The evolution of diet in the Lamprophiidae

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Declaration

I declare that this dissertation is my own, unaided work unless specifically acknowledged in the text. It has not been submitted previously for any degree or examination at any other university, nor has it been prepared under the aegis or with the assistance of any other body or organization or person outside of the University of the Witwatersrand, Johannesburg, South Africa.

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Abstract

Studying feeding biology in a phylogenetic context helps elucidate the factors that significantly influenced the evolutionary history of organisms. The snake lineage is one of the most morphologically and ecologically diverse clades of vertebrates due to a variety of traits (e.g. venom, body shape, gape size and habitat use) that have enabled their exceptional radiation. Recently, the Deep History Hypothesis (DHH) has been used to explain how divergence, deep in the evolutionary history of snakes, has resulted in present day niche preferences. The Competition-Predation Hypothesis (CPH) contrastingly attributes current ecological traits to recent species interactions. Diet has been a key factor in shaping snake diversity and ecology, and it has often been used as a proxy to understand current snake community structure and evolutionary trends in snakes.

I tested the validity of the two evolutionary hypotheses in the Lamprophiidae, a family of primarily African snakes. Furthermore, the evolution of lifestyle, fang types and body size in the Lamprophiidae was examined. Having sourced dietary data for ~300 species, a Hierarchical Cluster Analysis was performed, to group diet into eight broad clusters. A generalist diet comprised of lizards, aquatic vertebrates, small mammals, snakes and reptile eggs, was characteristic of 46% of extant species. Stochastic Character Mapping was performed to generate 50 possible evolutionary hypotheses, the majority of which suggested a generalist ancestral feeding condition with a tendency towards specialisation. Although the generalist feeding trait has largely been retained in many extant lamprophids, some species have a more specialised diet. From the phylogenetic reconstruction, it is evident that the ancestral lamprophid consumed a generalist diet in a terrestrial environment with a relatively small body size (400-600 mm) and possessed back fangs. Body size and fang morphology were correlated with diet indicating that these selective pressures have influenced the variety in prey consumption.

A phylogenetic signal from Pagel's lambda confirmed the divergence in diet while traits such as lifestyle, fang types and body size were constrained. Thus, the validity of DHH and CPH depends on the characters assessed and in this case, a combination of historical and contemporary influences is responsible for shaping the lamprophid community as a whole. The divergence in diet in the lamprophids is most likely influenced by competition or predation, as their interactions with other species within their habitat could be responsible for shaping their diet. This proves to be the case for the lamprophidae, however, studies on other groups of snakes, in different regions of the world have found that phylogeny is more influential on diet patterns. This study shows the importance in understanding ecological factors as a determinant of community ecology.

Key words: Divergent evolution, snake ecology, morphological trait reconstruction

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Introduction

The evolution of snakes

Snakes arose between 140 to 167 million years ago and their subsequent radiations have resulted in the diversity of snakes that we see today (Vitt and Caldwell 2009). Snakes represent one of the most morphologically diverse vertebrate clades in the world due largely to their exceptional radiation (Vitt and Caldwell 2009). Various traits have led to this radiation including the presence of venom (Daltry *et al.* 1996), body shape (Boback and Guyer 2003), change in gape size (Pough and Groves 1983) and specific habitat use (Alencar *et al.* 2013). Sites *et al*. (2011) showed that there have been multiple origins of many of these notable traits, that has led to a better understanding of the squamate phylogeny and it is a combination of these traits have shaped snake communities both in the past and the present. Habitat use and other feeding-related traits such as venom delivery systems (Fry *et al.* 2012) and macrostomatan head morphology (Vincent *et al.* 2006) are seen to be more derived in snakes, representing more recent radiation adaptations. These adaptations have played a major role in increasing the range of accessibility to prey of all shapes and sizes (Sites *et al.* 2011; Greene 1983).

Snakes can be found in all parts of the world except for polar regions and the deep oceans (Greene 1997). Their lifestyles range from terrestrial, cryptozoic, arboreal and aquatic to fossorial, with variations in the degree of specialisation within each of these categories (Martins *et al.* 2001; Pizzatto *et al.* 2007). Ecological traits such as home range size, lifestyle and habitat selection are often influenced by prey availability and vice versa (Glaudas and Alexander 2016). Diet and microhabitat are also shown to be closely correlated in snakes and the evolution of one has implications on the other (Savitzky 1983; Motta *et al.* 1995; Martins *et al.* 2001; Kohlsdorf *et al.* 2008). Therefore, it is important to explore the diversity and evolution of these traits within snake assemblages (Alencar *et al*. 2013). This may result in significant insights into the general patterns found in any group while also being able to explore the processes that generated them (Fry *et al*. 2008).

Snakes possess many distinctive features including highly modified skulls and jaw mechanisms (Greene 1983). This allows for increased skull flexibility, which ultimately aids a larger gape size (Secor and Diamond 2000; Sites *et al.* 2011). This unique morphology has a significant impact on the type of prey snakes are able to ingest as well as how they are able to keep up with their dietary demands (Greene 1983). Gape size is important in determining the type of prey a snake can eat (Rodriduez-Robles *et al.* 1999). Snakes are gape limited meaning that they swallow their prey whole and as a result foraging success increases with maximum ingestible prey size (Forsman and Lindell 1993). The most basal clade of living snakes are tiny burrowing animals with restricted gapes such as the worm-like blindsnakes (Scolecophidians), pipesnakes (Cylindrophiidae) and shield-tail snakes (Uropeltidae) (Scanlon and Lee 2010).

Snakes with a moderate gape include the sunbeam snakes (*Xenopeltis*), while large-gaped snakes include the surface-active clades such as pythons, colubroids and boas that represent a derived radiation (Scanlon and Lee 2010). Greene (1983) explained that higher henophidians (e.g. python and boas) possess a more mobile jaw apparatus and body structure, which enables them to immobilise their prey through constriction (Frazetta 1970; Greene and Burghardt 1978). This implies that snake evolution has involved consistent trends towards greater surface activity, increased body size, and an enlarged gape (Underwood 1967; Rodríguez-Robles *et al.* 1999).

Diet patterns of snakes

One of the most fundamental questions in biology concerns dietary breadth: How many closely related organisms are able to consume a diversity of prey items while other organisms are specialised to feed on only one or a few types of prey (Brischoux *et al.* 2009). The evolution of specialisation is largely based on the concept of both behavioural and physiological trade-offs in the environment including specialist-generalist trade-offs in terms of fitness, under different circumstances, that are fundamental to most models of specialisation (Fry 1996; Angilletta *et al.* 2003). In contrast, generalist feeders consume a larger variety of prey and are often opportunistic hunters. This variation in dietary breadth is commonly observed in snakes, making them model organisms to study broad-scale evolutionary patterns in diet and factors that influence their behaviour and community structure (Savitsky 1983; Pauwels *et al.* 2008).

The dietary demands of snakes are thought to be important in their evolutionary origin and radiation (Gans 1961; Rieppel 1980). Morphological features have been known to affect handling cost of certain prey sizes, as noted in vipers (Pough and Groves 1983). One way in which snakes adapt to feeding shifts are through evolutionary changes in body size. Body structure amongst different clades, in addition to different ecological traits, constitutes a core component of snake ecology. The repeated occurrence of a combination of morphological characteristics including stout bodies, large heads and fangs suggests that snakes possessing these features are specialised for a particular activity (Pough and Groves 1983). Pough (1977) noted that the ability to swallow prey items that are large in relation to the size of the snake appears to be a validation for the development of certain morphological characteristics. A large head, long jaws, and large gape facilitates the ingestion of bulky food items (Greene 1983), while smaller-bodied individuals consume smaller prey (Pough and Groves 1983; Greene 1997).

Many studies on the diet of early snakes have found that their diet was relatively narrow in terms of prey type and weight, as they predominantly ate eel-like fish, caecilians, and other elongate amphibians, amphisbaenians and other limbless lizards (Greene 1983; Rodriguez-Robles *et al.* 1999). These ancestral feeding habits have changed from frequent feeding on small prey such as lizards to infrequent feeding on very heavy prey (Greene 1983). Schmidt (1950), Frazetta (1970) and Rieppel (1978) have proposed that the early evolution of snakes was to some extent, a consequence of the rise of mammals, which led to adaptations for feeding on large prey (Gans 1961). This idea was evident in the most derived snakes that have a larger gape size compared to their ancestors, enabling them to feed on many mammals and other larger prey (birds and lizards) (Rodriguez-Robles and De Jesús-Escobar 1999).

Several adaptive processes drive the evolution of snake feeding behaviour and it has been generally accepted that snake venom primarily facilitates the immobilisation and digestion of prey, but this idea remains widely debated (Barlow *et al.* 2009). The development of the venom system along with unique dental morphology shows that venom played a vital role in the evolution and the success and diversity of snakes and consequently their feeding ecology (Scanlon and Lee 2010). The ‘overkill’ hypothesis of venom evolution postulates that variation in venom composition and diversity, is a result of neutral evolutionary processes rather than natural selection for lethality (Sasa 1999; Mebs 2001). By contrast, other authors have argued that venom diversity results from adaptation to species specific diets (e.g. Daltry *et al.* 1996; Wüster *et al.* 1999; Kordiš and Gubenšek 2000). It is likely that a combination of different factors, including body structure, has enabled the venom diversity we see today.

Several studies have investigated the correlations between specific prey types and maxillary morphology of snakes (Savitzky 1981; Vaeth *et al.* 1985; Jackson *et al.* 1999; Jackson and Fritts 2004). Savitzky (1981) found dental specialisation was correlated with a specific prey type, as hinged teeth in some snake genera, is associated with durophagy- an adaptation that prevents the teeth from breaking when a snake consumes hard-bodied prey. Other studies (Savitzky 1983; Cundall and Irish 1989; Greene 1989; Jackson and Fritts 2004) supported those findings and included further morphological modifications to encompass the hard-bodied prey, such as the presence of a large diastema in the maxillary dentition and an arched maxillary bone.

In contrast to this adaptation for consuming hard-bodied prey, substantially lengthened teeth have been reported in predators that prey on soft items such as slugs (Zweifel 1954), while piscivorous snakes are associated with having numerous, sharp, posteriorly curved teeth (Savitzky 1983; Knox and Jackson 2010). Some studies have reported multiple variations in dental morphology for egg-eating. Broadley (1979) showed that snakes that prey on soft-shelled eggs have broad, bladelike teeth to slice open the eggs for digestion. Contrastingly, snakes that are specialised for calcareous egg-eating are shown to have a few, small teeth, thought to facilitate regurgitation of the egg shell after its contents have been consumed (Savitzky 1983). Thus, from an ecomorphological perspective, there is a strong correlation between different types of maxillary dentition and preferred type of prey in colubroid snakes (Knox and Jackson 2010).

Feeding behaviour in snakes, driven by changes in body size and dental morphology, varies according to the location and geography of the species (Greene 1983). With changes in body size seen in various snakes, there have been cases of ontogenetic shifts in diet from ectothermic prey to endothermic prey (Shine 1980; Mushinsky *et al.* 1982; Henderson *et al.* 1987; Greene 1989; Henderson 1993; Shine *et al.* 1998; Rodriguez-Robles *et al.* 1999). This coincides with the shift from elongated to mammalian prey items in advanced snakes with larger gape sizes and venom systems (Rieppel 1978; Greene 1983). Factors such as microhabitat and climate can have an impact on food resources, as harsh conditions often mean reduced food availability whilst favourable environments have abundant prey (Toft 1985; Alencar *et al.* 2013). In addition, being an ambush or active forager, or diurnal or nocturnal also influences the type of food consumed, as some prey may only be active at night (Alencar *et al.* 2013). Different environments exhibit varying food availability, making spatial differences in prey availability a pertinent factor in snake habitat selection (Toft 1985). This is the main cause of the wide variations in diet among different families of snakes (Rodriguez-Robles *et al.* 1999).

Recently-diverged taxa are said to be ecologically similar, indicating a direct link between the evolutionary relatedness of species in a community and the characters that determine their distribution and abundance (Kraft *et al.* 2007). Most studies have focused on the Neotropics (Vitt and Vangilder 1983; Cadle and Greene 1993; Bellini *et al.* 2015), where a large diversity in the snake community exists. Vitt and Vangilder (1983) found that body size was correlated with diet and showed evidence of recent effects on shaping the snake community. Contrastingly, Cadle and Greene (1993) showed deep history impacts in the same community of Brazilian snakes. The focus needs to be shifted to other snake communities, such as those in Africa (Gartner and Greene 2008). This will lead to a better understanding of some of the more recently diverged taxa, including the lamprophiids and how they have changed over time.

Phylogenetic patterns in snakes

There is a large number of extant snake species (>3619; Uetz 2015). However, several factors significantly impede advances in understanding the evolutionary relationships of snakes (Zaher *et al.* 2009). The main restrictions include the inadequate taxonomic and genomic sampling among snakes and the limited range of morphological characters investigated thoroughly within the clade (Zaher *et al.* 2009). Despite these restrictions, a large number of morphological (Estes *et al.* 1988; Conrad 2008; Gauthier *et al.* 2012) and molecular (Townsend *et al.* 2004; Vidal and Hedges 2005; Wiens *et al.* 2010; Mulcahy *et al.* 2012; Wiens *et al.* 2012) studies have changed radically in their methodology, to produce many of the small-scale phylogenies seen today. Recently, Pyron *et al.* (2013a) reconstructed the squamate phylogeny to address previous classification problems and to incorporate new species in some of the families. This new phylogeny was used as a foundation on which the present work was established.

The clarification of phylogenetic relationships amongst closely-related taxa is critical to correctly inferring patterns of community structure, biogeography, character evolution, as well as evolution of biodiversity as a whole (Eggleton and Vane-Wright 1994; Riddle 1995; Harvey *et al*. 1996; Losos 1996; Ortolani and Caro 1996; Zamudio *et al*. 1997; Da Silva and Patton 1998; Roderick and Gillespie 1998). A reliable phylogeny allows researchers to test the authenticity of multiple models of evolutionary diversification, particularly in diverse organisms such as snakes (Patton and Smith 1992; Patton *et al*. 1994; Jackman *et al*. 1997; Losos *et al*. 1998; Gascon *et al*. 1998; Rodriguez-Robles and De Jesús-Escobar 1999). This aids in identifying instances of correlated character evolution (Brooks and McLennan 1991; Rodriguez-Robles and Greene 1996; Autumn *et al*. 1997; Vogler and Kelley 1998) and to assess whether a particular trait has evolved once or repeatedly within a lineage (Dial and Grismer 1992; Lanyon 1992; Greene 1994; Benabib *et al*. 1997; Mueller *et al*. 1998). With continuing efforts to improve our understanding in the field of phylogenetics and systematics with regards to snakes, many studies now look to incorporate morphological characters in addition to molecular data (Zaher *et al.* 2009).

Phylogenetically-based evolutionary ecology provides a framework to study patterns and determinants of community structure (Webb *et al.* 2002; Chazdon *et al.* 2003; Anderson *et al.* 2004). Colston *et al.* (2010) suggested that a necessary first step to examine the distribution of ecological characters among species in a phylogenetic context is with three possible scenarios. (1) Ecological characters have evolved randomly in the group, in which case sister species will tend to share some degree of ecological similarity, (2) ecological characters will tend to be more similar than expected under a random walk model (niche conservatism), as sister species are very similar to each other and (3) ecological characters are more different than expected by a random walk model, as sister species will have very different ecological strategies (divergence). This information is beneficial for exploring local community composition and the reflection of the regional species pool (Webb *et al.* 2002). Local communities are made up of both closely and distantly related species. Thus, the interplay of phylogenetic clustering and phylogenetic overdispersion will determine the relative contribution of the two evolutionary processes on shaping community structure (Webb *et al.* 2002; Cooper *et al.* 2008).

Two evolutionary hypotheses have been proposed to explain the ecological differences that have shaped current snake communities (Colston *et al.* 2010). The first is the Competition-Predation Hypothesis (CPH) that centres around recent effects, as closely related taxa diverge to partition available resources through interspecific competition or predation (Colston *et al.* 2010; Bellini *et al.* 2013). According to the CPH, species interactions drive the evolution of divergence in resource use and niche characteristics (food, time, and microhabitat) among species in local assemblages. This hypothesis predicts that ecological traits of coexisting species are independent of phylogeny, as major shifts in niche preferences result from interactions among species within present-day assemblages, as seen in many Amazonian snake communities (Henderson *et al.* 1979; Vitt and Vangilder 1983).

The second evolutionary hypothesis is the Deep History Hypothesis (DHH) that suggests that divergence deep in the evolutionary history of organisms have resulted in species maintaining their ancestral traits in present-day assemblages (Vitt and Pianka 2005). The DHH proposes that ecological traits of coexisting species can be predicted based on phylogeny, regardless of the present species community (Bellini *et al.* 2015). Evidence supporting this hypothesis has been shown, not only in the diets of 12 lizard families across four continents (Vitt and Pianka 2005), but also in snake diets of 196 species from across the world (Colston *et al.* 2010). The impact of the deep history of snakes is becoming increasingly evident in current snake communities across the globe (Burghart *et al.* 2000; Cadle and Greene 1993; de Queiroz and Rodriguez-Robles 2006). However, this is largely dependent on the individuals that make up a community and the functioning of natural communities has largely been dependent on interspecific competition for resources (Hanski 1987; Shorrocks 1990; Ray and Sunquist 2001; Krijger *et al.* 2001).

Lamprophiidae

The Lamprophiidae (Fitzinger 1843) is a late Eocene radiation of nocturnal and diurnal snakes (Kelly *et al.* 2011) that extend from Africa to Asia and Europe (Uetz 2015). The group incorporates many of the most charismatic of Africa's non-venomous snake species (Kelly *et al.* 2011). It includes many species such as the house snakes (*Boaedon* and *Lamprophis* spp.), sand snakes (*Psammophis* spp.) and stiletto snakes (*Atractaspis* spp.). The family has long been considered part of the much larger Colubridae family but has recently been elevated to the level of family (Pyron *et al*. 2011). The Colubridae are largely made up of nonvenomous snakes, but also include some species that are venomous. Colubrids with venom are often described as opisthoglyphous, meaning they have elongate, grooved teeth located at the back of the maxilla (Vidal 2002). The opisthoglyphous dentition appeared at least twice in the history of snakes and differs from that of proteroglyphous vipers and elapids that are front-fanged (Kardong 1982).

There are seven subfamilies recognised within the Lamprophiidae (Pyron *et al.* 2013a) with a total of ~308 species (Uetz 2015), many of which are endemic to Africa (Kelly *et al*. 2011). With the discovery of many new species and genetic regroupings of other species, this family has undergone multiple taxonomic changes over the last few years (Kelly *et al*. 2011). However, recent changes in the phylogeny, with incorporation of new species, have modified the defining characteristics of the family from being mainly non-venomous to now including many venomous species (Fry *et al*. 2012). As a result, there is greater morphological variation between the species of the different subfamilies than previously thought (Burbrink and Pyron 2009).

There is strong support for the monophyly of Lamprophiidae and all of its subfamilies (Vidal *et al.* 2008; Kelly *et al.* 2009; Kelly *et al.* 2011; Pyron *et al.* 2011) that include Atractaspidinae, Aparallactinae, Lamprophiinae, Prosymninae, Pseudaspidinae, Psammophiinae, and Pseudoxyrhophiinae (Pyron *et al.* 2013a). According to Pyron *et al.* (2013a), most currently-defined genera with the Lamprophiidae are monophyletic. However, within Aparallactinae, *Xenocalamus* is strongly placed within *Amblyodipsas*, and in Atractaspidinae, *Homoroselaps* is weakly placed in *Atractaspis* (Lawson *et al.* 2005; Kelly *et al.* 2009; Pyron *et al.* 2011; Pyron *et al.* 2013a; Pyron *et al.* 2013c). Superficially resembling the snake species within Elapidae and Viperidae, are the sister-genera *Atractaspis* and *Homoroselaps*, which fall into the Atractaspidine subfamily of the Lamprophiidae family (Fry *et al*. 2009).

The basic composition of Atractaspidinae with respect to the inclusion of *Homoroselaps* in the Lamprophiidae or Elapidae has been debated for over three decades (McCarthy 1985; McDowell 1968; Underwood and Kochva 1993; Cadle 1994; Zaher 1999; Slowinski and Keogh 2000; Kelly *et al.* 2003) This is due to similarities in many of the characteristics, in particular the elaborate, morphologically-specialised high-pressure front-fang venom systems used to conduct venom into their prey (Fry *et al.* 2008). These systems, including skeletal, muscle and gland components, show a characteristic, but different, pattern for each group (Fry *et al.* 2008). This inclusion of a proteroglyphous species in the family of mostly opistoglyphous and aglyphous snakes, has a significant impact on the type of prey consumed and is a unique trait for the lamprophids.

Aim

This study aims to describe the evolutionary pattern of diet in the family Lamprophiidae through the evaluation of the Deep History Hypothesis and the Competition-Predation Hypothesis on diet and other ecological and morphological traits. It, can then serve to answer important evolutionary and behavioural ecology questions for further studies within the Lamprophiidae.

Objectives

1. Test for the effect of phylogeny or competition as a determinant of current diet, lifestyle, fang morphology and body size in the lamprophids.

2. Evaluate whether the evolution of lamprophid diet and lifestyle are correlated.

3. Assess whether the evolution of diet is correlated with fang types in lamprophids.

4. Evaluate whether differences in body size have influenced the lamprophid diet evolution.

Methods

Data Collection

My dataset consisted of 136 of the 308 species in the Lamprophiidae (Uetz 2015). These 136 species were used because Pyron's phylogenetic tree, which is the most recently revised tree, showed only 136 closely related species for the Lamprophiidae (Pyron *et al.* 2013b). For each species I recorded the geographic location (region), diet, lifestyle, fang types and maximum body size (SVL and tail length) using field guides (Isemonger 1983; Branch 1998; Branch 2001; Marais 2004; Spawls *et al.* 2002; Alexander and Marais 2007), books and primary literature (Kofron 1990; Revault 1996; Vidal *et al.* 2008; Kelly *et al.* 2011; Fry *et al*. 2012; Kusamba *et al*. 2013; Cadle 2014). Lifestyle was categorised as terrestrial, arboreal, fossorial or semi-aquatic while fang type was classed as back-fanged, front-fanged or absent. All discrete variables were coded as presence-absence for each trait. Body size was recorded as the maximum body size (mm) for each species and I refer to snakes as small (< 500 mm), medium (500-1000 mm) and large (> 1000-2500 mm).

Data Analysis

Due to the high variation and wide range of prey types consumed, I performed a Hierarchical Cluster Analysis to group diets of 308 species into broad categories in SPSS statistics software (IBM 2013). A dendogram was generated in SPSS with various clusters and I selected the clusters of snake species based on homogenous diets that were different from each other. Each cluster was represented on a bar graph to comparatively see the consumption of the different prey types. The diet, lifestyle, fang types and body size information of 136 species was mapped on the most recent and comprehensive published phylogenetic tree for the family Lamprophiidae (Pyron *et al*. 2013a; Pyron *et al.* 2013b). The 136 species excluded an Elapid outgroup *Calliophis melanurus*, representing the most basal representative of a single taxon from the sister clade to the Lamprophiidae (Cadle 1988; Rong *et al.* 2010; Pyron *et al.* 2013a).

To reconstruct ancestral characteristics, I used Stochastic Character Mapping in the phytools package in R 3.2.1 (R Core Development Team 2014). This method of reconstruction uses Bayesian Inference that samples discrete character state reconstructions under a Markov process of shifts given the species' states and their phylogeny (Huelsenbeck *et al.* 2003) and mapping these characters onto phylogenies using a probabilistic approach rather than relying on parsimony (Bollback 2006). Stochastic Character Mapping considers stochastic changes at the internal nodes on a phylogeny and accounts for uncertainty in the historical character dynamics by creating multiple maps (Huelsenback *et al.* 2003). I generated 50 character histories (Price *et al.* 2015) for all discrete traits under three different types of likelihood models. To assess the best model for character reconstruction I used three models offered in the R 3.2.1 (R Core Development Team 2014) geiger package and compared ΔAIC and log likelihood (-lnL) values of the 50 character histories. The equal-rates (ER) model looks at all transitions in the parameter occurring at equal rates. The symmetric model (SYM) looks at forward and reverse transitions that share the same parameter and the all-rates-different (ARD) model looks at each rate as a unique parameter where all rates are different.

Pairwise evaluations were carried out between binary coded traits for diet and lifestyle as well as diet and fang types, respectively. I used Pagel's correlation in Mesquite 3.03 (Pagel 1999; Maddison and Maddison 2015) using 10 iterations within 1000 simulations. This was used to evaluate whether the rate of evolution of the two traits was independent. To investigate the relationship between diet and body size, I used the Phylogenetic ANOVA in the R Geiger package. I used Pagel's lambda in the R package geiger to test for a phylogenetic signal in the distribution of diet, lifestyle, fang types and body size (Revell 2012). This was used 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).

Results

Diet clusters

The Hierarchical Cluster Analysis on the diet of the Lamprophiidae revealed eight major diet clusters consisting of a variety of prey items including slug and snails (Kofron 1990) and centipedes to diets of fish, lizards and other snakes (Kusamba *et al.* 2013). A generalist diet was characteristic of 46% of extant lamprophid species (Fig. 1). The second-most prevalent diet cluster was the aquatic vertebrates with 18% of the lamprophids feeding on these prey (Fig. 1).

The dietary clusters consisted of the following: Type 1 diet consisted of 100% of the snakes that consumed lizards only (Fig. 2a). The majority of lamprophids in Type 2 were comprised of aquatic invertebrate consumers such as fish and frogs, with some species that also include lizards in their diet (36%; Fig. 2b). Sixty-two percent of the Type 3 diet was made up of snake eaters and other elongate prey such as legless skinks and amphisbaenids (Fig. 2c). However, 37% of lamprophids in the Type 3 diet ate lizards while 2% ate reptile eggs and snakes. In the Type 4 diet, 72% of species consumed reptile eggs, 22% also consumed lizards and 5% ate aquatic vertebrates in addition to reptile eggs (Fig. 2d).

Within the more specialised clusters such as the Type 5 diet, 90% of snakes ate centipedes or scorpions (arthropods) and only 10% also ate snakes (Fig. 2e). The Type 6 diet was primarily characterised by the consumption of soft-bodied invertebrates (71% of species) but 14% of snakes also included lizards or reptile eggs (14%) in their diet (Fig. 2f). Within the Type 7 diet 83% of snakes fed exclusively on slugs and snails with the remainder of species also eating snakes and lizards (Fig. 2g). The Type 8 diet consisted of generalists as the snakes included are a variety of prey classes in their diet including small mammals (33%), lizards (25%), aquatic vertebrates (19%) as well as birds (12%), snakes (9%) and reptile eggs (2%, Fig. 2h).

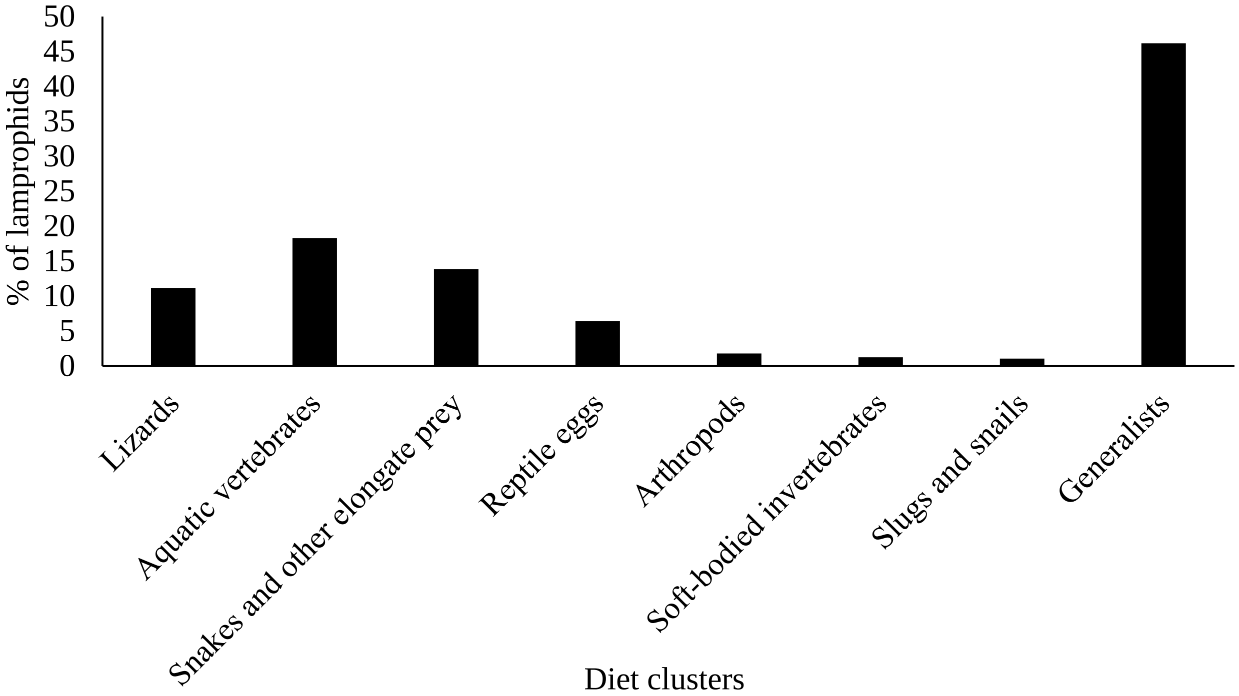

Figure 1. The percentage of all lamprophids consuming prey from eight diet clusters.

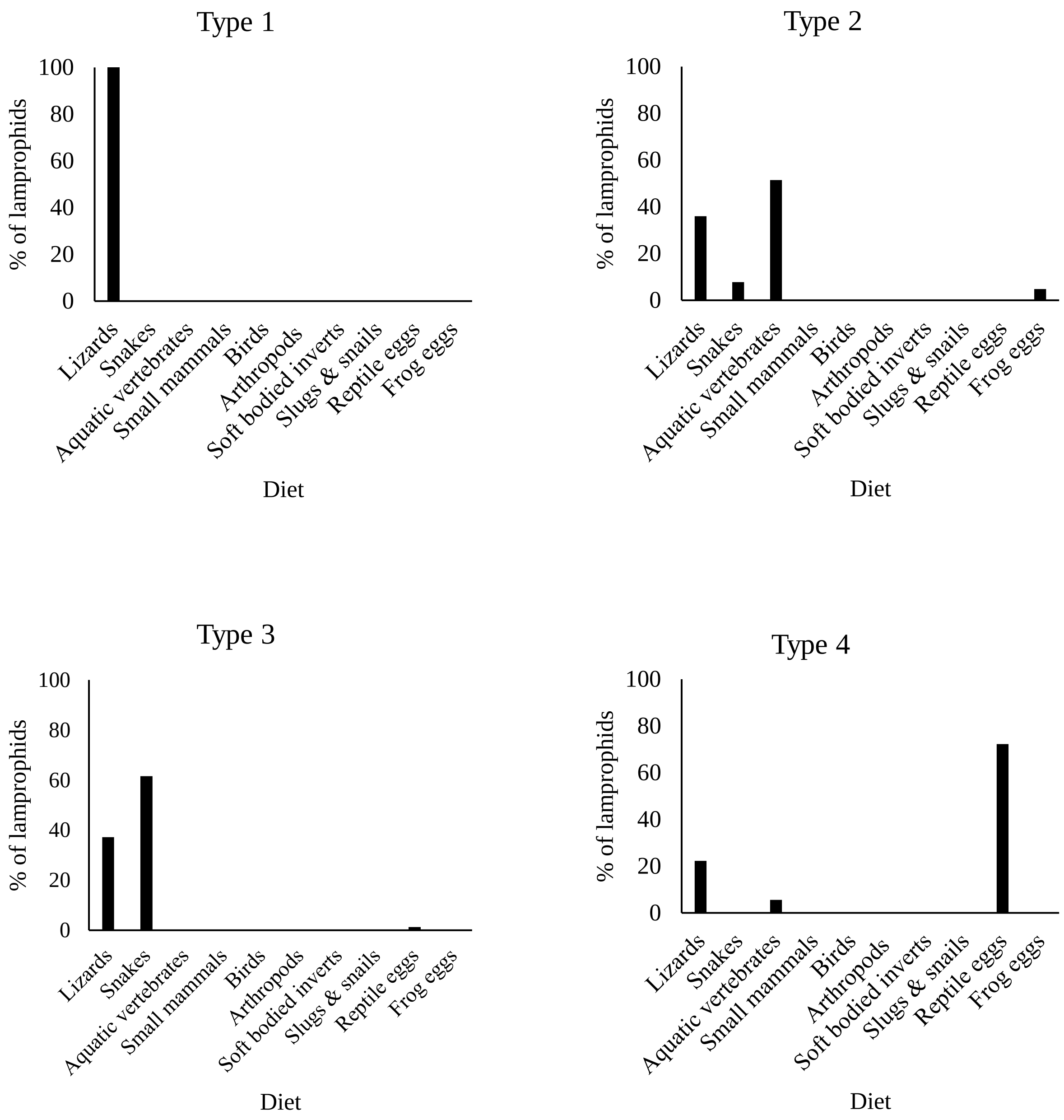

Figure 2. The percentage of all lamprophids consuming specific prey types within the first four of the eight diet clusters. 2a. Type 1-lizard cluster; 2b. Type 2- aquatic vertebrate cluster; 2c. Type 3- Snake and other elongate prey cluster; 2d. Type 4- Reptile egg cluster

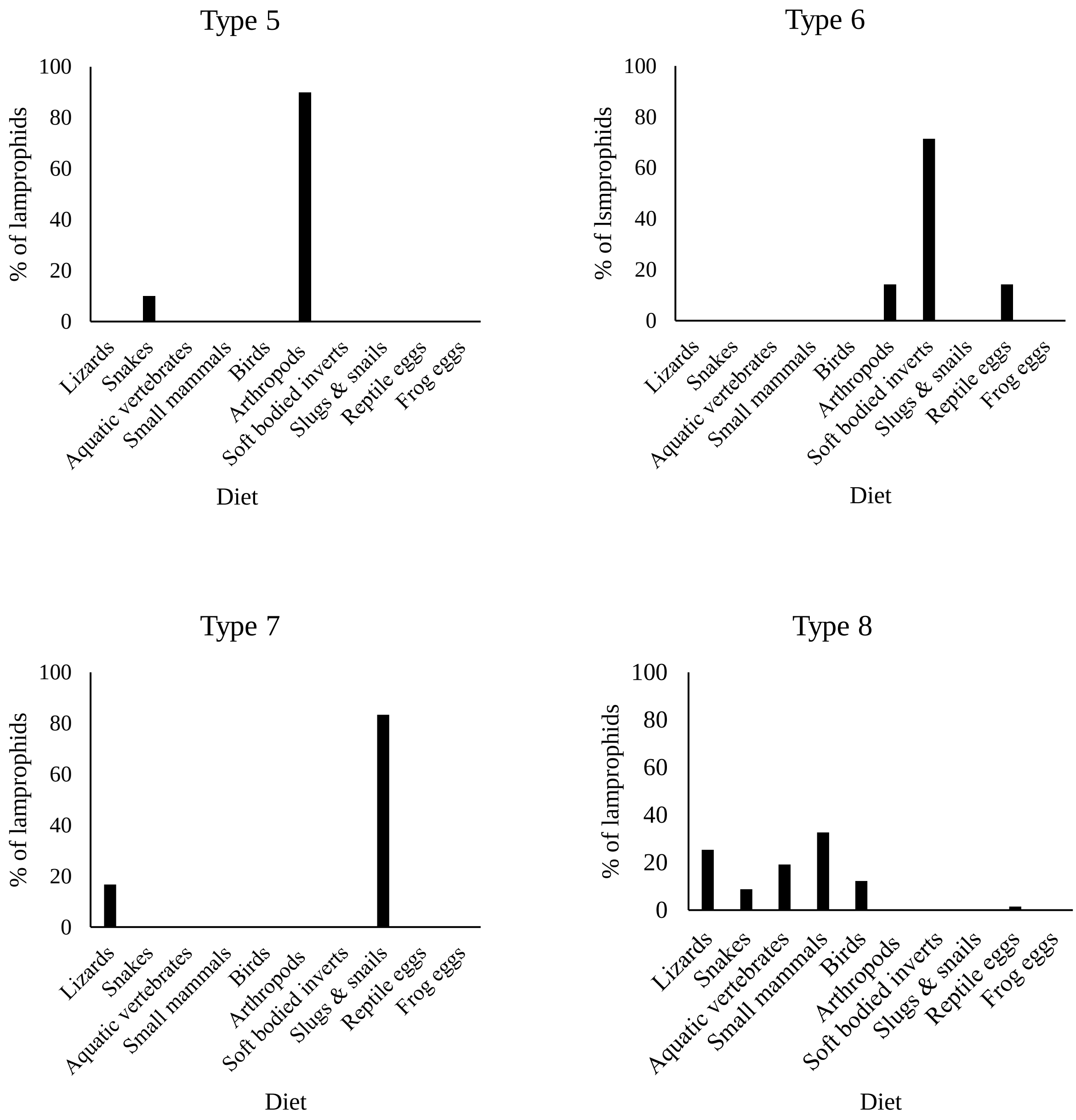

Figure 2. The percentage of all lamprophids consuming specific prey types within the last four of the eight diet clusters. 2e. Type 5- arthropod cluster; 2f. Type 6- soft-bodied invertebrate cluster; 2g. Type 7-Slugs and snails cluster; 2h. Type 8- generalist cluster

Phylogenetic reconstruction

My findings suggested a generalist ancestral feeding condition with a tendency towards subsequent specialisation (Fig. 3). The best model is one with the highest log likelihood (-lnL) and the lowest ΔAIC (Table 1; Paradis 2012). In this case the ER model is the best fit, with the lowest ΔAIC. Among the 50 character histories generated, 43 supported a generalist ancestral feeding pattern with a tendency towards a specialised diet (Fig. 3). The other possible ancestral condition generated by the most accurate depiction of the model (Fig. 3) was either an ophiophagy ancestor (6) or a soft-bodied invertebrate consumer (1).

Of the 136 species, 25 specialised on a Type 1 lizard diet, a trait which evolved relatively recently (Fig. 3). The consumption of Type 2 aquatic vertebrate diet is largely seen within the Pseudoxyrophinae, but also in the Lamprophiinae, Pseudaspidinae and Psammophiinae (Fig. 3). Sixteen species specialised on a Type 3 snake and other elongate prey diet and nine specialised on the Type 4 reptile eggs diet. Fifty-four of the 136 species had a Type 8 generalist diet having retained the ancestral condition. The specialisation in the Type 5 arthropod diet is an autapomorphy and the only autapomorphy in the Lamprophiidae (Fig. 3). Specialisation in Type 6 soft-bodied invertebrate diet and Type 7 slugs and snails diet have appeared independently, each at least twice. There was little evidence of dietary specialisation at a sub-family level as a large variety of prey was consumed within each sub-family.

Lifestyle reconstruction

Reconstruction of lifestyle showed that being terrestrial was the ancestral condition (Fig. 4). The terrestrial lifestyle has been retained across the phylogeny and the specialisations towards different lifestyles tends to be near the terminal branches. Arboreality has arisen within two sub-families and this lifestyle evolved earlier in the Pseudoxyrophiinae sub-family and more recently in the Psammophiinae. Semi-aquatic lamprophids evolved independently at least four times while fossoriality is restricted to the Atractaspidinae and Aparallactinae.

Fang type reconstruction

Reconstruction of fang types show that the ancestor of the lamprophids had back fangs (Fig. 5) The Atractaspidinae is the only sub-family that has front fangs (Deufal and Cundall 2003) and this occurrence is considered an autapomorphy representative of the whole subfamily. Prosymninae and Lamprophiinae have no fanged members. Psammophiinae, Aparallactinae and Pseudaspidinae included species with only back fangs, this is the ancestral condition with the exception of *Pseudaspis cana*, that has no fangs. Pseudoxyrophiinae showed the most variation as species have both back fangs and no fangs with no obvious trend apparent. Within their respective sub-families, species evolved their current fang type early during their evolution.

Table 1. The Maximum Likelihood estimate values for model parameters ER, SYM and ARD for diet in lamprophids.

Model	Parameters (n)	Log likelihood (-lnL)	Δ AIC
ER	1	-218.49	439.01
SYM	28	-187.17	445.37
ARD	56	-181.34	554.49

Body size evolution

Body size varies greatly within the Lamprophiidae ranging from individuals as small as 250 mm to as large as 2500 mm (Appendix 1). Phylogenetic reconstruction showed that the lamprophid ancestor was small, at a size of 400-600 mm (Fig. 6). Fifty-two species are over 1 m long and having a larger body size is a derived trait (Appendix 1). Prosymninae was the only sub-family with the most conserved body sizes amongst all lamprophids.

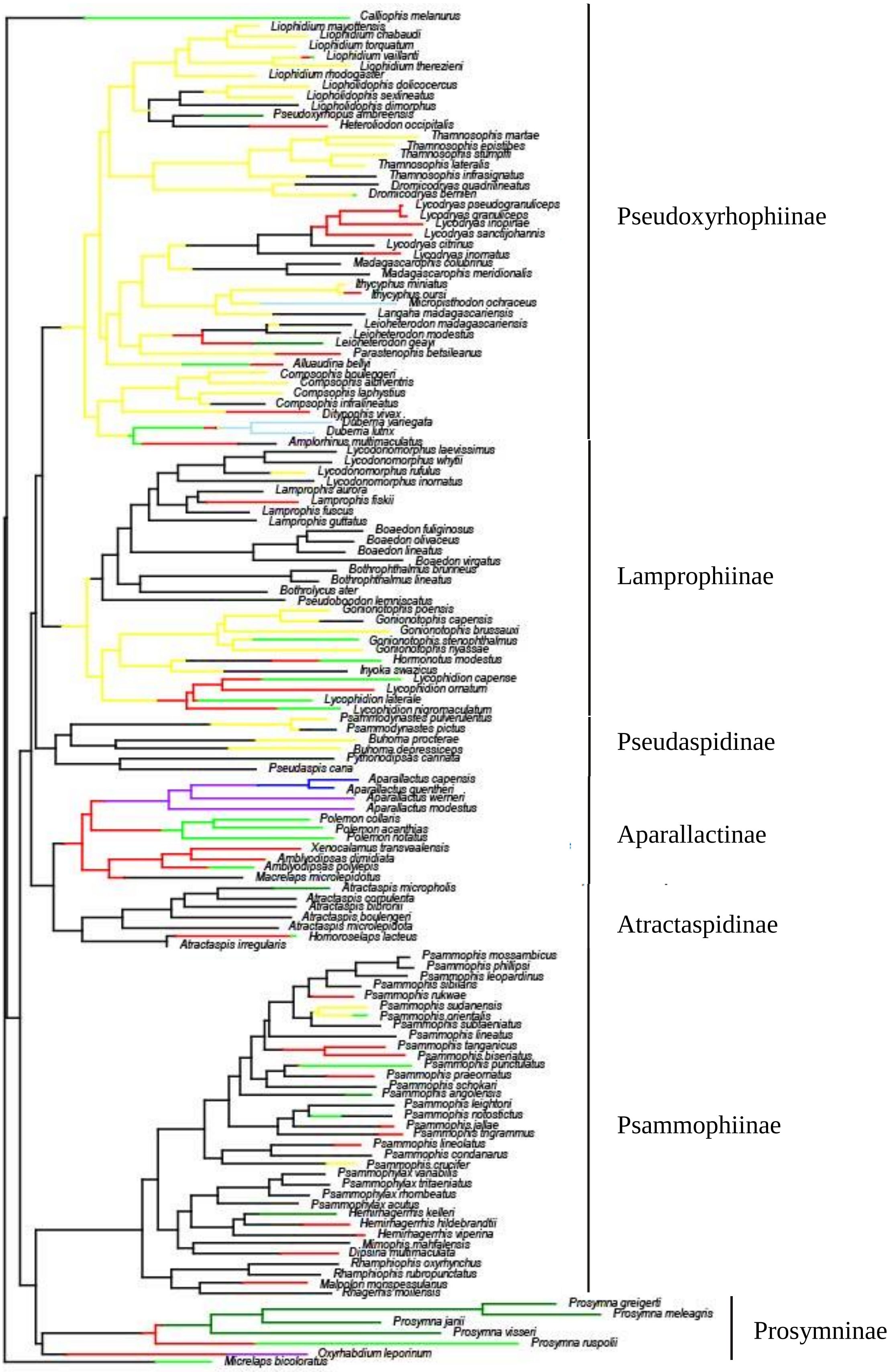

Figure 3. Stochastic character map showing that the ancestor of Lamprophiidae preyed on a generalist diet. Red- lizards (Type 1); yellow- aquatic vertebrates (Type 2); light green-

snakes and other elongate prey (Type 3); dark green- reptile eggs (Type 4); dark blue-arthropods (Type 5); purple- soft bodied invertebrates (Type 6); light blue-slugs and snails (Type 7) and black-generalist (Type 8).

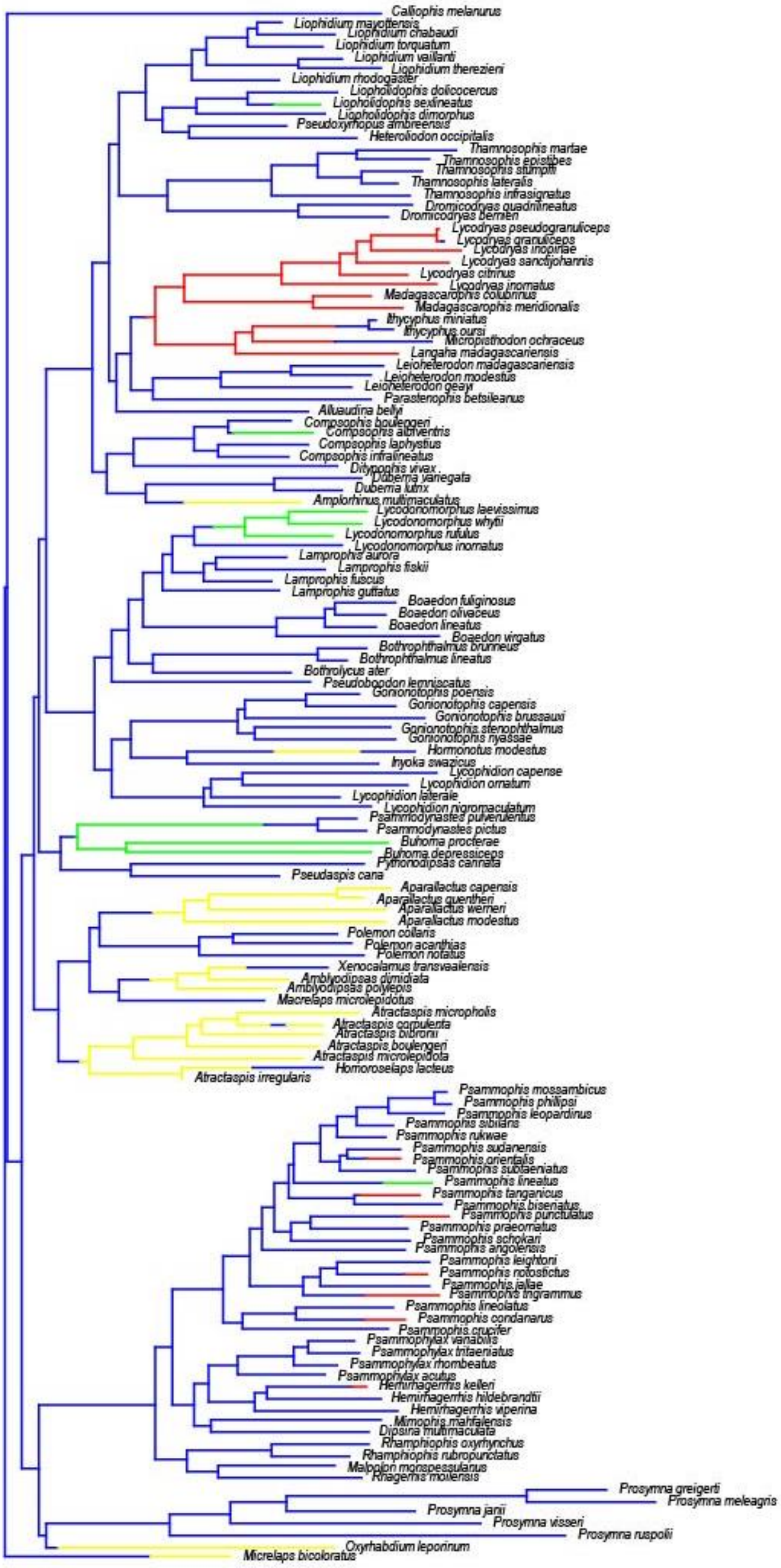

Figure 4. Stochastic character mapping showing terrestrial lifestyle as the ancestral trait. Blue- terrestrial; red- arboreal; green- semi-aquatic and yellow- fossorial.

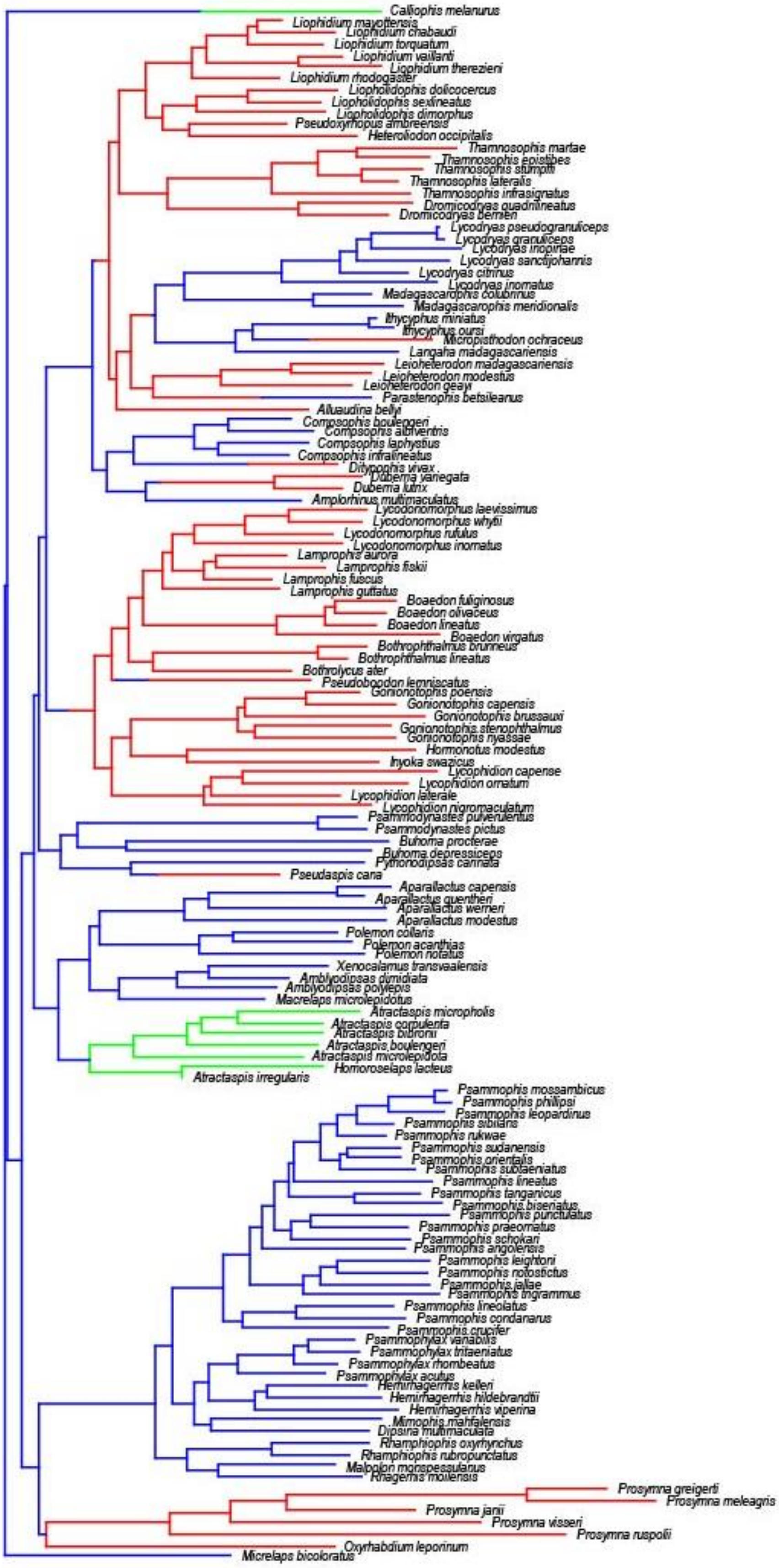

Figure 5. Stochastic character mapping reconstruction of type of fangs showing back fangs as the ancestral trait. Blue- back fangs; green- front fangs and red- no fangs.

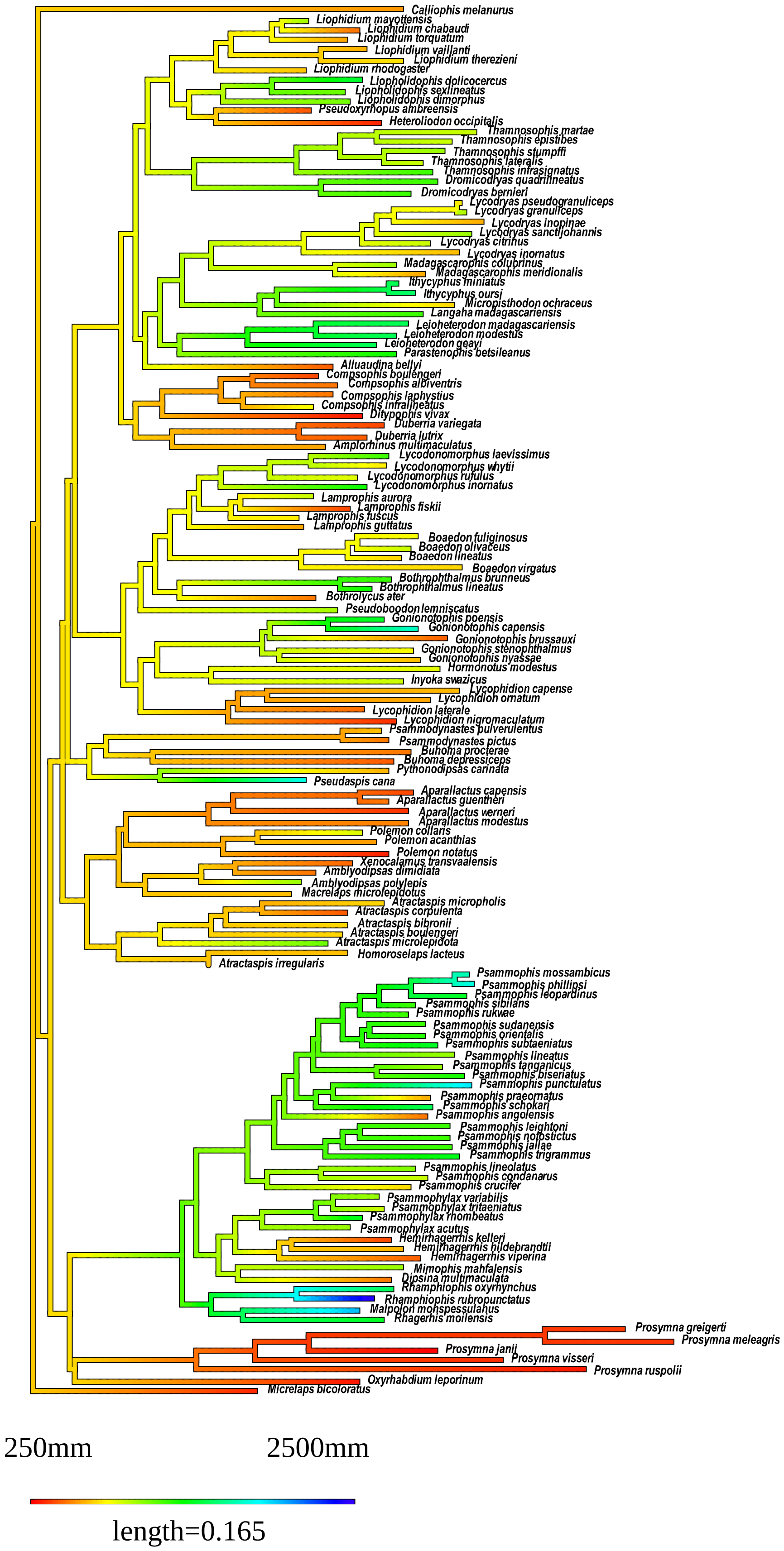

Figure 6. Stochastic mapping of the reconstruction of body size showing the ancestral body size between 400-600 mm.

Pagel’s lambda, which was used to test for a phylogenetic signal, showed strong support for lifestyle ($\lambda = 0.94$), types of fangs ($\lambda = 0.99$) and body size ($\lambda = 0.96$), while current diet patterns in the Lamprophiidae are largely independent of phylogeny ($\lambda = 0.47$).

Correlation analysis

Lifestyle and diet

Terrestrial lamprophids consumed a variety of organisms from a Type 1 lizard diet to Type 4 reptile egg diet, but they did not consume any arthropods nor soft-bodied invertebrates (Fig. 6). Arboreal species consumed a variety of prey comprising lizards (Type 1), snakes and other elongated prey (Type 3) and reptile eggs (Type 4; Fig. 7). Fossorial species were the only ones to consume arthropods (Type 5) and soft-bodied invertebrates (Type 6; Fig. 7). They also had a generalist diet, consuming snakes and other elongated prey (Type 3), with one species eating lizards (Type 1) and one species eating reptile eggs (Type 4). Semi-aquatic species predominantly consumed aquatic vertebrates (Type 2), while other semi-aquatic lamprophids were generalist feeders. Pagel’s correlation method revealed that diet of the lamprophids was not associated with a particular lifestyle with a few exceptions. A diet of arthropods (Type 5) was correlated with a terrestrial lifestyle ($P < 0.05$, $\Delta LnL = 75.85$, d.f = 3) and a soft-bodied invertebrate (Type 6) was correlated with a terrestrial ($P < 0.05$, $\Delta LnL = 79.67$, d.f = 3), arboreal ($P < 0.05$, $\Delta LnL = 52.72$, d.f = 3) and fossorial ($P < 0.01$, $\Delta LnL = 29.56$, d.f = 3) lifestyle.

Fang type and diet

Front-fanged snakes mostly consumed generalist prey (Type 8) but also specialised in snakes and other elongate prey (Type 3) and reptile eggs (Type 4; Fig. 7). Species with no fangs were found to eat all prey types except arthropods (Type 5; Fig. 7). Back-fanged lamprophids had the most varied diet, consuming all types of prey except slugs and snails (Type 7). Pagel’s correlation revealed that the diet of the Lamprophiidae is positively correlated with fang type within the family ($P < 0.05$). Aquatic vertebrate (Type 2) consumption was positively correlated with snakes that have all three fang types and the same correlation was evident for arthropod (Type 5) consumption. Slug and snail (Type 7) prey consumption was positively correlated with back fangs and no fangs. Generalist (Type 8) feeding was positively correlated with snakes that had back and front fangs as well as no fangs.

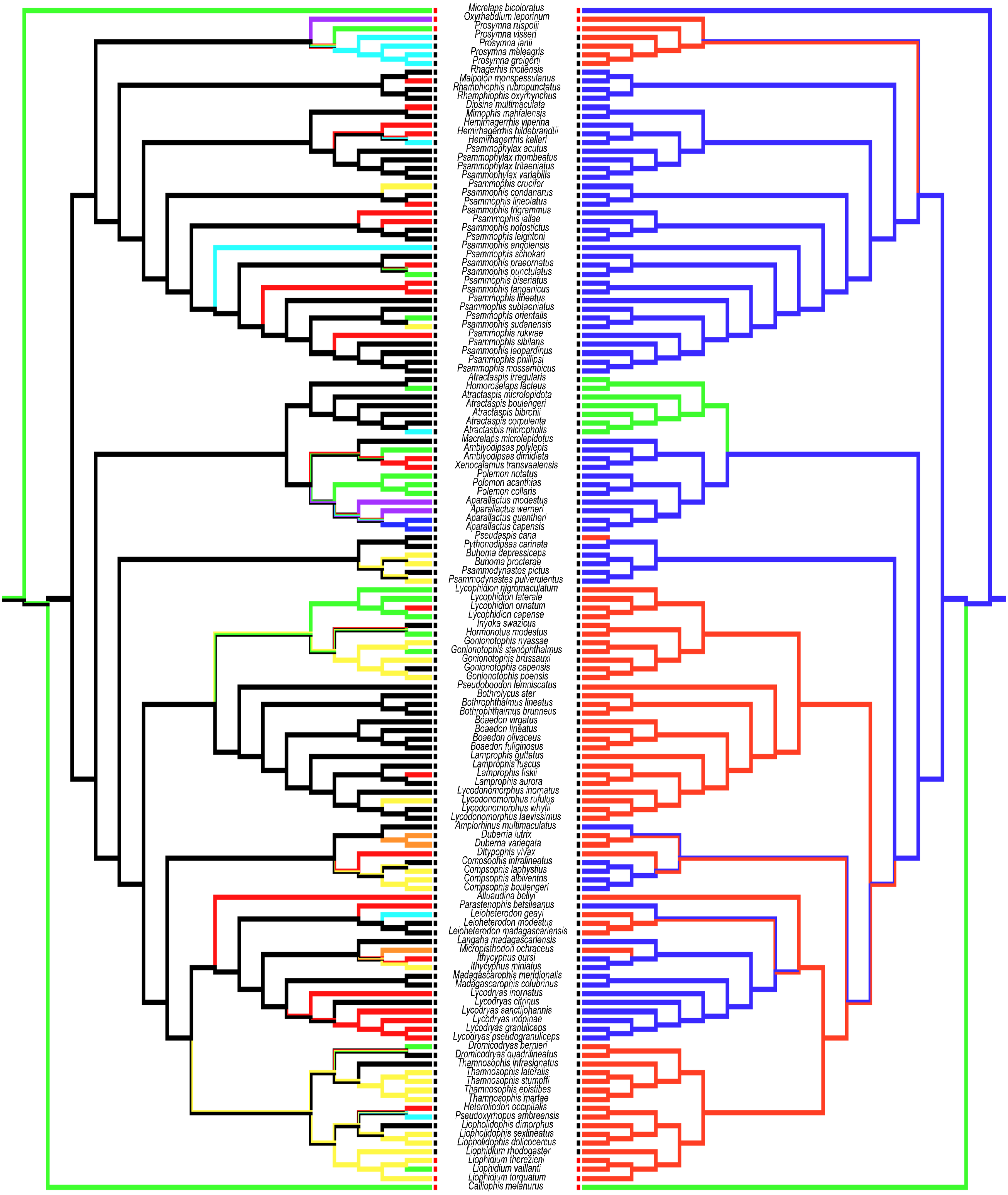

Figure 7. Mirror tree showing the correlation of fang type and diet in the Lamprophiidae. Left: Red- lizards (Type 1); yellow- aquatic vertebrates (Type 2); light green- snakes (Type 3); dark green- reptile eggs (Type 4); dark blue- arthropods (Type 5); purple- soft bodied invertebrates (Type 6); light blue-slugs and snails (Type 7) and black-generalist (Type 8). Right: Red- no fangs; blue- back fangs; green- front fangs.

Body size and diet

The Phylogenetic ANOVA, found that body size was correlated with diet (F = 4.64, P < 0.05, d.f = 1). Snakes consuming generalists, have larger variations in body size. In contrast, snakes consuming smaller prey such as arthropods and soft-bodied invertebrates have small body sizes (Fig. 8).

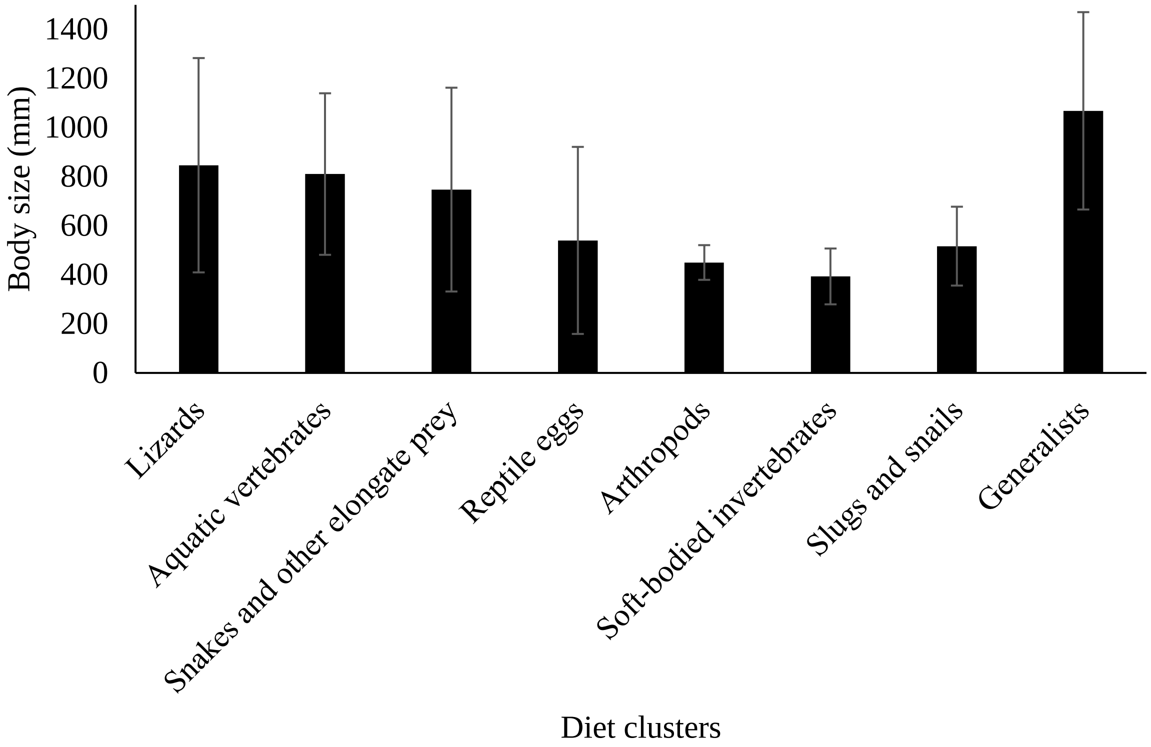

Figure 8. Maximum body size (mm) variation of the lamprophids within each of the eight diet clusters. Standard bars represent standard statistical error.

Discussion

From the stochastic character mapping, it is evident that the ancestral lamprophid consumed a generalist diet in a terrestrial environment, had a relatively small body size and possessed back fangs. Many extant lamprophids remain generalist feeders, but many have specialised on specific prey types such as arthropods or slugs and snails. This has resulted in a divergence in diet as species have experienced independent adaptations to exploit novel prey types. A study by Colston *et al.* (2010) showed that dietary divergence within a clade may be an evolutionary response to morphological adaptations, shown in this study through the correlation of body size and fang type with diet.

Thus, in the Lamprophiidae, the specialisation of diet is a derived trait and is supported by the idea that shifts in diet begin by incorporating a new prey class as a less important component of diet (de Queiroz and Rodriguez-Robles 2006). This idea is supported within the Lamprophiidae as species within different subfamilies specialise on specific prey items, however, at a sub-family level the trend is for a generalist diet. This divergence in diet indicates that species of the same genus (despite similar morphological or other ecological traits) consume different diets and there could be various factors contributing to this diet pattern.

Many diet-specialist snakes tend to extract nutrients from their prey more efficiently than generalists (Britt *et al.* 2006) and the nutritional value of these new prey types may be higher in comparison to the ancestral prey. Two species within the Lamprophiidae, the southern African genus *Duberria* and the Madagascan species *Micropisthodon ochraceus*, efficiently extract nutrients from slugs and snails (Britt and Bennett 2008). This specialisation has occurred independently in these species and is attributed to slugs and snails being a valuable food source in addition to their abundance (Arnold 1993). Arnold (1977) suggested that the propensity to feed on slugs is a heritable trait (Britt *et al.* 2006). Many snakes include gastropods as a dominant prey type in their diet, making them specialists that possess superior energetic efficiencies than generalist snakes (Krieger *et al.* 1971; Pianka 1974).

Ophiophagy is found in lamprophids from several sub-families suggesting that it is not a unique trait and it may in fact be related to body morphology (Kusamba *et al.* 2013). The consumption of elongated prey is probably associated with a low ingestion and high weight ratio (Greene 1983) allowing a wide range of elongate prey to be eaten. Kusamba *et al*. (2013) reported ophiophagy in *Polemon* that were able to consume large typhlopid snakes, similar in length to the *Polemon* predator. This behaviour has also been noted in the Elapidae where ophiophagy is also common (Kgaditse 2016). As lamprophid and elapid snakes are both gape limited, the slender body structure and ability to consume elongate prey has been facilitated by an ophiophagous diet.

In contrast to the body structure of ophiophagus snakes, it has been suggested that some piscivorous snakes possess a narrow elongated head (Marx and Rabb 1972), which is hydro-dynamically advantageous and allows for a faster strike rate under water (Young 1991; Hibbits 2000), increasing the chances of prey capture (Drummond 1983; Alfaro 2002). The narrow elongate head is characteristic in some piscivorous lamprophids such as the

Madagascan snakes *Liopholidophus, Thamnosophis* and *Compsophis,* indicating that an elongate head with a different body structure is an adaptation for consuming aquatic vertebrates. This correlation in body structure and specific prey type may have driven a wide variety of prey to be eaten within the Lamprophiidae.

The results of the phylogenetic signal concurrently with the stochastic character mapping in the Lamprophiidae indicate that whilst lifestyle, fangs and body size have retained their ancestral characteristics, diet has been influenced by recent interactions within the family. This wide variety in lamprophid diet suggests that diet divergence has taken place, in contrast to niche conservatism in the morphological and other ecological traits. This is attributed to inter/intraspecific competition as competitive interactions have led to lamprophids favouring some prey types over others. This then supports the Competition-Predation Hypothesis. Lamprophids within the same sub-family have evolved to have different diets to each other despite similarity in body size, lifestyle and fang types. These results are somewhat surprising as species that have shared ancestry and are morphologically similar, usually have similar adaptive traits (Hibbitts and Fitzgerald 2005).

Every lineage that makes up a community has a set of traits that permits only certain options in terms of resource use and ecological interactions. The present behavioural ecology among lamprophids is only understood in terms of recent effects (Cadle and Greene 1993). Bellini *et al.* (2015) found that the assemblage in the temperate snake community of South America was a result of an admixture of evolutionary independent lineages causing closely related species to share similarities in diet, morphology, ecology, life history and ecological niches. In contrast, my study shows that species have retained ancient diet characteristics in only some sub-families (i.e., Psammophiinae, Atractaspidinae and Lamprophiinae). However, other traits such as lifestyle, types of fangs and body size show strong phylogenetic inertia resulting in phylogenetic niche conservatism. This indicates that on a niche-specific level, there is a lot more going on and the primary drivers of the large variation in diet are competition with other predators and prey abundances within the habitat.

Many of the other studies that found evidence of the Competition-Predation Hypothesis, have been conducted in the Neotropics on fewer species than within the Lamprophiidae and on species from several different snake families (Bellini *et al*. 2015, Vitt and Vangilder 1983, Cadle and Greene 1993, Schoener 1974, Henderson *et al.* 1979). In contrast, my study assesses one large family, indicating that there is large variation in diet among the lamprophids, despite their close taxonomic relations. The lamprophids are morphologically conserved but have diverged with regards to diet. Studies that included several families also included species with different morphological and ecological traits that could be responsible for variation in diet (Vitt and Vangilder 1983). This is further indication that niche conservatism exists in communities of distantly related species and divergent evolution can occur among closely related species.

Geographically, Neotropical studies (e.g., Vitt and Vangilder 1983; Bellini *et al.* 2015) cover a smaller area than my study. The lamprophids occur over the Afrotropics, parts of the Paleoarctic and the Indomalay ecozones, allowing them to fill niches that are unavailable to the Neotropical snakes (Nagy *et al.* 2003). This indicates the higher likelihood of external biotic factors influencing diet consumption in the Lamprophiidae (climate and microhabitat). Despite the occurrence of larger snakes in the Neotropics compared to the smaller lamprophids (Vitt and Vangilder 1983), lamprophids have a wider range of body sizes, enabling them to exploit a wider variety of prey as shown by the higher number of generalist prey consumed. The comparison of the lamprophids with Neotropical snakes serves to reflect on the uniqueness of this snake radiation across the three ecozones.

França *et al.* (2008) showed that both ecology and phylogeny are significant determinants of snake assemblages and morphological divergence can occur in response to ecological factors such as habitat use and diet. This shows that ecologically, traits are influenced by multiple selective forces, despite the fact that one trait may be conserved while the other has diverged (Vitt and Vangilder 1983). The relative importance of the Deep History Hypothesis and Competition-Predation Hypothesis depends on the characters assessed and these hypotheses are not necessarily mutually exclusive but rather they can act together to influence a community (Colston *et al.* 2010). In this case, a combination of historical and contemporary influences is at play but the divergence in diet on a large scale is predominantly caused by resource availability or competition with other snakes.

On a smaller scale, Pagel's correlation analysis indicated that body size and fang type are influential on prey type but the wide variety in diet consumption is not driven by their lifestyle. Despite no correlation between lifestyle and diet, the change from a terrestrial lifestyle to a fossorial one is likely to have facilitated the invertebrate prey consumption. Within the Aparallactinae, an interesting specialisation occurs with the *Aparallactus* spp. which are found to consume arthropods and soft-bodied invertebrates. Most species within this genus almost exclusively specialise on centipedes, but some species also eat earthworms (Gower and Rasmussen 2004). This suggests that the specialisation has occurred due to a change in lifestyle, as the dietary preference of Aparallactinae is not strongly associated with a particular group of prey (Colston *et al.* 2010). This idea is supported by the consumption of soft-bodied invertebrates by *Oxyrhabdium* as an adaption to a fossorial lifestyle.

Dietary divergence is often correlated with shifts in morphology (Schluter and Grant 1984), behaviour (Fryer and Iles 1972), and ecology (Smith *et al*. 1978), and is evident in this study with the positive correlation of fang types with diet. This indicates that the type of fang possessed by a lamprophid has enabled them to exploit certain types of prey. The dental morphology of snakes is traditionally focused on the venom-delivery system. Therefore, the ancestral trait of having back fangs, suggests that lamprophids have evolved from a venomous ancestor. Therefore, these findings support the idea that a venom system is ancestral in snakes, as proposed by Fry *et al.* (2012) and is further supported by the diversity of maxillary dentition and venom glands.

The idea of an ancestral venom system has been debated over the years as the presence of fangs and venom was originally seen as an apomorphic trait. Fry *et al.* (2012) hypothesised that the presence of venom is a plesiomorphic condition in snakes and is indirectly supported by my study as the loss of fangs in some lamprophids and changes in dental morphology have most likely occurred as a shift to a new prey type or prey capture technique (Fry *et al.* 2008). The front-fang condition of the *Atractaspis* is most likely an adaptation to a fossorial lifestyle, while the loss of the venom system in snakes is attributed to the evolution of a constriction method of prey capture (Fry *et al.* 2012). These results clearly indicate that these adaptations to alternate fang types are apomorphic and have evolved from a single back-fanged ancestor.

Within the Lamprophiidae, the mole snakes (*Psaudaspis cana*), with no fangs, secondarily lost their venom (Alexander and Marais 2007; Fry *et al.* 2003). Evans (2016) also showed that mole snakes possess specialised posterior maxilla with enlarged, specialised teeth that are unusual in shape and position in comparison to other species. This is further indication that lamprophids with no fangs show variation in their dental morphology and diet in addition to an external selective pressure has caused the loss of fangs. Mole snakes possess different dentition to other species in addition to a strophied mucoid gland (Taub 1967). They use their maxillary teeth and a slicing motion to hunt fossorial rodents and moles with the possibility of dispatching their prey underground, rather than pulling it to the surface (Evans 2016).

Having fangs is costly and species that have lost this trait most likely did so to feed on prey such as aquatic vertebrates, which can be consumed without the requirement of fangs but rather through constriction. Slugs and snails can also be consumed without fangs as they swallowed whole (Barlow *et al.* 2009; Fry *et al.* 2012). However, lamprophids that prey on aquatic vertebrates have different dental morphology to each other as some snakes have fangs while others do not. This was also noted in lamprophids that fed on slugs and snails. Barlow *et al.* (2009) showed strong evidence that variation in snake venom composition results from adaptive evolution driven by natural selection for different diets. My study indirectly supports this theory as changes in fang type also appear to be due to an adaptation to different prey types, and the back-fanged lamprophids, with variation in dental morphology, consumed a larger range of prey types, particularly lizards. Jackson and Fritts (2004) describe the presence of moderately sharp posterior dental edges in the Common Wolf snake, *Lycodon aulicus capucinus,* and propose that this is to facilitate cutting through the hard scales of their lizard prey. Lamprophids that prey on lizards most likely have the same dental morphology allowing them to exploit more prey types but this has not yet been researched comprehensively.

The incredible use of dental morphology has also been proposed by Branch *et al.* (1997). They indicated that the enlarged palatine fangs of *Pythonodipsas* may aid it in extracting prey from burrows. The Cape wolf snake *Lycophidion capense* also has conspicuously large maxillary teeth to extract lizards from their refuges (Alexander and Marais 2007). Mole snakes use their teeth in a slicing motion for hunting fossorial prey and dispatching it underground (Evans 2016). Lamprophids with back fangs that prey on aquatic vertebrates are distinguished by the possession of a single, enlarged posterior fang and highly acuminate, posteriorly angled teeth in many (Knox and Jackson 2010). It is thought that the function of the large fang is to puncture the skin of the slippery fish that are difficult to hold onto and release venom (Knox and Jackson 2010). Thus, the difference in dental morphology within the lamprophids may be a result of hunting habitat rather than prey morphology (Evans 2016).

Knox and Jackson (2010) conclude that selective pressures play a greater role in determining maxillary dentition than phylogenetic constraints, because colubrids were shown to have similar dental morphology to each other based on the prey they consumed. This idea may be applied to the front-fanged Atractaspidinae snakes (Tilbury and Verster 2016). Their dental morphology is similar to those of the vipers and elapids as they have relatively long fangs on short maxillae, a gap separating the pterygoid and palatine bones, a toothless pterygoid, and a snout tightly attached to the rest of the skull (Deufel and Cundall 2003). This also makes them different to rear-fanged lamprophids. Atractaspidinae species are fossorial and consume a wide variety of prey including mammals and reptiles. It is likely that their unique dental morphology is an adaptation to exploit a wider variety of prey compared to other fossorial lamprophids such as snakes of the Aparallactinae sub-family. This is further indication that selective pressures play an important role in the diet of snakes.

The correlation of body size and diet in the lamprophids shows that species within this family in general, do conform to the pattern of body size-prey relationship seen in many other snakes (Pough and Groves 1983; Shine *et al.* 1998; Boback and Guyer 2003). The generalist diet of early lamprophids may have facilitated some of the ecological shifts described here and the great diversification that occurred in their diet (Martins *et al*. 2002). My study supports the idea that prey selection is often influenced by the size of the predator as larger individuals in a species will eat larger prey compared to smaller individuals (Pough and Groves 1983; Greene 1997).

Differing prey size with snake body size is seen when there is a shift in prey consumption, as mammals and birds are larger than most reptiles and invertebrates (Shine 1994). The lamprophids show that maximum adult body size is accompanied by concurrent increases in the proportion of the diet types. This was largely composed of mammalian prey with a corresponding decrease in the importance of invertebrate prey. Many smaller bodied lamprophids have specialised on diets such as arthropods or soft-bodied invertebrates, while larger-bodied species feed on a wider range of prey. Larger bodied snakes that have a generalist diet, also include smaller bodied prey. Smaller prey items may not always be nutritious enough, so lamprophids are likely to incorporate larger prey into their diet (Greene 1997).

It is likely that larger-bodied snakes also encounter a larger variety of prey by traveling greater distances than do smaller-bodied snakes as they need to keep up with the energetic demands of their body (Greene 1997). The probability of finding prey increases but the cost of locomotion, predation and competition also increases. This may be the reason why the diet of the lamprophids has diverged and many large snakes specialise on specific diets such as lizards or aquatic vertebrates. However, due to the phylogenetic convergence of body size, there is no clear evidence that the divergence in diet is influenced by body size. It is possible that ontogenetic differences may play a role in prey selection and this was not considered in the present study.

Recommendations

Future studies should seek to investigate resource partitioning as a means of determining diet in local communities of lamprophids as many of these species occupy similar habitats. Rahman *et al.* (2014) showed that niche partitioning in sympatric species of the sister family Homalopsidae is not related to interspecific competition, but it is rather influenced by independent evolutionary history. This idea can also be tested in the Lamprophiidae since the divergence in diet is so apparent and varied. It is important to look at the local community structure in Africa and other regions where the lamprophids exist. Webb *et al.* (2002) suggested that in communities with closely related species, habitat filtering would play a role in the structure of local assemblages as niche conservatism would be evident. However, if the local community is a subset of distantly related species, competition is likely to play a bigger role in local community assemblage.

A closer look at the other morphological traits on diet patterns will most likely reveal interesting patterns. The individual evolutionary history of each subfamily within the Lamprophiidae could be used to specifically identify the impacts on current feeding behaviour. The Atractaspidinae is unique in comparison to other lamprophids in terms of fangs and diet and this has significant impact on measures of divergence in diet for the clade. It is evident that multiple factors are influencing the behavioural ecology of extant lamprophids.

Conclusion

This study outlines the evolution of ecological and morphological traits of the Lamprophiidae for the first time. This was also the first large scale study that assesses multiple factors and their impact on the diet within this family. The remarkable dietary divergence indicates that there are multiple factors at play. Possibly the most surprising finding is the ancestral condition for the family was back-fanged, which suggests that the ancestor was also venomous. It appears that the evolution of the fang condition has played a significant role in the dental morphology of extant lamprophids and the divergence in their diet.

Various lamprophids have relatively restricted distributions in various parts of Africa and many of them are highly cryptic. Exploring the diversity of ecological traits such as microhabitats and their evolution in snakes results in significant insights into the general patterns found in specific snake families. This allows for the application of modern comparative methodology to clarify plausible courses of evolution (Alencar *et al.* 2013). The Lamprophiidae have only recently been defined and an insight into their diet provides perspective on the ecology of the family.

Diet is an important determinant of snake ecology and phylogenetic comparative studies serve as a tool to investigate factors that significantly influence feeding behaviour. This is a good base study for further investigations into the feeding behaviour in the Lamprophiidae as significant insights can help in understanding the ecology of these species. Phylogenetic studies such as this look at past and recent effects of different environmental factors, thus providing useful tools to understand community ecology, behaviour and species assemblage. Although these patterns are seen in other snakes, the combination of unique traits on the lamprophid diet is indicative that this family of snakes needs to be studied further.

The Competition-Predation Hypothesis further indicates that recent factors are influencing the diet in the Lamprophiidae, but many recent studies on other groups of snakes have found that phylogeny is more influential on diet patterns in snakes (Colston *et al.* 2010, Bellini *et al.* 2015). The reality may therefore be more complicated than some analyses suggest because different snake communities are impacted differently by different ecological, geographical and morphological factors. In order to conclusively understand the current ecology of the lamprophids, further studies should look at incorporating information on sympatric snakes from other families. This will provide a better comparative study to the ecology of the Neotropics to the Afrotropics. There are limited studies on large scale diet patterns in snakes and since diet is such an important factor in determining snake ecology, more phylogenetic studies need to be conducted on the influence of past and recent effects on extant snake species.

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Appendix

Appendix 1. Diet, lifestyle, fang type, body size (mm) and geographic location data for all lamprophid snakes and the outgroup species. The sub-family for each species is also provided.

Subfamily	Species	Diet	Lifestyle	Fang type	Body Size (mm)	Geographic location
	Micrelaps bicoloratus	Snakes and other elongate prey	Fossorial	Back	330	East Africa
Prosymninane	*Oxyrhabdium leporinum*	Soft-bodied invertebrates	Fossorial	None	300	Philippine
Prosymninane	*Prosymna ruspolii*	Snakes and other elongate prey	Terrestrial	None	300	East Africa
Prosymninane	*Prosymna visseri*	Reptile eggs	Terrestrial	None	350	Southern Africa
Prosymninane	*Prosymna janii*	Reptile eggs	Terrestrial	None	250	Southern Africa
Prosymninane	*Prosymna greigerti*	Reptile eggs	Terrestrial	None	370	Central, West and East Africa
Prosymninane	*Prosymna meleagris*	Reptile eggs	Terrestrial	None	360	Central + West Africa
Psamophiinae	*Rhamphiophis oxyrhynchus*	Generalists	Terrestrial	Back	1500	East Africa
Psamophiinae	*Rhamphiophis rubropunctatus*	Generalists	Terrestrial	Back	2500	East Africa
Psamophiinae	*Malpolon monspessulanus*	Lizards	Terrestrial	Back	2000	Europe

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Subfamily	Species	Diet	Lifestyle	Fang type	Body Size (mm)	Geographic location
Psamophiinae	*Rhagerhis moilensis*	Generalists	Terrestrial	Back	1400	West Africa + Middle east
Psamophiinae	*Mimophis mahfalensis*	Generalists	Terrestrial	Back	1000	Madagascar
Psamophiinae	*Dipsina multimaculata*	Lizards	Terrestrial	Back	500	Southern Africa
Psamophiinae	*Hemirhagerrhis viperina*	Lizards	Terrestrial	Back	450	Southern Africa
Psamophiinae	*Hemirhagerrhis kelleri*	Reptile eggs	Arboreal	Back	400	East Africa
Psamophiinae	*Hemirhagerrhis hildebrandtii*	Lizards	Terrestrial	Back	640	East Africa
Psamophiinae	*Psammophylax acutus*	Generalists	Terrestrial	Back	1000	Central Africa + West
Psamophiinae	*Psammophylax rhombeatus*	Generalists	Terrestrial	Back	1400	Southern Africa
Psamophiinae	*Psammophylax variabilis*	Generalists	Terrestrial	Back	1000	Southern Africa + Central
Psamophiinae	*Psammophylax tritaeniatus*	Generalists	Terrestrial	Back	900	Southern Africa + Central
Psamophiinae	*Psammophis crucifer*	Aquatic vertebrates	Terrestrial	Back	710	Southern Africa
Psamophiinae	*Psammophis lineolatus*	Lizards	Terrestrial	Back	1050	Asia + Middle East
Psamophiinae	*Psammophis condanarus*	Generalists	Arboreal	Back	900	Asia

Appendix 1. Diet, lifestyle, fang type, body size (mm) and geographic location data for all lamprophid snakes and the outgroup species. The sub-family for each species is also provided.

Subfamily	Species	Diet	Lifestyle	Fang type	Body Size (mm)	Geographic location
Psamophiinae	*Psammophis trigrammus*	Lizards	Arboreal	Back	1380	Southern Africa
Psamophiinae	*Psammophis jallae*	Lizards	Terrestrial	Back	1200	Southern Africa + Central
Psamophiinae	*Psammophis leightoni*	Generalists	Terrestrial	Back	1200	Southern Africa
Psamophiinae	*Psammophis notostictus*	Generalists	Arboreal	Back	1200	Southern Africa
Psamophiinae	*Psammophis angolensis*	Reptile eggs	Terrestrial	Back	500	Central, South and East Africa
Psamophiinae	*Psammophis schokari*	Generalists	Terrestrial	Back	1500	Asia
Psamophiinae	*Psammophis punctulatus*	Snakes and other elongate prey	Arboreal	Back	1900	East Africa
Psamophiinae	*Psammophis praeornatus*	Lizards	Terrestrial	Back	600	Central + West Africa
Psamophiinae	*Psammophis tanganicus*	Lizards	Arboreal	Back	1000	East Africa
Psamophiinae	*Psammophis biseriatus*	Lizards	Terrestrial	Back	1280	East Africa
Psamophiinae	*Psammophis lineatus*	Generalists	Semi-aquatic	Back	1000	All Africa
Psamophiinae	*Psammophis subtaeniatus*	Generalists	Terrestrial	Back	1400	Central, South and East Africa

Appendix 1. Diet, lifestyle, fang type, body size (mm) and geographic location data for all lamprophid snakes and the outgroup species. The sub-family for each species is also provided.

Subfamily	Species	Diet	Lifestyle	Fang type	Body Size (mm)	Geographic location
Psamophiinae	*Psammophis sudanensis*	Aquatic vertebrates	Terrestrial	Back	1200	Central Africa
Psamophiinae	*Psammophis orientalis*	Snakes and other elongate prey	Arboreal	Back	1250	East Africa
Psamophiinae	*Psammophis rukwae*	Lizards	Terrestrial	Back	1200	West Africa
Psamophiinae	*Psammophis sibilans*	Generalists	Terrestrial	Back	1200	West + East Africa
Psamophiinae	*Psammophis leopardinus*	Generalists	Terrestrial	Back	1400	Southern Africa
Psamophiinae	*Psammophis mossambicus*	Generalists	Terrestrial	Back	1700	Central, South and East Africa
Psamophiinae	*Psammophis phillipsi*	Generalists	Terrestrial	Back	1800	Central Africa + West
Atractaspidinae	*Homoroselaps lacteus*	Snakes and other elongate prey	Terrestrial	Front	650	Southern Africa
Atractaspidinae	*Atractaspis irregularis*	Generalists	Fossorial	Front	660	Central Africa + East
Atractaspidinae	*Atractaspis microlepidota*	Generalists	Fossorial	Front	1100	West Africa
Atractaspidinae	*Atractaspis boulengeri*	Generalists	Fossorial	Front	700	Central Africa

Appendix 1. Diet, lifestyle, fang type, body size (mm) and geographic location data for all lamprophid snakes and the outgroup species. The sub-family for each species is also provided.

Subfamily	Species	Diet	Lifestyle	Fang type	Body Size (mm)	Geographic location
Atractaspidinae	*Atractaspis bibronii*	Generalists	Fossorial	Front	700	Southern Africa + east
Atractaspidinae	*Atractaspis micropholis*	Reptile eggs	Fossorial	Front	700	West Africa
Atractaspidinae	*Atractaspis corpulenta*	Generalists	Fossorial	Front	440	Central Africa
Aparallactinae	*Macrelaps microlepidotus*	Generalists	Terrestrial	Back	650	Southern Africa
Aparallactinae	*Amblyodipsas polylepis*	Snakes and other elongate prey	Fossorial	Back	1000	Southern Africa + east
Aparallactinae	*Xenocalamus transvaalensis*	Lizards	Terrestrial	Back	470	Southern Africa
Aparallactinae	*Amblyodipsas dimidiata*	Lizards	Fossorial	Back	500	Tanzania
Aparallactinae	*Polemon notatus*	Snakes and other elongate prey	Terrestrial	Back	320	Central Africa
Aparallactinae	*Polemon collaris*	Snakes and other elongate prey	Terrestrial	Back	860	Central Africa + West
Aparallactinae	*Polemon acanthias*	Snakes and other elongate prey	Terrestrial	Back	580	West Africa

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Subfamily	Species	Diet	Lifestyle	Fang type	Body Size (mm)	Geographic location
Aparallactinae	*Aparallactus modestus*	Soft-bodied invertebrates	Fossorial	Back	520	All Africa
Aparallactinae	*Aparallactus werneri*	Soft-bodied invertebrates	Fossorial	Back	360	Tanzania
Aparallactinae	*Aparallactus capensis*	Arthropods	Fossorial	Back	400	Southern Africa + east Africa
Aparallactinae	*Aparallactus guentheri*	Arthropods	Fossorial	Back	500	Southern Africa + east Africa
Pseudaspidinae	*Pythonodipsas carinata*	Generalists	Terrestrial	Back	630	Southern Africa
Pseudaspidinae	*Pseudaspis cana*	Generalists	Terrestrial	None	1800	Southern Africa + Central
Pseudaspidinae	*Psammodynastes pulverulentus*	Aquatic vertebrates	Terrestrial	Back	650	Asia
Pseudaspidinae	*Psammodynastes pictus*	Generalists	Terrestrial	Back	500	Asia
Pseudaspidinae	*Buhoma procterae*	Aquatic vertebrates	Semi-aquatic	Back	500	Tanzania
Pseudaspidinae	*Buhoma depressiceps*	Aquatic vertebrates	Semi-aquatic	Back	440	Central Africa + West
Lamprophiinae	*Lycophidion nigromaculatum*	Snakes and other	Terrestrial	None	350	West Africa

Appendix 1. Diet, lifestyle, fang type, body size (mm) and geographic location data for all lamprophid snakes and the outgroup species. The sub-family for each species is also provided.

Subfamily	Species	Diet	Lifestyle	Fang type	Body Size (mm)	Geographic location
		elongate prey				
Lamprophiinae	*Lycophidion laterale*	Snakes and other elongate prey	Terrestrial	None	480	Central Africa + West
Lamprophiinae	*Lycophidion capense*	Snakes and other elongate prey	Terrestrial	None	640	All Africa
Lamprophiinae	*Lycophidion ornatum*	Lizards	Terrestrial	None	600	Central Africa
Lamprophiinae	*Hormonotus modestus*	Snakes and other elongate prey	Terrestrial	None	850	Central Africa + West
Lamprophiinae	*Inyoka swazicus*	Generalists	Terrestrial	None	900	Southern Africa
Lamprophiinae	*Gonionotophis stenophthalmus*	Snakes and other elongate prey	Terrestrial	None	800	Central Africa + West
Lamprophiinae	*Gonionotophis nyassae*	Aquatic vertebrates	Terrestrial	None	650	All Africa
Lamprophiinae	*Gonionotophis brussauxi*	Aquatic vertebrates	Terrestrial	None	450	Central Africa

Appendix 1. Diet, lifestyle, fang type, body size (mm) and geographic location data for all lamprophid snakes and the outgroup species. The sub-family for each species is also provided.

Subfamily	Species	Diet	Lifestyle	Fang type	Body Size (mm)	Geographic location
Lamprophiinae	*Gonionotophis poensis*	Aquatic vertebrates	Terrestrial	None	1400	Central Africa + West
Lamprophiinae	*Gonionotophis capensis*	Generalists	Terrestrial	None	1750	All Africa
Lamprophiinae	*Pseudoboodon lemniscatus*	Generalists	Terrestrial	None	970	East Africa
Lamprophiinae	*Bothrolycus ater*	Generalists	Terrestrial	None	500	Central Africa
Lamprophiinae	*Bothrophthalmus brunneus*	Generalists	Terrestrial	None	1200	Central Africa
Lamprophiinae	*Bothrophthalmus lineatus*	Generalists	Terrestrial	None	1300	Central Africa + West
Lamprophiinae	*Boaedon virgatus*	Generalists	Terrestrial	None	700	Central Africa + West
Lamprophiinae	*Boaedon lineatus*	Generalists	Terrestrial	None	700	All Africa
Lamprophiinae	*Boaedon fuliginosus*	Generalists	Terrestrial	None	800	All Africa
Lamprophiinae	*Lamprophis guttatus*	Generalists	Terrestrial	None	600	Southern Africa
Lamprophiinae	*Lamprophis fuscus*	Generalists	Terrestrial	None	750	Southern Africa
Lamprophiinae	*Lamprophis aurora*	Generalists	Terrestrial	None	900	Southern Africa
Lamprophiinae	*Lamprophis fiskii*	Lizards	Terrestrial	None	400	Southern Africa
Lamprophiinae	*Lycodonomorphus inornatus*	Generalists	Terrestrial	None	1300	Southern Africa

Appendix 1. Diet, lifestyle, fang type, body size (mm) and geographic location data for all lamprophid snakes and the outgroup species. The sub-family for each species is also provided.

Subfamily	Species	Diet	Lifestyle	Fang type	Body Size (mm)	Geographic location
Lamprophiinae	*Lycodonomorphus rufulus*	Aquatic vertebrates	Semi-aquatic	None	850	Southern Africa
Lamprophiinae	*Lycodonomorphus laevissimus*	Generalists	Semi-aquatic	None	1200	Southern Africa
Lamprophiinae	*Lycodonomorphus whytii*	Generalists	Semi-aquatic	None	750	Southern Africa
Pseudoxyrophiinae	*Amplorhinus multimaculatus*	Generalists	Fossorial	Back	600	Southern Africa
Pseudoxyrophiinae	*Duberria variegata*	Slugs and snails	Terrestrial	None	400	Southern Africa
Pseudoxyrophiinae	*Duberria lutrix*	Slugs and snails	Terrestrial	None	450	Southern Africa
Pseudoxyrophiinae	*Ditypophis vivax*	Lizards	Terrestrial	None	300	Socotra
Pseudoxyrophiinae	*Compsophis boulengeri*	Aquatic vertebrates	Terrestrial	Back	400	Madagascar
Pseudoxyrophiinae	*Compsophis albiventris*	Aquatic vertebrates	Semi-aquatic	Back	500	Madagascar
Pseudoxyrophiinae	*Compsophis laphystius*	Aquatic vertebrates	Terrestrial	Back	500	Madagascar
Pseudoxyrophiinae	*Compsophis infralineatus*	Generalists	Terrestrial	Back	800	Madagascar
Pseudoxyrophiinae	*Alluaudina bellyi*	Lizards	Terrestrial	None	450	Madagascar
Pseudoxyrophiinae	*Parastenophis betsileanus*	Lizards	Terrestrial	Back	1290	Madagascar
Pseudoxyrophiinae	*Leioheterodon geayi*	Reptile eggs	Terrestrial	None	1500	Madagascar

Appendix 1. Diet, lifestyle, fang type, body size (mm) and geographic location data for all lamprophid snakes and the outgroup species. The sub-family for each species is also provided.

Subfamily	Species	Diet	Lifestyle	Fang type	Body Size (mm)	Geographic location
Pseudoxyrophiinae	*Leioheterodon Madagascargascariensis*	Generalists	Terrestrial	None	1500	Madagascar + Comoro
Pseudoxyrophiinae	*Leioheterodon modestus*	Generalists	Terrestrial	None	1200	Madagascar
Pseudoxyrophiinae	*Langaha Madagascargascariensis*	Generalists	Arboreal	Back	1200	Madagascar
Pseudoxyrophiinae	*Micropisthodon ochraceus*	Slugs and snails	Terrestrial	None	700	Madagascar
Pseudoxyrophiinae	*Ithycyphus miniatus*	Aquatic vertebrates	Terrestrial	Back	1500	Madagascar + Comoro
Pseudoxyrophiinae	*Ithycyphus oursi*	Lizards	Terrestrial	Back	1540	Madagascar
Pseudoxyrophiinae	*Madagascarophis colubrinus*	Generalists	Arboreal	Back	1000	Madagascar
Pseudoxyrophiinae	*Madagascarophis meridionalis*	Generalists	Arboreal	Back	600	Madagascar
Pseudoxyrophiinae	*Lycodryas inornatus*	Lizards	Arboreal	Back	650	Madagascar
Pseudoxyrophiinae	*Lycodryas citrinus*	Generalists	Arboreal	Back	900	Madagascar
Pseudoxyrophiinae	*Lycodryas sanctijohannis*	Lizards	Arboreal	Back	1000	Comoro
Pseudoxyrophiinae	*Lycodryas inopinae*	Lizards	Arboreal	Back	620	Madagascar
Pseudoxyrophiinae	*Lycodryas pseudogranuliceps*	Lizards	Arboreal	Back	710	Madagascar
Pseudoxyrophiinae	*Lycodryas granuliceps*	Lizards	Terrestrial	Back	1000	Madagascar
Pseudoxyrophiinae	*Dromicodryas quadrilineatus*	Generalists	Terrestrial	None	1200	Madagascar

Appendix 1. Diet, lifestyle, fang type, body size (mm) and geographic location data for all lamprophid snakes and the outgroup species. The sub-family for each species is also provided.

Subfamily	Species	Diet	Lifestyle	Fang type	Body Size (mm)	Geographic location
Pseudoxyrophiinae	*Dromicodryas bernieri*	Snakes and other elongate prey	Terrestrial	None	1200	Madagascar
Pseudoxyrophiinae	*Thamnosophis infrasignatus*	Generalists	Terrestrial	None	1200	Madagascar
Pseudoxyrophiinae	*Thamnosophis martae*	Aquatic vertebrates	Terrestrial	None	900	Madagascar
Pseudoxyrophiinae	*Thamnosophis epistibes*	Aquatic vertebrates	Terrestrial	None	900	Madagascar
Pseudoxyrophiinae	*Thamnosophis stumpffi*	Aquatic vertebrates	Terrestrial	None	1000	Madagascar
Pseudoxyrophiinae	*Thamnosophis lateralis*	Aquatic vertebrates	Terrestrial	None	900	Madagascar
Pseudoxyrophiinae	*Pseudoxyrhopus ambreensis*	Reptile eggs	Terrestrial	None	430	Madagascar
Pseudoxyrophiinae	*Heteroliodon occipitalis*	Lizards	Terrestrial	None	330	Madagascar
Pseudoxyrophiinae	*Liopholidophis dimorphus*	Generalists	Terrestrial	None	1080	Madagascar
Pseudoxyrophiinae	*Liopholidophis dolicocercus*	Aquatic vertebrates	Terrestrial	None	1430	Madagascar
Pseudoxyrophiinae	*Liopholidophis sexlineatus*	Aquatic vertebrates	Semi-aquatic	None	1100	Madagascar
Pseudoxyrophiinae	*Liophidium therezieni*	Aquatic vertebrates	Terrestrial	None	730	Madagascar

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Subfamily	Species	Diet	Lifestyle	Fang type	Body Size (mm)	Geographic location
Pseudoxyrophiinae	*Liophidium torquatum*	Aquatic vertebrates	Terrestrial	None	600	Madagascar
Pseudoxyrophiinae	*Liophidium mayottensis*	Aquatic vertebrates	Terrestrial	None	980	Comoro
Pseudoxyrophiinae	*Liophidium chabaudi*	Aquatic vertebrates	Terrestrial	None	490	Madagascar
	Calliophis melanurus	Snakes and other elongate prey	Terrestrial	Front	570	Asia