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The evolution and diversification of diet in elapids

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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.

M. Kgaditse

Mimmie Kgaditse, 22 July 2016

"In any study of evolutionary ecology, food relations appear as one of the most important aspects of the system of animate nature. There is quite obviously much more too living communities than the raw dictum "eat or be eaten," but in order to understand the higher intricacies of any ecological system, it is most easy to start from this crudely simple point of view."

- G. E. Hutchinson (1959) Homage to Santa Rosalia or why are there so many kinds of animals?

ABSTRACT

A central goal in macroecology is understanding the factors that have shaped broad-scale patterns among extant natural communities. Diet is widely cited as a key factor involved in shaping snake diversification. Amongst serpents, the adaptive radiation of elapids is unparalleled in terms of their sheer global distribution. My study was aimed at evaluating the variation in diet and how trends evolved throughout the radiation of the elapids. Based on the published natural history data of 303 elapid species, a cluster analysis revealed seven groups of species within which diet types were similar. The broad diet clusters included snake consumption, feeding on fish, ectotherms, endotherms, lizards, a generalist diet and lastly, a terrestrial invertebrate group that was the least prevalent diet type. Maximum Parsimony, Maximum Likelihood and Stochastic Character Mapping were used to trace the ancestral dietary condition in the Elapidae. Reconstructions demonstrated that starting from an ophiophagous ancestor, elapids still largely retain their early feeding habits. Despite the emergence of novel feeding patterns in the group, the predominantly conservative diet patterns suggest that niche conservatism has shaped elapid foraging dynamics. Members of the lineage characteristically feed on elongate ectothermic prey (e.g., squamates, caecilians, eels, earthworms) possibly owing to morphologically-mediated gape constraints. Phylogenetically corrected comparative methods were used to assess the influence of differences in body size, lifestyle and global scale spatial distribution of diet evolution. While lifestyle and distribution considerably influenced how diet patterns evolved, body size was not a significant determinant of the prey types taken. The lack of body size-diet association may be because larger-bodied elapids also opportunistically supplement their diet with smaller prey items. Overall, the findings indicate that recent ecological factors (e.g., lifestyle) coupled with long established factors (phylogeny, biogeography) have shaped elapid natural history patterns. This study is the first of its kind to offer a family-level, phylogenetically-based analysis on the evolutionary and contemporary feeding dynamics of the world’s most widespread snake family.

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1. INTRODUCTION

1.1. General overview

The feeding habits of animals are fundamental characteristics of their natural histories (Slip & Shine 1988). For instance, particular dietary regimes may impose constraints upon body size (Schwaner & Sarre 1990; Meik *et al.* 2010), locomotor behaviour (Mori 1991; Secor 1995), or reproductive strategy (Shine 1990; Forsman 1991). The type of prey eaten may also influence distribution and abundance (Slip & Shine 1988) and directly impacts on daily of activity patterns and habitat use (Huey & Pianka 1981; Plummer 1981). Moreover, dietary habits influence energy intake and survivorship which affect life-history variables either as direct phenotypic effects, or as the basis for the evolution of modified behaviour, physiology or morphology (Slip & Shine 1988; Higham 2007; Pleguezuelos *et al.* 2007).

The dietary characteristics of snakes are of particular interest as snakes possess extraordinary adaptations for locating, subduing and ingesting a large variety of prey (Gans 1983; Greene 1997)**.** Snakes are among the most remarkable of extant vertebrate radiations as evidenced by their widespread geographic distribution (Cadle 1987; Keogh 1998). The approximately 3672 species making up this clade comprise ~36% of the global reptile species diversity (Uetz & Hošek 2015). Snakes evolved some 140-170 million years ago and have since amassed a remarkable range of ecological, behavioural and biological variation (Vitt & Caldwell 2009). This clade demonstrates distinctive biological characteristics (e.g., elongate, legless body, ubiquitous carnivory, indeterminate growth, ectothermic physiology and complex cranial morphology). Serpents are therefore model candidates for investigating broad-scale evolutionary patterns in diet and their influence on species' ecomorphological diversity.

Diet is recognised as a central factor in having influenced the evolution of snakes (Greene 1983; Alencar *et al.* 2013) as snakes have evolved highly elaborate feeding mechanisms which have allowed them to consume a wide variety of prey (Greene 1997; Alencar *et al.* 2013). Early snakes are thought to have evolved from limbed tetrapods which fed predominantly on relatively small prey on a frequent basis (Greene 1983). Evidence suggests that some early ophidians occasionally captured and subdued heavier, bulkier prey items (Gans 1961). This dietary change to larger meals represented a significant ecological shift from that of their saurian predecessors (Greene 1983). The changes in the feeding habits of snakes also necessitated the evolution of pronounced cranial modifications for increased gape in response to relatively larger prey (Gans 1961). Examples of these morphological adaptations include the elongation of the quadrate, movable suspension of the supratemporal and greater mobility of the snout complex (Lee 1998; Rodriguez-Robles *et al.* 1999). Such innovations allowed the consumption of a greater diversity of prey species of various shapes and sizes (Greene 1983).

Extant members of major snake radiations such as boids (boas, pythons and erycines) and vipers show the largest degree of cranial kinesis of any vertebrate, feeding on prey as diverse in shape as pangolins, porcupines, lizards and large mammals, some of which can weigh more than the snake (Greene 1983; Secor *et al*. 1994; Warner 2009). As a result of these dietary shifts, modern snakes now occupy a great range of adaptive niches which might previously have been exploited by other lizards and vertebrates (Greene 1983). The feeding habits of snakes thus appear to lie at the heart of their origin and radiation. Extant snakes species are now adapted to terrestrial, fossorial, arboreal, marine and freshwater modes of life allowing them to occupy every continent, with the exception of Antarctica and oceanic pelagic areas (Greene 1997).

All extant snakes are placed in one of two major clades (Rodriguez-Robles *et al.* 1999; Fig. 1). The scolecophidians are the most basal living snakes forming a monophyletic clade comprised of small, blind, burrowing snakes which consume small-bodied prey on a frequent basis (Lee *et al*. 2007; Vidal *et al.* 2006). All other living snakes form the more ecologically and morphologically diverse Alethinophidia group, members of which feed relatively infrequently on large-bodied (primarily vertebrate) prey (Vidal *et al.* 2006). The majority of Alethinophidia is comprised of Macrostomata however it is not clear which alethinophidians fall within the macrostomatan clade (Rodriguez-Robles *et al.* 1999; Lee *et al.* 2007). The large-bodied, constricting boids are most basal in the macrostomatans (Wilcox *et al*. 2002). The remaining macrostomatans forming the Caenophidia or “advanced snakes” are a group that contains all known venomous snake species (Greene 1997; Fry *et al*. 2003).

The Caenophidia is highly diverse and species rich (>2500 species; Lee *et al*. 2007) despite being the most recently evolved superfamily of snakes, having evolved in the mid-Cenozoic (Greene 1983). Although several families make up the Caenophidia, only ~20% of species possess a front-fanged venom delivery system (Knight & Mindell 1994; Fry *et al.* 2003). These groups (all of which fall within the superfamily Colubroidea) include the atractaspids and two independently evolved monophyletic groups: (1) Viperidae (e.g., rattlesnakes, adders and vipers) and (2) Elapidae which is globally the most widespread of the families (Knight & Mindell 1994; Rodriguez-Robles *et al.* 1999; Alexander & Marais 2007).

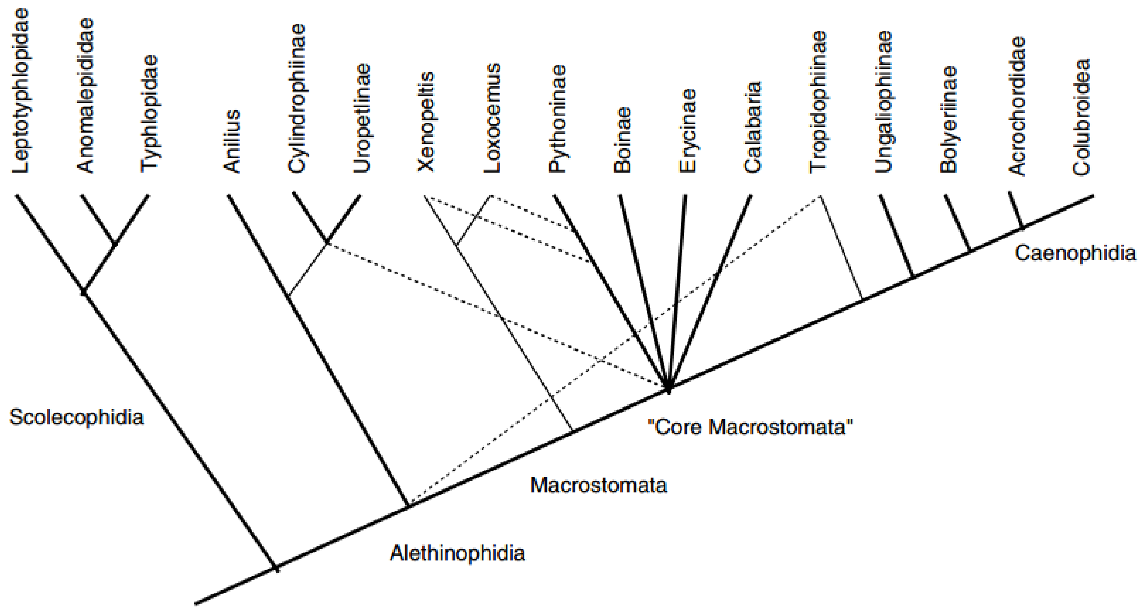


Figure 1. The currently accepted phylogeny of extant (Serpentes) (Lee *et al.* 2007). Thick solid lines show relationships which are supported by both morphological and molecular studies, thin lines are relationships derived from morphological analyses, while dotted lines represent relationships based on molecular data.

Known as proteroglyphs, the Elapidae are primarily characterised by the presence of two hollow, fangs on the relatively-immobile maxilla (Knight & Mindell 1994). Elapids include *Naja*, *Dendroaspis*, *Micrurus*, *Hydrophis*, *Elapsoidea* and their allies (Keogh 1998). The family consists of approximately 357 species (Uetz & Hošek 2015) in 61 genera which are widespread in both marine and terrestrial habitats over much of the tropical and subtropical areas of the world (Shine & Keogh 1996; Fig. 2). Terrestrial elapids occur in Australia, Africa (excluding Madagascar), Arabia, the Americas, Asia and Melanesia, while marine species inhabit large parts of the Pacific and Indian Oceans (Mengden 1983; Keogh 1998; Alexander & Marais 2007; Fig. 2). The Elapidae have thus adapted to many diverse habitats wherein they represent important components of the biota (Mengden 1983; Pincheira-Donoso *et al.* 2013). As a consequence of radiations spanning millions of years, elapids have evolved a considerable range of morphological, behavioural and ecological characteristics in response to selective pressures associated with their specific environments (Hutchinson & Donnellan 1993).

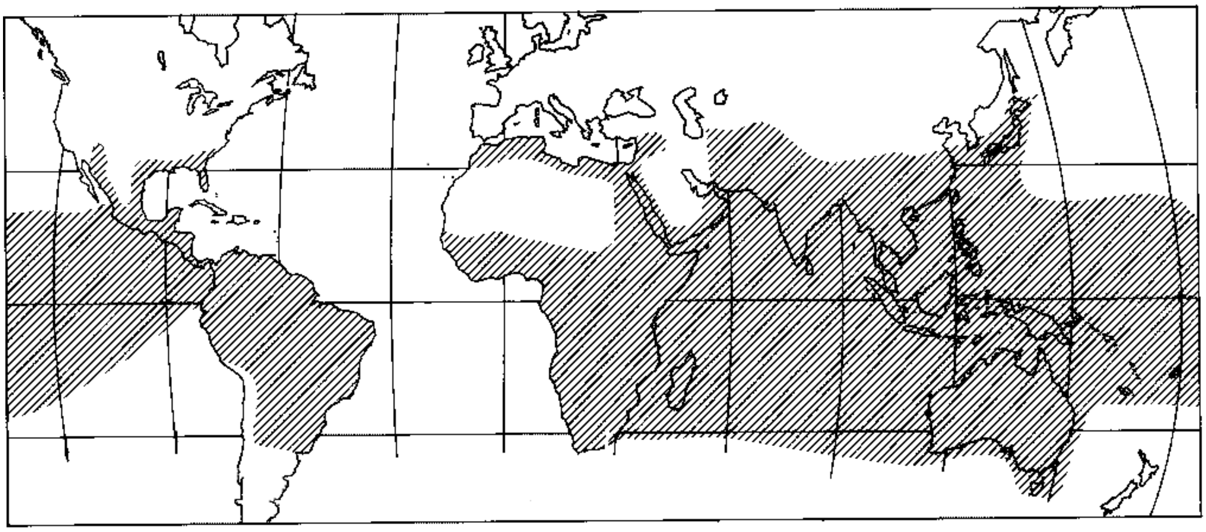


Figure 2. Global distribution of the Elapidae (taken directly from Hutchinson & Donnellan 1993).

Despite the widespread occurrence of members of the Elapidae and the importance of feeding biology in influencing the divergence of snakes, no study has yet attempted to highlight the evolutionary history of diet within this lineage. Investigating the diversity of dietary traits and how they evolved provides insight into the broad taxonomic and functional feeding patterns found within the Elapidae and provides a basis for comparing this clade with other snake groups. Moreover, revealing these diet traits allows for the investigation of the ecological or biogeographic processes which are responsible for the generation of observed patterns (Alencar *et al.* 2013). Although it is difficult to make inferences with absolute certainty about feeding in extinct snakes (Greene 1992), a number of methods have the potential to improve our understanding of diet evolution. One approach is to evaluate the prey consumed in the family in relation to phylogenetic relationships, then assess whether any concordant patterns in diet are evident (Greene 1983).

Phylogenetic reconstruction is an approach which may allow for the description of ancestral diet traits (Harrison & Langdale 2006). The method entails mapping the character states of extant species onto a phylogeny (the presumed evolutionary history of the taxon; Martins *et al.* 2002; Bollback 2007) to infer nodes at which changes in the characteristic of interest has likely occurred. In so doing, it is possible to track patterns of character change along a phylogeny and thus deduce a historical framework for understanding the evolution of the various traits (Bollback 2007). Although several phylogenetic trees have been formulated for a wide range of snake groups (e.g., Wilcox *et al.* 2002; Lee *et al.* 2007; Pyron *et al.* 2013), such assessments on ophidian dietary trait evolution have seldom been attempted. Exceptions are Greene (1992), Rodríguez-Robles *et al*. (1999) and Alencar, *et al*. (2013) who have used character mapping to infer the historical trajectories of feeding ecology in some boid, colubrid and viperid clades.

Rodríguez-Robles *et al*. (1999) evaluated the taxonomic variation in dietary composition and foraging strategies in erycrine boas to find that the relative abundance of rodent prey had greatly facilitated the diversification of ancestral erycines. A similar study was carried out on the feeding ecology of *Bothrops*, a Neotropical pitviper genus (Greene 1992). A reconstruction of past feeding habits suggested that ancestral *Bothrops* likely fed on a broad variety of prey and that the generalist diet showed by early *Bothrops* may have enabled various ecological shifts within the genus and the subsequent range expansion that took place in the Americas (Martins *et al*. 2002). More recently, Alencar, *et al*. (2013) described the evolution and diversification of diet and correlated microhabitat use in the tribe Pseudoboini (Family Colubridae). They revealed that Pseudoboine snakes feed mainly on lizards and small mammals having evolved to forage arboreally (Alencar, *et al*. 2013). The systematics of the Elapidae has recently undergone extensive revision (Slowinski & Keogh 2000; Pyron *et al.* 2013).The availability of an up-to-date and comprehensive phylogeny for this group in addition to natural history data provides an empirical basis for detecting evolutionary and contemporary patterns in their feeding attributes.

Investigating the diet characteristics of elapids in a phylogenetic context can further clarify the ecomorphological and biogeographic factors that influenced the evolution of diet in the group (Rodríguez-Robles *et al*. 1999) and shed light on the origin of biodiversity in general. An evaluation of this nature is essential given that fundamental relationships may exist between diet and other natural history traits in any organism (Hawe & Peres 2013). For instance, body size has been recognised as a determinant of diet types in a number of vertebrates (Fleming 1991; Forsman 1991). The Elapidae have a wide range of body sizes (Appendix 2) and it has been suggested that pronounced body size variations between squamate populations were tightly correlated with the types of prey available to them (Aubret 2012; Keehn *et al.* 2013). These findings collectively support the notion that the size and diversity of prey consumed may be an important driver of body size evolution (and *vice versa*) in gape-limited predators. The range of body sizes and dietary divergence of extant elapids thus presents an ideal system to examine the evolutionary relationship between dietary profile and body size.

The Elapidae are globally widespread and member species are adapted to a wide range of habitats. It is likely that natural selection has led to patterns in the spatial variation of diet preferences within the clade (Rossman *et al.* 1996). For example, in the colubrid *Thamnophis elegans*, differences in the preference for slugs as food is heritable and varies between inland and coastal populations as a result of genetic polymorphism (Arnold 1992). Alternatively, significant geographic variation in diet at varying spatial scales may relate primarily to geographic shifts in prey abundance and availability (Shine 1987). An example of this has been documented in south Australian tigersnakes (*Notechis*) which, occupying proximate islands, encounter vastly different prey availability depending upon the occurrence of seabird colonies (Schwaner & Sarre 1990). The tigersnakes inhabiting these islands exhibit marked differences in prey type and body size (Schwaner & Sarre 1990). Members of the Elapidae generally form distinct taxonomic clades which are restricted to particular continents. They have adapted to foraging terrestrially, in arboreal habitats, subterranean environments and in water. It is therefore essential to assess the spatial dietary variation amongst biogeographic regions, in addition to doing so at a smaller spatial scale.

In this study, I provide a description of the broad-scale dietary variation within the family Elapidae and explore how dietary traits evolved during the diversification of the clade. In order to uncover the processes involved in the evolution of diet in this diverse clade, a number of questions are addressed:

(1) What are the broad diet types consumed by members of the Elapidae?
(2) What dietary characteristics did ancestral elapids likely display?
(3) How did the dietary traits of elapids change during subsequent radiations?
(4) What factors were influential in determining the evolutionary trajectory of diet in the Elapidae?

1.2. Aims and objectives

This project aims to collate feeding records of the Elapidae to not only outline their present day feeding characteristics, but provide a basis for understanding the evolutionary processes that led to contemporary foraging dynamics within the group. Such an evaluation offer opportunities for comparing fundamental aspects of elapid feeding ecology with other advanced snake groups. The objectives were to:

(1) Describe the broad diet groups in the Elapidae.
(2) Reconstruct the dietary condition of ancestral elapids.
(3) Describe the evolutionary trajectory of diet traits within the Elapidae.
(4) Assess the evolutionary relationship between diet and maximum body size.
(5) Evaluated if or how the dietary characteristics vary amongst biogeographic regions.
(6) Investigate if or how diet evolution is related to lifestyle differences among elapid species.
(7) Use findings to compare elapid feeding habits to those of other snake families.

1.3. Description of the elapid family

1.3.1. Taxonomy and origin

Members of Elapidae consist of various divergent monophyletic lineages, with an unequal spread of generic and species level richness among clades and biogeographic regions (Keogh 1998):

(1) The greatest number of genera and species of elapids inhabit Australia (Sanders *et al.* 2008).
(2) Melanesian elapids found in the Solomon Islands, New Guinea and Fiji occur solely in these areas whilst showing intermediate levels of specific and generic richness (Keogh 1998; Keogh *et al*. 1998).
(3) African representatives such as *Dendroaspis*, *Elapsoidea*, *Pseudohaje*, *Walterinnesia*, and *Naja* are also intermediate in specific and generic richness (Keogh 1998).
(4) While the American coral snake lineage consists of only two closely-related genera, one of these genera has high species richness with more than 80 species. The other genus, *Micruroides*, is monotypic (Slowinski 1995; Keogh 1998; Uetz & Hošek 2015).
(5) The continental Asian elapid radiation has an impressive species richness of cobras (*Naja*, *Ophiophagus Hannah*), coral snakes (10 *Calliophis* spp) and terrestrial kraits (13 *Bungarus* spp) (Mengden 1983; Keogh 1998).
(6) Two groups of more than 60 species make up the sea snake lineage: (1) *Laticauda* is partially aquatic, returning to land to lay their eggs (Heatwole 1999); (2) The

viviparous hydrophiids (*Aipysurus*, *Hydrophis*, *Emydocephalus*, *Ephalophis greyae* and *Parahydrophis mertoni*) are fully aquatic (Keogh *et al*. 1998; Alexander & Marais 2007). Hydrophiids and *Laticauda* evolved a marine lifestyle independently from terrestrial Australasian elapids less than 5 million years ago (Keogh 1998). Today they occur in a range of marine habitats throughout the Indo-West Pacific with the greatest number of species in the Indo-Australian biodiversity hotspot (Heatwole 1999).

The divisions among and within elapid groups have been the subject of a long standing debate (Alexander & Marais 2007). Originally, terrestrial forms and sea snakes were placed in two subfamilies (i.e., Elapinae and Hydrophiinae; Boulenger 1896) while some studies have divided them into separate families (Alexander & Marais 2007). The early history of elapids remains ambiguous (Keogh 1998). Some evidence suggests that the African *Elapsoidea* and *Aspidelaps* are the most basal of living elapids which, in agreement with Cadle (1982; 1987), points to an African origin. A recent study contrastingly supports the Asian *Calliophis* as the most primitive lineage (Pyron *et al*. 2013). Cadle (1987) indicates that Asian elapids are comprised of representatives from every one of the subfamilies recognized by McDowell (1987), suggesting an Asian origin. Keogh (1998) similarly showed that the Asian radiation is the sister group to major American, Australian and African elapid lineages (Graham Alexander pers. comm.).

Keogh (1998) supports the contention that Asia is the geographic origin, with dispersal to other parts of the range during the Miocene. He states that dispersal to the New World likely occurred by way of the Bering Straits and to Australia through south-east Asia after the collision of the Australian and Asian tectonic plates (Keogh 1998). This idea seems unlikely given that the Bering Strait was a land bridge during the ice age which would have precluded ectotherms (Graham Alexander pers. comm.). The hypothesis further fails to explain why the distribution of New World elapids is restricted to South America and southern parts of the USA. A more plausible explanation is that the Elapidae arrived in the Americas by way of long-jump dispersal.

1.3.2. Biology and ecology

Most elapids are active-foraging predators feeding mainly on relatively small-bodied prey on a more frequent basis than do ambush-foraging snakes such as vipers (Huey & Pianka 1981).

Exceptions to this generalization is are *Acanthophis* (Shine 1980a), *Dendroaspis* (Greene 1997) and *Hoplocephalus* (Fitzgerald *et al*. 2002) which employ the “sit-and-wait” foraging strategy to capture relatively larger-bodied prey items. Actively foraging entails elapids travelling in pursuit of prey however, the daily movements and home ranges of most elapids remain inadequately quantified (Hutchinson & Donnellan 1993). Low population densities and high vagility suggest that elapids may cover relatively large areas in search of mates or food resources (Shine 1987; Reed 2003). The habitat use by a particular snake species appears to relate primarily to the availability of basic requirements such as suitable cover and prey types (Schwaner & Sarre 1990).

Elapids use a wide range of habitats (lifestyles) and this comes with significant morphological modifications to optimise performance within specific habitats (Lillywhite & Henderson 1993; Rozar 2010). The morphological similarities of elapids leading different lifestyles transcend generic boundaries, implying that convergent evolution is in effect. This means that natural selection is driving species to evolve similar morphological features in response to particular environmental selection pressures (Hugueny & Pouilly 1999). Arboreal taxa such as *Hoplocephalus*, *Dendroaspis* and *Pseudohaje* have evolved a unique set of morphological traits in accordance with foraging in trees. This habitat presents a number of challenges - branches can be narrow, fragile and present a highly discontinuous substrate over which to move (Greene 1997; Pizzatto *et al*. 2007; Rozar 2010). A snake’s ability to bridge gaps and negotiate narrow branches determines the extent of available habitat and therefore the availability of prey (Greene 1997; Rozar 2010). To overcome these challenges, arboreal snakes tend to be slender and have highly flexible vertebral columns (Greene 1997). Long, slender-bodies with long tails aid in climbing by spreading the body’s mass widely across several points of contact and also facilitating movement through the narrow spaces among branches (Pizzatto *et al*. 2007; Rozar 2010).

A great deal of morphological similarity also exists among fossorial species. Fossorial snakes are often distinguishable by a high number of ventral scales and a short tail, which is tipped by one or more spines used as a lever for pushing off (Seigel *et al*. 1987; Greene 1997). Burrowing elapids are typically shorter than a metre, although *Elapsoidea sundevallii* (Spawls & Branch 1995) and *Micropekhis ikaheka* (O’shea 2005) may reach a length of 2.1 m. Burrowing elapids also typically have compact heads that are indistinct from the neck and fused body scales to absorb the forces of tunnelling and minimise friction with the ground.

Aspidelaps scutatus has a broad, flat head with modified rostral scales and uses its snout to open tunnels, then scoop soil out in a loop created by retracting the neck laterally (Greene 1997; Alexander & Marais 2007). Specialised fossorial snakes tend to have poor vision and most of them actively hunt by locating the chemical cues of prey (Greene 1984; Seigel *et al*. 1987; Alexander & Marais 2007).

Freshwater elapids as *Naja annulata* and *N. christyi* possess a flat, broad head that has a wide gape for feeding on fish and frogs. The body is cylindrical and large, with a long tail (Spawls & Branch 1995). Amongst serpents, sea snakes exhibit the most dramatic morphological specialisations for life in water. These foragers can dive to depths exceeding 100 m and remain submerged for up to two hours (Elfes *et al*. 2013). The cross-sectional body shape of terrestrial snakes is circular compared to dorsoventrally-elongate (greater body height compared to width) sea snakes (Brischoux & Shine 2011). This body form creates an efficient underwater thrust, even with the bodily distension resulting from ingesting large-bodied prey (Brischoux & Shine 2011). The tail of marine species is vertically flattened and fin-like for rapidly propelling the predators through water (Heatwole 1999).

Elapids vary greatly in size with snout-vent lengths (SVL) up to 4 m and 5.7 m having been recorded for *Dendroaspys polylepis* and *Ophiophagus Hannah*, respectively (Mehrtens 1987; Alexander & Marais 2007). At the other extreme are small-bodied species such as *Simoselaps minimus, Neelaps calonotus* and *Drysdalia mastersii* which respectively reach maximum SVLs of 194, 251 and 271 mm (Shea *et al*. 1993). Members of the Elapidae also demonstrate varying body forms according to foraging mode, amongst other factors. For instance, fast-moving active foraging *Demansia* have slender bodies and long tapering tails (Shine 1980b), while *Acanthophis* is comparatively short and thick-bodied to accommodate large-bodied prey (Shine 1980a).

2. MATERIALS AND METHODS

2.1 Species traits

I gathered data from the literature (peer reviewed journals, books, field guides and online resources) on the prey types, maximum body size, global scale distribution and lifestyle of elapids (Appendix 3). These included 303 species making up ~85% of all elapid species (Appendix 3). A Hierarchical Cluster Analysis was used to define broad dietary categories using the Ward's clustering method (Kaufman & Rousseeuw 2009) in the SPSS 22 (2014) software. Species points with Euclidean distance measures of > 90% similarity were considered clusters (Appendix 1). The resulting clusters delineate groups of species with markedly similar diet characteristics. Four characters that were then reconstructed:

1. The resulting diet groups defined by the cluster analysis (i.e., diet clusters Type 1-7). Details pertaining to the cluster outputs are described in chapter 3.1 and Appendix 1.
2. Lifestyle, denoting the species' foraging environment was defined as either ground-dwelling, burrowing, arboreal or partly to fully aquatic, according to the following criteria:

a) Ground-dwelling: surface active/terrestrial hunters which mainly forage at ground-level (including rocky areas).
b) Burrowing: elapids which live in some form of excavation be it shallow or deep. Examples include burrows (fossorial), loose soil or leaf litter (cryptozoic). These species may frequently occur above ground (e.g., to forage) and are thus capable of leading both a subterranean and terrestrial existence (subfossorial).
c) Arboreal: regularly climbing to forage. They may hunt above ground-level (in trees and shrubs) in addition to doing so at the ground-level.
d) Aquatic: predominantly or exclusively feeds in either marine or freshwater environments.
e) Semiaquatic: hunts in freshwater, but may occasionally/rarely feed at terrestrial or above ground environments (semiaquatic).

3. Broad-scale biogeographic occurrence: regions included Neotropical, Afrotropical, Indo-Malaysian, Palearctic, New Guinean and Australian elapids, while the marine assemblage was treated as belonging to a biogeographic single group.
4. Body size (mm) which is represented by the maximum total length (SVL and tail length).

2.2. Ancestral state reconstruction

The four traits were then mapped onto the most recent and inclusive published phylogenetic tree for the family encompassing 143 (~46%) of the species assessed (Pyron *et al*. 2013). The tree and data matrix of this phylogeny are available in NEXUS format from the DataDryad repository (10.5061/dryad.82h0m). To infer the direction of character evolution within Elapidae, I rooted the tree with the inclusion of a non-elapid outgroup species (Graham *et al*. 2002). This is because the root of this clade represents its deepest and most basal split thereby allowing for the definition of the historical sequence of all subsequent character changes (Rota-Stabelli & Telford 2008). I chose *Micrelaps bicoloratus* (from sister clade Lamprophiidae) as the most appropriate outgroup (i.e., closely related to the elapids) since a greater distance between the root node and first outgroup node creates long outgroup branches potentially leading to spurious inferences on trait evolution (Swofford *et al.*1996; Graham *et al.* 2002; Pyron *et al*. 2013). *Micrelaps bicoloratus* is a venomous, rear-fanged snake endemic to East Africa (Branch & Branch 2005). This small (~200-300 mm) fossorial serpent has a diet that is comprised of other reptiles which it hunts at night (Branch & Branch 2005; Spawls *et al.* 2014).

To reconstruct ancestral characteristics, I used Maximum Parsimony (Bollpack 2006) and carried out optimisations in Mesquite 2.75 (Maddison & Maddison 2008). Given that a character such as diet can assume multiple states, changes from one character state to another were treated as unordered as they do not necessarily follow a clear, logical evolutionary sequence between transitions (Wilkinson 1992; Maddison & Maddison 2008). Maximum parsimony reconstruction minimises the number of character changes required to produce the terminal character distributions on phylogenies (Harriĝson & Langdale 2006). Given that the parsimony method selects for less complex character histories to explain present day traits, it has been argued that the technique may underestimate the variance and uncertainty involved in trait evolution (Bollpack 2006; Harrison & Langdale 2006).

I used Stochastic Character Mapping (SCC) as an alternative and comparative reconstruction approach as it accommodates the uncertainty in ancestral states of the group by means of Bayesian inference (Huelsenbeck *et al*. 2003; Bollpack 2006). I used the “make.simmap” function in the R 3.03 (2014) “phytools” package to perform Stochastic Character Mapping. The function first fits a continuous-time reversible Markov model (MCMC) for the evolution of diet. Using the terminal states on the phylogeny, the model samples random character histories for discretely-coded data (Bollback 2006). The uncertainty in the overall rate of character change and state frequencies (character history) was accounted for by creating multiple (n = 100) maps (Huelsenbeck *et al*. 2003). Finally, the “ace” function in the “ape” package in R 3.03 (2014) was used to calculate the conditional likelihood of each diet type occurring at each node of the tree. This probabilistic approach is referred to as a Maximum Likelihood reconstruction which represents a third widely utilised method of ancestral state optimisation.

The R 3.03 (2014) programme offers three alternative models for simulating the evolution of diet using Stochastic Character Mapping or Maximum Likelihood. These include the equal rates (ER) model which keeps all transition rates of diet traits equal. The symmetric (SYM) model restricts the parameter values for forward and backward transition rates between states to being equal, while the all rates different option (ARD) ensures that transition rates are all unique. I utilised the Akaike Information Criterion (AIC) and sample-size corrected AICc as a measure of the relative strength of models for the data. The delta AIC along with the maximum-likelihood estimate (LnL) were computed to compare models. The number of observations for AIC computation was taken as the number of trait values observed.

2.3 Diet correlation with maximum body size, lifestyle and broad-scale geographic distribution

In order to assess whether the various characters histories covaried, I tested for nonrandom association in the distribution of states on the phylogeny. Two phylogenetically independent comparative methods were utilised in analysing trait coevolution depending on whether data were continuously or discretely coded. A phylogenetic Anova (with 1000 simulations) was used in the R 3.2.3 (2014) ‘geiger’ package for the analysis of body size (maximum total length, mm) and diet associations given that the former is continuously coded.

For discrete characters, Pagel's (1994) correlation method was used in Mesquite 2.47 (Maddison & Maddison 2008). This method evaluates the observed likelihood ratios of two models to assess whether the rates of evolution of two characters is independent (Pagel 1994). In one model, the rate of change in one character is independent of the state of the other, while in the second model, the rates of change depend on the state of the other character (Pagel 1994). The significance of the difference in the ratios was tested by running Monte Carlo tests using an intensity of likelihood search of 10 iterations and 1000 simulated replicates of data (Maddison & Maddison 2008). Traits were treated as binary characters and all possible pairwise comparisons were analysed (Pagel 1994; Maddison & Maddison 2008). The level of significance was set at $P < 0.05$ in both types of evaluations. This method controls for the influence of phylogeny by evaluating associations in states at nodes across the entire phylogeny rather than simply comparing along the tips of the cladogram (Garland *et al*. 1992).

3. RESULTS

3.1. Diet clusters of extant elapids

Dietary records were collected for 303 elapid species. Eleven prey classes consisting of a variety of mammals, birds, lizards, snakes, amphibians, fish and their eggs, the eggs of lizards and snakes, as well as terrestrial and marine invertebrates comprised the dietary profile (Appendix 3). The hierarchical cluster analysis revealed seven broad dietary categories which were relatively evenly proportioned (Fig 4; Appendix 1). The diet groups making up the dietary profile consisted of:

Type 1: Squamates, but with a prevalence of snakes (Fig. 3.a)

Type 2: Fish, their eggs and marine invertebrates (Fig. 3.b). Both the Type 1 and Type 2 diet types each constituted ~19.0% of the prey groups consumed by elapids (Fig. 4).

Type 3: Ectotherms, but especially amphibians and lizards comprised 16.0% of elapid species diets (Fig. 3.c; Fig. 4).

Two clusters appeared to prey on a broad representation of most prey classes. Type 4 encompassed the majority endothermic prey eaters. For instance, 80.3% of bird consumers, 61.3% of mammal consumers and 68.6% of bird egg consumers belonged to this diet cluster. (Fig. 3.d; Appendix 2). Type 5 (generalist diet) had a functionally more uniform mix of prey classes (Fig.3.e; Fig. 4).

Type 6: Primarily lizard based diet with some reptile egg consumption which made up 13.0% of the overall diet profile (Fig 3.f; Fig. 4).

Type 7: Terrestrial invertebrate was the least prevalent diet type consumption (8.0% of species). *Toxicocalamus* comprised the majority of this diet cluster (Fig. 3.g; Fig. 4).

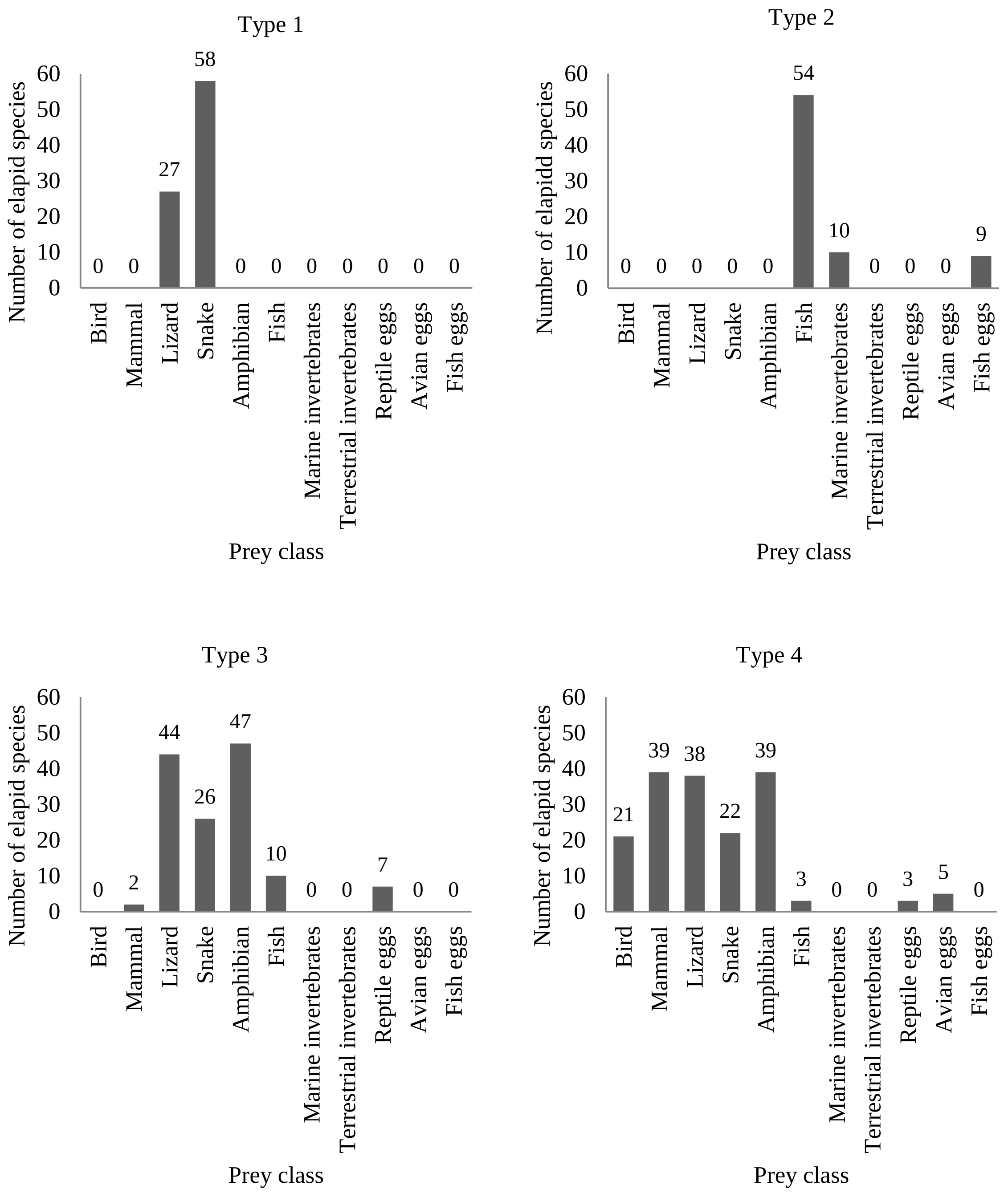
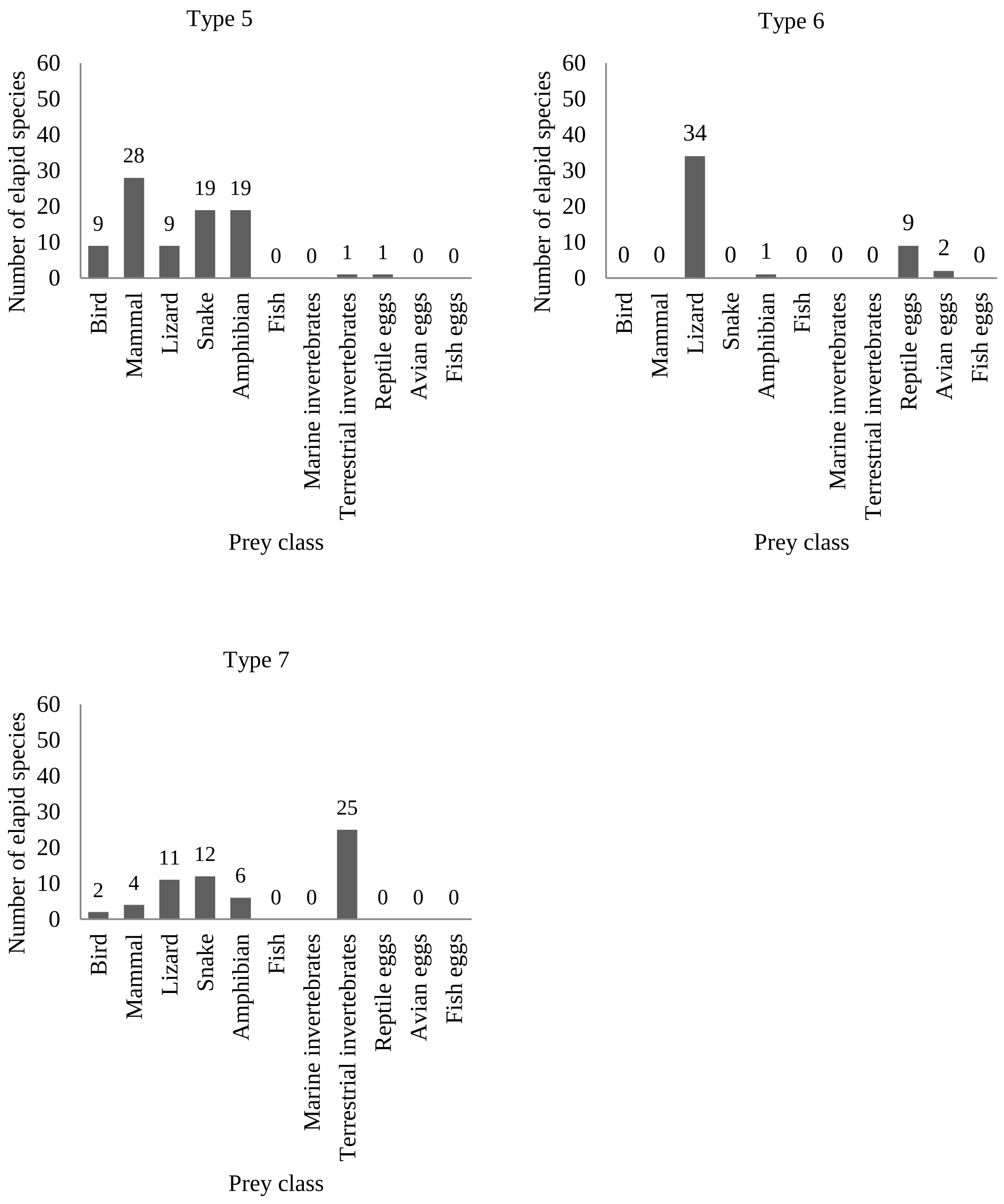


Figure 3. The number of species in the Elapidae recorded as consumers of various prey classes in each of seven diet clusters.



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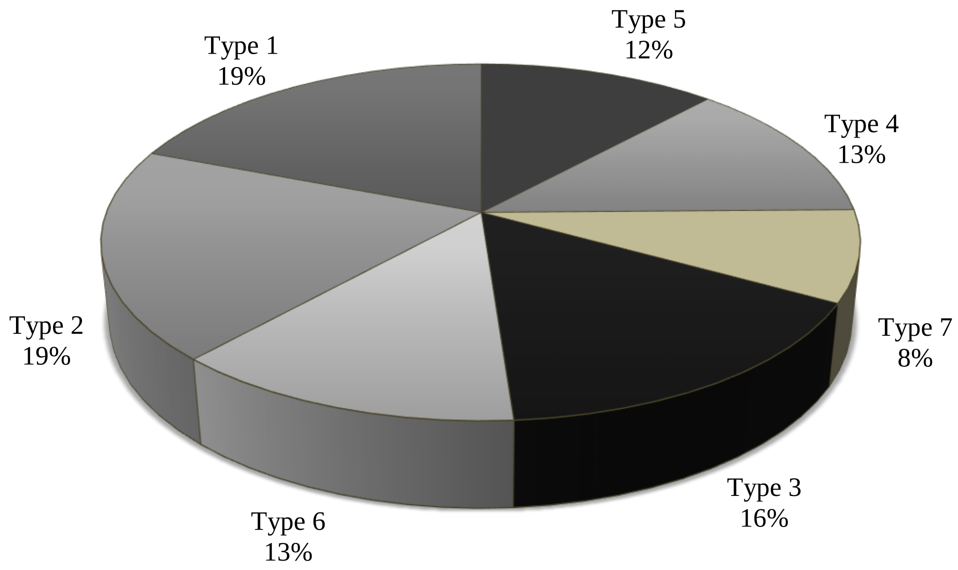

Figure 4. The percentage of elapid species consuming prey from the seven diet clusters comprising the diet profile of the family.

3.2. Model selection

The lower AIC/c and △AIC/c estimates indicate substantial support for the SYM model, whereas the ER and ARD models were highly unlikely to fit the data (Table 1. Burnham and Anderson 2002; Harmon *et al*. 2010). The higher Log likelihood estimation of the ARD model suggests moderate support, indicating that it is the next best model for explaining elapid diet data.

Table 1. The Maximum Likelihood estimate; number of free parameters; AIC, △AIC, AIC and △AICc values for the ER, SYM and ARD models of parameter values for various diet types in Elapidae.

Model	Parameters (n)	Log likelihood	AIC	△AIC	AICc	△AICc
ER	1	-209.3	420.6	29.2	420.7	21.2
SYM	21	-174.7	391.4	0	399.4	0
ARD	42	-161	415.9	24.5	454.3	54.9

3.3. Parsimony

The parsimony reconstruction indicated that the ancestral elapid most likely consumed a Type 1 diet (Fig. 6). This type of diet was evident in 15/139 of the extant species represented in the Pyron *et al.* (2013) phylogeny (Fig. 6). According to this reconstruction, the ancestral condition was lost in some lineages and re-evolved independently three times in elapid history (Fig. 6). The consumption of Type 1 prey is most prevalent diet type throughout the radiation of the speciose coral snake lineage indicating that it is symplesiomorphic (a shared ancestral condition) (Fig. 6).

The consumption of a Type 2 diet evolved relatively late in the elapid radiation (Fig. 6). This diet type appeared independently at least four times to occur in 36 of the species assessed (Fig. 6). Not surprisingly, Type 2 prey consumption was most evident throughout the evolutionary history of *Hydrophis* and *Laticauda* (Fig. 6). Parsimonious inferences suggest that Type 2 feeding likely evolved in an ancestor that fed on Type 1, Type 3, Type 4 and/or Type 5 (Fig. 6). *Micrurus surinamensis*, is the only member of its largely terrestrial radiation to specialise in Type 2 prey from precursors which included Type 1 forms their diet (Fig. 6).

A diet comprised of Type 3 food items evolved at least seven times in elapid history with the generally apomorphic trait now occuring in 25 of the taxa evaluated (Fig. 6). Excluding Type 1 feeding, feeding mainly on Type 3 groups was the dominant dietary feature among coral snakes (Fig. 6). The ancestral species of the clade encompassing *Elapsoidea semiannulata*, *Bungarus candidus*, *B. multicinctus*, *Naja multifasciata* and *N. annulata* ate a wide range of prey types (i.e., Type 5 and/or Type 4; Fig. 6). However, a dietary narrowing ultimately occurred resulting in the greater Type 3 specialisation now seen in the taxa (Fig. 6). The taxonomic group with the longest history of feeding solely on Type 3 encompasses *Denisonia devisi*, *Drysdalia coronoides*, *Hemiaspis damelli* and the *Austrelaps* genus (Fig. 6). The predecessors of this clade were probably strict consumers of a Type 2 diet (Fig. 6).

A Type 4 and Type 5 diet evolved relatively late and is most notable in the recent radiation of *Naja* and their closest relatives e.g., *Walterinasia aegyptia*, *Hemachatus haemachatus*, *Elapsoidea* and *Bungarus* (Fig. 8).The clade’s most recent forebearers appear to have fed on Type 3 prey types before broadening their diet (Fig. 6). In lineages where Type 4 prey is eaten, the Type 3 diet transitioned to a Type 5 diet before Type 4 became the predominant diet pattern (Fig. 6). Type 4 diet and Type 5 diets and their widespread nature within the family resulted from 13 and 5 independent evolutionary events respectively (Fig. 6).

Eating prey from the Type 6 cluster is generally a primitive trait within the Elapidae (Fig. 6). Feeding on Type 6 prey arose no fewer than four times (Fig. 6). The ancestors of *Drysdalia mastersii* possibly switched from consuming a diet largely comprised of Type 3 but narrowed it to saurophagy (Fig. 6). The elapid giving rise to *Echiopsis atriceps* may have narrowed its dietary range from one that is Type 4 to a diet consisting of Type 6 prey (Fig. 6). Contrary to most members of its lineage, the ancestor of *Micrurus dissoleucus* switched from feeding on other Type 1 groups to a more specialised Type 6 based diet (Fig. 6). Type 6 consumption is a long-established feeding pattern in the elapids preceding the taxon incorporating *Furina*, *Simoselaps*, *Suta*, and *Aspidomorphus* (Fig. 6). The forebearer to these genera may have also consumed a much broader diet including Type 4, but later narrowed its feeding habits (Fig. 6).

Incorporating Type 5 into the diet appears to be the most derived, specialised dietary condition occurring in just six extant species (Figs 6-10). An invertebrate-based diet appeared independently in four recent evolutionary events (Fig. 6). It is a common characteristic of *Toxicocalamus loriae*, *T. preussi* and *Demansia psammophis* (Fig. 6).The forebearer to this clade had a diet consisting of Type 4 prey (Fig. 6). Over time, feeding on Type 6 and Type 3 items became the dominant dietary characteristic for extended periods until incorporating invertebrates became characteristic of the taxa (Fig. 6). Like most other coral snakes, *Micrurus hemprichii* had a long history of snake consumption until eventually type 7 prey (i.e., onycophorans) were also incorporated into the diet (Fig. 6).

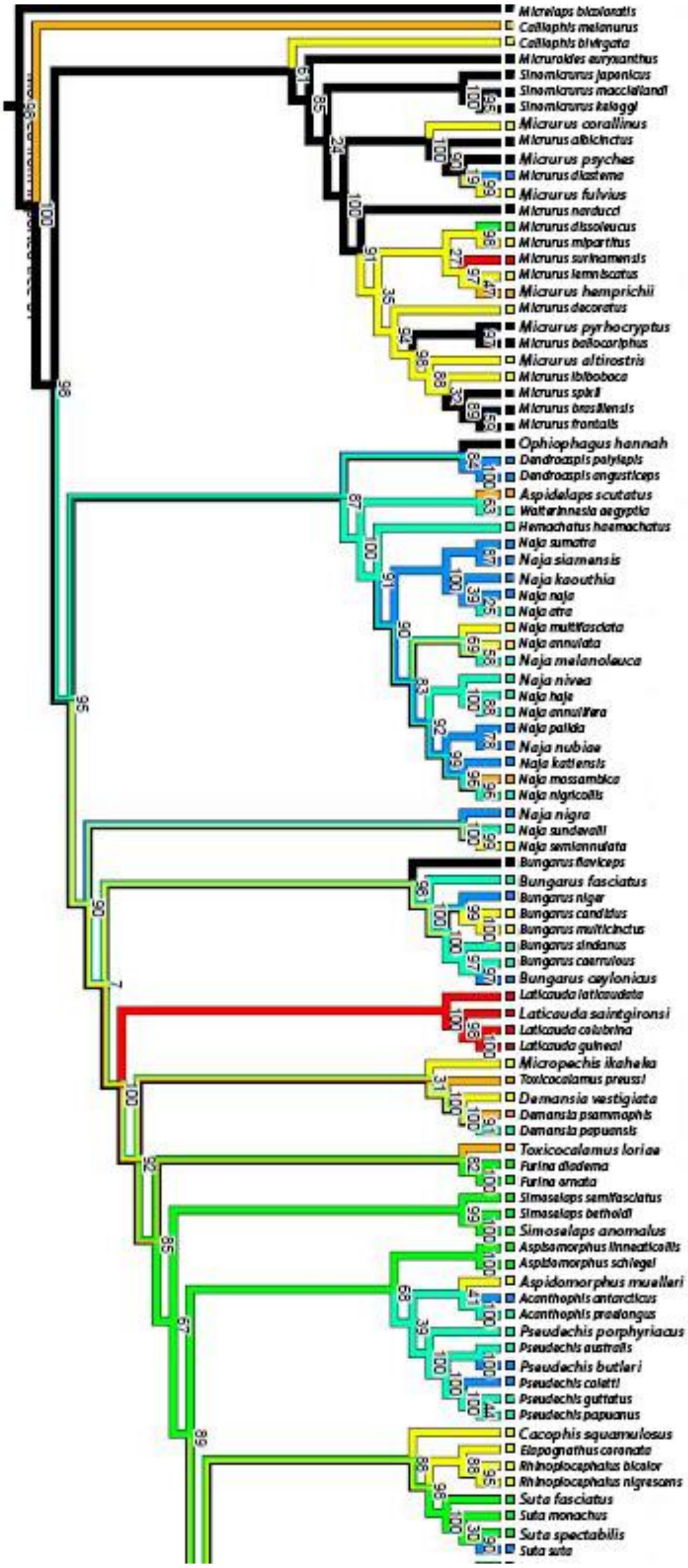

Figure 6. The ancestral reconstruction of diet in the Elapidae. The colours depict the following: black (Type 1), red (Type 2), yellow (Type 3), dark blue (Type 4), light blue (Type 5), green (Type 6) and orange (Type 7).

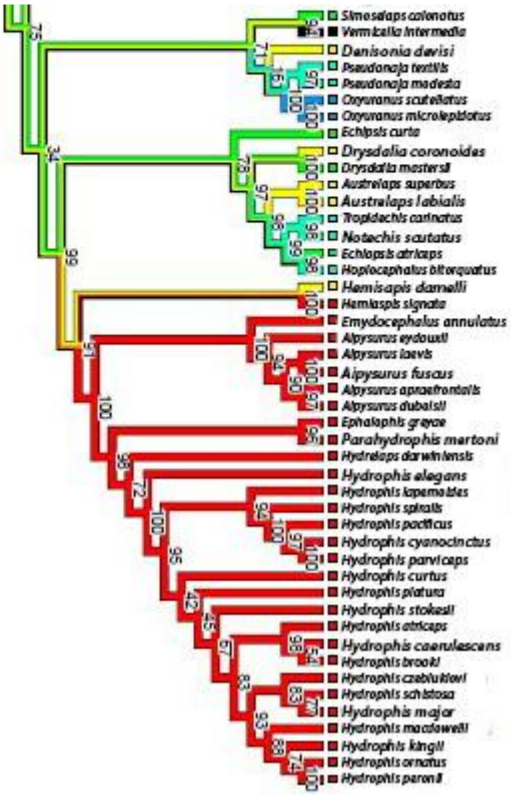

Figure 6. The ancestral reconstruction of diet in the Elapidae. The colours depict the following: black (Type 1), red (Type 2), yellow (Type 3), dark blue (Type 4), light blue (Type 5), green (Type 6) and orange (Type 7).

3.4. Maximum Likelihood

Several of the evolutionary diet patterns observed in the parsimony hypothesis were repeated in the maximum likelihood hypotheses. Most importantly, results of the technique suggest that the consumption of Type 1 prey is the most likely ancestral diet type (Fig. 7; Table 2). Thereafter, this hypothesis interprets Type 3 consumption as the most prevalent diet type throughout the evolution of Elapidae (Fig. 7). A Type 1 diet is an important plesiomorphic feature amongst coral snakes, but is relatively uncommon throughout the evolution of most other clades (Fig. 7). Type 4 and Type 5 foraging evolved relatively late and most notably in the ancestor of *Naja* and their close relatives as well as *Pseudechis* (Fig. 7). Type 2 consumption was a derived characteristic which evolved independently in two events corresponding to the *Hydrophis* and *Laticauda* groups (Fig. 7). By far the most recent and least prevalent type of diet was foraging on Type 7 prey (Fig. 7).

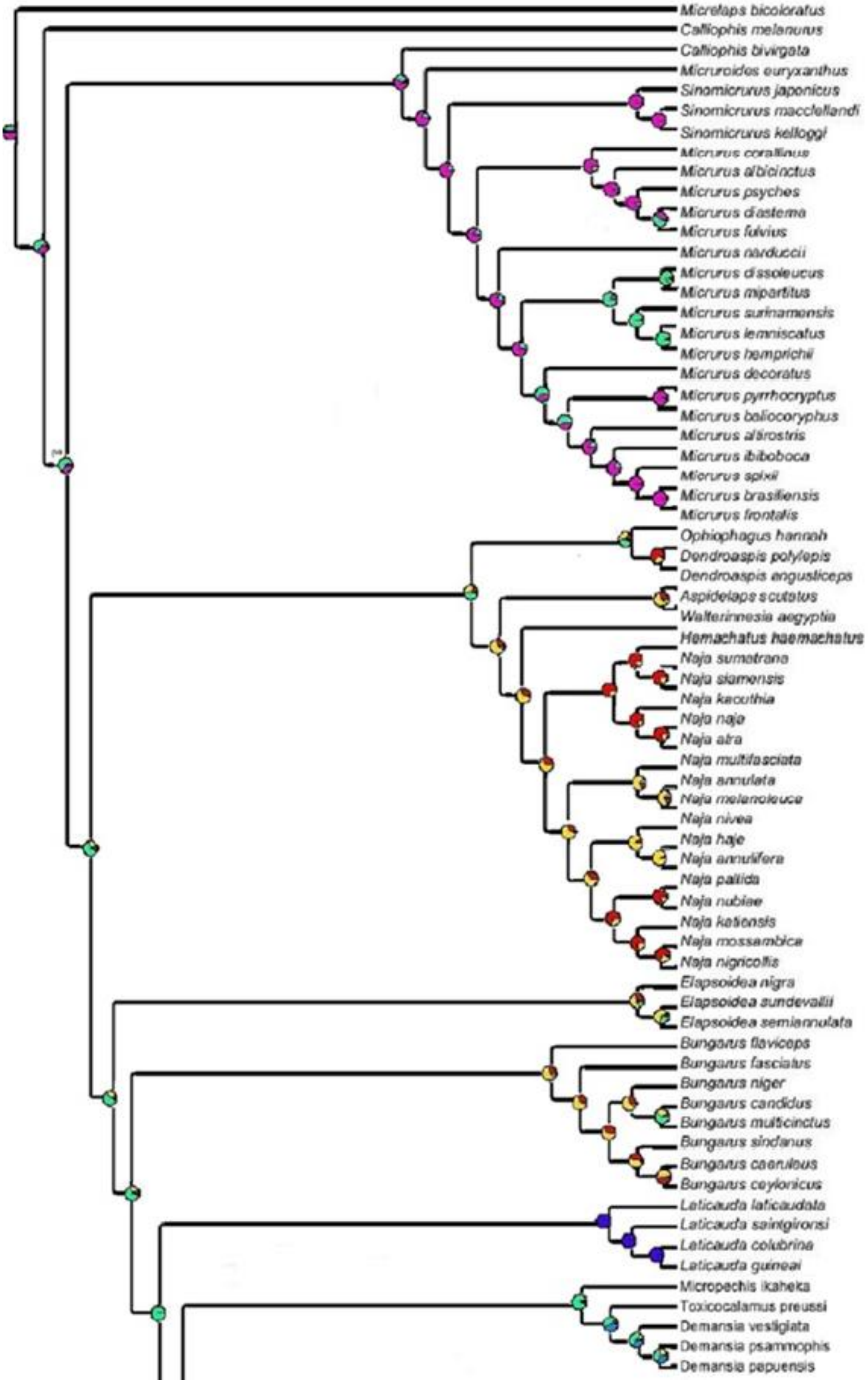

Figure 7. A maximum likelihood based reconstruction of diet in the Elapidae. Pie charts indicate the likelihood of particular diet types occurring at each node in the phylogeny. Diet types included the consumption of: Type 1 (purple), Type 3 (light blue), Type 4 (red), Type 6 (green), Type 7 (black), Type 2 (dark blue) and a Type 5 (orange) diet groups.

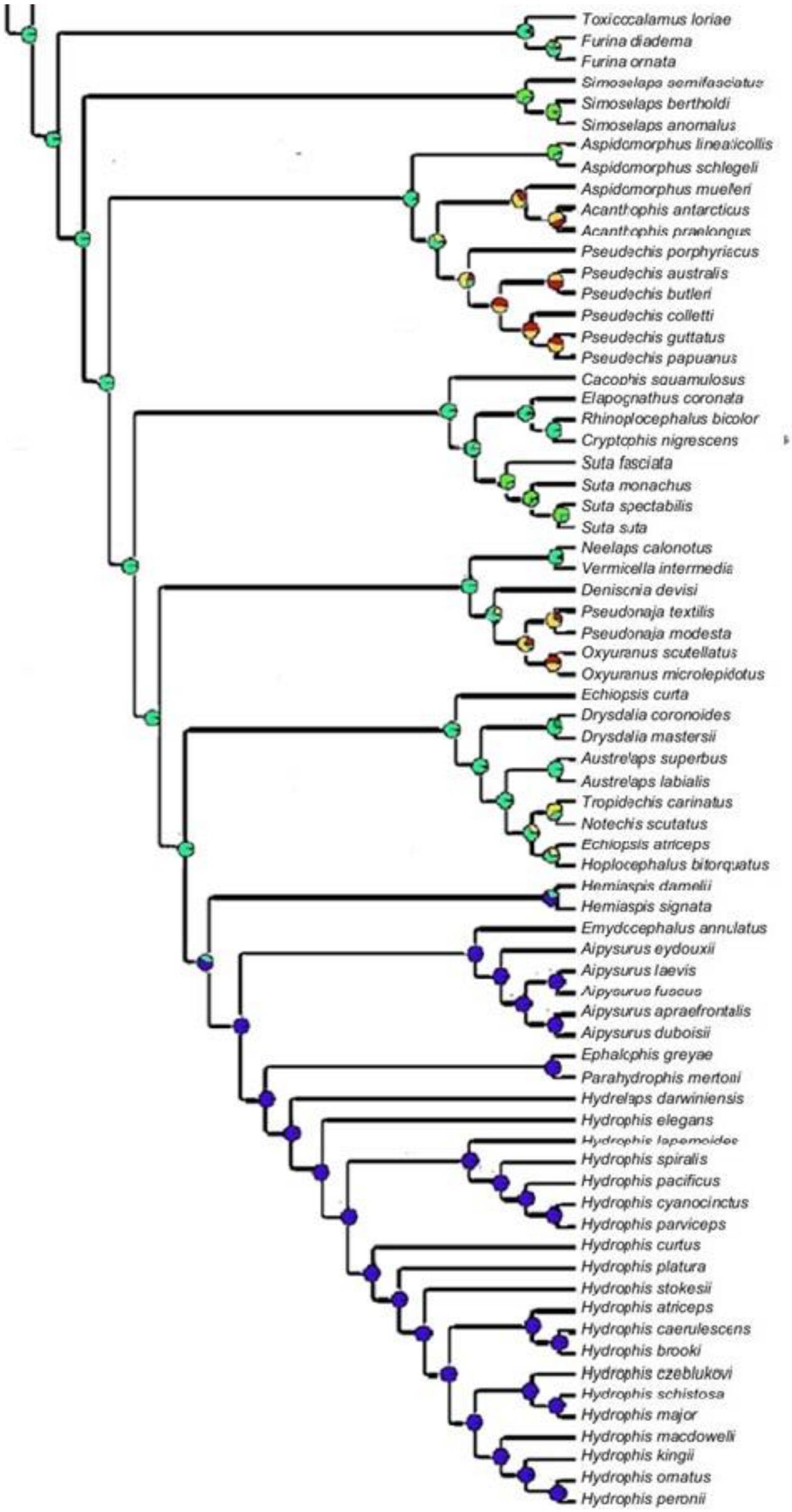

Figure 7. A maximum likelihood based reconstruction of diet in the Elapidae. Pie charts indicate the likelihood of particular diet types occurring at each node in the phylogeny. Diet types included the consumption of: Type 1 (purple), Type 3 (light blue), Type 4 (red), Type 6 (green), Type 7 (black), Type 2 (dark blue) and a Type 5 (orange) diet groups.

Table 2. The scaled probabilities of seven diet clusters occurring at the root node of elapid phylogeny.

Diet group	Type 1	Type 2	Type 3	Type 4	Type 5	Type 6	Type 7
Scaled likelihood at the-root node	0.57	0.00	0.28	0.03	0.03	0.05	0.04

3.5. Stochastic Character Mapping (Bayesian Inference)

This approach supports the idea that the ancestral elapid predominantly ate Type 1 if not other Type 3 prey groups (Table 3).The 100 stochastically modelled histories revealed patterns that were common in the alternative reconstructions. The technique indicates that Type 1 is most likely to transition into feeding on other Type 3 prey and this was the earliest diet shift within the clade (Table 4). Another recurring pattern was the depiction of a Type 4 or Type 5 diet as a trait that evolved relatively recently in the clade. Similar findings were seen with the evolution of Type 2 foraging. Parsimonious inferences suggest that Type 2 consumption evolved from an ancestor which fed on a very broad diet type (Fig. 7), however, ML & summarised SCC data indicate that Type 2 consumption most probably arose from a consumer of Type 3 prey (Fig. 8; Table 4). The inclusion of a sizable representation of Type 7 cluster is the newest dietary condition in elapids (Table 5). The model suggests that for the 100 stochastically created evolutionary hypotheses, elapids have spent the majority of their existence feeding on Type 1 prey (Table 5).

Table 3. The number of trees from of the 100 stochastically mapped histories which supported a particular diet groups as the possible ancestral condition.

	Type 1	Type 2	Type 3	Type 4	Type 5	Type 6	Type 7
Number of trees supporting the ancestral diet type	48	0	45	4	1	1	1

Table 4. The numbers of transitions which occurred between diet types in 100 stochastically mapped trees. On average trees had 110.38 changes between states.

Diet guild	Type 1	Type 2	Type 3	Type 4	Type 5	Type 6	Type 7
Type 1		0	11.59	0	0	0	0
Type 2	0		0.67	0	0	0.16	0
Type 3	9.45	1.89		3.63	5.86	6.51	4.37
Type 4	0	0	3.25		26.22	2.64	2.49
Type 5	0	0	4.27	28.55		0	1.15
Type 6	0	1.65	14.24	7.58	0		0
Type 7	0	0	1.45	0.84	0.3	0	

Table 5. The mean raw and proportional amount of time spent consuming seven diet types within the elapid snake family.

Diet group	Type 1	Type 2	Type 3	Type 4	Type 5	Type 6	Type 7
Raw	1.66	1.1	1.4	1.17	1.1	1.12	0.33
Proportional	0.21	0.14	0.18	0.15	0.14	0.14	0.04

3.6. Differences in the diets of elapids among biogeographic regions

Broad-scale biogeographic differences were observed in the prevalence of different dietary groups. The typical Australian elapid diet is largely comprised of Type 6 prey (Fig. 8). This is the case in 34.0% of species in this region while a further 22.0% feed on Type 3 diet (Fig. 8). The least prevalent diet type within Australian lineages was that of Type 7 (0.03%; Fig. 8). In contrast, Type 7 represented the most important diet group within the nearby New Guinean region, with 61.1% of species feeding on these prey (Fig. 8). Afrotropical elapid diets were charactersed by the consumption of Type 4 (41.4%) and Type 5 (27.6%) feeding patterns (Fig. 8). Type 1 prey were the most widely recorded diet type amongst Indo-Malaysian, Palearctic and Neotropical species (Fig. 8).

Amongst Indo-Malaysian elapids, 40.0% fed on Type 1 prey, while 20.0% of species in this region ate prey from the Type 4 or Type 5 clusters (Fig. 8). Over two thirds of the Palearctic species assessed fed on snakes while the rest fed on broad range of mainly Type 4 prey (Fig. 8). Type 1 was the diet most widely recorded among Neotropical elapid assemblages and this was the case for approximately 53.8% of species of species within this region (Fig. 8). Type 3 diet (21.4%) made up the second most important diet group within the Neotropical radiation followed by the Type 5 diet (8.7%). Neotropical assemblages were the only terrestrial radiation to include prey of the Type 2 cluster (however minor) into their diet (1.8%; Fig. 8). No Neotropical species ate prey from the Type 4 prey cluster (Fig. 8).

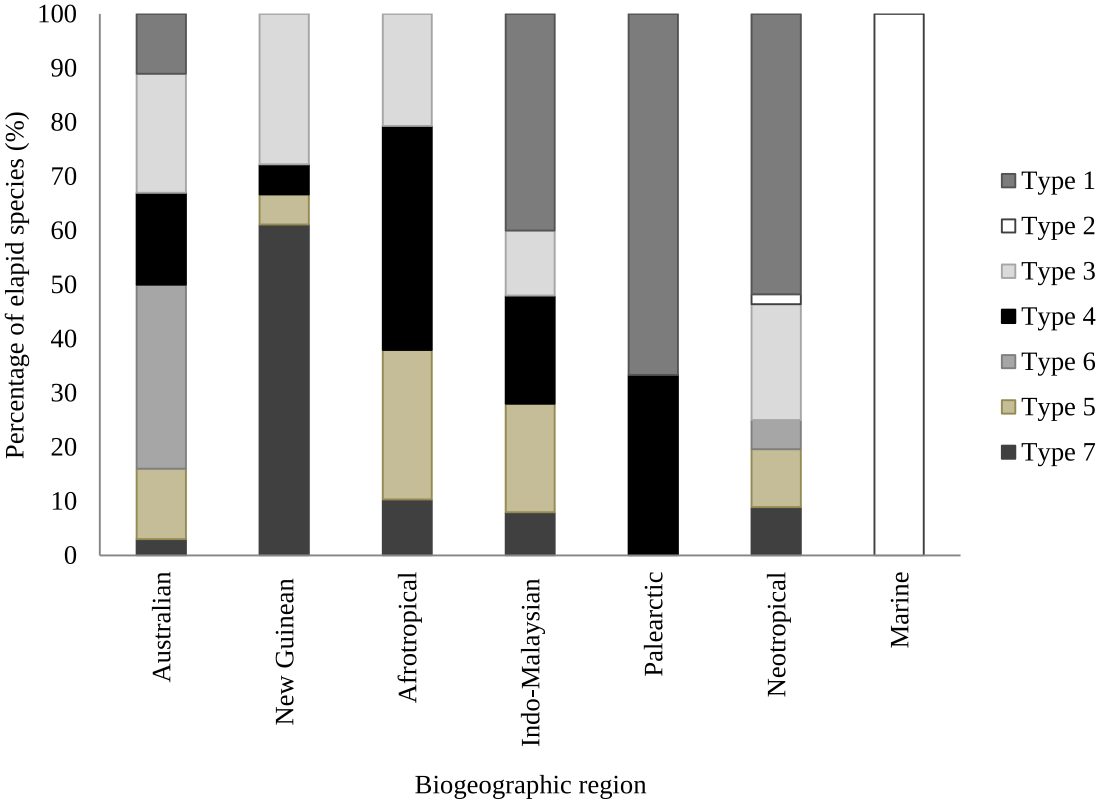

Figure 8. The dietary characteristics of elapid species occurring in seven biogeographic regions.

3.7. Evolutionary differences in diet types across biogeographic regions

In multiple pairwise comparisons of diet types and geographic regions, analyses showed that the model for correlated evolution fit the data significantly better than the alternative model of independence. For instance, evolving on the Australian landmass was significantly associated with the evolution of Type 6 consumption (P < 0.01, △LnL = 6.09, d.f = 4) (Fig. 9; Table 6). New Guinean elapid assemblages evolved primarily taking Type 7 prey (P < 0.05, △LnL = 3.30, d.f = 4) (Fig. 9; Table 6). Elapids forming part of the Afrotropical radiation were markedly inclined to forage on prey from the Type 3 (P < 0.01, △LnL = 3.89, d.f = 4), Type 4 (P < 0.05, △LnL = 1.96, d.f = 4), Type 5 (P < 0.01, △LnL=-5461.05, d.f = 4) and Type 6 (P < 0.01, △LnL = 7.84, d.f = 4) diet clusters (Fig. 9; Table 6).

The radiation of the family in Indo-Malaysian regions was related to the consumption of various prey forms such as Type 1 (P<0.05, △LnL = 3.24, d.f = 4), Type 4 (P<0.05,

$\triangle$LnL = 2161.00, d.f = 4), Type 5 ($P<0.05$, $\triangle$LnL = 4.50, d.f = 4) and Type 6 ($P < 0.01$, $\triangle$LnL = 2335.00, d.f = 4) feeding patterns (Fig. 9; Table 6). Palearctic assemblages also evolved to take on a Type 4 diet ($P < 0.05$, $\triangle$LnL = 4.00, d.f = 4) in addition to one comprised of Type 1 prey forms ($P < 0.01$, $\triangle$LnL = 6.79, d.f = 4) (Table 6). In contrast Neotropical snakes showed a relationship with feeding on Type 1 prey ($P < 0.01$, $\triangle$LnL = 12.61, d.f = 4), whereas no statistically meaningful associations were seen with the consumption of Type 4 prey ($P = 0.16$, $\triangle$LnL = 0.89, d.f = 4) (Fig. 9; Table 6).

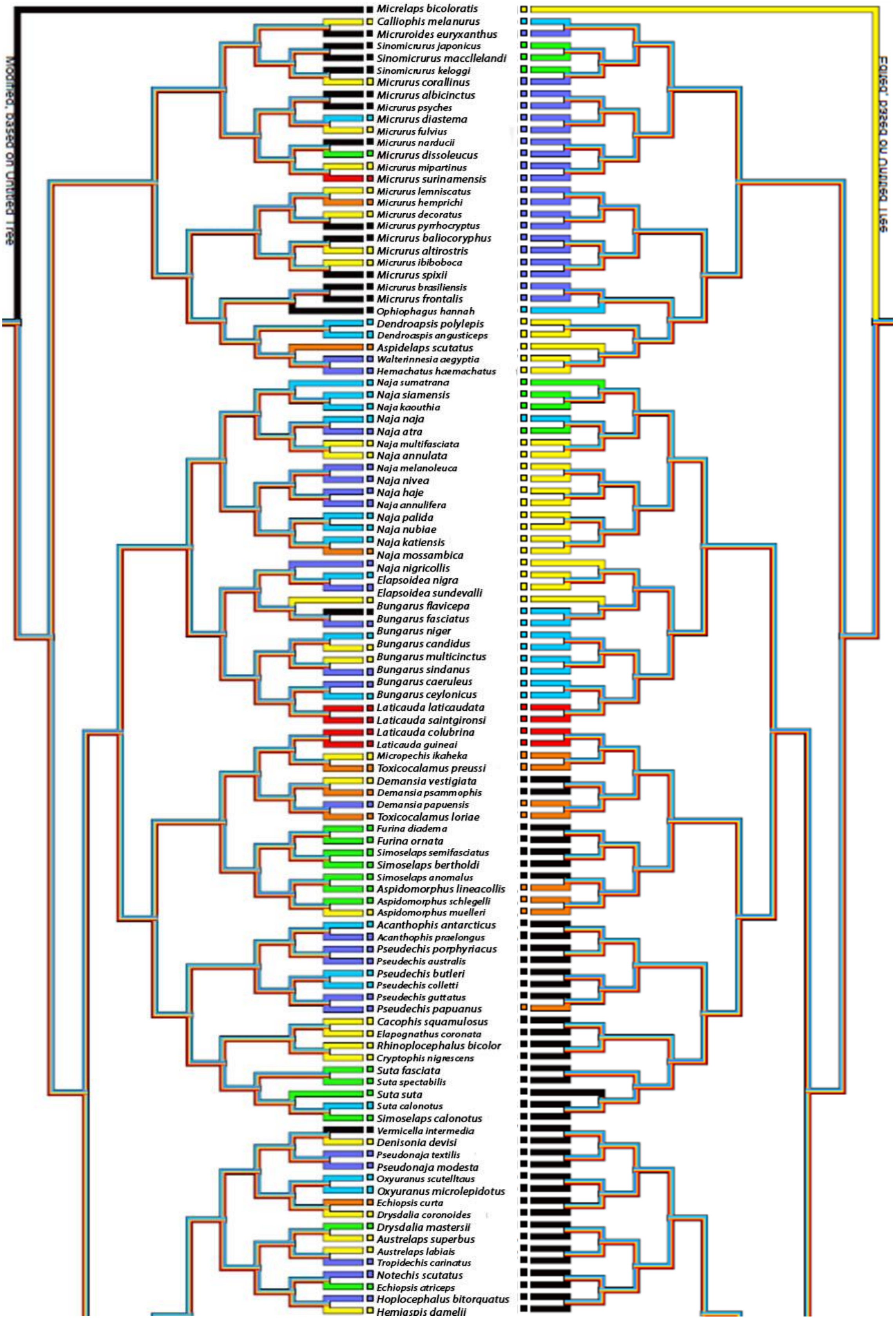

Figure 9. Mirror tree view of the reconstructed diet (left) and broad scale geographic distribution of the Elapidae. On the left branch colours are as follows: black (snakes), red (Type 2), green (Type 6), yellow (Type 3), light blue (Type 5), dark blue (Type 4), and orange (Type 7). In the regional reconstruction: Australian (black), Indo-Malaysian (blue), Palearctic (green), Neotropical (dark blue), Afrotropical (yellow) and marine (red).

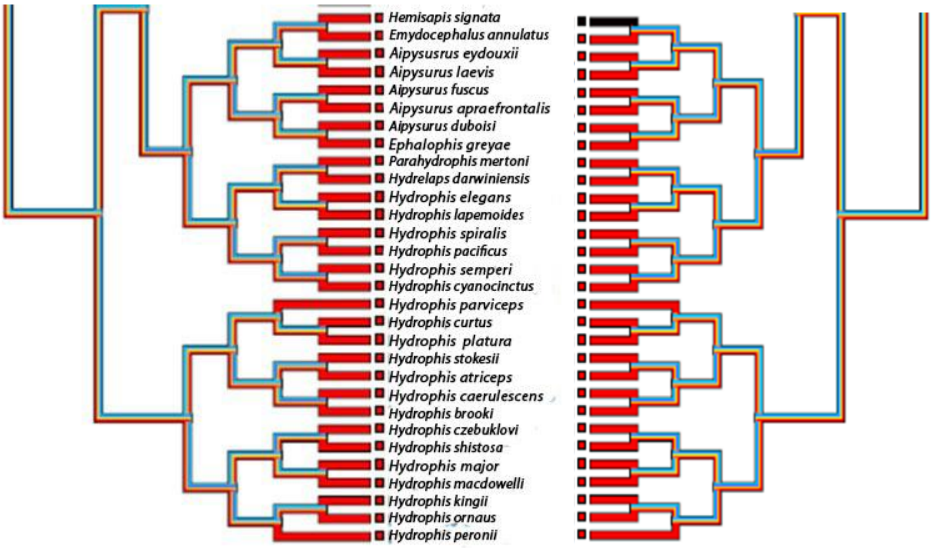

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Table 6. Pagel's correlation output on the evolutionary covariation in diet types across different biogeographic regions. Results are presented as P values with the differences in log likelihoods (△LnL) occurring within brackets. For each pairwise comparison the degrees of freedom are 4.

Zoogeographic region	Type 1	Type 2	Type 3	Type 4	Type 5	Type 6	Type 7
Australian	0.13 (2.00)	**< 0.02 (2.74)**	0.25 (1.66)	0.12 (2.31)	0.09 (2.6658)	**< 0 001 (6.09)**	0.08 (2.53)
New Guinean	0.42 (0.58)	**< 0.001 (5.40)**	0.70 (0.86)	0.29 (1.93)	0.34 (1.81)	0.44 (0.69)	**< 0.05 (3.30)**
Marine	0.16 (2.11)	**< 0.001 (18.85)**	0.23 (2.33)	**< 0.05 (4.04)**	**< 0.05 (4.90)**	0.207 (1.97)	0.07 (2.37)
Afrotropical	0.32 (1.97)	0.32 (2.09)	**< 0.001 (3.89)**	**< 0.04 (1.96)**	**< 0.01 (- 5461.15)**	**< 0.001 (7.84)**	0.05 (1.07)
Indo-Malaysian	**< 0.01 (3.24)**	**< 0.01 (4.21)**	0.29 (0.85)	**< 0.01 (- 2161.00)**	**< 0.05 (4.50)**	**< 0.001 (- 2335.00)**	0.15 (9.96)
Palearctic	**< 0 001 (6.79)**	0.20 (2.40)	0.34 (4.38)	**< 0.01 (4.00)**	0.18 (2.24)	0.45 (0.70)	0.26 (2.09)
Neotropical	**< 0.001 (12.61)**	**< 0.001 (1.75)**	0.27 (2.09)	0.16 (0.89)	0.13 (2.15)	**< 0.02 (1.39)**	0.4 (- 25075.78)

3.8. Differences in the diet characteristics in relation to lifestyle

Amonst the 303 elapids evaluated the largest group (32.0%) are ground-dwelling hunters (Appendix 3). Although Type 1 prey were consumed by elapids leading both arboreal (26.7% of Type 1 consumers) and ground-dwelling (4.4% of Type 1 feeding species) lifestyles, the vast majority (68.9%) of snake feeders were burrowers (Fig. 10.a). Type 7 consumption was, likewise, associated with a primarily cryptozoic to fossorial existence (68.0 %), while 16.0% of species in this dietary cluster were either climbers or surface active (Fig. 10.a). Approximately 50.0% of Type 6 consumers were ground-dwelling hunters, while the other half burrow to some degree (Fig. 10.a). Nearly 66.6% of the elapid species consuming a Type 4 diet were largely ground-dwelling (Fig. 10.a). Arboreal to semiarboreal (19.4%) species were also prominent within the Type 4 cluster compared to burrowing (8.3%) and semiaquatic (5.6%) forms (Fig. 10.a). Snakes foraging on a Type 5 diet were similarly mainly terrestrial (56.3%), secondarily arboreal (21.9%) while also having a sizable representation of burrowing species (18.8%; Fig. 10.a). Most (66.7%) of the semiaquatic elapids, for the most part, preyed on Type 3 prey (Fig. 10. a).

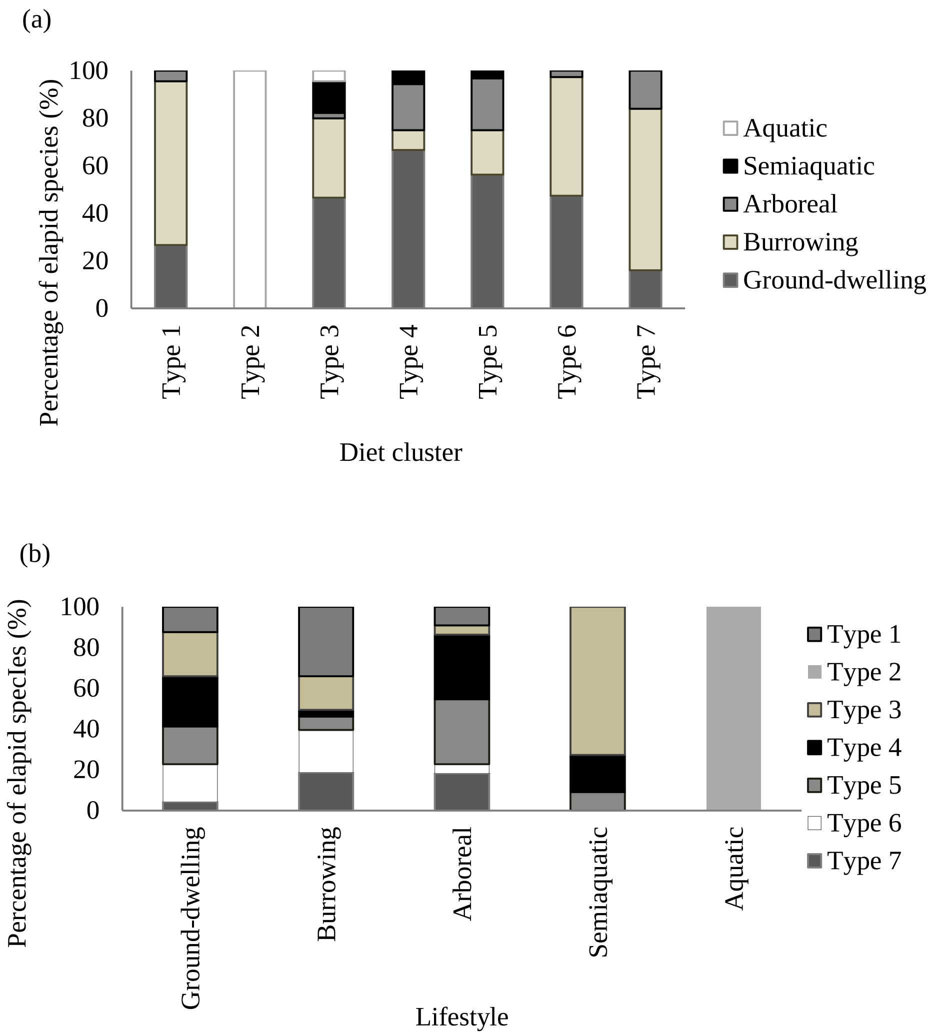

Figure 10. The variation in the consumption of seven diet groups among elapids with different lifestyles. Data are represented as (a) the percentage of elapids in each diet cluster which lead a particular lifestyle or (b) the percentage of species in each lifestyle category known to prey upon each diet cluster.

3.9. Lifestyle and diet

The reconstruction suggests that elapids evolved from a burrowing ancestor and that this plesiomorphy occurs in 29% of the extant species represented in Pyron *et al.*'s (2013) tree, and 30% of the overall species assessed (Fig. 11; Appendix 3). Elapids which burrow or inhabit leaf litter evolved to feed on Type 1 ($P < 0.01$, $\triangle LnL = 3.02$, d.f = 4), Type 3 ($P < 0.05$, $\triangle LnL = 6.00$, d.f = 4) and Type 6 ($P < 0.05$, $\triangle LnL = 4.27$, d.f = 4) prey items (Fig 11; Table 7). From this ancestor, the first terrestrial elapids appeared relatively early in the history of the family and this particular mode of living became the most prolific throughout the clade (Fig. 11). Being terrestrial was linked to feeding on several diets including Type 4 ($P < 0.05$, $\triangle LnL = 3.98$, d.f = 4), Type 5 ($P < 0.05$, $\triangle LnL = 3.89$, d.f = 4), Type 6 ($P < 0.05$,

$\triangle$LnL = 3.22, d.f = 4) and Type 7 ($P < 0.05$, $\triangle$LnL = 4.06, d.f = 4) feeding patterns (Fig. 11; Table 7).

Type 3 diet (with an emphasis on amphibian prey) has been a defining characteristic throughout the short semiaquatic elapid evolutionary period ($P < 0.01$, $\triangle$LnL = 6.02, d.f = 4) (Table 7). This mode of life represented the most apomorphic of all lifestyles in the family (Fig. 11). Arboreality is yet another derived trait which evolved in at least four evolutionary events which were linked with eating a Type 4 ($P < 0.01$, $\triangle$LnL = 7.83, d.f = 4) or Type 5 diet ($P < 0.01$, $\triangle$LnL = 5.71, d.f = 4) (Fig. 11; Table 7).

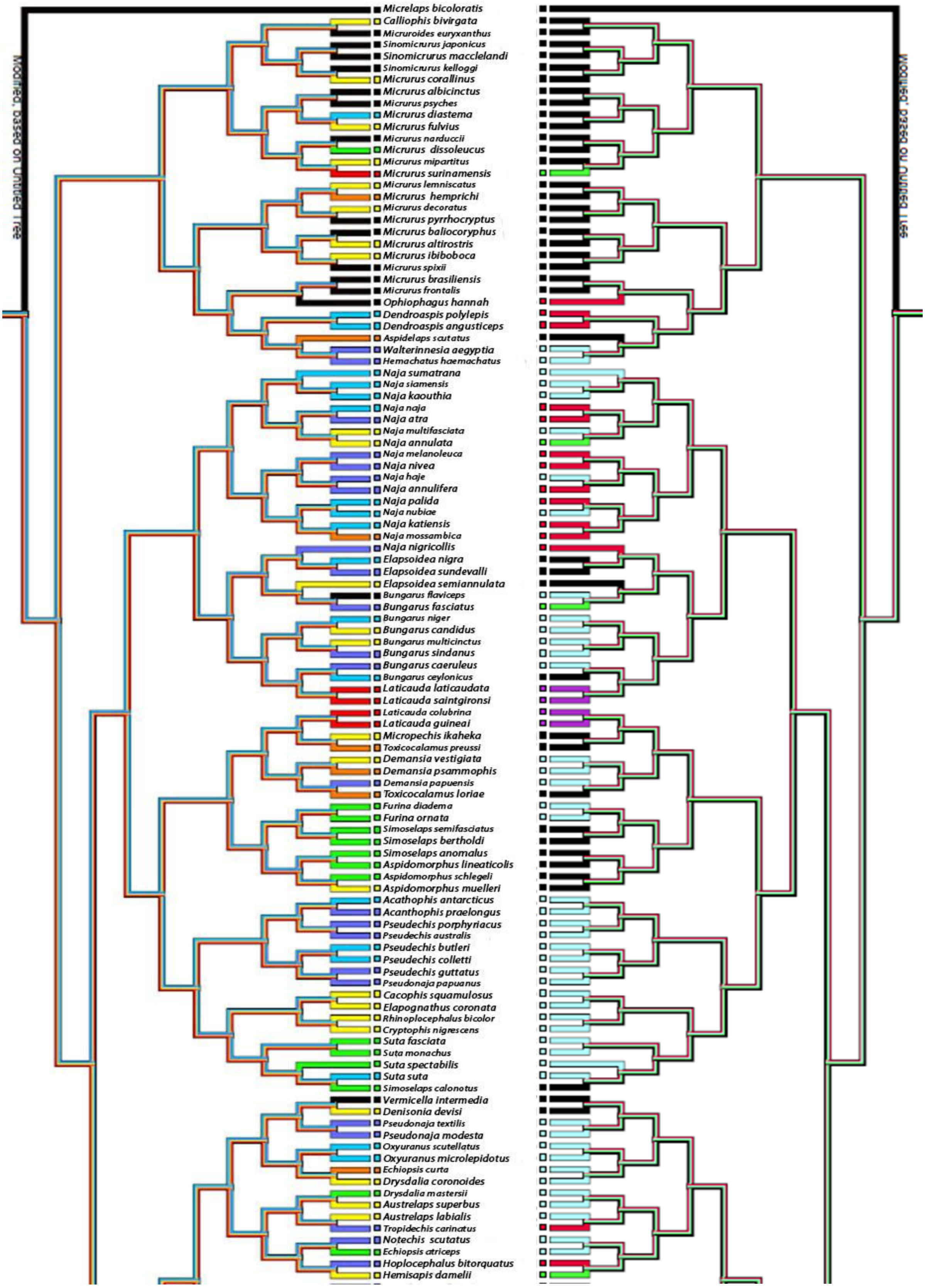

Figure 11. The maximum likelihood reconstructed mirror trees of diet (left) and lifestyle (right) for the Elapidae. In the diet reconstruction colours are as follows: black (Type 1), red (Type 2), yellow (Type 3), dark blue (Type 4), light blue (Type 5), green (Type 6), orange (Type 7). Lifestyle reconstruction colours indicate the following: red (burrowing), yellow (aquatic), green (ground-dwelling), purple (arboreal), blue (semiaquatic).

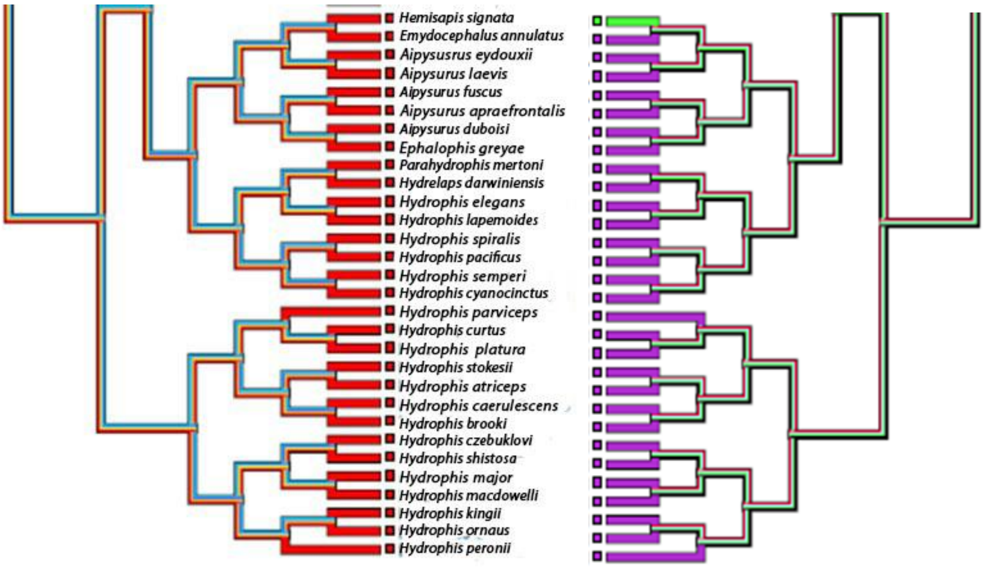

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Table 7. Results of Pagel’s correlation on the association in the rates of lifestyle and diet evolution. Data are shown as P values and differences in log likelihoods (△LnL) are bracketed. For each pairwise comparison the degrees of freedom are 4.

Lifestyle	Type 1	Type 2	Type 3	Type 4	Type 5	Type 6	Type 7
Ground-dwelling	0.15 (-149.71)	**< 0.001 (6.54)**	0.27 (1.00)	**< 0.05 (3.98)**	**< 0.05 (3.89)**	**< 0.05 (3.22)**	**< 0.01 (4.06)**
Burrowing	**< 0.001 (3.02)**	**< 0.001 (7.37)**	**< 0.01 (6.00)**	0.31 (2.31)	0.08 (5.36)	**< 0.05 (4.27)**	0.34 (1.52)
Arboreal	0.129 (2.15)	**< 0.001 (1.75)**	0.08 (2.08)	**< 0.001 (7.83)**	**< 0. 001 (5.71)**	0.15 (2.13)	0.24 (4.21)
Semiaquatic	0.10 (1.52)	**< 0.05 (1.89)**	**< 0.001 1(6.02)**	0.44 (0.86)	0.11 (1.36)	0.70 (0.60)	0.26 (1.00)
Aquatic	**< 0.001 (1.57)**	**< 0.001 (14.11)**	**< 0.001 (5.24)**	0.26 (1.35)	0.08 (1.34)	0.19 (1.80)	**< 0.01 (3.11)**

Table 8. The scaled likelihoods of different lifestyle categories at the root node of the Elapid phylogeny.

Diet group	Burrowing	Arboreal	Ground-dwelling	Semiaquatic	Aquatic
Scaled likelihoods at the root node	0.9683	0.0006	0.0304	0.0006	0.0001

3.10. Body size and diet

Intial evaluations of the mean maximum total lengths of elapids using standard statistical tests revealed significant differences in the sizes of species consuming different diet types (ANOVA: $P < 0.01$, $F = 75349.74$, d.f = 1). However, there is a strong phylogenetic signal in the body size patterns of the Elapidae (Phylogenetic Anova: $P = 0.994$, $F= 0.436$; Fig. 12). This indicates that species probably have similar body sizes as a function of shared common history rather than diet differences.

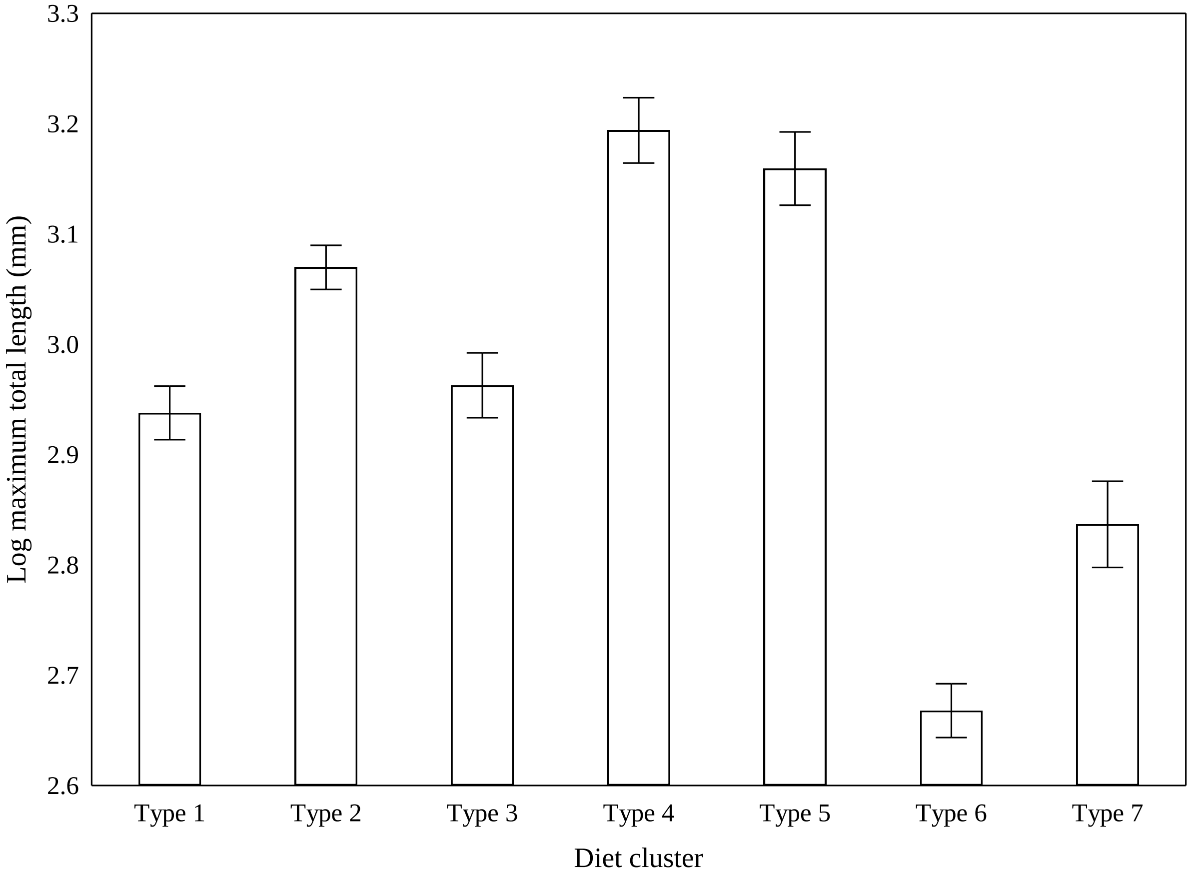

Figure 12. Differences in the log maximum total lengths (mm) of elapids consuming different diet types. Error bars represent standard error.

4. DISCUSSION

4.1. Diet evolution

My analyses show that ancestral elapids were likely to be fossorial and fed on snakes and lizards (Type 1). Most extant elapid snakes consume prey in the Type 1 or Type 2 diet characterised by the consumption of fish, especially eels and gobies. From a functional (morphological) standpoint, the ancestral and contemporary elapid feeding patterns are characterised by the consumption of elongate prey. This suggests that the overarching dietary patterns is one of niche conservatism, where the observed evolutionary change in a feature is either slow or absent (Wiens *et al*. 2010). The reasons behind the pattern of elapids consuming elongate prey may be constrained by their body shape as they tend to be slender snakes. Broader diet types such as those seen in the Type 4 (generalist) or Type 5 (endotherm inclusive) diet clusters are a relatively derived characteristic within the Elapidae. Prey type also appears to be related to biogeographic area of occurrence and lifestyle.

The reason behind elapid snakes consuming elongate prey is primarily attributed to head morphology (Cobb 2004; Jackson *et al*. 2004). Most elapids, relative to vipers and pythons, are slender with a narrow head possessing shorter mandibles and quadrates which constrains the gape size and the range of ingestible prey sizes (Greene 1983; Greene 1997). The difference in mass between the snake predator and its prey is described as the weight ratio, while the ingestion ratio quantifies the relative width of prey to the predator’s head (Greene 1983; Greene 1987). A slender, small-headed snake feeding on relatively bulky items such as birds and mammals would show disproportionately high ingestion and weight ratios (Jackson *et al*. 2004; Greene 1983). With the consumption of long items, elapids and their prey may be roughly the same width keeping the ingestion ratio low, while the predator is able to achieve a high weight ratio (Jackson *et al*. 2004). Despite lacking adaptations for a wide gape, elapids are able to circumvent possible prey width restrictions on prey size, thus allowing for larger meals or a more varied range of prey (Cobb 2004). This may have facilitated ecological shifts to the diverse habitats in which the elongate prey occur. Moreover, specialising on long prey may have released them from competition with vipers, boas and other snake families known to eat heavy-bodied prey

Generalist diets inclusive of endotherms appears to be a relatively derived characteristic in elapids. This finding is supported by all three of my reconstruction hypotheses. Queiroz and Rodriguez-Robles (2006) states that such shifts in diet generally originate through the incorporation of new prey types as secondary dietary components. It is unclear what forces may be responsible for producing these patterns. Competitive interactions between ecologically similar elapids for limited resources may be leading to character displacements, facilitating ecological shifts to broader, more opportunistic diets than previously seen in the family. While squamate consumption has been the typical diet type in the Elapidae, noticeable niche divergences have emerged as a result of many independent adaptations.

4.2. Diet and the biogeographic regions

For many faunal assemblages, geographically separate groups experience vastly different selective pressures due to different ecological conditions (Tremblay & Cherel 2003) and histories (Olson *et al*. 1995). The evolutionary course of the various diet types varied significantly across biogeographic regions. Each of the biogeographic regions has a unique diet evolution pattern which has been influenced by ecological and biogeographic factors associated with the area. For instance, species making up the Australian assemblage are the result of a single evolutionary radiation that occurred approximately 10-18 million years ago (Grundler & Rabosky 2014). Despite being a recent radiation, this clade includes forms which exploit most terrestrial habitats on the continent (Shine 1995). Within these habitats, Australian elapids feed on prey ranging from small insects and tadpoles, to other snakes and various marsupials. The diversity and adaptive success of these predators is probably due to the fact that the elapid which first arrived on this continent did so in the absence of any other ophidian competitors which traditionally occupied various niches on other continental landmasses (Grundler & Rabosky 2014). The ancestral forms were able to morphologically and ecologically diversify to fill different predatory roles before any other snake group had a chance to arrive in Australia (Shine 1995).

Pagel’s correlation revealed that evolving in Australia was significantly associated with the consumption of Type 6 prey (lizards and reptile eggs). This is to be expected given that the typically arid and warm conditions on this continent are ideal for fostering a dominance of reptilian prey while limiting the region’s capacity to support endotherms. Endotherms have higher metabolic rates than ectotherms at a given mass (Nagy 1987). Endotherms require more food to maintain a constant body temperature (Pough 1980). In contrast, the ectothermic physiology of reptilian prey means that they can withstand extended periods of food scarcity typical of the Australian continent (Pough 1980). Australian diet patterns are therefore likely a function of physiological and biogeographical factors (Shine 1983).

It was indicated that for most of their evolution, coral snakes of the Americas were inclined to feed on snakes and lizards, fish, ectotherms and terrestrial invertebrate diets. A detailed analysis of Neotropical elapid diets reveals that although their food groups are taxonomically diverse, they are generally dominated by elongate ectothermic prey (Appendix 3). A sizable representation of the lizards consumed are skinks and amphisbaenids and *Micrurus narducci* even consumes the autotomized tails of lizards (Harry Greene pers. comm.). Aquatic coral snakes primarily eat eels but knifefish are also taken. Moreover, coral snakes consume a considerable number of amphibian prey. The overwhelming majority of amphibians consumed are caecilians at just over 88% of the reported records (Appendix 3). Feeding patterns observed in coral snakes appear to echo those seen in the Elapidae in general, where the diet is constrained prey body shape. Greene (1984) found the diet of the primarily ophiophagus *Micrurus fulvius* to be more closely associated with prey length, while relative prey diameters were comparable.

Coral snakes are morphologically conservative, each with a slender body and a small head that is barely distinct from the neck (Greene 1997). Their skulls have a low number of scales and their quadrate and mandibular bones are short (Greene 1983; Cobb 2004). The reason behind these predators going for the elongate prey that characterise their diet may strongly correlate with skull morphology. Bearing in mind how coral snakes are structured, it would be advantageous for them to select prey that will not require these predators to have a very wide gape to swallow them. This is further demonstrated by the fact that, despite the widespread availability of avian and mammalian prey in the Americas, coral snakes do not feed on them (Table 4; Appendix 3). In cross section, the body profile of birds and small mammals would generally be larger in diameter than the typical lizard, thus necessitating a large gape to swallow them (Greene 1997). This suggests that, owing prey width constraints, Neotropical coral snakes are actively selecting their prey on an item to item basis (Greene 1997).

Afrotropical snakes demonstrate by far the broadest diet profile within species (Appendix 3). The rates of evolution of a generalist diet inclusive of endotherms were significantly associated with evolving within Africa (Table 6). Most terrestrial and aquatic prey classes, with the exception of fish eggs, are eaten by Afrotropical elapids. Elapids within this region also have the widest range of body sizes. Species consuming a broader range of prey would require the necessary range of cranial and skeletal dimensions to swallow and process their varied prey items. Furthermore, different body types would be required to optimally navigate the different habitats in which a broader range of prey may occur (see chapter 1.4). However given the low correlation between body size and diet the wide range of diets is probably a function of factors other than the predator’s length (Fig. 13). A possible interpretation may lie in the impressive ecological and taxonomic variety of African elapids. The Afrotropical elapid fauna has a generic richness which is second only to that of the Australian radiation (Keogh 1998). Within this elapid radiation, morphologically varied groups are found which also occur in a great diversity of habitats.

4.3. Diet and lifestyle

The results of Pagel’s correlation show that, for much of their evolution, elapids leading different lifestyles differed in the consumption of the various diet types (Table 7). This indicates that diet signifies an important axis of variation amongst ground-dwelling, climbing, burrowing and aquatic hunters. However no all-encompassing explanation for these differences is apparent. The majority of modern ground-dwelling elapids demonstrate broad dietary patterns having evolved to feed on prey from a number of diet clusters throughout their history (Table 7). The reasons for the generalist diet patterns of ground-dwelling predators may lie in their tendency to travel large distances over which they may encounter a wider variety of potential prey types.

In a similar vein, over the course of their evolution, arboreal elapids typically evolved to forage on a broad diet which consists primarily of birds and mammals (Table 7). Two explanations may account for the patterns seen. Firstly, active foraging is considered the typical foraging strategy amongst the Elapidae, however consummate climbing elapids such as *Dendroapsis* and *Hoplocephalus* exhibit ambush predation remaining sedentary for several days at a single site awaiting the arrival of prey (Greene 1997; Fitzgerald *et al*. 2002). Given the long intervals between meals, ambush foragers elapids may be inclined to take large-bodied prey such as endotherms to maximise energy intake (Greene 1983).

Hoplocephalus has a relatively broad distribution and the home ranges of *H. stephensii* have been reported to greatly exceed those of even much larger-bodied elapids such as *Pseudonaja textilis* and *Pseudechis porphyriacus* (Fitzgerald *et al*. 2002). The tree-dwelling *Pseudohaje goldii* is widely distributed through central Africa from Kenya westwards to Nigeria and parts of Ghana (Akani *et al*. 2005). Luiselli *et al*. (2000) similarly reports that Green mambas show an extensive distribution and are able to persist in a wide variety of the habitats provided there are thickets and trees to hide in. A widespread distribution may well explain why tree dwelling elapids feed on a broad spectrum of prey, given that more varied prey are likely to be encountered in a larger home range. Conversely, these distribution patterns could be owing to a scarcity of spatial and trophic resources as arboreal elapids may occur syntopically with other large-bodied arboreal snake species (Luiselli *et al.* 2002). The utilisation of the greater habitat range combined with evolving to feed on a comprehensive array of prey could allow climbing elapids to avoid the presence of conspecifics or other potential competitors (Fitzgerald *et al*. 2002).

While above ground foraging has its own associated diet types, Pagel's correlation revealed that foraging below ground often entailed feeding on a broad range of prey types (i.e., snakes, lizards and other ectotherms, endotherms and terrestrial invertebrates) (Fig. 11). The ancestral elapid probably inhabited leaf litter or lived below surface level. As previously highlighted, most elapids feed on elongate ectothermic prey (see chapter 4.1), however it is among subterranean foragers (especially coral snakes) that this pattern is most apparent. For instance, Appendix 4 indicates the typical prey forms taken by elapids which burrow, demonstrating the dominance of one morphological prey type among the great taxonomic diversity eaten. These diet characteristics may result from morphological restrictions that prevent elapids possessing narrower, more specialized head morphologies from taking on larger bodied prey. This supposition is more comprehensively explained in chapter 4.1. Most of the prey classes evaluated in this study with the exception of avifauna (and their eggs), or fish (and their eggs) are available in cryptozoic and fossorial environments. This implies that the diet of burrowing elapids reflects prey selection based on morphology as opposed to prey availability within these habitats.

Despite showing some morphological selection for prey shapes typical of ectotherms, most burrowing elapids can be considered diet generalists (I noted a wide array of invertebrate and vertebrate prey with high class-level diversity). However, genera such as *Toxicocalamus*, *Sinomicrurus*, *Simoselaps*, *Vermicella* and *Brachyurophis* show relative dietary specialisation suggesting that they avoid most other available prey while targeting others. The majority of terrestrial invertebrate consumers are found within leaf litter or below ground (Appendix 3). This diet cluster is the rarest and most specialised dietary condition in the Elapidae. Greene (1983) states the overall feeding biology of snakes is characterised by infrequent feeding on relatively large prey items. It is likely that because of their small size, terrestrial invertebrates are often too small to offer enough nutritional value for the extended intervals between meals. In the family as a whole, primarily foraging on terrestrial invertebrates may thus be a less optimal foraging strategy.

The most important example of terrestrial invertebrate consumers lies in the genus *Toxicocalamus* wherein 88% of species eat earthworms (Appendix 3). This prey type is possibly favoured because of their high protein content which may compensate for the cost required to locate prey in complex subterranean environments. Alternatively, *Toxicocalamus* select thise particular prey for their low processing and handling costs given that earthworms are relatively defenceless soft-bodied invertebrates (Greene 1982). Blindsnakes which are favoured by *Sinomicrurus*, *Simoselaps* and *Vermicella* are small-bodied, with reduced vision and possess no venom or the ability to inflict a powerful bite (Alexander & Marais 2007). These diet preferences, similar to those of terrestrial invertebrate feeders, could be due to selection for more vulnerable prey.

Elapid species which specialise in eating reptile eggs (e.g., *Brachyurophis*) hunt for them in subterranean galleries. The dentition of *B. semifasciatus* is greatly modified with the anterior teeth being reduced in size and number while those of the pterygoid are posteriorly enlarged and blade like to apply considerable force to the eggshells (Scanlon & Shine 1988). The consumption of eggs, either avian or reptilian, may have simply evolved as a form of trophic opportunism among species whose ancestors fed on prey which lay eggs (Alencar *et al*. 2013; Travaglia-Cardoso *et al*. 2014). The benefits of feeding on this prey is further enhanced by the food group being a high energy food source that has low handling costs given that they are defenceless.

Semiaquatic elapids possess the most derived lifestyle type amongst the Elapidae (Fig. 11). The divergence into underwater foraging may have resulted from opportunistic foraging on the aquatic prey which met the morphological characters generally selected for by elapid predators (see chapter 4.1). Nowhere is this more apparent than in *Micrurus surinamensis*, the only member of the typically burrowing coral snakes that specialises in fish consumption (O'Shea 2008; Carillo de Espinoza 1983). This predator spends the majority of its life in slow moving water bodies where it feeds on knifefish, catfish and swamp eels (Carillo de Espinoza 1983; Schlüter *et al*. 2004; Avila *et al*. 2012). This diet type likely recently evolved so the species could capitalise on the elongate water dwelling fish which the rest of its congeners were not exploiting (see chapters 4.1 & 4.2).

Amongst marine elapids, eels and goby-like fish are consumed by the greatest number of predator species and most prey species are relatively sedentary, dwelling on the sea bottom, or within burrows and reef crevices (Seigel *et al*. 1987). This suggests that even with the major ecological shift to living in marine areas, active foraging prevails as the primary mode of hunting prey among elapids given that they would have to actively pursue prey within their frequent habitats. Nevertheless, several modes of feeding were used by sea snakes: (1) *Aipysurus foliosquama* actively hunts a variety of small fish in shallows and reefs (Heatwole 1999; Mirtschin & Davis 1992); (2) *Hydrophis platurus* ambushes a wide range of pelagic fish (Whitaker & Captain 2004; Alexander & Marais 2007); (3) *Emydocephalus annulatus* has the most unique mode of feeding known amongst snakes (Shine *et al*. 2004). This species forages by moving slowly but as they investigate crevices and burrows for fish eggs (Shine *et al*. 2004). The snakes frequently feed on a large number of markedly smaller defenceless and immobile prey - a mode of feeding reminiscent of browsing (Shine *et al*. 2004).

The correlations between traits suggest that diet and lifestyle often respond to some common evolutionary force or that one serves as a selective force for shifts in the other. This is in keeping with predictions that where and how an elapid forages played a key role in influencing diet diversification within the lineage. There was however no obvious pattern or explanation to feeding dynamics amongst guilds. In some cases, foraging strategies appear to simply reflect differential exposure to varied prey in the microhabitats inhabited by predators. Contrastingly, the morphologically mediated diet patterns in burrowing elapids could be owing to gape limitations associated with the slender cranial design required to forage in narrow tunnels (Greene 1997). At the broadest level, competition for limited resources (intraspecific and/or interspecific) may have promoted diversification into previously unoccupied or underutilized niches allowing these snakes to exploit a greater variety of prey (Shine 1991). Because we have yet to quantify the relative importance of each possible factor, future studies on the sympatric ecology of snake groups could clarify the specifics of why and how lifestyles and foraging dynamics interact.

4.4. Body size and diet

The phylogenetic Anova revealed that differences in body size and diet are not interrelated in the Elapidae (Fig. 12). These findings go against what is generally reported with respect to snake-prey size dynamics. A number of studies addressing this have indicated that prey selection tends to be strongly influenced by predator sizes (Downes 2002). Not surprisingly, in many species of snakes, larger-bodied predators tend to eat bigger-sized prey than do smaller-bodied individuals of the same predatory species (Shine 1991b). Among snakes, these intraspecific relationships regarding prey and predator size have been recognised in several species of the families Acrochordidae (Shine, 1986); Boidae (Slip & Shine 1988); Colubridae (Fitch 1982); Typhlopidae (Shine & Webb 1990) and Viperidae (Pough & Groves 1983). These patterns could be due to larger-bodied snakes being more capable of capturing, subduing and consuming larger-bodied prey (Shine 1991; Reading & Jofre 2013). Moreover, given that predators of varying sizes may hunt in different ways, amongst different habitats and at different times, these factors may significantly influence the prey types encountered (Shine 1991b). Alternatively, larger predators may be selecting larger prey because of their greater caloric value (Greene 1997).

In the case that these patterns persisted in Elapidae, species attaining a greater maximum size might have shown significant associations with the consumption of an endothermic diet. In contrast, smaller-sized elapids may be expected to consume more lizards, terrestrial invertebrates and other ectotherms. For example in *Bothrops moojeni*, amongst many other vipers, an ontogenetic diet shift occurs, characterized by the consumption of lizards and amphibians by younger vipers, whilst adults ingested birds and mammals (Andrade & Abe 1996). Similarly in *Vipera berus* ectotherms (i.e., lizards) formed the primary dietary component of smaller-bodied snakes, while large-bodied snakes fed on mammals (Brito 2004; Santos *et al*. 2008). Analogous diet shifts with increasing snake size have also been observed in members of Colubridae and certain sea snake species (Seigel *et al*. 1987). Unlike the relatively flattened body cross-section of lizards and amphibians those of birds and small mammals are more spherical requiring a proportionately larger gape to consume (Arnold 1993; Reading & Jofré (2013).

Body size was also expected to interrelate with diet breadth since large-bodied snakes may have a greater gape and hence be capable of ingesting a wide range of prey sizes and shapes (Shine 1991b; Greene 1997). Moreover, bigger-bodied snakes may encounter more types of prey by searching over wider distances than smaller counterparts (Greene 1997). For instance Reading & Jofré (2013) reported that the largest of *Coronella austriaca* were able to prey upon all the prey species accessible to them, while the smallest snakes were limited to the small-bodied prey because of their limited gape. In Elapidae however, a significant correlation between greater body length and a generalist diet was not evident (Fig. 12).

Instead the phylogenetically-based analyses of this study revealed that diet is a poor predictor of historical body size patterns which were instead phylogenetically structured. Others studies such as Shine (1977, 1987), Garcia and Drummond (1988) and Cobb (2004) have also documented little or no snake-prey size relationships. The most likely explanation for the lack of association may be that despite being able to take on larger-sized prey, elapids of a greater size continue to feed on small-bodied prey if the opportunity presents itself (Pough & Groves 1983; Arnold 1993; Greene 1997). For *Thamnophis sirtalis* and several other colubrid and viperid taxa, large-bodied individuals reportedly ingested bigger-sized prey than did smaller conspecifics, but did so without disregarding small-bodied prey (Greene 1997). This may be because for those slightly larger-bodied snakes, smaller prey may be nutritious yet energetically cheap to handle without the added cost of having to find a better item (Shine 1991; Greene 1997). Because of these feeding patterns, there may be a certain degree of correlation with maximum prey size but not minimum prey size, resulting in a telescoping pattern described by Arnold (1993).

Terribile *et al*. (2009) found that various environmental models did not significantly explain global interspecific patterns in the average body size of elapids. The study supports observations that, in general, representatives of Elapidae are morphologically conservative (Slowinski 1995; Terribile *et al*. 2009). In the present study, trends in body sizes have been structured and constrained by long-established phylogenetic characteristics rather than recent ecological factors such as prey types. It is however, also possible that predator-prey size dynamics may be explained in ways not assessed within this study. For instance, future studies should consider the influence of sexual dimorphism and ontogenetic differences in the sizes of prey taken.

Studies on a wide variety of snakes have suggested that natural selection may be a major evolutionary force driving differences in body size or energy requirements between the sexes (Shine 1994, Vincent *et al*. 2004). There may be selection for male and female elapids to reduce competition for limited trophic resources by growing to markedly dimorphic sizes (Shine 1991). This may be the case in female *Laticauda colubrina* which achieve a greater size than male conspecifics and subsequently take bigger prey species than the smaller-bodied sex (Heatwole 1999). Dietary dimorphisms may result from the larger-bodied sex being physically capable of taking on larger-bodied prey than the smaller sex or an inclination for the sexes to forage in different habitats (Shine 1991). Researchers tend to combine data for both sexes in published dietary analyses meaning that the actual dietary variation between male and female elapids may be underestimated. Given that intersexual morphometric (maximum total length) data could only be acquired for fewer than half of the species assessed, I could not ascertain whether significant dietary divergences occurred between the sexes throughout elapid evolution.

There may be a considerable divergence in the types of prey taken by juvenile and adult-elapids. The commonly reported pattern of juvenile snakes taking on prey different from those of adult conspecifics was found in *Acanthophis antarcticus* (Seigel *et al*. 1987). Juvenile *A. antarcticus* tend to prey on lizards whereas adults would feed on more robust mammalian species (Seigel *et al.* 1987). Various investigations into the developmental restrictions in snake feeding and have also reported age-mediated prey size discrimination (Cobb 2004; Reading & Jofré 2013). My findings therefore do not suggest that body size plays absolutely no role in elapid foraging ecology because it is possible that intraspecifically or between individuals there may exist age-specific differences in prey selection. The vast majority of our understanding on the trophic relations of snakes is based on the diets of adults, meaning that we have yet to get the full picture on the size dynamics related to feeding.

5. CONCLUSION

The present study set out to highlight the evolutionary history of diet traits within a lineage which is speciose, medically important and represents an important trophic component in ecosystems around the world. This research is the first attempt at evaluating the natural history patterns of the elapid group in relation to their taxonomic relationships. Moreover, unlike most macroevolutionary studies on the drivers of species assemblages, my analyses accounted for the phylogenetic non-independence of species data. Such extensive evaluations on snake foraging ecology are scarce because snakes are often cryptic or rare, their stomachs are often empty making dietary analyses challenging and the taxonomic relationships of some groups remain unresolved (Seigel *et al*. 1987). I considered the Elapidae a model group on which to investigate the complexities of feeding dynamics given their impressive ecomorphological and species diversity and unequalled global distribution relative to other snake groups.

The remarkable adaptive success of the family is most vividly expressed within the sea snake lineage. The subfamily Hydrophiinae, despite being a very recently evolved lineage, is the most ecologically diverse group of marine reptiles which further makes up ~90% of extant marine reptile species (Sanders *et al*. 2008; Elfes *et al*. 2013). While most other sea snakes species are restricted to shallow coastal areas where prey abundance is high, *Hydrophis platurus* feeds at the water's surface which has allowed its range extends into the open ocean (Heatwole 1999). This species is now the most widely distributed ophidian species in the world (Rasmussen *et al*. 2001; Alexander & Marais 2007). The explosive speciation and adaptive radiation of *Hydrophiines* within a relatively short evolutionary period suggests that traits specific to this lineage are likely to have been involved in its adaptive success. Sanders *et al*. (2008) cites greater adaptive phenotypic plasticity as a possible factor in addition to key innovations which have allowed the clade to quickly capitalise on open ecological opportunities for diversification.

Amongst the possible diet covariates assessed in this study, lifestyle diversification was likely the most pertinent covariate in influencing the radiation of elapids today. This is demonstrated by the lack of body size correlation with diet or several other environmental variables (Terribile *et al*. 2009). Furthermore, the most widespread elapid group occurs in marine areas transcending various biogeographic regions. By evolving to forage in the world's oceans, sea snakes "went where no snake has gone before". Evolving to forage in climatically suitable waters devoid of other serpents may thus be the single biggest factor responsible for the widespread global distribution of marine living elapids allowing them to exploitat open niches. The same factors are likely influenced invasions into varied terrestrial habitats.

Despite the marked differentiation in resource use amongst sea snakes, they, similar to their terrestrial counterparts, still feed on characteristically elongate ectothermic prey (Seigel *et al*. 1987). The present study has demonstrated that the ancestral elapid was a likely a burrowing predator which fed on squamates (see chapter 3; Fig. 13). These foraging dynamics are still largely maintained within the group. I postulate that the appearance of elapids within the squamate-rich Asian regions may have offered special circumstances of prey size, shape and abundance which promoted the early radiation of primitive elapids. In the absence of morphological adaptations such as those typically seen in vipers and boas for taking heavier/bulkier prey forms, this has proven to be the optimal foraging strategy for the Elapidae. These observations serve to indicate that a complex interplay of proximate (e.g., varying prey availability in different microhabitats) and historical factors (e.g., zoogeography) determined the macroevolutionary diet patterns of the Elapidae.

Reconstructions unanimously show evidence of an emergence of apomorphic feeding habits (i.e., generalist and endotherm inclusive), a finding which I have superficially attributed to competition among ecologically similar predators (see chapter 4.1). The study could have been better served by statistically assessing the role of competitive interactions as a driver of recent diet shifts. Rabosky & Lovette (2008) phylogenetically quantified the influence of competition on species diversification by fitting density-dependent models. Alternatively, comparisons of disparity and range overlap could be made between sister taxa, although modern advancements offer explicit competition-based models of trait evolution (Price *et al*. 2015). Furthermore, because several factors can operate simultaneously to shape the characteristics of natural communities (Hartmann *et al*. 2009), future research should aim to isolate other clade-specific factors involved in generating differences in resource use among the Elapidae.

I further noted that results were dependent on whether the tree was rooted and the state of the outgroup condition. While it is largely agreed that rooting a tree is a necessary component of character reconstruction, there appears to be no universal criterion for selecting the outgroup species (Smith 1999; Graham *et al*. 2002; Rota-Stabelli & Telford 2008; Harry Greene pers. comm.; Alex Pyron pers. comm). I further acknowledge that, as in most studies on snake assemblages, the diet, lifestyle and maximum body size data may be marred by sampling biases in the literature used as a basis for analyses (e.g., fossorial or small forms may be undersampled owing to their greater crypticity).

Despite possible shortfalls, this assessment of the broad evolutionary characteristics of elapid foraging dynamics, offers a valuable basis for comparing them with other snake groups. From a functional standpoint, the general diet of elapids is comparatively reminiscent of those seen in the Atractaspididae (African burrowing asps). Representatives of the lineage are typically slender bodied with small heads which are indistinct from the neck, but they exhibit a range of specific cranial adaptations (e.g., “side-stabbing” dentition, quill-shaped heads and undercut jaws) for hunting and consuming fossorial squamates and elongate vertebrates in their burrows (Shine *et al.* 2006a; Alexander & Marais 2007; Warner 2009).

In contrast, extensive historical evaluations of viperid and boid clades demonstrate that they have evolved to feed on broad diets often inclusive of large-bodied mammalian prey. Rodríguez-Robles *et al.* (1999) evaluated the historical and taxonomic variation in erycine boa foraging and concluded that the radiation of erycine ancestors intercepts with that of their primarily rodent prey throughout the predator's range. In the *Bothrops* pitviper genus, a reconstruction of past feeding habits suggested that ancestral forms of the group were probably diet generalists, an overriding characteristic which is maintained within the lineage (Martins *et al*. 2002). Most basal snake groups exhibit markedly constrained gape from having retained primitive cranial morphology and kinetics and they consequently feed on elongate or small prey. This indicates that the consumption of heavier and bulkier prey (such as in vipers and boas) and the morphological adaptations associated with it are relatively derived in comparison to elapid or atractastapid attributes.

Similar comprehensive family, tribe or genus level assessments as presented here are limited despite an increase in studies on the natural history and ecological characteristics of serpents in recent years. Since diet is the most important niche dimension determining the ecological divergence of snake assemblages (Seigel *et al.* 1987), similar phylogenetic comparative studies can act as a valuable tool for identifying the causes of adaptive variation or the phenotypic and lineage diversity of predators (Rodriguez-Robles 2002). This information can be utilised to generate testable hypotheses regarding the organisation of other predatory assemblages (Cadle & Greene 1993; Rodríguez-Robles 2002; Hartmann *et al.* 2009). For these reasons, I plan to use a subset of the techniques and principles utilised in this study to carry out an investigation of the spatiotemporal variation in the ecological characteristics of African snake assemblages as well as the mechanisms driving them. Snakes represent important components of trophic systems and exert an important influence on overall ecosystem dynamics. Prioritising research focused on their historical and curent attributes is therefore essential for understanding diversity patterns at large.

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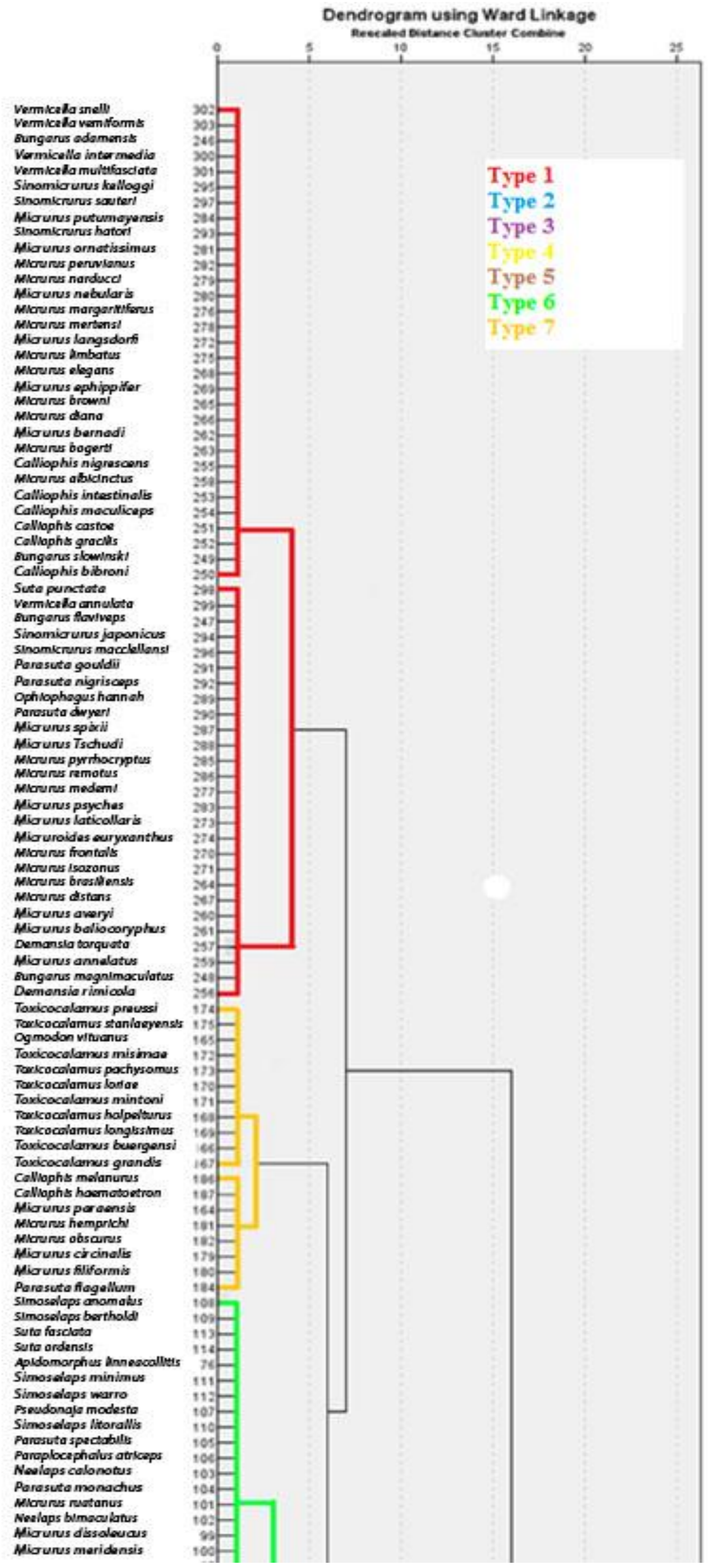
APPENDIX

Appendix 1. Hierarchical cluster analysis dendrogram showing relatively homogenous diet groups in the Elapidae. The greater the distances between joined clusters, the greater the differences in these diet clusters



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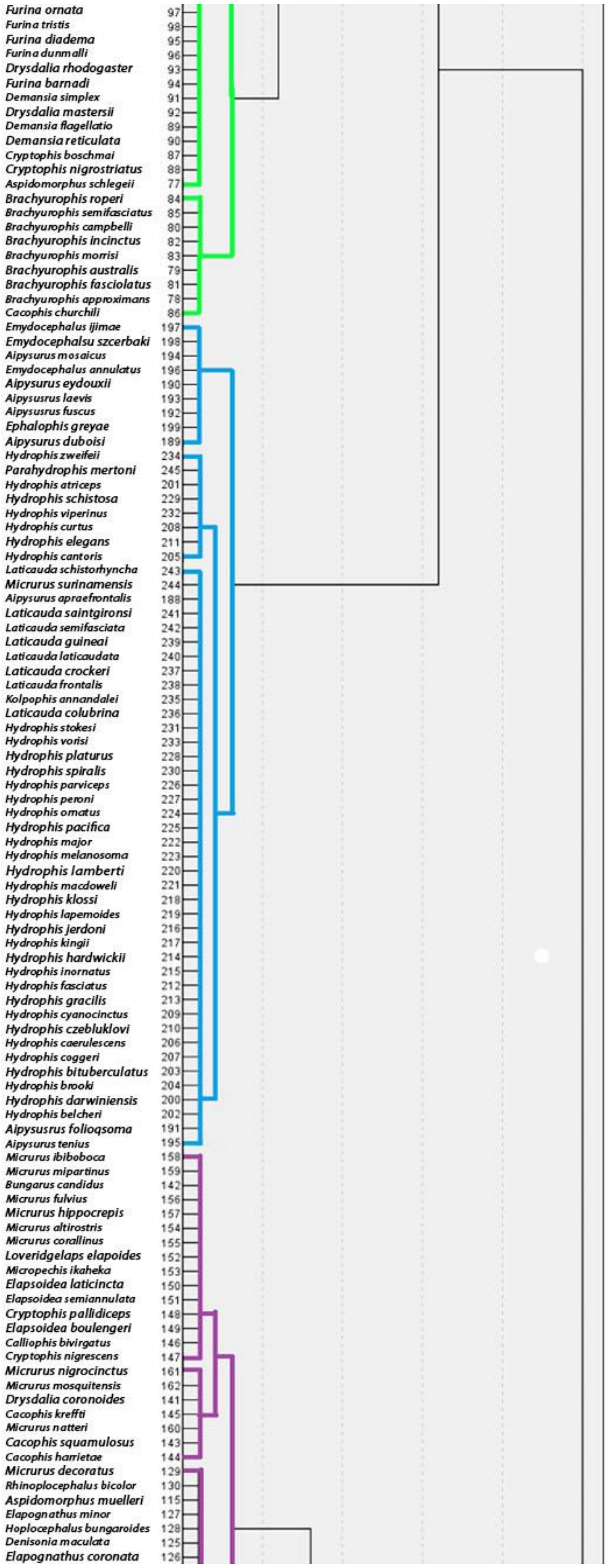

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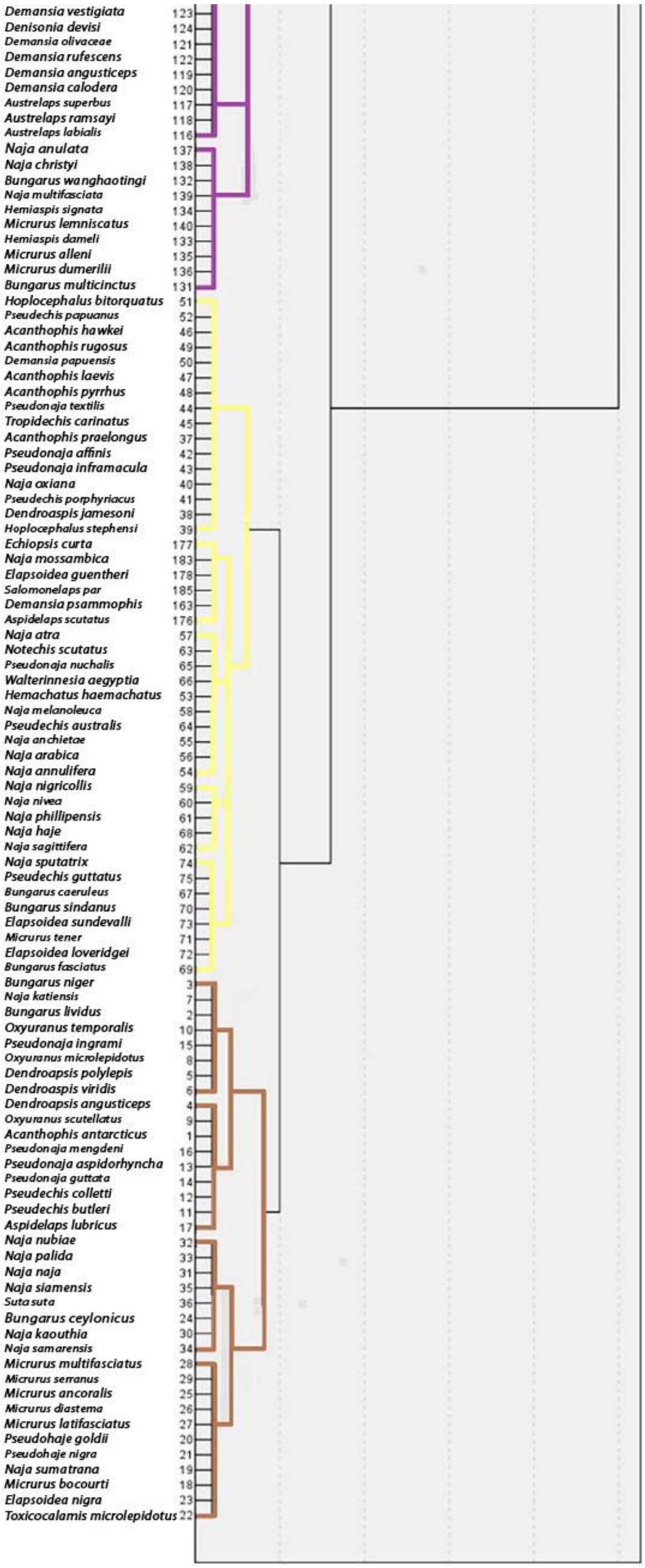
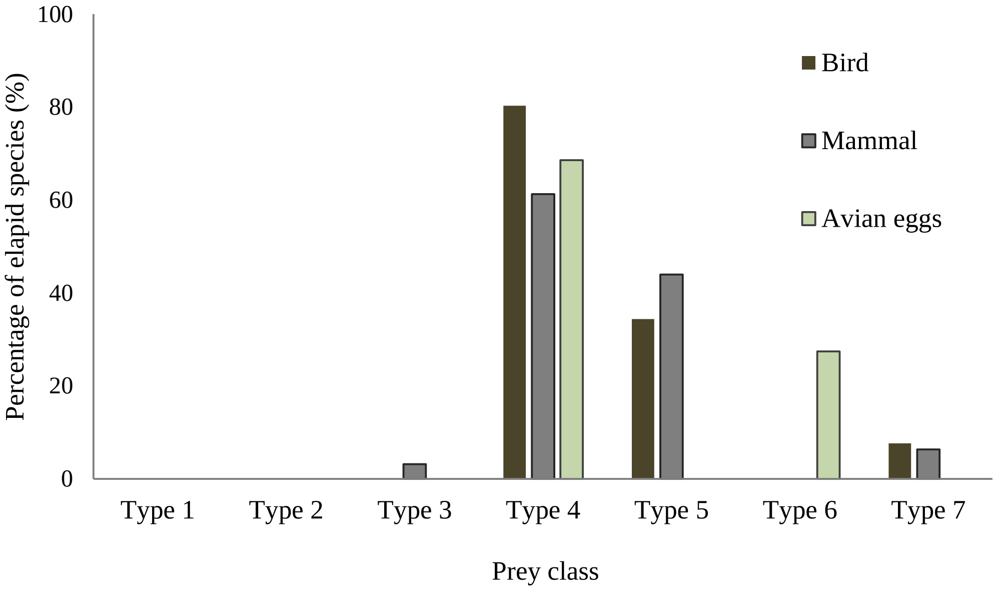


Appendix 2. The percentage of elapid species known to predate birds, mammals and avian eggs which were assigned to various diet clusters.



Appendix 3. Diet classes recorded as presence-absence data (1 & 0 respectively) for each of the 303 elapid species assessed. Abbreviations are as follows: b - birds, m-mammals, l - lizards, s - snakes, a - amphibians, f - fish, mi - marine invertebrates, ti - terrestrial invertebrates, re - reptile eggs, ae - avian eggs, fe - fish eggs; Grd – ground-dwelling, Aqu - aquatic, Bur - burrowing, Arb - arboreal, SA - semiaquatic; MTL - maximum total length (mm). The corresponding source references are provided.

		Prey class														
Species	Authority, year of description	b	m	l	s	a	f	mi	ti	re	ae	fe	MTL (mm)	Lifestyle	Region	Reference
Acanthophis antarcticus	(Shaw, 1802)	1	1	1	0	0	0	0	0	0	0	0	1000	Grd	Aus	93; 155; 182; 183
Acanthophis hawkei	Wells & Wellington, 1985	0	1	1	0	1	0	0	0	0	0	0	1300	Grd	Aus	29
Acanthophis laevis	Macleay, 1878	0	1	1	0	1	0	0	0	0	0	0	1100	Grd	Aus	155; 182
Acanthophis praelongus	Ramsay, 1877	1	1	1	0	1	0	0	0	0	0	0	750	Grd	Aus	155; 182; 183
Acanthophis pyrrhus	Boulenger, 1898	0	1	1	0	1	0	0	0	0	0	0	700	Grd	Aus	182; 183
Acanthophis rugosus	Loveridge, 1948	0	1	1	0	1	0	0	0	0	0	0	700	Grd	Aus	155; 182
Aipysurus apraefrontalis	Smith, 1926	0	0	0	0	0	1	0	0	0	0	0	1080	Aqu	Mar	57
Aipysurus duboisii	Bavay, 1869	0	0	0	0	0	1	0	0	0	0	1	1100	Aqu	Mar	57

Aipysurus eydouxii	(Gray, 1849)	0	0	0	0	0	1	1	0	0	0	1	1500	Aqu	Mar	57
Aipysurus foliosquama	Smith, 1926	0	0	0	0	0	1	0	0	0	0	1	1000	Aqu	Mar	57; 93
Aipysurus fuscus	(Tschudi, 1837)	0	0	0	0	0	1	1	0	0	0	1	950	Aqu	Mar	57
Aipysurus laevis	Lacépède, 1804	0	0	0	0	0	0	0	0	0	0	1	2000	Aqu	Mar	10; 33; 57; 177
Aipysurus mosaicus	Sanders, Rasmussen, Elmberg, Mumpuni, Guinea, Blias, Lee & Fry, 2012	0	0	0	0	0	1	0	0	0	0	0		Aqu	Mar	169
Aipysurus tenuis	Lönnberg & Andersson, 1913	0	0	0	0	0	1	0	0	0	0	0	1020	Aqu	Mar	93
Aspidelaps lubricus	(Laurenti, 1768)	0	1	1	1	0	0	0	0	1	0	0	800	B	Afr	2; 162
Aspidelaps scutatus	Smith, 1849	0	1	1	1	1	0	0	1	0	0	0	750	B	Afr	2; 162
Aspidomorphus lineaticollis	(Werner, 1903)	0	0	1	0	0	0	0	0	0	0	0	400	B	NG	152
Aspidomorphus muelleri	(Schlegel, 1837)	0	0	1	0	1	0	0	0	0	0	0	600	B	NG	152
Aspidomorphus schlegeli	(Günther, 1872)	0	0	1	0	0	0	0	0	0	0	0	425	B	NG	152; 169
Austrelaps labialis	(Jan, 1859)	0	0	1	0	1	0	0	0	0	0	0	1200	Grd	Aus	183
Austrelaps ramsayi	(Krefft, 1864)	0	0	1	0	1	0	0	0	0	0	0	1700	Grd	Aus	29
Austrelaps superbus	(Günther, 1858)	0	0	1	0	1	0	0	0	0	0	0	1700	Grd	Aus	29; 93
Brachyurophis approximans	(Glauert, 1954)	0	0	1	0	0	0	0	0	1	0	0	370	B	Aus	29; 93
Brachyurophis australis	(Krefft, 1864)	0	0	1	0	0	0	0	0	1	0	0	500	B	Aus	29; 93
Brachyurophis campbelli	(Kinghorn, 1929)	0	0	0	0	0	0	0	0	1	0	0	400	B	Aus	29; 128
Brachyurophis fasciolatus	(Günther, 1872)	0	0	1	0	0	0	0	0	1	0	0	400	B	Aus	93
Brachyurophis incinctus	(Storr, 1968)	0	0	0	0	0	0	0	0	1	0	0	300	B	Aus	93; 29
Brachyurophis morrisi	(Horner, 1998)	0	0	0	0	0	0	0	0	1	0	0	263	B	Aus	29
Brachyurophis roperi	(Kinghorn, 1931)	0	0	0	0	0	0	0	0	1	0	0	400	B	Aus	29
Brachyurophis semifasciatus	Günther, 1863	0	0	0	0	0	0	0	0	1	0	0	400	B	Aus	10; 29; 93
Bungarus adamanensis	Biswas & Sanyal, 1978	0	0	0	1	0	0	0	0	0	0	0	1000	Grd	IM	178
Bungarus caeruleus	(Schneider, 1801)	0	0	0	1	0	0	0	0	0	0	0	1750	Grd	Pal	178
Bungarus candidus	(Linnaeus, 1758)	0	1	1	1	1	0	0	0	0	0	0	1600	Grd	IM	33; 34
Bungarus ceylonicus	Günther, 1864	0	0	1	1	1	0	0	0	0	0	0	900	B	IM	175
Bungarus fasciatus	(Schneider, 1801)	0	1	0	1	1	0	0	0	0	0	0	2250	Grd	IM	33; 99

Bungarus flaviceps	Reinhardt, 1843	0	1	1	1	1	1	0	0	1	0	0	2070	Grd	IM	33; 76
Bungarus lividus	Cantor, 1839	0	0	1	1	0	0	0	0	0	0	0	1000	Grd	IM	136; 187
Bungarus magnimaculatus	Wall & Evans, 1901	0	1	0	1	0	0	0	0	0	0	0	1300	Grd	IM	33; 76
Bungarus multicinctus	Blyth, 1861	0	0	1	1	0	0	0	0	0	0	0	1354	Grd	IM	33; 34; 99
Bungarus niger	Wall, 1908	0	1	1	0	1	1	0	0	0	0	0	1295	Grd	IM	136; 178; 187
Bungarus sindanus	Boulenger, 1897	0	1	0	1	0	0	0	0	0	0	0	1518	Grd	IM	178; 187
Bungarus slowinski	Kuch, Kizirian, Nguyen, Lawson, Donnelly & Mebs, 2005	0	1	1	1	1	0	0	0	0	0	0	1350	Grd	Pal	33
Bungarus wanghaotingi		0	1	0	1	1	1	0	0	0	0	0	1100	Grd	IM	33; 76
Cacophis churchilli	Wells & Wellington, 1985	0	0	1	0	1	0	0	0	1	0	0	600	Grd	Aus	93
Cacophis harrietae	Krefft, 1869	0	0	1	1	1	0	0	0	1	0	0	400	Grd	Aus	29; 93; 138
Cacophis krefftii	Günther, 1863	0	0	1	1	1	0	0	0	1	0	0	330	Grd	Aus	29; 93; 138
Cacophis squamulosus	(Duméril, Bibron & Duméril, 1854)	0	0	1	1	1	0	0	0	1	0	0	900	Grd	Aus	10
Calliophis bibroni	(Jan, 1858)	0	0	0	1	0	0	0	0	0	0	0	880	Grd	Aus	33
Calliophis bivirgata	(Boie, 1827)	0	0	1	1	1	0	0	0	0	0	0	1850	B	Aus	33
Calliophis castoe	Smith, Ogale, Deepak & Giri, 2012	0	0	0	1	0	0	0	0	0	0	0	540	B	Aus	178
Calliophis gracilis	Gray, 1835	0	0	0	1	0	0	0	0	0	0	0	740	B	Aus	33
Calliophis haematoetron	Smith, Manamendra-Arachchi & Somaweera, 2008	0	0	0	1	0	0	0	1	0	0	0		B	Aus	178
Calliophis intestinalis	(Laurenti, 1768)	0	0	0	1	0	0	0	0	0	0	0	710	B	Aus	33
Calliophis maculiceps	(Günther, 1858)	0	0	0	1	0	0	0	0	0	0	0	480	B	Aus	33; 76
Calliophis melanurus	(Shaw, 1802)	0	0	0	1	0	0	0	1	0	0	0	350	B	Aus	178
Calliophis nigrescens	(Günther, 1862)	0	0	0	1	0	0	0	0	0	0	0	1140	Grd	Aus	178
Cryptophis boschmai	(Brongersma & Knaap Van Meeuven, 1961)	0	0	1	0	0	0	0	0	0	0	0	450	Grd	Aus	29; 93
Cryptophis nigrescens	(Günther, 1862)	0	0	1	1	1	0	0	0	0	0	0	1200	Grd	Aus	10; 29; 93
Cryptophis nigrostriatus	(Krefft, 1864)	0	0	1	0	0	0	0	0	0	0	0	600	Grd	Aus	29; 93

Cryptophis pallidiceps	(Günther, 1858)	0	0	1	1	1	0	0	0	0	0	0	630	Grd	Aus	29; 93
Demansia angusticeps	(Macleay, 1888)	0	0	1	0	1	0	0	0	0	0	0	> = 850	Grd	Aus	27; 29; 104
Demansia calodera	Storr, 1978	0	0	1	0	1	0	0	0	0	0	0	> = 650	Grd	Aus	27; 29; 104
Demansia flagellatio	Wells & Wellington, 1985	0	0	1	0	0	0	0	0	0	0	0	> = 700	Grd	Aus	27; 29
Demansia olivacea	(Gray, 1842)	0	0	1	0	1	0	0	0	0	0	0	850	Grd	Aus	29; 93; 104; 138
Demansia papuensis	(Macleay, 1877)	0	1	1	0	1	0	0	0	0	0	0	1800	Grd	Aus	29; 93; 104
Demansia psammophis	(Schlegel, 1837)	0	1	1	1	1	0	0	1	0	0	0	1100	Grd	Aus	93; 104; 138
Demansia reticulata	(Gray, 1842)	0	0	1	0	0	0	0	0	0	0	0	> = 800	Grd	Aus	29; 104
Demansia rimicola	Scanlon, 2007	0	0	1	1	0	0	0	0	0	0	0	> = 900	Grd	Aus	27; 29; 104
Demansia rufescens	Storr, 1978	0	0	1	0	1	0	0	0	0	0	0	> = 700	Grd	Aus	29; 104
Demansia simplex	Storr, 1978	0	0	1	0	0	0	0	0	0	0	0	600	Grd	Aus	29; 93; 104; 138
Demansia torquata	(Günther, 1862)	0	0	1	1	0	0	0	0	0	0	0	850	Grd	Aus	29; 93; 104
Demansia vestigiata	(De Vis, 1884)	0	0	1	0	1	0	0	0	0	0	0	1600	Grd	Aus	10; 29; 39; 104
Dendroaspis angusticeps	(Smith, 1849)	1	1	1	0	0	0	0	0	0	0	0	2500	Arb	Afr	162
Dendroaspis jamesoni	(Traill, 1843)	1	1	1	0	1	0	0	0	0	0	0	2500	Arb	Afr	78; 162
Dendroaspis polylepis	Günther, 1864	1	1	0	0	0	0	0	0	0	0	0	4300	Arb	Afr	2; 162
Dendroaspis viridis	(Hallowell, 1844)	1	1	0	0	0	0	0	0	0	0	0	2300	Arb	Afr	162
Denisonia devisii	(Waite & Longman, 1920)	0	0	1	0	1	0	0	0	0	0	0	600	B	Aus	29; 93; 144
Denisonia maculata	(Steindachner, 1867)	0	0	1	0	1	0	0	0	0	0	0	500	B	Aus	29; 93; 138
Drysdalia coronoides	(Günther, 1858)	0	0	1	1	1	0	0	0	1	0	0	500	Grd	Aus	29; 93
Drysdalia mastersii	(Krefft, 1866)	0	0	1	0	0	0	0	0	0	0	0	400	Grd	Aus	29; 93; 147
Drysdalia rhodogaster	(Jan & Sordelli, 1873)	0	0	1	0	0	0	0	0	0	0	0	450	Grd	Aus	29; 93
Echiopsis curta	(Schlegel, 1837)	1	1	1	0	1	0	0	1	0	0	0	700	Grd	Aus	10; 29; 93
Elapognathus coronata	(Schlegel, 1837)	0	0	1	0	1	0	0	0	0	0	0	600	Grd	Aus	29; 93
Elapognathus minor	(Günther, 1863)	0	0	1	0	1	0	0	0	0	0	0	450	Grd	Aus	93
Elapsoidea boulengeri	Boettger, 1895	0	0	1	1	1	0	0	0	0	0	0	700	B	Afr	2; 162; 169
Elapsoidea guentheri	Bocage, 1866	0	0	1	1	1	0	0	1	0	0	0	620	B	Afr	2; 162
Elapsoidea laticincta	(Werner, 1919)	0	0	1	1	1	0	0	0	0	0	0	550	B	Afr	162

Elapsoidea loveridgei	Parker, 1949	0	1	1	1	1	0	0	0	1	0	0	650	B	Afr	162
Elapsoidea nigra	Günther, 1888	0	0	0	0	1	0	0	0	0	0	0	600	B	Afr	162
Elapsoidea semiannulata	Bocage, 1882	0	0	1	1	1	0	0	0	0	0	0	700	C-F	Afr	2; 162
Elapsoidea sundevallii	Smith, 1848	0	1	1	1	1	0	0	0	0	0	0	1380	C-F	Afr	2; 162
Emydocephalus annulatus	Krefft, 1869	0	0	0	0	0	0	0	0	0	0	1	1050	Aqu	Mar	120
Emydocephalus ijimae	Stejneger, 1898	0	0	0	0	0	0	0	0	0	0	1	-	Aqu	Mar	57; 93
Emydocephalus szczerbaki	Dotsenko, 2011	0	0	0	0	0	0	0	0	0	0	1	-	Aqu	Mar	57; 93
Ephalophis greyae	Smith, 1931	0	0	0	0	0	1	0	0	0	0	1	660	Aqu	Mar	57; 93
Furina barnadi	(Kinghorn, 1939)	0	0	1	0	0	0	0	0	0	0	0	500	Grd	Aus	29; 93
Furina diadema	(Schlegel, 1837)	0	0	1	0	0	0	0	0	0	0	0	450	Grd	Aus	29
Furina dunmalli	(Worrell, 1955)	0	0	1	0	0	0	0	0	0	0	0	750	Grd	Aus	29; 93
Furina ornata	(Gray, 1842)	0	0	1	0	0	0	0	0	0	0	0	700	Grd	Aus	29
Furina tristis	(Günther, 1858)	0	0	1	0	0	0	0	0	0	0	0	1000	Grd	Aus	10; 29; 93
Hemachatus haemachatus	(Bonnaterre, 1790)	1	1	1	1	1	0	0	0	0	0	0	1500	Grd	Afr	2; 162
Hemiaspis damelii	(Günther, 1876)	0	0	1	0	1	1	0	0	0	0	0	750	Grd	Aus	29; 93
Hemiaspis signata	(Jan, 1859)	0	0	1	1	1	1	0	0	0	0	0	900	Grd	Aus	93
Hoplocephalus bitorquatus	(Jan, 1859)	0	1	1	0	1	0	0	0	0	0	0	1200	Arb	Aus	29; 93
Hoplocephalus bungaroides	Schlegel, 1837	0	0	1	0	1	0	0	0	0	0	0	1000	Grd	Aus	10; 29; 93
Hoplocephalus stephensi	Krefft, 1869	1	1	1	0	1	0	0	0	0	0	0	1200	Arb	Aus	29; 93
Hydrelaps darwiniensis	Boulenger, 1896	0	0	0	0	0	1	0	0	0	0	0	500	Aqu	Mar	57; 93; 177
Hydrophis atriceps	Günther, 1864	0	0	0	0	0	1	1	0	0	0	0	1200	Aqu	Mar	33; 57; 76
Hydrophis belcheri	(Gray, 1849)	0	0	0	0	0	1	0	0	0	0	0	932	Aqu	Mar	57
Hydrophis bituberculatus	Peters, 1873	0	0	0	0	0	1	0	0	0	0	0	1050	Aqu	Mar	33
Hydrophis brookii	Günther, 1872	0	0	0	0	0	1	0	0	0	0	0	1035	Aqu	Mar	33; 57
Hydrophis caerulescens	(Shaw, 1802)	0	0	0	0	0	1	0	0	0	0	0	1090	Aqu	Mar	33; 178
Hydrophis cantoris	Günther, 1864	0	0	0	0	0	1	1	0	0	0	0	1450	Aqu	Mar	33; 76
Hydrophis coggeri	(Kharin, 1984)	0	0	0	0	0	1	0	0	0	0	0	1200	Aqu	Mar	57; 125; 183
Hydrophis curtus	(Shaw, 1802)	0	0	0	0	0	1	1	0	0	0	0	1500	Aqu	Mar	10; 33; 57
Hydrophis cyanocinctus	Daudin, 1803	0	0	0	0	0	1	0	0	0	0	0	1885	Aqu	Mar	33; 57
Hydrophis czeblukovi	(Kharin, 1984)	0	0	0	0	0	1	0	0	0	0	0	1200	Aqu	Mar	57; 177

Hydrophis elegans	(Gray, 1842)	0	0	0	0	0	1	1	0	0	0	0	2100	Aqu	Mar	10; 57; 100
Hydrophis fasciatus	(Schneider, 1799)	0	0	0	0	0	1	0	0	0	0	0	1100	Aqu	Mar	33; 76
Hydrophis gracilis	(Shaw, 1802)	0	0	0	0	0	1	0	0	0	0	0	1025	Aqu	Mar	33; 76; 101
Hydrophis hardwickii	(Gray, 1834)	0	0	0	0	0	1	0	0	0	0	0	1200	Aqu	Mar	76; 93
Hydrophis inornatus	(Gray, 1849)	0	0	0	0	0	1	0	0	0	0	0	1089	Aqu	Mar	33; 177
Hydrophis jerdoni	(Gray, 1849)	0	0	0	0	0	1	0	0	0	0	0	1100	Aqu	Mar	57; 76; 178
Hydrophis kingii	Boulenger, 1896	0	0	0	0	0	1	0	0	0	0	0	1900	Aqu	Mar	57
Hydrophis klossi	Boulenger, 1912	0	0	0	0	0	1	0	0	0	0	0	1190	Aqu	Mar	33
Hydrophis lamberti	Smith, 1917	0	0	0	0	0	1	0	0	0	0	0	1250	Aqu	Mar	33
Hydrophis lapemoides	(Gray, 1849)	0	0	0	0	0	1	0	0	0	0	0	960	Aqu	Mar	33; 57
Hydrophis macdowelli	Kharin, 1983	0	0	0	0	0	1	0	0	0	0	0	1200	Aqu	Mar	57; 177
Hydrophis major	(Shaw, 1802)	0	0	0	0	0	1	0	0	0	0	0	1600	Aqu	Mar	57; 177
Hydrophis melanosoma	Günther, 1864	0	0	0	0	0	1	0	0	0	0	0	1390	Aqu	Mar	33; 57
Hydrophis ornatus	(Gray, 1842)	0	0	0	0	0	1	0	0	0	0	0	1150	Aqu	Mar	33; 57; 76; 177
Hydrophis pacificus	Boulenger, 1896	0	0	0	0	0	1	0	0	0	0	0	1500	Aqu	Mar	57
Hydrophis parviceps	Smith, 1935	0	0	0	0	0	1	0	0	0	0	0	890	Aqu	Mar	33; 121; 125
Hydrophis peronii	(Duméril, 1853)	0	0	0	0	0	1	0	0	0	0	0	1500	Aqu	Mar	10; 33; 57; 177
Hydrophis platurus	(Linnaeus, 1766)	0	0	0	0	0	1	0	0	0	0	0	1100	Aqu	Mar	10; 33; 57; 162
Hydrophis schistosus	Daudin, 1803	0	0	0	0	0	1	1	0	0	0	0	1580	Aqu	Mar	10; 33; 57; 76
Hydrophis spiralis	(Shaw, 1802)	0	0	0	0	0	1	0	0	0	0	0	2750	Aqu	Mar	10; 57; 76
Hydrophis stokesii	(Gray, 1846)	0	0	0	0	0	1	0	0	0	0	0	2000	Aqu	Mar	10; 33; 57; 177
Hydrophis viperinus	(Schmidt, 1852)	0	0	0	0	0	1	1	0	0	0	0	925	Aqu	Mar	33; 57; 76
Hydrophis vorisi	Kharin, 1984	0	0	0	0	0	1	0	0	0	0	0	1200	Aqu	Mar	57; 93
Hydrophis zweifeli	(Kharin, 1985)	0	0	0	0	0	1	1	0	0	0	0	-	Aqu	Mar	93
Kolpophis annandalei	(Laidlaw, 1901)	0	0	0	0	0	1	0	0	0	0	0	520	Aqu	Mar	33
Laticauda colubrina	(Schneider, 1799)	0	0	0	0	0	1	0	0	0	0	0	3600	Aqu	Mar	10; 33; 57; 76
Laticauda crockeri	Slevin, 1934	0	0	0	0	0	1	0	0	0	0	0	499	Aqu	Mar	37; 57
Laticauda frontalis	(De Vis, 1905)	0	0	0	0	0	1	0	0	0	0	0	905	Aqu	Mar	29; 57
Laticauda guineai	Heatwole, Busack & Cogger, 2005	0	0	0	0	0	1	0	0	0	0	0		Aqu	Mar	29

Laticauda laticaudata	(Linnaeus, 1758)	0	0	0	0	0	1	0	0	0	0	0	1100	Aqu	Mar	17; 18; 33; 57; 76
Laticauda saintgironsi	Cogger & Heatwole, 2005	0	0	0	0	0	1	0	0	0	0	0		Aqu	Mar	17; 18; 169
Laticauda schistorhyncha	(Günther, 1874)	0	0	0	0	0	1	0	0	0	0	0	806	Aqu	Mar	37; 57; 169; 187
Laticauda semifasciata	(Reinwardt, 1837)	0	0	0	0	0	1	0	0	0	0	0	1995	Aqu	Mar	10; 57; 169
Loveridgelaps elapoides	(Boulenger, 1890)	0	0	1	1	1	0	0	0	0	0	0	1000	Grd	NG	10
Micropechis ikaheka	Lesson, 1830	0	0	1	1	1	0	0	0	0	0	0	2100	C-F	NG	10
Micruroides euryxanthus	(Kennicott, 1860)	0	0	1	1	0	0	0	0	0	0	0	550	C-F	Neo	10
Micrurus albicinctus	Amaral, 1925	0	0	0	1	0	0	0	0	0	0	0	573	C-F	Neo	25
Micrurus alleni	Schmidt, 1936	0	0	1	0	1	1	0	0	0	0	0	1340	Grd	Neo	8; 25
Micrurus altirostris	(Cope, 1860)	0	0	1	1	1	0	0	0	0	0	0	1310	C-F	Neo	25
Micrurus ancoralis	Jan, 1872	0	0	0	1	1	0	0	0	0	0	0	1510	C-F	Neo	82
Micrurus annellatus	Peters, 1871	0	0	1	1	0	0	0	0	0	0	0	730	C-F	Neo	25
Micrurus averyi	Schmidt, 1939	0	0	1	1	0	0	0	0	0	0	0	715	C-F	Neo	25
Micrurus baliocoryphus	(Cope, 1862)	0	0	1	1	0	0	0	0	0	0	0	1449	C-F	Neo	25; 34; 117
Micrurus bernadi	(Cope, 1887)	0	0	0	1	0	0	0	0	0	0	0	826	C-F	Neo	25
Micrurus bocourti	(Jan, 1872)	0	0	0	0	1	0	0	0	0	0	0	820	C-F	Neo	25; 73
Micrurus bogerti	Roze, 1967	0	0	0	1	0	0	0	0	0	0	0	770	C-F	Neo	25
Micrurus brasiliensis	Roze, 1967	0	0	1	1	0	0	0	0	0	0	0	1513		Neo	25
Micrurus browni	Schmidt & Smith, 1943	0	0	0	1	0	0	0	0	0	0	0	1000	C-F	Neo	25; 73
Micrurus circinalis	(Duméril, Bibron & Duméril, 1854)	0	0	1	1	0	0	0	1	0	0	0	537	C-F	Neo	25
Micrurus corallinus	(Merrem, 1820)	0	0	1	1	1	0	0	0	0	0	0	987	C-F	Neo	10; 25; 165
Micrurus decoratus	(Jan, 1858)	0	0	1	0	1	0	0	0	0	0	0	670	C-F	Neo	25
Micrurus diana	Roze, 1983	0	0	0	1	0	0	0	0	0	0	0	998		Neo	25
Micrurus diastema	(Duméril, Bibron & Duméril, 1854)	0	0	0	1	1	0	0	0	0	0	0	900	C-F	Neo	25; 165
Micrurus dissoleucus	Cope, 1860	0	0	1	0	0	0	0	0	0	0	0	650	C-F	Neo	25; 73
Micrurus distans	Kennicott, 1860	0	0	1	1	0	0	0	0	0	0	0	1075	C-F	Neo	25
Micrurus dumerilii	Jan, 1858	0	0	1	0	0	1	0	0	0	0	0	948	C-F	Neo	25; 165
Micrurus elegans	Jan, 1858	0	0	0	1	0	0	0	0	0	0	0	1000	C-F	Neo	25; 73
Micrurus ephippifer	(Cope, 1886)	0	0	0	1	0	0	0	0	0	0	0	926	C-F	Neo	25; 73

Micrurus filiformis	(Günther, 1859)	0	0	1	1	0	0	0	1	0	0	0	960		Neo	25
Micrurus frontalis	Duméril, Bibron & Duméril, 1854	0	0	1	1	0	0	0	0	0	0	0	1418	C-F	Neo	25; 34
Micrurus fulvius	(Linnaeus, 1766)	0	0	1	1	1	0	0	0	0	0	0	1000	C-F	Neo	10; 25
Micrurus hemprichii	(Jan, 1858)	0	0	1	1	0	0	0	1	0	0	0	917	C-F	Neo	25
Micrurus hippocrepis	(Peters, 1862)	0	0	1	1	1	0	0	0	0	0	0	710	Grd	Neo	25; 73
Micrurus ibiboboca	(Merrem, 1820)	0	0	1	1	1	0	0	0	0	0	0	1330	C-F	Neo	25; 165
Micrurus isozonus	(Cope, 1860)	0	0	1	1	0	0	0	0	0	0	0	1550	C-F	Neo	25; 165
Micrurus langsdorffi	(Wagler, 1824)	0	0	0	1	0	0	0	0	0	0	0	770	C-F	Neo	25
Micrurus laticollaris	Peters, 1870	0	0	1	1	0	0	0	0	0	0	0	800	C-F	Neo	25; 73
Micrurus latifasciatus	Schmidt, 1933	0	0	0	1	1	0	0	0	0	0	0	1140	C-F	Neo	25; 73
Micrurus lemniscatus	(Linnaeus, 1758)	0	0	1	1	1	1	0	0	0	0	0	1450	Grd	Neo	25; 34
Micrurus limbatus	Fraser, 1964	0	0	0	1	0	0	0	0	0	0	0	735	C-F	Neo	25; 73
Micrurus margaritiferus	Roze, 1967	0	0	0	1	0	0	0	0	0	0	0	773		Neo	25; 26
Micrurus medemi	Roze, 1967	0	0	1	1	0	0	0	0	0	0	0	666		Neo	25
Micrurus meridensis	Roze, 1989	0	0	1	0	0	0	0	0	0	0	0	390		Neo	25
Micrurus mertensi	Schmidt, 1936	0	0	0	1	0	0	0	0	0	0	0	1115		Neo	25
Micrurus mipartitus	(Duméril, Bibron & Duméril, 1854)	0	0	1	1	1	0	0	0	0	0	0	1200	C-F	Neo	25
Micrurus mosquitensis	Schmidt, 1933	0	0	1	1	1	0	0	0	1	0	0	750		Neo	25; 169
Micrurus multifasciatus	Jan, 1858	0	0	0	1	1	0	0	0	0	0	0	1130	C-F	Neo	25; 73
Micrurus narduccii	(Jan, 1863)	0	0	0	1	0	0	0	0	0	0	0	1157	C-F	Neo	25; 26
Micrurus nattereri	Schmidt, 1952	0	0	1	1	1	0	0	0	1	0	0	1300		Neo	25; 169
Micrurus nebularis	Roze, 1989	0	0	0	1	0	0	0	0	0	0	0	557	Grd	Neo	25
Micrurus nigrocinctus	(Girard, 1854)	0	0	1	1	1	0	0	0	1	0	0	1150	Arb	Neo	25
Micrurus obscurus	(Jan, 1872)	0	0	1	1	0	0	0	1	0	0	0	1345		Neo	25; 169
Micrurus ornatissimus	(Jan, 1858)	0	0	0	1	0	0	0	0	0	0	0	848		Neo	25; 26; 169
Micrurus paraensis	Da Cunha & Nascimento, 1973	0	0	0	1	0	0	0	1	0	0	0	530	C-F	Neo	25
Micrurus peruvianus	Schmidt, 1936	0	0	0	1	0	0	0	0	0	0	0	543		Neo	25; 26
Micrurus psyches	(Daudin, 1803)	0	0	1	1	0	0	0	0	0	0	0	910		Neo	25; 117
Micrurus putumayensis	Lancini, 1962	0	0	0	1	0	0	0	0	0	0	0	805		Neo	25; 26

Micrurus pyrrhocryptus	(Cope, 1862)	0	0	1	1	0	0	0	0	0	0	0	1241	C-F	Neo	8; 25
Micrurus remotus	Roze, 1987	0	0	1	1	0	0	0	0	0	0	0	567		Neo	25; 169
Micrurus ruatanus	(Günther, 1895)	0	0	1	0	0	0	0	0	0	0	0	681	C-F	Neo	25
Micrurus serranus	Harvey, Aparicio & Gonzalez, 2003	0	0	0	1	1	0	0	0	0	0	0	822	C-F	Neo	25
Micrurus spixii	Wagler, 1824	0	0	1	1	0	0	0	0	0	0	0	1600	C-F	Neo	8; 10; 25; 165
Micrurus surinamensis	(Cuvier, 1817)	0	0	0	0	0	1	0	0	0	0	0	1350	C-F	Neo	8; 10; 25; 129
Micrurus tener	Baird & Girard, 1853	0	1	1	1	1	0	0	0	1	0	0	1217	C-F	Neo	25
Micrurus tschudii	Jan, 1858	0	0	1	1	0	0	0	0	0	0	0	880	Arb	Neo	25; 26
Naja anchietae	Bocage, 1879	1	1	1	1	1	0	0	0	0	0	0	2310	Grd	Afr	169
Naja annulata	Peters, 1876	0	0	0	0	1	1	0	0	0	0	0	2700	SA	Afr	162
Naja annulifera	Peters, 1854	1	1	1	1	1	0	0	0	0	0	0	2245	Arb	Afr	2; 169
Naja arabica	Scortecci, 1932	1	1	1	1	1	0	0	0	0	0	0		Grd	Afr	184
Naja atra	Cantor, 1842	1	1	1	1	1	1	0	0	0	0	0	1650	Grd	IM	99
Naja Christyi	(Boulenger, 1904)	0	0	0	0	1	1	0	0	0	0	0	1400	SA	Afr	162
Naja haje	(Linnaeus, 1758)	0	1	0	1	1	0	0	0	0	1	0	2500	Grd	Afr	162
Naja kaouthia	Lesson, 1831	0	1	0	1	1	0	0	0	0	0	0	2300	Grd	IM	33; 76
Naja katiensis	Angel, 1922	0	1	0	1	0	0	0	0	0	0	0	1000	Arb	Afr	162
Naja melanoleuca	Hallowell, 1857	1	1	1	1	1	0	0	0	0	0	0	2700	Grd	Afr	2; 162
Naja mossambica	Peters, 1854	1	1	1	1	1	0	0	1	0	0	0	1500	Grd	Afr	2; 162
Naja multifasciata	(Werner, 1902)	0	0	0	1	1	1	0	0	0	0	0	800	Grd	Afr	162
Naja naja	(Linnaeus, 1758)	1	1	0	1	1	0	0	0	0	0	0	2200	SA	IM	178
Naja nigricollis	Reinhardt, 1843	1	1	1	1	1	0	0	0	0	1	0	2000	Arb	Afr	2; 162
Naja nivea	(Linnaeus, 1758)	1	1	1	1	1	0	0	0	0	1	0	1700	Arb	Afr	2; 162
Naja nubiae	Wüster & Broadley, 2003	1	1	0	1	1	0	0	0	0	0	0	1510	Grd	Afr	36; 184
Naja oxiana	(Eichwald, 1831)	1	1	1	0	1	0	0	0	0	0	0	1900	Grd	Afr	10; 178
Naja pallida	Boulenger, 1896	1	1	0	1	1	0	0	0	0	0	0	1500	Arb	Afr	162
Naja philippinensis	Taylor, 1922	0	1	1	1	1	0	0	0	0	1	0	2000	Grd	IM	33; 169
naja sagittifera	Wall, 1913	0	1	1	0	1	0	0	0	0	1	0	635	Grd	IM	178
Naja samarensis	Peters, 1861	0	1	0	1	1	0	0	0	0	0	0	1200	Grd	IM	169
Naja siamensis	Laurenti, 1768	0	1	0	1	1	0	0	0	0	0	0	1600	Grd	IM	33
naja sputatrix	Boie, 1827	0	1	1	1	1	0	0	0	0	0	0	1500	Grd	IM	33
Naja sumatrana	Müller, 1890	0	1	0	0	1	0	0	0	0	0	0	1500	Grd	IM	33
Neelaps bimaculatus	(Duméril, Bibron & Duméril, 1854)	0	0	1	0	0	0	0	0	0	0	0	450	C-F	Aus	29; 93; 128

Neelaps calonotus	(Duméril, Bibron & Duméril, 1854)	0	0	1	0	0	0	0	0	0	0	0	280	C-F	Aus	29; 93
Notechis scutatus	(Peters, 1861)	1	1	1	1	1	1	0	0	0	0	0	2100	Grd	Aus	10; 29
Ogmodon vitianus	Peters, 1864	0	0	0	0	0	0	0	1	0	0	0	300	C-F	Pol	10
Ophiophagus Hannah	(Cantor, 1836)	0	0	1	1	0	0	0	0	0	0	0	5850	Arb	IM	33; 76; 99
Oxyuranus microlepidotus	(Mccoy, 1879)	0	1	0	0	0	0	0	0	0	0	0	2500	Grd	Aus	10; 29
Oxyuranus scutellatus	Peters, 1867	1	1	1	0	0	0	0	0	0	0	0	3500	Grd	Aus	10; 29
Oxyuranus temporalis	Doughty, Maryan, Donnellan & Hutchinson, 2007	0	1	0	0	0	0	0	0	0	0	0	1600	Grd	Aus	29; 169
Parahydrophis mertoni	(Roux, 1910)	0	0	0	0	0	1	1	0	0	0	0	600	Aqu	Mar	10; 177
Parasuta dwyeri	(Worrell, 1956)	0	0	1	1	0	0	0	0	0	0	0	500	C-F	Aus	93
Parasuta flagellum	(Mccoy, 1878)	0	0	1	0	0	0	0	1	0	0	0	400	C-F	Aus	29; 93
Parasuta gouldii	(Gray, 1841)	0	0	1	1	0	0	0	0	0	0	0	600	C-F	Aus	29; 93
Parasuta monachus	(Storr, 1964)	0	0	1	0	0	0	0	0	0	0	0	530	Grd	Aus	29; 93
Parasuta nigriceps	(Günther, 1863)	0	0	1	1	0	0	0	0	0	0	0	600	C-F	Aus	29; 93
Parasuta spectabilis	(Krefft, 1869)	0	0	1	0	0	0	0	0	0	0	0	400	Grd	Aus	29; 93
Paroplocephalus atriceps	(Storr, 1980)	0	0	1	0	0	0	0	0	0	0	0	500	Arb	Aus	21; 29; 93
Pseudechis australis	(Gray, 1842)	1	1	1	1	1	0	0	0	0	0	0	3000	Grd	Aus	29; 93
Pseudechis butleri	Smith, 1982	0	1	1	**1**	0	0	0	0	0	0	0	1800	Grd	Aus	29; 93
Pseudechis colletti	Boulenger, 1902	0	1	1	0	0	0	0	0	0	0	0	2000	Grd	Aus	29; 93
Pseudechis guttatus	De Vis, 1905	0	1	1	1	1	0	0	0	0	0	0	2000	Grd	Aus	29; 93
Pseudechis papuanus	Peters & Doria, 1878	0	1	1	0	1	0	0	0	0	0	0	2450	Grd	Aus	10; 29; 182
Pseudechis porphyriacus	(Shaw, 1794)	1	1	1	0	1	0	0	0	0	0	0	2101	Grd	Aus	93
Pseudohaje goldii	(Boulenger, 1895)	0	1	0	0	1	0	0	0	0	0	0	2700	Arb	Afr	162
Pseudohaje nigra	Günther, 1858	0	1	0	0	1	0	0	0	0	0	0	2200	Arb	Afr	162
Pseudonaja affinis	Günther, 1872	1	1	1	0	1	0	0	0	0	0	0	2000	Grd	Afr	29; 93; 156
Pseudonaja aspidorhyncha	(Mccoy, 1879)	0	1	1	0	0	0	0	0	0	0	0	1500	Grd	Afr	29; 177; 183
Pseudonaja guttata	(Parker, 1926)	0	1	1	0	0	0	0	0	0	0	0	1400	Grd	Afr	29; 93
Pseudonaja inframacula	(Waite, 1925)	1	1	1	0	1	0	0	0	0	0	0	1500	Grd	Afr	29; 93
Pseudonaja ingrami	(Boulenger, 1908)	0	1	0	0	0	0	0	0	0	0	0	1760	Grd	Afr	93

Pseudonaja mengdeni	Wells & Wellington, 1985	1	1	1	1	0	0	0	0	0	0	0	1300	Grd	Afr	29; 169
Pseudonaja modesta	(Günther, 1872)	0	0	1	0	0	0	0	0	0	0	0	600	Grd	Afr	93
Pseudonaja nuchalis	Günther, 1858	1	1	1	1	1	0	0	0	0	0	0	1500	Grd	Afr	29; 93
Pseudonaja textilis	(Duméril, Bibron & Duméril, 1854)	1	1	1	0	1	0	0	0	0	0	0	2500	Grd	Afr	29; 93
Rhinoplocephalus bicolor	Müller, 1885	0	0	1	0	1	0	0	0	0	0	0	400	Grd	Afr	29; 93
Salomonelaps par	(Boulenger, 1884)	0	0	1	1	1	0	0	1	0	0	0	1200	Grd	NG	10; 93
Simoselaps anomalus	(Sternfeld, 1919)	0	0	1	0	0	0	0	0	0	1	0	210	C-F	Aus	29; 93
Simoselaps bertholdi	(Jan, 1859)	0	0	1	0	0	0	0	0	0	1	0	330	C-F	Aus	29; 93
Simoselaps littoralis	(Storr, 1968)	0	0	1	0	0	0	0	0	0	0	0	400	C-F	Aus	29; 93
Simoselaps minimus	(Worrell, 1960)	0	0	1	0	0	0	0	0	0	0	0	220	C-F	Aus	29; 93
Simoselaps warro	(De Vis, 1884)	0	0	1	0	0	0	0	0	0	0	0	400	C-F	Aus	29; 93
Sinomicrurus hatori	(Takahashi, 1930)	0	0	0	1	0	0	0	0	0	0	0	980	C-F	Pal	102; 169
Sinomicrurus japonicus	(Günther, 1868)	0	0	1	1	0	0	0	0	0	0	0	600	C-F	Pal	102
Sinomicrurus kelloggi	(Pope, 1928)	0	0	0	1	0	0	0	0	0	0	0	800	C-F	IM	33; 102
Sinomicrurus macclellandi	(Reinhardt, 1844)	0	0	1	1	0	0	0	0	0	0	0	840	C-F	Pal	33; 76; 99
Sinomicrurus sauteri	(Steindachner, 1913)	0	0	0	1	0	0	0	0	0	0	0	980	C-F	Pal	102
Suta fasciata	(Rosen, 1905)	0	0	1	0	0	0	0	0	0	0	0	600	Grd	Aus	29; 93; 144
Suta ordensis	(Storr, 1984)	0	0	1	0	0	0	0	0	0	0	0	750	Grd	Aus	10; 29
Suta punctata	(Boulenger, 1896)	0	0	1	1	0	0	0	0	0	0	0	500	Grd	Aus	10; 29; 93
Suta suta	(Peters, 1863)	0	1	0	1	1	0	0	0	0	0	0	900	Grd	Aus	10
Toxicocalamus buergersi	(Sternfeld, 1913)	0	0	0	0	0	0	0	1	0	0	0	365	C-F	NG	100; 169
Toxicocalamus grandis	(Boulenger, 1914)	0	0	0	0	0	0	0	1	0	0	0	960	C-F	NG	100
Toxicocalamus holopelturus	Mcdowell, 1969	0	0	0	0	0	0	0	1	0	0	0	620	C-F	NG	100
Toxicocalamus longissimus	Boulenger, 1896	0	0	0	0	0	0	0	1	0	0	0	800	C-F	NG	24; 100; 169
Toxicocalamus loriae	(Boulenger, 1898)	0	0	0	0	0	0	0	1	0	0	0	690	C-F	NG	100
Toxicocalamus mintoni	Kraus, 2009	0	0	0	0	0	0	0	1	0	0	0		C-F	NG	100
Toxicocalamus misimae	Mcdowell, 1969	0	0	0	0	0	0	0	1	0	0	0	468	C-F	NG	100
Toxicocalamus pachysomus	Kraus, 2009	0	0	0	0	0	0	0	1	0	0	0		C-F	NG	100

Toxicocalamus preussi	(Sternfeld, 1913)	0	0	0	0	0	0	0	1	0	0	0	765	C-F	NG	100
Toxicocalamus spilolepidotus	Mcdowell, 1969	0	0	0	0	1	0	0	1	0	0	0	780	C-F	NG	100
Toxicocalamus stanleyanus	Boulenger, 1903	0	0	0	0	0	0	0	1	0	0	0	610	C-F	NG	100
Tropidechis carinatus	(Krefft, 1863)	1	1	1	0	1	0	0	0	0	0	0	1000	Arb	Aus	10; 29; 142
Vermicella annulata	(Gray, 1841)	0	0	1	1	0	0	0	0	0	0	0	1000	C-F	Aus	10; 29; 93
Vermicella intermedia	Keogh & Smith, 1996	0	0	0	1	0	0	0	0	0	0	0	650	C-F	Aus	29; 128
Vermicella multifasciata	(Longman, 1915)	0	0	0	1	0	0	0	0	0	0	0	540	C-F	Aus	10; 29; 128
Vermicella snelli	Storr, 1968	0	0	0	1	0	0	0	0	0	0	0	> = 500	C-F	Aus	29
Vermicella vermiformis	Keogh & Smith, 1996	0	0	0	1	0	0	0	0	0	0	0	> = 600	C-F	Aus	29
Walterinnesia aegyptia	Lataste, 1887	1	1	1	1	1	0	0	0	0	0	0	1350	Grd	Afr	162
Micrelaps bicoloratis (outgroup)	(Sternfeld, 1908)	0	0	0	1	0	0	0	0	0	0	0	320	C-F	Afr	15

Appendix 4. Broad summary of prey types taken by burrowing elapid genera and species.

Burrowing genus or species	Prey taken
Aspidomorphus spp (n=3)	Eats skinks
Aspidelaps spp (n=2)	Primarily take amphibians or legless skinks
Brachyurophys (n=8)	All eat reptile eggs along with small or burrowing lizards (37.5%)
Calliophis spp (n=9)	All take snakes (esp. blindsnakes) with a secondary representation of termites and other narrow bodied insects and their eggs
Denisonia spp (n=2)	Both spp primarily take frogs with lizards being the other prey type
Elapsoidea spp (n=7)	Primarily taking skinks and amphisbaenids in addition to snakes and amphibians.
Micropekhis ikaheka	Small mammal, lizards, snakes and amphibians
Micruroides euryxanthus	Lizards and blindsnakes
Micrurus (n=61)	A group largely known to eat squamates
Neelaps (n=2)	100% take elongate (*Lerista*) skinks
Ogmodon vituanus	Earthworms and other soil arthropods
Parasuta spp (n=4)	All take lizards
Simoselaps (n=5)	All consume small-bodied lizards
Sinomicrurus spp (n=5)	All consume snakes
Toxicocalamus spp (n=11)	88% feed on earthworms

Vermicella spp (n=5)	100% feed on blindsnakes