossorial' and arboreal with semi-arboreal into 'arboreal'.

3. Results

Of the 3951 snake species listed, information on swimming ability was available for 454 (11 %) (Table 1; Fig. 1). However, 382 of these (84 %) were fully-aquatic or semi-aquatic snakes and 62 (14 %) were terrestrial. Swimming was reported for only 3 arboreal, 3 semi-arboreal, 4 burrowing and no semi-fossorial snakes. The swimming ability of the remaining 3497 (89 %) species remains unknown, and this proportion rises to 98 % if aquatic species are excluded. These values contrast with the common claim that all snakes can swim (Table S1).

Regarding snake phylogeny, almost all the available information concentrated on a few modern lineages (Table 2; Fig. 2). This means that based on the review of the evidence it was impossible to infer any evolutionary scenario about the swimming ability of snakes.

Among the sources used to find swimming information, non-scientific websites were the most rewarding. Data (e.g. videos) were collected for 304 snake species. Interestingly, although most snake

Table 1

Number of snake species for which swimming ability has been reported from the scientific literature or via internet searches (Swim Review) according to major lifestyle categories. The number of snake species tested (or observed) by the authors is given (Swim Tests), as well as the number of species for which this information is new (Swim New). The total number of snake species per lifestyle category is provided (N tot). By excluding aquatic species (fully-aquatic, semi-aquatic), previous data were heavily biased towards terrestrial species.

Life Style	Swim Review	Swim Tests	Swim New	N tot
Fully-aquatic	*64*	*4*	*0*	*64*
Semi-aquatic	*318*	*12*	*0*	*318*
Terrestrial	62	40	26	1400
Arboreal	3	17	17	349
Semi-Arboreal	3	13	12	396
Burrower	4	10	9	821
Semi-Burrower	0	7	7	603
Total	454	103	71	3951

species for which videos were recovered were aquatic (N=250) or terrestrial (N=46), non-academic videos showed that five swimming species were arboreal or semi-arboreal and three were burrowing. Using scientific publications, 77 species were identified as able to swim, mainly aquatic and semi-aquatic (N=69), but also one arboreal and seven terrestrial species. Using the PRISMA procedure, 105 species were found to be swimming (95 aquatic, 10 terrestrial). Naturalistic books provided information on 75 species (69 aquatic, five terrestrial, one burrowing).

The tests and few opportunistic observations (5 species) allowed us to obtain information on 103 snake species; for 71 of these this information was new. Importantly, this new information partially filled ecological and phylogenetic gaps (Tables 1, 2; Fig. 2). Swimming ability is now available for the major snake lifestyles and most important lineages (e.g. 7 new "non-aquatic" families). We show that at least the scolecophidians that were tested were able to swim; *Anilius* and *Calabaria* can swim, etc. Even purely fossorial and particularly stocky snakes such as *Eryx colubrinus* or *E. conicus* can swim, as can extremely slender arboreal snakes such as *Imantodes cenchoa* or *Oxybelis fulgidus*. Therefore, the targeted tests we performed shed light on the swimming ability of living snakes in general.

4. Discussion

In a very broad phylogenetic sense, all terrestrial animals have an aquatic origin. However, this is not necessarily true on a finer scale, where certain lineages have evolved from terrestrial lineages, such as snakes, which are descended from terrestrial squamates. Not all terrestrial animals can swim and would quickly drown if placed in water. This is the case for many amniotes, insects, arachnids and molluscs (Heller et al., 1997; Woods and Lane, 2016). For example, while some mammals or birds are good swimmers, others cannot swim (Brown et al., 1982; Lawson et al., 2015). Similarly, although land tortoises can sometimes float, they are generally at risk of rapid drowning once in the water (Jacobson, 1994). The original swimming ability of vertebrates and invertebrates was therefore lost in different lineages that became terrestrial. Knowing whether this loss of ability occurred in certain snake lineages could shed light on the processes of specialisation towards lifestyles that do not involve swimming, such as strictly burrowing or arboreal species.

For snakes, our survey results show that once aquatic species were excluded, the information available on swimming ability was very limited. In fact, it was almost non-existent for the majority of key lineages of the phylogenetic tree and for morphologies and lifestyles that are very common. Swimming was reported in only 72 non-aquatic species (2 %) and in only nine of the 25 non-aquatic families included in this study (total number of families N=31). No information in the literature was available for the blind snakes (Scolecophidia), represented by 5 families and 462 species. Only 0.8 % of arboreal snakes and 0.2 % of burrowing snakes were known to be able to swim, although these groups contain 18.9 % and 36.0 % of known snakes respectively. Even among terrestrial species, which account for 35.4 % of snakes and are more easily observed, swimming has only been documented in 4.4 % of all cases. In other words, we did not know whether species that are very heavily built and burrowing (e.g. *Eryx* sp.), very slender cylindrical and burrowing (e.g. *Leptotyphlops* sp.), or extremely slender and arboreal (e.g. *Imantodes* sp.) were actually able to swim. Based on these fragmentary data it was a rather fragile position to declare that all species can swim (Table S1).

However, our experimental results, which fill in some of these
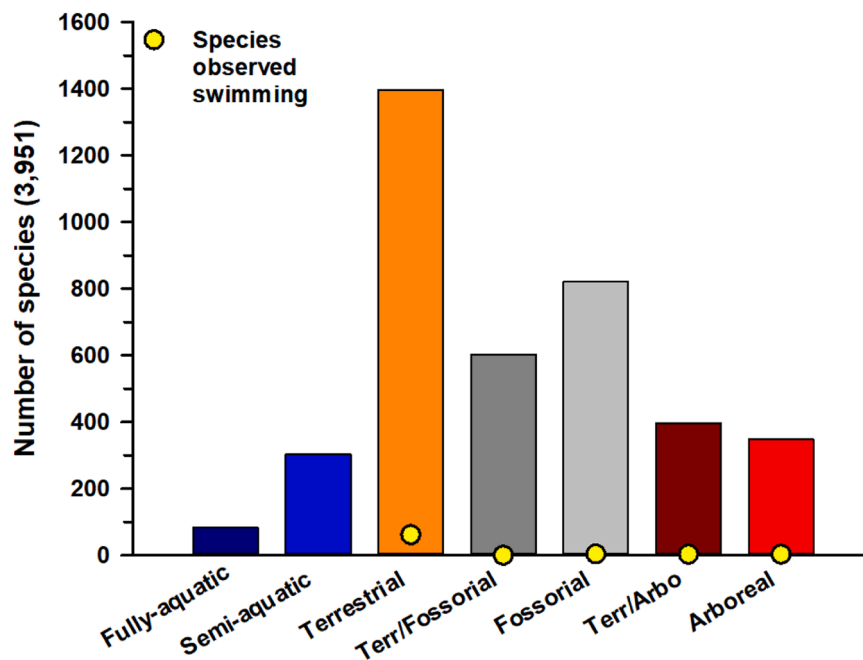

Fig. 1. Broad categories of lifestyle in snakes (N=3951 species). Bars provide the number of species in each category. The yellow circles show the number of species where swimming ability has been observed or confidently inferred.

Table 2

Number of snake species for which swimming ability has been reported from the scientific literature or via internet searches (Review) according to the main snake families used in this study (N=31). Test correspond to the species for which swimming ability was tested (or observed) by the authors. For both, "Non-Aquatic" means that fully-aquatic or semi-aquatic species were excluded from counting. Swim tot correspond to the total number of snakes species per family for which swimming ability is documented after combination of new species tested with species reviewed. The total number of snake species per family is provided (N tot).

Family	Review		Test			
	All taxa	Non-Aquatic	All taxa	Non-Aquatic	Swim tot	Ntot
Acrochordidae	3				3	3
Aniliidae			1	1	1	1
Anomalepididae			1	1	1	21
Anomochilidae						3
Atractaspididae	1	1	1	1	1	72
Boidae	5	1	12	10	14	64
Bolyeriidae						2
Calabariidae			1	1	1	
Colubridae	262	27	42	36	292	2046
Cyclocoridae						8
Cylindrophiidae	1	1	1	1	1	15
Elapidae	92	13	12	5	97	386
Gerrhopilidae						23
Homalopsidae	47		1		47	57
Lamprophiidae	10		2	2	12	89
Leptotyphlopidae						142
Loxocemidae			1	1	1	1
Pareidae			1	1	1	39
Prosymnidae						16
Psammophiidae	3	3	4	4	6	55
Pseudaspididae	1				1	4
Pseudoxyrhophiidae	2				2	89
Pythonidae	9	9	7	7	14	38
Tropidophiidae			1	1	1	35
Typhlopidae			1	1	1	275
Uropeltidae						61
Viperidae	17	16	13	13	25	373
Xenodermidae			1	1	1	28
Xenopeltidae	1	1			1	2
Xenophidiidae						2
Xenotyphlopidae						1
Total sp. (N)	**454**	**72**	**103**	**87**	**525**	**3951**
Total Family (N)	**14**	**9**	**18**	**17**	**22**	**31**

Fig. 2. Simple phylogeny of living snakes (Streicher and Ruane, 2018) and swimming ability in the main lineages. Circles indicates lineages where swimming was observed, a lack of circle indicates a lack of information. Orange circles: data retrieved from the review of the evidence. Blue circles: new data obtained in this study by testing snakes + several new observations.

important gaps, suggest that experts such as H. Lillywhite (2014) were indeed right. It seems that likely all snakes can swim, regardless of their lineage or lifestyle. However, very few scolecophidian snakes have been tested, so it remains possible that some species cannot swim, especially the highly elongate forms (e.g. certain *Leptotyphlops sp.*). The ability to swim is not information that is regularly reported, either in the scientific literature or in naturalist observations. Many zoologists may have observed snakes swimming or drowning, but this information is not easily accessible. It would be desirable for this to become available, at least to complete our data on key taxa. Scientific publications provide reliable information, non-academic websites less so. However, most reports of terrestrial species observed swimming were found on the internet. Indeed, many people take and post videos and photos of animals, both in the field and in captivity (e.g. a snake in a swimming pool). However, species that are inaccessible to the public (e.g. highly fossorial, strictly arboreal, nocturnal) escape observation. Further, we have not found any reports of snakes that cannot swim - negative information is more difficult to gather. Opportunistically, researchers and breeders could easily carry out tests in the field or on captive individuals but this information is also lacking. In our expanded sample, only a poorly know amphibian, *Boulengerula fischeri*, was found not to swim (Table S3). However, this observation should be treated with caution as only one individual was tested; if the observation of swimming is conclusive for a species, its absence is not.
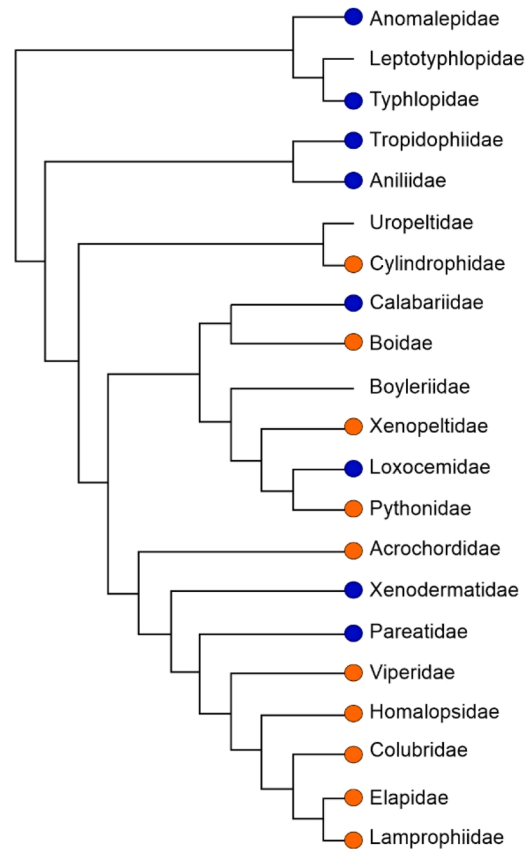
In practice, given the great species richness of snakes, we have made only a modest contribution to filling in the gaps in neglected lineages and lifestyles. However, the fact that we have targeted key lineages and that all the snake species studied, as well as other elongate animals (but not all, Table S3) are able to swim suggests that in taxa that use lateral vertebral flexion during locomotion (on land or in water), lateral undulation is likely to be closely linked to the ability to swim. Yet, the specific body kinematics used for crawling and swimming differ significantly. In water, in order for the propulsive forces to exceed resistive ones and to induce displacement, the propagation of lateral undulations from the head to the rear of the animal must take a particular form. Generally, the amplitude of the undulations increases and the whole body interacts with the fluid at all times. Physically, the main difference is that when the body of the animal undulates in water, it sets the water in motion, which can carry momentum away and thus modify the equilibrium of forces of the locomotion problem by the added fluid inertia. These constraints do not apply in terrestrial locomotion, whether the whole body is in contact with a solid substrate, or only a few points constitute the solid support as when moving through branches. A specific and similar pattern of lateral undulations during swimming has been observed in two species of snakes (*Pantherophis guttata* and *Nerodia fasciata*), but with peculiarities in a third species, *Hydrophis platurus*, whose body is laterally flattened (Graham et al., 1987; Jayne, 1985). Moreover, an electromyographic study of epaxial muscle activity in the two Colubrids revealed differences between the lateral undulations produced on land and in water (Jayne, 1988). In addition to lateral undulations, individuals must control their buoyancy, roll stability and be able to choose a course. Remarkably, fossorial and arboreal snakes have been able to do this, demonstrating that they have indeed mastered

complex aspects of swimming.

Considering the taxonomic and ecological diversity of snakes, it is possible that there is a continuum of lateral undulation modalities that are effective in a range of environments from water through granular fluids (e.g. sand), intermediate (e.g. grass providing semi-rigid support points), continuous solids (e.g. rock) and discontinuous solids (e.g. branches). Most snakes are capable of crossing different environments during their lifetime, and relatively limited modifications to their undulatory movements would enable them to do so quite easily. However, at present, it is even not known how amphibious snakes modify their lateral undulations when navigating between land and water. Consequently, we are far from understanding how snakes adapt their lateral undulations to the environments they pass through. A giant earthworm (fossorial annelid) anecdotally tested, which swam in a manner similar to that observed in squamates (unpublished), offers an extension in invertebrates to anguilliform swimming, which would be facilitated in limbless and elongate land animals.

The ability to swim is not a discriminating criterion for testing hypotheses about the evolution of snakes. We need to look at questions that are more specific. Comparing athletic performance and swimming efficiency between species could prove more useful. Do snakes representing early-diverging lineages swim differently from terrestrial, arboreal, or burrowing species from late-diverging evolutionary radiations? How do the anatomical adaptations of snakes to aquatic or marine life affect swimming kinematics? What are the hydrodynamic consequences associated with the diversity of lateral undulations? To answer these questions, it is necessary to collect swimming kinematics from a wide range of snakes, extract the relevant information (frequency and amplitude of undulations, swimming speed, etc.) and compare it with the morphology and ecology of the species. Despite the long history of biomechanical analyses of kinematic data of animal swimming since the pioneering works of Gray (1933a,b,c), at present, kinematic data for snakes are, however, very scarce, unfortunately. Likewise, flow field measurements around swimming snakes have only very recently been reported (Stin et al., 2023) and the link between kinematics and swimming energetics in the spirit of the works of Lighthill (1969, 1971) has not yet been given a definitive picture. Locomotor performance has been more extensively studied, especially for terrestrial and aquatic locomotion. Some results seem consistent with the hypothesis that snakes are faster in their primary environment, especially highly aquatic ones with a more laterally compressed body form (Wang et al., 2013). Nevertheless, others show that more terrestrial species could swim faster than most aquatic species (Brischoux et al., 2010; Shine et al., 2003). During our test, we also observed several terrestrial or arboreal species with higher swimming performance than true sea snakes despite the compressed body form of marine species. It should be noted that the particular context of the tests we conducted, with motivation to swim induced by a threatening experimenter, may have introduced biases that are not well understood. In addition, early experiences in an environment have an impact of locomotor performance too (Aubret et al., 2007). The relation between performance, kinematics and morphology is still unsolved, and the need to collect more data stay crucial.

Finally, a better understanding of swimming performance is useful for conservation purposes. Knowing whether a snake swims is not enough to know whether it is at risk of fatigue and drowning, for example after floods caused by the impounding of dams, or by extreme rainfall events that are increasing in frequency and intensity as a result of climate change.

CRediT authorship contribution statement

Hugues Gossuin: Resources. **Olivier Chateau:** Resources. **Guillaume Fosseries:** Writing – review & editing, Writing – original draft, Visualization, Validation, Methodology, Investigation, Formal analysis, Data curation. **Chany Banzept:** Resources. **Pierre Banzept:** Resources. **Ramiro Godoy-Diana:** Writing – review & editing. **Xavier Bonnet:** Writing – review & editing, Visualization, Validation, Supervision, Methodology, Investigation, Funding acquisition, Formal analysis, Data curation, Conceptualization. **Anthony Herrel:** Writing – review & editing, Investigation. **Dimitri Lefebvre:** Investigation. **Philippe Gaucher:** Resources. **Antoine Joris:** Resources. **Margo Traimond:** Resources. **Antoine Gouygou:** Resources. **Karim Daoues:** Resources.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Acknowledgments

Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.zool.2024.126223.

Data Availability

Data will be totally available after paper acceptance

References

Aubret, F., Bonnet, X., Shine, R., 2007. The role of adaptive plasticity in a major evolutionary transition: early aquatic experience affects locomotor performance of terrestrial snakes. Funct. Ecol. 21, 1154–1161. https://doi.org/10.1111/j.1365-2435.2007.01310.x.

Bradnam, K.R., Fass, J.N., Alexandrov, A., Baranay, P., Bechner, M., Birol, I., Boisvert, S., Chapman, J.A., Chapuis, G., Chikhi, R., Chitsaz, H., Chou, W.-C., Corbeil, J., Del Fabbro, C., Docking, T.R., Durbin, R., Earl, D., Emrich, S., Fedotov, P., Fonseca, N.A., Ganapathy, G., Gibbs, R.A., Gnerre, S., Godzaridis, É., Goldstein, S., Haimel, M., Hall, G., Haussler, D., Hiatt, J.B., Ho, I.Y., Howard, J., Hunt, M., Jackman, S.D., Jaffe, D.B., Jarvis, E.D., Jiang, H., Kazakov, S., Kersey, P.J., Kitzman, J.O., Knight, J.R., Koren, S., Lam, T.-W., Lavenier, D., Laviolette, F., Li, Y., Li, Z., Liu, B., Liu, Y., Luo, R., MacCallum, I., MacMantes, M.D., Maillet, N., Melnikov, S., Naquin, D., Ning, Z., Otto, T.D., Paten, B., Paulo, O.S., Phillippy, A.M., Pina-Martins, F., Place, M., Przybylski, D., Qin, X., Qu, C., Ribeiro, F.J., Richards, S., Rokhsar, D.S., Ruby, J.G., Scalabrin, S., Schatz, M.C., Schwartz, D.C., Sergushichev, A., Sharpe, T., Shaw, T.I., Shendure, J., Shi, Y., Simpson, J.T., Song, H., Tsarev, F., Vezzi, F., Vicedomini, R., Vieira, B.M., Wang, J., Worley, K.C., Yin, S., Yiu, S.-M., Yuan, J., Zhang, G., Zhang, H., Zhou, S., Korf, I.F., 2013. Assemblathon 2: evaluating de novo methods of genome assembly in three vertebrate species, 2047-217X-2–10 GigaScience 2. https://doi.org/10.1186/2047-217X-2-10.

Branch, B., 1998. Field guide snakes and other reptiles of Southern Africa. Struik Publishers.

Brischoux, F., Kato, A., Ropert-Coudert, Y., Shine, R., 2010. Swimming speed variation in amphibious seasnakes (Laticaudinae): A search for underlying mechanisms. J. Exp. Mar. Biol. Ecol. 394, 116–122. https://doi.org/10.1016/j.jembe.2010.08.001.

Brown, S.G., Dunlap, W.P., Maple, T.L., 1982. Notes on water-contact by a captive male lowland gorilla. Zoo. Biol. 1, 243–249. https://doi.org/10.1002/zoo.1430010308.

Burbrink, F.T., Grazziotin, F.G., Pyron, R.A., Cundall, D., Donnellan, S., Irish, F., Keogh, J.S., Kraus, F., Murphy, R.W., Noonan, B., Raxworthy, C.J., Ruane, S., Lemmon, A.R., Lemmon, E.M., Zaher, H., 2020. Interrogating genomic-scale data for Squamata (lizards, snakes, and amphisbaenians) shows no support for key

traditional morphological relationships. Syst. Biol. 69, 502–520. https://doi.org/10.1093/sysbio/syz062.

Caldwell, M.W., Nydam, R.L., Palci, A., Apesteguía, S., 2015. The oldest known snakes from the Middle Jurassic-Lower Cretaceous provide insights on snake evolution. Nat. Commun. 6, 5996. https://doi.org/10.1038/ncomms6996.

Caldwell, M.W., Simões, T.R., Palci, A., Garberoglio, F.F., Reisz, R.R., Lee, M.S.Y., Nydam, R.L., 2021. *Tetrapodophis amplectus* is not a snake: re-assessment of the osteology, phylogeny and functional morphology of an Early Cretaceous dolichosaurid lizard. J. Syst. Palaeontol. 19, 893–952. https://doi.org/10.1080/14772019.2021.1983044.

Campbell, J.A., Smith, E.N., Hall, A.S., 2018. Caudals and calyces: the curious case of a consumed Chiapan colubroid. J. Herpetol. 52, 458–471. https://doi.org/10.1670/18-042.

Cogger, H., 2014. Reptiles and amphibians of Australia. CSIRO publishing.

Da Silva, F.O., Fabre, A.-C., Savriama, Y., Ollonen, J., Mahlow, K., Herrel, A., Müller, J., Di-Poï, N., 2018. The ecological origins of snakes as revealed by skull evolution. Nat. Commun. 9. https://doi.org/10.1038/s41467-017-02788-3.

Fachini, T.S., Onary, S., Palci, A., Lee, M.S.Y., Bronzati, M., Hsiou, A.S., 2020. Cretaceous blind snake from Brazil fills major gap in snake evolution. iScience 23, 101834. https://doi.org/10.1016/j.isci.2020.101834.

Figueroa, A., 2016. Phylogenetic relationships and evolution of snakes. Univ. N. Orleans Theses Diss.

Frolich, L.M., Biewener, A.A., 1992. Kinematic and electromyographic analysis of the functional role of the body axis during terrestrial and aquatic locomotion in the salamander *Ambystoma tigrinum*. J. Exp. Biol. 162, 107–130. https://doi.org/10.1242/jeb.162.1.107.

Garberoglio, F.F., Apesteguía, S., Simões, T.R., Palci, A., Gómez, R.O., Nydam, R.L., Larsson, H.C.E., Lee, M.S.Y., Caldwell, M.W., 2019. New skulls and skeletons of the Cretaceous legged snake *Najash*, and the evolution of the modern snake body plan. Sci. Adv. 5, eaax5833. https://doi.org/10.1126/sciadv.aax5833.

Graham, J.B., Lowell, W.R., Rubinoff, I., Motta, J., 1987. Surface and subsurface swimming of the sea snake *Pelamis Platurus*. J. Exp. Biol. 127, 27–44. https://doi.org/10.1242/jeb.127.1.27.

Gray, J., 1933a. Studies in animal locomotion: I. The movement of fish with special reference to the eel. J. Exp. Biol. 10, 88–104. https://doi.org/10.1242/jeb.10.1.88.

Gray, J., 1933b. Studies in animal locomotion: II. the relationship between waves of muscular contraction and the propulsive mechanism of the eel. J. Exp. Biol. 10, 386–390. https://doi.org/10.1242/jeb.10.4.386.

Gray, J., 1933c. Studies in animal locomotion: III. the propulsive mechanism of the whiting (*Gadus Merlangus*). J. Exp. Biol. 10, 391–400. https://doi.org/10.1242/jeb.10.4.391.

Harrington, S.M., de Haan, J.M., Shapiro, L., Ruane, S., 2018. Habits and characteristics of arboreal snakes worldwide: arboreality constrains body size but does not affect lineage diversification. Biol. J. Linn. Soc. 125, 61–71. https://doi.org/10.1093/biolinnean/bly097.

Hartmann, P.A., Hartmann, M.T., Martins, M., 2009. Ecology of a snake assemblage in the Atlantic Forest of southeastern Brazil. Pap. éIs. Avulsos De. Zool. 49, 343–360. https://doi.org/10.1590/S0031-10492009002700001.

Heller, J., Sivan, N., Hodgson, A.N., 1997. Reproductive biology and population dynamics of an ovoviviparous land snail, *Lauria cylindracea* (Pupillidae). J. Zool. 243, 263–280. https://doi.org/10.1111/j.1469-7998.1997.tb02781.x.

Hsiang, A.Y., Field, D.J., Webster, T.H., Behlke, A.D., Davis, M.B., Racicot, R.A., Gauthier, J.A., 2015. The origin of snakes: revealing the ecology, behavior, and evolutionary history of early snakes using genomics, phenomics, and the fossil record. BMC Evolut. Biol. 15, 87. https://doi.org/10.1186/s12862-015-0358-5.

Índice taxonómico reptiles Ecuador [WWW Document], 2023. URL https://bioweb.bio/faunaweb/reptiliaweb/IndiceTaxonomico (accessed 4.5.23).

Jacobson, E.R., 1994. Causes of mortality and diseases in tortoises: a review. J. Zoo. Wildl. Med. 25, 2–17.

Jayne, B.C., 1982. Comparative morphology of the semispinalis-spinalis muscle of snakes and correlations with locomotion and constriction. J. Morphol. 172, 83–96. https://doi.org/10.1002/jmor.1051720108.

Jayne, B.C., 1985. Swimming in constricting (*Elaphe g. guttata*) and nonconstricting (*Nerodia fasciata pictiventris*) colubrid snakes. Copeia 1985, 195–208. https://doi.org/10.2307/1444809.

Jayne, B.C., 1988. Muscular mechanisms of snake locomotion: An electromyographic study of lateral undulation of the Florida banded water snake (*Nerodia fasciata*) and the yellow rat snake (*Elaphe obsoleta*). J. Morphol. 197, 159–181. https://doi.org/10.1002/jmor.1051970204.

Jayne, B.C., 2020. What defines different modes of snake locomotion? Integr. Comp. Biol. 60, 156–170. https://doi.org/10.1093/icb/icaa017.

Klein, C.G., Pisani, D., Field, D.J., Lakin, R., Wills, M.A., Longrich, N.R., 2021. Evolution and dispersal of snakes across the Cretaceous-Paleogene mass extinction. Nat. Commun. 12, 5335. https://doi.org/10.1038/s41467-021-25136-y.

Lawson, B., Duff, J.P., Beckmann, K.M., Chantrey, J., Peck, K.M., Irvine, R.M., Robinson, R.A., Cunningham, A.A., 2015. Drowning is an apparent and unexpected recurrent cause of mass mortality of common starlings (*Sturnus vulgaris*). Sci. Rep. 5, 17020. https://doi.org/10.1038/srep17020.

Lighthill, M.J., 1969. Hydromechanics of aquatic animal propulsion. Annu. Rev. Fluid Mech. 1, 413–446. https://doi.org/10.1146/annurev.fl.01.010169.002213.

Lighthill, M.J., 1971. Large-amplitude elongated-body theory of fish locomotion. Proc. R. Soc. Lond. Ser. B. Biol. Sci. 179, 125–138. https://doi.org/10.1098/rspb.1971.0085.

Lillywhite, H.B., 2014. How snakes work: structure, function and behavior of the world's snakes. Oxford University Press.

Ludington, A.J., Hammond, J.M., Breen, J., Deveson, I.W., Sanders, K.L., 2023. New chromosome-scale genomes provide insights into marine adaptations of sea snakes

(*Hydrophis*: Elapidae). BMC Biol. 21, 284. https://doi.org/10.1186/s12915-023-01772-2.

Luiselli, L., Filippi, E., Capula, M., 2005. Geographic variation in diet composition of the grass snake (*Natrix natrix*) along the mainland and an island of Italy: the effects of habitat type and interference with potential competitors. Herpetol. J. 15, 221–230.

Macrì, S., Aalto, I.-M., Allemand, R., Di-Poï, N., 2023. Reconstructing the origin and early evolution of the snake brain. Sci. Adv. 9, eadi6888. https://doi.org/10.1126/sciadv.adi6888.

Mahood, Q., Van Eerd, D., Irvin, E., 2014. Searching for grey literature for systematic reviews: challenges and benefits. Res. Synth. Methods 5, 221–234. https://doi.org/10.1002/jrsm.1106.

Mann, A., Pardo, J.D., Maddin, H.C., 2022. Snake-like limb loss in a Carboniferous amniote. Nat. Ecol. Evol. 6, 614–621. https://doi.org/10.1038/s41559-022-01698-y.

Mateo, S., 2020. Procédure pour conduire avec succès une revue de littérature selon la méthode PRISMA. Kin. ésithérapie, la Rev. 20, 29–37. https://doi.org/10.1016/j.kine.2020.05.019.

Mathou, A., Bonnet, X., Daoues, K., Ksas, R., Herrel, A., 2023. Evolutionary convergence of muscle architecture in relation to locomotor ecology in snakes. J. Anat. 242, 862–871. https://doi.org/10.1111/joa.13823.

Meinertzhagen, I.A., Lemaire, P., Okamura, Y., 2004. The neurobiology of the ascidian tadpole larva: recent developments in an ancient chordate. Annu. Rev. Neurosci. 27, 453–485. https://doi.org/10.1146/annurev.neuro.27.070203.144255.

Miralles, A., Marin, J., Markus, D., Herrel, A., Hedges, S.B., Vidal, N., 2018. Molecular evidence for the paraphyly of Scolecophidia and its evolutionary implications. J. Evolut. Biol. 31, 1782–1793. https://doi.org/10.1111/jeb.13373.

Murphy, J.C., 2007. Homalopsid snakes, evolution in the mud. Krieger Publishing Company.

Myers, E.W., Sutton, G.G., Delcher, A.L., Dew, I.M., Fasulo, D.P., Flanigan, M.J., Kravitz, S.A., Mobarry, C.M., Reinert, K.H.J., Remington, K.A., Anson, E.L., Bolanos, R.A., Chou, H.-H., Jordan, C.M., Halpern, A.L., Lonardi, S., Beasley, E.M., Brandon, R.C., Chen, L., Dunn, P.J., Lai, Z., Liang, Y., Nusskern, D.R., Zhan, M., Zhang, Q., Zheng, X., Rubin, G.M., Adams, M.D., Venter, J.C., 2000. A whole-genome assembly of *Drosophila*. Science 287, 2196–2204. https://doi.org/10.1126/science.287.5461.2196.

Nishino, A., Okamura, Y., Piscopo, S., Brown, E.R., 2010. A glycine receptor is involved in the organization of swimming movements in an invertebrate chordate. BMC Neurosci. 11, 6. https://doi.org/10.1186/1471-2202-11-6.

Palci, A., Hutchinson, M.N., Caldwell, M.W., Lee, M.S.Y., 2017. The morphology of the inner ear of squamate reptiles and its bearing on the origin of snakes. R. Soc. Open Sci. 4, 170685. https://doi.org/10.1098/rsos.170685.

Peng, C., Ren, J.-L., Deng, C., Jiang, D., Wang, J., Qu, J., Chang, J., Yan, C., Jiang, K., Murphy, R.W., Wu, D.-D., Li, J.-T., 2020. The genome of Shaw's sea snake (*Hydrophis curtus*) reveals secondary adaptation to its marine environment. Mol. Biol. Evol. 37, 1744–1760. https://doi.org/10.1093/molbev/msaa043.

Peng, C., Wu, D.-D., Ren, J.-L., Peng, Z.-L., Ma, Z., Wu, W., Lv, Y., Wang, Z., Deng, C., Jiang, K., Parkinson, C.L., Qi, Y., Zhang, Z.-Y., Li, J.-T., 2023. Large-scale snake genome analyses provide insights into vertebrate development. Cell 186, 2959–2976.e22. https://doi.org/10.1016/j.cell.2023.05.030.

Rautsaw, R.M., Schramer, T.D., Acuña, R., Arick, L.N., DiMeo, M., Mercier, K.P., Schrum, M., Mason, A.J., Margres, M.J., Strickland, J.L., Parkinson, C.L., 2021. Genomic adaptations to salinity resist gene flow in the evolution of Floridian watersnakes. Mol. Biol. Evol. 38, 745–760. https://doi.org/10.1093/molbev/msaa266.

Roscito, J.G., Sameith, K., Kirilenko, B.M., Hecker, N., Winkler, S., Dahl, A., Rodrigues, M.T., Hiller, M., 2022. Convergent and lineage-specific genomic differences in limb regulatory elements in limbless reptile lineages. Cell Rep. 38, 110280. https://doi.org/10.1016/j.celrep.2021.110280.

Segall, M., Cornette, R., Fabre, A.-C., Godoy-Diana, R., Herrel, A., 2016. Does aquatic foraging impact head shape evolution in snakes? Proc. R. Soc. B: Biol. Sci. 283, 20161645. https://doi.org/10.1098/rspb.2016.1645.

Shine, R., 1987. Ecological comparisons of island and mainland populations of Australian tigersnakes (*Notechis*: Elapidae). Herpetologica 43, 233–240.

Shine, R., Cogger, H.G., Reed, R.R., Shetty, S., Bonnet, X., 2003. Aquatic and terrestrial locomotor speeds of amphibious sea-snakes (Serpentes, Laticaudidae). J. Zool. 259, 261–268. https://doi.org/10.1017/S0952836902003242.

Starace, F., 2013. Serpents et amphisbènes de Guyane française. Ibis Rouge, Matoury.

Stin, V., Godoy-Diana, R., Bonnet, X., Herrel, A., 2023. Measuring the 3D wake of swimming snakes (*Natrix tessellata*) using volumetric particle image velocimetry. J. Exp. Biol. 226, jeb245929. https://doi.org/10.1242/jeb.245929.

Streicher, J.W., Ruane, S., 2018. Phylogenomics of snakes. in: Encyclopedia of life sciences. John Wiley & Sons, Ltd, pp. 1–8. https://doi.org/10.1002/9780470015902.a0027476.

Strong, C.R.C., Scherz, M.D., Caldwell, M.W., 2022. Convergence, divergence, and macroevolutionary constraint as revealed by anatomical network analysis of the squamate skull, with an emphasis on snakes. Sci. Rep. 12, 14469. https://doi.org/10.1038/s41598-022-18649-z.

Tingle, J.L., Garner, K.L., Astley, H.C., 2024. Functional diversity of snake locomotor behaviors: A review of the biological literature for bioinspiration. Ann. N. Y. Acad. Sci., nyas.15109 https://doi.org/10.1111/nyas.15109.

Uetz, P., Freed, P., Aguilar, R., Reyes, F., Hošek, J., 2024. The Reptile Database [WWW Document]. URL http://www.reptile-database.org (accessed 4.5.23).

Visser, D., 2015. Asian pitvipers: Breeding experience & wildlife. Chimaira, Frankfurt am Main.

Wang, S., Lillywhite, H.B., Tu, M.-C., 2013. Locomotor performance of three sympatric species of sea kraits (*Laticauda* spp.) from Orchid Island, Taiwan. Zool. Stud. 52, 43. https://doi.org/10.1186/1810-522X-52-43.

Woods, H.A., Lane, S.J., 2016. Metabolic recovery from drowning by insect pupae. J. Exp. Biol. 219, 3126–3136. https://doi.org/10.1242/jeb.144105.

Yi, H., Norell, M.A., 2015. The burrowing origin of modern snakes. Sci. Adv. 1, e1500743. https://doi.org/10.1126/sciadv.1500743.

Zaher, H., Mohabey, D.M., Grazziotin, F.G., Wilson Mantilla, J.A., 2023. The skull of *Sanajeh indicus*, a Cretaceous snake with an upper temporal bar, and the origin of ophidian wide-gaped feeding. Zool. J. Linn. Soc. 197, 656–697. https://doi.org/10.1093/zoolinnean/zlac001.