

## Ancestral Reconstruction of Diet and Fang Condition in the Lamprophiidae: Implications for the Evolution of Venom Systems in Snakes

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**ABSTRACT.**—The Colubroidea includes all venomous and some nonvenomous snakes, many of which have extraordinary dental morphology and functional capabilities. It has been proposed that the ancestral condition of the Colubroidea is venomous with tubular fangs. The venom system includes the production of venomous secretions by labial glands in the mouth and usually includes fangs for effective delivery of venom. Despite significant research on the evolution of the venom system in snakes, limited research exists on the driving forces for different fang and dental morphology at a broader phylogenetic scale. We assessed the patterns of fang and dental condition in the Lamprophiidae, a speciose family of advanced snakes within the Colubroidea, and we related fang and dental condition to diet. The Lamprophiidae is the only snake family that includes front-fanged, rear-fanged, and fangless species. We produced an ancestral reconstruction for the family and investigated the pattern of diet and fangs within the clade. We concluded that the ancestral lamprophiid was most likely rear-fanged and that the shift in dental morphology was associated with changes in diet. This pattern indicates that fang loss, and probably venom loss, has occurred multiple times within the Lamprophiidae. There is also evidence that front fangs arose from a rear-fanged condition, and this has occurred independently more than once within the family. Our findings provide insight into fang and dental condition in relation to diet and support the hypothesis of a venomous ancestor for the Lamprophiidae.

Snakes represent one of the most morphologically diverse vertebrate clades (Vitt and Caldwell, 2009) with adaptive success that can be attributed to various factors including the evolution of various venom types, divergence of body shapes, changes in habitat selection, and foraging mode (Sites et al., 2011). Most importantly, snakes possess distinctively modified kinetic skulls and jaws, and this unique morphology has increased the diversity of prey sizes that snakes are able to subdue and ingest (Greene, 1983). Snakes are also renowned for their venom and dental morphology, and it has been generally accepted that snake venom primarily facilitates the immobilization and digestion of prey (Savitzky, 1980; Barlow et al., 2009). Associated with the evolution of venom are fangs and various glands which deliver venom into their prey (Fry et al., 2012; Kerckamp et al., 2015).

Historically, the presence of venom and fangs in snakes was considered a derived condition that arose independently multiple times within advanced snakes (Vidal and Hedges, 2005), a thinking that was based on the fact that the early-branching clades such as the pythonids and boids all lacked fangs and are considered nonvenomous. However, several studies on venom evolution indicate venomous ancestors at several nodes in the Caenophidia phylogeny, with subsequent losses in venom and fangs in certain clades. Recent work has concluded that the lamprophiid subfamilies Atractaspidinae and Aparallactinae (Portillo et al., 2019) and Pseudoxyrhophiinae (Burbrink et al., 2019) all had rear-fanged ancestry and that fang evolution is linked closely to diet and, although suggestive, this does not directly shed light on the ancestral condition for the Lamprophiidae as a whole.

Jackson (2002, 2003, 2007) made significant contributions to the knowledge and understanding of the superfamily Colubroidea, which includes all venomous snakes and is the group in which tubular fangs evolved. Jackson posits that the possession of a venom system is ancestral to the Colubroidea, as they possess a Duvernoy's gland that has evolved and

specialized into a venom gland and independently within the three front-fanged clades (elapids, viperids, and atractaspidids). Because of the confusion in terminology with regard to Duvernoy's gland, the designation of venom gland is preferred by some scientists (Jackson et al., 2017). Fry et al. (2008) support the idea of a single colubroid common ancestor but with reference to venom glands, resulting in a mounting consensus that the ancestral condition for Colubroidea was venomous. Jackson (2003) defines a snake fang as "a long, pointed maxillary tooth modified to carry and dispense venom into the tissue of prey," a definition that includes enlarged (ungrooved) teeth that function the same way as 'traditional venom conducting fangs.' We adopt Jackson's broad definition because it sheds light on snakes that have a range of dental morphology and are considered to be nonvenomous.

Jackson (2007) examined several colubroid fang types, including grooved, ungrooved, and deeply grooved to the extent of forming a closed canal, and a tubular structure with a suture line. Jackson argued that the suture line in tubular fangs resulted from the closing of the two sides of a deep groove, but concluded that the ancestral colubroid had tubular fangs while the subsequent evolution of grooved fangs was the result of heterochrony (Jackson and Fritts, 1995; Jackson, 2007). If the possession of fangs is the ancestral state for Colubroidea, it follows that the loss of fangs has occurred on several occasions in the evolution of snakes (Jackson, 2003, 2007). A concomitant loss of the production of venom also seems likely because, at least in some instances, the presence of fangs is tightly linked to that of venom production (Kerckamp et al., 2015).

If venom systems have been lost in some species of the Colubroidea, it follows that the loss must be advantageous under specific situations, such as in snakes which specialize on easy-to-handle, nondangerous prey (Pintor et al., 2010; Casewell et al., 2013). McCue (2006) showed that venom production caused an 11% increase in the resting metabolic rate of *Crotalus atrox*. A relatively high metabolic cost of venom production could have driven the selection for the loss of both venom and fangs in certain clades where venom was not essential for prey handling. Various studies have described the relationship

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between dental morphology and diet (Britt et al., 2009; Knox and Jackson, 2010), venom and diet (Daltry et al., 1996; Fry et al., 2003, 2008, 2012; Casewell et al., 2013; Burbrink et al., 2019; Portillo et al., 2019). However, there is limited information on the broad-scale phylogenetic and ecological factors driving fang and dental morphology and diet in the Lamprophiidae as a whole.

We used ancestral reconstruction in the Lamprophiidae to investigate the pattern of fang evolution and assessed its relationship to diet evolution within the clade. The Lamprophiidae is an ideal clade for this investigation because it is the only family of snakes that includes species that possess front fangs, rear fangs, or no fangs, making member species diverse with regard to fang structure. Members of the Lamprophiidae also consume an array of prey, ranging from various vertebrates to soft- and hard-bodied invertebrates. We hypothesized that the possession of fangs was the ancestral condition for the Lamprophiidae. Currently, there are seven subfamilies recognized within the Lamprophiidae: Aparallactinae, Atractaspidae, Lamprophiinae, Psammophiinae, Prosymninae, Pseudaspidae, and Pseudoxyrophiinae (Vidal et al., 2008).

#### MATERIALS AND METHODS

Our dataset consisted of 134 of the 315 species in the Lamprophiidae (Uetz, 2018). We were necessarily limited to the species that were included in the latest published phylogeny (Zheng and Wiens, 2016). For each species, we sourced published data on diet and fang condition (See Appendix 1 for diet data and references). Because of the high variation in prey types consumed by lamprophiids, we performed a hierarchical cluster analysis in SPSS Statistics for Windows (Version 22.0., IBM Corporation, Armonk, New York) to identify broad diet categories. We identified categories based on the dominant prey consumed by each species. Because of the nature of cluster analyses, a cluster that included lamprophiid species that specialized on particular prey types also included additional prey items that may have sometimes been included in the diet (i.e., a species that primarily consumes lizards may also occasionally eat frogs). In cases where we could not explicitly separate these species, they were included within a type category. Generalist prey were the most diverse to quantify and, as a result, a cluster grouped snakes that consumed mammals and birds with those that also included lizards in their diet. Fang type was categorized as rear-fanged, front-fanged, or fangless.

Primary data sources on diet for the lamprophiids were limited (see Appendix 1) and, as a result, we also sourced information from various secondary sources such as field guides, blogs, citizen science data, and additional reliable websites that included diet information. Taking our data acquisition limitations into consideration, we have sourced the most complete diet dataset at each level for the lamprophiids. Information on diet and fang types of the 134 species was then mapped onto the most recent and comprehensive published phylogenetic tree for the family Lamprophiidae (Zheng and Wiens, 2016). The ancestral states were reconstructed using stochastic character mapping in the phytools package in R 3.4.2 (Revell, 2012), a method of reconstruction that uses Bayesian Inference. Discrete character state reconstructions were sampled under a Markov process of shifts, given the species states and their phylogeny (Huelsenbeck et al., 2003). Characters were then mapped onto phylogenies using a probabilistic approach

(Bollback, 2006). For both traits (diet and fang condition), we generated 50 stochastic character histories (Price et al., 2015).

To assess the best model type for character reconstruction, we used three models offered in the R 3.4.2 geiger package (Harmon et al., 2008) and compared the sample-size corrected Akaike information criterion  $\Delta$ AIC and log likelihood ( $-\ln L$ ) values. The equal-rates (ER) model maintains all transitions in the parameter occurring at equal rates; the symmetric model (SYM) assesses forward and reverse transitions that share the same parameter; and the all-rates-different (ARD) model ensures each rate parameter is unique. The best model was selected based on the smallest  $\Delta$ AIC and highest log likelihood ( $-\ln L$ ) values (Burnham and Anderson, 2003). Pagel's correlation method was utilized in Mesquite 3.31 (Pagel, 1999; Maddison and Maddison, 2015) to evaluate whether the rates of evolution in diet and fang type were independent using 10 iterations within 1,000 simulations. A mirror tree in Mesquite was used to show the evolutionary patterns of diet and fang types using stochastic character mapping. We used Pagel's lambda ( $\lambda$ ) in the R package geiger to test for a phylogenetic signal in the distribution of diet and fang types (Revell, 2012) in order to get an understanding of the phylogenetic constraint in species resemblance without looking at divergence date and other comprehensive phylogenetic information (Blomberg et al., 2003). Closely related species will tend to have similar dietary or dental morphology.

#### RESULTS

*Diet Clusters.*—The hierarchical cluster analysis revealed eight major diet groups for 134 lamprophiids (Table 1).

*Ancestral Reconstruction of Diet.*—Our findings suggest that the ancestral state was a generalist diet with a tendency toward specialization in some clades (Fig. 1). The best model was the ER model (lowest  $\Delta$ AIC; Table 2), and all of the 50 evolutionary hypotheses generated supported a generalist ancestral feeding state (Fig. 1). Of the 134 species, 40% of extant lamprophiids retained the ancestral diet condition (Table 3). The aquatic vertebrate feeders span across the Pseudoxyrophiinae, but some also occur in the Lamprophiinae, Pseudaspidae, and Psammophiinae. Arthropod specialization was the only autapomorphy within the clade and specialization in a soft-bodied invertebrate diet and snail diet have both appeared twice independently.

*Ancestral Reconstruction of Fang Type.*—Stochastic character mapping revealed that the ancestral lamprophiid was rear-fanged (Fig. 1). The Atractaspidae is the only subfamily that has front-fanged species with the trait being autapomorphic (Fig. 1). Prosymninae and Lamprophiinae have only fangless members. Psammophiinae, Aparallactinae, and Pseudaspidae included species with only rear fangs, with the exception of *Pseudaspis cana*, which has no fangs (but has enlarged teeth on the posterior maxilla). Pseudoxyrophiinae showed the most variation, as they include species that have rear fangs or are fangless. Within their respective subfamilies, species evolved their current fang condition early in the radiation of the family, with the exception of Pseudoxyrophiinae.

*Fang Type and Diet.*—Between the two front-fanged groups, *Atractaspis* and *Homoroselaps*, *Atractaspis* is a generalist while *Homoroselaps* specializes on elongate prey (Fig. 1; Table 3). Fangless species eat all prey types except arthropods and soft-bodied invertebrates. Rear-fanged lamprophiids have the most varied diet, consuming all types of prey except slugs and snails (Fig. 1; Table 3). Pagel's correlation revealed that the diet of the

TABLE 1. The hierarchical cluster analysis performed on lamprophiids, which revealed eight major diet groups.

Diet cluster	Prey types within cluster
Type 1	Lizard specialists (lizard eaters)
Type 2	Frogs and/or fish, but some species also included lizards (aquatic vertebrate eaters)
Type 3	Mainly snakes and other elongate prey such as legless skinks and amphisbaenids and occasionally lizards (elongate prey eaters)
Type 4	Reptile eggs (reptile egg-eaters)
Type 5	Centipedes or scorpions (arthropod eaters)
Type 6	Soft-bodied invertebrates (soft-bodied invertebrate eaters)
Type 7	Slugs and snails (snail eaters; not included in Type 6 because of specialization of only one genus of the Lamprophiidae and identified as such in the cluster analysis)
Type 8	A variety of prey classes including small mammals, lizards, and aquatic vertebrates as well as birds, snakes, and reptile eggs (generalists)

Lamprophiidae is strongly linked with fang type within the family ( $P < 0.05$ ). Pagel's lambda showed a strong phylogenetic signal for fang type ( $\lambda = 0.99$ ;  $P > 0.05$ ), whereas diet distribution was independent of phylogeny ( $\lambda = 0.49$ ;  $P < 0.05$ ).

DISCUSSION

Our findings strongly support the hypothesis that the ancestral condition for lamprophiids was a generalist diet with rear fangs. The plesiomorphic condition of having rear fangs

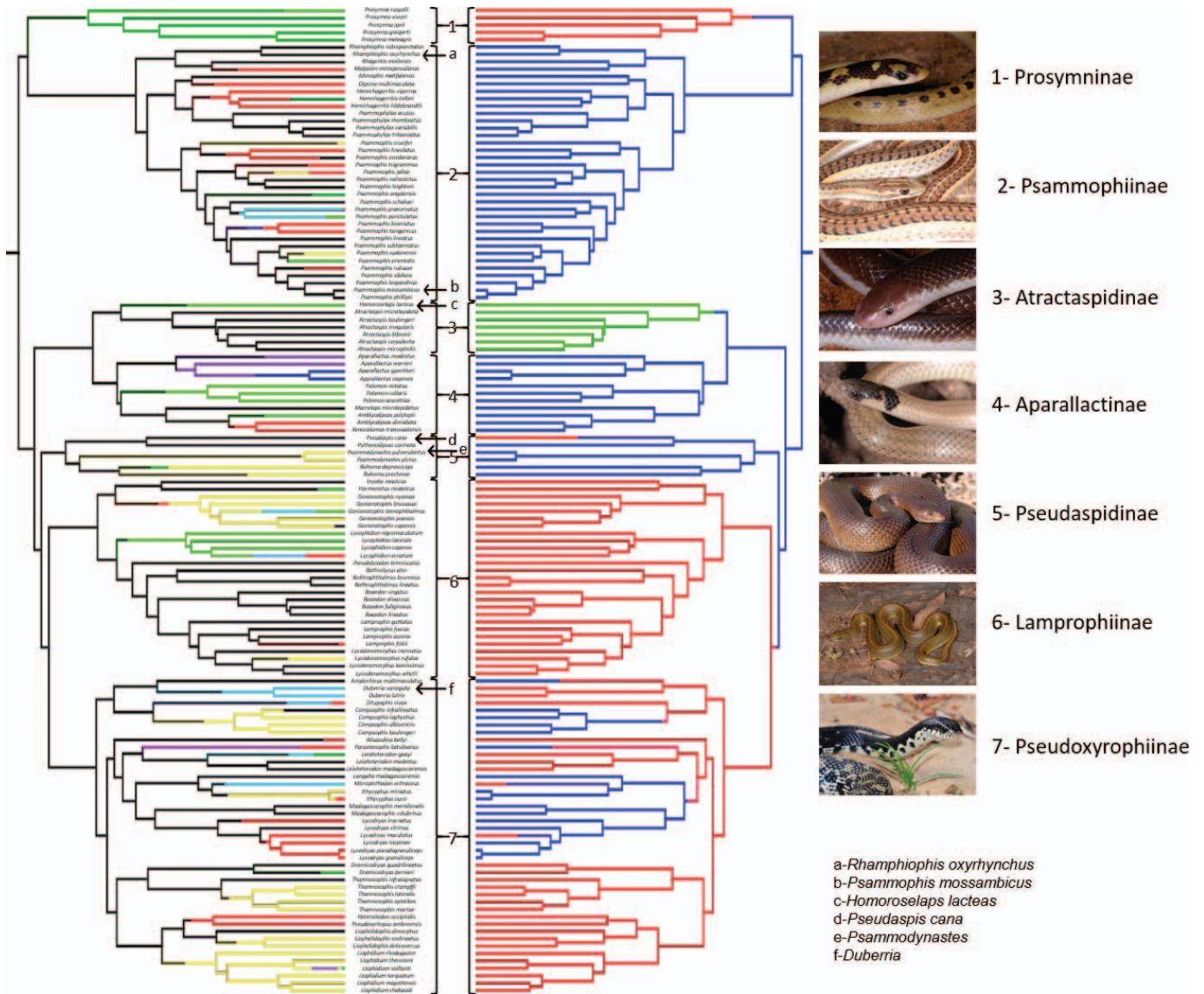


FIG. 1. Mirror tree showing the correlation of fang type and diet in the Lamprophiidae from a Stochastic Character Mapping reconstruction. Left: Red, lizard eaters; yellow, aquatic vertebrate eaters; light green, elongate prey eaters; dark green, reptile egg-eaters; dark blue, arthropod eaters; purple, soft-bodied invertebrate eaters; light blue, slugs and snail eaters; and black, generalists. Right: Red, no fangs; blue, rear fangs; green, front fangs. Photographs by Graham Alexander.

TABLE 2. The maximum likelihood estimate values for model parameters ER, SYM, and ARD for diet in lamprophiids. The best model has the lowest  $\Delta$ AIC and highest log likelihood ( $-\ln L$ ) values.

Model	Parameters (n)	Log likelihood ( $-\ln L$ )	$\Delta$ AIC
ER	1	210.95	423.93
SYM	28	178.40	428.26
ARD	56	173.88	542.67

suggests that all lamprophiids have evolved from a venomous ancestor. Thus, we deduce that the presence of venom in the Lamprophiidae is also plesiomorphic, and our findings indirectly support the hypothesis of a fanged colubroid ancestor with subsequent evolution to front fangs and rear fangs. The detection of a phylogenetic signal indicated that within subfamilies, fang morphology tends to be constrained, with some exceptions (e.g., Atractaspidinae; Portillo et al., 2019). Therefore, changes in dental morphology and the loss of fangs in some lamprophiids have most likely occurred as a shift to novel prey types or prey capture methods, as evidenced by the divergence in diet. The emergence of front-fang types is apomorphic in many subfamilies (Burbrink et al., 2019; Portillo et al., 2019), but many lamprophiids have also retained their ancestral fang morphology.

Because venom systems can be metabolically costly (McCue, 2006), species that have lost this trait were most likely able to do so because they feed on prey that are easy to subdue without venom. For example, slugs and snails present little retaliation to predation in both the lamprophiid genera *Duberria* and *Micropisthodon* and the snail-eating colubrid genera *Pareas* and *Dipsas* (Sazima, 1989; Götz, 2002; Barlow et al., 2009). Rather, the use of teeth allows these snakes to extract the snail from its shell without the need for envenomation. In addition to teeth, it is likely that glands in the mouth aid in the consumption of snails and evolved as an independent trait (de Oliveira et al., 2017). Such examples of convergent evolution to eat slugs and snails support the hypothesis that the loss of fangs is related to specializations in diet.

Many diet-specialist snakes tend to extract nutrients from their prey more efficiently than do generalists (Britt et al., 2006), and the nutritional value of these new prey types may be higher in comparison to the ancestral prey. The specialization on slugs and snail consumption occurred independently in various species and is attributed to slugs and snails being an abundant and valuable food source (Arnold, 1993). Arnold (1977) suggested that the propensity to feed on slugs is a heritable trait (Britt et al., 2006), and many snakes include gastropods as a dominant prey type in their diet, making them specialists that possess superior energetic efficiencies in comparison to generalists (Krieger et al., 1971; Pianka, 1974). The evolution of the venom system within this context indicates that slug and snail

eaters have lost their fangs and that venom may be used as an alternate means of handling prey.

Within the Lamprophiidae, the mole snake (*Pseudaspis cana*) has no fangs (Alexander and Marais, 2007) and has secondarily lost its venom system (Fry et al., 2003). Evans et al. (2019) showed that mole snakes possess specialized, enlarged posterior maxillary teeth that are unusual in shape and position. Mole snakes use these enlarged maxillary teeth as part of a unique biting action that causes slicing of prey and during male–male combat (Alexander and Marais, 2007) and may also employ them to dispatch fossorial rodents and moles in the confines of their burrows, rather than pulling them to the surface (Branch et al., 1997). By Jackson's definition of a fang, the unique dental structure of the mole snake resembles that of a fang which has lost its ability to deliver venom, which further supports the idea of venom loss in the Lamprophiidae.

Dental morphology has an important function in prey capture, and several adaptations allow handling of slippery prey within the Lamprophiidae. The use of large maxillary teeth to extract lizards from refuges is seen in the Cape Wolf Snake (*Lycophidion capense*; Alexander and Marais, 2007), while it has been reported that the use of hinged teeth is a specialization to durophagy in several lamprophiids (Savitzky, 1981). Adaptations to feeding on skinks have occurred in the rear-fanged *Psammodynastes* species, and this requires grooved teeth that can conduct venom. The fang is a means of subduing the prey (Greene, 1989) and introducing venom into it (Jackson and Fritts, 1996). Clearly, variations in dental morphologies have allowed many snakes to exploit a range of prey items that may not have been previously available to them.

A generalist diet was characteristic of 40% of lamprophiids, which was defined as snakes that included multiple prey items of different shapes and sizes. The fang condition varies for generalists and can be attributed to the functional characteristic of different prey shapes. Many lamprophiids that are generalists include mammals in their diet that can be subdued by constriction (e.g., *Lamprophis* species) or by envenomation (e.g., many *Psammophis* species). Therefore, diversification of dental morphology can depend on prey characteristics and can play an important role in shaping feeding ecology (Cundall and Greene, 2000).

The Lamprophiidae also includes the front-fanged species in the Atractaspidinae. *Atractaspis* have superficially similar dental morphology to those of the vipers, as they possess relatively long fangs on a short maxilla. But despite the superficial similarities in fang condition, there are major differences in their function, such as the maxillary rotation that occurs in the latter (Deufel and Cundall, 2003). *Atractaspis* envenomates prey by stabbing downwards and backward with a single long fang from one side of the closed mouth while the snake crawls alongside its prey (Berkovitz and Shellis, 2016). Deufel and

TABLE 3. The percentage and number of lamprophiids (of total 134) assigned to each of the eight diet clusters and to each fang type.

Diet cluster	No. and % in cluster	No. ear fangs; %	No. fangs; %	No. front fangs; %
Lizards	26; 19%	20; 15%	6; 4%	0
Aquatic vertebrates	25; 19%	10; 7%	15; 11%	0
Elongate prey	15; 11%	6; 4%	8; 6%	1; 1%
Reptile-eggs	7; 5%	1; 1%	6; 4%	0
Arthropods	3; 2%	3; 2%	0	0
Soft-bodied invertebrates	1; 1%	0	1; 1%	0
Snails	3; 2%	0	3; 2%	0
Generalists	54; 40%	26; 19%	22; 16%	6; 4%

Cundall (2003) showed that *Atractaspis* have likely modified their prey-capture strategy for hunting in the confines of a burrow by eliminating mouth opening. Portillo et al. (2019) suggested that the unique, viper-like front fangs of *Atractaspis* may have evolved to facilitate the predation of rodent nestlings or squamates in tight burrows, as preying on animals in tight burrows limits mobility of the predator, a feeding behavior that appears to be unique amongst snakes.

Portillo et al. (2019) provide further insight on both burrowing asps and collared snakes with regard to snake dentition and diet and the adaptability of dentition within short periods of time to facilitate foraging strategies. *Atractaspis* is of special interest, as the independent evolution to front fangs would have required unique driving forces. Squamate prey is consumed across all atractaspidinae and aparallactine genera (Portillo et al. 2019) and, therefore, a fossorial habitat and a small body size may have been a driver for the front-fang evolution in *Atractaspis*. There is no evidence to suggest that the transition to a front-fanged state in the Atractaspidinae was preceded by a fangless intermediate, and it appears that the front-fang condition in the Lamprophiidae has evolved convergently with the front-fang venom systems of viperids and elapids (Kerckamp et al. 2015).

The evolution of diet and venom has been closely linked in various snakes (Fry et al., 2003; Barlow et al., 2009). While there are very limited data on venom composition for all lamprophiids, few studies have focused on rear-fanged non-front-fanged evolution and diet in some lamprophiids (Fry et al., 2008). In *Psammophis mossambicus*, neurotoxins have been linked to preying on mammals (Fry et al., 2008; Brust et al., 2013), and in *Rhamphiophis oxyrhynchus*, neurotoxic venom is thought to be used for prey envenomation (Lumsden et al., 2005). The complex composition of neurotoxins in non-front-fanged snakes suggests that different venoms have evolved independently (Lumsden et al., 2007). Additionally, Fry et al. (2003) highlight that snakes need a variety of toxin types to feed on a wide diversity of prey because different prey have different defense systems. The diversity in the diet of lamprophiids has very likely shaped their dental morphology and their venom composition.

Our study shows that the evolution of fang condition has had a significant impact on the dental morphology of extant lamprophiids and evolution of their diet. We also provide evidence for the independent loss of fangs and the independent evolution to front fangs from a rear-fanged ancestor in colubroid snakes. It is generally assumed that fangless species of snakes are not venomous while species with fangs are venomous, a generalization that may not be true in all cases. Clearly, the relationship between the possession of fangs and the production of venom requires further investigation. We provide insight into the ecological significance of differences in fang position and the driving forces underpinning the evolution of diet and dental morphology. More research is needed on venom protein evolution in relation to diet and greater focus should be given to the Lamprophiidae, which is comprised of species that are markedly different in both their diet and dental morphology. Diet is an important determinant of snake ecology and phylogenetic comparative studies serve as a tool to investigate factors, such as fang condition, that significantly influence feeding behavior.

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APPENDIX 1. Diet data with specific references.

Species	Diet	References
<i>Prosymna ruspolii</i>	Reptile eggs	Reptile eggs (Broadley, 1979; Spawls et al., 2006)
<i>Prosymna visseri</i>	Reptile eggs	Reptile eggs (Alexander and Marais, 2007; Broadley, 1979)
<i>Prosymna jani</i>	Reptile eggs	Reptile eggs (Alexander and Marais, 2007; Broadley, 1979)
<i>Prosymna greigerti</i>	Reptile eggs	Reptile eggs (Broadley, 1979)
<i>Prosymna meleagris</i>	Reptile eggs	Reptile eggs (Broadley, 1979)
<i>Rhamphiophis rubropunctatus</i>	Generalist	Small rodents and lizards (Spawls et al., 2006, 2018)
<i>Rhamphiophis oxyrhynchus</i>	Generalist	Lizards; small rodents, and snakes (Branch, 1991; Lumsden et al., 2005)
<i>Rhagerhis moilensis</i>	Generalist	Rodents, lizards, snakes and birds (Schleich, et al., 1996)
<i>Malpolon monspessulanus</i>	Lizards	Lizards (Carranza et al., 2006)
<i>Mimophis mahfalensis</i>	Generalist	Lizards, small mammals, snakes, and frogs (Glaw and Vences, 2007; IUCN, 2018)
<i>Dipsina multimaculata</i>	Lizards	Lizards (Alexander and Marais, 2007; Branch, 1991)
<i>Hemirhagerhis viperina</i>	Lizards	Lizards (Broadley, 1997)
<i>Hemirhagerhis kelleri</i>	Reptile eggs	Lizards and gecko eggs (Spawls et al., 2006)
<i>Hemirhagerhis hildebrandtii</i>	Lizards	Lizards (Spawls et al., 2002)
<i>Psammophylax acutus</i>	Generalist	Small mammals and frogs (Spawls et al., 2002)
<i>Psammophylax rhombeatus</i>	Generalist	Lizards, frogs, rodents, birds, and/or snakes (Alexander and Marais, 2007; Cottone and Bauer, 2010)
<i>Psammophylax variabilis</i>	Generalist	Lizards, frogs (Alexander and Marais, 2007; Soller, 2018), small mammals, fish, and/or birds
<i>Psammophylax tritaeniatus</i>	Generalist	Small mammals, frogs, lizards, and birds (Alexander and Marais, 2007)
<i>Psammophis crucifer</i>	Aquatic vertebrates	Lizards and frogs (Cottone and Bauer, 2010; Branch, 1991; Soller, 2018)
<i>Psammophis lineolatus</i>	Lizards	Lizards
<i>Psammophis condanarus</i>	Generalist	Lizards, bird chicks, frogs, rodents, and snakes
<i>Psammophis trigrammus</i>	Lizards	Lizards (Branch, 1991)
<i>Psammophis jallae</i>	Lizards	Lizards (Branch, 1991; Soller, 2018)
<i>Psammophis leightoni</i>	Generalist	Rodents, lizards, snakes, and amphibians (Branch, 1991; Soller, 2018)
<i>Psammophis notostictus</i>	Generalist	Lizards, rodents, and amphibians (Branch, 1991; Soller, 2018)
<i>Psammophis angolensis</i>	Generalist	Lizards (Loveridge, 1955), skink eggs, and frogs (Spawls et al., 2006, Branch, 1991)
<i>Psammophis schokari</i>	Generalist	Lizards, small mammals, and birds
<i>Psammophis praeornatus</i>	Lizards	Lizards
<i>Psammophis punctulatus</i>	Elongate prey	Lizards and snakes (Spawls et al., 2006)
<i>Psammophis biseriatus</i>	Lizards	Lizards (Spawls et al., 2006)
<i>Psammophis tanganicus</i>	Lizards	Lizards (Spawls et al., 2006)
<i>Psammophis lineatus</i>	Generalist	Frogs and small mammals (Soller, 2018)
<i>Psammophis subtaeniatus</i>	Generalist	Small birds, lizards (Branch, 1991), rodents, and frogs (Soller, 2018)
<i>Psammophis sudanensis</i>	Aquatic vertebrates	Lizards, snakes (Spawls et al., 2006) rodents, frogs, and small birds
<i>Psammophis orientalis</i>	Elongate prey	Lizards and snakes (Spawls et al., 2006)
<i>Psammophis rukwae</i>	Lizards	Lizards (Spawls et al., 2002)
<i>Psammophis sibilans</i>	Generalist	Amphibians, lizards, and small mammals (Spawls et al., 2002)
<i>Psammophis leopardinus</i>	Generalist	Snakes, rodents, lizards, and birds (Soller, 2018)
<i>Psammophis mossambicus</i>	Generalist	Lizards, snakes, (Branch, 1991), rodents, frogs, and birds (Spawls et al., 2002, 2006; Soller, 2018)
<i>Psammophis phillipsi</i>	Generalist	Lizards (Leaché et al., 2006), small mammals, frogs, and snakes
<i>Homoroselaps lacteus</i>	Elongate prey	Lizards and snakes (Branch, 1991)
<i>Atractaspis microlepidota</i>	Generalist	Lizards, small mammals (Spawls et al., 2006), burrowing reptiles, and amphibians (Alexander and Marais, 2007) snakes (Shine et al., 2006)
<i>Atractaspis boulengeri</i>	Generalist	Burrowing reptiles
<i>Atractaspis irregularis</i>	Generalist	Snakes, lizards, small mammals (Spawls et al., 2006), burrowing reptiles (Alexander and Marais, 2007)
<i>Atractaspis bibronii</i>	Generalist	Burrowing reptiles (Alexander and Marais, 2007), frogs, lizards, and small mammals (Shine et al., 2006) (Spawls et al., 2006)
<i>Atractaspis corpulenta</i>	Generalist	Snakes and lizards (Shine et al., 2006)
<i>Atractaspis micropholis</i>	Generalist	Small reptiles
<i>Aparallactus modestus</i>	Soft-bodied invertebrates	Earthworms (Underwood and Kochva, 1993; Vidal et al., 2008)
<i>Aparallactus werneri</i>	Arthropods	Centipedes and other small insects (Spawls et al., 2002)
<i>Aparallactus guentheri</i>	Arthropods	Centipedes (Spawls et al., 2006)
<i>Aparallactus capensis</i>	Arthropods	Centipedes (Spawls et al., 2006)
<i>Polemon notatus</i>	Elongate prey	Snakes (Kusamba et al., 2013)
<i>Polemon collaris</i>	Elongate prey	Snakes (Kusamba et al., 2013)
<i>Polemon acanthias</i>	Elongate prey	Snakes (Kusamba et al., 2013)
<i>Macrelaps microlepidotus</i>	Generalist	Frogs (Underwood and Kochva, 1993), small mammals, lizards, and snakes (Branch, 1991; Shine et al., 2006)
<i>Amblyodipsas polylepis</i>	Elongate prey	Lizards and snakes, sometimes frogs and amphisbaenians (Branch, 1991; Shine et al., 2006; Spawls et al., 2006)
<i>Amblyodipsas dimidiata</i>	Lizards	Worm lizards (Spawls et al., 2006; Branch, 1991)

## APPENDIX 1. Continued.

Species	Diet	References
<i>Xenocalamus transvaalensis</i>	Lizards	Lizards (Branch, 1991) and amphisbaenians (Shine et al., 2006; Alexander and Marais, 2007)
<i>Pseudaspis cana</i>	Generalist	Rodents (Spawls et al., 2006) lizards (Branch, 1991), small mammals, birds and their eggs (Alexander and Marais, 2007)
<i>Pythonodipsas carinata</i>	Generalist	Lizards and rodents (Branch, 1991)
<i>Psammodynastes pulverulentus</i>	Aquatic vertebrates	Lizards (Greene, 1989) and frogs (Miller and Zug, 2016)
<i>Psammodynastes pictus</i>	Aquatic vertebrates	Fish, frogs, and prawns (Baker, 2018)
<i>Buhome depressiceps</i>	Aquatic vertebrates	Frogs (Spawls et al., 2002, 2006)
<i>Buhome procterae</i>	Aquatic vertebrates	Frogs (Spawls et al., 2002)
<i>Inyoka swazicus</i>	Generalist	Lizards and birds (Alexander and Marais, 2007)
<i>Hormonotus modestus</i>	Elongate prey	Snakes (Spawls et al., 2002)
<i>Gonionotophis nyassae</i>	Elongate prey	Lizards (Branch, 1991) and small snakes (Spawls et al., 2006)
<i>Gonionotophis brussauxi</i>	Aquatic vertebrates	Lizards, snakes, and frogs (Spawls et al., 2002)
<i>Gonionotophis stenophthalmus</i>	Elongate prey	Lizards (Spawls et al., 2002) and snakes
<i>Gonionotophis poensis</i>	Aquatic vertebrates	Lizards (Spawls et al., 2006), snakes, and frogs
<i>Gonionotophis capensis</i>	Generalist	Lizards, snakes, rodents, and toads (Spawls et al., 2006)
<i>Lycophidion nigromaculatum</i>	Elongate prey	Lizards and snakes (Alexander and Marais, 2007)
<i>Lycophidion laterale</i>	Elongate prey	Lizards and snakes (Spawls et al., 2002)
<i>Lycophidion capense</i>	Elongate prey	Lizards (Branch, 1991) and small snakes (Spawls et al., 2006)
<i>Lycophidion ornatum</i>	Lizards	Lizards (Spawls et al., 2006; Cunha and Vogt, 2016)
<i>Pseudoboodon lemniscatus</i>	Generalist	Lizards, frogs, and rodents (Spawls, 2004)
<i>Bothrolycus ater</i>	Generalist	Small mammals and frogs (Tapley et al., 2016)
<i>Bothrophthalmus brunneus</i>	Generalist	Small mammals (Spawls et al., 2002)
<i>Bothrophthalmus lineatus</i>	Generalist	Small mammals (Spawls et al., 2002)
<i>Boaedon virgatus</i>	Generalist	Small mammals (Leaché et al., 2006)
<i>Boaedon olivaceus</i>	Generalist	Small mammals (Spawls et al., 2006)
<i>Boaedon fuliginosus</i>	Generalist	Small mammals (Branch, 1991) and lizards (Broadley, 1969; Spawls et al., 2006)
<i>Boaedon lineatus</i>	Generalist	Small mammals and frogs (Leaché et al., 2006)
<i>Lamprophis guttatus</i>	Generalist	Lizards (Branch, 1991) and rodents (Alexander and Marais, 2007)
<i>Lamprophis fuscus</i>	Generalist	Lizards and rodents (Branch, 1991)
<i>Lamprophis aurora</i>	Generalist	Rodents, lizards, and frogs (Broadley, 1969; Alexander and Marais, 2007)
<i>Lamprophis fiskii</i>	Lizards	Lizards (Branch, 1991)
<i>Lycodonomorphus inornatus</i>	Generalist	Lizards, rodents, and snakes (Broadley, 1969)
<i>Lycodonomorphus rufulus</i>	Aquatic vertebrates	Frogs (Branch and Hanekom, 1987) tadpoles, fish (Branch, 1991), and rodents (Alexander and Marais, 2007)
<i>Lycodonomorphus laevisissimus</i>	Generalist	Frogs, tadpoles, and fish (Raw, 1973)
<i>Lycodonomorphus whytii</i>	Aquatic vertebrates	Amphibians (Loveridge, 1955) and possibly fish (Spawls et al., 2002)
<i>Amplorhinus multimaculatus</i>	Generalist	Frogs, lizards (Branch, 1991), and mice (Alexander and Marais, 2007)
<i>Duberria variegata</i>	Slugs and snails	Slugs and snails (Bates, 1998; Branch, 1991; Spawls et al., 2006)
<i>Duberria lutrix</i>	Slugs and snails	Slugs and snails (Branch, 1991; Bates, 1998; Spawls et al., 2006)
<i>Dityopphis vivax</i>	Lizards	Lizards
<i>Compsophis infralineatus</i>	Generalist	Frogs and mammals (Glaw and Vences, 2007)
<i>Compsophis laphystius</i>	Aquatic vertebrates	Frogs and their clutch (Glaw and Vences, 2007; Kaloloha et al., 2011)
<i>Compsophis albiventris</i>	Aquatic vertebrates	Frogs and lizards (Glaw and Vences, 2007; Eudeline et al., 2015)
<i>Compsophis boulengeri</i>	Aquatic vertebrates	Frogs and lizards (Glaw and Vences, 2007)
<i>Alluaudina bellyi</i>	Lizards	Lizards (Glaw and Vences, 2007)
<i>Parastenophis betsileanus</i>	Lizards	Lizards and invertebrates (Glaw and Vences, 2007; Kaloloha et al., 2011)
<i>Leioheterodon geayi</i>	Reptile eggs	Reptile eggs (Glaw and Vences, 2007)
<i>Leioheterodon modestus</i>	Generalist	Lizards, frogs, birds, small mammals, and reptile eggs (Glaw and Vences, 2007)
<i>Leioheterodon madagascariensis</i>	Generalist	Birds, mammals, reptile eggs, frogs, and lizards (Mori and Tanaka, 2001; Glaw and Vences, 2007)
<i>Langaha madagascariensis</i>	Generalist	Frogs, lizards, and birds (Glaw and Vences, 2007)
<i>Micropisthodon ochraceus</i>	Slugs and snails	Slugs and snails and lizards (Glaw and Vences, 2007)
<i>Ithyocyphus miniatus</i>	Aquatic vertebrates	Lizards and frogs (Glaw and Vences, 2007)
<i>Ithyocyphus oursi</i>	Lizards	Lizards, chameleon, geckos (Glaw and Vences, 2007)
<i>Madagascarophis meridionalis</i>	Generalist	Chameleons, geckos, frogs, and small mammals (Glaw and Vences, 2007)
<i>Madagascarophis colubrinus</i>	Generalist	Frogs, lizards, chameleons, birds, small mammals, and snakes (Glaw and Vences, 2007)
<i>Lycodryas inornatus</i>	Lizards	Lizards (Glaw and Vences, 2007)
<i>Lycodryas citrinus</i>	Generalist	Lizards, frogs, snakes, and birds (Glaw and Vences, 2007)
<i>Lycodryas maculatus</i>	Lizards	Lizards (Glaw and Vences, 2007)
<i>Lycodryas inopiniae</i>	Lizards	Lizards (Glaw and Vences, 2007)
<i>Lycodryas pseudogranuliceps</i>	Lizards	Lizards (Glaw and Vences, 2007)
<i>Lycodryas granuliceps</i>	Lizards	Lizards (Glaw and Vences, 2007)
<i>Dromicodryas quadrilineatus</i>	Generalist	Lizards and mammals (Glaw and Vences, 2007)
<i>Dromicodryas bernieri</i>	Elongate prey	Lizards, small snakes (Glaw and Vences, 2007)



## APPENDIX 1. Continued.

Species	Diet	References
<i>Thamnosophis infrasinatus</i>	Generalist	Newts, lizards, small mammals, frogs, and chameleons (Glaw and Vences, 2007)
<i>Thamnosophis stumpffi</i>	Aquatic vertebrates	Frogs and lizards (Glaw and Vences, 2007)
<i>Thamnosophis lateralis</i>	Aquatic vertebrates	Frogs and lizards (Glaw and Vences, 2007)
<i>Thamnosophis epistibes</i>	Aquatic vertebrates	Frogs and lizards (Glaw and Vences, 2007)
<i>Thamnosophis martaie</i>	Aquatic vertebrates	Frogs and lizards (Glaw and Vences, 2007)
<i>Heteroliodon occipitalis</i>	Lizards	Lizards (Glaw and Vences, 2007)
<i>Pseudoxyrhopus ambreensis</i>	Lizards	Lizards (Glaw and Vences, 2007)
<i>Liopholidophis dimorphus</i>	Generalist	Frogs and millipedes (Cadle, 1996, 2003, 2014; Glaw and Vences, 2007)
<i>Liopholidophis sexlineatus</i>	Aquatic vertebrates	Frogs (Cadle, 1996, 2003, 2014; Glaw and Vences, 2007)
<i>Liopholidophis doliocercus</i>	Aquatic vertebrates	Frogs (Cadle, 1996, 2003, 2014; Glaw and Vences, 2007)
<i>Liophidium rhodogaster</i>	Aquatic vertebrates	Fish and lizards (Glaw and Vences, 2007)
<i>Liophidium therezieni</i>	Aquatic vertebrates	Fish and lizards (Glaw and Vences, 2007)
<i>Liophidium vaillantii</i>	Elongate prey	Snakes (Cadle, 1999; Glaw and Vences, 2007)
<i>Liophidium torquatum</i>	Aquatic vertebrates	Fish and lizards (Glaw and Vences, 2007)
<i>Liophidium mayottensis</i>	Aquatic vertebrates	Fish and lizards (Glaw and Vences, 2007; Scherz, 2018)
<i>Liophidium chabaudi</i>	Aquatic vertebrates	Fish and lizards (Glaw and Vences, 2007)

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