Diversity and diversification of uropeltid snakes

Filipa Leão Sampaio

University College London

March 2020

Thesis submitted for the degree of Doctor of Philosophy

Declaration

I, Filipa Leão Sampaio, confirm that the work presented in this thesis is my own. Where information has been derived from other sources, I confirm that this has been indicated in the thesis.

Statement of authorship

Unpublished sequence data generated by David Gower and colleagues were used in Chapters 2 and 3. Tissue samples collected pre-2000 were provided by Wildlife Heritage Trust, Sri Lanka (thanks to Rohan Pethiyagoda); and the University of Kerala, Thiruvanathapuram, India. Molecular lab work (extractions and amplifications) with fresh tissue samples was conducted by Cornelia Simon Nutbrown (UCL MRes) and me in the NHM molecular labs, and sequencing was carried out at UCL GEE Sequencing facility with the assistance of Fraser Simpson, Wendy Hart and Farrell Mackenzie. Part of the molecular lab work was carried out in collaboration with Ullasa Kodandaramaiah and Vivek Cyriac at IISER Thiruvananthapuram, India, and with Mendis Wickramasinghe and Nethu Wickramasinghe at IBMBB, University of Colombo, Sri Lanka. I carried out the molecular lab work with fluid preserved historical specimens in the NHM ancient DNA lab with Selina Brace's assistance. Shotgun sequencing was done in the NHM sequencing facility (Andy Briscoe and Claire Griffin). For Chapter 3, BPP analyses were conducted by Tomas Flouri and Paschalia Kapli (UCL), and BAMM analyses were implemented by Julia Day. For Chapter 4, I conducted visits to natural history collections to examine specimens and collect a set of metric traits used in analyses; ventral counts were done by me, David Gower and colleagues. I assembled datasets, analysed the data, prepared figures and tables, wrote a first draft, and incorporated edits and comments from David Gower and Julia Day.

Abstract

Fossorial snakes are key to understanding snake origins and trends of fossoriality in early snake evolution. However, they are generally understudied due to their secretive lifestyle, making them less likely to be encountered without special effort. Given their phylogenetic position and fossorial habits, this PhD project aims to study the evolution of a major radiation of fossorial snakes – the family Uropeltidae. Currently there are eight recognised genera and ca. 56 species, distributed in the Western Ghats of India and Sri Lanka. They show morphological traits that are adaptations to fossoriality, which have never been studied in detail, or with quantitative approaches. Their heads are adapted for headfirst burrowing, hence being important structures to study adaptation to the physical environment. Moreover, snakes in this group are commonly known as shieldtails due to the unusual structures on their tails, whose diversity and function are poorly known. This project employs an integrative approach to generate a taxonomically comprehensive molecular phylogeny for uropeltids, and to study lineage and phenotypic diversity and diversification patterns. This work provides insights into spatial, temporal and morphological patterns of diversification in these organisms and understand the impact that fossoriality has on biotic diversification. In summary, this thesis advances the understanding of evolutionary relationships among uropeltids, uncovering unexpectedly high levels of uropeltid molecular diversity. Moreover, results estimated constant lineage accumulation rates in uropeltids, and a pattern of early burst of phenotypic evolution in tail tip traits. These results suggest that while this is not a case of adaptive radiation, tail tip morphology might have played an important ecological role early on in the diversification of the Uropeltidae.

Impact Statement

This study presents new insights into the evolutionary history and diversification patterns of uropeltids, a group of fossorial (burrowing) snakes that has generally been poorly understood due to their secretive habits and confusing taxonomic history. Despite recent advances in understanding their evolutionary relationships, a comprehensive phylogeny has not been available due to the lack of samples available for assembling molecular datasets. For the first time, uropeltid mitochondrial sequence data were generated from fluid-preserved museum specimens up to at least 120 years old, enabled by advances in molecular techniques originally employed in ancient DNA studies. This highlights the potential for historical specimens stored in natural history collections as a source of DNA for future studies. Molecular data revealed exceptionally high levels of diversity (higher than predicted by current uropeltid taxonomy), showing how part of vertebrate biological diversity remains to be discovered. Analysis of phenotypic diversification was made possible by examining and collecting external trait data from specimens housed in museum collections. Results revealed a curious pattern with different tail morphologies evolving early on in the evolutionary history of the clade, a pattern that has not been detected for other snakes. These findings might allow for a better understanding of trends of morphological evolution across fossorial squamate reptiles.

This study generated a taxonomically comprehensive dataset for a species rich clade endemic to the Western Ghats and Sri Lanka biodiversity hotspot. In combination with other recent and hopefully future diversification studies of other organismal groups, the data and analyses presented here will help to improve understanding of the evolutionary origins of the exceptional biodiversity in this region. The improved understanding of evolutionary, biogeographic, and ecomorphological patterns of uropeltid diversity presented in this thesis will also, ultimately, improve conservation assessments for these generally neglected snakes.

The outputs of the work conducted have resulted in the publication of a new species description (Appendix paper 1), with another under revision (Appendix paper 2), and future manuscripts will focus on the molecular phylogenetics and

evolutionary diversification in uropeltids. Once manuscripts for the data and analyses generated in this thesis are published, all morphological and sequence data will be publicly available so that they can be incorporated in other studies, though in practice this might be more straightforward with molecular datasets. Preliminary results have been presented at the BES Macroecology SIG (London, 2017), Young Systematists' Forum (London, 2018), and the Biennial Conference of the Systematics Association (Bristol, 2019).

Furthermore, this study demonstrates the importance of natural history collections as biodiversity repositories, and how methodological advances can help bring historical collections into modern research.

Acknowledgments

First of all, I wish to thank my supervisors, David Gower and Julia Day, for their encouragement, support and advice throughout the development of this thesis. Would like to extend my thanks to my viva examiners, Paul Upchurch and Wolfgang Wüster, for their comments and suggestions on the thesis.

Thanks to colleagues who collected samples and generated DNA sequence data before I started this project, and to Connie Simon Nutbrown for generating sequence data during her MRes project that were also used in this thesis. Thanks to Frederico Martins for training in the Sanger sequencing protocol, and to Fraser Simpson, Wendy Hart and Farrell Mackenzie at UCL GEE Sequencing facility for assistance in DNA sequencing. I would also like to thank Selina Brace and Ian Barnes for access to the NHM ancient DNA lab, and a special thanks to Selina for lab support and training, and discussion on the bioinformatics workflow. Thanks to Peter Foster for the maintenance of the NHM servers and for always replying so promptly to my requests. Thank you to Tomas Flouri and Paschalia Kapli at UCL for discussion on species delimitation methods and for help setting up analyses in BPP. Ollie Crimmen provided useful references for collections preservation methods. Thanks to Carla Bardua, Aki Watanabe, and Ashleigh Marshall for help with different aspects of microCT reconstruction and landmarking, Dan Sykes for help with Drishti, and Brett Clark with Avizo assistance.

Thanks to members of the NHM Vertebrates group for the friendly work environment, advice and helpful discussions: Ariane Standing, Chiho Ikebe, Mark Wilkinson, Ralf Britz, Deepak V, Jeff Streicher, Steve Mahoney, María Torrez Sanchez, Natalie Cooper, Gabriela Bittencourt, Ollie Crimmen, Patrick Campbell, Chun Kamei, Ana Serra Silva. To the postgraduate community in the museum, I am appreciative of the companionship and advice throughout - Debbie Glass, Dinarzarde Raheem, Carla Bardua, Natalia Fraija, Helen Jenkins, Tom Pennance, João Leite, just to name a few. And to Eileen Cox and Anna Hutson thanks for administrative support.

To Jen Olori, many thanks for welcoming me at SUNY Oswego, teaching me all about uropeltid skulls and for sharing literature. To Susan, thanks for taking me in and being such a great housemate during my stay, and both for showing me around upstate NY.

Thanks to Ashok Captain and Varad Giri for assistance with logistics during my visit to India. I am grateful to Ullasa Kodandaramaiah at IISER Thiruvananthapuram for welcoming us into his lab, and to the lab members for such a welcoming stay. Thanks to Vivek Cyriac for help in the lab and for sharing his uropeltid knowledge. Many thanks to

Mendis and Nethu Wickramasinghe for being so welcoming and for all their assistance during my visit to Colombo.

For access to collections and/or specimen loans I would like to thank The Natural History Museum, London, UK (Patrick Campbell, Jeff Streicher), Muséum national d'Histoire naturelle, Paris, France (Nicolas Vidal and colleagues), Museum für Naturkunde, Berlin, Germany (Frank Tillack, Mark-Oliver Rödel), American Museum of Natural History, New York, USA (Frank Burbrink, David Kirzirian, Lauren Vonnahme), Muséum d'histoire naturelle de la Ville de Genève, Switzerland (Andreas Schmitz), Museum of Comparative Zoology, Harvard University, Boston, USA (José Rosado), National Museum of Natural History, Smithsonian Institution, Washington DC, USA (Addison Wynn, Esther Langan), California Academy of Sciences, San Francisco, USA (Lauren Scheinberg, Erica Ely), Bombay Natural History Society, Mumbai, India (Rahul Khot), IISER Thiruvananthapuram, India (Ullasa Kodandaramaiah, Vivek Cyriac), Herpetological Foundation of Sri Lanka, Colombo, Sri Lanka (Mendis Wickramasinghe, Nethu Wickramasinghe), National Museum, Colombo, Sri Lanka (NMSL) (Lankana Somarathna), National Centre for Biological Sciences, India (Varad Giri).

This project was funded by a London NERC DTP studentship and research training support grant. EU SYNTHESYS grants covered a two-week visit to MNHN, Paris and a one-week visit to MfN, Berlin to work on the herpetological collections and access to CT-scanning facilities. An AMNH Collection Study Grant covered a one-week visit to work on the collection in New York. Visits to collect trait data in collections in Harvard, Washington DC and San Francisco, and a research stay in Jen Olori's lab at SUNY Oswego were supported by a UCL Bogue Fellowship. An award from the Systematics Association and Linnean Society's Systematics Research Fund covered a visit to labs and collections in India and Sri Lanka. A Systematics Association Student Travel Scholarship covered costs to present a poster at the Biennial Conference of the Systematics Association in Bristol.

Thanks to the ladies at the yellow door for giving me a sense of community in London. Huge thanks to Ellie, Jan and Simon for their friendship and keeping me sane.

Obrigada aos meus pais e à Mafalda for todo o apoio apesar das minhas ausências. Não teria chegado aqui sem vocês.

Table of contents

List of tables

List of figures

Chapter 1 – Introduction

1.1 Snakes and fossoriality in early snake evolution

Snakes (Serpentes) are a clade of squamate reptiles most closely related to the paraphyletic 'lizards' (Townsend et al., 2004; Vidal and Hedges, 2005). There are over 3700 living species of snakes (Uetz and Hošek, 2019) with a worldwide distribution except Antarctica (Burbrink and Crother, 2011). Snakes, while maintaining a relatively conservative body pattern, elongated and limbless, have been able to successfully adapt to a variety of different habitats (Bellairs, 1968) and include terrestrial, arboreal, aquatic and fossorial (burrowing) species.

There is agreement that one of the basal most phylogenetic divisions within extant snakes is between the small fossorial Scolecophidia Cope, 1864 (blindsnakes and threadsnakes) and the typically larger and ecologically more diverse Alethinophidia Nopsca, 1923, a group that includes all other extant snakes (Vidal and Hedges, 2002; Vidal et al., 2008; Wiens et al., 2008; Scanlon and Lee, 2011; Streicher and Wiens, 2016) (Figure 1-1). The relationships among Scolecophidia have been under debate as to whether the group is mono- or paraphyletic, but a recent study by Miralles et al. (2018), employing a dense sampling across scolecophidians, found support for the paraphyly of scolecophidian snakes (Figure 1-2). The relationships among the major groups of alethinophidians is also not entirely clear (McDiarmid et al., 1999), with disagreements between morphological and molecular evidence.

Alethinophidians can be divided into the probably non-monophyletic henophidians, comprising a broad number of taxa including uropeltoids, boas and pythons; and the monophyletic caenophidians ('advanced' or 'higher' snakes) which contain the majority of living snakes, including colubrids, elapids and viperids (Heise et al., 1995). Snakes can also be further characterised phenotypically as macrostomatan, which are able to engulf prey with a diameter exceeding that of the snake's head (Rieppel, 2012); or non-macrostomatan, which include the small fossorial snakes scolecophidians, aniliids (*Anilius*) and uropeltoids (cylindrophiids, anomochilids and uropeltids) (Rieppel, 2012). Somewhat confusingly, Macrostomata is also a higher taxon in some classifications of snakes that were

underpinned by a phylogenetic hypothesis of monophyly of macrostomatan alethinophidians, though Burbrink et al.'s (2019) analysis of a large genomic squamate dataset did not find support for a monophyletic Macrostomata. Harrington and Reeder (2017) suggested this phenotype evolved once and was independently lost in anilids, uropeltids and cylindrophiids.

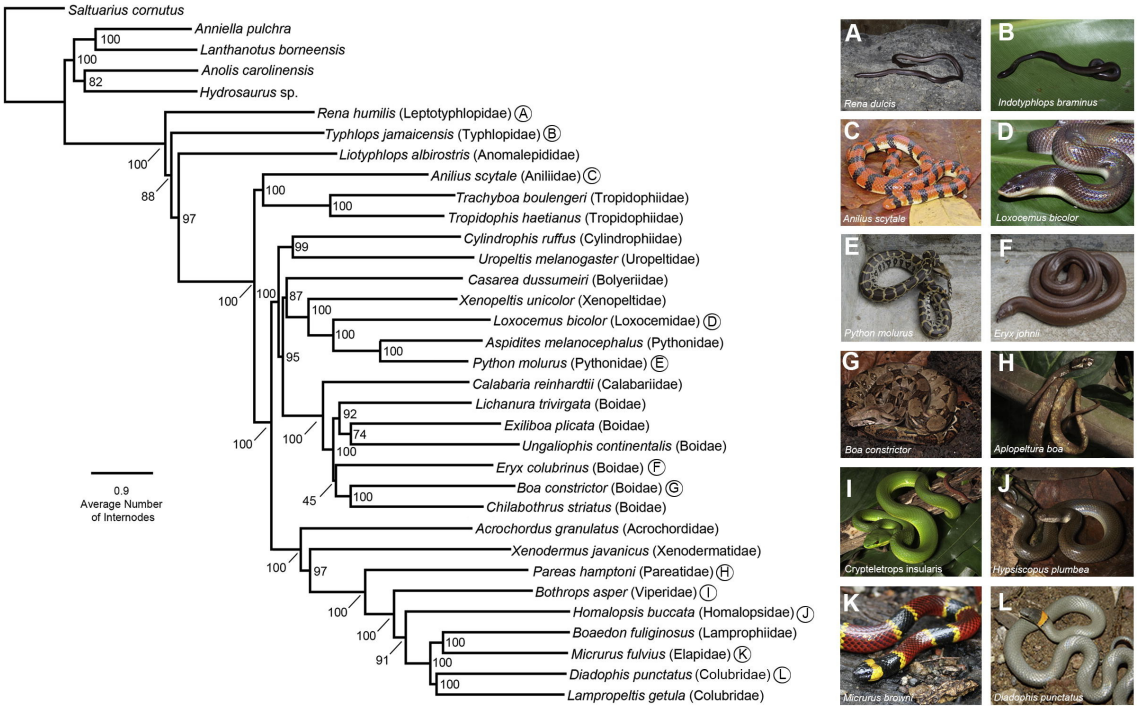


Figure 1-1 Tree estimated from concatenated likelihood analysis (RAxML) of 3776 ultra-conserved elements loci (1,398,192 bp; 52% missing data) from sequence capture, only including loci with no more than 50% missing taxa per locus. Numbers at nodes indicate bootstrap support value (Streicher and Wiens, 2016).

There are several extant groups of fossorial snakes including scolecophidians, aniliids and uropeltoids, as well as some macrostomatan atractaspidids, colubrids and elapids (Cundall and Irish, 2008) that together do not constitute a monophyletic group. Even though snakes are generally well-studied organisms, fossorial snakes are relatively poorly known vertebrates due to their relatively secretive lifestyle, making them less likely to be encountered without special effort. Nevertheless, fossorial snakes are key to understanding snake origins and early evolution that has long been a subject of debate.

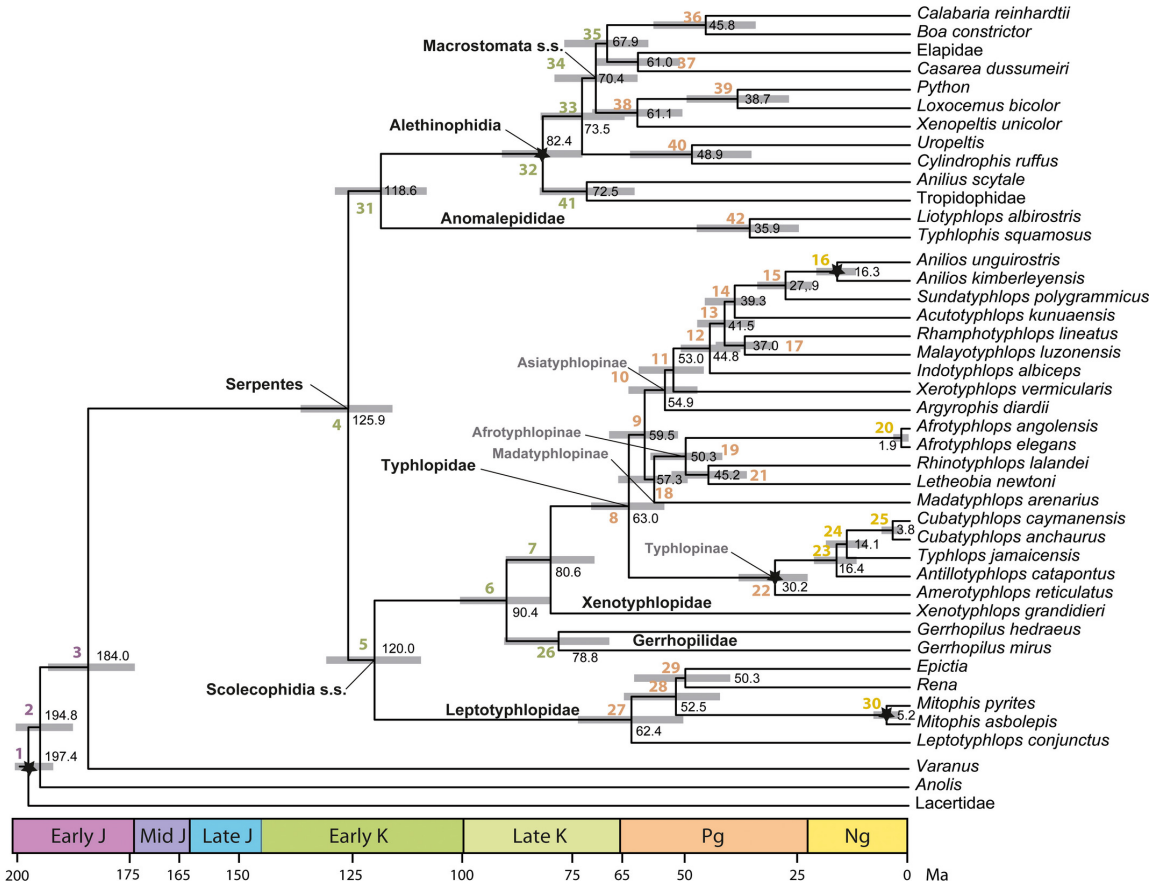


Figure 1-2 Time tree from Miralles et al. (2018) based on 14 loci, with a relaxed uncorrelated lognormal clock, and a birth-death tree prior inferred in BEAST. Grey bars at nodes depict 95% credibility intervals for divergence events.

Fossorial squamates have specialised features that are adaptations to moving and feeding within the soil environment. Modifications associated with burrowing habits include body elongation, and limb reduction or absence, gaining a snake-like form (Bellairs, 1968). There are several groups of squamate reptiles that have undergone partial or complete limb reduction, this having occurred at least 25 times during squamate evolution (Wiens et al., 2006). There is a diverse range of limb loss in fossorial lizards – in the Pygopodidae, only the hind pair are visible; the amphisbaenian *Bipes* only have front limbs; in the slow worm *Anguis fragilis*, neither pair of limbs is externally visible (Bellairs, 1968), and in some squamates there are no traces of limbs or (internally) of limb girdles. Fossorial squamates generally have small, even-sized scales (including those on the belly) which are not adapted for surface locomotion (Curran and Kauffeld, 1937). Underground, vision loses its importance. Most burrowing squamates have reduced visual capability and have

small or vestigial eyes with reduced complements of visual pigments (Curran and Kauffeld, 1937; Walls, 1942; Underwood, 1970; Simões et al., 2015). Mechanical stress is also an influence, with most burrowing squamates having their eyes covered by a transparent spectacle or even by typical head scales, which prevents dirt from entering (Underwood, 1970). Many fossorial squamates also have a short tail (Bellairs, 1970).

It is hypothesised that snakes in an early phase in their evolutionary history passed through either a profound aquatic or a burrowing phase (Coates and Ruta, 2000; Burbrink and Crother, 2011; Longrich et al., 2012; and references therein). These two competing hypotheses have been used to explain how snakes gained their legless, elongated snake-like form. Paleontological data for early snakes are patchy and poorer than for some other reptile groups, and interpretation of snake origins has also relied heavily on evidence derived from the anatomy of extant taxa (Bellairs, 1968). Snake ancestry and early evolution remain patchily understood due partly to a lack of intermediate forms in the fossil record (Longrich et al., 2012; Hsiang et al., 2015). The earliest known fossils that can be attributed to Serpentes are typically considered to be in the region of 100 million years old (though see Caldwell et al. (2015) for a claim that snakes extend in the fossil record to ~167–143 million years ago (Ma)).

For most of the past two decades, support for the aquatic origin of snakes has come from part of the fossil record (marine fossils with hindlimbs – e.g. *Pachyrachis problematicus* (Caldwell and Lee, 1997; Scanlon et al., 1999)) and most of the support for the burrowing origin has come from extant snakes, including phylogenetic evidence (due to the number of fossorial clades at or near the base of the snake tree). Studies on the molecular phylogenetics of lizards and snakes point to the paraphyly of scolecophidians at the base of snake phylogeny, with authors suggesting a fossorial ancestral snake (Wiens et al., 2012; Miralles et al., 2018). More recently in this debate, Martill et al. (2015) reported a squamate fossil from the Early Cretaceous that they interpreted as providing evidence that snakes evolved from burrowing rather than marine ancestors.

Based on snake visual anatomical features, Walls (1942) argued that ancestral snakes were burrowers with greatly reduced eyes, and that subsequently

most snakes came above ground and underwent extensive radiation as surface-living types. Based on the evolution of visual opsin genes of scolecophidians and of other squamates, recent results have indicated that it is unlikely that the ancestral snake was as fossorial as living scolecophidians because they are extremely specialised burrowers with visual systems too reduced to represent the ancestral condition (Simões et al., 2015). Harrington and Reeder's (2017) ancestral state reconstruction of macrostomatan and limbelessness phenotypes suggests that the ancestral snake would not have been phenotypically macrostomatan, but that also would not have been a specialised burrower like extant scolecophidians, which is in accordance with evidence that the visual systems of the ancestral snake would not have been as reduced as in extant fossorial snakes (Simões et al., 2015).

Other recent studies have investigated the link between skull (Da Silva et al., 2018; Watanabe et al., 2019) and inner ear (Yi and Norell, 2015; Palci et al., 2017) shape and ecology in a phylogenetic framework to understand the ecological origin of snakes. Yi and Norell (2015) studied the inner ear structure to test fossoriality quantitatively in stem snakes, and their results were interpreted as showing that fossoriality was prevalent in the lineages leading to crown snakes (which included the fossil *Dinilysia*). However, Palci et al. (2017) rebutted those results with a more complete taxonomic sampling and based on its inner ear shape and placement in morphospace with extant species, suggested a different ecological assignment to the fossil *Dinilysia*, which they argue that while it might have been fossorial as in Yi and Norell (2015), they also found evidence for semi-aquatic habits. Still, Palci et al. (2017) refrained from making predictions for an ancestral ecology of snakes. Da Silva et al.'s (2018) findings based on the analyses of skull shape propose that the most recent common ancestor of crown snakes might have had a small skull adapted for fossoriality, though less specialised than scolecophidians. Nevertheless, Da Silva et al. (2018) results suggested that the ancestor of snakes and their sister group would have been non-fossorial, indicating a terrestrial to fossorial transition in the origin of snakes. A non-aquatic origin for snakes has also been proposed by other morphometric skull studies (Watanabe et al., 2019), as well as ancestral state reconstruction of habitats (Hsiang et al., 2015).

There are multiple extant fossorial snake lineages and the study of the morphology, ecology, phylogeny and evolution of less deeply phylogenetically nested lineages of burrowing snakes has potentially important implications for understanding trends of fossoriality in early snake evolution (Olori, 2010; Olori and Bell, 2012). Given their phylogenetic position and fossorial habits, this thesis will focus on the systematics and diversification of the Uropeltidae — a major group of fossorial alethinophidian non-caenophidian snakes.

1.2 Study organisms - uropeltid snakes

The Superfamily Uropeltoidea Müller is comprised of three families – Uropeltidae Müller, 1832, Cylindrophiidae Fitzinger, 1843 and Anomochilidae Cundall, Wallach, and Rossman, 1993. They form the largest evolutionary radiation of fossorial alethinophidians (based on extant representatives). Uropeltoids are also known as Asian anilioids due to traditionally its members being associated with the (now believed to be) distantly related South American Aniliidae Stejner, 1907, whose sole extant member is *Anilius scytale* (McDiarmid et al., 1999). These four families used to be considered a monophyletic group comprising the only living non-macrostomatan alethinophidian snakes, characterised by fossoriality and small mouth gape (Lee and Scanlon, 2002), but molecular data has provided strong evidence that they are not monophyletic (Vidal and David, 2004).

Cylindrophiidae, or Asian pipe snakes, is a monogeneric family endemic to South and Southeast Asia, occurring in Sri Lanka (one species), southern China (three species), and Malay Archipelago (10 species) — Indonesia, Malaysia, Borneo, Myanmar (Burma), Singapore, Thailand, Laos, Cambodia, and Vietnam (McDiarmid et al., 1999; Cundall, 2003; Kieckbusch et al., 2018). They live predominantly in leaf litter or loose soil and may be more common near water (Cundall, 2003). There is one genus and 14 species described in this family (Uetz and Hošek, 2019). It is more widespread than Uropeltidae and currently considered taxonomically less diverse. Cylindrophiids also appear to be morphologically less diverse than uropeltids, but this has not been studied in detail.

Anomochilidae is a family comprised by one genus and three species (Uetz and Hošek, 2019), distributed in Indonesia, Malaysian Peninsula and Borneo

(Cundall, 1993; McDiarmid et al., 1999; Das et al., 2008). All three species of *Anomochilus* are recorded in Borneo, making the island the possible centre of diversification of this poorly known genus (Das et al., 2008). For anomochilids, only a few specimens (less than 20) have been available in collections to perform morphological assessments, which has made it difficult to understand the biology and systematics of this group (Das et al., 2008).

Uropeltidae are endemic to a relatively restricted geographic range but have a high number of species when compared with the other uropeltoid families. Commonly known as shieldtails, the family currently has eight recognised genera, and a total of 56 species (Uetz and Hošek, 2019). They are distributed in Sri Lanka and in the Western Ghats of peninsular India (Figure 1-3) (Cadle et al., 1990; McDiarmid et al., 1999; Bossuyt et al., 2004), a known global biodiversity hotspot with high levels of endemism (Myers et al., 2000; Bossuyt et al., 2004). The heterogenous topography and diverse climates with monsoon seasons in the Western Ghats and Sri Lanka support high levels of vegetation and faunal diversity (Gunawardene et al., 2007). The island of Sri Lanka and India are part of the same continental plate, and are presently separated by the Palk strait. During the Pleistocene ice ages, when sea level was low, the strait formed a land bridge allowing organismal dispersal between the two regions, hence sharing sister taxa (reviewed in Bossuyt et al., 2004).

Uropeltids are small (total length approx. 18-58 cm), cylindrical, smooth-scaled snakes. Uropeltids have morphological traits that are adaptations to fossoriality, having strongly reinforced skulls for head-first burrowing, and reduced eyes. They exhibit seemingly high levels of morphological diversity, which have never been studied in detail or using a quantitative approach. The different snout shapes are likely associated with distinct digging behaviours, microhabitat use and/or diet, but this is largely unexplored. Several studies report uropeltid skull qualitative variation and description (Rieppel and Zaher, 2002; Cundall and Irish, 2008; Comeaux et al., 2010; Olori, 2010; Olori and Bell, 2012). Uropeltid tails also have distinct morphologies. Snakes in this group are commonly known as shieldtails due to their unusual blunt or obliquely flattened tail covered with heavily keeled scales and sometimes tipped with spines (terminal scute as in Pyron et al. (2016)),

with a bony plate underneath, which tends to be mistaken for the head (Gans, 1976). Among the different genera tails structures differ in size and shape, and their diversity and evolution are poorly understood. Regarding function, it has been suggested they use it as a plug in the soil to block tunnels from predators, which would have constituted a selective advantage (Gans, 1976). For plates with examples see Figures 1-4 to 1-8.

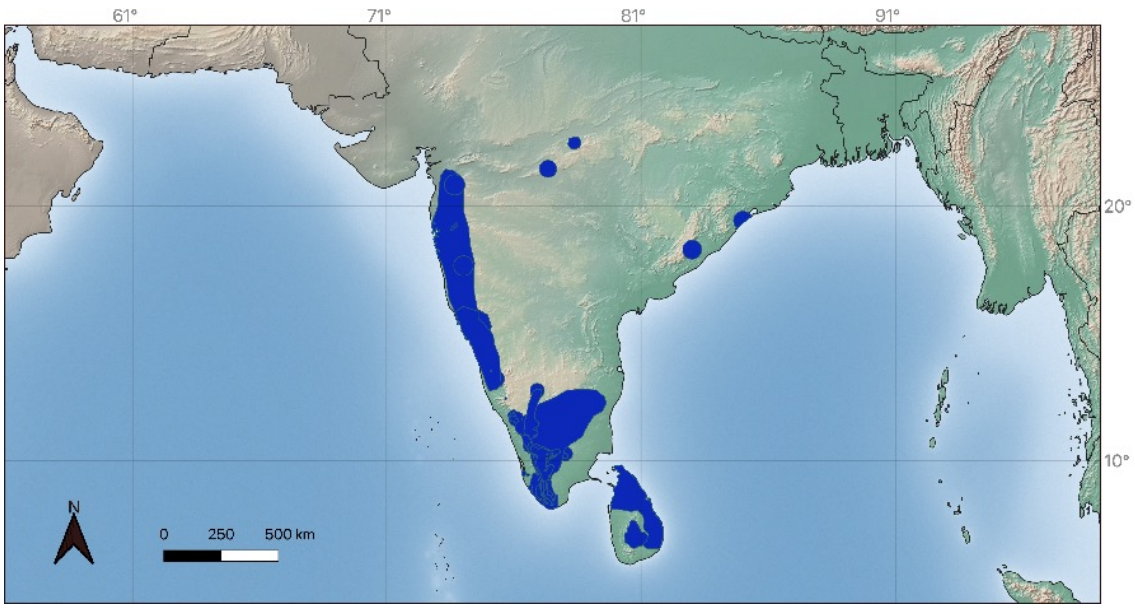


Figure 1-3 Map with distribution of the Uropeltidae family shaded in dark blue according to IUCN (2018). Shaded relief and water raster downloaded from http://www.naturalearthdata.com/.

Many Indian uropeltids occur at high elevations, in moist and cool (lower than 20ºC) forest environments, typically inhabiting shola forests – tropical evergreen forests – as well as plantations (e.g. rubber, coffee) (Rajendran, 1985). In Sri Lanka, endemic *Rhinophis* species are known to occur at different elevation levels (lowland, mid-elevations and high mountains), and occupy both wet and dry areas (Cadle et al., 1990). Rajendran (1985) has reported they are not found during day time, and can be encountered in burrows in the soil of one to two meters in depth, or under logs and rocks. From what is known uropeltids feed mostly on earthworms (Rajendran, 1985). Little information on reproductive modes is available, other than

Figure 1-4 *Melanophidium punctatum* specimen (BMNH 72.1.2.6). Scale in millimetres. (Photo credit: Natural History Museum, London photo unit).

Figure 1-5 *Teretrurus sanguineus* specimen (BMNH 1946.1.16.62). Scale in millimetres. (Photo credit: Natural History Museum, London photo unit).

Figure 1-6 *Uropeltis phipsonii* specimen (BMNH 97.7.19.2). Scale in millimetres. (Photo credit: Natural History Museum, London photo unit).

Figure 1-7 *Plectrurus aureus* specimen (BMNH 1946.1.1.54). Scale in millimetres. (Photo credit: Natural History Museum, London photo unit).

Figure 1-8 *Rhinophis punctatus* specimen (CAS 226068). Scale in millimetres. (Photo credit: Natural History Museum, London photo unit).

they are ovoviviparous (Rajendran, 1985). Some species have a brightly coloured ventral side, usually red or yellow tones. The bright colouration is suggested to have evolved as a warning signal to avoid predation from birds (Cyriac and Kodandaramaiah, 2019). However, there is generally little information on development, sexual dimorphism, ecology and patterns of geographic variation (Olori and Bell, 2012).

Partly because of their morphological traits, but also their fossorial lifestyle which makes them underrepresented in natural history collections, the evolutionary relationships and taxonomic classification of uropeltids have long been contentious (Cadle et al., 1990). Uropeltid taxonomy is extremely confusing, with most of it having been established in the late 1800s and early 1900s, written extremely briefly, often not explained with clear character descriptions, examined for small sample sizes, as well as poor locality data (Gower et al., 2008). Many synonymies proposed during this period (see McDiarmid et al. (1999) and Pyron et al. (2016) for synonymy lists), have not been readdressed in detail. This has been exacerbated by most of the type and historical specimens residing in European collections, not easily accessible by most researchers in South Asia. After a long break in taxonomic activity, there have been several uropeltid species recently documented based on external morphological characters. The lack of well understood morphological characters leads to misidentification of specimens, but these recent studies have started tackling this issue by expanding the range of useful morphological characters used in their systematics. Recent work has seen the description of species that were new to science (e.g. *Melanophidium khairei* (Gower et al., 2016), *Rhinophis roshanpererai* (Wickramasingue et al., 2017), *R. erangaviraji* (Wickramasinghe et al., 2009)), and hidden in synonymy (e.g. *Uropeltis bicatenata* (Gower et al., 2008)). However, besides morphological characters, molecular data has been instrumental for taxonomic purposes, and its analyses has led to taxonomic reassignments (e.g. *Pseudotyphlops*, *Uropeltis melanogaster* and *U. phillipsi*, now in the genus *Rhinophis* (Pyron et al., 2016)).

Based on albumin immunological data using protein electrophoresis, Cadle et al.'s (1990) study on uropeltids (ca. 11 species) made advances in inferring the evolutionary relationships among uropeltids, despite the small subset of taxa, and

established biogeographic scenarios for the family. The authors found the monophyly of Sri Lankan taxa, and a paraphyletic Indian assemblage with respect to the Sri Lankan group. Based on these findings, Cadle et al. (1990) suggested an Indian origin for the family with subsequent radiation into Sri Lanka. These results have found support in recent phylogenetic studies based on cranial datasets (Olori and Bell, 2012) and molecular data (Bossuyt et al., 2004; Pyron et al., 2016; Cyriac and Kodandaramaiah, 2017). Because the lowland species *R. travancoricus* was found as the Indian sister taxon of the Sri Lankan *Rhinophis*, Cadle et al. (1990) further hypothesised an initial radiation of lowland environments in Sri Lanka with subsequent (single or multiple) radiation(s) into montane biomes within the island.

Further phylogenetic work was conducted based on morphological cranial characters (Rieppel and Zaher, 2002; Comeaux et al., 2010; Olori and Bell, 2012), still with fairly limited sampling (less than 10 species), and with molecular data (Bossuyt et al., 2004; Pyron et al., 2016; Cyriac and Kodandaramaiah, 2017). A recent study (Cyriac and Kodandaramaiah, 2017), increased taxon sampling (ca. 40 species), offering a more complete understanding of uropeltid molecular phylogenetic relationships, and estimated the split between Uropeltidae and Cylindrophidae + Anomochilidae ca. 56 Ma (Figure 1-9). In their study, Cyriac and Kodandaramaiah (2017) suggested that uropeltid lineage diversification rates have been influenced by changes in temperature and environment during the Cenozoic era (65 million years to the present).

Despite advances in inferring the phylogenetic relationships among uropeltids, incomplete taxon sampling has not allowed the testing of the monophyly of all genera, and several species have not yet been sampled in molecular phylogenetic analyses. This has been hindered by the lack of tissue samples available to conduct molecular work. Incomplete taxon sampling is known to impact diversification patterns estimates (Moen and Morlon, 2014), so that a more taxonomically comprehensive tree might reveal different lineage diversification patterns. Moreover, despite the seemingly high levels of morphological variation across uropeltid species, both in head and terminal tail scute shape (Gans, 1976), this has never been studied in detail or with quantitative approaches, and the evolutionary pressures that drive uropeltid morphological shape are not understood

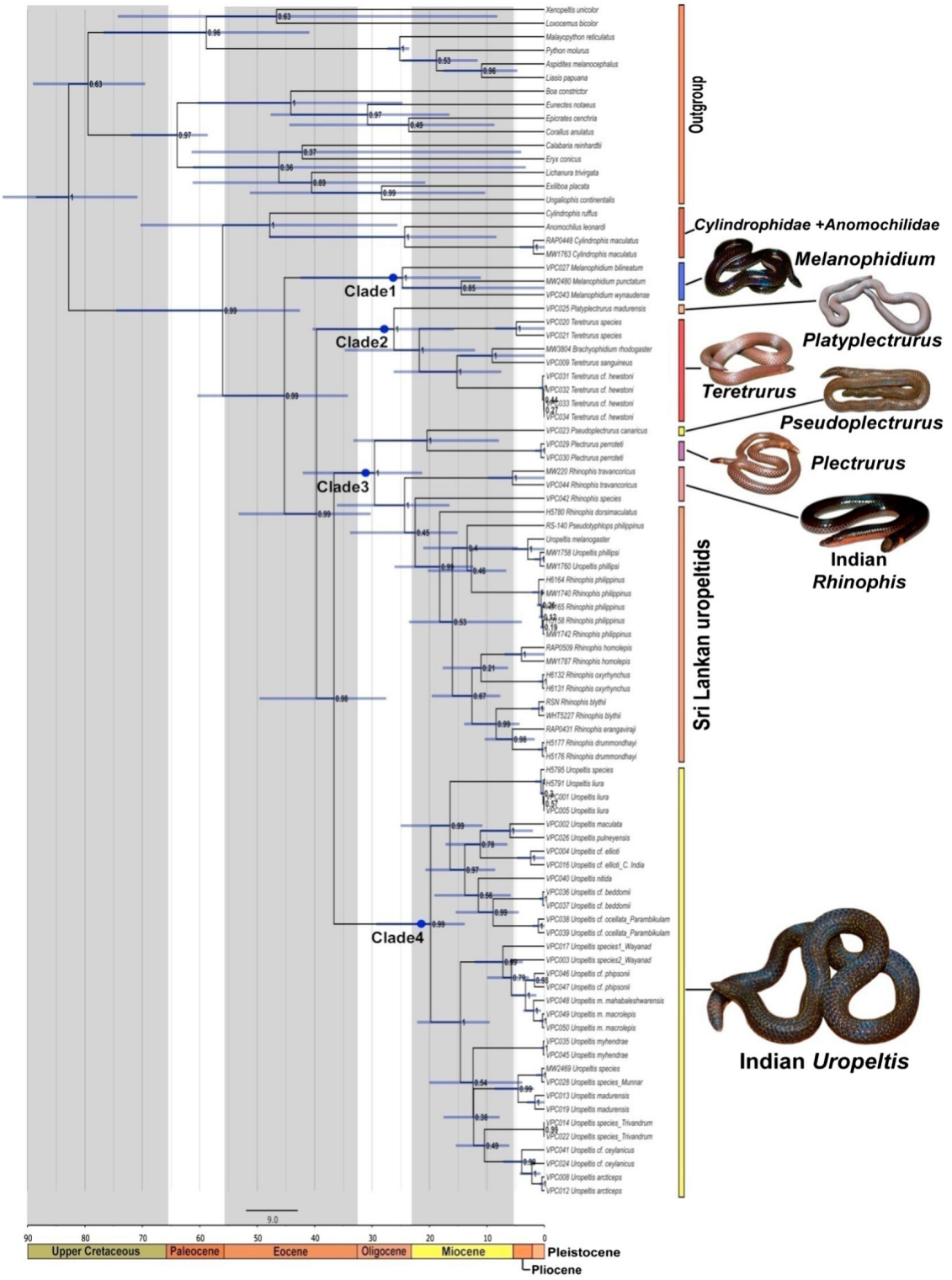


Figure 1-9 Cyriac and Kodandaramaiah (2017) ultrametric dated tree of Uropeltidae and outgroups, with divergence time estimates inferred in BEAST. Node support values indicate posterior probabilities and node bars indicate the 95% confidence intervals.

(Olori, 2010). Additionally, the biotic exchange between India and Sri Lanka, as well as the adaptation to a new environment with a greater ecological diversity of habitats which allows the snakes to occur in a higher diversity of habitats might have acted as promotors of diversification, but this is yet to be tested with a broader Sri Lankan taxon sampling.

Recently there has been an encouraging number of studies of herpetofauna lineages endemic to the Indian subcontinent biodiversity hotspot (Deepak and Karanth, 2018; Lajmi et al., 2018; Meegaskumbura et al., 2019). Understanding patterns of phenotypic and lineage diversification in uropeltids will allow to offer a comparative set of data for a speciose fossorial squamate clade to better understand how, where and when this diversity arose in the Western Ghats-Sri Lankan biodiversity hotspot, and perhaps offer some insights into evolutionary trends in fossoriality in squamate reptiles.

1.3 Thesis aims

Given uropeltids' fossorial habits and their phylogenetic position among extant snake lineages, the study of the morphology, ecology, phylogeny and evolution of this lineage has potentially important implications for understanding early snake evolution. For burrowing vertebrates occurring in a relatively small area, uropeltids are exceptionally speciose and surprisingly morphologically diverse, such that they prompt many questions in evolutionary biology. This thesis aims to understand uropeltid lineage and phenotypic diversity and diversification patterns and is based on an integrative approach. This includes generating an extensive and taxonomically comprehensive molecular dataset from traditional Sanger-sequencing and high throughput sequencing, as well as morphological data in the form of external metric and meristic characters. Molecular phylogenies, including sequence data from ethanol preserved natural history collections specimens, are used to infer the evolutionary relationships among these snakes, testing current generic classification and inferring for the first time relationships among several species. In addition, molecular species delimitation methods are used to provide a new perspective on the species-level diversity of Uropeltidae. Dating analyses with fossil calibrations are used to infer the timing of India to Sri Lanka biotic exchange events, and patterns

of lineage diversification. Finally, trait data are analysed using phylogenetic comparative methods to understand the major axes of morphological variation across uropeltids, and infer patterns of phenotypic diversification, including if the radiation is adaptive.

Chapter 2 – A near-complete molecular phylogeny of uropeltid snakes harnessing natural history collections as a DNA source

Abstract

Natural history collections are important biodiversity repositories, harbouring zoological specimens collected all over the world during the last 250 years. Recent advances in wet lab methods and sequencing technology allow the recovery of short, damaged DNA fragments, expected to occur in old specimens. Still, there is not yet a method available known to work without fail, which is made more difficult by the uncertain preservation history of most specimens in collections. Being able to retrieve DNA from type and historical material would offer a huge advantage for organisms not easily collected or with an unclear taxonomy. Uropeltid snakes are an ideal candidate to test these new methodologies. Uropeltidae is a clade of small fossorial snakes (approx. 56 species) endemic to the Western Ghats of India and Sri Lanka. Because of their burrowing habits, they are not easily encountered without effort, and the confusing taxonomic status of some of the species was established a century ago. Recent studies have focused on understanding the molecular phylogenetic relationships among this family of snakes using freshly collected genetic resources, but have been hindered by the lack of tissue samples available, with only ca. 41 species included in the latest study. In addition, the identity of sampled specimens is sometimes unclear because of ongoing taxonomic uncertainty. Here, ancient DNA protocols and high throughput sequencing were employed to generate mitochondrial sequence data from ethanol-preserved uropeltid specimens, including types of poorly known species. New shotgun sequence data from museum specimens were combined with a 'traditional' Sanger sequencing data matrix, to infer uropeltid phylogenetic relationships using Bayesian and Maximum Likelihood approaches. A total of 44 specimens were sampled, with HTS data successfully generated for 22 of 44 sampled historical specimens. Analyses corroborated the monophyly of all genera except in the case of the paraphyly of *Teretururus* with respect to *Brachyophidium*, which is in agreement with previous studies in that this part of uropeltid generic taxonomy might require

taxonomic revision. These new analyses allowed several species to be sampled in molecular phylogenetics for the very first time, thus helping also to resolve taxonomic uncertainty.

2.1 Introduction

Uropeltidae Müller, 1832 is a clade of small fossorial snakes endemic to peninsular India and Sri Lanka, a well-known biodiversity hotspot (Myers et al., 2000). There are eight genera and 56 species currently recognised in the family (Uetz and Hošek, 2019). This has generally been a poorly understudied squamate clade due to their fossorial and secretive habits and confusing taxonomic history, which was for the most part established in the late 1800s and early 1900s. In the last decade there has been a resurgence in taxonomic activity, with several new species being described – often based solely on external morphological characters – and other species resurrected from synonymy and/or moved to different genera (Gower et al., 2008, 2016; Wickramasinghe et al., 2009; Aengals and Ganesh, 2013; Pyron et al., 2016; Jins et al., 2018).

Attempts to analyse evolutionary relationships among uropeltids were initially based on few taxa and immunological data (Cadle et al., 1990) or cranial characters (Rieppel and Zaher, 2002), but more recent studies have built phylogenies for the family based on mitochondrial and nuclear sequence data (Pyron et al., 2016; Cyriac and Kodandaramaiah, 2017; Jins et al., 2018). Phylogenetic relationships among Uropeltidae require further examination because there are incongruences in the relationships among genera among the latest analyses (Cyriac and Kodandaramaiah, 2017; Jins et al., 2018). In addition, although all genera have been represented in the latest molecular phylogenetic studies, the monophyly of some genera (e.g. *Plectrurus*) has not yet been tested because several species have yet to be included in analyses. This might be due in part to the fact that fossorial squamates are not easily encountered and collected without special effort, resulting in relatively few fresh tissue samples available for molecular studies. Therefore, some species have rarely been collected and are known only from very few museum records with poor locality data, for which there are no tissue samples available. Thus, uropeltid snakes are an ideal candidate group to test the utility of recent

molecular approaches that aim to generate DNA sequence data from natural history collections' specimens. Most uropeltid specimens in European and North American natural history collections are old, of uncertain preservation history, and possibly formalin-fixed. From the early 1900s, fixing specimens in formalin became common practise for vertebrate fluid-preserved specimen preparation, before storing them in ethanol (Simmons, 2014). There are several challenges in sequencing ancient DNA or DNA from specimens from historical natural history collections (reviewed in Dabney, Meyer and Pääbo, 2013): i) DNA degraded into short fragments (Pääbo, 1989); ii) high occurrence of nucleotide substitutions from C to T at the 5' and G to A at the 3', with nucleotide misincorporations caused by cytosine deamination occurring more frequently in single stranded overhangs at the 5' of ancient DNA strands (Briggs et al., 2007; Brotherton et al., 2007); iii) cross-linkage between DNA strands or between DNA and other molecules, which does not allow the strands to be separated and thus preventing DNA polymerases moving along a strand (Pääbo, 1989). Additionally, samples fixed in formalin are also known to have DNA misincorporations in the form of C to T and G to A (Williams et al., 1999; Wong et al., 2014), and cross-linkage between DNA and proteins (Gilbert et al., 2007 and references therein). Due to these issues with DNA fragmentation and quality, traditional PCR based approaches aiming to amplify specific fragments of DNA are typically not appropriate to obtain sequence data from historical fluid-preserved specimens. Advances in high-throughput sequencing (HTS) technologies, including whole genome shotgun sequencing and sequence capture, have made it possible to use fragmented DNA to obtain large amounts of sequence data and even whole genomes from degraded DNA fragments. State of the art bioinformatic tools have been an important associated development to assemble reads de novo or by potentially aligning them to a reference genome. Recent studies using these HTS methods on herpetological fluid-preserved and in some cases formalin-fixed specimens have had varying levels of success (Hykin et al., 2015; Ruane and Austin, 2017; McGuire et al., 2018), so that yet there is not a one-fits-all methodology to obtain sequence data from this type of samples. Molecular data from type and historical museum specimens would be very useful to resolve outstanding issues in uropeltid taxonomy, especially through matching of extant populations of known

locality data with historical type specimens. Additionally, being able to generate DNA sequence data from historical museum specimens would greatly help to maximise taxon sampling to build near-complete phylogenies, and to understand phylogenetic relationships within the family Uropeltidae.

2.1.1 Aims

To generate a comprehensive phylogeny for the family Uropeltidae, combining 'traditional' Sanger sequencing data, as well as HTS data from fluid-preserved specimens.

2.1.2 Hypotheses

i) Whole genome shotgun sequencing is suitable to obtain large amounts of mitochondrial sequence data for DNA extracted from fluid-preserved museum specimens, ii) all eight currently recognised uropeltid genera are monophyletic, iii) Sri Lankan uropeltids are monophyletic, consistent with being the result of a single colonisation event from Indian ancestors.

2.2 Materials and methods

2.2.1 Sampling

A total of 252 samples of Uropeltidae, including representatives for all genera and the majority of currently recognised species, were used to infer phylogenetic relationships in this family of snakes. A number of tissues were made available by the supervisory team and colleagues to conduct molecular lab work for the present study. Additional sequence data were retrieved from GenBank and included in the phylogenetic analyses. Details on sample codes, species, locality, and GenBank accession numbers for all samples included in the analyses are listed in Appendix Table 2-1.

2.2.2 DNA extraction, amplification and sequencing of fresh tissue samples

Genomic DNA was extracted from absolute ethanol-preserved muscle or liver tissue samples using Qiagen's DNeasy Blood and Tissue kit (Qiagen, Valencia, CA). DNA was amplified using PCR for four mitochondrial (mtDNA) markers: 12S rRNA (*12s*),

16s rRNA (*16s*), NADH dehydrogenase subunit 4 (*nd4*) and cytochrome b (*cytb*), and two nuclear (nuDNA) loci: oocyte maturation factor (*cmos*) and prolactin receptor (*prlr*).

Mitochondrial genes are usually more variable than nuclear genes, providing data that typically offer greater resolution at shallower phylogenetic levels, and therefore are useful for their potential to resolve more recent divergences. The mtDNA markers *12s*, *16s*, *nd4* and *cytb* and nuDNA loci *cmos* have been used in previous phylogenetic studies of uropeltids (Bossuyt et al., 2004; Pyron et al., 2016; Cyriac and Kodandaramaiah, 2017; Jins et al., 2018) and, as such, sequences were available from NCBI that could be incorporated into the dataset from this study. *Cmos* is a relatively conserved marker that is typically useful to infer deeper phylogenetic divergences among extant reptiles (Saint et al., 1998). A preliminary analysis with this marker (data not shown) confirmed that it was relatively slow evolving and not very informative at the species level. An additional nuclear marker was thus selected that would be more variable than *cmos* – *prlr* has been shown to be variable and relatively rapidly evolving in other squamates (Townsend et al., 2008) and proved easy to amplify for uropeltids with the primers reported by that study. Detailed information on PCR protocols and DNA sequencing can be found in Appendix 2-1 and Appendix Table 2-2. Sequence chromatograms were checked by eye and edited using Geneious v8.1.9 (Kearse et al., 2012) (Biomatters). Heterozygous positions in nuclear sequences were scored with IUPAC ambiguity codes.

2.2.3 Archival DNA samples

2.2.3.1 Taxon sampling

Small pieces of body wall muscle tissue were sampled as minimally invasively as possible from 44 uropeltid museum specimens (Appendix Table 2-3). Specimens were chosen from a range of different collection dates (1801 to 1977), and also included type specimens with the aim that DNA sequence data for these would help resolve taxonomic issues impeding accurate and precise identification of vouchers sampled for fresh tissue. Because formalin was used to fix specimens for preservation only from the early 1900s, it is expected that specimens deposited in

the collection prior to that will not have been in contact with formalin, and the generally soft state of many of these specimens was considered to be consistent with that interpretation. None of the historical museum specimens sampled for tissue has associated preservation data, so it was unknown what type of alcohol they were stored in now or in the past. Tissue collection was performed in a lab space where no DNA extractions or amplifications had been previously carried out to reduce the likelihood of DNA contamination.

2.2.3.2 DNA extraction and library build

To avoid potential contamination from modern DNA (e.g. PCR products) that can be expected to be more prevalent in post-PCR molecular laboratories (Fulton, 2012), DNA extraction and library build for these samples were carried out in a dedicated ancient DNA lab in the Natural History Museum, London. All surfaces had been pre-sterilised with a diluted bleach solution, and dissecting materials were cleaned with bleach and kept under UV light prior to use. These steps were performed in batches of 11 samples plus one negative control in order to test for contaminants. See Appendix Table 2-3 for information on samples used, and Appendix 2-2 and Appendix 2-3 for detailed DNA extraction and library build protocols, respectively.

2.2.3.3 High throughput sequencing

A total of 48 double indexed libraries (44 samples and four negative controls) were quantified and pooled together at an equimolar concentration (Natural History Museum (NHM) Sequencing Facility). Multiplexed samples were subjected to shotgun sequencing using a mid-output kit for 75 base pairs (bp) paired-ends reads on an Illumina NextSeq500 platform (NHM).

2.2.3.4 Bioinformatics

Reads were trimmed for Illumina adapters with AdapterRemoval v.2.2.4 (Schubert et al., 2016). Given that DNA damage is typically more likely to occur at the ends of fragments, three base pairs were removed from the 3' and 5' ends of each read (commands: --trim5p 3 --trim3p 3). As an additional quality check, reads' ends were

trimmed for both Ns and low-quality bases (--trimns --trimqualities). Minimum read length was set to 25 (--minlength 25) and overlapping paired reads (of at least 11 nucleotides by default) were merged (--collapsed) with a mismatch rate of three (--mm 3). Quality of trimmed reads was assessed with FastQC (http://www.bioinformatics. babraham.ac.uk/projects/fastqc) (results not shown).

In the absence of complete mitochondrial genomes of closely related taxa to be used as references in a mapping approach, a two-step approach was employed. First, a de novo assembly was carried out to obtain new draft reference partial mitochondrial genomes for each sample, and second, the trimmed reads were mapped to the newly generated references. Multiple kmer sizes (17, 27, 37, 47, 57) were used in a de novo assembly using Velvet v.1.2.10 (Zerbino and Birney, 2008). Kmer length is an important choice for a successful assembly, though it has been noted that kmer size selection is not straightforward, and that analysing a set of different kmer lengths helps to achieve higher genome coverage (Bi et al., 2012). This approach has been previously employed in studies using ancient or museum specimen DNA for de novo genome assembly (Hykin et al., 2015; Seitz and Nieselt, 2017). The coverage cut-off value was initially set at 5, and if that was deemed too high (i.e., by having only a few contigs mapping against a reference), cut-offs of 3 and then of 1 were applied for selected samples. For each sample, contigs from all Velvet runs were imported into Geneious and using Map to Reference (in the Tools >Align/Assemble menu) contigs were mapped against a partial uropeltid mitochondrial genome (GenBank accession number: GC200594 – *Rhinophis* sp. nov. 2, which lacks the control regions). The Geneious mapper option was employed with a Medium-Low Sensitivity setting (except for sample FS85, for which Medium Sensitivity was applied, because with a lower sensitivity setting very few contigs would map to the reference sequence), with up to five iterations. Some assembled contigs showed mismatches in some positions (particularly toward the ends of contigs) due to incorporation of what were interpreted as deaminated bases. Consensus sequences were extracted and used as new references for each respective sample in a second step, mapping trimmed reads in Burrows Wheeler Aligner (BWA) aln (Li and Durbin, 2009). Default options were used except for no

seeding (-l1024), which has been suggested to work better for degraded DNA due to nucleotide mismatches from deamination that might occur in the seed region, forcing a global alignment of the reads to the reference sequence (Schubert et al., 2012; Rasmussen et al., 2015). Samtools v1.9 (Li et al., 2009) was used to remove unmapped reads, and to remove reads with mapping quality Phred scores of less than 30 (-q 30).

Picard MarkDuplicates v2.18.16 (http://broadinstitute.github.io/picard/) was used to remove PCR duplicates obtained during library builds. Mapping statistics on total reads, initial mapped reads, quality filtered reads (MAPQ30), and quality filtered reads with duplicates removed were calculated with Samtools (flagstat). DNA damage patterns were assessed by plotting nucleotide misincorporation in mapDamage 2.0 (Jónsson et al., 2013). Mean reads length and partial mitochondrial genome coverage were calculated with QualiMap v2.2.1 (Okonechnikov et al., 2015). Resulting BAM files were imported into Geneious, where consensus sequences for partial mitochondrial genomes for each sample were generated, and sequences (homologous with those generated by Sanger sequencing for fresh tissues) for up to four mitochondrial markers (*12s*, *16s*, *nd4* and *cytb*) were extracted. These data were then added to the data matrix of Sanger sequences for downstream phylogenetic analyses.

An attempt was made to retrieve nuclear sequences of interest (i.e. *cmos* and *prlr*) that might be expected to be present with lower coverage than mtDNA sequences. Trimmed reads were imported into Geneious and mapped to reference sequences (generated from Sanger sequencing and from GenBank), using the same settings and process as described above.

2.2.4 Sequence alignments, data partitions and model selection

Sequence data were aligned using ClustalW (Thompson et al., 1994) implemented in Geneious with default settings (gap open cost = 15; gap extended cost = 6.66). Ambiguously aligned positions in *12s* and *16s* alignments were removed using Gblocks v0.91b (Castresana, 2000) via an online server (http://phylogeny.fr, Dereeper et al. 2008) selecting the 'less stringent' options. tRNA regions were

removed from *nd4* sequences. Protein coding gene alignments (*cytb*, *nd4*, *cmos* and *prlr*) were checked for stop codons and reading frame shifts.

Preliminary analyses with individual gene trees did not find incongruences in topology between different markers (analyses not shown). Alignments were concatenated and assembled into two datasets: 1) Sanger sequencing data for uropeltids; 2) combined Sanger and NextSeq data. Dataset 1 included 230 samples and 3373bp [*12s*: (n=227, 372bp, 387bp before Gblocks); *16s*: (n=213, 463bp, 517bp before Gblocks); *nd4*: (n=207, 697bp); *cytb*: (n=126, 715bp); *cmos*: (n=181, 570bp); *prlr*: (n=178bp, 556bp)]. Dataset 2 included 252 samples with a total of 3379bp [(*12s*: n=249, 378bp, 388bp before Gblocks); *16s*: (n=235, 463bp, 522bp before Gblocks); *nd4*: (n=228, 697bp); *cytb*: (n=147, 715bp); *cmos*: (n=181, 570bp); *prlr*: (n=178, 556bp)]. Details of localities, GenBank accession numbers, and information on which dataset they were part of for all Uropeltidae samples included in the analyses are listed in Appendix Table 2-1.

Concatenated datasets were analysed with PartitionFinder v2.1.1 (Lanfear et al. 2016; Lanfear et al. 2012; Guindon et al. 2010), to find the best-fit partition schemes and models of nucleotide substitution for the phylogenetic analyses, applying the Bayesian information criterion (BIC) and implementing a greedy search algorithm. Data were partitioned by gene for *12s* and *16s*, and by gene and codon position for the protein coding genes, giving a total of 14 possible partitions. For datasets 1 and 2, the best-fit scheme consisted of a single partition under GTR+I+G.

2.2.5 Phylogenetic analyses

Phylogenetic relationships were inferred using Bayesian Inference (BI) and Maximum Likelihood (ML). BI analyses were performed in MrBayes v3.2 (Ronquist et al., 2012), conducting two independent runs for $5x10^7$ generations, sampling every 5,000 generations, resulting in 10,000 trees. Runs were checked visually using Tracer v1.7.1 (Rambaut et al., 2018) to verify convergence of the runs and that effective sample sizes (ESS) were all >200. The first 25% trees were discarded as burn-in and the remaining trees used to determine posterior probability values (BPP) for branch support.

ML analyses were conducted using Garli (Genetic Algorithm for Rapid Likelihood Inference) v2.0 (Bazinet et al., 2014) with best trees estimated from 10 independent ML runs with a stepwise-addition algorithm. Branch support was assessed by 1000 non-parametric bootstrapping replicates. Bootstrap support values (BP) were added to the best tree with DendoPy SumTrees v4.4.0 (Sukumaran and Holder, 2010b, 2010a).

Analyses were carried out using the online CIPRES Science Gateway v3.1 server (Miller et al., 2010) (http://www.phylo.org/sub_sections/portal/). Phylogenetic trees were visualised and edited in R v.3.6.0 (R Development Core Team, 2019) with packages ape v5.3 (Paradis and Schliep, 2019) and phytools v.0.6-99 (Revell, 2012). Trees were rooted with a monophyletic *Melanophidium*, based on findings from previous studies that this genus is sister to all other uropeltids (Bossuyt et al., 2004; Pyron et al., 2016; Cyriac and Kodandaramaiah, 2017).

2.3 Results

2.3.1 Shotgun sequencing archival DNA recovery

Of the 44 samples included in the shotgun sequencing, 22 yielded contigs from Velvet that successfully mapped to the reference uropeltid partial mitochondrial genome (GenBank accession: GC200594). Despite the fact that some historical samples had relatively high levels of DNA concentration as determined with Qubit (Appendix Table 2-3), not all of them worked in terms of producing data that allowed for a de novo Velvet assembly and map to reference in Geneious approach. Lack of success for these samples is perhaps explained by poor DNA preservation and/or presence of contaminants. Summary statistics for mapped reads are available in Appendix Table 2-4. For the 22 samples that worked, BWA mapping results after quality trimming and duplicate removal revealed mean coverage depths between 2.3x and 78.2x, with less than 1% of the original reads being mapped for all samples, telling of poor endogenous mitochondrial DNA preservation. Read lengths were relatively short, averaging between 36.8 and 52bp, characteristic of post-mortem DNA degradation into small fragments (Dabney et al. 2013). Although the age of the sampled specimens is not always clear from their accession numbers, all 22 successfully sequenced samples had accession dates from the 1800s, and

at least eight of those were from the late 1800s, before the introduction of formalin preservation became common practice in natural history collections. All specimens collected in the 1970s from the CAS and USNM collections failed, perhaps because of formalin preservation.

MapDamage analyses revealed patterns of deamination at the ends of the reads, typical signatures of post-mortem DNA damage (Schubert et al., 2012; Jónsson et al., 2013), with a relative increase of frequency of C to T misincorporations at the 5' ends and an increase of G to A transitions at the 3' ends of the reads. For reference, nucleotide misincorporation pattern plots for a couple of samples mapped in BWA after quality trimming and duplicates removal are available in Appendix Figure 2-1 and Appendix Figure 2-2. Sequences of up to four mitochondrial markers (*12s*, *16s*, *nd4* and *cytb*) were extracted for the 22 samples and used in subsequent phylogenetic analyses, allowing the addition of taxa with few or no representatives available in the Sanger sequence dataset. No nuclear sequence data for *cmos* or *prlr* were retrieved from the shotgun data.

2.3.2 Phylogenetic analyses

For each of the two phylogenetic datasets (datasets 1 and 2), ML and BI analyses yielded similar topologies that were congruent for all well supported clades. The only exceptions were the relationships among some Indian *Rhinophis* (discussed below). Results for the more taxonomic complete dataset 2 (Sanger and shotgun data), are described in this section, and shown in Figure 2-1 to 2-4 for BI trees and Appendix Figure 2-3 to 2-6 for ML analyses. Additional figures for dataset 1 (Sanger data) BI and ML trees are provided for reference and can be found in Appendix Figure 2-7 and Appendix Figure 2-8, respectively.

Analyses of the concatenated mt and nuDNA datasets recovered strong support for the monophyly of all genera with the exception of *Teretrurus*, which is paraphyletic with respect to the monotypic genus *Brachyophidium*. Within Uropeltidae four well-supported main clades were found: Clade A (*Melanophidium*), Clade B (*Platyplectrurus* and *Teretrurus*+*Brachyophidium*), Clade C (*Uropeltis*) and Clade D (*Pseudoplectrurus*, *Plectrurus* and *Rhinophis*). Within *Melanophidium* (Clade A; Figure 2-1), all four currently recognised species were included in the

analyses and all are resolved as monophyletic with the exception of *M. wynaudense*, which is paraphyletic with respect to *M. khairei*. Terminal branches within *Melanophidium* are typically long, indicating high levels of genetic diversity within currently recognised species, particularly for *M. punctatum* and *M. wynaudense* for which six samples of each were included in the analyses. Clade B (Figure 2-2), sister to clades C and D, comprised a clade with the two described *Platyplectrurus* species recovered as sister (BPP=1, BP=100) to a clade including at least four well-supported lineages of *Teretrurus*, and *Brachyophidium*. Clade C (Figure 2-3), sister to clade D, included approximately 20 out of the 24 currently recognised *Uropeltis* species, and an additional ten other lineages that likely represent named (i.e. known synonyms) or as yet undescribed species. The two clades separated by the basal split within clade C comprise species with notably different external tail morphologies – taxa in clade C1 have Pyron et al.'s (2016) tail types III and IV (or type I and III of Smith (1943)), and those in clade C2 have tail type V (or Smith's (1943) type II). Within clade D (Figure 2-4), the monotypic *Pseudoplectrurus* is recovered as sister lineage to a well-supported group (BPP=1, BP=100) comprising all three described *Plectrurus* species. *Pseudoplectrurus*+*Plectrurus* are sister to all (Indian and Sri Lankan) *Rhinophis,* with this genus receiving maximum support.

Some disagreement between the results of the ML and BI analyses was identified regarding the relationships among some of the Indian *Rhinophis*. All analyses recovered a monophyletic *R. travancoricus* and a clade comprising all other sampled Indian *Rhinophis* (cf. *sanguineus* (sp. nov. 4 (*sanguineus* + *microlepis*))) except *R. goweri* and the relationships within the latter group are consistent between analyses. BI analysis recovered the *R. sanguineus* clade as sister to a well-supported clade (BPP=1) comprising all other *Rhinophis*. Within the latter clade, the Indian *R. travancoricus* is recovered as sister lineage to a clade (BPP=0.65) comprising the Indian species *R. goweri* and all Sri Lankan *Rhinophis*. *Rhinophis goweri* was nested within the Sri Lankan clade, but with low support (BPP=0.79). In contrast, ML analyses recovered *R. travancoricus* as sister to a poorly supported lineage (BP=44) comprising all other *Rhinophis*. Within the latter, the *R. sanguineus* clade is recovered as sister to a well-supported group (BP=99)

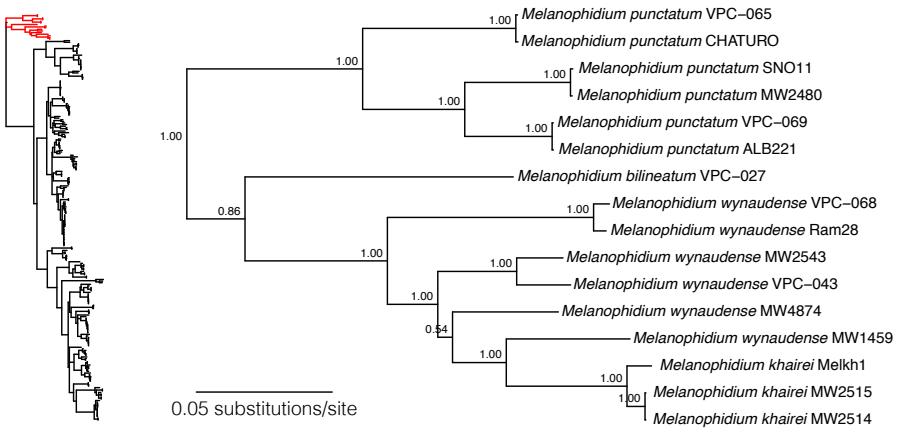


Figure 2-1 Subset BI phylogeny representing clade A. The whole tree is plotted on the left, with the position of clade A highlighted in red. Tree based on mt (*12s*, *16s*, *nd4* and *cytb*) and nucDNA markers (*cmos* and *prlr*) generated through Sanger and shotgun sequencing. Numbers at internal branches are Bayesian posterior probability (BPP) values (given to two decimal places).

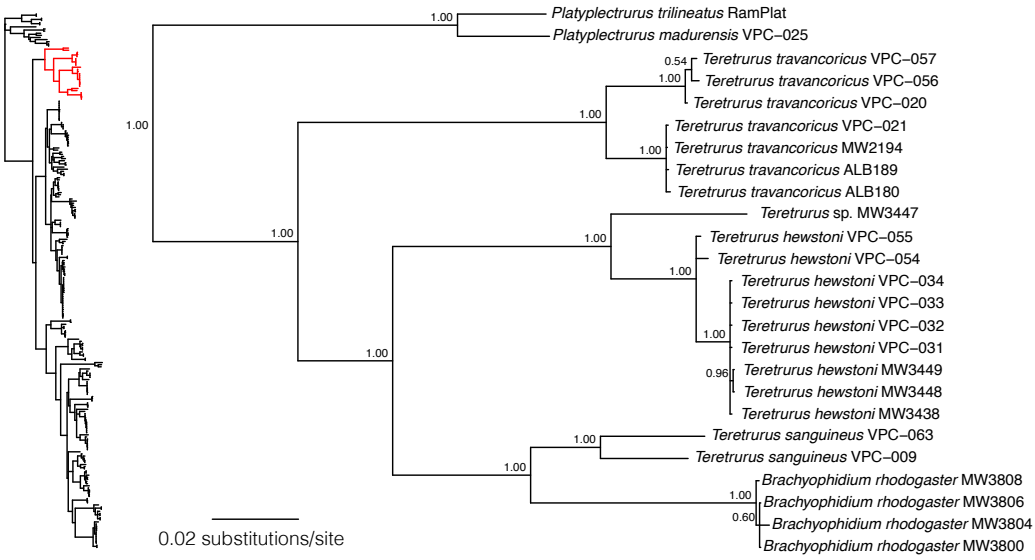


Figure 2-2 Subset BI phylogeny representing clade B. The whole tree is plotted on the left, with the position of clade B highlighted in red. Tree based on mt (*12s*, *16s*, *nd4* and *cytb*) and nucDNA markers (*cmos* and *prlr*) generated through Sanger and shotgun sequencing. Numbers at internal branches are Bayesian posterior probability (BPP) values (given to two decimal places).

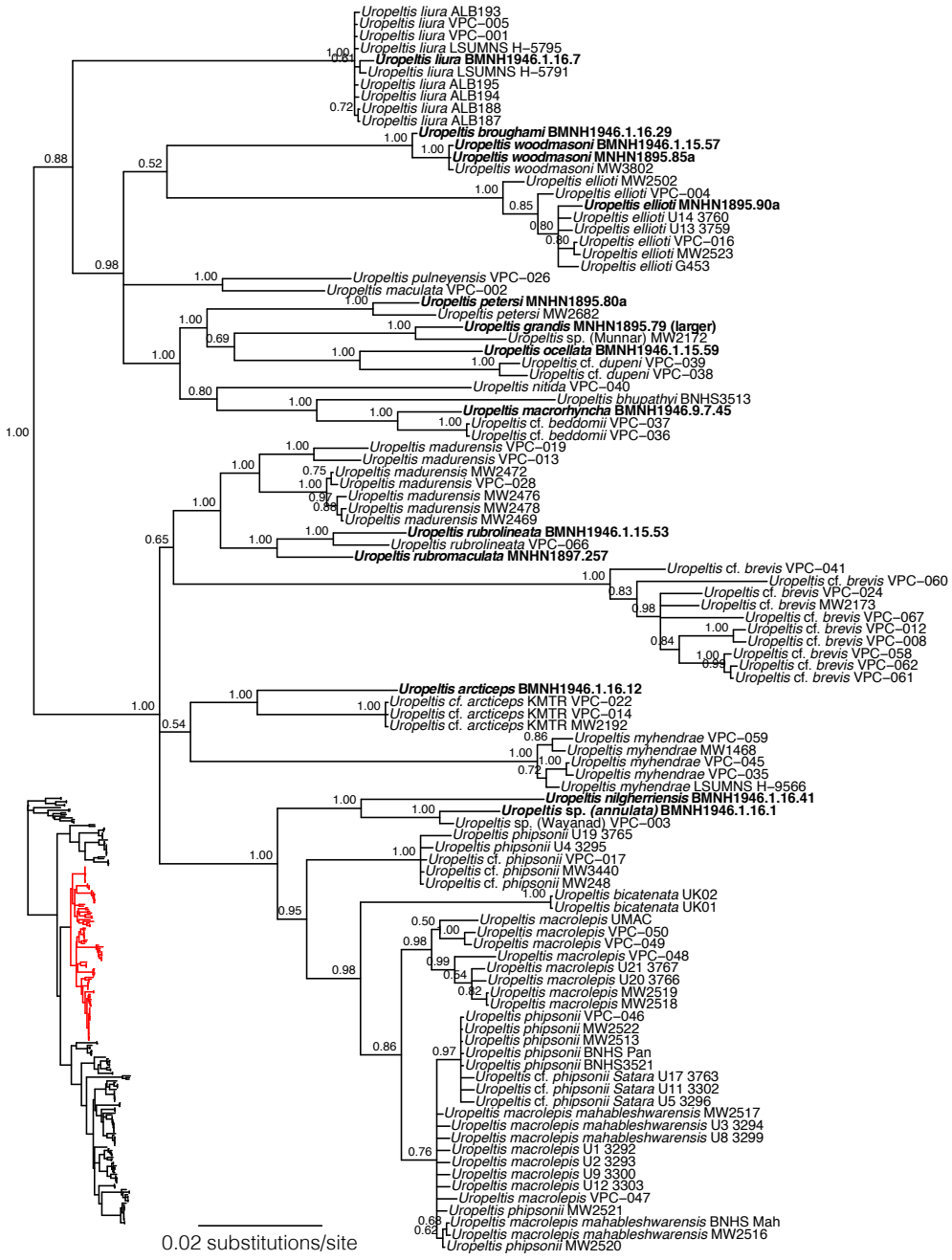


Figure 2-3 Subset BI phylogeny representing clade C. The whole tree is plotted on the left, with the position of clade C highlighted in red. Tree based on mt (*12s*, *16s*, *nd4* and *cytb*) and nucDNA markers (*cmos* and *prlr*) generated through Sanger and shotgun sequencing. Tips in bold indicate ethanol preserved samples obtained through shotgun sequencing. Numbers at internal branches are Bayesian posterior probability (BPP) values (given to two decimal places).

Figure 2-4 Subset BI phylogeny representing clade D. The whole tree is plotted on the left, with the position of clade D highlighted in red. Tree based on mt (*12s*, *16s*, *nd4* and *cytb*) and nucDNA markers (*cmos* and *prlr*) generated through Sanger and shotgun sequencing. Tips in bold indicate ethanol preserved samples obtained through shotgun sequencing. Numbers at internal branches are Bayesian posterior probability (BPP) values. Indian lineages coloured in black and Sri Lankan in grey.

including *R. goweri* and Sri Lankan *Rhinophis*. The Indian *R. goweri* is sister to the Sri Lankan clade but the monophyly of the latter receives low support (BP=24). Despite the inconsistent position of the Indian *R. goweri* between ML and BI analyses, there seems to be no compelling support for the placement of that species within the Sri Lankan radiation.

2.3.3 Phylogenetic placement of archival samples

Inclusion of archival samples showed that the holotype of *U. liura* (BMNH1946.1.16.7) clustered with all other samples identified as the same species. The holotype of *U. macrorhyncha* (BMNH1946.9.7.45) nested within the clade including *U. nitida*, *U. bhupathyi* and *U.* cf. *beddomii*, with strong support (BPP=1, BP=95) for being sister to *U.* cf. *beddomii*. There was maximum support for the holotype of *U. broughami* (BMNH1946.1.16.29) being the closest sampled relative of the sympatric *U. woodmasoni*. *Uropeltis woodmasoni* specimens BMNH1946.1.15.57 (type of *Silybura melanogaster*) and MNHN1895.85a (type of *Silybura nigra*) were recovered in a maximally supported lineage otherwise comprising a freshly sampled voucher of *U. woodmasoni*, which is consistent with the hypothesis that *S. nigra* and *S. melanogaster* are conspecific with (and synonyms of) *U. woodmasoni* (e.g. Smith 1943). A syntype of *U. petersi* MNHN1895.80a clustered with the recently collected (approximately 15–20 years ago) sample MW2682, identified as *U. petersi*. This finding contradicts Pyron et al.'s (2016) claim that this species has not been collected since its description in the late 1800s.

A syntype of *U. grandis* (MNHN1895.79, from the Annamalai Hills) was found to be sister to a sample (*Uropeltis* sp. Munnar MW2172) from Munnar that could not be identified at species level because the voucher was unavailable for examination. *Uropeltis ocellata* BMNH1946.1.15.59 (lectotype) was found in a maximally supported clade with two samples whose vouchers were identified as U. cf. *dupeni*. *Uropeltis dupeni* is currently considered a synonym of *U. ocellata*; however, the examination of the relevant types showed a substantial difference in the number of ventral scales and body shape, suggesting that these are likely not conspecific (D. Gower, pers. comm.). Specimen MNHN1895.90a is a syntype of *U.*

beddomii, but this sample was nested within the clade including all *U. ellioti* samples. Subsequent re-examination of the external morphology of specimen MNHN1895.90a suggests that it is likely *U. ellioti* and that it differs from the other *U. beddomii* types. Jins et al. (2018) suggested that MNHN1895.90a might have been mistakenly claimed to be a type of *U. beddomii.* One of the syntypes of *U. arcticeps* (BMNH1946.1.16.12), occurred as sister to samples identified as *U*. cf. *arcticeps* in a well supported lineage. The lectotype of *U. rubrolineata* (BMNH1946.1.15.53) was recovered with maximum support as sister to a fresh sample from a voucher identified as *U. rubrolineata*, and these samples were found to be most closely to *U. rubromaculata*, represented only by archival sample MNHN1897.257. *Uropeltis nilgherriensis* (holotype: BMNH1946.1.16.41), currently considered a synonym of *U. ceylanica* (e.g. Pyron et al. 2016), was recovered as sister to a lineage containing a sample that could not be immediately assigned to a species (*Uropeltis* sp. Wayanad VPC-003), and *Uropeltis* sp. (*annulata*) (BMNH 1946.1.16.1); the latter is the holotype of *Silybura nilgherriensis* var. *annulata*, also currently considered a synonym of *U. ceylanica* (McDiarmid et al., 1999).

In the monotypic genus *Pseudoplectrurus*, the *P. canaricus* sample MNHN1895.102 grouped as expected with the other available *P. canaricus* sample sequenced from fresh tissue. Within *Plectrurus*, there were only fresh tissue samples available for one of the species (*P. perrotetii*). ML analyses including DNA recovered from other *Plectrurus* species from archival specimens placed *P. guentheri* as sister to a poorly supported (BP=45) lineage including *P. aureus* and *P. perrotetii*, whereas BI analysis recovered a basal polytomy among the three congeners. Relationships within this genus are clearly yet to be resolved.

Among *Rhinophis*, HTS data for the archival type specimen for *R. philippinus* MNHN0.6994 further clarified the taxonomic confusion between *R. philippinus* and *Rhinophis* sp. nov. 2 (description in progress), with both analyses highlighting the genetic distinctiveness of the two sister lineages. The previously published sequence data for *Rhinophis* sp. nov. 2 had been erroneously reported as the superficially similar *R. philippinus*. The holotype of *R. saffragamus* (MNHN0.5621) was recovered in the same lineage with the two other available *R. saffragamus* samples sequenced from fresh tissue. *Rhinophis oxyrhynchus* ZMB3826 was

recovered as one of five major *R. oxyrhynchus* lineages, though its closest relative among the other samples for this taxon is not clearly resolved.

2.4 Discussion

Recent studies on the molecular phylogenetics of the family Uropeltidae have made some progress in unveiling the relationships of these often enigmatic fossorial squamates. Nevertheless, in a group of organisms with a historically confusing taxonomy and with relatively few tissue samples available to conduct wet lab work, novel molecular methods that make use of natural history collections' fluid-preserved specimens have proven successful in generating novel mitochondrial sequence data. These were added to existing and new Sanger multilocus datasets. Taxon and gene sampling were thus much greater than for previous studies, making substantial progress towards building a near-complete molecular phylogeny to understand the evolutionary relationships among and within genera, and offer some insights into species diversity and taxonomy.

2.4.1 Molecular phylogenetics of Uropeltidae and taxonomic implications

Previous works on Uropeltidae molecular phylogenetics had sampled all genera of the family but had not included many of the currently recognised species. The present study represents the most extensive molecular and taxonomic sampling of uropeltids across both India and Sri Lanka. This more complete taxonomic sampling of uropeltids has provided the basis for greater confidence in the inferred relationships of many taxa, and also provided novel insights into lineage diversity within the family.

To accomplish these achievements, this study successfully employed ancient DNA wet lab methods and whole genome shotgun sequencing to obtain DNA data for fluid-preserved historical specimens. Mitochondrial fragments from the regions of interest were recovered for 22 out of the 40 samples included in the shotgun sequencing. (See next section for further discussion on the assembly of mitogenomes). This allowed several extant populations (of sometimes uncertain identity) to be linked with type specimens. Examples of this are the clustering of the types of *U. liura*, *U. ellioti*, *U. petersi*, *P. canaricus*, *R. oxyrhynchus* and *R.*

saffragamus with more recently collected specimens identified as conspecific, providing confidence that the shotgun sequence data represent non-contaminated endogenous DNA, as well as confidence that the recently collected vouchers had been correctly identified. Perhaps more importantly, this methodology has generated molecular phylogenetic data for species for which no fresh tissue samples were available. This is the first time that *U. macrorhyncha*, *U. rubrolineata*, *P. guentheri* and *P. aureus*, among others, have been included in molecular phylogenetic analyses.

The relationships among genera found here are congruent with those inferred by Cyriac and Kodandaramaiah (2017) including that *Rhinophis* is more closely related to *Uropeltis* than to *Brachyophidium*, whereas other studies with smaller sample sizes instead found *Rhinophis* to be more closely related to *Brachyophidium* (Bossuyt et al., 2004; Pyron et al., 2016; Jins et al., 2018). Employing larger sample sizes, a broader taxon sampling and greater character sampling appears to have stabilised inferred relationships among major uropeltid lineages, and thus stabilised the genus-level taxonomy and classification. The inclusion of additional taxa in the analyses provided evidence for the first molecular test of the monophyly of *Platyplectrurus* and *Plectrurus*.

As in Cyriac and Kodandaramaiah (2017), *B. rhodogaster* is nested within a paraphyletic *Teretrurus*. This supports the synonymising of *Brachyophidium* Wall, 1921 with *Teretrurus* Beddome, 1886 (as proposed previously (Smith, 1943; Cadle et al., 1990; Rieppel and Zaher, 2002)), to remove the paraphyly of *Teretrurus*. In terms of major external features, the two genera differ only in that *Brachyophidium* lacks separate supraoculars. Additionally, the analyses here found additional support (from extended taxon and character sampling) for Cyriac and Kodandaramaiah's (2017) finding that *Teretrurus* comprises multiple, relatively deeply divergent lineages, some of which represent specimens that morphologically closely resemble the types of *T. hewstoni* and *T. travancoricus* – taxa that have long been considered synonyms of *T. sanguineus* (McDiarmid et al., 1999). Thus, the species-level taxonomy of *Teretrurus* requires revision, likely including the resurrection of some existing names.

Until recently the Sri Lankan *R. phillipsi* and *R. melanogaster* were classified within *Uropeltis* (e.g. Smith 1943, McDiarmid et al. 1999) but molecular phylogenetic results of analyses by Cadle et al. (1990), Bossuyt et al. (2004) and Pyron et al. (2013), and morphological features such as the separation of the nasal shields by the rostral prompted Pyron et al. (2016) to transfer these two species to *Rhinophis*. Even though Cyriac and Kodandaramaiah (2017) did not follow Pyron et al.'s (2016) classification, both that study and the present analyses provide additional support for Pyron et al.'s (2016) change in generic classification, with both species being nested within other *Rhinophis* species. Additionally, Pyron et al. (2016) synonymised the Sri Lankan *Pseudotyphlops* (previously considered a monotypic genus: *P. philippinus*) with *Rhinophis* in order to ensure monophyly of the latter, which is further supported here (and by Cyriac and Kodandaramaiah (2017)). Although previous studies (Pyron et al., 2016; Cyriac and Kodandaramaiah, 2017) could not precisely resolve the relationships of this lowland species (now under the name *R. saffragamus*), this study found it to be sister-taxon of a clade comprised by montane Sri Lankan species – *R. lineatus*, *R. zigzag*, *R. blythii*, *R. erangaviraji* and *R. drummondhayi* – though with low support values.

The molecular systematics results of this study also discovered higher amounts of lineage diversity than expected for several groups, indicating a potentially substantially higher number of valid species than currently recognised. This is exemplified by *Melanophidium* (recently reviewed by Gower et al. (2016)), for which all four currently described species were sampled (a first for molecular phylogenetic studies of Uropeltidae). For both *M. wynaudense* and *M. punctatum* multiple highly divergent lineages were discovered, suggesting cryptic species diversity. This ought to be further tested with species delimitation methods.

2.4.2 Museum specimen preservation and HTS success

Formaldehyde started being commercially produced in 1889 in Germany. At first used as an antiseptic, a physician (F. Blum) found its fixative properties in 1893, though apparently around the same time other workers arrived at similar findings. Subsequently, formalin was used in botanical, insect, fishes and reptiles' collections, among others. It is difficult to learn exact dates of when major museum

collections started using formaldehyde, but there are some mentions of formalin use in natural history collections in the literature. As early as 1908, Holt and Byrne (1908) referenced comments made by Koehler in 1896 on the use of formalin in fish collections. By then, formaldehyde was being used in collections in the fixation step before being preserved in alcohol, whereas before then specimens were typically preserved in alcohol without fixatives. As early as 1662, there are records of alcohol being used for specimen preservation. When travelling from fieldwork sites, specimens were often stored in spirits such as brandy or rum. Due to high costs and/or low availability of alcohol, specimens were often preserved in diluted concentrations, preserved in other substances such as vinegar, or oils, and used alcohol with additives such as alum or mercury. Additives were used to make alcohol a better preservative, especially when it had to be diluted. Industrial methylated spirits (IMS) went into production in 1855, which is cheaper than alcohol, and which is nowadays still used in some major collections (e.g. NHM, London). For an extensive review see Simmons (2014) and references therein.

A masters thesis (Carter, 2003) studying the impact of preservation methods on DNA quality touched on some of these points. The author found that in invertebrate fluid-preserved specimens i) DNA from IMS preserved specimen had poorer quality than for ethanol preserved specimens; ii) the dilution of ethanol in water was found to degrade DNA; iii) some additives in ethanol did not cause additional DNA degradation; iv) formaldehyde degraded DNA considerably, though it might still be possible to extract DNA.

The preservation history for the specimens used in this study has not been recorded, therefore the accession age acts as a guide to whether the specimen would have been exposed to formalin (with possible exposure to IMS as well as or instead of ethanol being much more difficult to infer). The oldest specimen for which DNA sequence data were successfully obtained from historical museum specimens in this study was accessioned in 1801 and the latest one from 1897. Before the 1900s formaldehyde was not commonly used in collections (Simmons, 2014). Note that not all specimens accessioned between those dates worked, so that other factors might be at play. All historical specimens from later than that date failed, so

that the lab methods employed in this study do not seem to be suitable for formalin preserved specimens.

Previous studies employing HTS methods for obtaining DNA data from herpetological fluid-preserved specimens as old as 145 years old or as young as 30 have had varying degrees of success (Hykin et al., 2015; Ruane and Austin, 2017; McGuire et al., 2018). As those authors have mentioned, one would expect it to be easier to successfully extract good quality DNA from specimens preserved in ethanol, rather than those fixed in formaldehyde before being preserved in ethanol, which is known to degrade DNA. Still, DNA could not be extracted/sequenced from all pre-1900 samples included in this study or in other studies that have generated endogenous DNA sequence data from historical specimens (Ruane and Austin, 2017; McGuire et al., 2018). Given the typical lack of preservation history records, there might not be a one-fits-all successful DNA extraction method. Still, there might be extraction methods more effective for specimens that have likely been fixed in formaldehyde due to their accession age (Campos and Gilbert, 2012; Hykin et al., 2015; Ruane and Austin, 2017).

2.4.3 Mitogenome assembly from HTS data for snakes

A feature of alethinophian snakes' mitochondrial genomes is the duplicate control regions (CRs). These occur in the 5' end of *12s*, and a duplicated region is located between the NADH dehydrogenase subunit 1 (*nd1*) and subunit 2 (*nd2*) (Kumazawa et al., 1996; Dong and Kumazawa, 2005; Jiang et al., 2007). CRs are often almost identical copies, but there are snake lineages where the two CRs have different sizes, and snake mitochondrial genomes can further vary by having other arrangements including fragment insertions (Jiang et al., 2007; Yan et al., 2008; Qian et al., 2018). It has also been noted that the two CRs might be very similar within species, but are highly variable between species (Dong and Kumazawa, 2005). In the largest study on snake mitochondrial evolution up to date, Qian et al. (2018) found 11 different types of mt gene arrangements in snakes from 14 families. Though that study did not include uropeltids, these would have nested in a clade otherwise characterised by the most common type of mitochondrial organisation, with a duplicated CR and translocated $tRNA^{LEU}$ (Qian et al., 2018). Douglas and

Gower (2010) obtained a near-complete mt genome for a sample of *Rhinophis* sp. nov. 2 (reported as *R. philippinus* in that paper) and confirmed it to have a duplicate CR (though those regions were not sequenced) and a translocated $tRNA^{LEU}$.

Duplicate CRs are the likely reason why it was not possible to obtain complete mitochondrial data from de novo assembly of short read shotgun sequence data, as duplicated sequences would be difficult to place in their correct position in the mt genome. Afterwards, when scaffolding Velvet contigs using a reference sequence in Geneious, it was still not possible to correctly place contigs to create a complete circular sequence. Even though results from using only *Rhinophis* sp. nov. 2 as a reference were described, the mapping did not work either when using complete mitochondrial sequences available for the proximate uropeltid outgroups *Cylindrophis ruffus* (Genbank assession number: NC_007401) and *Python bivittatus* (NC_021479), as sequences in the CR were too divergent. Further examination of one of the samples (FS25) with good coverage overall, found incompletely assembled CR sequences, with the 5' end region of the CRs missing (analyses not shown).

Because obtaining complete mt genomic sequences could not be accomplished in a straightforward approach without references for the CRs, only the mtDNA fragments obtained through Sanger sequencing were extracted from the partial genomes, which was adequate to achieve this study's aims. Future work could focus on assembling complete mitogenomes from the same raw HTS data, as these might be of relevance if uropeltid species were to be included in further studies on the evolution of snake mitochondrial genomes and/or if more uropeltid mitogenomes were sequenced from fresh tissue samples.

2.4.4 Shieldtail dispersal between India and Sri Lanka

It was first Cadle et al.'s (1990) study based on allozymes and albumin immunology that found evidence for Indian uropeltids to be paraphyletic, inferring *R. travancoricus*, a low to mid-elevation species endemic to the southern Western Ghats of India (Rajendran, 1985), sister to a clade comprising all sampled Sri Lankan uropeltids. Based on these findings, Cadle et al. (1990) suggested an Indian origin for shieldtails, and proposed a single colonisation event from lowland India to Sri

Lanka, with diversification occurring in the island and species adapting from lowlands to montane habitats.

There are four Indian *Rhinophis* species currently recognised – *R. travancoricus, R. sanguineus, R. fergusonianus* and *R. goweri*. The present study has incorporated molecular phylogenetic data for all, except for *R. fergusonianus*, which is known from only one specimen (BMNH1946.1.16.77) (McDiarmid et al., 1999) for which the HTS DNA library build was not successful. Additionally, data for *Rhinophis* sp. nov. 4, *R*. cf. *sanguineus* and *R. microlepis* (typically considered a synonym of *R. sanguineus* (McDiarmid et al., 1999)) were included. Whereas previous molecular phylogenetic studies have included samples of only *R. travancoricus* and *R. sanguineus*, and have found the same pattern of paraphyletic Indian *Rhinophis* lineages as successive sister taxa to the monophyletic Sri Lankan uropeltids (Cadle et al., 1990; Bossuyt et al., 2004; Pyron et al., 2016; Cyriac and Kodandaramaiah, 2017; Jins et al., 2018), the greater taxonomic sampling in this study has provided a somewhat less clear picture, with the single *R. goweri* sample being found either with low support outside the Sri Lankan clade in ML trees, or found nested with low support within a Sri Lankan clade in BI analyses.

Rhinophis goweri is endemic to low to mid elevations tropical dry evergreen forest area in the Eastern Ghats in Southern India (Aengals and Ganesh, 2013), which is a drier locality than where other Indian *Rhinophis* inhabit (D. Gower, pers. comm.). Despite the inconsistent and poorly supported position of the Indian *R. goweri*, there seems to be no compelling support for the placement of that species within the Sri Lankan radiation, and thus no compelling rejection of Cadle et al.'s (1990) hypothesis of a single dispersal of lowland, dry adapted taxa from India to Sri Lanka. Alternatively, if *R. goweri* is in fact nested within a Sri Lankan lineage, this would be indicative of a 'back-dispersal' of a single lowland lineage back to South India. This 'back to India' pattern is observed in several other vertebrate and invertebrate lineages, such as freshwater fishes, frogs and freshwater crabs (Bossuyt et al., 2004; Meegaskumbura et al., 2019).

The lack of clarity on the monophyly of Sri Lankan *Rhinophis* due to the inconclusively resolved relationships of *R. goweri* is likely a result of obtaining sequence data only for *12s* and *16s* markers for a single specimen. Future studies

including more genetic data for this species might be able to elucidate the phylogenetic placement of this species more precisely and allow firmer conclusions to be drawn regarding the biogeographic history of the genus in South India and Sri Lanka.

2.5 Conclusions

This study was successful in generating HTS data from fluid preserved specimens, by utilising ancient DNA lab methods. The protocols employed here proved useful for samples accessioned in collections before 1897, but failing for specimens accessioned more recently that are more likely to have been exposed to formalin. Future studies could attempt to apply lab protocols appropriate for formalin preserved samples to try and generate sequence data from samples accessioned in collections after the early 1900s. Additionally, even though it was not one of the aims of this study, due to the relatively high number of mitochondrial fragments recovered in the shotgun sequencing, it might be possible to assemble complete mitochondrial genomes from the data generated. For that, complete reference sequences of Uropeltidae species are necessary and will enable uropeltids to be included in future studies focusing on the evolution of snake mitogenomes.

The findings of this study provide the most complete understanding of shieldtail phylogenetic relationships to date by including all but six of the 56 currently recognised species (species missing: *R. fergusonianus*, *R. porrectus*, *R. punctatus*, *U. ceylanica*, *U. dindigalensis*, *U. shortii*), plus yet undescribed species and synonyms that likely require resurrection. The monophyly of all genera has been corroborated, with the exception of *Tereturus* (paraphyletic with respect to *Brachyophidium*), providing a clear basis for taxonomic revisionary work. This multilocus dataset will be employed in lineage divergence dating and diversification analyses, for which a sound taxonomy is necessary.

Chapter 3 – Lineage diversification in a species-rich clade of fossorial squamates (Serpentes: Uropeltidae)

Abstract

Understanding diversification patterns can elucidate the processes shaping evolutionary radiations. Densely sampled phylogenies are fundamental for addressing questions on the tempo and mode of diversification in radiations. Lineage diversification patterns were tested for uropeltids, a species rich radiation of fossorial snakes endemic to the Western Ghats of India and Sri Lanka. Based on a taxonomically near-comprehensive molecular dataset, species delimitation methods were employed to delimit OTUs to be included in subsequent analyses. A multilocus, fossil calibrated time-tree was built and used as input in lineage diversification analyses. Results recovered a much higher number of putative species than currently recognised (111 vs. 56). Uropeltidae display constant rates of net diversification through time, and there was no evidence found of an early rapid burst of diversification for the clade that dispersed to and radiated within Sri Lanka, which would be the typical pattern expected for adaptive radiations. Shifts in net diversification rate seem to be uncommon in speciose tropical continental radiations, which often lack evidence of adaptive radiations. No evidence for uropeltid adaptive radiation on the island (Sri Lanka) might be explained by biogeographic factors, but more studies in the region with other endemics are necessary to understand overall patterns of organismal diversification in the Western Ghats and Sri Lanka. Although reasons for the low diversification rate and constant lineage accumulation in uropeltids are not entirely understood, here it is proposed that it might be typical of organisms adapted to fossoriality.

3.1 Introduction

Identifying patterns and understanding processes shaping evolutionary radiations has long been a main aim in evolutionary biology (Simpson, 1953; Ricklefs, 2007). Diversification rate estimates (difference between speciation and extinction rates) are an important parameter in macroevolution studies, and can be used to

understand aspects of evolutionary radiations (Morlon, 2014). For instance, adaptive radiations are usually identified by displaying a pattern of early burst with rapid diversification followed by a slowdown in rates over time as niches become filled (Phillimore and Price, 2008; Rabosky and Lovette, 2008). The most well-studied examples of evolutionary radiations are adaptive and often occur in islands or island-like systems such as isolated lakes – for example, Darwin's finches in the Galápagos (Grant and Grant, 2008), Caribbean *Anolis* lizards (Losos et al., 1998) and cichlid fishes (Seehausen, 2006). However, not all radiations are adaptive (reviewed in Rundell and Price, 2009; Simões et al., 2016) – for example, North American woodland salamanders (Kozak et al., 2006). Investigating the tempo and mode of species diversification aids in detecting patterns and can uncover evolutionary processes that generate evolutionary radiations over large time scales and geographical areas (Slater et al., 2010; Derryberry et al., 2011). Obtaining diversification rates for a variety of organisms may allow a better understanding of the influence that the age of the clade (young vs. old), geographical area (continental vs. island), and behavioural habits (fossorial vs. ground dwelling, for instance) may have in shaping radiations.

Complete (or near-complete) phylogenetic reconstructions with reliable estimates of species divergence times provide a framework for inferring the tempo and mode of lineage diversification (Ricklefs, 2007). Greater completeness of taxon sampling of extant species in phylogenies increases accuracy of estimates of diversification rates (Heath et al., 2008), with less complete species sampling likely to generate patterns that are consistent with declines in lineage diversification rates through time (Rabosky and Lovette, 2008 and references therein). Clades of non-model organisms typically have incompletely resolved taxonomies, which complicates assessments of the degree of completeness of taxon sampling in diversification rate studies. In such cases, molecular species delimitation methods have been deemed appropriate for the identification of independent evolutionary lineages to understand evolutionary processes to be employed in downstream phylogenetic analyses (Carstens et al., 2013). In understudied organismal groups for which assigning samples to species is not clear, studies have used a combination of single-locus species discovery analyses and multilocus coalescent

validation methods to assign candidate species or operational taxonomic units (OTUs) (Carstens et al., 2013 and references therein). Consistency between different methods often gives more confidence in defining putative species (e.g. Amador et al., 2018). When employing these methodologies there are limitations associated with the characteristics of the data analysed, such as sampling coverage, number of samples per species, effective population size, or species divergence times (Zhang et al., 2011; Talavera et al., 2013; Ahrens et al., 2016; Luo et al., 2018). Additionally, there are other caveats associated with the methods like the inability to distinguish between population and species level structure which might lead to inaccurate delimitation, overestimating species numbers (Sukumaran and Knowles 2017). Due to these issues, these methods may serve as a first approach to understand unrecognised species diversity and to test for the possible occurrence of cryptic species (Zhang et al., 2011), and come up with putative species for future taxonomic assessments (Carstens et al., 2013). Still, while molecular species delimitation methodologies help generate hypothesis of candidate species, these ought to be further tested in an integrative taxonomy framework (Dayrat, 2005; Padial et al., 2010) with morphological, spatial, and ecological data.

Uropeltid snakes are a useful system to study diversification patterns and test hypotheses of evolutionary radiations in both continental and island settings. Uropeltidae is a species rich family of fossorial snakes endemic to the Western Ghats of India and Sri Lanka, with 56 species currently recognised (Uetz and Hošek, 2019) (40 endemic to India and 16 in Sri Lanka). Cyriac and Kodandaramaiah's (2017) study of the molecular phylogenetics and diversification patterns of uropeltids found the split between Uropeltidae and its sister group *Cylindrophis* + *Anomochilus*, presently distributed in Southeast Asia and Sri Lanka, to have occurred at the Paleocene-Eocene boundary (ca. 56 million years ago (Ma)). At this time, mainland India and Asia are considered to have been in contact, potentially allowing organismal exchange between these two areas (Ali and Aitchison 2008). Thus, Cyriac and Kodandaramaiah (2017) hypothesised a continental Asia origin for Uropeltoidea (Uropeltidae + (Cylindrophidae + Anomochilidae)), followed by a split where Uropeltidae diversified in India and Cylindrophidae + Anomochilidae in

Southeast Asia. Cyriac and Kodandaramaiah (2017) also estimated that the split between the Indian uropeltids and the nested SL radiation occurred ca. 22 Ma. Based on this dated phylogeny in combination with diversification analyses, the authors suggested that surface Cenozoic climatic fluctuations had a role in shaping the temporal patterns of diversification in the fossorial uropeltids. While this study made advances in understanding diversification dynamics in uropeltids, it was based on relatively limited sampling. Cyriac and Kodandaramaiah (2017) included ca. 40 species, of which 10 were species endemic to Sri Lanka. A more complete molecular phylogeny for Uropeltidae was built in Chapter 2. This phylogeny displayed seemingly high levels of molecular diversity within some currently recognised species (e.g. *Melanophodium wynaudense*, *M. punctatum*, *Rhinophis travancoricus*, *R. oxyrhynchus*, *Uropeltis ellioti*), indicating that the true species diversity of the family is perhaps currently underestimated. Although uropeltid taxonomy is understood to be fairly stable at the generic level, at the species level it has been more contentious due to sparse sampling in previous molecular studies, as well as ambiguous external morphological characters (Pyron et al., 2016). Further investigations into diversification patterns among uropeltids will be facilitated by having a more complete species-level phylogeny. Employing molecular species delimitation methods offers one approach to identifying species-level lineages for use in diversification studies, and might assist ongoing taxonomic revisionary studies.

3.1.1 Aims

Based on the molecular phylogenetic tree generated in Chapter 2, this chapter employed species delimitation methods to attempt to infer uropeltid species diversity. Based on these results, a taxonomically densely sampled multilocus calibrated time tree using multiple fossil calibrations was generated, and used to estimate divergence times for uropeltids. Finally, the time tree was used to infer temporal patterns of lineage diversification, in which evidence was sought for an early burst pattern of lineage diversification for the entire clade, and for a change in lineage diversification rate associated with the dispersal of uropeltids to (and radiation within) the island of Sri Lanka.

3.1.2 Hypotheses

i) Is the current diversity of uropeltids underestimated?; ii) Did divergence across uropeltid genera occurred simultaneously?; iii) How did geological and climatic events shape uropeltid diversification?; iv) Were rates of species diversification constant over time, i.e. not showing a signature of early burst?

3.2 Materials and methods

A single-locus data matrix is required for analysis using single-locus species delimitation methods. Mitochondrial DNA (mtDNA) data were selected for this study because of the denser sampling that was available and the greater genetic divergence among closely related individuals. A multilocus data set was subsequently assembled based on results from the species delimitation methods and employed in molecular dating analyses.

3.2.1 Sequence alignments, data partitions and model selection

Sequence data were aligned using ClustalW (Thompson et al., 1994) implemented in Geneious v.1.8.9 (Kearse et al., 2012) with default settings (gap open cost = 15; gap extended cost = 6.66). Ambiguously aligned positions in *12s* and *16s* alignments were removed using Gblocks v0.91b (Castresana, 2000) via an online server (http://phylogeny.fr, Dereeper et al. 2008) selecting the 'less stringent' options. tRNA regions were removed from *nd4* sequences. Protein coding gene (*cytb*, *nd4*, *cmos* and *prlr*) alignments were checked for stop codons and reading frame shifts.

Alignments were concatenated and assembled into two datasets: 3.1) concatenated mtDNA data for all samples of uropeltids with sequences available in GenBank or generated in Chapter 2, to use as input in single-locus delimitation analyses; 3.2) multilocus data (i.e. mt- and nuclear (nuDNA) DNA) for outgroups and a subset of uropeltid samples representative of putatively species-level OTUs (operational taxonomic units) resulting from the species delimitation analyses for use in divergence dating analyses. Dataset 3.1 included 252 samples with a total of 2253bp [(*12s*: n=249, 378bp, 388bp before Gblocks); *16s*: (n=235, 463bp, 522bp before Gblocks); *nd4*: (n=228, 697bp); *cytb*: (n=147, 715bp). Dataset 3.2 included

155 samples and 3350bp [*12s*: (n=153, 349bp, 405bp before Gblocks); *16s*: (n=153, 454bp, 533bp before Gblocks); *nd4*: (n=141, 697bp); *cytb*: (n=113, 715bp); *cmos*: (n=131, 570bp); *prlr*: (n=103, 565bp)]. Details of sample localities, GenBank accession numbers (for published data), and datasets are given in Appendix Table 2-1. GenBank accession numbers for outgroup samples which were part of dataset 3.2 and used in the dating analyses are listed in Appendix Table 3-1.

Concatenated datasets were analysed with PartitionFinder v2.1.1 (Guindon et al., 2010; Lanfear et al., 2012, 2016), to find the best-fit partition schemes and models of nucleotide substitution for the phylogenetic analyses, applying the Bayesian information criterion (BIC) and implementing a greedy search algorithm. Data were partitioned by gene for *12s* and *16s*, and by gene and by codon position for the protein coding genes, giving a total of 14 possible partitions. For dataset 3.1, the best-fit scheme consisted of a single partition under GTR+I+G. For dataset 3.2, the following models were best fitting for two subsets: GTR+I+G (*12s*, *16s*, *nd4* 1st position, *nd4* 2nd position, *cytb* 1st position, *cytb* 2nd position, *cmos* 1st position, *cmos* 2nd position, *cmos* 3rd position, *prlr* 1st position, *prlr* 2nd position, *prlr* 3rd position), and TIM+G (*nd4* 3rd position and *cytb* 3rd position).

3.2.2 Molecular phylogenetics for uropeltid mitochondrial DNA dataset

A tree for the concatenated mtDNA matrix (dataset 3.1) was generated using MrBayes v3.2 (Ronquist et al., 2012) conducting two independent runs for 1x10^{7} generations, sampling every 1,000 generations, resulting in 10,000 trees. Data partitions and substitution models were implemented based on the PartitionFinder results. The option sumt contype=allcompat was used to ensure the consensus tree was binary, which is necessary for input in the species delimitation method mPTP (Kapli et al., 2017). Run convergence was determined in Tracer v1.7.1 (Rambaut et al., 2018) with all runs having ESS values >200. The first 25% trees were discarded as burn-in and the remaining trees used to determine Bayesian posterior probability (BPP) values for branch support. Tree was rooted with *Melanophidium* in R v.3.5.1 (R Development Core Team, 2019) with ape's v5.3 (Paradis and Schliep, 2019) function root(), based on findings from previous studies

that this genus is sister to all other uropeltids (Bossuyt et al., 2004; Pyron et al., 2016; Cyriac and Kodandaramaiah, 2017).

An ultrametric tree (an input requirement for the species delimitation method bGMYC (Reid and Carstens, 2012)), was built for the same dataset (3.1) in BEAST2 v.2.4.8 (Bouckaert et al., 2014). Beauti v2.4.8 (Drummond et al., 2012) was used to generate xml files, implementing data partitions and substitution models based on PartitionFinder results. An initial run was conducted under an uncorrelated lognormal relaxed clock model, linking all sites as they all belong to the same locus, to determine clock model evolution. A parameter for standard deviation of the uncorrelated log-normal relaxed clock (ucld.stdev) close to 0 is representative of low rate variation among branches and a strict clock is more appropriate, while values closer to 1 are indicative of higher rate variation and the locus should be analysed under a relaxed clock for better analytical performance (Brown and Yang, 2011). A strict clock model was selected (after an initial run in which ucld.stdev was <<1), using a Yule model as the tree prior. Three independent analyses were run for 100 million generations sampling every 10,000 generations. Convergence of runs was detected as reported above. Runs were merged in LogCombiner (Drummond et al., 2012), and a maximum clade credibility (MCC) tree was obtained using TreeAnnotator (Drummond et al., 2012), discarding 10% of trees as burnin. Additionally, the three runs were merged in LogCombiner discarding 10% as burnin, and 100 trees were resampled from the posterior probability distribution. MrBayes and Beast2 runs were conducted in the CIPRES Science Gateway v3.1 server (Miller et al., 2010) (http://www.phylo.org/sub_sections/portal/).

3.2.3 Species delimitation

This study employed four different approaches to species delimitation based on DNA sequence data. The general mixed Yule-coalescent model (GMYC) (Pons et al., 2006) uses branching events in an ultrametric tree to model divergence between species, based on a Yule process, and coalescence between lineages sampled from the same species, while assuming that coalescent events occur at a higher rate than speciation events. The Bayesian implementation of the GMYC method (bGMYC) is able to account for phylogenetic uncertainty in tree topology and branch

lengths using Markov chain Monte Carlo (MCMC) simulations. Additionally, bGMYC also allows the selection of a point estimate of species limits instead of a default mean probability (0.5). Lower values of the probability threshold (example: 0.1) tend to cluster samples together, while higher values (example: 0.9) will split samples into a higher number of putative species. The Poisson tree processes (PTP) (Zhang et al., 2013) is another single-locus species delimitation method, that models branching events based on branch length (i.e., number of substitutions). Unlike (b)GMYC, this method does not require an ultrametric tree as input. PTP can be calculated using a ML heuristic search, which provides bootstrap support values for the species delimitation, or with its Bayesian implementation (bPTP) which uses MCMC to calculate posterior probabilities for species delimitations. The multi-rate PTP (mPTP) method (Kapli et al., 2017) accounts for different evolutionary rates for each species, which may result in fewer putative species than PTP results. This method can also be implemented with a heuristic search as well as with a MCMC sampling for inferring support values. Finally, Bayesian Phylogenetics and Phylogeography (BPP) (Yang and Rannala, 2010) is a multilocus, multispecies coalescent method that implements a reversible jump MCMC (rjMCMC) algorithm to calculate posterior probabilities for different models of species delimitation. BPP is able to accommodate uncertainty in gene tree topology and branch lengths, and processes such as incomplete lineage sorting due to ancestral polymorphism. The model uses two types of parameters based on population genetics – population size (θ) and species divergence time (τ) (Rannala and Yang, 2003).

3.2.3.1 Single-locus species delimitation

In a first set of bGMYC analyses implemented in R, 100 trees from the posterior distribution of the BEAST analyses (to allow for the stochasticity of tree space) were run for 50,000 generations, discarding the first 40,000 generations, with a thinning of 100. GMYC tends to be successful when the rate of coalescence is higher than the speciation rate (bGMYC software manual, available at http://nreid.github.io). By examining the result of the MCMC run with the checkrates() function, log ratio values (coalescent rate/Yule rate) were found to be below zero. The bGMYC manual suggests that values <0 are an indication that the model might not be a good fit for

the data, such that the results of the run cannot be treated as reliable. One of the reasons for this might be that the divergences among the main clades are too ancient and there might be high rate heterogeneity across major lineages within the group (Talavera et al., 2013). To attempt to overcome this, four major clades were extracted from the MCC tree using the function extract.clades() implemented in the ape package v.5.3 (Paradis and Schliep, 2019) in R, and each clade was analysed individually in a second set of bGMYC analyses: i) *Melanophidium*; ii) *Teretrurus* + *Platyplectrurus*; iii) *Uropeltis*; iv) *Pseudoplectrurus* + *Plectrurus* + *Rhinophis*. Analyses ran for $1x10^6$ generations, with a thinning of 100, with the first 10% of samples discarded. Convergence of the MCMC chains was assessed visually by plotting the results of the runs, and the plots obtained with checkrates() showed log ratio values above zero. Multiple probability thresholds of delimitation ranging from 0.1 to 0.9 in intervals of 0.1 were implemented with the R command bgmyc.point(), 0.1 being the most conservative and 0.9 being more liberal in terms of estimated number of species.

To allow for a direct comparison of results among the different analyses, bPTP and mPTP analyses were run for the same four main clades used in bGMYC analyses, extracting clades in R as above. bPTP was run for $1x10^6$ MCMC iterations, sampling every 100, with a burnin of 10%. The mPTP method was also employed, running both ML and MCMC searches, the latter analyses running for $1x10^8$ iterations, sampling every 10,000 steps, with a burnin of 10%.

3.2.3.2 Multilocus species delimitation

Results from single-locus species delimitation analyses were compared and used to designate the putative species to be included in the multilocus delimitation software BPP v4 (Flouri et al., 2018). Because there is a limit on the number of species in the guide tree (for more than 30 species the program runs into memory issues; T. Flouri, pers. comm.) BPP analyses were conducted using the same four clades used in the single locus delimitation analyses. Analysis A10 compares species delimitation models based on a user specified fixed tree that guides the Markov chain (Yang and Rannala, 2010; Rannala and Yang, 2013), which should decrease computational time. The guide trees employed for each clade were based

on the BI tree inferred from the concatenated mitochondrial and nuclear dataset from Chapter 2, randomly resolving polytomies using ape's multi2di() function in R. Multiple sequence alignments were assembled for each clade, and for each locus (concatenated mtDNA, *prlr*, and *cmos*) – information on number of samples and length of alignments in Appendix Table 3-2.

Multiple BPP analyses were conducted, implementing different prior combinations for ancestral population sizes (θ) and divergence times (τ), based on those previously applied in studies of squamate reptiles and amphibians (Leaché and Fujita, 2010; Bellati et al., 2015; Gehara et al., 2017). Prior values were converted from a gamma to an inverse gamma distribution IG(α,β), because the latter is implemented in the most recent version of BPP, by preserving the priors mean (β/(α-1)) and variance ($\beta^2/((\alpha-1)^{2*}(\alpha-2))$) the same. The priors in the different settings assumed: i) large ancestral population sizes and deep divergences among species (θ ~ IG(3, 0.2) and τ ~ IG(3, 0.2); θ and τ with mean = 0.1 and variance = 0.01); ii) small ancestral population sizes and recent divergences (θ ~ IG(4, 0.003) and τ ~ IG(4, 0.003); θ and τ with mean = 0.001 and variance = $5x10^{-7}$); iii) large ancestral population sizes and recent divergences (θ ~ IG(3, 0.2); τ ~ IG(4, 0.003)). To account for rate variation among loci a symmetric Dirichlet prior was set with α = 5. After a burnin of 10^6 samples, each analysis ran for $4x10^6$ steps with a sampling frequency of 10 (i.e. 400,000 samples were logged). All prior combinations ran four times in total, twice for each of the two rjMCMC algorithms (0 and 1) available in BPP to test reliability of results. The results of the multiple runs were compared to identify potential convergence problems.

3.2.4 Molecular dating

3.2.4.1 Fossil calibrations

Because there are no known uropeltid fossils, 44 additional extant snake species representative of several (sub)families were added to the dataset as outgroups (Appendix Table 3-1) so that snake fossil calibrations employed in previous molecular dating studies of uropeltids and other snakes (Cyriac and Kodandaramaiah, 2017; Deepak et al., 2018) could be used here. To assemble a more complete dataset and reduce the amount of missing data, it was necessary

to create chimeric data for some outgroup species, by combining GenBank DNA sequence data from different individual specimens and studies. Six node calibrations were selected, informed particularly by Head (2015) and Head et al. (2016). (i) Oldest divergence within Alethinophidia, with a minimum age of 93.9 Ma and soft maximum 100.5 Ma (Head, 2015) based on *Haasiophis terrasanctus* Tchernov *et al.*, 2000. Based on earlier phylogenetic analyses, Head (2015) recommended using *H. terrasanctus* to calibrate the minimum age of the basal divergence within non-*Anilius,* non-tropidophiid alethinophidians, but the application here is based on evidence that *H. terrasanctus* might be a stem rather than crown alethinophidian, as unconstrained phylogenetic analyses in Hsiang et al. (2015) found *Haasiophis* in a clade sister to Alethinophidia (see also Zaher et al., 2019). (ii) Divergence between Boinae and Erycinae, with a minimum age of 58 Ma (Jaramillo et al., 2007; Head, 2015) and soft maximum age of 64 Ma (Woodburne et al., 2014; Head, 2015) based on the boine *Titanoboa cerrejonensis* Head et al., 2009. (iii) Divergence between *Corallus* and (*Chilabothrus*+(*Epicrates*+*Eunectes*)), with a minimum age of 50.2 Ma (Head, 2015) and soft maximum 64 Ma (Woodburne et al., 2014; Head, 2015) based on *Corallus priscus* Rage, 2001. (iv) Divergence between *Acrochordus javanicus* and (*A. ararfurae*+*A. granulatus*), with a minimum age of 18.05 Ma (Head et al., 2016) and maximum 23.0±0.05 Ma (Sanders et al., 2010; Hilgen et al., 2012; Head et al., 2016) based on *Acrochordus dehmi* (Hoffstetter, 1964). (v) Divergence between Crotalinae and Viperinae, with a minimum age of 20.0 Ma and maximum 23.8 Ma (Agustí et al., 2001; Head et al., 2016) based on the viperine *Vipera aspis* complex (Szyndlar and Rage, 1999). (vi) Divergence between non-acrochordid, non-xenodermatid caenophidians and their closest extant relatives, with a minimum age of 50.5 Ma and maximum 72.1 Ma (Head et al., 2016; see also Zaher et al., 2019) based on *Procerophis sahnii* (Rage et al., 2008). The implementation of these six calibrations in BEAST is shown in Appendix Table 3-3.

3.2.4.2 BEAST analyses

To estimate divergence times among uropeltid lineages, a single sample per species was selected based on the results of the single-locus species delimitation analyses,

which guided the number and identity of species-level lineages. Samples with maximum sequence coverage were used where possible, excluding samples for which only two molecular markers were available and from the same locality as a closely related 'putative' species. Based on the single-locus species delimitation results, dating analyses were conducted with a subset of 111 uropeltid OTUs (dataset 3.2 (Appendix Table 2-1); plus 44 outgroup species (Appendix Table 3-1)). The concatenated matrix (i.e. mtDNA and nuDNA) was analysed in BEAST2, using BEAUti v.2.4.8 to generate the xml files. Data partitions and substitution models were selected based on the PartitionFinder results for dataset 3.2. A strict clock model was selected for all loci, unlinked across loci, (after an initial run to test clock model evolution, under a lognormal relaxed clock unlinked across loci in which ucld.stdev was <1 for all loci), using a Yule model as tree prior. Detailed calibration settings are available in Appendix Table 3-3. Three independent analyses were run for 100 million generations sampling every 10,000 generations using the CIPRES server. Run convergence was determined in Tracer v1.7.1 with most ESS values >200, except for rates of substitution for the TIM+G model (all values above 100). Runs were merged in LogCombiner, and a maximum clade credibility (MCC) tree was obtained using TreeAnnotator, discarding the first 10% of trees as burnin. MCC tree was visualised and edited with a geological time scale with R packages phytools (Revell, 2012), PHYLOCH (Heibl, 2008), strap (Bell and Lloyd, 2015) and CODA (Plummer et al., 2006), based on the script available here: https://taming-the-beast.org/tutorials/FBD-tutorial/.

3.2.5 Estimating lineage diversification

Lineage diversification was investigated using a number of methods. Analyses were conducted only with the Uropeltidae clade, which was extracted from the consensus concatenated dated MCC tree from this chapter using the R package ape v. 5.3 extract.clade() function, so that outgroups would not be included in the analyses. The Uropeltidae tree contained n=111 species (56 of which correspond to named species, and 55 additional, putatively species-level OTUs, as estimated using single-locus species delimitation methods). To visualise the tempo of diversification a lineage-through-time (LTT) plot was generated using the ltt()

function in the ape package. The gamma (γ) statistic of Pybus and Harvey (2000) was also generated using the ape package gammaStat() function, to detect departures from the constant rate pure-birth Yule model. Significant negative γ indicates deceleration in diversification rates, representative of early lineage diversification, γ=0 shows a constant diversification rate, while positive γ values indicate an increase in rates in more recent diversification events (Pybus and Harvey, 2000). In order to test if the uropeltid radiation diversified under a distinct rate regime, the programs BAMM2.5 (Bayesian Analysis of Macroevolutionary Mixtures, Rabosky *et al.*, 2013; Rabosky, 2014) and BAMMTOOLS2.0 (Rabosky et al., 2014) were employed, also using the consensus concatenated dated tree. The following priors were generated using BAMM: expected number of shifts=1; lambda Init.Prior=3.04; lambda ShiftPrior=0.02; mu Init.Prior=3.04; lambda TimeVariablePrior=1.

3.3 Results

3.3.1 Species delimitation

For the *Melanophidum* clade, which has four species currently recognised (Uetz and Hošek, 2019), different threshold values applied in bGMYC were fairly consistent, identifying between 11 and 12 different, putative species-level lineages, while bPTP identified 12 (Table 3-1). For Clade B comprising *Teretrurus*, *Brachyophidium* and *Platyplectrurus*, bGMYC results ranged between nine and 12 putative species-level lineages, with bPTP finding 11. *Platyplecturus* presently has two species recognised, and both *Teretrurus* and *Brachyophidium* currently are considered monotypic genera (Pyron et al., 2016), though Cyriac and Kodandaramaiah (2017) found at least four distinct molecular lineages of *Teretrurus* + *Brachyophidium* in their study. *Teretrurus sanguineus* currently includes several synonyms, of which at least some of which appear to be valid. Most of the additional, putative species-level lineages found by bGMYC and bPTP within Clade B are within *Teretrurus*. Between 48 and 51 lineages were found by bGMYC for Clade D comprising *Plectrurus*, *Pseudoplectrurus* and *Rhinophis*, while bPTP found 49. Results for *Plectrurus* and *Pseudoplectrurus* were consistent with the currently recognised species for those genera, with some *Rhinophis* having more putative

species diversity than was identified from examination of vouchers. For Clade C comprising *Uropeltis*, bGMYC found support for between 21 and 48 putative species-level lineages, and bPTP recovered 44. Comparing the different methods, mPTP consistently detected a more conservative number of putative species-level lineages compared with the other single-locus delimitation analyses (Table 3-1). The taxon sampling includes a number of paraphyletic 'species' (based on voucher identifications) and obvious singletons, which mPTP tends to clump together with other nested or sister lineages, respectively (Kapli et al., 2017). Consequently, results from mPTP were not considered further for comparison with the other delimitation methods employed in the present study.

There are no precise guidelines for which bGMYC threshold is likely to yield the most accurate results, and most workers have seemingly arbitrarily selected those generated using a midpoint value. In this study, bGMYC results from application of a threshold of 0.6 were mostly consistent with results obtained from bPTP (Table 3-1 and Appendix Table 3-4) and so these were used to select the putative species-level units to be included in the guide tree in the BPP analyses. The exceptions occurred in *Uropeltis*, where different numbers of 'species' were identified by bGMYC 0.6 and bPTP (43 and 44, respectively). Beyond simple counts

Table 3-1 Number of putative species found in different species delimitation analyses. Results from single locus delimitation analyses used to inform species input into the multilocus method BPP are highlighted in bold.

Method	Clade A	Clade B	Clade C	Clade D
	Melanophidium	*Teretrurus*, *Brachyophidium*, *Platyplectrurus*	*Uropeltis*	*Plectrurus, Pseudoplectrurus, Rhinophis*
bGMYC 0.1	11	9	21	48
bGMYC 0.2	12	9	26	48
bGMYC 0.3	12	10	29	49
bGMYC 0.4	12	10	34	49
bGMYC 0.5	12	10	39	49
bGMYC 0.6	**12**	**11**	**43**	**49**
bGMYC 0.7	12	11	45	50
bGMYC 0.8	12	11	46	50
bGMYC 0.9	12	12	48	51
bPTP	**12**	**11**	**44**	**49**
mPTP multi	5	7	17	36

there were also some discordances between the bGMYC 0.6 and bPTP results in the composition of the 'species' units, which were assessed on a case by case basis, as follows. In both analyses, the *U. broughami* sample BMNH1946.1.16.29 was grouped in the same 'species' unit as its sister lineage comprising all *U. woodmasoni* samples. These two species are morphologically similar (e.g. they have the derived condition of 19 midbody dorsal scale rows) but specimens attributed to each species are very distinct in, for example, the number of ventral scales (>200 in *broughami* versus < 180 in *woodmasoni*: see Appendix Table 4-1), therefore for input in BPP they were retained as distinct species. The two samples of *Uropeltis* cf. *dupeni* VPC-038 and VPC-039 were grouped as a single 'species' by bGMYC but as different 'species' by bPTP. The two specimens are from nearby localities and lack obvious morphological differences (D. Gower, pers. comm.) and so were grouped into a single species for BPP and divergence analyses input. *Uropeltis ellioti* VPC-004 was recovered as a singleton (the sole sampled member of a species as determined by molecular species delimitation) in bGMYC analysis and clustered with a monophyletic lineage of other *U. ellioti* samples in bPTP – because this sample is a singleton, it was used as its own single 'species' lineage in BPP. *Uropeltis phipsonii* U19 3765 grouped with other *U. phipsonii* samples in the bGMYC results but was a separate 'species' in the bPTP results – only *12s* data are available for this sample, so it was not considered as distinct from other *U. phipsonii* samples for input in BPP and divergence analyses.

The preliminary results from BPP varied substantially depending on the starting parameters (details not shown). Overall, for the four clades, settings assuming small ancestral population sizes and recent divergences tended to split samples into more species (values closer to 1), though it still clustered together all *Plectrurus* species, as well as *Uropeltis woodmasoni* and *U. broughami*, for instance. The other two settings employed, suggesting large ancestral population sizes and either deep or recent divergences among species, resulted in similar delimitations and tended to cluster together more species. Due to the need to further investigate the settings to be employed in BPP analyses to assign sensible delimitations based on a multilocus dataset, further analyses were not pursed in the

present work. Therefore, results recovered from the bPTP and bGMYC 0.6 threshold analyses (111 uropeltid OTUs) were taken forward for the dating analysis.

3.3.2 Divergence time estimates of the uropeltid radiation

Based on the concatenated tree (mt and nuDNA) (Figure 3-1 and Table 3-2), the age of the uropeltid radiation (oldest divergence within the clade) was estimated at 61 Ma (95% high posterior density (HPD): 53.2–69.6), in the Paleocene. Melanophidum, the sister genus to all other uropeltids, was estimated to have started diversifying 41.2 Ma (95% HPD: 35.53–47.78). The clade comprising *Platyplectururus* + (*Teretrurus* + *Brachyophidium*) split from its sister clade 52.39 Ma (95% HPD: 45.66–59.66), and started diversifying 37.42 Ma (95% HPD: 31.9–43.4), during the Eocene. *Uropeltis* diverged from the clade comprising *Rhinophis* + (*Pseudoplectrurus* + *Plectrurus*) 48.65 Ma (95% HPD: 42.49–55.62), with *Uropeltis* undergoing initial diversification much later at the Oligocene–Miocene boundary 23.78 Ma (95% HPD: 20.56–27.49). The clade comprising *Rhinophis* + (*Pseudoplectrurus* + *Plectrurus*) was estimated to initially diversify during the Eocene, 41.75 Ma (95% HPD: 36.46–47.86). Indian and Sri Lankan *Rhinophis* were estimated to have split 34.53 Ma (95% HPD: 30.11–39.57), with the origin of the extant Sri Lankan lineages estimated at 27.48 Ma (95% HPD: 23.94–31.53).

Though the phylogenetic position of the Indian species *R. goweri* is not clear (see Chapter 2), BEAST2 analysis recovered this species within the Sri Lankan clade, estimating the split between *R. goweri* and *R. dorsimaculatus* at 18.17 Ma (95% HPD: 12.97–23.49). Much of the estimated species diversification within genera occurred in the late Miocene and Pliocene, starting at 10 Ma, with the exception of *Melanophidium* which seemed to have undergone species diversification earlier in the Miocene.

The posterior distribution for the divergence times of the calibrated nodes differed substantially from the prior constraints for nodes I) 143.4 Ma (95% HPD: 125.09–162.59), V) 63.97 Ma (95% HPD: 54.55–73.89), and VI) 124.59 Ma (95% HPD: 108.39–141.32). These have older ages than the calibration priors, which were set up with the following means: I) 93.9 Ma, V) 20 Ma, and VI) 50.5 Ma.

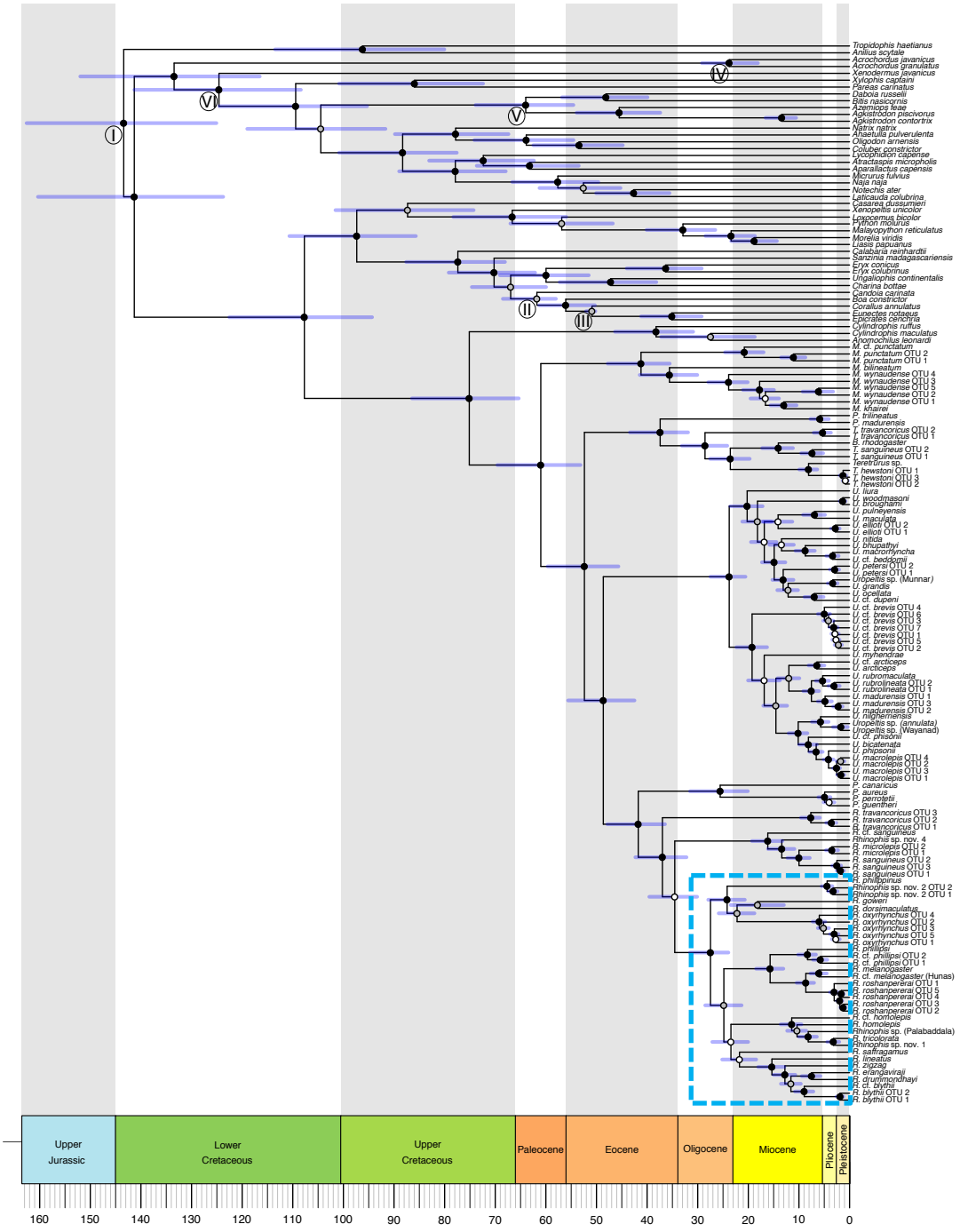


Figure 3-1 Multilocus time calibrated MCC tree inferred in BEAST2. Roman numerals on nodes correspond to fossil calibrations as in Appendix Table 3-3. Branch support indicated by coloured circles on nodes with Bayesian posterior probability (BPP) values (black: ≥ 0.95; grey: <0.95 and ≥ 0.75; white: < 0.75). Blue bars denote 95% high posterior density (HPD) credible intervals for node ages. Uropeltidae Sri Lankan clade clustered within dashed light blue box.

Table 3-2 Uropeltidae clade ages estimated in BEAST2. Uropeltoidea is a superfamily comprising the families Uropeltidae, Cylindrophidae and Anomochilidae.

	Present study		Cyriac and Kodandaramaiah (2017)
Clade	Mean node age (Ma) (95% HPD)	Geological time period	Mean node age (Ma) (95% HPD)
Split between Uropeltoidea and other Henophidia	107.71 (94.33,122.55)	Lower Cretaceous	82.83 (70.87, 94.28)
Split between Uropeltidae + (Cylindrophidae + Anomochilidae)	75.13 (65.36, 86.45)	Upper Cretaceous	56.02 (42.59, 74.57)
Uropeltidae	61 (53.16, 69.58)	Paleocene	ca. 45 (33.9, 55.8)
Melanophidium	41.2 (35.53,47.78)	Eocene	
Platyplectrurus + *Teretrurus*	37.42 (31.9, 43.4)	Eocene	
Uropeltis	23.78 (20.56, 27.49)	Oligocene	
(*Pseudoplectrurus* + *Plecturus*) + *Rhinophis*	41.75 (36.46, 47.86)	Eocene	
Sri Lankan *Rhinophis*	27.48 (23.94, 31.53)	Oligocene	
Split between Indian and Sri Lankan species	34.53 (30.11, 39.57)	Eocene-Oligocene boundary	22 (15.13, 33.77)

3.3.3 Diversification dynamics

The pattern of diversification generated using BAMM indicated that net speciation rates remained more or less constant over time (Figure 3-2 A). Although this method has received criticism (Meyer and Wiens, 2018; Meyer et al., 2018), this has been strongly refuted (Rabosky, 2018, 2019), and the results from BAMM are supported by other methods employed here. A constant rate of diversification is supported by the lineage-through-time (LTT) plot (Figure 3-3) and the gamma statistic (0.0667, p-value = 0.9469). In addition, the BAMM analysis did not identify any rate shifts (i.e. there were zero core shifts, BF = 1) (Figure 3-2 B). Generated mean rates of speciation from BAMM for the uropeltid radiation were estimated at 0.09 lineages per million years (0.07–0.11 upper/lower 90% HPD).

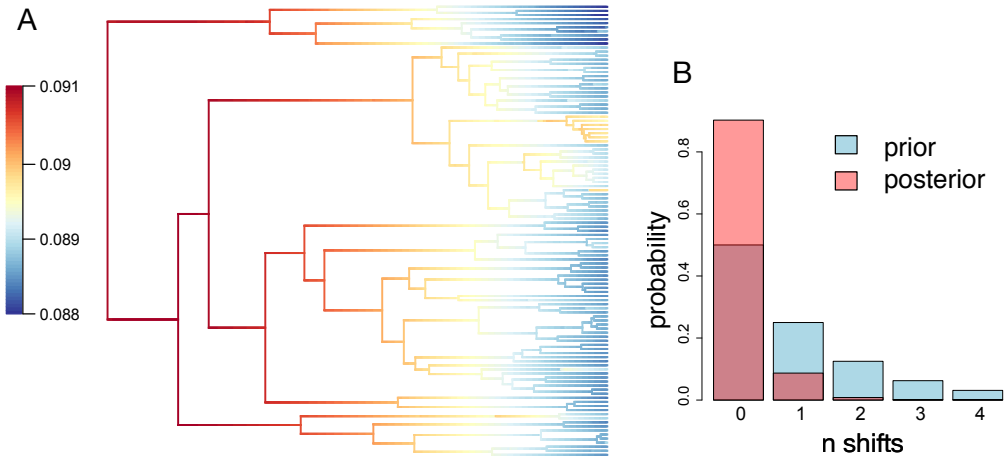


Figure 3-2 A) Phylorate plot generated in BAMMtools with mean speciation rates (cool colours = slower rates, warm colours = faster) along each branch of the Uropeltidae phylogeny, allowing assessment of rate shifts along the tree. B) Histogram of the prior (blue) and posterior (red) distribution of the number of rate shifts in BAMM analysis.

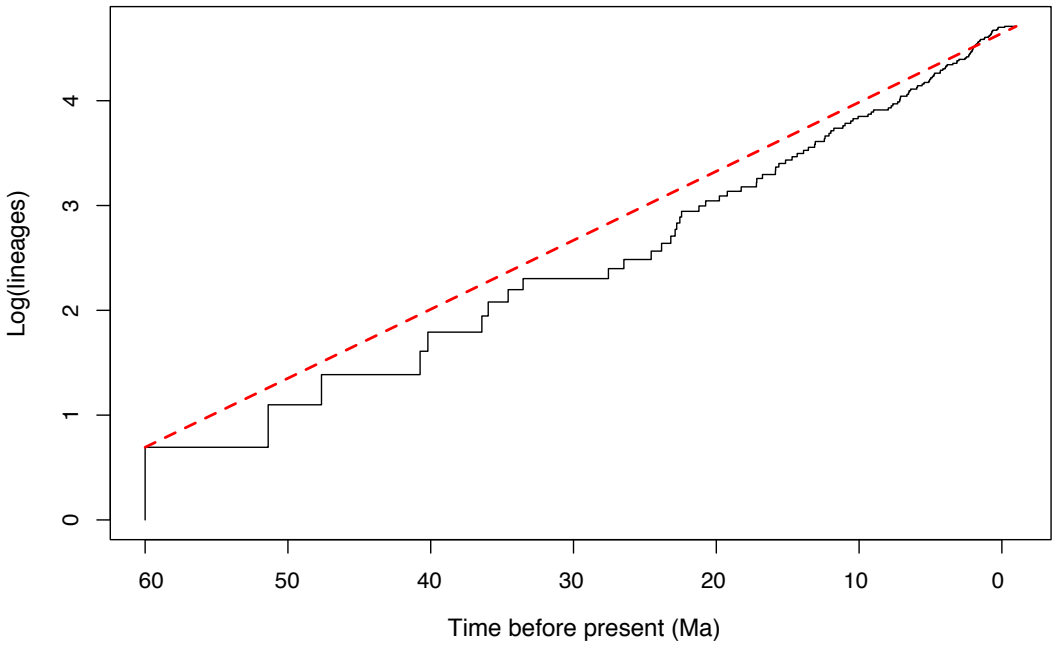


Figure 3-3 Plot of number of lineages on a log scale through time (using ape) derived from the dated Uropeltidae MCC tree (black line). Dashed red line represents number of lineages expected under a constant rate of lineage diversification.

3.4 Discussion

This study highlights that species diversity in uropeltids, an overall poorly studied group of fossorial squamates, has previously been underestimated. Using molecular species delimitation methods, this study finds evidence for a much higher number of potential candidate species than currently recognised. Based on these findings, the most comprehensive calibrated phylogeny of the family Uropeltidae was generated, pushing back the estimated origin of the group to the Late Paleocene ca. 61 Ma (95% HPD: 53.16–69.58), as opposed to the Middle Eocene, ca. 45 Ma (95% HPD: 55.8–33.9, Cyriac and Kodandaramaiah, 2017). Diversification in uropeltids is inferred to have followed a constant rate of lineage accumulation, a pattern that has been observed in other tropical mainland clades. However, there was no evidence for an increase of diversification rate associated with the clade that dispersed to and radiated within the island of Sri Lanka.

3.4.1 Increase in estimated species-level diversity of a poorly known fossorial vertebrate clade

Molecular diversity in uropeltids is considerably higher than expected, with 116 putative species recovered by PTP and 115 by bGMYC (threshold 0.6), which if correct would imply a 100% increase of species in this group. This was particularly pronounced for three genera: *Melanophidium*, with the discovery of multiple deeply divergent lineages (four species currently described vs. 12 recovered by PTP), *Uropeltis* (24 vs. 44 species) and *Rhinophis* (20 vs. 49 species). The high discrepancy between the number of species currently described and the number recovered in the different species delimitation analyses probably partly reflect the reality of a poorly studied group of organisms with undescribed diversity, but might also reflect caveats with sampling and methodological issues associated with DNA-based species delimitation.

Issues arise from conducting analyses with an unbalanced sampling, which is known to influence PTP results (Zhang et al., 2013). Species-level paraphyly (as in Funk and Omland, 2003) and singletons tend to decrease accuracy in mPTP, by either over splitting samples into smaller groups or grouping nested putative species together (Kapli et al., 2017), hence results from this method were not considered

for further inspection. Even though it has been suggested that shortcomings from implementing analyses such as GMYC with datasets with low sample sizes per species can be overcome by increasing the phylogenetic scope of the study (Talavera et al., 2013), in this case bGMYC results for the full dataset were deemed unreliable, and so the dataset was subdivided into four smaller clades to conduct species delimitation analyses. Nevertheless, Ahrens et al. (2016) found that with GMYC singletons are not necessarily an issue and that population genetics parameters, such as effective population size, are more relevant in obtaining a higher accuracy in the delimitation, so that delimitation accuracy for species with small sample sizes is only negatively affected if it reflects differences in effective populations among species. All analyses of mtDNA failed to separate the closely related species *U. woodmasoni* and *U. broughami*, which could be due to these being recently evolved species, for which single locus methods tend to underestimate species diversity (Machado et al., 2018), and/or that only one sample of *U. broughami* was available for this study. Even though mtDNA has been widely used in molecular evolution studies due to its advantages (reviewed in Galtier et al., 2009), which in turn have made it popular for implementing species delimitation methods (e.g. Blair and Bryson, 2017; Machado et al., 2018), issues that potentially compromise its accuracy (e.g. introgression, incomplete lineage sorting) provide arguments towards analysing mtDNA data with multilocus coalescent methods such as BPP (Yang and Rannala, 2010). Nevertheless, results from the single-locus (mtDNA, in this case) species delimitation methods implemented here were useful to discover molecular diversity that strongly indicates underestimated species diversity, and to highlight cases where cryptic species might occur (*U. brevis, R. oxyrhynchus*). However, these results alone are insufficient to conclusively delimit species and make reliable taxonomic conclusions and actions. This would ideally be further investigated with increased sample sizes for each taxon, multilocus datasets and inferences using coalescence-based approaches. Additionally, analysing results in light of morphological variation and better geographical data will increase information towards resolving uropeltid taxonomy and a better understanding of the evolutionary history of the group.

3.4.2 Molecular dating of the Uropeltidae

The current study estimated the divergence between Uropeltidae and (Cylindrophidae + Anomochilidae) to have occurred 75.13 Ma (95% HPD: 65.36–86.45) which is much older than had been previously estimated. The recent study by Cyriac and Kodandaramaiah (2017) employed a smaller, but still relatively broad sampling of uropeltids and estimated the divergence between Uropeltidae + (Cylindrophidae + Anomochilidae) at 56.02 Ma (95% HPD: 42.59–74.57), near to the Paleocene-Eocene boundary. Other studies investigating the higher evolutionary relationships among snakes have estimated younger dates for this divergence, while being based on very limited uropeltoid sampling e.g. Miralles et al. (2018) estimated divergence between Uropeltidae (one sample each of *R. melanogaster* and *R. phillipsi* combined into a chimeric sample; erroneously named as *Uropeltis*) and *Cylindrophis* sp.) at 48.9 Ma (95% HPD: 36 – 62.4); Harrington and Reeder (2017) estimated divergence between *R. melanogaster* (as *U. menalogaster*) and *Cylindrophis* sp. at 46.17 Ma (95% HPD: 34.95–64.59); or sometimes studies only report mean values for the age of the nodes without confidence interval values, e.g. Zheng and Wiens (2016) estimated the split between Uropeltidae + (Cylindrophidae + Anomochilidae) at 44.43 Ma (analyses conducted with 13 uropeltid species). The oldest divergence within Uropeltidae is estimated in this study to have occurred 61 Ma (95% HPD: 53.16–69.58), while Cyriac and Kodandaramaiah (2017) estimated it at ca. 45 Ma (95% HPD: 33.9–55.8) in the Eocene, which partly overlaps with the current estimate. Reasons for these dating discrepancies, with this study uncovering generally older dates of divergence, could be due to a number of factors. The higher-level studies were mostly based on nuclear sequence data, which tend to give younger dates (Zheng et al., 2011). Across snakes and other vertebrates, mitochondrial data sometimes suffer saturation of the 3rd codon in protein coding genes, which might bias estimates towards older dates (Phillips, 2009; Lukoschek et al., 2012). Basal internal branches of the tree are prone to saturation particularly when the outgroup taxa are very divergent from the group of interest (Duchêne et al., 2014), which might be the case in the dataset employed for this analysis. Because of the poor fossil record among uropeltids, there are no reliable calibrations within the group. As such, selection of

outgroups in this study was fairly wide in taxonomic scope, and species distantly related to uropeltids were added to the dataset to be able to employ multiple fossil calibrations.

While it is not necessarily an issue to have posterior distribution values that do not match the specified priors, the BEAST analysis reported here produced considerably older estimates than expected for some of the (especially older) calibrated nodes such as the root. Heled and Drummond (2012) found that when calibration was set up under a strict clock instead of a relaxed clock, the posterior distribution did not match the prior, being instead influenced by the data. Additionally, when employing multiple independent calibrations, it has been found that priors interact with each other (Heled and Drummond, 2012), and different calibration schemes can impact estimates of evolutionary rates and timescales (Duchêne et al., 2014).

Cyriac and Kodandaramaiah (2017) employed a similar set of molecular markers to those analysed in this study (here the mitochondrial *cytb* and nuclear *prlr* were added to the sequence matrix). Cyriac and Kodandaramaiah (2017) used some of the same fossil calibrations (I, II, VI) as this study with slightly different dates (though exact settings applied in BEAST by the former study are not clear), and included another calibration (*Morelia riversleigensis* Smith and Plane, 1985 vide Scanlon, 2001 to date the crown Pythonidae node) not employed in this study. These factors make it difficult to establish the reason for the difference in obtained divergence dates between these two studies. Preliminary assessments removing one calibration prior at a time had no visible effect on the posterior distributions of calibrated notes (analyses not shown). To fully understand the impact of the interaction of the calibration priors and data, analyses could be run without the sequence data (Barba-Montoya et al., 2017), and this should also be pursued.

Further analyses investigating the difference between executing divergence dating analyses using only mitochondrial or nuclear data, as well as the impact that different calibration schemes might have on node ages would be helpful to improve divergence age estimates within the family Uropeltidae. The fact that dating estimates obtained here are diffuse, with large HPD ranges, adding to the fact that they are fairly disparate from previous studies, makes it problematic to try and test,

post hoc, potentially causal climatic and geological events that might explain divergence times. The main aim of the dating analysis carried out here was to generate a species-level ultrametric tree and to examine species-level diversification through time.

3.4.3 Tempo and mode of diversification

Net diversification of the uropeltid radiation, which is largely composed of mainland taxa, follows a constant rate of lineage accumulation, as opposed to displaying an early burst and slowdown in rates, the latter being a signature of adaptive radiation (Schluter, 2000). A pattern of constant net diversification has been identified in other tropical continental radiations, for example South American ovenbirds and woodcreepers (Derryberry et al., 2011), African catfishes and spiny eels (Day et al., 2013, 2017, respectively) and African toads (Liedtke et al., 2016), and might be a common characteristic in these systems. However, despite the uropeltid radiation containing an insular clade (35 out of 111 OTUs) that radiated following dispersal from the mainland, there is no evidence for any substantial shift in net diversification during the Sri Lankan radiation. Thus, the colonisation of Sri Lanka does not seem to have led to a subsequent rapid burst of diversification of *Rhinophis*, because no rate shifts were identified (Figure 3-2) and therefore there is no evidence that these insular taxa diversified at a different rate to mainland clades.

Here, the colonisation of Sri Lanka was estimated to have occurred in the Oligocene (oldest divergence among extant Sri Lankan lineages 27.48 Ma (95% HPD: 23.94–31.53)), though Cyriac and Kodandaramaiah (2017) reported a younger estimate at 22 Ma (95% HPD: 15.13–33.77). Both these estimates are older than other island system radiations where a rapid burst of diversification has been identified e.g. Lake Tanganyikan cichlid fishes 9-12 Ma (Day et al., 2008), Malagasy vanga birds ca. 20 Ma (Reddy et al., 2012), Andean clearwing butterflies 15.2 Ma (95% HPD: 13.2–25.6 Ma) (De-Silva et al., 2016). Although this study recovered generally older divergence dates than previous studies, a similar pattern of constant diversification rates has been reported for Sri Lankan shrub frogs (*Pseudophilautus*), which colonised Sri Lanka ca. 30 Ma (Meegaskumbura et al., 2019). Given that the sister genus of *Pseudophilautus* (*Raorchestes*) is endemic to

the Western Ghats and has a similar diversification timing and dynamic (Vijayakumar et al., 2016), Meegaskumbura et al. (2019: 20) suggested that a synchronous uplift of the Indian Western Ghats and Sri Lankan highlands might explain the "coincident and gradual radiations" in both lineages. Though Meegaskumbura et al. (2019) also note that there are no reliable dates yet available in the literature for the uplift of Sri Lankan mountains. Very few studies have investigated diversification patterns of endemic radiations within Sri Lanka, so it is not clear how prevalent this pattern is. The relatively slow net speciation rate for uropeltids, 0.09 lineages per million years (90% HPD: 0.07–0.11), is in agreement with previous findings that fossorial snakes and other fossorial squamate reptile lineages tend to have lower rates of diversification than lineages inhabiting arboreal environments (Bars-Closel et al., 2017; Cyriac and Kodandaramaiah, 2017) so that microhabitat might be a major factor in the diversification dynamics of uropeltids. It is not clearly understood how fossorial microhabitats might constrain net diversification, but it has been suggested that relatively poor organismal dispersal ability or the relatively homogeneous environment and restricted niche diversity might play a role (Bars-Closel et al., 2017).

Incomplete species sampling (less than 80%) tends to underestimate the number of more recent nodes and over represent deeper nodes, biasing results towards a slowdown in rates of lineage diversification (Cusimano and Renner, 2010; reviewed in Moen and Morlon, 2014), exaggerating a pattern associated with an early burst effect. Nevertheless, the analyses conducted here failed to sample only seven (*R. fergusonianus*, *R. porrectus*, *R. punctatus*, *U. beddomii*, *U. ceylanica*, *U. dindigalensis*, *U. shorttii*) out of the 56 species currently described (Uetz and Hošek, 2019), so that in this case, there is no indication that missing species is an issue. On the other hand, analyses included a relatively high number of OTUs compared with the number of species currently recognised, based on the single locus mitochondrial lineages species delimitation analyses. introducing a taxonomic bias by overestimating the number of OTUs, while it might potentially account for cryptic diversity, it might lead to a bias in diversification estimates by boosting the number of more recent nodes. Thus, overestimating the number of species might have the tendency to erase a signal of early burst. Furthermore, the generally older estimates

of divergence times (compared with those inferred in previous studies) might have influenced the inference of diversification patterns. The relatively high density of older node ages estimated in the dating analysis would tend to create a pattern of early burst of diversification (Burbrink and Pyron, 2011), though this was not observed for uropeltids. It is unclear how the combination of these factors might have impacted the inference of diversification patterns. Additionally, reliable estimates of uropeltid diversification rates is further challenged by the lack of fossil record for the group.

Due to limitations of diversification methods in estimating diversification rates through time, future analyses could include maximum likelihood approaches (e.g. RPANDA (Morlon et al., 2016), ClaDS (Maliet et al., 2019)) to compare with BAMM results (Burin et al., 2019).

3.5 Conclusion

Uropeltidae is one of the largest radiations of extant fossorial squamates, with exceptional amounts of species diversity in this broader grouping within a relatively small geographic region. This study shows that the number of species of uropeltids in India and Sri Lanka has so far been underestimated, with a much higher number of lineages uncovered than the species currently recognised. Further investigation into taxonomic morphological characters and geographical data will be necessary to make further inferences of any necessary taxonomic revisions and assess how common cryptic taxa are in the clade. Divergence times of Uropeltidae and of all major clades within the family were estimated based on a multilocus dataset with 111 putative species. The calibrated time tree estimated older dates than previously assessed (Cyriac and Kodandaramaiah, 2017), which might be the result of the fossil calibrations applied, warranting further investigation into the settings employed in the dating analyses. This will enable inference of climatic and biogeographic events that might explain lineage diversification patterns in uropeltids. Diversification analyses show no evidence for rate shifts increase or decrease in the evolution of uropeltid snake lineages. These findings are in accordance with other vertebrate continental radiations where despite the high levels of extant diversity there is no evidence for lineages evolving under a pattern

of early burst (Liedtke et al., 2016). Nonetheless, constant lineage accumulation with relatively slow rates might be the result of lack of ecological niche specialisation in a fossorial clade, but future work with ecomorphological traits and detailed ecological data will help further elucidate the evolutionary dynamics of this clade.

Chapter 4 – Morphological evolution in an evolutionary radiation of fossorial snakes (Serpentes: Uropeltidae)

Abstract

As with other aspects of the biology of fossorial taxa, the diversity and diversification of phenotypic traits of head-first burrowing vertebrates is relatively understudied. Shieldtails (Serpentes: Uropeltidae) are a family of small fossorial snakes, endemic to Sri Lanka and peninsular India. There are eight genera and 56 species currently recognised. This is a poorly understood group, partly due to their secretive habits and confusing taxonomic history. Although uropeltids seem to exhibit high levels of morphological diversity and have some highly distinct phenotypic features, their morphology has not been studied using a quantitative approach. A large dataset was generated for 22 external traits from 975 historical specimens housed in natural history collections. These data were combined with a new dated multilocus phylogeny, to determine phylomorphospace occupation of overall body shape, and investigate patterns of morphological diversification through time. Results show a wide range of uropeltid body and head shapes across the clade, with the most speciose genera *Uropeltis* and *Rhinophis* occupying different areas of morphospace, mainly due to differences in tail tip morphologies. The data provide evidence for an early burst pattern of evolution for tail traits. The decoupling of uropeltid lineage diversification rates, with constant lineage accumulation rates, from phenotypic diversification is indicative that this is not a typical case of adaptive radiation. The pattern of uropeltid tail shape diversification indicates that most tail shape variation developed early on in the evolutionary history of the family, which might be indicative of an ecomorphological function of the tail terminal scutes.

4.1 Introduction

Understanding processes that constrain or promote organismal diversification is one of the main aims of evolutionary biology. One of the processes that is considered to have generated much organismal ecomorphological diversity is adaptive radiation, where the rapid ecological and morphological diversification of

an ancestor into multiple lineages is driven by access to novel environments (Simpson, 1953; Schluter, 2000). There are different kinds of events that promote radiations and bursts of phenotypic diversification. These include, but are not limited to, extinction of competitors, which fosters the occurrence of a species in a new environment, the colonisation of a new region, such as dispersal to islands, or the development of key innovations providing access to new ecological opportunities (Simpson, 1953; Heard and Hauser, 1995; Schluter, 2000; Gavrilets and Vose, 2005; Yoder et al., 2010). These past processes should in theory leave signatures in phenotypic traits of extant taxa and it should be able to inferred them by application of phylogenetic comparative methods (PCMs) (Blomberg et al., 2003; Harmon et al., 2003; Freckleton and Harvey, 2006). For example, in adaptive radiations, novel ecological opportunity favours an initial burst of phenotypic diversification during early cladogenesis as organisms diversify into new niches, with a subsequent slowdown in rates of evolution as niches become filled over time (Simpson, 1944, 1953; Schluter, 2000; Gavrilets and Vose, 2005; Rabosky and Lovette, 2008).

While most classic, textbook examples of adaptive radiations are found in lineages endemic to insular systems such as islands or lakes – West Indies anoles (Losos et al., 1998; Harmon et al., 2005), vangas in Madagascar (Jønsson et al., 2012), East African cichlids (Seehausen, 2006), Galapagos finches (Grant and Grant, 2008) – adaptive radiations are not exclusive to these environments, also having been reported in, for example, continental anoles (Pinto et al., 2008). Conversely, there are examples of non-adaptive radiation, in which diversification is accompanied by negligible ecomorphological differentiation (Rundell and Price, 2009), and have been observed in plethodontid salamanders (Kozak et al., 2006), and *Achatinella* land snails of Hawaii (Cameron et al., 1996) for example.

The Western Ghats of India and the highlands of Sri Lanka are together one of the world's biodiversity hotspots, with high levels of threatened endemism (Myers et al., 2000). The Indian subcontinent is thought to have gone through long periods of isolation, breaking away from South America-Africa in the mid-Jurassic (ca. 170 million years ago (Ma)) and from Madagascar in the late Cretaceous (ca. 90 Ma). This period of isolation came to an end in the Paleogene (ca. 50-55 Ma), when the

northern part of the Indian subcontinent collided with Eurasia, causing the uplift of the Himalayas, and allowing for biotic exchange between these two regions (reviewed in Ali and Aitchison 2008). The formation of the peninsular Indian Deccan Traps flood basalts, derived from a period of intense volcanism around the time of the Cretaceous-Tertiary boundary (66 Ma), is considered to have had massive climatic and environmental effects, causing large scale extinctions (Courtillot et al., 1986; Officer et al., 1987). The then unoccupied niches provided opportunity for in-situ diversification of some of the original Gondwanan organisms that survived decimation (Datta-Roy and Praveen Karanth, 2009) as well as for invasions from the Eurasian continent. Sri Lanka is a shelf island, separated from Southern India by the Palk Strait, with a sea-floor corridor at least 20m deep, which has been exposed for parts of the Quaternary at times when sea-level was lower (2.59 Ma to 11.7 ka) (Ali 2018 and references therein). Despite the fact that this corridor has permitted organism movement between the two regions, there is a high level of island endemism (Bossuyt et al., 2004), so that prolonged environmental factors might have restricted organismal dispersal across any land bridges that arose between the two regions (Ali, 2018). The Western Ghats and Sri Lanka make for an interesting biogeographic region, with some herpetofauna endemics having high levels of diversity (Van Bocxlaer et al., 2009; Datta-Roy et al., 2012; Meegaskumbura et al., 2019). However, thus far very few studies have been conducted to understand how the diversity in this hotspot was assembled in time and space.

Uropeltids (Serpentes: Uropeltidae), commonly known as shieldtails, are a family of small fossorial snakes, endemic to Sri Lanka and peninsular India. Despite having a relatively small geographic range and all members of the group being burrowers in relatively moist soils, this is a very speciose clade, with eight genera and 56 species currently recognised (Uetz and Hošek, 2019), and a higher number of Operational Taxonomic Units (OTUs) have been uncovered in molecular phylogenetic analyses of the group (Chapter 3 of this thesis). Uropeltidae is a poorly understood group, partly due to their secretive habits and confusing taxonomic history. Uropeltids have features associated with adaptation to a fossorial lifestyle – a relatively conserved body plan, elongated and limbless, and a small, reinforced skull for head first burrowing. Different head shapes – rounded or keeled snouts –

are likely associated with distinct microhabitat use, diet and/or burrowing styles, as is known to occur in other, better studied fossorial squamates such as amphisbaenians (Kearney and Stuart, 2004). The most distinctive and unusual characteristic in uropeltid snakes is their tail structures that have given them their common name. Some species have a blunt or even an obliquely flattened tail covered with heavily keeled scales, and sometimes tipped with two short, stout spines, or a domed rough cap (Smith, 1943; Gans, 1976; Pyron et al., 2016). The function of these structures is not entirely understood but it has been hypothesised they might be used to aggregate a soil plug to avoid predation in burrows, or head mimicry by directing predators towards their reinforced tails while digging a burrow with their heads and trying to escape (Gans, 1976). Even though uropeltids superficially seem to exhibit high levels of morphological diversity and have some highly distinct phenotypic features (e.g., pointed or broad heads; simple or elaborate tails), their morphology has never been studied using a quantitative comparative approach. Thus, it is not clearly understood how morphological diversity in uropeltids is assembled across clades, or in space and time. The quantification and analysis of morphological diversity in the context of a phylogeny will allow for a better understanding of the evolutionary history of Uropeltidae.

4.1.1 Aims

Generate a quantitative dataset of ecologically relevant morphological characters for the family Uropeltidae, for a comprehensive taxonomic sampling with specimens from natural history collections. Using a densely sampled calibrated phylogeny from Chapter 3, analyse phylomorphospace occupation of uropeltid species and identify the major axes of external phenotypic variation. Determine patterns of trait diversification through time and test hypothesis of adaptive radiation via detection of early bursts.

4.1.2 Hypotheses

i) Uropeltidae, a clade of soil burrowers, established their phenotypic diversity through adaptive radiation (a process not generally identified among burrowing taxa); (ii) Sri Lankan *Rhinophis* evolved via adaptive radiation after dispersing into

uropeltid-free ecospace from India; (iii) Sri Lankan and Indian uropeltids occupy different areas of morphospace; iv) morphospace occupation is largely defined by higher clade (generic) membership.

4.2 Materials and methods

All analyses were conducted in R v3.6.0 (R Development Core Team, 2019), with functions used detailed below.

4.2.1 Data collection

A total of 975 type and historical Uropeltidae specimens were examined from natural history collections (Appendix Table 4-1) through loans and visits to collections. Specimens included in the analyses covered all of the genera and almost all of the currently recognised species (Uetz and Hošek, 2019), representing a total of 83 putatively species-level taxonomic units. Data were taken on average for 11.8 specimens per species, with sample sizes varying between one and 43. For 20 species less than five specimens were available in museum collections. For example, *Rhinophis fergusonianus* is known only from the type specimen.

Trait selection relied on aspects of the morphology that were thought to be ecologically or functionally relevant. This is challenging because little is known about uropeltid biology and ecology, especially at the species level. Most of what is known is that uropeltids burrow in soil and eat invertebrates, especially worms (Rajendran, 1985). In other fossorial squamates, different head shapes are associated with distinct burrowing behaviours (e.g. amphisbaenians - Kearney and Stuart, 2004). Mouth width limits prey size, especially in non-macrostomatan snakes (King, 2002). In snakes, as in other vertebrates, eye size is related with behavioural ecology and may reflect adaptation to environment (Walls, 1942; Liu et al., 2012), with fossorial species tending to have smaller eyes due to functional degeneration (Underwood, 1970). Relative body girth has been shown to be a trait correlated with trophic specialisation in some snakes (Sherratt et al., 2018). Vertebral number is also an ecologically relevant feature in vertebrates, with a high number of vertebrae possibly being associated with body elongation and increased flexibility along the spine (Claverie and Wainwright, 2014; Sherratt et al., 2019), which could be hypothesised

to be important for burrowing ability in uropeltids. The rough tail scute in uropeltids has been hypothesised to increase the adhesion of soil particles, aiding to form a mud plug in tunnels when burrowing in the soil (Gans, 1976). Twenty-two linear measurements of features of the body, head and tail were taken from museum specimens to capture shape variation, as described in Appendix Table 4-2 (Figure 4-1): total length (TL), midbody circumference (MbC), tail circumference (tC), midbody width (MbW), tail width (tW), tail length (tL), terminal scute base length (SL), terminal scute base width (SW), head length 1 (HL-SL), head length 2 (HL-P), head height (HH1.P), head width (HW), mouth width (IL-IL), lower jaw length 1 (IL-M), lower jaw length 2 (IL-ST), eye diameter (E), eye-naris distance (E-N), eye-snout distance (E-ST), eye-supralabial distance (E-SL), partial anterior head height (RH), inter-ocular distance (E-E), internarial distance (N-N). TL, MbC and tC were measured to the nearest 1mm. TL was measured with a measuring tape, and circumferences were measured by wrapping a piece of thin thread around the specimen and then measuring its length against a measuring tape. All other linear measurements were taken with a digital calliper to the nearest 0.1mm under a dissection microscope. Bilateral measures were taken on the right side of the specimen, unless that side was damaged. Additional metric characters were calculated based on some of the raw measurements. Snout to vent length (SVL) was obtained by subtracting tail length (tL) from total length (TL). TL is quicker to measure than SVL because there is no need to locate the vent. Rostrum projection (RP) was calculated by subtracting lower jaw length 1 from lower jaw length 2. The distance by which the rostrum projects in front of the mouth is very short in many uropeltids, and so if measured directly would likely be associated with a relatively larger measurement error.

Two meristic characters were taken, useful both for species identification and in some cases to differentiate between males and females (see below): number of ventral (V) and subcaudal (SC) scales. Ventral scale counts were recorded following Gower & Ablett (2006). The number of subcaudal scales was recorded for both the right and left side on the tail, and the mean was used in the analyses. In most snakes, including uropeltids, there is a direct correspondence between the number of ventral scale counts and number of vertebrae (Alexander and Gans,

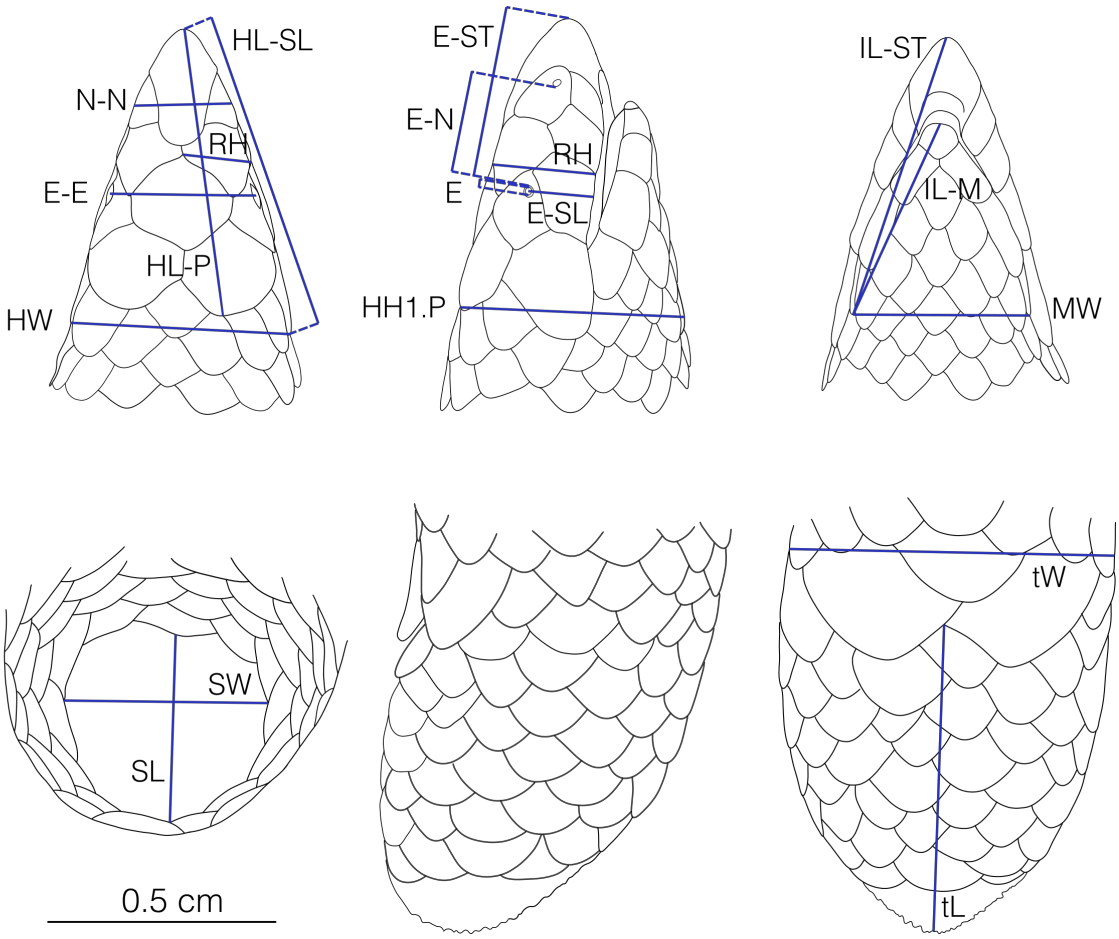


Figure 4-1 Linear measurements taken around the head (top) and tail (bottom) of uropeltid specimens. Dorsal view on the left side, lateral view in the centre, and ventral view on the right side. Character description in Appendix Table 4-2. Illustration of a *Rhinophis lineatus* specimen (CAS 226024) (based on photo by NHM photo unit; Gower and Maduwage (2011)).

1966). Therefore, in the absence of x-ray images, the number of external ventral scales was used as a proxy for number of body segments.

Data were collected for both male and female specimens, not only to increase the number of specimens per species, but because there is little information available in the literature regarding sexual dimorphism in uropeltids (Jins et al., 2018). In snakes, it is common to determine sex by observing the presence or absence of hemipenes through a small midventral incision at the base of the tail, but because uropeltids have short tails and small hemipenes in males, this method is often not appropriate. Thus, various additional methods were mostly used to help

determine sex. The presence of hemipenes was confirmed in a few specimens using X-ray micro-computed tomography scans of tails, where ornamentation structures (typically spines) were mineralised. In some cases, sex was determined through small, approximately midventral incisions in the body wall to determine the presence of eggs or oviducts for females, and epididymis for males. To avoid dissecting all specimens, sex was also inferred by examining the number of ventral scales, subcaudals and relative tail length (tL/SVL) for each species, where these had a bimodal distribution (Wall, 1919; Guibé, 1948; Constable, 1949; Gower et al., 2008; Jins et al., 2018). Where there is sexual dimorphism, females tend to have higher ventral counts or (more frequently) relatively shorter tails and fewer subcaudals. Specimens with relatively longer tails and more subcaudals were therefore identified as male. For some species, such as in *Melanophidium* spp. and *Rhinophis oxyrhynchus,* these characters did not show a clearly bimodal distribution, and therefore if the specimens were not dissected, sex was scored as "?". The dataset comprised 367 females, 338 males and 270 unassigned specimens. No other characters are known to be sexually dimorphic in uropeltids, and tail length was not included in multivariate analyses to avoid detecting morphological differences due to sexual dimorphism. Sexes were pooled together in the analyses.

Data were taken for specimens of a wide range of sizes (and, possibly, maturity) within some species. Other than the presence of internal organs such as yolky ova, foetuses and/or oviducts in females or epididymis in males, with thickened walls, insufficient information is available for uropeltids to be able to distinguish between sexually immature 'juveniles' and sexually mature 'adults' of similar sizes. Other investigations, such as histology of testes, were beyond the scope of this project. It is likely that for some species sexually immature specimens were included in the dataset. As mentioned above, some species are only known from relatively small sample sizes, and where these are all made up of relatively small specimens, there is no way of knowing whether that happens to be a species with a short total length or a biased sample of juvenile specimens. To avoid including smaller individuals in the analyses (which may or may not be juveniles), outliers in

the lower quartile for each species were checked by visualising boxplots, and a total of 20 specimens were removed from the dataset.

4.2.2 Molecular phylogeny

To analyse the morphological data within a phylogenetic framework, a multilocus calibrated tree generated in Chapter 3 was employed in downstream analyses. The phylogeny included OTUs based on single locus species delimitation methods, which tend to oversplit species with singletons (see discussion in Chapter 3). Because it was not possible to assign morphological groups for all tips, closely related OTUs that might represent species complexes in the tree were pruned to only include one tip per species included in the morphological dataset, using the package ape v5.3 (Paradis and Schliep, 2019) in R. Species that were in the morphological dataset but not included in the molecular phylogeny were added to the tree based on their morphology. *Rhinophis* cf. *zigzag* was added as sister taxa to *R. zigzag*, *Rhinophis* sp. nov. 3 added as sister to *R.* cf. *homolepis*, *U. beddomii* added as sister to *U*. cf. *beddomii*, *U.* cf. *madurensis* added as sister to *U. madurensis*, *U.* cf. *ocellata* added as sister to *U. ocellata*, *U. dupeni* added as sister to *U.* cf. *dupeni*, *U. brevis* added as sister to *U.* cf. *brevis*, *U.* cf. *petersi* added as sister to *U. petersi*. *Rhinophis punctatus* and *R. porrectus* superficially resemble each other and are hypothesised to be closely related to *R. dorsimaculatus* (Gower and Wickramasinghe, 2016), and so were added to the *R. dorsimaculatus* terminal branch. *Uropeltis macrolepis mahableshwarensis* (debatably a species rather than subspecies) was added to the node splitting *U. phipsonii* and *U. macrolepis*. Finally, *U. dindigalensis* was added as sister to *U. woodmasoni* + *U. broughami*, the only other two *Uropeltis* species with 19 midbody scale rows (all other *Uropeltis* species have 17). For tips that were added as sisters to particular taxa, new terminal branches were added halfway along the internal branch subtending its sister taxon (whether a single species or a clade). Polytomies in the tree formed by adding new tips to clades were randomly resolved using apes's function multi2di() by adding branches of length zero. Species in the morphological dataset for which it was not possible to confidently assign a position onto the tree were excluded from further analyses. This excluded six species (*R. fergusonianus*, *Rhinophis* sp.

(Bambarabotuwa), *Rhinophis* sp. (Palabaddala), *U. ceylanica*, *U*. cf. *ceylanica*, and *U. shorttii*), such that the final dataset of taxa in the phylogeny consisted of 77 species. The topology of the tree used in analyses is provided in Appendix Figure 4-1.

4.2.3 Statistical analyses for user measurement error

To test for measurement errors, 22 specimens were measured twice. For this subset of samples, raw variables were tested for normality using the Shapiro-Wilk test (R function shapiro.test()). Because residuals for all variables were not under a normal distribution, the non-parametric test Wilcoxon paired-sample test (wilcox.test()) was used to calculate for differences in the means between the two groups of measurements, with results showing that means were not significantly different ($p>0.05$).

4.2.4 Missing data

In most cases, empty data cells in the raw data were not a problem because data for the same character for other specimens of the same species still allowed species means to be calculated. In one case an estimated rather than measured value for a single character (eye diameter) was employed. This was for *R*. cf. *blythii*, which is known from only a single specimen (WHT5209). It was not possible to measure eye diameter confidently because the animal was preserved close to skin shedding, such that the eye was not clearly visible though the position and an approximate idea of the maximum eye size could be determined from the bulge of the scale overlying the eye. Eye size and head shape and escalation did not appear to be substantially different from specimens of *R. blythii*. For the 21 specimens of *R. blythii* for which both head length (HL) and eye diameter (E) were measured, HL is 10.3–17.33 times E (mean = 13.33). Thus, E was estimated from HL (7.6 mm) in WHT5209 as 0.57 mm based on the same average proportion occurring in *R. blythii*. From photographs, the approximate likely eye size of WHT5209 based on the overlying scale bulge is estimated at 0.6–0.7 mm, so an estimated eye size of 0.6 was entered into the data set for multivariate analysis. This option was taken to

avoid deleting an entire species (*R.* cf. *blythii*) or character (E) from the data set because of a single empty cell.

4.2.5 Size correction

Data were log-transformed and species means were calculated for each variable (R function aggregate()). Size-free variables were obtained by conducting a phylogenetic regression, or phylogenetic generalised least squares (PGLS), which allows the non-independence of residuals due to the common shared ancestry of species to be accounted for (Felsenstein, 1985; Mundry, 2014). Phylogenetic size correction of traits was conducted by fitting a phylogenetic regression for each log-transformed variable against logSVL, used as a measure of body size. PGLS was implemented in the R package phytools (Revell, 2012) using the phyl.resid() function (Revell, 2009, 2010), with residuals being computed with simultaneous estimation of their phylogenetic signal using Pagel's λ (Pagel, 1999) through maximum likelihood. This option has been shown to perform better than if regression is executed without phylogenetic correction or with the assumption of evolution by Brownian Motion (BM) prior to assessing the phylogenetic signal of the residuals (Revell, 2010). λ values were > 0.9 for the residuals of all traits.

4.2.6 Multivariate statistics and phylogenetic comparative analyses

To quantify body shape variation among uropeltids, linear measurements were employed in principal components analyses (PCA), which allow the visualisation of species morphospace occupation (Ricklefs and Miles, 1994). Multivariate methods like PCA are commonly used to reduce the dimensionality of a dataset with multiple continuous traits. A subset of axes that explain most of the variation are extracted and treated as univariate shape data, before analysing the data with phylogenetic comparative methods (PCMs).

Because PCAs assume samples' independence, recently developed methods allow to conduct phylogenetic PCAs (pPCA) that account for the shared evolutionary history of the species and subsequent non-independence of the samples (Revell, 2009; Polly et al., 2013). While pPCA scores can in theory be used in subsequent PCMs as shape variables, they are correlated with each other and

across axes, which is not the case with standard principal components (PC) (Polly et al., 2013). Also, pPC scores are not phylogenetically independent (Revell, 2009; Polly et al., 2013; Uyeda et al., 2015), and if applied to PCMs they still require model selection and should be analysed with phylogenetic methods (Revell, 2009; Polly et al., 2013; Uyeda et al., 2015). When fitting evolutionary models to pPC scores independence of the axes is assumed, which then is not the case (Uyeda et al., 2015). Applying PCMs on (p)PC axes may lead to a biased inference of evolutionary models observed for the individual axes towards particular patterns, due to the method of calculating the PCA, and results are often difficult to interpret (Revell, 2009; Monteiro, 2013; Polly et al., 2013; Uyeda et al., 2015). Because of these issues, for comparative purposes both phylogenetic and standard PCAs were conducted to understand morphospace occupation and the major axes of shape variation in the dataset. Then, a subset of standard PC scores was used in subsequent comparative analyses, along with individual traits residuals to understand patterns of phenotypic diversification.

A correlation matrix of the corrected residuals was used in a non-phylogenetic PCA (R function prcomp()), as well on a pPCA, implemented in the R package phytools (phyl.pca()), to identify the major axes of variation while accounting for the effect of phylogenetic non-independence of species (Revell, 2009; Polly et al., 2013). Morphospace occupation was visualised in bivariate plots for different PC axes, assessing the loadings to identify the variables that explain most of the variation along each axis. Phylomorphospace – the phylogeny projected onto bivariate morphospace – was plotted to allow the visualisation of shape differences in a phylogenetic perspective (phylomorphospace() function in phytools) (Sidlauskas, 2008; Revell, 2012) for both the PCA and pPCA plots. This method estimates ancestral states of the internal nodes through a maximum likelihood approach (Revell, 2012). To reduce the dimensionality of the data, the scores from a subset of (p)PC axes accounting for 95% of the shape variation were extracted and used in downstream analyses.

4.2.7 Phylogenetic signal

In the presence of phylogenetic signal, more closely related species tend to have more similar traits, produce more similar residuals from the phylogenetic regression, and occupy similar areas of morphospace (Blomberg and Garland, 2002; Blomberg et al., 2003; Symonds and Blomberg, 2014). To test the influence of phylogeny on shape, phylogenetic signal was estimated for size-corrected traits from PGLS and (p)PC scores that explained 95% of the variation (for both the phylogenetic corrected and standard PCAs), calculating Pagel's λ (Pagel, 1999) and Blomberg's K (Blomberg et al., 2003) statistics, employing the phylosig() function in the R package phytools. Additionally, a multivariate version of Blomberg's K (K_{mult}, Adams 2014) was used to test for phylogenetic signal simultaneously across (p)PC axes scores for axes one to five (together explaining 95% of the variation), and one to 18 using geomorph 3.1.2 (Adams et al., 2019) physignal() function. A λ value closer to zero is indicative of no phylogenetic signal with traits being less similar among closely related species than expected, whereas λ values closer to one indicate an increasingly strong phylogenetic signal under BM (Pagel, 1999). Blomberg's K also tests phylogenetic signal of a trait compared to the expectation for the variable to evolve under BM. A value of K below one means that there is less phylogenetic signal and traits are more variable than expected under BM. A K value close to one indicates that a trait has phylogenetic signal as expected under BM, while a value above one suggests that closely related species are more similar than expected under a BM model of trait evolution (Blomberg et al., 2003).

4.2.8 Disparity through time

To identify patterns of phenotypic diversification over time, disparity through time (DTT; Harmon et al. 2003) plots were calculated for standard PC scores for axes one to five, and for selected size corrected traits. Due to a high rate of false positives that tend to occur in the original GEIGER's method (Harmon et al., 2008), DTT curves were computed using the rank envelope test (Murrell, 2018). The DTT method allows assessments of whether trait disparity between and within clades is higher or lower than expected under a null model of BM. In the rank envelope test, the DTT curve has a global rank value that summarises how extreme that curve is

in comparison to all other curves, by assessing its maximum deviation from the median curve (Murrell, 2018). Visually, if the DTT curve falls outside the 95% confidence envelope, then the null hypothesis is rejected and the curve is significantly different to a BM distribution. The rank envelope test also outputs a global measure of the most extreme disparity value, with the resulting p-value informing whether the level of disparity is lower or higher than under the null hypothesis of traits evolving under BM. Analyses were conducted with 5000 simulations. R code available at https://www.researchgate.net/publication/333827660_generalmulti-rankDTTR.

4.2.9 Models of evolution

To determine the evolutionary models that best explain the patterns of trait evolution in the data, different models were fitted to individual PC scores (axes 1-5, which together explain 95% of the variation) and to residuals of selected single traits, using the R package GEIGER v.2.0 (Harmon et al., 2008; Pennell et al., 2014) fitContinuous() function, which applies a maximum likelihood method, identifying the best fit model by assessing Akaike information criterion corrected for small sample sizes (AICc) scores. The models assessed were the following: BM assumes trait similarity due to common ancestry under a random walk, with changes accumulating proportionally to time (Felsenstein, 1988); early burst (EB) is characterised by an early period of rapid trait evolution, with a slowdown in rates over time, often associated with adaptive radiation (Harmon et al., 2010); Ornstein–Uhlenbeck (OU) models the evolution of phenotypic traits under a specific case of BM, where traits evolve under a random walk with a strong stabilising selection around a selective optimum, or multiple optima (Hansen, 1997; Butler and King, 2004). Best model fit was estimated with ΔAICc and AICc weights (AICw). ΔAICc is the difference between each model and the best model, so that the best model has a Δ value of zero.

4.2.10 Node height test

To infer rates of trait evolution through time, node height tests were conducted with GEIGER's nh.test() function for the individual traits residuals. This test calculates the

absolute value of phylogenetic independent contrasts of a trait and compares those to the contrasts of the height (distance from root) of the nodes expected under a BM model of evolution. A significant negative relationship between absolute rate contrasts and node height is indicative of a slowdown in rates of trait evolution, which is consistent with an early burst or niche-filling mode of trait evolution (Freckleton and Harvey, 2006).

4.3 Results

4.3.1 Morphospace occupation

The first two principal component (PC) axes of Uropeltidae shape variation are depicted in Figure 4-2, and phylomorphospace occupation across the first five PC axes is shown in Figure 4-3 and Appendix Figure 4-2 for both standard and phylogenetic PCAs, respectively. The variance explained by each character for all (p)PCs is in Appendix Table 4-3 and Appendix Table 4-4. Results for PCA and pPCA are very similar across PC1 and PC2 axes, with regards to species positions across the plots and with regards to variable loadings explaining the variation along those axes. Only results for PCA are further detailed here.

The first five axes account for 95.2% of the variation in the standard PCA, and these were retained for further comparative analyses. Most of the overall shape variation is explained by PC1 (68.6%), which is mostly correlated with trait elongation. Almost all variables have high loadings towards negative values of PC1, with species in negative areas of this axis displaying larger features, such as having proportionally larger heads and wider bodies. PC1 explained some of the intrageneric variation, with *Rhinophis* and *Uropeltis*, the most speciose clades, occupying the largest areas of morphospace, by having the widest range of values along this axis. *Rhinophis* exhibits the greatest variation along PC1, but this is largely attributable to the extreme shape of a single species, the largest known uropeltid *R. saffragamus*. *Rhinophis saffragamus* has the lowest score on PC1, and this species has a wide body, relatively large head, and a large but flat tail scute. In contrast, *R. punctatus* and *R. porrectus*, which have the highest scores on this axis, have much more slender bodies, with minute heads and enlarged, conical tail scutes.

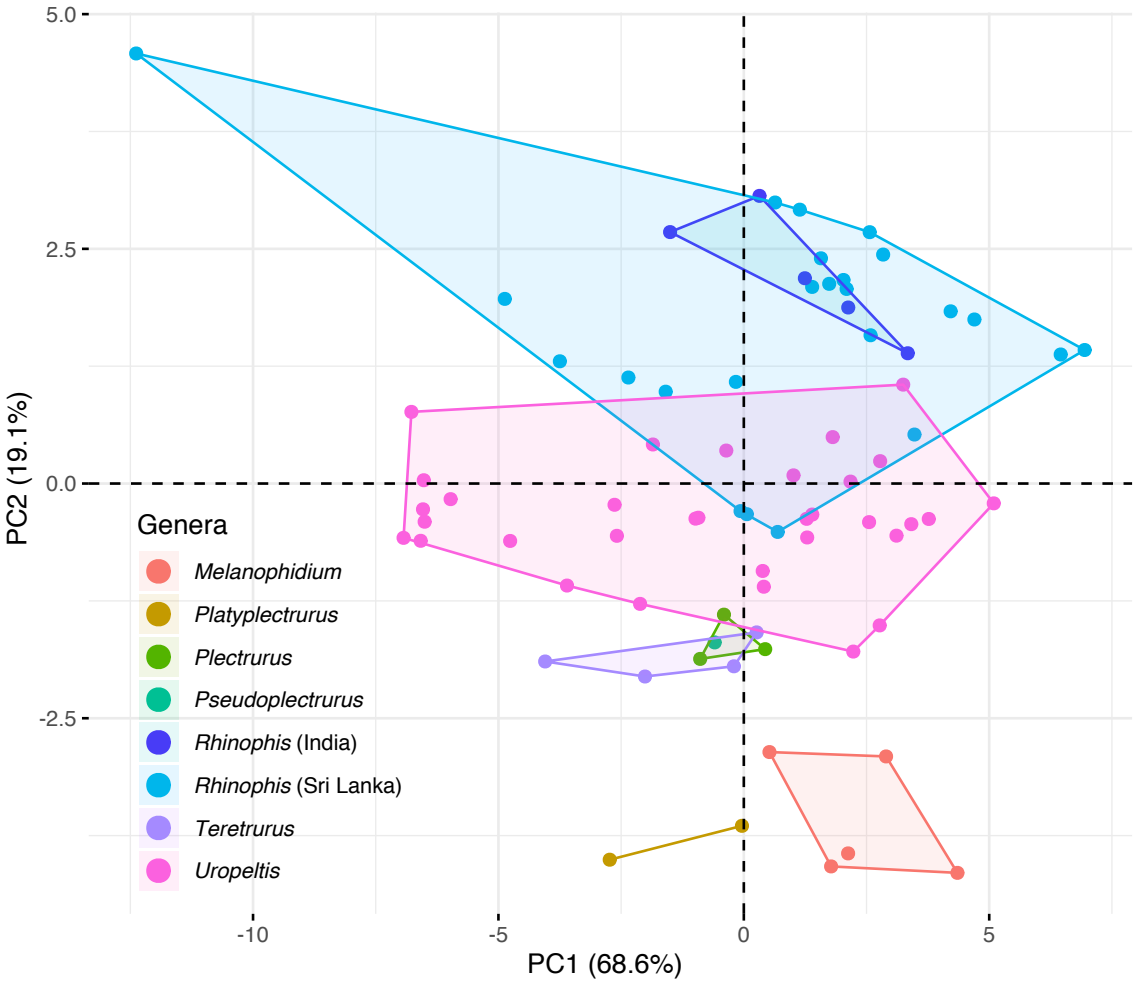


Figure 4-2 Morphospace occupation (PC1 vs. PC2) of Uropeltidae based on species means, coloured by genus, with genera bound by convex hulls. For *Rhinophis*, different tones of blue distinguish Indian (dark blue) and Sri Lankan (light blue) species. The light blue circle on the far left represents *R. saffragamus*.

PC2 explains 19.1% of the shape variation and separates most genera, with some exceptions of overlap. Most of the variation along PC2 is correlated with tail scute dimensions and rostrum projection, with *Rhinophis* species occupying positive areas of PC2 having larger tail shields and more prominent, pointed snouts. At the other end of that axis, *Melanophidium* and *Platyplectrurus* species have blunt, shorter snouts and tails with typically small and/or less radically modified terminal scutes. A clade of Sri Lankan *Rhinophis* that have smaller terminal scutes and less prominent snouts, occupy the same area of the PC1 vs PC2 morphospace as some *Uropeltis* species. Likewise, a few *Uropeltis* species with a more prominent and pointed, *Rhinophis*-like snout, occupy areas of the plot with higher PC2 scores,

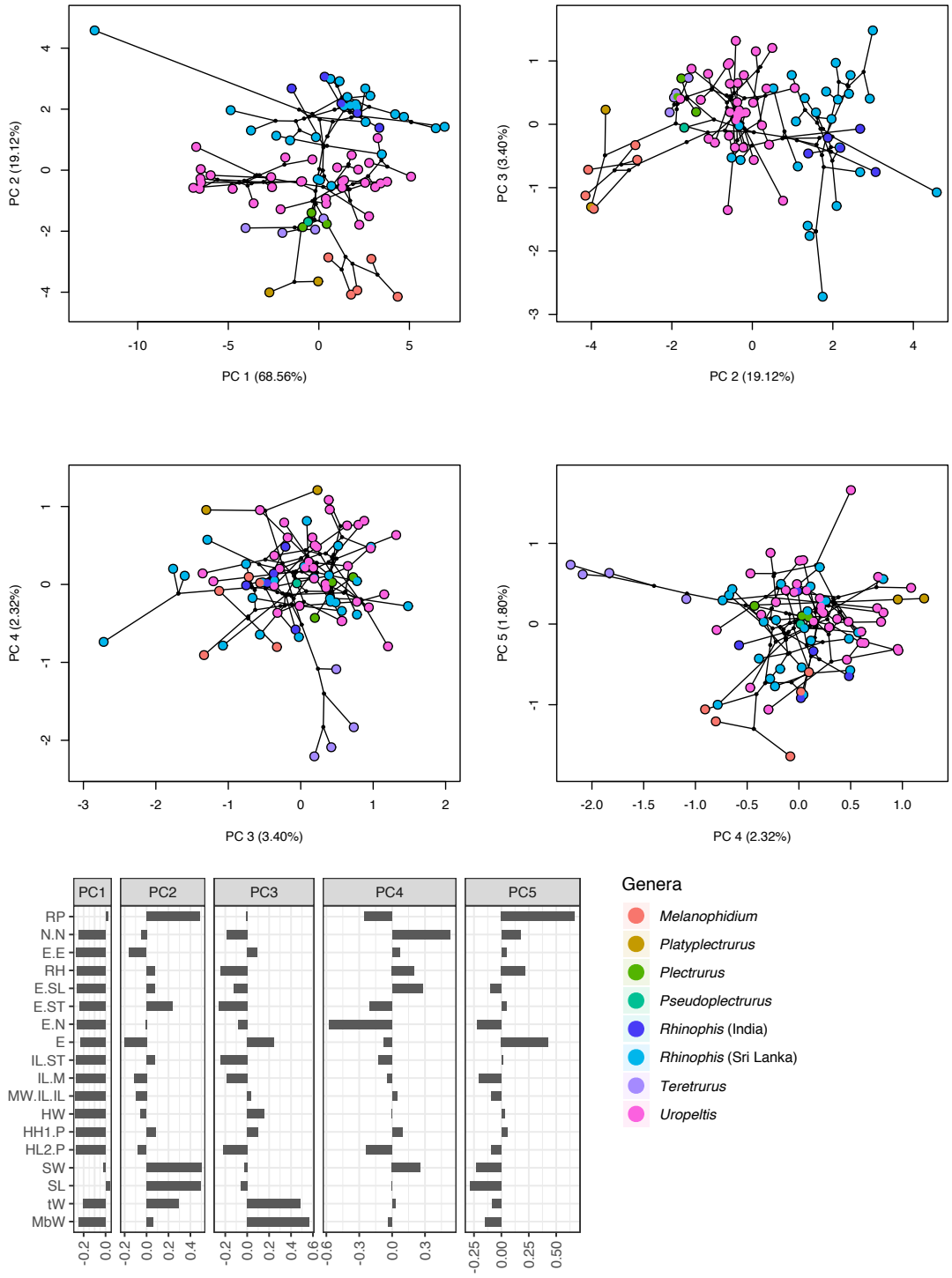


Figure 4-3 Phylomorphospace occupation of the standard PCA scores (PC1 vs. PC2, PC2 vs. PC3, PC3 vs. PC4, PC4 vs. PC5), with species coloured according to genus. Graphical representation of loadings for axes 1 to 5 (bar plots created in R using ggplot2 (Wickham, 2009)).

where mostly *Rhinophis* occur. There is also overlap between *Teretrurus* and *Pseudoplectrurus* + *Plectrurus*, in the PC1 vs PC2 morphospace.

Regarding geographical areas, *Rhinophis* is the only genus distributed in both South India and Sri Lanka. All other genera only occur in India. The Indian *Rhinophis* species (dark blue coloured circles in the plots) occupy a very distinct area of morphospace from other Indian uropeltids. This is mostly explained by their enlarged tail scute, a defining characteristic of the genus (with a few exceptions). However, when the five sampled species of Indian *Rhinophis* are compared to the 24 sampled Sri Lankan *Rhinophis*, the continental species occupy a considerably smaller area of morphospace, which nests within the morphospace occupied by their Sri Lankan congeners. The insular species have diverged to occupy by far the largest area of morphospace, which partly also overlaps with the continental *Uropeltis*, indicating some convergence of body forms with this genus.

4.3.2 Phylogenetic signal

Overall phylogenetic signal in the multivariate data, calculated for multiple axes simultaneously, is not very strong for PC axes 1 to 5 (K_{mult}=0.7, p=0.001) or axes 1 to 18 (K_{mult}=0.68, p=0.001) under what is expected under a BM model of evolution. For individual PC axes, significant phylogenetic signal was detected only in PC2, (K=3.2, p-value < 0.05; λ=1.01, p-value < 0.05). Along PC2 there is a clear separation between most of the genera (Figure 4-2). For PC axes 1 and 3 to 5, there is little phylogenetic signal in multivariate shape (Appendix Table 4-5). Regarding residuals of individual variables, strong phylogenetic signal was detected for tail scute dimensions (SL: K=3.39, p-value < 0.05; λ=1.01, p-value < 0.05; SW: K=3.08, p-value < 0.05; λ=1.01, p-value < 0.05) and rostrum projection (RP: K=1.68 p-value < 0.05; λ=0.97, p-value < 0.05) (Appendix Table 4-6), with K values > 1 indicating that traits are more similar than expected under BM. These variables explain most of the variation along PC2.

4.3.4 Phenotypic disparity through time

Application of the rank envelope method identified the PC1 curve to closely follow the null model of BM evolution through most of the plot, demonstrating a lack of

high or low morphological disparity through time for this axis (Figure 4-4). The PC2 line falls outside the 95% confidence envelope for a single time point, with the data curve being close to the lower interval curve most of the time, showing some indication of an early evolutionary burst in shape disparity and subsequent decline in the rate of multivariate evolution. For PC2, in that time point there is a higher amount of between clade trait variation than expected under the null model. The rank envelope test finds support for two late bursts in PC3 disparity, with higher within clade disparity at those time periods than expected under BM. The DTT plot shows that PC4 and PC5 disparity does not deviate significantly from that expected under BM evolution, except for more recent increases in disparity within clades. The global rank p-value was significant (0.0002<p< 0.007).

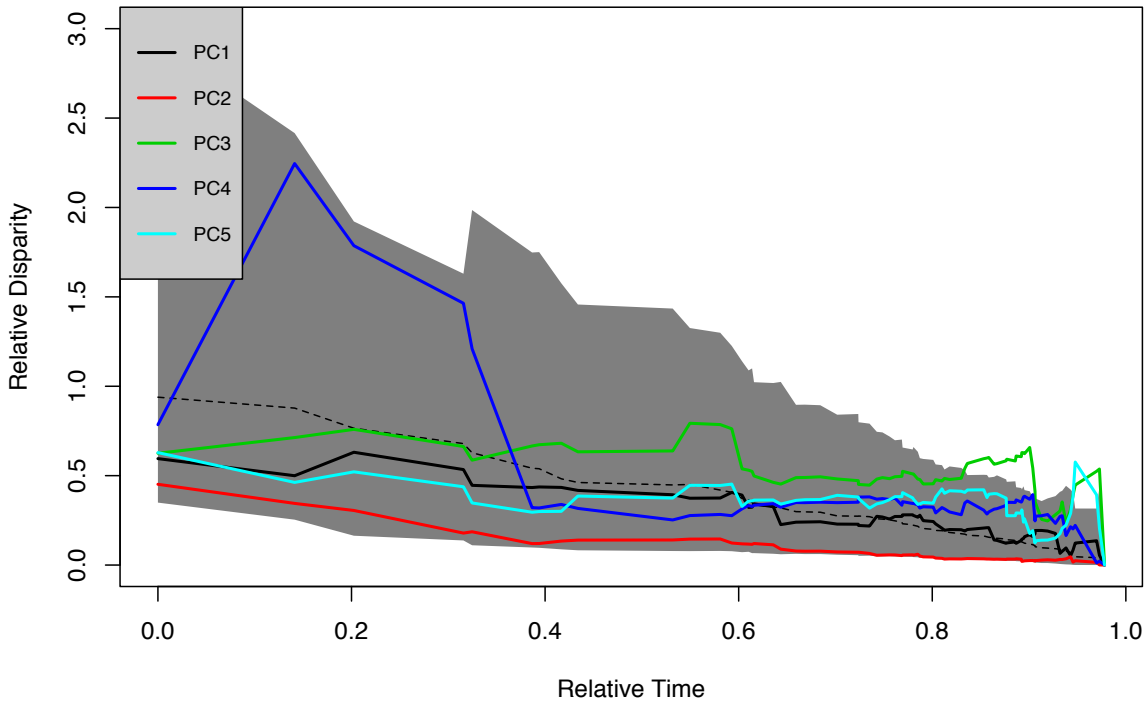


Figure 4-4 DTT plot with curves for standard PC1-5 scores, each axis curve represented by a solid line with a different colour. Dashed line represents the median curve representing the null model under BM evolution based on 5000 simulations. The 95% confidence envelope is represented by the grey shaded area.

Fitting models of evolution in these axes further supports these patterns of morphological diversification (Table 4-1). For PC1 the best fitting model is OU, but only having 50% of the AICc weight, with BM having 38% and EB 12,7%. While BM has less weight, it cannot be ruled out as a significantly poorer fit than OU. Furthermore, the pattern of disparity for the PC1 DTT curve is more consistent with a BM model. For PC2, Akaike weights provide support for EB, while for PCs 3-5, OU is the best fitting model.

Table 4-1 AICc scores and weights for BM, OU and EB models of evolution, fitted to PC1-5 scores.

PC axis	Model	log-likelihood	AICc	deltaAICc	weight AICc
PC1	BM	-187.29614	378.754446	0.5617747	0.3755506
	OU	-185.93195	378.192671	0	0.4973433
	EB	-187.29621	380.921189	2.728518	0.127106
PC2	BM	-92.38167	188.925503	7.508829	0.02270267
	OU	-92.38167	191.092108	9.675434	0.00768431
	EB	**-87.543953**	**181.416674**	**0**	**0.96961303**
PC3	BM	-89.517149	183.196461	11.55584	0.00308238
	OU	**-82.655928**	**171.640623**	**0**	**0.99587448**
	EB	-89.517312	185.363392	13.72277	0.00104314
PC4	BM	-62.118339	128.39884	1.4657	0.29244508
	OU	**-60.302187**	**126.93314**	**0**	**0.60857898**
	EB	-62.118436	130.56564	3.6325	0.09897593
PC5	BM	-59.913995	123.990152	4.562746	0.08985901
	OU	**-56.549319**	**119.427406**	**0**	**0.87972998**
	EB	-59.91413	126.157026	6.729621	0.03041101

DTT analyses showed different patterns of morphological evolution among individual traits (Figure 4-5 and Appendix Figure 4-3). The tail scute dimensions (SW and SL) were found to have disparity values significantly different to those expected under BM, with the curves for these two traits falling below the rank envelope for long time periods, where disparity within clades is lower than expected (SW p-value=0.004; SL p-value=0.004), which is consistent with an early burst. Midbody width (MbW; p-value=0.003), distance between the eye and lip (E-SL; p-value=0.01), and anterior partial head height (RH; p-value=0.02) were found to have late bursts of diversity, with disparity within clades being higher than expected under

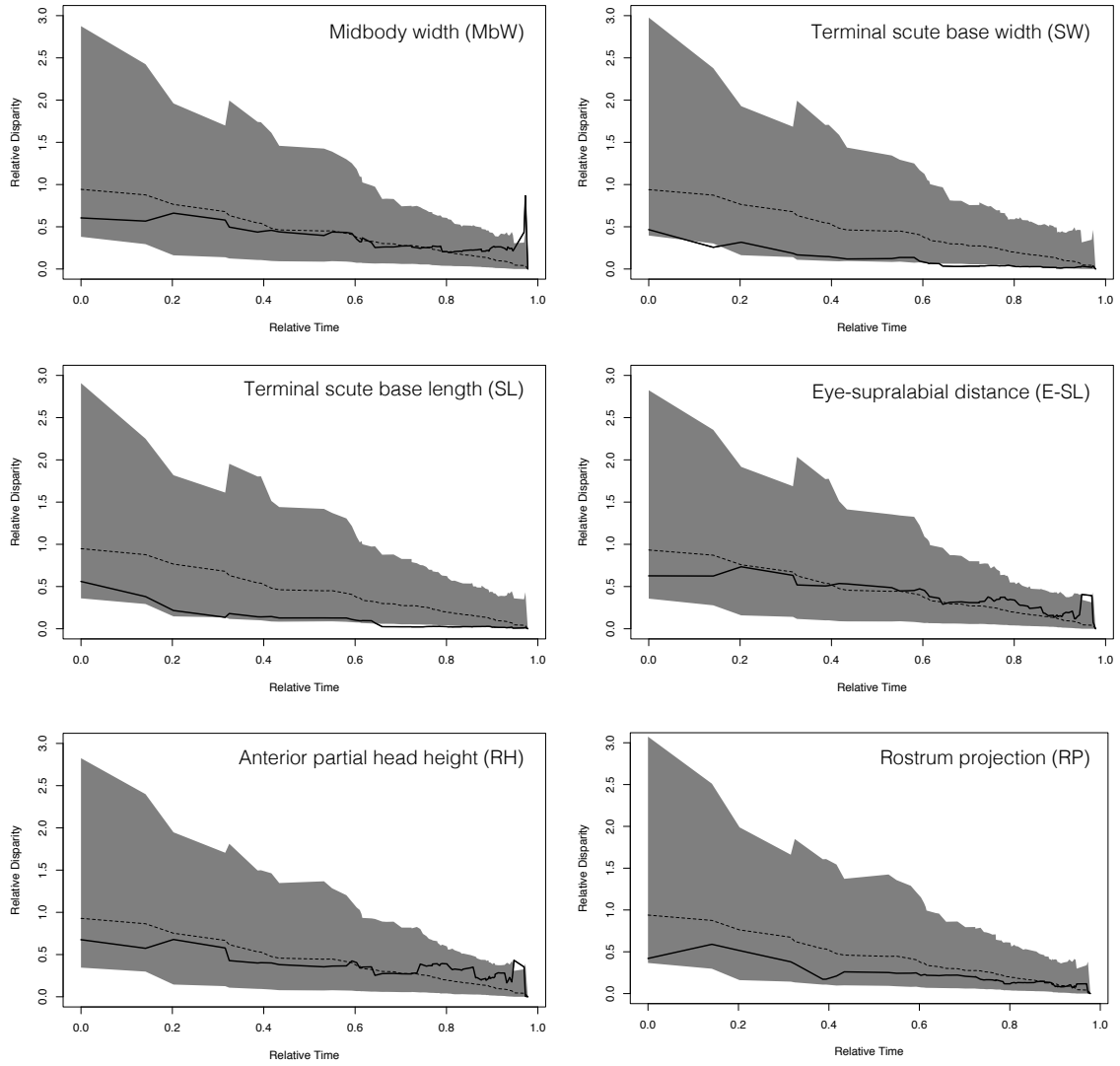


Figure 4-5 DTT plots with curves for a subset of individual traits residuals, represented by the full black curve in each plot. Dashed line represents the median curve representing the null model under BM evolution based on 5000 simulations. Grey shaded area represents the 95% confidence envelope.

BM. All other traits do not deviate in disparity through time from the null expectation under BM (p-values > 0.05). Assessing model fit for individual variables (Appendix Table 4-7), tail scute dimensions (SW and SL) have high support for evolving under a model of EB. Most other variables were found to follow a BM model of evolution, with the exception of midbody width (MbW), distance between eye and lip (E-SL), and anterior partial head height (RH), which followed an OU model of phenotypic evolution. An OU model suggests a stabilising selection of trait evolution, which might drive species to overlap in morphospace around trait optima values.

Nevertheless, for any given trait that significantly deviates from the null model, median disparity is within the 95% envelope of the null model for most of the clade's evolutionary history.

Moreover, the node height test found a significant negative relationship between absolute contrasts for tail traits and node age (SL: estimate = -0.0005 ± 0.0001, t = -3.9, p-value = 0.0002; SW: estimate = -0.0006 ± 0.0002, t = -3.7, p-value = 0.0004) (Figure 4-6), consistent in an early burst in trait evolution near the root. This suggests that rate of trait evolution has decreased with time for these variables, consistent with niche-filling model of trait evolution. For all other variables, results were not statistically significant.

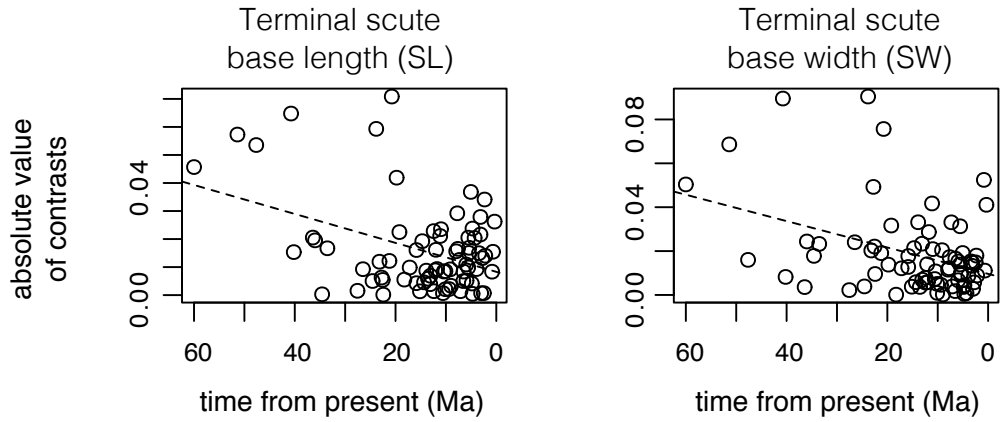


Figure 4-6 Node height test plots showing absolute contrasts for tail scute traits against node height depicting rate of morphological evolution.

4.4 Discussion

This work has generated a large, novel and quantitative dataset of external phenotypic traits thought to be ecologically relevant, for a near-comprehensive sampling of uropeltid species. This is the first dataset of this kind for this family. Analytical results elucidate the large degree and pattern of shape diversity observed across uropeltid genera and species. Disparity analyses suggest that tail scute dimensions seemed to have evolved through an early burst of shape evolution, slowing down as possibly niches became filled. However, there is no evidence for early burst in the evolution of other traits. Later in the radiation there is evidence of

relatively high subclade disparity, which is often interpreted as a signal of evolutionary convergence.

4.4.1 Body shape variation in uropeltids

PCA analyses reveals that most of the variation (95.2%) is explained by the first five PCs, with PC1 and PC2 combined explaining 87.7%. PC1 explains 68.6% of the total shape variation and represents enlargement of most traits. Uropeltid species with proportionally small heads and thin bodies occur towards positive values of PC1, while in negative coordinates along this axis occur species with bigger heads and wider bodies relative to their total length. Sri Lankan *Rhinophis* is the clade with the widest range of values, with *R. saffragamus* constituting an outlier in lower values of PC1. Along this axis, there is overlap between the different genera, suggesting the occurrence of similar forms among different genera. PC2 (19.1%) is correlated mainly with terminal tail scute dimensions and relative size of rostrum. Towards positive values of PC2 occur species with proportionally bigger terminal scutes and elongated rostrums. This axis explains most of the variation between the different genera, with some areas of overlap. Genera are generally well circumscribed and largely differentiated in the PC1 vs. PC2 (phylo)morphospace, based on tail scute and rostrum features (reflected in PC2), with some repeated patterns of variation among genera, which is reflected by overlap along PC1. The most species-rich genera — *Uropeltis* and *Rhinophis* — are the most overall phenotypically derived subclades and occupy the largest areas of the PC1 vs. PC2 (phylo)morphospace. They have fairly similar occupation extents on the plot except for *R. saffragamus* which is an extreme outlier.

Offering a phylogenetic perspective, the phylomorphospace PC1 vs. PC2 plot (Figure 4-3) shows overlap between phylogenetic non-sister groups: i) *Teretrurus* and *Plectrurus* + *Pseudoplectrurus*, and ii) some Sri Lankan *Rhinophis* and Indian *Uropeltis*. The overlap between *Uropeltis* and *Rhinophis* partly reflects data for traits that have led to taxonomic confusion in these genera. Until as recently as 2016, the Sri Lankan species *R. melanogaster* and *R. phillipsi* were part of the genus *Uropeltis*. Taxonomic confusion stemmed from the unusually (for *Rhinophis*) small terminal scute in these species, but molecular evidence led to a change in

generic classification for these species (Pyron et al., 2016). Additionally, the *Uropeltis* taxa in this overlap region include some species whose generic classification has been questioned (Pyron et al., 2016) because they have the *Rhinophis*-like feature of the rostral separating the nasals (e.g. *U. pulneyensis*, *U. grandis*: see Jins et al., 2018). The overlap could indicate that some species in these genera might have converged into similar body shapes, but this ought to be investigated with further tests (e.g. SURFACE (Ingram and Mahler, 2013)).

Rhinophis occupy the most distinct area of (phylo)morphospace, which is largely explained by tail scute dimensions and the most extreme degrees of rostrum projection. Indian *Rhinophis* occupy a small area of morphospace, distinct from all other Indian subclades, but not distinct from Sri Lankan *Rhinophis*. Despite dispersing from a continental land mass to an island and radiating there, there is no indication that island colonisation gave rise to exceptionally different forms (with the exception of a single oddity – *R. saffragamus*, though even that species seems to depart in morphology much more than ecology, as far as it is known). The Sri Lankan *R. safframagus* is phenotypically an outlier, having the most extreme negative value of PC1 and in the most positive value of PC2. This is one of the longest known uropeltid species (the longest *R. saffragamus* specimen recorded for this study was 560 mm, while the mean for all species ranged between 150 and 450 mm (Appendix Table 4-1)). This species has enlarged features relative to their total length (e.g. a proportionally bigger head and wider body), and their tail scutes, while wide and rugose, are flat unlike most *Rhinophis*. No information regarding specialised diet or different use of substrate in this species is available. This species seemingly has a large distribution in the wet, intermediate and dry areas of Sri Lanka (Pyron et al., 2016 and references therein), which is relatively unusual for uropeltids, which typically have small distributions. Additionally, *R. saffragamus* has some other unusual and distinctive taxonomic characteristics. This is one of the few uropeltids (and the only *Rhinophis*) with 19 dorsal scale rows, and it has relatively few ventral scales (samples recorded in this study had between 133 and 154 ventrals) (Appendix Table 4-1). This is the only *Rhinophis* species in which the rostral does not separate the nasal scales, which is one of the main characteristics that distinguishes *Rhinophis* from the other uropeltid genera.

4.4.2 Patterns of phenotypic diversification

Patterns of accumulation of disparity through time of most measured traits of uropeltid morphology, either analysed individually or with multivariate data, follow a BM model of evolution, where trait variance is proportional to the shared evolutionary history of the taxa. However, multivariate PC2 falls outside close to the edge of the confidence envelope, and individual tail scute (but not rostrum) traits showed significant departure from what was expected under BM. Instead, PC2 and tail scute traits are a better fit to an EB model, with average disparity values in tail scute dimensions being lower between subclades than expected under the null assumption of BM. Maximum likelihood model fitting revealed support for the EB model of trait evolution for both of the measured tail scute traits (SW and SL) based on AIC weight, suggesting these traits diversified rapidly early on in the evolutionary history of the clade. Therefore, morphological disparity for tail shape is partitioned among rather than within major sub-clades (Harmon et al., 2003), which is in agreement with the visual aid of the phylomorphospace – in which major (sub)clades are differentiated along the PC2 axis and major subclades share patterns of variation along PC1 (and other PCs). Tail scute dimensions are partly constrained by phylogeny, with residuals of variables displaying strong phylogenetic signal (both with $K > 3$). The ability to interpret evolutionary rates and processes from phylogenetic signal is limited, but increase in phylogenetic signal (where $K > 1$) has been found to be associated with non-adaptive processes (e.g. heterogeneous rate genetic drift), but also with niche shifts (Revell et al., 2008). During an adaptive radiation, niche-filling would be expected, with lineage and phenotypic diversification rates decreasing over time (Schluter, 2000). Also, the node height test showed a significant negative relationship between relative node age and traits residuals contrast values, which indicates the rate of evolution of these traits decreased through time (Slater and Pennell, 2014). The node height test plot (Figure 4-6) confirms that the highest levels of disparity for tail scute traits residuals are towards the base of the tree, between 60 and 40 Ma, during cladogenesis of the major clades, followed by a sharp decrease in absolute value of contrasts. This was followed by another increase at 20 Ma, associated with the formation of subclades (particularly within *Uropeltis* and *Rhinophis*) with a subsequent decrease until recent

times. Thus, although there is not much indication of EB evolution for uropeltid phenotypes overall, there is for uropeltid tail scutes.

DTT plots show high levels of average subclade disparity for midbody width, eye-supralabial distance, and anterior partial head height (Figure 4-5). For these traits, subclades have diversified greatly and sometimes overlap with each other in morphospace. There is strong evidence that these features have followed an OU mode of evolution. Analyses of multivariate trait data found the same patterns for PC3 and PC5 (Figure 4-4), which is indicative of possible convergence of phenotypes across subclades, and is consistent with the phylomorphospace plots (Figure 4-3). Across uropeltids there is a wide range of body widths, and both thinner and wider bodies seem to occur independently in multiple clades. In amphisbaenians, wider bodies have a higher efficiency cost for digging (Navas et al., 2004). This could be indicative that in uropeltids there is perhaps a range of fossorial behaviours, with some species being more or less dedicated burrowers and/or adapted to fossoriality in different soil types.

4.4.3 Evolution of uropeltid tails

The EB pattern observed for tail scute shape is consistent with adaptive radiation sensu Schluter (2000), though EB is not characteristic of all adaptive radiations, being absent for morphological data of several well-studied cases of adaptive radiations (Harmon et al., 2010). Nonetheless, phenotypic density-dependence in uropeltids is not accompanied by a shift in lineage diversification, so that uropeltid tail shape evolution does not seem to be correlated with an increase in species diversity. Results from Chapter 3 LTT plot revealed that uropeltid lineage diversification has been steady, with no declines in diversification rates (γ = 0667, p-value=0.9469), unlike the expectation of an adaptive radiation where rates decline as a result of niche filling (Schluter, 2000; Rabosky and Lovette, 2008). These results could be due to caveats in the analyses (over-sampling species in the diversification analysis could have erased an EB effect; lack of fossil data to study lineage diversification). Still, there are growing amounts of evidence from recent works for a disconnection between phenotypic traits and lineage diversification rates in some taxa (Derryberry et al., 2011; Désamoré et al., 2018; Crouch and Ricklefs, 2019;

Folk et al., 2019). Crouch and Ricklefs (2019) suggested this might be the product of ecomorphological diversification in major clades occurring early on in the evolutionary history of the group, which for uropeltids is corroborated with DTT plots and the high phylogenetic signal of the tail scute traits.

It is not straightforward to interpret the processes underlying the patterns of uropeltid phenotypic diversity discovered here, but the EB pattern for tail traits might suggest that tails diversified under strong ecomorphological constraints. As far as is known, all uropeltids prey on invertebrates (perhaps being earthworm specialists) in relatively moist, often upland soils of (at least prior to human modification) tropical rain forests (Gans, 1976, 1993; Rajendran, 1985). Despite diversity in body size and shape and head shape, there is no evidence of substantial diversification into many distinct niches to any similar degree to that which characterises the most famous examples of adaptive radiations (e.g. Caribbean *Anolis* lizard ecomorph adaptations to different ecological niches (Losos et al., 2006)). However, one could argue that soils might present fewer niches than above ground habitats (lacking water bodies, vegetation, or other primary production; having substantial probable constraints in e.g. limited oxygen, and physical forces exerted during locomotion in dense media).

The tail scutes of *Rhinophis* and *Uropeltis* reflect internal ossified structures (Hoffstetter and Gasc, 1969). Having bony caudal shields, which can occur in both (fossorial) snakes and amphisbaenians, has been hypothesised to be adaptation for defensive behaviour, by directing attacks to the posterior part of the body, where a reinforced tail increases the chances of surviving attacks (Greene, 1973). Still, the function of modified tail scutes in uropeltids is not entirely clear. It has been proposed they use their tail as a plug in the soil to avoid predation in the soil burrows (Gans, 1976). Additionally, it has been suggested that the tail shield might serve for defence, with the caudal display directing attacks away from the head and towards a reinforced tail when on the surface, either voluntarily or when unearthed by potential predators, though Gans (1976) did not report this behaviour for particular species. However, in *U. pulneyensis* it has been observed that while the head burrows in the soil, the snake showed a caudal display, where the tail resembles a head by mimicking its movement (Melvinselvan and Nibedita, 2016).

Defensive characters such as body armour have been found to follow a pattern of EB in agamid lizards, suggesting that anti-predation phenotypic features might have had had an important role in the diversification of the group (Broeckhoven et al., 2016). Though in this agamid study case, this EB pattern was accompanied by shifts in lineage diversification rates, which is not the case in uropeltids. So, although there is no compelling evidence at present that different tail scute morphologies in uropeltids are adaptations to different abiotic factors, perhaps different tail scute morphologies reflect adaptation to different predator-driven selective pressures i.e. biotic more than abiotic aspects of niche. The variety of tail shields (e.g. keratinised dome, flat or oblique plate (Gans, 1976)) might be indicative of different ecological or behavioural purposes, but this is yet to be tested.

4.4.4 Methodological considerations

PC axes are widely used to understand patterns of trait evolution, partly because they reduce dimensionality of the raw data, which allows the identification of overall patterns of morphological evolution. However, results for disparity and model evolution analyses based on PC axes being treated as univariate traits are not necessarily straightforward to interpret. In this study, examining only PC axes obscured some of the signal in the size-corrected single traits and made interpretation more difficult. Comparison of results of the analyses of principal components scores and of individual traits, aided the interpretation of which traits are consistent with BM and which ones are responsible for non-random evolutionary patterns (Murrell, 2018). For example, when analysing patterns in the DTT plots, if the inference was made based on the variable loadings for the individual PC axes, it would misleadingly suggest that for PC2 multiple traits with the highest loadings (beyond only tail scutes) were causing the observed EB pattern. However, when analysed individually, rostrum projection (RP) does not deviate from BM, while both the terminal tail scute traits (SL and SW) display EB patterns. Therefore, even though analyses had to be conducted for each individual trait, in a way defeating the purpose of reducing the dimensionality of the dataset and working with less individual variables, analysing traits one by one felt like the best approach to more precisely understand the patterns observed. Furthermore, by analysing PC scores

instead of individual axes, the power to identify signals of deviation from the null model could also be lost, due to the averaging of the Brownian with the non-Brownian traits (Murrell, 2018).

4.4.5 Study limitations and future directions

For this study, there was limitation in the sample size, with 20 species having fewer than five individuals available for the analyses. While sample sizes available in collections were limited in some cases, it is not clear the impact that it might have had on the results. The results of this study are also based on a set of linear measurements of external phenotypic traits, which remains a widely used methodology to understand overall morphological variation and trends in diversification patterns (Mahler et al., 2010; Derryberry et al., 2011; Vidal-Garcia and Keogh, 2015; Sherratt et al., 2017; Friedman et al., 2019; Price et al., 2019). This method is cost effective, requiring only a pair of callipers and a low power microscope, and it allows data to be generated for larger sample sizes than, for example, micro-CT scan studies.

Future studies might find it useful to employ more novel methods to explore shape variation in individual features. This could be achieved with three-dimensional (3D) geometric morphometrics of high-dimensional landmark and semi-landmark data on skulls and ossified tails scutes based on micro-CT scans of museum specimens, or for similar scans (or photogrammetry reconstructions) of external shape of heads and tails. Future work focusing solely on ossified cranial features might provide a better insight into the impact of fossoriality in head shape. In amphisbaenians, a clade of fossorial squamates, snout shape (shovel-, spade-, keel-snouted) has been found to be correlated with specific burrowing behaviours, while mandibles appear to be more correlated with diet patterns (Gans, 1968; Kearney and Stuart, 2004; Kazi and Hipsley, 2018) and similar patterns could be tested for in uropeltids. Variation in tail tip morphology also seems to occur in the fossorial amphisbaenians (Mott et al., 2008; Hoogmoed et al., 2009; Gomes and Maciel, 2012; Teixeira et al., 2014), but this is yet to be studied with quantitative approaches in those taxa.

While some ecological and behavioural work has been done in the 1970s and 1980s, regarding diet – uropeltids feed mostly on invertebrates (Rajendran, 1985) – or uropeltid digging style – wedge-shaped skulls have been linked to the way they move through the substrate (Gans, 1976) – detailed work has not been conducted across a broad range of species. Therefore, due to the lack of behavioural or ecological data available for uropeltids, it is not possible to test for possible correlation between phenotypic traits and particular ecologies or behaviours. One approach that might allow the lack of field ecological records to be circumvented would be to employ abiotic variables from geographic information systems (GIS) layers (e.g. WorldClim-Global climate data; https://www.worldclim.org). However, that would also require precise and accurate locality data for uropeltid samples, which is challenging because for many historical voucher specimens this information might not be available given that locality data for many specimens is highly imprecise (personal observation). Recording new locality occurrence data along with information regarding local ecological variables would be beneficial for future studies.

4.5 Conclusion

Analysing a set of linear morphological traits in a phylogenetic framework is useful to determine major patterns of phenotypic variation, and to identify overall trends in diversification patterns through time. Results from this study show a wide array of uropeltid body and head shapes across the clade. Notably, it finds evidence for an EB pattern of evolution for tail traits, even though evidence of phenotypic EB patterns are rare in comparative datasets (Harmon et al., 2010). The decoupling of uropeltid lineage diversification rates, with no rate shifts, from morphological diversification is indicative that this is not a case of adaptive radiation. Uropeltid tail shape variation is partitioned among rather than within major sub-clades, suggesting that tail shapes developed early on in the evolutionary history of the family, which might suggest a strong ecomorphological function of the tail scutes. While results are not straightforward to interpret, here it is hypothesised that an enlarged terminal caudal shape, with a keratinised or ossified underlying structure, might have been advantageous in defending from predators.

It seems reasonable that much of the focus when trying to understand processes of evolution in head-first burrowers has been towards head features (Sherratt et al., 2014; Kazi and Hipsley, 2018). The present study demonstrates that extending the study to other features such as tail structures might help uncover interesting patterns and hopefully elucidate processes of diversification in fossorial vertebrates. To fully understand the drivers of variation in tail scute morphology and patterns of diversification in uropeltids, and possibly across fossorial squamates, will require future studies focusing on species ecology and behaviour of tail function.

Chapter 5 — Conclusions

5.1 Summary of thesis findings

The main aims of the present work were to generate a taxonomically comprehensive molecular phylogeny of the Uropeltidae, and to study lineage and phenotypic diversity and diversification patterns. In summary, the analyses of the molecular and morphological datasets generated for this work have: i) advanced understanding of evolutionary relationships among uropeltids, which will be informative in future taxonomic studies; ii) demonstrated the usefulness of ancient DNA methods in generating (at least) mitochondrial sequence data from fluid-preserved historical museum specimens; iii) uncovered unexpectedly high levels of uropeltid molecular diversity; iv) estimated rates of lineage diversification to have been constant over time; v) identified an early burst pattern of phenotypic evolution in tail tip traits, suggesting that tail tip morphology might have played an important ecological role early on in the diversification of the family.

To accomplish this, a new large multilocus dataset of uropeltid DNA sequence data was generated, which enabled the most taxonomically comprehensive phylogeny to be inferred for the Uropeltidae family to date (Chapter 2). The molecular dataset used in this study was built from published sequence data (21.8%) (Bossuyt et al., 2004; Pyron et al., 2016; Cyriac and Kodandaramaiah, 2017; Jins et al., 2018), as well as newly generated sequence data. Additionally, sequence data were generated from type and historical fluid-preserved museum specimens. This was aided by recently developed ancient DNA molecular techniques appropriate for damaged and fragmented DNA, typical of ancient and historical samples. These methods allowed the generation of DNA sequence data, with almost complete mitochondrial genomes in some cases, enabling the addition of taxa in the molecular dataset, some of which up until now were not available for molecular work. This resulted in a phylogenetic tree with all but six of the 56 currently described uropeltid species, in addition to yet undescribed taxa or known synonyms, which will be exceptionally useful in future taxonomic revisionary work.

The taxonomically near-comprehensive uropeltid phylogenetic tree built in Chapter 2 was essential as input in species delimitation methods, so that a single

sample per species could be included in the dated tree (one of the assumptions of using a Yule model tree prior). Results from Chapter 3 single locus species delimitation analyses provided evidence that the number of uropeltid species has been underestimated, and 111 OTUs were used as input in dating analyses. Even though the dating analyses inferred divergence dates older than expected, results were useful for obtaining relative divergence dating between main clades and lineages to be used as input in diversification analyses.

Work reported in Chapter 4 generated a large amount of ecomorphological trait data from 975 museum specimens across Uropeltidae. This thesis is the first time phenotypic data have been generated and analysed in a quantitative approach for uropeltid snakes to study shape variation though time. Results found evidence for a decoupling between lineage and phenotypic diversification patterns. While lineage diversification was estimated to have been constant over time, with no evidence for rate shifts (Chapter 3), trait data analyses uncovered a pattern of early burst of phenotypic change for the tail terminal scute, suggesting that uropeltid tails diversified early on in the evolution of the family (Chapter 4). Thus, while this is not a classic case of adaptive radiation as initially hypothesised, this evolutionary radiation seems to display a pattern of disparification in which a species or clade radiates into a new area of morphospace without an associated increase in net diversification rate (Simões et al., 2016). Although there is not much literature available regarding the behaviour and ecological requirements of each uropeltid sub-clade, here it is suggested that larger and more elaborate terminal scutes might have played a role in enabling uropeltids to adapt to new ecological niches.

5.2 Herpetofauna diversity and diversification patterns in the Western Ghats-Sri Lanka biodiversity hotspot

There have been a few studies in recent years on the diversification patterns of Western Ghats-Sri Lanka biodiversity hotspot herpetofaunal endemics, testing for hypotheses of adaptive radiations and inferring the effects of past climate on diversification patterns. Lajmi and Karanth (2019) estimated the origin of *Hemidactylus* geckos in Peninsular India 39–32 million years ago (Ma), having found an early increase in lineage diversification rates, followed by a slowdown in rates,

typical of adaptive radiations. The implementation of ancestral state reconstructions on habitat type further revealed a dry adapted ancestor, with the authors suggesting that the change from a humid to dry climate at the Eocene–Oligocene boundary might have promoted diversification of dry adapted lineages in these geckos (with multiple humid lineages evolving independently later on). With an Indian origin for the radiation, multiple dispersals of *Hemidactylus* into Sri Lanka occurred in the Miocene when Sri Lanka and South India where connected by a land bridge for the two Sri Lankan endemic wet zone species, and more recent dispersals for the dry zone species co-occurring in both areas (Lajmi et al., 2018). Nevertheless, there is no evidence that rapid lineage accumulation in the Indian radiation was accompanied by an early burst in phenotypic disparity (Lajmi et al., 2019). Deepak and Karanth's (2018) study of the fan-throated lizards *Sitana* estimated an origin for the genus ca. 18 Ma in the mid-Miocene, during a monsoon climate, with an increase in lineage diversification 11 Ma possibly promoted by aridification in the late Miocene. The origin of diversification of *Pseudophilautus* frogs in Sri Lanka has been estimated to have occurred ca. 30 Ma in the Oligocene, with an ancestral form predicted to have been adapted to wet and cool lowland areas of India and Sri Lanka (Meegaskumbura et al., 2019). No evidence was found for adaptive radiation to have occurred in the island, with Meegaskumbura et al. (2019) suggesting that constant rates of linage diversification perhaps reflect that climate and habitats suitable for these frogs were not abundant at the time of origin of the radiation.

How does the uropeltid radiation compare with other Indian and Sri Lankan endemics? It is difficult to compare due to the variety of patterns observed, just in these three examples alone. While in *Hemidactylus* there have been multiple colonisations from India to Sri Lanka, here and previous uropeltid studies have found only evidence of one event. Additionally, in the *Pseudophilautus* frogs there is an indication for a back to India dispersal, a pattern also common in the region (Bossuyt et al., 2004). For uropeltids, there is no firm evidence for a similar (back-to-India) pattern because the position of the Indian *R. goweri* within the Sri Lankan radiation was poorly supported in the phylogenetic analyses. Thus, the sister species to the Sri Lankan uropeltid radiation is still unclear. However, for a long time it has been suggested that a dry adapted taxon dispersed from the lowlands of

South India into Sri Lanka (Cadle et al., 1990). A better understanding of uropeltid species occurrence regarding altitude and climate might help understand temporal dynamics and adaptation to climates and habitats in the origin of sub-clade diversifications.

While not many diversification studies are available for fossorial radiations, and not many have looked into herpetofaunal phenotypic diversification in this region, these recent studies reveal a diverse evolutionary dynamic of endemic radiations. The decoupling between lineage and phenotypic diversification patterns (constant lineage diversification and a pattern of early burst of morphological variation in Uropeltidae, and diversity dependent lineage accumulation without early clade morphological disparity typical of adaptive radiation in *Hemidactylus* geckos) are not straightforward to explain, and more studies on diversification across the Indian subcontinent might help better understand common patterns across organisms.

As for the results reported here for uropeltids, some of these other studies of Western Ghats-Sri Lanka herpetofauna have found a higher number of putative species based on molecular phylogenies and species delimitation methods (Deepak and Karanth, 2018; Lajmi and Karanth, 2019). This highlights the high levels of undescribed biodiversity in less conspicuous and less well studied tropical vertebrates.

5.3 Future directions

Findings reported in Chapter 2 demonstrate the potential that ancient DNA methods have for generating DNA sequence data from ethanol preserved historical museum specimens. However, it seems that for specimens that might have been recent enough to have been accessed in collections at a time when formalin fixation became a common approach, the methodology employed here might not be successful, so it would be worth trying other methods that have been developed for those samples (Campos and Gilbert, 2012; Ruane and Austin, 2017; McGuire et al., 2018). For some samples for which the methods were successful, almost complete mitochondrial genomic data were generated. However, complete mitochondrial genomes could not be easily assembled with de novo methods due

to the nearly identical duplicated control region of alethinophidian snakes, and the lack of a complete closely related reference genome made it impossible to align contigs to a reference for this highly variable genomic region. Applying different bioinformatic tools that are able to deal with repetitive regions in genome assembly might enable generation of complete mitochondrial genomes that could be analysed with comparative datasets that aim to understand the evolution and structure of snake mitochondrial genomes (Dong and Kumazawa, 2005; Jiang et al., 2007; Yan et al., 2008; Douglas and Gower, 2010; He et al., 2010; Qian et al., 2018).

Further taxonomic and/or character sampling might be able to clarify the phylogenetic relationships of some species (e.g. position of the Indian *R. goweri* inside or outside the Sri Lankan clade?). Generating densely sampled molecular datasets and including more samples per putative species would be useful to be employed in species delimitation methods. For example, depending on the analyses (e.g. mPTP or GMYC) and type of dataset (e.g. large or small population sizes), having singletons – species with only one sample – in the analyses tends to either over splitting or over clustering (Kapli et al., 2017; Dellicour and Flot, 2018), although singletons are not supposed to be problematic for BPP, a multilocus coalescent method (Yang and Rannala, 2017). Additionally, analysing these results in light of morphological taxonomic traits (e.g. scale counts, head scales proportions) would be beneficial for future studies aiming to clarify the taxonomic status of known synonyms or potentially cryptic complexes.

In Chapter 4, linear morphometric trait data were used to quantify and understand external morphological diversity in uropeltids. Even though linear morphometrics is still widely used to identify patterns of morphological variation (Vidal-Garcia and Keogh, 2015; Garcia-Porta et al., 2016; Reynolds et al., 2016; Price et al., 2019), more novel techniques employing two and three dimensional (3D) geometric morphometrics have been developed that allow morphological features to be studied in detail, including improved capturing of variation in shape. Three dimensional geometric morphometrics has been used recently to study bony anatomical features of a range of organisms. The evolution of cranial shape has been studied in organisms such as Darwin's finches and the Hawaiian honeycreepers, which are classic examples of adaptive radiation (Tokita et al.,

2016), and the evolution of skull shape in fossorial herpetofauna, such as Caribbean amphisbaenians (Kazi and Hipsley, 2018) and caecilian amphibians (Bardua et al., 2019). Uropeltid snakes are a great example of a speciose clade of organisms with reinforced skulls adapted to head-first burrowing, which seem to be fairly diverse, and perhaps offer some examples of convergent evolution (Figure 5-1 to 5-3), and these more novel methods applied to skeletal anatomy might capture other aspects of the morphological variation that external measurements cannot. Moreover, shape variation in uropeltid tails, particularly the more elaborate tails of species in the genera *Uropeltis* and *Rhinophis*, is difficult to capture using linear metric and meristic characters because of a lack of obvious landmarks. Additionally, qualitative traits related with tail spines and ridges are difficult to define. The lack of clear landmarks could be overcome by the placement of semi-landmarks across the surface (e.g. study on egg shape (Attard et al., 2018)). Skeletal data can be obtained with X-ray micro-computed tomography (micro-CT), a non-destructive technique that produces a 3D model of an object allowing the visualisation and analyses of hard tissue (e.g. bony) features. It is anticipated that these novel methods employing high dimensional datasets exploring bony structures of the head and tail of uropeltids would provide more insights into the shape diversity and evolution of these particular structures, and perhaps their ecology. The former could be tackled by analysing quantitative measures of skull and tail shield plate shape within the context of a dated, molecular phylogeny to understand how tempo and mode of evolution have shaped uropeltid cranial and shield tail diversity. These analyses would allow comparison between diversity and diversification patterns assessed using bony features analysed with 3D geometric morphometrics and external trait data analysed with multivariate statistics. So far, heads and tails of ca. 150 specimens have been scanned for about 65 taxonomic units, and over 70 specimens' skulls have been segmented to be employed in preliminary analyses.

The processes that might be driving the pattern of constant lineage diversification and early burst of tail phenotypic disparity in uropeltids are not understood. Gathering data that documents variation in the ecology (e.g. diet, soil substrate), behaviour and precise distribution of uropeltids, would not only increase our understanding of uropeltid natural history and distribution, but also would enable

these factors to be incorporated in quantitative analyses to identify correlates with lineage and morphological diversification, greatly benefiting our understanding of the diversity and diversification of shieldtails.

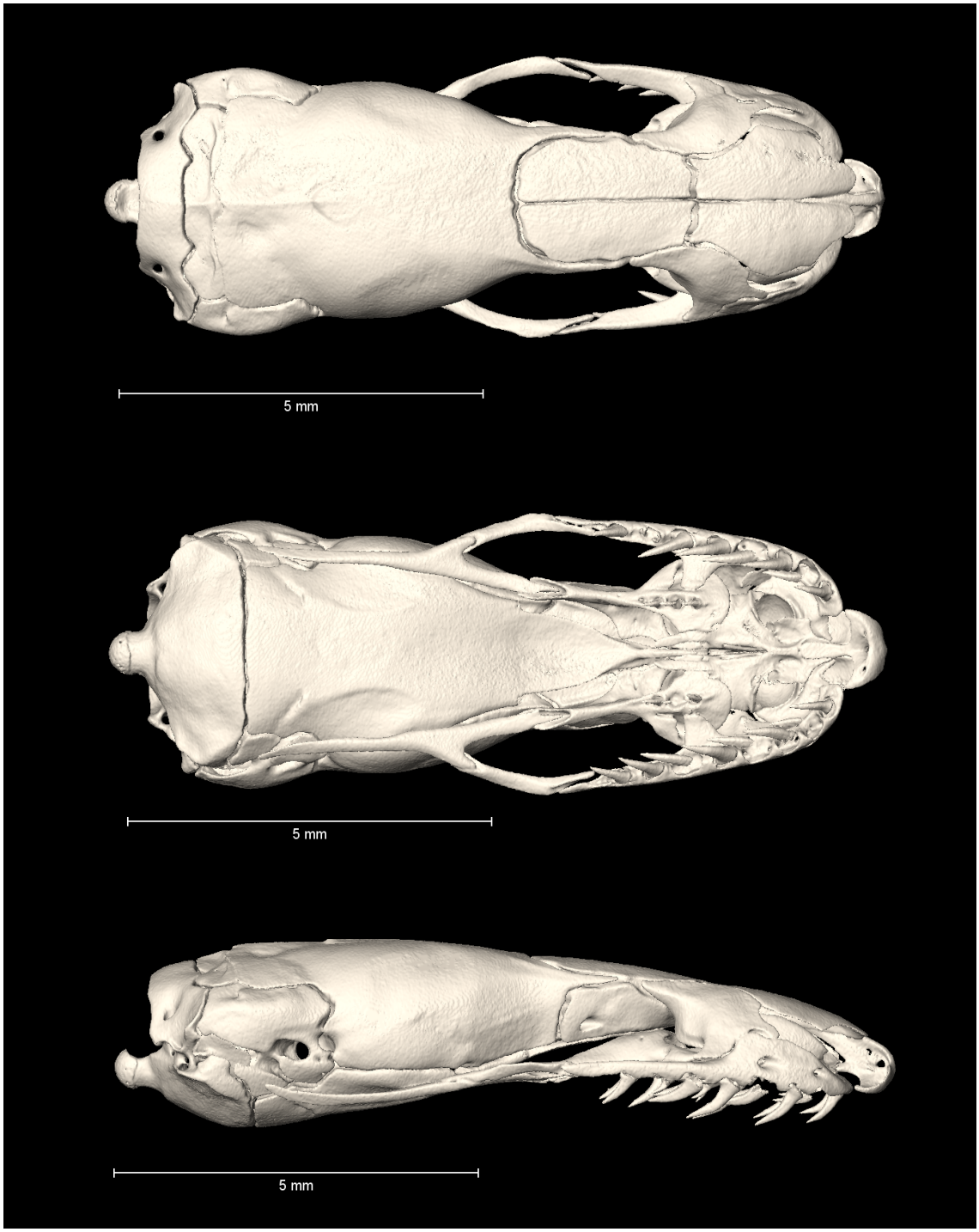


Figure 5-1 *Melanophidium bilineatum* skull (specimen MNHN 1895.111) in dorsal (top), ventral (centre) and lateral (bottom) views. Scale bars: 5 millimetres.

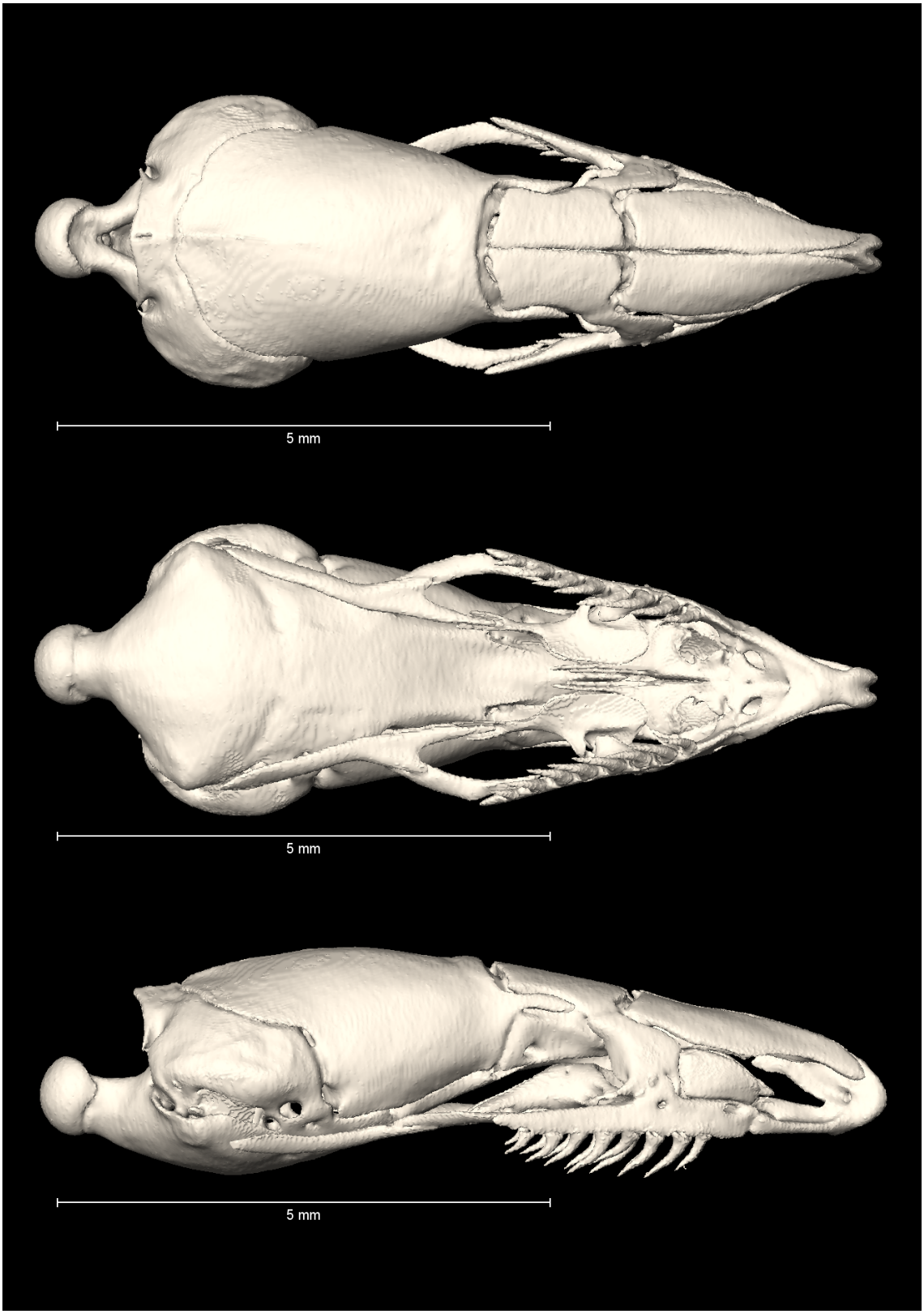


Figure 5-2 *Uropeltis broughami* skull (specimen MNHN1895.89) in dorsal (top), ventral (centre) and lateral (bottom) views. Scale bars: 5 millimetres.

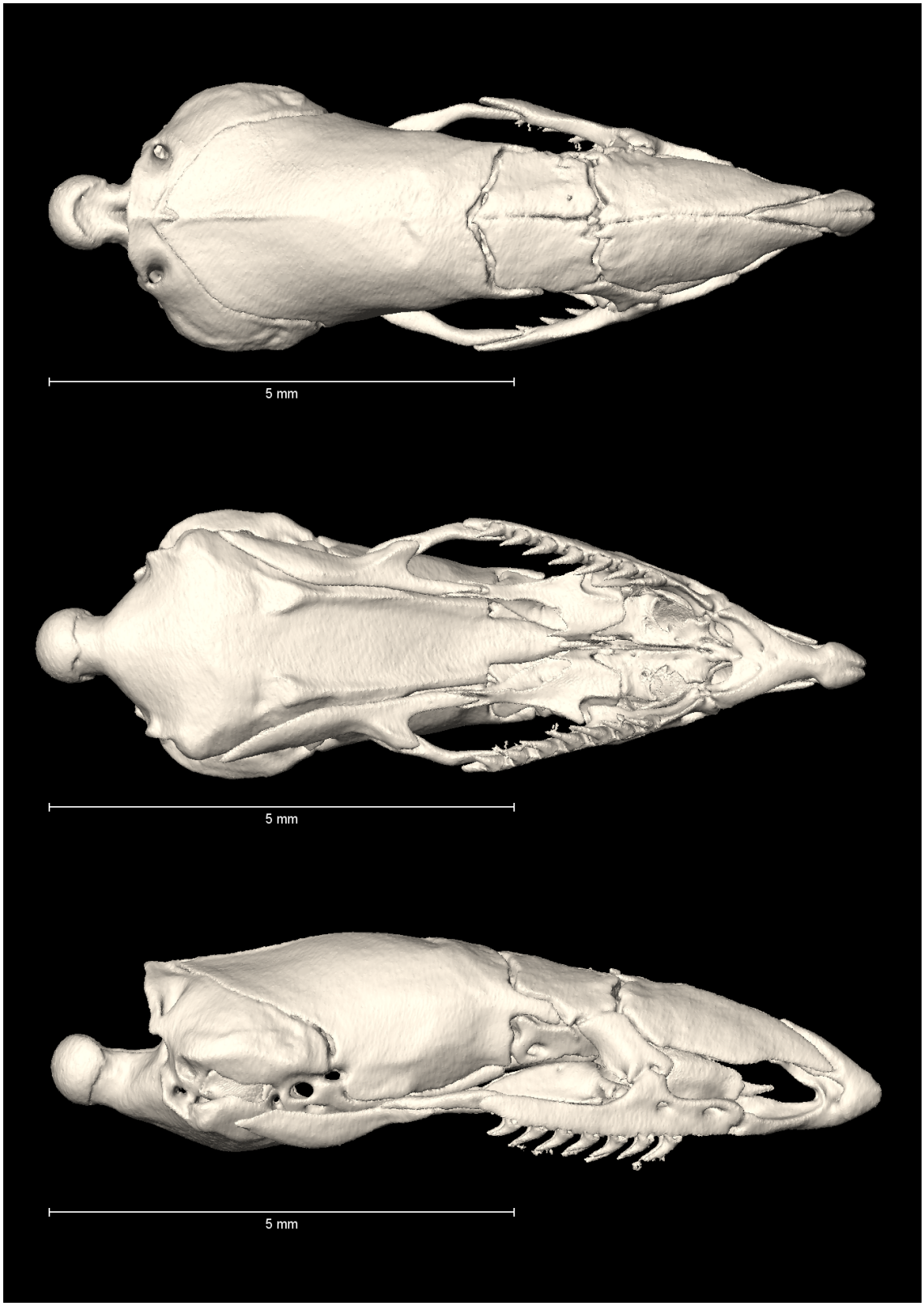


Figure 5-3 *Rhinophis punctatus* skull (specimen BMNH 71.11.13.1) in dorsal (top), ventral (centre) and lateral (bottom) views. Scale bars: 5 millimetres.

References

Adams, D. C. (2014) 'A Generalized K Statistic for Estimating Phylogenetic Signal from Shape and Other High-Dimensional Multivariate Data', *Systematic Biology*, 63(5), pp. 685–697. doi: 10.1093/sysbio/syu030.

Adams, D. C., Collyer, M. L. and Kaliontzopoulou, A. (2019) 'Geomorph: Software for geometric morphometric analyses. R package version 3.1.0 (https://cran.r-project.org/package=geomorph)'.

Aengals, R. and Ganesh, S. R. (2013) '*Rhinophis goweri* - a new species of Shield-tailed snake from the Southern Eastern Ghats, India', *Russian Journal of Herpetology*, 20(1), pp. 61–65.

Agustí, J., Cabrera, L., Garcés, M., Krijgsman, W., Oms, O. and Parés, J. M. (2001) 'A calibrated mammal scale for the Neogene of Western Europe. State of the art', *Earth-Science Reviews*, 52(4), pp. 247–260. doi: 10.1016/S0012-8252(00)00025-8.

Ahrens, D., Fujisawa, T., Krammer, H.-J., Eberle, J., Fabrizi, S. and Vogler, A. P. (2016) 'Rarity and Incomplete Sampling in DNA-Based Species Delimitation', *Systematic Biology*, 65(3), pp. 478–494. doi: 10.1093/sysbio/syw002.

Alexander, A. A. and Gans, C. (1966) 'The pattern of dermal-vertebral correlation in snakes and amphisbaenians', *Zoologische Mededelingen*, 41(11), pp. 171–190.

Ali, J. R. (2018) 'Islands as biological substrates: Continental', *Journal of Biogeography*, 45(5), pp. 1003–1018. doi: 10.1111/jbi.13186.

Ali, J. R. and Aitchison, J. C. (2008) 'Gondwana to Asia: Plate tectonics, paleogeography and the biological connectivity of the Indian sub-continent from the Middle Jurassic through latest Eocene (166-35 Ma)', *Earth-Science Reviews*, 88(3–4), pp. 145–166. doi: 10.1016/j.earscirev.2008.01.007.

Amador, L., Parada, A., D'Elía, G. and Guayasamin, J. M. (2018) 'Uncovering hidden specific diversity of Andean glassfrogs of the Centrolene buckleyi species complex (Anura: Centrolenidae)', *PeerJ*, 6, p. e5856. doi: 10.7717/peerj.5856.

Arévalo, E., Davis, S. K. and Sites, J. W. (1994) 'Mitochondrial DNA Sequence Divergence and Phylogenetic Relationships among Eight Chromosome Races of the *Sceloporus grammicus* Complex (Phrynosomatidae) in Central Mexico', *Systematic Biology*, 43(3), pp. 387–418. doi: 10.1093/sysbio/43.3.387.

Attard, M. R. G., Sherratt, E., McDonald, P., Young, I., Vidal-García, M. and Wroe, S. (2018) 'A new, three-dimensional geometric morphometric approach to assess egg shape', *PeerJ*, 6, p. e5052. doi: 10.7717/peerj.5052.

Barba-Montoya, J., dos Reis, M. and Yang, Z. (2017) 'Comparison of different strategies for using fossil calibrations to generate the time prior in Bayesian molecular clock dating', *Molecular Phylogenetics and Evolution*, 114, pp.

386–400. doi: 10.1016/J.YMPEV.2017.07.005.

Bardua, C., Wilkinson, M., Gower, D. J., Sherratt, E. and Goswami, A. (2019) 'Morphological evolution and modularity of the caecilian skull', *BMC Evolutionary Biology*, 19(1), p. 30. doi: 10.1186/s12862-018-1342-7.

Bars-Closel, M., Kohlsdorf, T., Moen, D. S. and Wiens, J. J. (2017) 'Diversification rates are more strongly related to microhabitat than climate in squamate reptiles (lizards and snakes)', *Evolution*, 71(9), pp. 2243–2261. doi: 10.1111/evo.13305.

Bazinet, A. L., Zwickl, D. J. and Cummings, M. P. (2014) 'A gateway for phylogenetic analysis powered by grid computing featuring GARLI 2.0', *Systematic Biology*, 63(5), pp. 812–818. doi: 10.1093/sysbio/syu031.

Bell, M. A. and Lloyd, G. T. (2015) 'strap: an R package for plotting phylogenies against stratigraphy and assessing their stratigraphic congruence', *Palaeontology*, 58(2), pp. 379–389. doi: 10.1111/pala.12142.

Bellairs, A. d'A. (1968) *Reptiles*. Hutchinson's University Library.

Bellairs, A. d'A. (1970) *The life of reptiles, Volume 1*. Universe Books.

Bellati, A., Carranza, S., Garcia-Porta, J., Fasola, M. and Sindaco, R. (2015) 'Cryptic diversity within the *Anatololacerta* species complex (Squamata: Lacertidae) in the Anatolian Peninsula: Evidence from a multi-locus approach', *Molecular Phylogenetics and Evolution*, 82, pp. 219–233. doi: 10.1016/J.YMPEV.2014.10.003.

Bi, K., Vanderpool, D., Singhal, S., Linderoth, T., Moritz, C. and Good, J. M. (2012) 'Transcriptome-based exon capture enables highly cost-effective comparative genomic data collection at moderate evolutionary scales', *BMC Genomics*, 13(1), p. 403. doi: 10.1186/1471-2164-13-403.

Blair, C. and Bryson, R. W. (2017) 'Cryptic diversity and discordance in single-locus species delimitation methods within horned lizards (Phrynosomatidae: *Phrynosoma*)', *Molecular Ecology Resources*, 17(6), pp. 1168–1182. doi: 10.1111/1755-0998.12658.

Blomberg, S. P. and Garland, T. (2002) 'Tempo and mode in evolution: phylogenetic inertia, adaptation and comparative methods', *Journal of Evolutionary Biology*, 15(6), pp. 899–910. doi: 10.1046/j.1420-9101.2002.00472.x.

Blomberg, S. P., Garland, T. and Ives, A. R. (2003) 'Testing for phylogenetic signal in comparative data: behavioral traits are more liable', *Evolution*, 57(4), pp. 717–745. doi: 10.1111/j.0014-3820.2003.tb00285.x.

Van Bocxlaer, I., Biju, S., Loader, S. P. and Bossuyt, F. (2009) 'Toad radiation reveals into-India dispersal as a source of endemism in the Western Ghats-Sri Lanka biodiversity hotspot', *BMC Evolutionary Biology*, 9(1), pp. 1–10. doi: 10.1186/1471-2148-9-131.

Bossuyt, F., Meegaskumbura, M., Beenaerts, N., Gower, D. J., Pethiyagoda, R., Roelants, K., Mannaert, A., Wilkinson, M., Bahir, M. M., Manamendra-Arachchi, K., Ng, P. K. L., Schneider, C. J., Oommen, O. V and Milinkovitch,

M. C. (2004) ‘Local Endemism Within the Western Ghats-Sri Lanka Biodiversity Hotspot’, *Science*, 306(5695), pp. 479–481. doi: 10.1126/science.1100167.

Bouckaert, R., Heled, J., Kühnert, D., Vaughan, T., Wu, C.-H., Xie, D., Suchard, M. A., Rambaut, A. and Drummond, A. J. (2014) ‘BEAST 2: A Software Platform for Bayesian Evolutionary Analysis’, *PLoS Computational Biology*, 10(4), p. e1003537. doi: 10.1371/journal.pcbi.1003537.

Brace, S., Diekmann, Y., Booth, T. J., Faltyskova, Z., Rohland, N., Mallick, S., Ferry, M., Michel, M., Oppenheimer, J., Broomandkhoshbacht, N., Stewardson, K., Walsh, S., Kayser, M., Schulting, R., Craig, O. E., Sheridan, A., Pearson, M. P., Stringer, C., Reich, D., Thomas, M. G. and Barnes, I. (2018) ‘Population Replacement in Early Neolithic Britain’, *bioRxiv*, p. 267443. doi: 10.1101/267443.

Briggs, A. W., Stenzel, U., Johnson, P. L. F., Green, R. E., Kelso, J., Prü, K., Meyer, M., Krause, J., Ronan, M. T., Lachmann, M. and Pä, S. (2007) ‘Patterns of damage in genomic DNA sequences from a Neandertal’, *Proceedings of the National Academy of Sciences*, 104(37), pp. 14616–14621. doi: 10.1073/pnas.0704665104.

Broeckhoven, C., Diedericks, G., Hui, C., Makhubo, B. G. and Mouton, P. le F. N. (2016) ‘Enemy at the gates: Rapid defensive trait diversification in an adaptive radiation of lizards’, *Evolution*, 70(11), pp. 2647–2656. doi: 10.1111/evo.13062.

Brotherton, P., Endicott, P., Sanchez, J. J., Beaumont, M., Barnett, R., Austin, J. and Cooper, A. (2007) ‘Novel high-resolution characterization of ancient DNA reveals C > U-type base modification events as the sole cause of post mortem miscoding lesions’, *Nucleic Acids Research*, 35(17), pp. 5717–5728. doi: 10.1093/nar/gkm588.

Brown, R. P. and Yang, Z. (2011) ‘Rate variation and estimation of divergence times using strict and relaxed clocks’, *BMC Evolutionary Biology*. BioMed Central, 11(1), p. 271. doi: 10.1186/1471-2148-11-271.

Burbrink, F. T., Grazziotin, F. G., Pyron, R. A., Cundall, D., Donnellan, S., Irish, F., Keogh, J. S., Kraus, F., Murphy, R. W., Noonan, B., Raxworthy, C. J., Ruane, S., Lemmon, A. R., Lemmon, E. M. and Zaher, H. (2019) ‘Interrogating genomic-scale data for Squamata (lizards, snakes, and amphisbaenians) shows no support for key traditional morphological relationships’, *Systematic Biology*. doi: 10.1093/sysbio/syz062.

Burbrink, F. T. and Crother, B. I. (2011) ‘Evolution and taxonomy of snakes’, in *Reproductive biology and phylogeny of snakes*. CRC Press, pp. 19–53.

Burbrink, F. T., Lawson, R. and Slowinski, J. B. (2000) ‘Mitochondrial DNA phylogeography of the polytypic North American rat snake (*Elaphe obsoleta*): a critique of the subspecies concept’, *Evolution; international journal of organic evolution*, 54(6), pp. 2107–2118. doi: 10.1554/0014-3820(2000)054.

Burbrink, F. T. and Pyron, R. A. (2011) 'The impact of gene-tree/species-tree discordance on diversification-rate estimation', *Evolution*, 65(7), pp. 1851–1861. doi: 10.1111/j.1558-5646.2011.01260.x.

Burin, G., Alencar, L. R. V, Chang, J., Alfaro, M. E. and Quental, T. B. (2019) 'How Well Can We Estimate Diversity Dynamics for Clades in Diversity Decline?', *Systematic Biology*, 68(1), pp. 47–62. doi: 10.1093/sysbio/syy037.

Butler, M. A. and King, A. A. (2004) 'Phylogenetic Comparative Analysis: A Modeling Approach for Adaptive Evolution', *The American naturalist*. The University of Chicago Press, 164(6), pp. 683–695. doi: 10.1086/426002.

Cadle, J. E., Dessauer, H. C., Gans, C. and Gartside, D. F. (1990) 'Phylogenetic relationships and molecular evolution in uropeltid snakes (Serpentes: Uropeltidae): allozymes and albumin immunology', *Biological Journal of the Linnean Society*, 40(3), pp. 293–320. doi: 10.1111/j.1095-8312.1990.tb00541.x.

Caldwell, M. W., Nydam, R. L., Palci, A. and Apesteguía, S. (2015) 'The oldest known snakes from the Middle Jurassic-Lower Cretaceous provide insights on snake evolution', *Nature Communications*, 6, p. 5996. doi: 10.1038/ncomms6996.

Caldwell, M. W. and Lee, M. S. Y. (1997) 'A snake with legs from the marine Cretaceous of the Middle East', *Nature*, 386(6626), pp. 705–709. doi: 10.1038/386705a0.

Cameron, R. A. D., Cook, L. M. and Hallows, J. D. (1996) 'Land snails on Porto Santo: adaptive and non-adaptive radiation', *Philosophical Transactions of the Royal Society of London. Series B: Biological Sciences*, 351(1337), pp. 309–327. doi: 10.1098/rstb.1996.0025.

Campos, P. and Gilbert, T. (2012) 'DNA extraction from formalin-fixed material.', in Shapiro, B. and Hofreiter, M. (eds) *Ancient DNA: Methods and Protocols, Methods in Molecular Biology*. Humana Press, pp. 81–85. doi: 10.1007/978-1-61779-516-9.

Carstens, B. C., Pelletier, T. A., Reid, N. M. and Satler, J. D. (2013) 'How to fail at species delimitation', *Molecular Ecology*, 22(17), pp. 4369–4383. doi: 10.1111/mec.12413.

Carter, J. D. (2003) *The effects of preservation and conservation treatments on the DNA of museum invertebrate fluid preserved collections. M.Phil. thesis*. National Museum of Wales. Available at: https://amgueddfa.cymru/media/16607/MPhil-DNA-preservation.pdf.

Castresana, J. (2000) 'Selection of Conserved Blocks from Multiple Alignments for Their Use in Phylogenetic Analysis', *Molecular Biology and Evolution*, 17(4), pp. 540–552. doi: 10.1093/oxfordjournals.molbev.a026334.

Claverie, T. and Wainwright, P. C. (2014) 'A Morphospace for Reef Fishes: Elongation Is the Dominant Axis of Body Shape Evolution', *PLoS ONE*, 9(11), p. e112732. doi: 10.1371/journal.pone.0112732.

Coates, M. and Ruta, M. (2000) 'Nice snake, shame about the legs.', *Trends in*

ecology & evolution, 15(12), pp. 503–507. doi: https://doi.org/10.1016/S0169-5347(00)01999-6.

Comeaux, R. S., Olori, J. C. and Bell, C. J. (2010) 'Cranial osteology and preliminary phylogenetic assessment of *Plectrurus aureus* Beddome, 1880 (Squamata: Serpentes: Uropeltidae)', *Zoological Journal of the Linnean Society*, 160(1), pp. 118–138. doi: 10.1111/j.1096-3642.2009.00595.x.

Constable, J. D. (1949) 'Reptiles from the Indian Peninsula in the Museum of Comparative Zoology', *Bulletin of the Museum of Comparative Zoology*, 103, pp. 59–160.

Courtillot, V., Besse, J., Vandamme, D., Montigny, R., Jaeger, J.-J. and Cappetta, H. (1986) 'Deccan flood basalts at the Cretaceous/Tertiary boundary?', *Earth and Planetary Science Letters*, 80(3–4), pp. 361–374. doi: 10.1016/0012-821X(86)90118-4.

Crouch, N. M. A. and Ricklefs, R. E. (2019) 'Speciation Rate Is Independent of the Rate of Evolution of Morphological Size, Shape, and Absolute Morphological Specialization in a Large Clade of Birds', *The American Naturalist*, 193(4), pp. E78–E91. doi: 10.1086/701630.

Cundall, D. (1993) 'The systematic relationships of the snake genus *Anomochilus*', *Zoological Journal of the Linnean Society*, 109, pp. 275–299. doi: 10.1111/j.1096-3642.1993.tb02536.x.

Cundall, D. (2003) 'Pipe snakes (Cylindrophiidae)', in Hutchins, M., Murphy, J. B., and Schlager, N. (eds) *Grzimek's Animal Life Enclyclopedia, 2nd edition. Vol. 7, Reptiles*. Gale Group, Farmington Hills, ML, pp. 395–397.

Cundall, D. and Irish, F. (2008) 'The snake skull', in *Biology of the Reptilia 20*, pp. 349–692.

Curran, C. H. and Kauffeld, C. (1937) *Snakes and their ways*. Harper & Brothers.

Cusimano, N. and Renner, S. S. (2010) 'Slowdowns in Diversification Rates from Real Phylogenies May Not be Real', *Systematic Biology*, 59(4), pp. 458–464. doi: 10.1093/sysbio/syq032.

Cyriac, V. P. and Kodandaramaiah, U. (2017) 'Paleoclimate determines diversification patterns in the fossorial snake family Uropeltidae Cuvier, 1829', *Molecular Phylogenetics and Evolution*, 116, pp. 97–107. doi: 10.1016/j.ympev.2017.08.017.

Cyriac, V. P. and Kodandaramaiah, U. (2019) 'Conspicuous colours reduce predation rates in fossorial uropeltid snakes', *PeerJ*, 7, p. e7508. doi: 10.7717/peerj.7508.

Dabney, J., Knapp, M., Glocke, I., Gansauge, M.-T. M.-T., Weihmann, A., Nickel, B., Valdiosera, C., Garcia, N., Paabo, S., Arsuaga, J.-L. J.-L., Meyer, M., García, N., Pääbo, S., Arsuaga, J.-L. J.-L. and Meyer, M. (2013) 'Complete mitochondrial genome sequence of a Middle Pleistocene cave bear reconstructed from ultrashort DNA fragments', *Proceedings of the National Academy of Sciences of the United States of America*, 110(39), pp. 1–6. doi: 10.1073/pnas.1314445110.

Dabney, J., Meyer, M. and Pääbo, S. (2013) 'Ancient DNA damage', *Cold Spring Harbor perspectives in biology*, 5(7), p. a012567. doi: 10.1101/cshperspect.a012567.

Das, I., Lakim, M., Lim, K. K. P., Hui, T. H., As, I. N. D., Akim, M. A. L. and Im, K. E. K. P. L. (2008) 'New Species of *Anomochilus* from Borneo (Squamata: Anomochilidae)', *Journal of Herpetology*, 42(3), pp. 584–591. doi: https://doi.org/10.1670/07-154.1.

Datta-Roy, A., Singh, M., Srinivasulu, C. and Karanth, K. P. (2012) 'Phylogeny of the Asian *Eutropis* (Squamata: Scincidae) reveals an "into India" endemic Indian radiation', *Molecular Phylogenetics and Evolution*, 63(3), pp. 817–824. doi: 10.1016/J.YMPEV.2012.02.022.

Datta-Roy, A. and Praveen Karanth, K. (2009) 'The Out-of-India hypothesis: What do molecules suggest?', *Journal of Biosciences*, 34(5), pp. 687–697. doi: 10.1007/s12038-009-0057-8.

Day, J. J., Peart, C. R., Brown, K. J., Friel, J. P., Bills, R. and Moritz, T. (2013) 'Continental diversification of an African catfish radiation (Mochokidae: *Synodontis*)', *Systematic Biology*, 62(3), pp. 351–365. doi: 10.1093/sysbio/syt001.

Day, J. J., Fages, A., Brown, K. J., Vreven, E. J., Stiassny, M. L. J., Bills, R., Friel, J. P. and Rüber, L. (2017) 'Multiple independent colonizations into the Congo Basin during the continental radiation of African *Mastacembelus* spiny eels', *Journal of Biogeography*, 44(10), pp. 2308–2318. doi: 10.1111/jbi.13037.

Day, J. J., Cotton, J. A. and Barraclough, T. G. (2008) 'Tempo and mode of diversification of Lake Tanganyika cichlid fishes', *PLoS ONE*, 3(3), p. e1730. doi: 10.1371/journal.pone.0001730.

Dayrat, B. (2005) 'Towards integrative taxonomy', *Biological Journal of the Linnean Society*, 85(3), pp. 407–415. doi: 10.1111/j.1095-8312.2005.00503.x.

De-Silva, D. L., Elias, M., Willmott, K., Mallet, J. and Day, J. J. (2016) 'Diversification of clearwing butterflies with the rise of the Andes', *Journal of Biogeography*, 43(1), pp. 44–58. doi: 10.1111/jbi.12611.

Deepak, V. and Karanth, P. (2018) 'Aridification driven diversification of fan-throated lizards from the Indian subcontinent', *Molecular Phylogenetics and Evolution*, 120, pp. 53–62. doi: 10.1016/j.ympev.2017.11.016.

Deepak, V., Ruane, S. and Gower, D. J. (2018) 'A new subfamily of fossorial colubroid snakes from the Western Ghats of peninsular India', *Journal of Natural History*, 52(45–46), pp. 2919–2934. doi: 10.1080/00222933.2018.1557756.

Dellicour, S. and Flot, J.-F. F. (2018) 'The hitchhiker's guide to single-locus species delimitation', *Molecular Ecology Resources*, 18(6), pp. 1234–1246. doi: 10.1111/1755-0998.12908.

Dereeper, A., Guignon, V., Blanc, G., Audic, S., Buffet, S., Chevenet, F., Dufayard, J. F., Guindon, S., Lefort, V., Lescot, M., Claverie, J. M. and Gascuel, O. (2008) 'Phylogeny.fr: robust phylogenetic analysis for the non-specialist',

Nucleic acids research, 36, pp. W465–W469. doi: 10.1093/nar/gkn180.

Derryberry, E. P., Claramunt, S., Derryberry, G., Chesser, R. T., Cracraft, J., Aleixo, A., Pérez-Emán, J., Remsen Jr., J. V. and Brumfield, R. T. (2011) 'Lineage diversification and morphological evolution in a large-scale continental radiation: the neotropical ovenbirds and woodcreepers (Aves: Furnariidae)', *Evolution*, 65(10), pp. 2973–2986. doi: 10.1111/j.1558-5646.2011.01374.x.

Désamoré, A., Laenen, B., Miller, K. B. and Bergsten, J. (2018) 'Early burst in body size evolution is uncoupled from species diversification in diving beetles (Dytiscidae)', *Molecular Ecology*, 27(4), pp. 979–993. doi: 10.1111/mec.14492.

Dong, S. and Kumazawa, Y. (2005) 'Complete Mitochondrial DNA Sequences of Six Snakes: Phylogenetic Relationships and Molecular Evolution of Genomic Features', *Journal of Molecular Evolution*, 61(1), pp. 12–22. doi: 10.1007/s00239-004-0190-9.

Douglas, D. A. and Gower, D. J. (2010) 'Snake mitochondrial genomes: phylogenetic relationships and implications of extended taxon sampling for interpretations of mitogenomic evolution', *BMC Genomics*, 11(1), p. 14. doi: 10.1186/1471-2164-11-14.

Drummond, A. J., Suchard, M. A., Xie, D. and Rambaut, A. (2012) 'Bayesian Phylogenetics with BEAUti and the BEAST 1.7', *Molecular Biology and Evolution*. Oxford University Press, 29(8), pp. 1969–1973. doi: 10.1093/molbev/mss075.

Duchêne, S., Lanfear, R. and Ho, S. Y. W. (2014) 'The impact of calibration and clock-model choice on molecular estimates of divergence times', *Molecular Phylogenetics and Evolution*, 78, pp. 277–289. doi: 10.1016/J.YMPEV.2014.05.032.

Felsenstein, J. (1985) 'Phylogenies and the Comparative Method', *The American Naturalist*, 125(1), pp. 1–15. doi: 10.1086/284325.

Felsenstein, J. (1988) 'Phylogenies and quantitative characters', *Annual Review of Ecology and Systematics*, 19(1), pp. 445–471.

Flouri, T., Jiao, X., Rannala, B. and Yang, Z. (2018) 'Species Tree Inference with BPP Using Genomic Sequences and the Multispecies Coalescent', *Molecular Biology and Evolution*, 35(10), pp. 2585–2593. doi: 10.1093/molbev/msy147.

Folk, R. A., Stubbs, R. L., Mort, M. E., Cellinese, N., Allen, J. M., Soltis, P. S., Soltis, D. E. and Guralnick, R. P. (2019) 'Rates of niche and phenotype evolution lag behind diversification in a temperate radiation', *Proceedings of the National Academy of Sciences of the United States of America*, 116(22), pp. 10874–10882. doi: 10.1073/pnas.1817999116.

Freckleton, R. P. and Harvey, P. H. (2006) 'Detecting Non-Brownian Trait Evolution in Adaptive Radiations', *PLoS Biology*, 4(11), p. e373. doi: 10.1371/journal.pbio.0040373.

Friedman, S. T., Martinez, C. M., Price, S. A. and Wainwright, P. C. (2019) 'The

influence of size on body shape diversification across Indo-Pacific shore fishes', *Evolution*, 73(9), pp. 1873–1884. doi: 10.1111/evo.13755.

Fulton, T. L. (2012) 'Setting up an ancient DNA laboratory', in Shapiro, B. and Hofreiter, M. (eds) *Methods in molecular biology. Ancient DNA: methods and protocols.* Humana Press, pp. 1–11.

Funk, D. J. and Omland, K. E. (2003) 'Species-Level Paraphyly and Polyphyly: Frequency, Causes, and Consequences, with Insights from Animal Mitochondrial DNA', *Annual Review of Ecology, Evolution, and Systematics*, 34(1), pp. 397–423. doi: 10.1146/annurev.ecolsys.34.011802.132421.

Galtier, N., Nabholz, B., Glémin, S. and Hurst, G. D. D. (2009) 'Mitochondrial DNA as a marker of molecular diversity: a reappraisal', *Molecular ecology*, 18(22), pp. 4541–50. doi: 10.1111/j.1365-294X.2009.04380.x.

Gans, C. (1968) 'Relative success of divergent pathways in amphisbaenian specialization', *The American Naturalist*, 102(926), pp. 345–362. doi: 10.1086/28254810.1086/282548.

Gans, C. (1976) 'Aspects of the biology of uropeltid snakes', in *Morphology and biology of reptiles*, pp. 191–204.

Gans, C. (1993) 'Fossorial amphibians and reptiles: their distributions as environmental indicators', in *Proceedings of the International and Interdisciplinary Symposium Ecology and Landscape Management in Sri Lanka. Margraf Scientific Books Weikersheim*, pp. 189–199.

Garcia-Porta, J., Morales, H. E., Gómez-Díaz, E., Sindaco, R. and Carranza, S. (2016) 'Patterns of diversification in islands: A comparative study across three gecko genera in the Socotra Archipelago', *Molecular Phylogenetics and Evolution*. Elsevier Inc., 98, pp. 288–299. doi: 10.1016/j.ympev.2016.02.007.

Gavrilets, S. and Vose, A. (2005) 'Dynamic patterns of adaptive radiation', *Proceedings of the National Academy of Sciences*, 102(50), pp. 18040–18045. doi: 10.1073/PNAS.0506330102.

Gehara, M., Barth, A., Oliveira, E. F. de, Costa, M. A., Haddad, C. F. B. and Vences, M. (2017) 'Model-based analyses reveal insular population diversification and cryptic frog species in the *Ischnocnema parva* complex in the Atlantic forest of Brazil', *Molecular Phylogenetics and Evolution*, 112, pp. 68–78. doi: 10.1016/J.YMPEV.2017.04.007.

Gilbert, M. T. P., Haselkorn, T., Bunce, M., Sanchez, J. J., Lucas, S. B., Jewell, L. D., van Marck, E. and Worobey, M. (2007) 'The Isolation of Nucleic Acids from Fixed, Paraffin-Embedded Tissues-Which Methods Are Useful When?', *PLoS ONE*, 2(6). doi: 10.1371/journal.pone.0000537.

Gomes, J. O. and Maciel, A. O. (2012) 'A new species of *Amphisbaena* Linnaeus (Squamata, Amphisbaenidae) from the state of Maranhão, northern Brazilian Cerrado', *Zootaxa*, 3572(3572), pp. 43–54. doi: 10.11646/zootaxa.3572.1.6.

Gower, D. J., Giri, V., Captain, A. and Wilkinson, M. (2016) 'A reassessment of

Melanophidium Günther, 1864 (Reptilia: Serpentes: Uropeltidae) from the Western Ghats region of peninsular India, with the description of a new species', 4085(4), pp. 481–503. doi: 10.11646/zootaxa.4085.4.2.

Gower, D. J. and Ablett, J. D. (2006) 'Counting ventral scales in Asian anilioid snakes', *Herpetological Journal*, 16(3), pp. 259–263.

Gower, D. J., Captain, A. and Thakur, S. S. (2008) 'On the taxonomic status of *Uropeltis bicatenata* (Günther) (Reptilia: Serpentes: Uropeltidae)', *Hamadryad*, 33(1), pp. 64–82.

Gower, D. J. and Maduwage, K. (2011) 'Two new species of Rhinophis Hemprich (Serpentes: Uropeltidae) from Sri Lanka', *Zootaxa*, 68(2881), pp. 51–68. doi: 10.11646/zootaxa.2881.1.4.

Gower, D. J. and Wickramasinghe, L. J. M. (2016) 'Recharacterization of *Rhinophis dorsimaculatus* Deraniyagala, 1941 (Serpentes: Uropeltidae), including description of new material', *Zootaxa*, 4158(2), pp. 203–212. doi: 10.11646/zootaxa.4158.2.3.

Grant, P. R. and Grant, B. R. (2008) *How and Why Species Multiply: The Radiation of Darwin's Finches*. Princeton Univ. Press.

Greene, H. W. (1973) 'Defensive Tail Display by Snakes and Amphisbaenians', *Journal of Herpetology*, 7(3), p. 143. doi: 10.2307/1563000.

Guibé, J. (1948) 'Étude du dimorphisme sexuel chez trois espéces du genre Silybura (Ophidien)'.

Guindon, S., Dufayard, J.-F., Lefort, V., Anisimova, M., Hordijk, W. and Gascuel, O. (2010) 'New Algorithms and Methods to Estimate Maximum-Likelihood Phylogenies: Assessing the Performance of PhyML 3.0', *Systematic Biology*, 59(3), pp. 307–321. doi: 10.1093/sysbio/syq010.

Gunawardene, N. R., Daniels, A. E. D., Gunatilleke, I. A. U. N., Gunatilleke, C. V. S., Karunakaran, P. V, Nayak, K. G., Prasad, S., Puyravaud, P., Ramesh, B. R., Subramanian, K. A., Vasanthy, G., Daniels, D. A., Gunatilleke, I. A. U. N., Gunatilleke, C. V. S., Karunakaran, P. V, Nayak, G. K., Prasad, S., Puyravaud, P., Ramesh, B. R., Subramanian, K. A. and Vasanthy, G. (2007) 'A brief overview of the Western Ghats – Sri Lanka biodiversity hotspot', *Current Science*, 93(11), pp. 1567–1572.

Hansen, T. F. (1997) 'Stabilizing selection and the comparative analysis of adaptation', *Evolution*, 51(5), pp. 1341–1351. doi: 10.1111/j.1558-5646.1997.tb01457.x.

Harmon, L. J., Schulte, J. A., Larson, A. and Losos, J. B. (2003) 'Tempo and mode of evolutionary radiation in iguanian lizards.', *Science*, 301(5635), pp. 961–964. doi: 10.1126/science.1084786.

Harmon, L. J., Kolbe, J. J., Cheverud, J. M. and Losos, J. B. (2005) 'Convergence and the multidimensional niche', *Evolution*, 59(2), pp. 409–421. doi: 10.1111/j.0014-3820.2005.tb00999.x.

Harmon, L. J., Weir, J. T., Brock, C. D., Glor, R. E. and Challenger, W. (2008)

'GEIGER: Investigating evolutionary radiations', *Bioinformatics*, 24(1), pp. 129–131. doi: 10.1093/bioinformatics/btm538.

Harmon, L. J., Losos, J. B., Jonathan Davies, T., Gillespie, R. G., Gittleman, J. L., Bryan Jennings, W., Kozak, K. H., McPeek, M. A., Moreno-Roark, F., Near, T. J., Purvis, A., Ricklefs, R. E., Schluter, D., Schulte II, J. A., Seehausen, O., Sidlauskas, B. L., Torres-Carvajal, O., Weir, J. T. and Mooers, A. Ø. (2010) 'Early bursts of body size and shape evolution are rare in comparative data', *Evolution*, 64(8), pp. 2385–2396. doi: 10.1111/j.1558-5646.2010.01025.x.

Harrington, S. M. and Reeder, T. O. D. W. (2017) 'Phylogenetic inference and divergence dating of snakes using molecules, morphology and fossils: new insights into convergent evolution of feeding morphology and limb reduction', *Biological Journal of the Linnean Society*, 121(2), pp. 379–394. doi: 10.1093/biolinnean/blw039.

He, M., Feng, J. and Zhao, E. (2010) 'The complete mitochondrial genome of the Sichuan hot-spring keel-back (Thermophis zhaoermii; Serpentes: Colubridae) and a mitogenomic phylogeny of the snakes', *Mitochondrial DNA*, 21(1), pp. 8–18. doi: 10.3109/19401730903505867.

Head, J. J. (2015) 'Fossil calibration dates for molecular phylogenetic analysis of snakes 1: Serpentes, Alethinophidia, Boidae, Pythonidae', *Paleontologica Electronica*, 18(1), pp. 1–17. doi: 10.26879/487.

Head, J. J., Mahlow, K. and Müller, J. (2016) 'Fossil calibration dates for molecular phylogenetic analysis of snakes 2: Caenophidia, Colubroidea, Elapoidea, Colubridae', *Palaeontologia Electronica*, 19(2), pp. 1–21. doi: 10.26879/625.

Heard, S. B. and Hauser, D. L. (1995) 'Key evolutionary innovations and their ecological mechanisms', *Historical Biology*, 10(2), pp. 151–173. doi: 10.1080/10292389509380518.

Heath, T. A., Hedtke, S. M. and Hillis, D. M. (2008) 'Taxon sampling and the accuracy of phylogenetic analyses', *Journal of Systematics and Evolution*, 46(3), pp. 239–257. doi: 10.3724/SP.J.1002.2008.08016.

Heibl, C. (2008) 'PHYLOCH: R language tree plotting tools and interfaces to diverse phylogenetic software packages. Avaliable online at: http://www.christophheibl.de/Rpackages.html'.

Heise, P. J., Maxson, L. R., Dowling, H. G. and Hedges, S. B. (1995) 'Higher-level snake phylogeny inferred from mtDNA 12S rRNA and 16S rRNA', *Molecular Biology and Evolution*, 12(2), pp. 259–265. doi: 10.1093/oxfordjournals.molbev.a040202.

Heled, J. and Drummond, A. J. (2012) 'Calibrated Tree Priors for Relaxed Phylogenetics and Divergence Time Estimation', *Systematic Biology*, 61(1), pp. 138–149. doi: 10.1093/sysbio/syr087.

Hilgen, F. J., Lourens, L. J., Van Dam, J. A., Beu, A. G., Boyes, A. F., Cooper, R. A., Krijgsman, W., Ogg, J. G., Piller, W. E. and Wilson, D. S. (2012) 'The Neogene Period', in *The Geologic Time Scale*. Elsevier, pp. 923–978. doi: 10.1016/B978-0-444-59425-9.00029-9.

Hoffstetter, R. and Gasc, J. P. (1969) 'Vertebrae and ribs of modern reptiles', in *Biology of the Reptilia 1(5)*, pp. 201–310.

Holt, E. W. L. and Byrne, L. W. (1908) 'Second report on the fishes of the Irish Atlantic slope', *Fisheries Ireland Scientific Investigations 1906*, (5), pp. 1–63.

Hoogmoed, M. S. ., Pinto, R. R. ., Rocha, W. A. Da and Pereira, E. G. . (2009) 'A New Species of *Mesobaena* Mertens, 1925 (Squamata: Amphisbaenidae) from Brazilian Guiana, with a Key to the Amphisbaenidae of the Guianan region', *Herpetologica*, 65(4), pp. 436–448. doi: 10.1655/08-062.1.

Hsiang, A. Y., Field, D. J., Webster, T. H., Behlke, A. D., Davis, M. B., Racicot, R. A. and Gauthier, J. A. (2015) 'The origin of snakes: revealing the ecology, behavior, and evolutionary history of early snakes using genomics, phenomics, and the fossil record', *BMC Evolutionary Biology*, 15(1), p. 87. doi: 10.1186/s12862-015-0358-5.

Hykin, S. M., Bi, K. and McGuire, J. A. (2015) 'Fixing formalin: A method to recover genomic-scale DNA sequence data from formalin-fixed museum specimens using high-throughput sequencing', *PLoS ONE*, 10(10), pp. 1–16. doi: 10.1371/journal.pone.0141579.

Ingram, T. and Mahler, D. L. (2013) 'SURFACE: detecting convergent evolution from comparative data by fitting Ornstein-Uhlenbeck models with stepwise Akaike Information Criterion', *Methods in Ecology and Evolution*. Edited by T. Hansen, 4(5), pp. 416–425. doi: 10.1111/2041-210X.12034.

IUCN (2018) *The IUCN Red List of Threatened Species. Version 2018-1. http://www.iucnredlist.org. Downloaded on July 2019.*

Jaramillo, C. A., Bayona, G., Pardo-Trujillo, A., Rueda, M., Torres, V., Harrington, G. J. and G. Mora (2007) 'The palynology of the Cerrejón Formation (upper Paleocene) of northern Colombia', *Palynology*. GeoScienceWorld, 31(1), pp. 153–189. doi: 10.2113/gspalynol.31.1.153.

Jiang, Z. J., Castoe, T. A., Austin, C. C., Burbrink, F. T., Herron, M. D., McGuire, J. A., Parkinson, C. L. and Pollock, D. D. (2007) 'Comparative mitochondrial genomics of snakes: extraordinary substitution rate dynamics and functionality of the duplicate control region', *BMC Evolutionary Biology*, 7(1), p. 123. doi: 10.1186/1471-2148-7-123.

Jins, V. J., Sampaio, F. L. and Gower, D. J. (2018) 'A new species of *Uropeltis* Cuvier, 1829 (Serpentes: Uropeltidae) from the Anaikatty Hills of the Western Ghats of India', *Zootaxa*, 4415(3), pp. 401–422. doi: 10.11646/zootaxa.4415.3.1.

Jónsson, H., Ginolhac, A., Schubert, M., Johnson, P. L. F. and Orlando, L. (2013) 'mapDamage2.0: fast approximate Bayesian estimates of ancient DNA damage parameters', *Bioinformatics*, 29(13), pp. 1682–1684. doi: 10.1093/bioinformatics/btt193.

Jønsson, K. A., Fabre, P. H., Fritz, S. A., Etienne, R. S., Ricklefs, R. E., Jorgensen, T. B., Fjeldsa, J., Rahbek, C., Ericson, P. G. P., Woog, F., Pasquet, E. and Irestedt, M. (2012) 'Ecological and evolutionary determinants for the adaptive

radiation of the Madagascan vangas', *Proceedings of the National Academy of Sciences*, 109(17), pp. 6620–6625. doi: 10.1073/pnas.1115835109.

Kapli, P., Lutteropp, S., Zhang, J., Kobert, K., Pavlidis, P., Stamatakis, A. and Flouri, T. (2017) 'Multi-rate Poisson Tree Processes for single-locus species delimitation under Maximum Likelihood and Markov Chain Monte Carlo', *Bioinformatics*. Narnia, 33(11), pp. 1630–1638. doi: 10.1093/bioinformatics/btx025.

Kazi, S. and Hipsley, C. A. (2018) 'Conserved evolution of skull shape in Caribbean head-first burrowing worm lizards (Squamata: Amphisbaenia)', *Biological Journal of the Linnean Society*, 125(1), pp. 14–29. doi: 10.1093/biolinnean/bly086/5053605.

Kearney, M. and Stuart, B. L. (2004) 'Repeated evolution of limblessness and digging heads in worm lizards revealed by DNA from old bones', *Proc R Soc Lond B Biol Sci*. The Royal Society, 271(1549), pp. 1677–1687. doi: 10.1098/rspb.2004.2771.

Kearse, M., Moir, R., Wilson, A., Stones-Havas, S., Cheung, M., Sturrock, S., Buxton, S., Cooper, A., Markowitz, S., Duran, C., Thierer, T., Ashton, B., Meintjes, P. and Drummond, A. (2012) 'Geneious Basic: An integrated and extendable desktop software platform for the organization and analysis of sequence data', *Bioinformatics*, 28(12), pp. 1647–1649. doi: 10.1093/bioinformatics/bts199.

Kieckbusch, M., Mader, F., Kaiser, H. and Mecke, S. (2018) 'A new species of *Cylindrophis* Wagler, 1828 (Reptilia: Squamata: Cylindrophiidae) from Boano Island, northern Maluku Province, Indonesia', *Zootaxa*, 4486(3), pp. 236–250. doi: 10.11646/zootaxa.4486.3.2.

King, R. B. (2002) 'Predicted and observed maximum prey size - snake size allometry', *Functional Ecology*, 16(6), pp. 766–772. doi: 10.1046/j.1365-2435.2002.00678.x.

Kocher, T. D., Thomas, W. K., Meyer, A., Edwards, S. V, Pääbo, S., Villablanca, F. X. and Wilson, A. C. (1989) 'Dynamics of mitochondrial DNA evolution in animals: Amplification and sequencing with conserved primers', *Proceedings of the National Academy of Sciences of the United States of America*, 86(16), pp. 6196–6200. doi: 10.1073/pnas.86.16.6196.

Kozak, K. H., Weisrock, D. W. and Larson, A. (2006) 'Rapid lineage accumulation in a non-adaptive radiation: phylogenetic analysis of diversification rates in eastern North American woodland salamanders (Plethodontidae: *Plethodon*)', *Proceedings of the Royal Society B: Biological Sciences*, 273(1586), pp. 539–546. doi: 10.1098/rspb.2005.3326.

Kumazawa, Y., Ota, H., Nishida, M. and Ozawa, T. (1996) 'Gene Rearrangements in Snake Mitochondrial Genomes: Highly Concerted Evolution of Control-Region-Like Sequences Duplicated and Inserted into a tRNA Gene Cluster', *Molecular Biology and Evolution*, 13(9), pp. 1242–1254. doi: 10.1093/oxfordjournals.molbev.a025690.

Lajmi, A., Bansal, R., Giri, V. and Karanth, P. (2018) 'Phylogeny and biogeography of the endemic *Hemidactylus* geckos of the Indian subregion suggest multiple dispersals from Peninsular India to Sri Lanka', *Zoological Journal of the Linnean Society*, 186(1), pp. 286–301. doi: 10.1093/zoolinnean/zly047/5049994.

Lajmi, A. and Karanth, P. K. (2019) 'Eocene–Oligocene cooling and the diversification of *Hemidactylus* geckos in Peninsular India', *Molecular Phylogenetics and Evolution*. Elsevier BV, p. 106637. doi: 10.1016/j.ympev.2019.106637.

Lajmi, A., Verma, A. and Karanth, K. P. (2019) 'Repeated evolution of terrestrial lineages in a continental lizard radiation', *Journal of Evolutionary Biology*. Wiley. doi: 10.1111/jeb.13544.

Lanfear, R., Calcott, B., Ho, S. Y. W. and Guindon, S. (2012) 'PartitionFinder: combined selection of partitioning schemes and substitution models for phylogenetic analyses', *Molecular Biology and Evolution*, 29(6), pp. 1695–1701. doi: 10.1093/molbev/mss020.

Lanfear, R., Frandsen, P. B., Wright, A. M., Senfeld, T. and Calcott, B. (2016) 'PartitionFinder 2: New Methods for Selecting Partitioned Models of Evolution for Molecular and Morphological Phylogenetic Analyses', *Molecular Biology and Evolution*, 34(3), pp. 772–773. doi: 10.1093/molbev/msw260.

Lawson, R., Slowinski, J. B., Crother, B. I. and Burbrink, F. T. (2005) 'Phylogeny of the Colubroidea (Serpentes): New evidence from mitochondrial and nuclear genes', *Molecular Phylogenetics and Evolution*, 37(2), pp. 581–601. doi: 10.1016/J.YMPEV.2005.07.016.

Leaché, A. D. and Fujita, M. K. (2010) 'Bayesian species delimitation in West African forest geckos (*Hemidactylus fasciatus*)', *Proceedings of the Royal Society B: Biological Sciences*. The Royal Society, 277(1697), pp. 3071–3077. doi: 10.1098/rspb.2010.0662.

Lee, M. S. and Scanlon, J. D. (2002) 'Snake phylogeny based on osteology, soft anatomy and ecology', *Biological Reviews*, 77, pp. 333–401. doi: 10.1017/s1464793102005924.

Li, H., Handsaker, B., Wysoker, A., Fennell, T., Ruan, J., Homer, N., Marth, G., Abecasis, G., Durbin, R. and 1000 Genome Project Data Processing Subgroup (2009) 'The Sequence Alignment/Map format and SAMtools', *Bioinformatics*, 25(16), pp. 2078–2079. doi: 10.1093/bioinformatics/btp352.

Li, H. and Durbin, R. (2009) 'Fast and accurate short read alignment with Burrows-Wheeler transform', *Bioinformatics*, 25(14), pp. 1754–1760. doi: 10.1093/bioinformatics/btp324.

Liedtke, H. C., Müller, H., Rödel, M. O., Menegon, M., Gonwouo, L. G. N., Barej, M. F., Gvoždík, V., Schmitz, A., Channing, A., Nagel, P. and Loader, S. P. (2016) 'No ecological opportunity signal on a continental scale? Diversification and life-history evolution of African true toads (Anura: Bufonidae)', *Evolution*, 70(8), pp. 1717–1733. doi: 10.1111/evo.12985.

Liu, Y., Ding, L., Lei, J., Zhao, E. and Tang, Y. (2012) 'Eye size variation reflects habitat and daily activity patterns in colubrid snakes', *Journal of Morphology*, 273(8), pp. 883–893. doi: 10.1002/jmor.20028.

Longrich, N. R., Bhullar, B.-A. S. and Gauthier, J. A. (2012) 'A transitional snake from the Late Cretaceous period of North America', *Nature*, 488(7410), pp. 205–208. doi: 10.1038/nature11227.

Losos, J. B., Jackman, T. R., Larson, A., Queiroz, K. de and Rodríguez-Schettino, L. (1998) 'Contingency and Determinismin Replicated Adaptative Radiations of Island Lizards', *Science*, 279(1998), pp. 2115–2118. doi: 10.1126/science.279.5359.2115.

Losos, J. B., Glor, R. E., Kolbe, J. J. and Nicholson, K. (2006) 'Adaptation, speciation, and convergence: a hierarchical analysis of adaptive radiation in Caribbean *Anolis* lizards', *Annals of the Missouri Botanical Garden*, 93(1), pp. 24–33. doi: 10.3417/0026-6493(2006)93[24:ASACAH]2.0.CO;2.

Lukoschek, V., Scott Keogh, J. and Avise, J. C. (2012) 'Evaluating Fossil Calibrations for Dating Phylogenies in Light of Rates of Molecular Evolution: A Comparison of Three Approaches', *Systematic Biology*, 61(1), p. 22. doi: 10.1093/sysbio/syr075.

Luo, A., Ling, C., Ho, S. Y. W. and Zhu, C. D. (2018) 'Comparison of methods for molecular species delimitation across a range of speciation scenarios', *Systematic Biology*, 67(5), pp. 830–846. doi: 10.1093/sysbio/syy011.

Machado, V. N., Collins, R. A., Ota, R. P., Andrade, M. C., Farias, I. P. and Hrbek, T. (2018) 'One thousand DNA barcodes of piranhas and pacus reveal geographic structure and unrecognised diversity in the Amazon', *Scientific Reports*, 8(1), p. 8387. doi: 10.1038/s41598-018-26550-x.

Mahler, D. L., Revell, L. J., Glor, R. E. and Losos, J. B. (2010) 'Ecological opportunity and the rate of morphological evolution in the diversification of Greater Antillean anoles', *Evolution*, 64(9), pp. 2731–2745. doi: 10.1111/j.1558-5646.2010.01026.x.

Maliet, O., Hartig, F. and Morlon, H. (2019) 'A model with many small shifts for estimating species-specific diversification rates', *Nature Ecology & Evolution*, 3(7), pp. 1086–1092. doi: 10.1038/s41559-019-0908-0.

Marr, M. M., Brace, S., Schreve, D. C. and Barnes, I. (2018) 'Identifying source populations for the reintroduction of the Eurasian beaver, *Castor fiber* L. 1758, into Britain: evidence from ancient DNA', *Scientific Reports*, 8(1), p. 2708. doi: 10.1038/s41598-018-21173-8.

Martill, D. M., Tischlinger, H. and Longrich, N. R. (2015) 'A four-legged snake from the Early Cretaceous of Gondwana', *Science*, 349(6246), pp. 416–419. doi: 10.1126/science.aaa9208.

McDiarmid, R. W., Campbell, J. A. and Toure, T. (1999) *Snake Species of the World: A Taxonomic and Geographic Reference. Volume 1*.

McGuire, J. A., Cotoras, D. D., O'Connell, B., Lawalata, S. Z. S., Wang-Claypool, C. Y., Stubbs, A., Huang, X., Wogan, G. O. U., Hykin, S. M., Reilly, S. B., Bi,

K., Riyanto, A., Arida, E., Smith, L. L., Milne, H., Streicher, J. W. and Iskandar, D. T. (2018) 'Squeezing water from a stone: high-throughput sequencing from a 145-year old holotype resolves (barely) a cryptic species problem in flying lizards', *PeerJ*. PeerJ Inc., 6, p. e4470. doi: 10.7717/peerj.4470.

Meegaskumbura, M., Senevirathne, G., Manamendra-Arachchi, K., Pethiyagoda, R., Hanken, J. and Schneider, C. J. (2019) 'Diversification of shrub frogs (Rhacophoridae, *Pseudophilautus*) in Sri Lanka – Timing and geographic context', *Molecular Phylogenetics and Evolution*, 132, pp. 14–24. doi: 10.1016/J.YMPEV.2018.11.004.

Melvinselvan, G. and Nibedita, D. (2016) 'Defelsive caudal display in *Uropeltis pulneyensis* Beddome 1863 (Serpentes: Uropeltidae) from Palani Hills, Western Ghats, India', *Russian Journal of Herpetology*, 23(1), pp. 77–80.

Meyer, A. L. S., Román-Palacios, C. and Wiens, J. J. (2018) 'BAMM gives misleading rate estimates in simulated and empirical datasets', *Evolution*, 72(10), pp. 2257–2266. doi: 10.1111/evo.13574.

Meyer, A. L. S. and Wiens, J. J. (2018) 'Estimating diversification rates for higher taxa: BAMM can give problematic estimates of rates and rate shifts', *Evolution*, 72(1), pp. 39–53. doi: 10.1111/evo.13378.

Meyer, M. and Kircher, M. (2010) 'Illumina sequencing library preparation for highly multiplexed target capture and sequencing', *Cold Spring Harbor Protocols*, 2010(6), p. pdb-prot5448. doi: 10.1101/pdb.prot5448.

Miller, M. A., Pfeiffer, W. and Schwartz, T. (2010) 'Creating the CIPRES Science Gateway for inference of large phylogenetic trees', in *2010 Gateway Computing Environments Workshop (GCE)*. IEEE, pp. 1–8. doi: 10.1109/GCE.2010.5676129.

Miralles, A., Marin, J., Markus, D., Herrel, A., Hedges, S. B. and Vidal, N. (2018) 'Molecular evidence for the paraphyly of Scolecophidia and its evolutionary implications', *Journal of Evolutionary Biology*, 31(12), pp. 1782–1793. doi: 10.1111/jeb.13373.

Moen, D. and Morlon, H. (2014) 'Why does diversification slow down?', *Trends in Ecology & Evolution*. Elsevier Current Trends, 29(4), pp. 190–197. doi: 10.1016/J.TREE.2014.01.010.

Monteiro, L. R. (2013) 'Morphometrics and the comparative method: studying the evolution of biological shape', *Hystrix, the Italian Journal of Mammalogy*, 24(1), pp. 25–32.

Morlon, H. (2014) 'Phylogenetic approaches for studying diversification', *Ecology Letters*, 17(4), pp. 508–525. doi: 10.1111/ele.12251.

Morlon, H., Lewitus, E., Condamine, F. L., Manceau, M., Clavel, J. and Drury, J. (2016) 'RPANDA: an R package for macroevolutionary analyses on phylogenetic trees', *Methods in Ecology and Evolution*, 7(5), pp. 589–597. doi: 10.1111/2041-210X.12526.

Mott, T., Rodrigues, M. T., De Freitas, M. A. and Silva, T. F. S. (2008) 'New Species

of Amphisbaena with a Nonautotomic and Dorsally Tuberculate Blunt Tail from State of Bahia, Brazil (Squamata, Amphisbaenidae)', *Journal of Herpetology*, 42(1), pp. 172–175. doi: 10.1670/07-074R2.1.

Mundry, R. (2014) *Statistical Issues and Assumptions of Phylogenetic Generalized Least Squares*, *Modern Phylogenetic Comparative Methods and Their Application in Evolutionary Biology*. doi: 10.1007/978-3-662-43550-2_6.

Murrell, D. J. (2018) 'A global envelope test to detect non-random bursts of trait evolution', *Methods in Ecology and Evolution*, 9(7), pp. 1739–1748. doi: 10.1111/2041-210X.13006.

Myers, N., Mittermeier, R. A., Mittermeier, C. G., da Fonseca, G. A. B. and Kent, J. (2000) 'Biodiversity hotspots for conservation priorities.', *Nature*, 403(6772), pp. 853–8. doi: 10.1038/35002501.

Navas, C. A., Antoniazzi, M. M., Carvalho, J. E., Chaui-Berlink, J. G., James, R. S., Jared, C., Kohlsdorf, T., Dal Pai-Silva, M. and Wilson, R. S. (2004) 'Morphological and physiological specialization for digging in amphisbaenians, an ancient lineage of fossorial vertebrates', *Journal of Experimental Biology*, 207(14), pp. 2433–2441. doi: 10.1242/jeb.01041.

Officer, C. B., Hallam, A., Drake, C. L. and Devine, J. D. (1987) 'Late Cretaceous and paroxysmal Cretaceous/Tertiary extinctions', *Nature*, 326(6109), pp. 143–149. doi: 10.1038/326143a0.

Okonechnikov, K., Conesa, A. and García-Alcalde, F. (2015) 'Qualimap 2: advanced multi-sample quality control for high-throughput sequencing data', *Bioinformatics*. Narnia, 32(2), p. btv566. doi: 10.1093/bioinformatics/btv566.

Olori, J. C. (2010) 'Digital Endocasts of the Cranial Cavity and Osseous Labyrinth of the Burrowing Snake *Uropeltis woodmasoni* (Alethinophidia: Uropeltidae)', *Copeia*, 2010(1), pp. 14–26. doi: 10.1643/CH-09-082.

Olori, J. C. and Bell, C. J. (2012) 'Comparative skull morphology of uropeltid snakes (Alethinophidia: Uropeltidae) with special reference to disarticulated elements and variation', *PloS one*, 7(3), p. e32450. doi: 10.1371/journal.pone.0032450.

Pääbo, S. (1989) 'Ancient DNA: Extraction, characterization, molecular cloning, and enzymatic amplification', *Proceedings of the National Academy of Sciences*, 86(6), pp. 1939–1943. doi: 10.1073/pnas.86.6.1939.

Padial, J. M., Miralles, A., De la Riva, I. and Vences, M. (2010) 'The integrative future of taxonomy', *Frontiers in Zoology*, 7(1), p. 16. doi: 10.1186/1742-9994-7-16.

Pagel, M. (1999) 'Inferring the historical patterns of biological evolution', *Nature*, 401(6756), pp. 877–884. doi: 10.1038/44766.

Palci, A., Hutchinson, M. N., Caldwell, M. W. and Lee, M. S. Y. (2017) 'The morphology of the inner ear of squamate reptiles and its bearing on the origin of snakes', *Royal Society Open Science*, 4(8), p. 170685. doi: 10.1098/rsos.170685.

Palumbi, S. R., Martin, A., Romano, S., McMillan, W. O., Stice, L. and Grabowski, G. (1991) *The Simple Fool's Guide to PCR, Version 2.0, privately published document compiled by S. Palumbi. Dept. Zoology, Univ. Hawaii, Honolulu, HI, 96822.*

Palumbi, S. R. (1996) 'Nucleic acids II: the polymerase chain reaction.', in Hillis, D., Moritz, C., and Mable, B. K. (eds) *Molecular systematics*. Sunderland, Massachusetts: Sinauer Associates, pp. 205–247.

Paradis, E. and Schliep, K. (2019) 'ape 5.0: an environment for modern phylogenetics and evolutionary analyses in R', *Bioinformatics*, 35(3), pp. 526–528. doi: 10.1093/bioinformatics/bty633.

Pennell, M. W., Eastman, J. M., Slater, G. J., Brown, J. W., Uyeda, J. C., FitzJohn, R. G., Alfaro, M. E. and Harmon, L. J. (2014) 'geiger v2.0: an expanded suite of methods for fitting macroevolutionary models to phylogenetic trees', *Bioinformatics*, 30(15), pp. 2216–2218. doi: 10.1093/bioinformatics/btu181.

Phillimore, A. B. and Price, T. D. (2008) 'Density-Dependent Cladogenesis in Birds', *PLoS Biology*, 6(3), p. e71. doi: 10.1371/journal.pbio.0060071.

Phillips, M. J. (2009) 'Branch-length estimation bias misleads molecular dating for a vertebrate mitochondrial phylogeny', *Gene*, 441(1–2), pp. 132–140. doi: 10.1016/J.GENE.2008.08.017.

Pinto, G., Mahler, D. L., Harmon, L. J. and Losos, J. B. (2008) 'Testing the island effect in adaptive radiation: rates and patterns of morphological diversification in Caribbean and mainland *Anolis* lizards', *Proceedings of the Royal Society of London, Series B*, 275(1652), pp. 2749–57. doi: 10.1098/rspb.2008.0686.

Plummer, M., Best, N., Cowles, K. and Vines, K. (2006) 'CODA: convergence diagnosis and output analysis for MCMC', *R News*, 6(1), pp. 7–11.

Polly, P. D., Lawing, A. M., Fabre, A.-C. and Goswami, A. (2013) 'Phylogenetic Principal Components Analysis and Geometric Morphometrics', *Hystrix, the Italian Journal of Mammalogy*. Associazione Teriologica Italiana, 24(1), pp. 33–41. doi: 10.4404/hystrix-24.1-6383.

Pons, J., Barraclough, T. G., Gomez-Zurita, J., Cardoso, A., Duran, D. P., Hazell, S., Kamoun, S., Sumlin, W. D. and Vogler, A. P. (2006) 'Sequence-Based Species Delimitation for the DNA Taxonomy of Undescribed Insects', *Systematic Biology*, 55(4), pp. 595–609. doi: 10.1080/10635150600852011.

Price, S. A., Friedman, S. T., Corn, K. A., Martinez, C. M., Larouche, O. and Wainwright, P. C. (2019) 'Building a Body Shape Morphospace of Teleostean Fishes', *Integrative and Comparative Biology*, 59(3), pp. 716–730. doi: 10.1093/icb/icz115.

Pybus, O. G. and Harvey, P. H. (2000) 'Testing macro-evolutionary models using incomplete molecular phylogenies', *Proceedings of the Royal Society of London. Series B: Biological Sciences*, 267(1459), pp. 2267–2272. doi: 10.1098/rspb.2000.1278.

Pyron, R. A., Ganesh, S. R., Sayyed, A., Sharma, V., Wallach, V. and Somaweera, R. (2016) 'A catalogue and systematic overview of the shield-tailed snakes (Serpentes: Uropeltidae)', *Zoosystema*, 38(4), pp. 453–506. doi: 10.5252/z2016n4a2.

Qian, L., Wang, H., Yan, J., Pan, T., Jiang, S., Rao, D. and Zhang, B. (2018) 'Multiple independent structural dynamic events in the evolution of snake mitochondrial genomes', *BMC Genomics*, 19(1), p. 354. doi: 10.1186/s12864-018-4717-7.

R Development Core Team (2019) 'R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria. URL https://www.R-project.org/'.

Rabosky, D. L., Santini, F., Eastman, J., Smith, S. A., Sidlauskas, B., Chang, J. and Alfaro, M. E. (2013) 'Rates of speciation and morphological evolution are correlated across the largest vertebrate radiation', *Nature Communications*, 4(1), p. 1958. doi: 10.1038/ncomms2958.

Rabosky, D. L. (2014) 'Automatic detection of key innovations, rate shifts, and diversity-dependence on phylogenetic trees', *PLoS ONE*, 9(2). doi: 10.1371/journal.pone.0089543.

Rabosky, D. L., Grundler, M., Anderson, C., Title, P., Shi, J. J., Brown, J. W., Huang, H. and Larson, J. G. (2014) 'BAMMtools: an R package for the analysis of evolutionary dynamics on phylogenetic trees', *Methods in Ecology and Evolution*, 5(7), pp. 701–707. doi: 10.1111/2041-210X.12199.

Rabosky, D. L. (2018) 'BAMM at the court of false equivalency: A response to Meyer and Wiens', *Evolution*, 72(10), pp. 2246–2256. doi: 10.1111/evo.13566.

Rabosky, D. L. (2019) 'Phylogenies and Diversification Rates: Variance Cannot Be Ignored', *Systematic Biology*, 68(3), pp. 538–550. doi: 10.1093/sysbio/syy079.

Rabosky, D. L. and Lovette, I. J. (2008) 'Density-dependent diversification in North American wood warblers', *Proceedings of the Royal Society B: Biological Sciences*, 275(1649), pp. 2363–2371. doi: 10.1098/rspb.2008.0630.

Rajendran, M. V. (1985) *Studies in Uropeltid Snakes*. Madurai Kamaraj University.

Rambaut, A., Drummond, A. J., Xie, D., Baele, G. and Suchard, M. A. (2018) 'Posterior Summarization in Bayesian Phylogenetics Using Tracer 1.7', *Systematic Biology*, 67(5), pp. 901–904. doi: 10.1093/sysbio/syy032.

Rannala, B. and Yang, Z. (2003) 'Bayes Estimation of Species Divergence Times and Ancestral Population Sizes Using DNA Sequences From Multiple Loci', *Genetics*, 164(4).

Rannala, B. and Yang, Z. (2013) 'Improved reversible jump algorithms for Bayesian species delimitation', *Genetics*, 194(1), pp. 245–53. doi: 10.1534/genetics.112.149039.

Rasmussen, S., Allentoft, M. E., Nielsen, K., Orlando, L., Sikora, M., Sjögren, K.-G., Pedersen, A. G., Schubert, M., Van Dam, A., Kapel, C. M. O., Nielsen, H. B.,

Brunak, S., Avetisyan, P., Epimakhov, A., Khalyapin, M. V., Gnuni, A., Kriiska, A., Lasak, I., Metspalu, M., Moiseyev, V., Gromov, A., Pokutta, D., Saag, L., Varul, L., Yepiskoposyan, L., Sicheritz-Pontén, T., Foley, R. A., Lahr, M. M., Nielsen, R., Kristiansen, K. and Willerslev, E. (2015) 'Early divergent strains of Yersinia pestis in Eurasia 5,000 years ago', *Cell*, 163(3), pp. 571–82. doi: 10.1016/j.cell.2015.10.009.

Reddy, S., Driskell, A., Rabosky, D. L., Hackett, S. J. and Schulenberg, T. S. (2012) 'Diversification and the adaptive radiation of the vangas of Madagascar', *Proceedings of the Royal Society B: Biological Sciences*. The Royal Society, 279(1735), pp. 2062–2071. doi: 10.1098/rspb.2011.2380.

Reid, N. M. and Carstens, B. C. (2012) 'Phylogenetic estimation error can decrease the accuracy of species delimitation: a Bayesian implementation of the general mixed Yule-coalescent model', *BMC Evolutionary Biology*, 12(1), p. 196. doi: 10.1186/1471-2148-12-196.

Revell, L. J. (2009) 'Size-correction and principal components for interspecific comparative studies', *Evolution*, 63(12), pp. 3258–3268. doi: 10.1111/j.1558-5646.2009.00804.x.

Revell, L. J. (2010) 'Phylogenetic signal and linear regression on species data', *Methods in Ecology and Evolution*, 1(4), pp. 319–329. doi: 10.1111/j.2041-210X.2010.00044.x.

Revell, L. J. (2012) 'phytools: an R package for phylogenetic comparative biology (and other things)', *Methods in Ecology and Evolution*, 3(2), pp. 217–223. doi: 10.1111/j.2041-210X.2011.00169.x.

Revell, L. J., Harmon, L. J. and Collar, D. C. (2008) 'Phylogenetic Signal, Evolutionary Process, and Rate', *Systematic Biology*, 57(4), pp. 591–601. doi: 10.1080/10635150802302427.

Reynolds, R. G., Collar, D. C., Pasachnik, S. A., Niemiller, M. L., Puente-Rol??n, A. R., Revell, L. J., Puente-rolón, A. R. and Revell, L. J. (2016) 'Ecological specialization and morphological diversification in Greater Antillean boas', *Evolution*, 70(8), pp. 1882–1895. doi: 10.1111/evo.12987.

Ricklefs, R. E. (2007) 'Estimating diversification rates from phylogenetic information', *Trends in Ecology & Evolution*, 22(11), pp. 601–610. doi: 10.1016/J.TREE.2007.06.013.

Ricklefs, R. E. and Miles, D. B. (1994) 'Ecological and evolutionary inferences from morphology: An ecological perspective', in *Ecological morphology: Integrative organismal biology*. Chicago, IL: University of Chicago Press, pp. 13–41.

Rieppel, O. (2012) '"Regressed" Macrostomatan Snakes', *Fieldiana Life and Earth Sciences*, 5(5), pp. 99–103. doi: 10.3158/2158-5520-5.1.99.

Rieppel, O. and Zaher, H. (2002) 'The skull of the Uropeltinae (Reptilia, Serpentes), with special reference to the otico-occipital region', *Bulletin of The Natural History Museum. Zoology Series*, 68(02), pp. 123–130. doi: 10.1017/s0968047002000146.

Ronquist, F., Teslenko, M., Mark, P. van der, Ayres, D. L., Darling, A., Höhna, S., Larget, B., Liu, L., Suchard, M. A. and Huelsenbeck, J. P. (2012) 'MrBayes 3.2: efficient Bayesian phylogenetic inference and model choice across a large model space', *Systematic Biology*, 61(3), pp. 539–542. doi: 10.1093/sysbio/sys029.

Ruane, S. and Austin, C. C. (2017) 'Phylogenomics using formalin-fixed and 100+ year old intractable natural history specimens', *Molecular Ecology Resources*, 17(5), pp. 1003–1008. doi: 10.1111/1755-0998.12655.

Rundell, R. J. and Price, T. D. (2009) 'Adaptive radiation, nonadaptive radiation, ecological speciation and nonecological speciation', *Trends in Ecology & Evolution*, 24(7), pp. 394–399. doi: 10.1016/J.TREE.2009.02.007.

Saint, K. M., Austin, C. C., Donellan, S. C., Hutchinson, M. N., Donnellan, S. C. and Hutchinson, M. N. (1998) 'C-mos, a nuclear marker useful for squamate phylogenetic analysis', *Molecular phylogenetics and evolution*, 10(2), pp. 259–263. doi: 10.1006/mpev.1998.0515.

Sanders, K. L., Mumpuni, Hamidy, A., Head, J. J. and Gower, D. J. (2010) 'Phylogeny and divergence times of filesnakes (*Acrochordus*): Inferences from morphology, fossils and three molecular loci', *Molecular Phylogenetics and Evolution*, 56(3), pp. 857–867. doi: 10.1016/j.ympev.2010.04.031.

Scanlon, J. D., Lee, M. S. Y., Caldwell, M. W. and Shine, R. (1999) 'The palaeoecology of the primitive snake *Pachyrhachis*', *Historical Biology*, 13(2–3), pp. 127–152. doi: 10.1080/08912969909386578.

Scanlon, J. D. and Lee, M. S. (2011) 'The major clades of living snakes: morphological evolution, molecular phylogeny, and divergence dates', in *Reproductive biology and phylogeny of snakes*. CRC Press, pp. 55–95.

Schluter, D. (2000) *The ecology of adaptive radiation*. OUP Oxford.

Schubert, M., Ginolhac, A., Lindgreen, S., Thompson, J. F., AL-Rasheid, K. A. S., Willerslev, E., Krogh, A. and Orlando, L. (2012) 'Improving ancient DNA read mapping against modern reference genomes', *BMC Genomics*, 13(1). doi: 10.1186/1471-2164-13-178.

Schubert, M., Lindgreen, S. and Orlando, L. (2016) 'AdapterRemoval v2: Rapid adapter trimming, identification, and read merging', *BMC Research Notes*. BioMed Central, 9(1), pp. 1–7. doi: 10.1186/s13104-016-1900-2.

Seehausen, O. (2006) 'African cichlid fish: a model system in adaptive radiation research', *Proceedings of the Royal Society B: Biological Sciences*, 273(1597), pp. 1987–1998. doi: 10.1098/rspb.2006.3539.

Seitz, A. and Nieselt, K. (2017) 'Improving ancient DNA genome assembly', *PeerJ*, 5, p. e3126. doi: 10.7717/peerj.3126.

Sherratt, E., Gower, D. J., Klingenberg, C. P. and Wilkinson, M. (2014) 'Evolution of Cranial Shape in Caecilians (Amphibia: Gymnophiona)', *Evolutionary Biology*, 41(4), pp. 528–545. doi: 10.1007/s11692-014-9287-2.

Sherratt, E., Vidal-García, M., Anstis, M. and Keogh, J. S. (2017) 'Adult frogs and

tadpoles have different macroevolutionary patterns across the Australian continent', *Nature Ecology and Evolution*, 1(9), pp. 1385–1391. doi: 10.1038/s41559-017-0268-6.

Sherratt, E., Coutts, F. J., Rasmussen, A. R. and Sanders, K. L. (2019) 'Vertebral evolution and ontogenetic allometry: The developmental basis of extreme body shape divergence in microcephalic sea snakes', *Evolution & Development*, 21(3), pp. 135–144. doi: 10.1111/ede.12284.

Sherratt, E., Rasmussen, A. R. and Sanders, K. L. (2018) 'Trophic specialization drives morphological evolution in sea snakes', *Royal Society Open Science*, 5(3), p. 172141. doi: 10.1098/rsos.172141.

Sidlauskas, B. (2008) 'Continuous and arrested morphological diversification in sister clades of characiform fishes: a phylomorphospace approach', *Evolution*, 62(12), pp. 3135–3156. doi: 10.1111/J.1558-5646.2008.00519.X.

Da Silva, F. O., Fabre, A. C., Savriama, Y., Ollonen, J., Mahlow, K., Herrel, A., Müller, J. and Di-Poï, N. (2018) 'The ecological origins of snakes as revealed by skull evolution', *Nature Communications*, 9(1), pp. 1–11. doi: 10.1038/s41467-017-02788-3.

Simmons, J. E. (2014) *Fluid preservation: a comprehensive reference.* Rowman & Littlefield.

Simões, B. F., Sampaio, F. L., Jared, C., Antoniazzi, M. M., Loew, E. R., Bowmaker, J. K., Rodriguez, A., Hart, N. S., Hunt, D. M., Partridge, J. C. and Gower, D. J. (2015) 'Visual system evolution and the nature of the ancestral snake', *Journal of Evolutionary Biology*, 28(7), pp. 1309–1320. doi: 10.1111/jeb.12663.

Simões, M., Breitkreuz, L., Alvarado, M., Baca, S., Cooper, J. C., Heins, L., Herzog, K. and Lieberman, B. S. (2016) 'The Evolving Theory of Evolutionary Radiations', *Trends in Ecology & Evolution*, 31(1), pp. 27–34. doi: 10.1016/J.TREE.2015.10.007.

Simpson, G. G. (1944) *Tempo and mode in evolution*. New York: Columbia University Press.

Simpson, G. G. (1953) *The major features of evolution*. New York: Columbia Univ. Press.

Slater, G. J., Price, S. A., Santini, F. and Alfaro, M. E. (2010) 'Diversity versus disparity and the radiation of modern cetaceans', *Proceedings of the Royal Society B: Biological Sciences*, 277(1697), pp. 3097–3104. doi: 10.1098/rspb.2010.0408.

Slater, G. J. and Pennell, M. W. (2014) 'Robust Regression and Posterior Predictive Simulation Increase Power to Detect Early Bursts of Trait Evolution', *Systematic Biology*, 63(3), pp. 293–308. doi: 10.1093/sysbio/syt066.

Smith, M. A. (1943) *Fauna of British India. Vol. III Serpentes*. Taylor and Francis.

Streicher, J. W. and Wiens, J. J. (2016) 'Phylogenomic analyses reveal novel

relationships among snake families', *Molecular Phylogenetics and Evolution*, 100, pp. 160–169. doi: 10.1016/j.ympev.2016.04.015.

Sukumaran, J. and Holder, M. T. (2010a) 'DendroPy: a Python library for phylogenetic computing', *Bioinformatics*, 26(12), pp. 1569–1571. doi: 10.1093/bioinformatics/btq228.

Sukumaran, J. and Holder, M. T. (2010b) 'SumTrees: Phylogenetic tree summarization. 4.4.0. Available at https://github.com/jeetsukumaran/DendroPy.'

Symonds, M. R. E. and Blomberg, S. P. (2014) 'A Primer on Phylogenetic Generalised Least Squares', in *Modern Phylogenetic Comparative Methods and Their Application in Evolutionary Biology*. Springer Berlin Heidelberg, pp. 105–130. doi: 10.1007/978-3-662-43550-2_5.

Talavera, G., Dincă, V. and Vila, R. (2013) 'Factors affecting species delimitations with the GMYC model: insights from a butterfly survey', *Methods in Ecology and Evolution*, 4(12), pp. 1101-1110. doi: 10.1111/2041-210X.12107.

Teixeira, M., Dal Vechio, F., Neto, A. M., Trefaut, M., Teixeira Jr, M., Vechio, F. D., Neto, A. M. and Rodrigues, M. T. (2014) 'A New Two-Pored *Amphisbaena* Linnaeus, 1758, from Western Amazonia, Brazil (Amphisbaenia: Reptilia)', *South American Journal of Herpetology*. Brazilian Society of Herpetology, 9(1), pp. 62–74. doi: 10.2994/SAJH-D-14-00004.1.

Thompson, J. D., Higgins, D. G. and Gibson, T. J. (1994) 'CLUSTAL W: improving the sensitivity of progressive multiple sequence alignment through sequence weighting, position-specific gap penalties and weight matrix choice', *Nucleic acids research*, 22(22), pp. 4673–4680. doi: 10.1093/nar/22.22.4673.

Tokita, M., Yano, W., James, H. F. and Abzhanov, A. (2016) 'Cranial shape evolution in adaptive radiations of birds: comparative morphometrics of Darwin's finches and Hawaiian honeycreepers'. doi: 10.1098/rstb.2015.0481.

Townsend, T., Larson, A., Louis, E. and Macey, J. R. (2004) 'Molecular phylogenetics of squamata: the position of snakes, amphisbaenians, and dibamids, and the root of the squamate tree', *Systematic Biology*, 53(5), pp. 735–757. doi: 10.1080/10635150490522340.

Townsend, T. M., Alegre, R. E., Kelley, S. T., Wiens, J. J. and Reeder, T. W. (2008) 'Rapid development of multiple nuclear loci for phylogenetic analysis using genomic resources: an example from squamate reptiles', *Molecular phylogenetics and evolution*, 47(1), pp. 129–42. doi: 10.1016/j.ympev.2008.01.008.

Uetz, P. and Hošek, J. (2019) *The Reptile Database*, *Available from: http://www.reptile-database.org (June 2019)*.

Underwood, G. (1970) 'The Eye', in Gans, C. and Parsons, T. S. (eds) *Biology of the Reptilia. Volume 2. Morphology B.* Academic Press, pp. 1–97.

Uyeda, J. C., Caetano, D. S. and Pennell, M. W. (2015) 'Comparative Analysis of Principal Components Can be Misleading', *Systematic Biology*. Narnia, 64(4), pp. 677–689. doi: 10.1093/sysbio/syv019.

Vidal-Garcia, M. and Keogh, J. S. (2015) 'Convergent evolution across the Australian continent: Ecotype diversification drives morphological convergence in two distantly related clades of Australian frogs', *Journal of Evolutionary Biology*, 28(12), pp. 2136–2151. doi: 10.1111/jeb.12746.

Vidal, N., Azvolinsky, A., Cruaud, C. and Hedges, S. B. (2008) 'Origin of tropical American burrowing reptiles by transatlantic rafting', *Biology Letters*. The Royal Society, 4(1), pp. 115–118. doi: 10.1098/rsbl.2007.0531.

Vidal, N. and David, P. (2004) 'New insights into the early history of snakes inferred from two nuclear genes', *Molecular Phylogenetics and Evolution*, 31(2), pp. 783– 787. doi: 10.1016/j.ympev.2004.01.001.

Vidal, N. and Hedges, S. B. (2002) 'Higher-level relationships of caenophidian snakes inferred from four nuclear and mitochondrial genes', *Comptes rendus biologies*, 325(9), pp. 987–995. doi: 10.1016/S1631-0691(02)01509-3.

Vidal, N. and Hedges, S. B. (2005) 'The phylogeny of squamate reptiles (lizards, snakes, and amphisbaenians) inferred from nine nuclear protein-coding genes', *Comptes Rendus Biologies*, 328(10–11), pp. 1000–1008. doi: 10.1016/j.crvi.2005.10.001.

Vijayakumar, S. P., Menezes, R. C., Jayarajan, A. and Shanker, K. (2016) 'Glaciations, gradients, and geography: multiple drivers of diversification of bush frogs in the Western Ghats Escarpment', *Proceedings of the Royal Society B: Biological Sciences*, 283(1836), p. 20161011. doi: 10.1098/rspb.2016.1011.

Wall, F. (1919) 'Notes on a collection of snakes made in the Nilgiri Hills and the adjacent Wynaad', *Journal of the Bombay Natural History Society*, 26(2), pp. 552–584.

Walls, G. L. (1942) *The vertebrate eye and its adaptive radiation*. New York.

Watanabe, A., Fabre, A.-C., Felice, R. N., Maisano, J. A., Müller, J., Herrel, A. and Goswami, A. (2019) 'Ecomorphological diversification in squamates from conserved pattern of cranial integration', *Proceedings of the National Academy of Sciences of the United States of America*, 116(29), pp. 14688–14697. doi: 10.1073/pnas.1820967116.

Wickham, H. (2009) *Ggplot2 : elegant graphics for data analysis*. New York: Springer.

Wickramasinghe, L. J. M., Vidanapathirana, D. R., Wickramasinghe, N. and Ranwella, P. N. (2009) 'A new species of *Rhinophis* Hemprich, 1820 (Reptilia: Serpentes: Uropeltidae) from Rakwana massif, Sri Lanka', *Zootaxa*, 2044(1), pp. 1–22. doi: 10.11646/zootaxa.2044.1.1.

Wickramasingue, L. J. M., Vidanapathirana, D. R., Rajeev, M. D. G. and Gower, D. J. (2017) 'A new species of *Rhinophis* Hemprich, 1820 (Serpentes: Uropeltidae) from the central hills of Sri Lanka', *Zootaxa*, 4263(1), pp. 153–164. doi: 10.11646/zootaxa.4263.1.7.

Wiens, J. J., Kuczynski, C. A., Smith, S. A., Mulcahy, D. G., Sites, J. W., Townsend,

T. M. and Reeder, T. W. (2008) 'Branch lengths, support, and congruence: testing the phylogenomic approach with 20 nuclear loci in snakes', *Systematic Biology*, 57(3), pp. 420–431. doi: 10.1080/10635150802166053.

Wiens, J. J., Hutter, C. R., Mulcahy, D. G., Noonan, B. P., Townsend, T. M., Sites, J. W. and Reeder, T. W. (2012) 'Resolving the phylogeny of lizards and snakes (Squamata) with extensive sampling of genes and species', *Biology Letters*, 8(6), pp. 1043–1046. doi: 10.1098/rsbl.2012.0703.

Wiens, J. J., Brandley, M. C. and Reeder, T. W. (2006) 'Why does a trait evolve multiple times within a clade? Repeated evolution of snakelike body form in squamate reptiles', *Evolution*, 60(1), pp. 123–41. doi: 10.1554/05-328.1.

Williams, C., Pontén, F., Moberg, C., Söderkvist, P., Uhlén, M., Pontén, J., Sitbon, G. and and Lundeberg, J. (1999) 'A high frequency of sequence alterations is due to formalin fixation of archival specimens', *The American journal of pathology*. Elsevier, 155(5), pp. 1467–1471. doi: 10.1016/S0002-9440(10)65461-2.

Wong, S. Q., Li, J., Tan, A. Y., Vedururu, R., Pang, J. M. B., Do, H., Ellul, J., Doig, K., Bell, A., McArthur, G. A., Fox, S. B., Thomas, D. M., Fellowes, A., Parisot, J. P. and Dobrovic, A. (2014) 'Sequence artefacts in a prospective series of formalin-fixed tumours tested for mutations in hotspot regions by massively parallel sequencing', *BMC Medical Genomics*. BioMed Central, 7(1), p. 23. doi: 10.1186/1755-8794-7-23.

Woodburne, M. O., Goin, F. J., Bond, M., Carlini, A. A., Gelfo, J. N., López, G. M., Iglesias, A. and Zimicz, A. N. (2014) 'Paleogene Land Mammal Faunas of South America; a Response to Global Climatic Changes and Indigenous Floral Diversity', *Journal of Mammalian Evolution*, 21(1), pp. 1–73. doi: 10.1007/s10914-012-9222-1.

Yan, J., Li, H. and Zhou, K. (2008) 'Evolution of the Mitochondrial Genome in Snakes: Gene Rearrangements and Phylogenetic Relationships', *BMC Genomics*. BioMed Central, 9(1), p. 569. doi: 10.1186/1471-2164-9-569.

Yang, Z. and Rannala, B. (2010) 'Bayesian species delimitation using multilocus sequence data', *Proceedings of the National Academy of Sciences*, 107(20), pp. 9264–9269. doi: 10.1073/pnas.0913022107.

Yang, Z. and Rannala, B. (2017) 'Bayesian species identification under the multispecies coalescent provides significant improvements to DNA barcoding analyses', *Molecular Ecology*, 26(11), pp. 3028–3036. doi: 10.1111/mec.14093.

Yi, H. and Norell, M. A. (2015) 'The burrowing origin of modern snakes', *Science Advances*, 1(10), p. e1500743. doi: 10.1126/sciadv.1500743.

Yoder, J. B., Clancey, E., Des Roches, S., Eastman, J. M., Gentry, L., Godsoe, W., Hagey, T. J., Jochimsen, D., Oswald, B. P., Robertson, J., Sarver, B. A. J., Schenk, J. J., Spear, S. F. and Harmon, L. J. (2010) 'Ecological opportunity and the origin of adaptive radiations', *Journal of Evolutionary Biology*, 23(8),

pp. 1581–1596. doi: 10.1111/j.1420-9101.2010.02029.x.

Zaher, H., Murphy, R. W., Arredondo, J. C., Graboski, R., Machado-Filho, P. R., Mahlow, K., Montingelli, G. G., Quadros, A. B., Orlov, N. L., Wilkinson, M., Zhang, Y.-P. and Grazziotin, F. G. (2019) 'Large-scale molecular phylogeny, morphology, divergence-time estimation, and the fossil record of advanced caenophidian snakes (Squamata: Serpentes)', *PLOS ONE*, 14(5), p. e0216148. doi: 10.1371/journal.pone.0216148.

Zerbino, D. R. and Birney, E. (2008) 'Velvet: algorithms for de novo short read assembly using de Bruijn graphs', *Genome research*. Cold Spring Harbor Laboratory Press, 18(5), pp. 821–9. doi: 10.1101/gr.074492.107.

Zhang, C., Zhang, D.-X., Zhu, T. and Yang, Z. (2011) 'Evaluation of a Bayesian Coalescent Method of Species Delimitation', *Systematic Biology*. Narnia, 60(6), pp. 747–761. doi: 10.1093/sysbio/syr071.

Zhang, J., Kapli, P., Pavlidis, P. and Stamatakis, A. (2013) 'A general species delimitation method with applications to phylogenetic placements', *Bioinformatics*, 29(22), pp. 2869–2876. doi: 10.1093/bioinformatics/btt499.

Zheng, Y., Peng, R., Kuro-o, M. and Zeng, X. (2011) 'Exploring Patterns and Extent of Bias in Estimating Divergence Time from Mitochondrial DNA Sequence Data in a Particular Lineage: A Case Study of Salamanders (Order Caudata)', *Molecular Biology and Evolution*, 28(9), pp. 2521–2535. doi: 10.1093/molbev/msr072.

Zheng, Y. and Wiens, J. J. (2016) 'Combining phylogenomic and supermatrix approaches, and a time-calibrated phylogeny for squamate reptiles (lizards and snakes) based on 52 genes and 4162 species', *Molecular Phylogenetics and Evolution*, 94, pp. 537–547. doi: 10.1016/j.ympev.2015.10.009.

Appendix 2-1 PCR protocol and Sanger sequencing.

A list of primer sequences, references, and PCR cycle conditions for each primer pair is available in Appendix Table 2-2. Amplifications were carried out in 15—25μL volumes, containing a final concentration of 1x Reaction Buffer, 2-3.2mM $MgCl_2$, 0.2—0.4mM each dNTP, 0.2—0.4μM each primer, 0.5—0.75 units of GoTaq DNA Polymerase (5u/μL, Promega), and 1—2μL template DNA. Reactions that failed to amplify or that yielded multiple unspecific bands with normal PCR cycles were repeated with touchdown PCR (TD); when that failed, reactions were repeated with the KAPA2G Robust HotStart ReadyMix PCR Kit (Kapa Biosystems) carrying out 15μL reactions using 1x HotStart ReadyMix, 0.4μM each primer and template DNA. When using this kit, cycling conditions were as follows: 95ºC(3'), 35x [95ºC(15"), 55ºC(15"), 72ºC(30")], 72ºC(1'). PCR products were stained with GelRed and visualised on 1% agarose gels under UV light.

Successful amplifications were purified using MicroClean (Microzone) and sequenced in forward and reverse directions using the same primers as in the amplification step, and dye labelled using BigDye Terminator v3.1 cycle sequencing kit (Applied Biosystems) on an ABI3730xl DNA Analyzer (University College London).

Appendix 2-2 Archival DNA extraction followed a modified version of the protocol reported by Dabney et al. (2013), as implemented in previous ancient DNA (aDNA) studies (Brace et al., 2018; Marr et al., 2018).

Tissue samples (1.65-7.4mg) were cut into smaller pieces, added to 180µL ATL buffer (Qiagen, Valencia, CA) and 20µL proteinase K, and incubated overnight at 56ºC in a thermo-mixer. Samples were centrifuged for 2 minutes at maximum speed, and the supernatant was added to 13mL of binding buffer (final concentrations: 5M guanidine hydrochloride, 40% isopropanol, 0.05% Tween-20, and 90mM sodium acetate) in silica spin columns (High Pure Viral Nucleic Acid Large Volume Kit, Roche). Tubes were centrifuged for 4 minutes at 2,500 RPM, rotated 90º and centrifuged again at 3,000 RPM for 2 minutes, and dry spun at 10,000 RPM for 1 minute. Silica membranes were washed twice with 650µL PE buffer (Qiagen) at 10,000 RPM for 1 minute, and then dry spun for 1 minute at maximum speed. Columns were placed in clean 1.5mL tubes and eluted twice in 50µL TET buffer (final concentrations: 10mM Tris-HCL, 1mM EDTA, 0.05% Tween-20), incubated for 5 minutes and centrifuged at maximum speed for 1 minute. DNA extractions were stored in a freezer at -20ºC.

Appendix 2-3 Archival DNA library build followed a modified version of the protocol reported by Meyer and Kircher (2010), without DNA fragmentation (Brace et al., 2018).

For the blunt end repair step, a mix was prepared of buffer Tango (1x), dNTPs (100µM each), ATP (1mM), T4 Polynucleotide Kinase (0.5U/µL) and T4 DNA polymerase (0.1U/µL, Thermo Fisher Scientific). 40µL of this mix was added to 30µL of DNA extract (total volume 70µL), and incubated at 25ºC for 15 minutes and at 12ºC for 5 minutes. Samples were subsequently purified using a Qiaquick PCR Purification Kit (Qiagen). 200µL of PB buffer was added to these samples, transferred to a spin column and centrifuged at 10,000 RPM for 1 minute. 650µL PE buffer was then added into each column and spun, followed by a final step of dry spinning to discard any residual buffer. Each sample was eluted in 22µL of EB buffer and then centrifuged. An adapter ligation mix was prepared by mixing T4 DNA Ligase Buffer (1x), PEG-4000 (5%), T4 DNA Ligase (0.125U/µL, Thermo Fisher Scientific) and adapter mix (100µM each). 20µL of sample was added to 20µL of this mix (total volume 40µL), and incubated at 22ºC for 30 minutes, followed by the Qiaquick purification step as reported above. An adapter fill mix was prepared with ThermoPol Buffer (1x), dNTPs (each 25mM) and Bst DNA Polymerase Large Fragment (0.3U/µL, Thermo Fisher Scientific). 20µL of sample was added to 20µL of master mix (total volume 40µL), and incubated at 37ºC for 20 minutes, followed by the Qiaquick purification step as reported above. A mix was prepared of AmpliTaq Buffer (1x), $MgCl_2$ (2.5mM), dNTPs (200µM each), BSA (0.4mg/mL), AmpliTaq Gold (0.05U/µL, Thermo Fisher Scientific), index primer P5 (0.4µM), index primer P7 (0.4µM). 40µL of this mix was added to 10µL of sample (total volume 50µL). Three index PCR reactions were carried out per library, to avoid excessive volumes and in case one reaction failed. Cycling conditions were as follows: 94ºC(2'), [20x 94ºC(40"), 60ºC(40"), 72ºC(40")], 72ºC(10'). PCR was followed by a purification step in a regular post-PCR room with a Qiaquick PCR Purification Kit, making a final elution of 60µL of library per sample. A total of 48 libraries were prepared.

Appendix Table 2-1 Uropeltidae samples used in Chapters 2 and 3 phylogenetic analyses. Information regarding species name, sample code, country, sampling locality, and molecular markers amplified — GenBank accession numbers for published sequences; cells with "x" denote new unpublished sequence data — and information on datasets.

Species	Sample code	Country	Locality	*12s*	*16s*	*nd4*	*cytb*	*cmos*	*prlr*	Dataset		
										1	2 3.1	3.2
Brachyophidium rhodogaster	MW3800	India	Sacred Heart College, Shembagganur, Kodaikanal, Tamil Nadu	x	x	x	x	x	x	x	x	x
Brachyophidium rhodogaster	MW3804	India	Sacred Heart College, Shembagganur, Kodaikanal, Tamil Nadu	AY700992	AY701023	x	x	x	x	x	x	
Brachyophidium rhodogaster	MW3806	India	Sacred Heart College, Shembagganur, Kodaikanal, Tamil Nadu	x	x	x	x	x	x	x	x	
Brachyophidium rhodogaster	MW3808	India	Sacred Heart College, Shembagganur, Kodaikanal, Tamil Nadu	x	x	x	x	x	x	x	x	
Melanophidium bilineatum	VPC-027	India	Kakkayam, Malabar WLS	x	MF775170	MF775253		MF775211	x	x	x	x
Melanophidium khairei	Melkh1	India		KX898253			KX898254			x	x	
Melanophidium khairei	MW2514	India	Amboli, Maharashtra	x	x	x	x	x	x	x	x	x
Melanophidium khairei	MW2515	India	Amboli, Maharashtra	x	x	x	x	x	x	x	x	
Melanophidium punctatum	ALB221	India	Sengaltheri, Tamil Nadu	x	x	x	x	x	x	x	x	x
Melanophidium punctatum	CHATURO	India	Chattancode, Kerala	x	x	x	x	x	x	x	x	x
Melanophidium punctatum	MW2480	India		AY700993	AY701024	x	x	x	x	x	x	x
Melanophidium punctatum	SNO11	India	Valparai	x	x	x		x	x	x	x	
Melanophidium punctatum	VPC-065	India	Marudhamala, Vithura	x	x	x		x	x	x	x	

Species	Sample code	Country	Locality	*12s*	*16s*	*nd4*	*cytb*	*cmos*	*prlr*	Dataset		
										1	2 3.1	3.2
Melanophidium punctatum	VPC-069	India	Kalakkad	x	x	x		x	x	x	x	
Melanophidium wynaudense	MW1459	India		x	x	x	x	x	x	x	x	x
Melanophidium wynaudense	MW2543	India	Jammanahally	x	x	x	x	x	x	x	x	x
Melanophidium wynaudense	MW4874	India		x	x	x		x	x	x	x	x
Melanophidium wynaudense	Ram28	India		x	x	x	x	x	x	x	x	x
Melanophidium wynaudense	VPC-043	India	ARRS, Agumbe	x	MF775171	MF775254		MF775212	x	x	x	x
Melanophidium wynaudense	VPC-068	India	Wayanad Wild, Lekkadi, Wayanad	x	x					x	x	
Platyplectrurus madurensis	VPC-025	India	Observatory, Kodaikanal	MF775132	MF775172	MF775255		MF775213	x	x	x	x
Platyplectrurus trilineatus	RamPlat	India	Anamallai Shola	x	x	x	x	x	x	x	x	x
Plectrurus aureus	MNHN 1895.107	India	Wynand, Chambra hills near Kalpatty,Malabar	x	x	x	x				x	x
Plectrurus guentheri	BMNH 1946.1.16.32	India	Walagut (Walaghat), below Sispara	x	x	x	x				x	x
Plectrurus guentheri	MNHN 1895.105	India		x	x	x	x				x	
Plectrurus perrotetii	MW3239	India		x	x	x	x	x	x	x	x	x
Plectrurus perrotetii	MW3241	India	Nilgiri, Tamil Nadu	x	x	x	x	x	x	x	x	
Plectrurus perrotetii	VPC-029	India	Ooty Govt. College, Ooty	MF775133	MF775173	MF775256		MF775214		x	x	
Plectrurus perrotetii	VPC-030	India	Ooty Govt. College, Ooty	MF775134	MF775174	x		MF775215		x	x	
Pseudoplectrurus canaricus	MNHN 1895.102	India	Kurha Mukh	x	x	x	x				x	
Pseudoplectrurus canaricus	VPC-023	India	Kudremukh Peak	MF775135	MF775175	MF775257		MF775216	x	x	x	x
Rhinophis blythii	LSUMNS H-5781	Sri Lanka	Talawakella	AY701018	AY701049	x	x	x	x	x	x	x
Rhinophis blythii	RS-N	Sri Lanka		KC347332	KC347370	KC347517		KC347409		x	x	
Rhinophis blythii	WHT5221	Sri Lanka	Ingestre Estate	AY701019	AY701050	x	x	x	x	x	x	x

Species	Sample code	Country	Locality	*12s*	*16s*	*nd4*	*cytb*	*cmos*	*prlr*	Dataset		
										1	2 3.1	3.2
Rhinophis blythii	WHT5223	Sri Lanka	Ingestre Estate	AY701020	AY701051	x	x	x	x	x	x	
Rhinophis blythii	WHT5224	Sri Lanka	Ingestre Estate	x	x	x	x	x	x	x	x	
Rhinophis blythii	WHT5225	Sri Lanka	Ingestre Estate	x	x	x	x	x	x	x	x	
Rhinophis blythii	WHT5227	Sri Lanka	Ingestre Estate	AY701021	AY701052	x	x	x		x	x	
Rhinophis cf. *blythii*	WHT5209	Sri Lanka	Ingestre Estate	x	x	x	x	x	x	x	x	x
Rhinophis dorsimaculatus	LSUMNS H-5779	Sri Lanka	Marichchikkadi	x	x	x		x		x	x	
Rhinophis dorsimaculatus	LSUMNS H-5780	Sri Lanka	Marichchikkadi	AY701009	AY701040	x	x	x	x	x	x	x
Rhinophis dorsimaculatus	MW2014-63	Sri Lanka	Sannar, Vidattalativu	x	x	x				x	x	
Rhinophis drummondhayi	LSUMNS H-5697	Sri Lanka	Pingarawa Estate, Namunukula	x	x	x		x		x	x	
Rhinophis drummondhayi	LSUMNS H-5778	Sri Lanka	Above Namunkula	AY700996	AY701027	x	x	x	x	x	x	x
Rhinophis drummondhayi	LSUMNS H-5784	Sri Lanka	Talawakella	AY700995	AY701026	x	x	x	x	x	x	
Rhinophis drummondhayi	MW1721	Sri Lanka	Cannavarella Group, near Passara, Badulla, Province of Uva	AY700994	AY701025	x	x	x	x	x	x	
Rhinophis drummondhayi	SBH194102	Sri Lanka		Z46447	Z46477		AF544673	AF544719		x	x	
Rhinophis drummondhayi	WHT5176	Sri Lanka	Madulsima	AY700997	AY701028	x	x	x	x	x	x	
Rhinophis drummondhayi	WHT5177	Sri Lanka	Madulsima	AY700998	AY701029	x	x	x	x	x	x	
Rhinophis drummondhayi	WHT5179	Sri Lanka	Bibilegama	x	x	x	x	x	x	x	x	
Rhinophis drummondhayi	WHT5180	Sri Lanka	Bibilegama	x	x	x	x	x	x	x	x	
Rhinophis drummondhayi	WHT5245	Sri Lanka	Bibilegama, Namunukula	x	x	x		x	x	x	x	
Rhinophis erangaviraji	RAP0431	Sri Lanka		KC347333	KC347371	KC347503	KC347490			x	x	x
Rhinophis goweri	CESS194	India		x	x					x	x	x

Species	Sample code	Country	Locality	*12s*	*16s*	*nd4*	*cytb*	*cmos*	*prlr*	Dataset		
										1	2 3.1	3.2
Rhinophis homolepis	LSUMNS H-5863	Sri Lanka	Gampola, Illawatura	x	x	x	x	x	x	x	x	x
Rhinophis homolepis	MW2016-100	Sri Lanka	Rambukpitiya, Nawalapitiya	x	x	x	x			x	x	
Rhinophis homolepis	MW2016-101	Sri Lanka	Rambukpitiya, Nawalapitiya	x	x	x	x			x	x	
Rhinophis homolepis	MW2018-100	Sri Lanka	Deraniyagala	x	x	x	x	x	x	x	x	
Rhinophis homolepis	RAP0509	Sri Lanka		KC347334	KC347372	KC347522	KC347489			x	x	
Rhinophis homolepis	WHT5246	Sri Lanka	Gampola	x	x	x	x	x	x	x	x	
Rhinophis homolepis	ZMB3827	Sri Lanka		x	x	x	x				x	
Rhinophis cf. *homolepis* 1	MW1787	Sri Lanka	near Rakwana, Ratnapura, Province of Sabaragamuwa	AY701015	AY701046	x	x	x	x	x	x	x
Rhinophis lineatus	WHT5208	Sri Lanka	Harasbedda	x	x	x	x	x	x	x	x	x
Rhinophis lineatus	WHT5218	Sri Lanka	Harasbedda	x	x	x	x	x	x	x	x	
Rhinophis lineatus	WHT5788	Sri Lanka	Ragala-Udapussellawa	x	x	x	x	x	x	x	x	
Rhinophis melanogaster	KU0143	Sri Lanka	Lulkandura	x	x	x	x	x	x	x	x	x
Rhinophis melanogaster	LSUMNS H-5794	Sri Lanka	Kandy area	x	x	x	x	x		x	x	
Rhinophis melanogaster	WHT5159	Sri Lanka	Hantane Estate	x	x	x	x	x	x	x	x	
Rhinophis melanogaster	WHT5160	Sri Lanka	Hantane Estate	x	x	x	x	x	x	x	x	
Rhinophis melanogaster	WHT5170	Sri Lanka	Hantane Estate	x	x	x	x	x	x	x	x	
Rhinophis cf. *melanogaster*	Rmel_Hunas	Sri Lanka	Hunas falls, Elkaduwa	x	x	x			x	x	x	x
Rhinophis microlepis	DVM01	India		x	x	x		x	x	x	x	
Rhinophis microlepis	MW4876	India		x	x	x	x	x	x	x	x	x
Rhinophis microlepis	VPC-064	India	Chandhanathodu, Periya, Wayanad	x	x	x		x	x	x	x	x
Rhinophis oxyrynchus	KU0043	Sri Lanka	Mihinthale	x	x	x	x	x	x	x	x	x

Species	Sample code	Country	Locality	*12s*	*16s*	*nd4*	*cytb*	*cmos*	*prlr*	Dataset		
										1	2 3.1	3.2
Rhinophis oxyrynchus	KU0065	Sri Lanka	Mihinthale	x	x	x	x		x	x	x	
Rhinophis oxyrynchus	LSUMNS H-6131	Sri Lanka		AY701013	AY701044	x	x	x	x	x	x	x
Rhinophis oxyrynchus	LSUMNS H-6132	Sri Lanka	Polonarywa	AY701014	AY701045	x	x	x	x	x	x	
Rhinophis oxyrynchus	Rvid1	Sri Lanka	Sannar, Vidattalativu		x	x				x	x	
Rhinophis oxyrynchus	Rvid2	Sri Lanka	Sannar, Vidattalativu	x	x	x			x	x	x	x
Rhinophis oxyrynchus	WHT5255_35	Sri Lanka	Nichchiyagama	x	x	x	x			x	x	x
Rhinophis oxyrynchus	ZMB3825	Sri Lanka		x	x	x	x				x	x
Rhinophis philippinus	KU0046	Sri Lanka	Ampitiya, Kandy	x	x	x	x	x	x	x	x	x
Rhinophis philippinus	MNHN0.6994	Sri Lanka		x	x	x	x				x	
Rhinophis phillipsi	LSUMNS H-5696	Sri Lanka		AF512739	AF512739					x	x	
Rhinophis phillipsi	LSUMNS H-5788	Sri Lanka					AF471034	AF471100		x	x	
Rhinophis phillipsi	MW1758	Sri Lanka	Moussakanda Estate, Gammaduwa, Matale, Central Province	AY701012	AY701043	x	x		x	x	x	
Rhinophis phillipsi	MW1760	Sri Lanka	near Gammaduwa, Matale, Central Province	AY701011	AY701042	x	x	x	x	x	x	x
Rhinophis phillipsi	WHT5269	Sri Lanka	Mousakanda	x	x	x	x	x	x	x	x	
Rhinophis cf. *phillipsi*	KNU027	Sri Lanka	Riverston	x	x	x	x	x	x	x	x	x
Rhinophis cf. *phillipsi*	MW2018-101	Sri Lanka	Riverston	x	x	x	x	x	x	x	x	
Rhinophis cf. *phillipsi*	WHT5786	Sri Lanka	Pussellawa	x	x	x	x	x	x	x	x	x
Rhinophis roshanpererai	KU0296	Sri Lanka	Between Ududumbara-Hasalaka	x	x	x	x	x	x	x	x	x
Rhinophis roshanpererai	WHT5172	Sri Lanka	Robery Estate, Badulla	x	x	x	x	x	x	x	x	x
Rhinophis roshanpererai	WHT5187	Sri Lanka	Robery Estate, Badulla	x	x	x	x	x		x	x	x

Species	Sample code	Country	Locality	*12s*	*16s*	*nd4*	*cytb*	*cmos*	*prlr*	Dataset		
										1	2 3.1	3.2
Rhinophis roshanpererai	WHT5202	Sri Lanka	Robery Estate, Badulla	x	x	x	x	x	x	x	x	x
Rhinophis roshanpererai	WHT5203	Sri Lanka	Robery Estate, Badulla	x	x	x	x	x	x	x	x	
Rhinophis roshanpererai	WHT5210	Sri Lanka	Harasbedda	x	x	x	x	x	x	x	x	x
Rhinophis roshanpererai	WHT5229	Sri Lanka	Harasbedda	x	x	x	x	x		x	x	
Rhinophis saffragamus	MNHN0.5621	Sri Lanka		x	x	x	x				x	
Rhinophis saffragamus	RS-140	Sri Lanka		KC347331	KC347369	KC347492		KC347408		x	x	
Rhinophis saffragamus	WHTPp	Sri Lanka		x	x	x	x	x	x	x	x	x
Rhinophis sanguineus	BUB1584	India		x	x	x		x	x	x	x	x
Rhinophis sanguineus	BUB1588	India		x	x	x		x	x	x	x	
Rhinophis sanguineus	VPC-042	India	CCRI, Seegudu, Chickmangalore	x	MF775176	MF775258		MF775217	x	x	x	x
Rhinophis sanguineus	VPC-052	India	Elimbilerimala, Mepadi, Wayanad	x	x	x		x	x	x	x	x
Rhinophis sanguineus	VPC-053	India	Elimbilerimala, Mepadi, Wayanad	x	x	x		x	x	x	x	
Rhinophis cf. *sanguineus*	MW1477	India	near Attappadi, Kerala	x	x	x		x	x	x	x	x
Rhinophis sp. (Palabaddala)	KU0125	Sri Lanka	Palabaddala, Sripadaya	x	x	x	x	x	x	x	x	x
Rhinophis sp. nov. 1	MW2018-112	Sri Lanka	Burusgala, Deniyaya	x	x	x		x	x	x	x	x
Rhinophis sp. nov. 1	MW2018-113	Sri Lanka	Burusgala, Deniyaya	x	x	x		x	x	x	x	
Rhinophis sp. nov. 1	MW2018-114	Sri Lanka	Burusgala, Deniyaya	x	x	x	x		x	x	x	
Rhinophis sp. nov. 2	KNU017	Sri Lanka	Ilukkumbura	x	x	x	x	x	x	x	x	x
Rhinophis sp. nov. 2	LSUMNS H-5684	Sri Lanka		x	x	x	x		x	x	x	
Rhinophis sp. nov. 2	LSUMNS H-6164	Sri Lanka	Palatenne	AY701016	AY701047	x	x	x	x	x	x	x
Rhinophis sp. nov. 2	LSUMNS H-6165	Sri Lanka	Palatenne	AY701017	AY701048	x	x	x	x	x	x	

Species	Sample code	Country	Locality	*12s*	*16s*	*nd4*	*cytb*	*cmos*	*prlr*	Dataset		
										1	2 3.1	3.2
Rhinophis sp. nov. 2	LSUMNS H-6179	Sri Lanka		AF512740	AF512740					x	x	
Rhinophis sp. nov. 2	MW1740	Sri Lanka	Kandehena, near Rattota, Matale, Central Province	AY701008	AY701039	GQ200594	GQ200594	x	x	x	x	
Rhinophis sp. nov. 2	MW1742	Sri Lanka	Kandehena, near Rattota, Matale, Central Province	AY701005	AY701036	x	x	x	x	x	x	
Rhinophis sp. nov. 2	MW1755	Sri Lanka	Dombawela	x	x	x	x		x	x	x	
Rhinophis sp. nov. 2	WHT5155	Sri Lanka	Kalugaltenna, Knuckles	x	x	x	x	x	x	x	x	
Rhinophis sp. nov. 2	WHT5157	Sri Lanka	Kalugaltenna	AY701006	AY701037	x	x	x	x	x	x	
Rhinophis sp. nov. 2	WHT5158	Sri Lanka	Kalugaltenna	AY701007	AY701038	x	x	x	x	x	x	
Rhinophis sp. nov. 4	DVM02	India		x	x	x		x	x	x	x	
Rhinophis sp. nov. 4	VPC-051	India	Wayanad Wild, Lekkadi, Wayanad	x	x	x		x	x	x	x	x
Rhinophis travancoricus	MW2181	India		x	x	x	x	x	x	x	x	x
Rhinophis travancoricus	MW220	India	TBGRI, Palode, Kerala	AY701010	AY701041	x	x	x	x	x	x	x
Rhinophis travancoricus	VPC-044	India	Harrison-Malayalam, Konni	MF775136	MF775177	MF775259		MF775218	x	x	x	x
Rhinophis tricolorata	WHT5790	Sri Lanka	Udugama	x	x	x	x	x	x	x	x	x
Rhinophis zigzag	WHT5243	Sri Lanka	Bibilegama, Namunukula	x	x	x	x	x	x	x	x	x
Teretrurus hewstoni	MW3438	India		x	x	x	x	x	x	x	x	x
Teretrurus hewstoni	MW3448	India	Wayanad, Kerala	x	x	x	x		x	x	x	
Teretrurus hewstoni	MW3449	India	Wayanad, Kerala	x	x	x	x	x	x	x	x	
Teretrurus hewstoni	VPC-031	India	Anjukunnu, Mananthawadi, Wayanad	MF775137	MF775178	x		MF775219	x	x	x	
Teretrurus hewstoni	VPC-032	India	Anjukunnu, Mananthawadi, Wayanad	MF775138	MF775179	MF775260		MF775220	x	x	x	
Teretrurus hewstoni	VPC-033	India	Anjukunnu, Mananthawadi, Wayanad	MF775139	MF775180	MF775261		MF775221	x	x	x	

Species	Sample code	Country	Locality	*12s*	*16s*	*nd4*	*cytb*	*cmos*	*prlr*	Dataset		
										1	2 3.1	3.2
Teretrurus hewstoni	VPC-034	India	Anjukunnu, Mananthawadi, Wayanad	MF775140	MF775181	MF775262		MF775222	x	x	x	
Teretrurus hewstoni	VPC-054	India	Elimbilerimala, Mepadi, Wayanad	x	x	x		x	x	x	x	x
Teretrurus hewstoni	VPC-055	India	Elimbilerimala, Mepadi, Wayanad	x	x	x			x	x	x	x
Teretrurus sanguineus	VPC-009	India	Kambilipara shole, Marayoor	MF775121	MF775159	MF775242		MF775201	x	x	x	x
Teretrurus sanguineus	VPC-063	India	Periyar Tiger Reserve	x	x	x		x	x	x	x	x
Teretrurus sp.	MW3447	India		x	x	x	x	x	x	x	x	x
Teretrurus travancoricus	ALB180	India	Oothu, Tamil Nadu	x	x	x	x	x	x	x	x	x
Teretrurus travancoricus	ALB189	India	Oothu, Tamil Nadu	x	x	x	x	x	x	x	x	
Teretrurus travancoricus	MW2194	India		x	x	x	x	x	x	x	x	
Teretrurus travancoricus	VPC-020	India	Pandimotta, Shendhurney WLS	MF775141	MF775182	MF775263		MF775223	x	x	x	x
Teretrurus travancoricus	VPC-021	India	Kakachi, KMTR	MF775142	MF775183	MF775264		MF775224		x	x	
Teretrurus travancoricus	VPC-056	India	Pandimotta, Shendhurney WLS (nr. Ponmudi)	x	x	x		x	x	x	x	
Teretrurus travancoricus	VPC-057	India	Pandimotta, Shendhurney WLS (nr. Ponmudi)	x	x			x	x	x	x	
Uropeltis arcticeps	BMNH 1946.1.16.12	India		x	x	x	x				x	x
Uropeltis cf. *arcticeps* (KMTR)	MW2192	India		x	x	x	x	x	x	x	x	x
Uropeltis cf. *arcticeps* (KMTR)	VPC-014	India	KMTR	MF775126	MF775164	MF775247		MF775206	x	x	x	
Uropeltis cf. *arcticeps* (KMTR)	VPC-022	India	Manjolai, KMTR	MF775148	MF775189	MF775269		MF775230		x	x	
Uropeltis bhupathyi	BNHS3513	India	Anaikatty, Coimbatore District, Tamil Nadu		MH114930	MH114931	x			x	x	x
Uropeltis bicatenata	UK01	India	Fangal Gavan, Maharashtra	x	x	x	x	x	x	x	x	x
Uropeltis bicatenata	UK02	India	Fangal Gavan, Maharashtra	x	x	x	x	x	x	x	x	

Species	Sample code	Country	Locality	*12s*	*16s*	*nd4*	*cytb*	*cmos*	*prlr*	Dataset		
										1	2 3.1	3.2
Uropeltis broughami	BMNH 1946.1.16.29	India	Sirumallay (Sirumalai) Hills, Madura District (now Dindigul District)	x	x	x	x				x	x
Uropeltis cf. *beddomei*	VPC-036	India	Kuchimudi, Parsmbikulam TR	MF775143	MF775184	MF775265		MF775225	x	x	x	x
Uropeltis cf. *beddomei*	VPC-037	India	Kuchimudi, Parsmbikulam TR	MF775144	MF775185	x		MF775226	x	x	x	
Uropeltis cf. *brevis*	MW2173	India	Munnar, Idukki, Kerala	AY701000	AY701031	x	x	x	x	x	x	x
Uropeltis cf. *brevis*	VPC-008	India	Vallakadavu, Periyar	MF775122	MF775160	MF775243		MF775202	x	x	x	x
Uropeltis cf. *brevis*	VPC-012	India	Vallakadavu, Periyar	MF775123	MF775161	MF775244		MF775203		x	x	
Uropeltis cf. *brevis*	VPC-024	India	Athirapally, Trissur	MF775145	MF775186	MF775266		MF775227	x	x	x	x
Uropeltis cf. *brevis*	VPC-041	India	Poopara, Parambikulam TR	MF775147	x	MF775268		MF775229	x	x	x	x
Uropeltis cf. *brevis*	VPC-058	India	Kulamanur, Idukki	x	x	x		x	x	x	x	x
Uropeltis cf. *brevis*	VPC-060	India	Ponmudi	x	x	x		x	x	x	x	x
Uropeltis cf. *brevis*	VPC-061	India	Elapara, Idukki	x	x	x		x	x	x	x	
Uropeltis cf. *brevis*	VPC-062	India	Elapara, Idukki	x	x	x		x	x	x	x	
Uropeltis cf. *brevis*	VPC-067	India	Kannur, Kerala	x	x	x				x	x	x
Uropeltis cf. *dupeni*	VPC-038	India	Karianchola, Parambikulam TR	MF775149	MF775190	MF775270			x	x	x	
Uropeltis cf. *dupeni*	VPC-039	India	Pandaravara, Parambikulam TR	MF775150	MF775191	MF775271		MF775231	x	x	x	x
Uropeltis ellioti	G453	India	Eastern Ghats	x	x	x		x	x	x	x	
Uropeltis ellioti	MNHN 1895.90a	India		x	x	x	x				x	
Uropeltis ellioti	MW2502	India	Ooruvasal, Maralyur, Idukki District, Kerala	AY700999	AY701030	x	x	x	x	x	x	x
Uropeltis ellioti	MW2523	India	Pachmarhi, Madhya Pradesh	x	x	x	x	x	x	x	x	x
Uropeltis ellioti	U13 3759	India		KR814596						x	x	

Species	Sample code	Country	Locality	*12s*	*16s*	*nd4*	*cytb*	*cmos*	*prlr*	Dataset		
										1	2 3.1	3.2
Uropeltis ellioti	U14 3760	India		KR814595						x	x	
Uropeltis ellioti	VPC-004	India	Mysore	MF775125	MF775163	MF775246		MF775205	x	x	x	
Uropeltis ellioti	VPC-016	India	Satpura	MF775127	MF775165	x		x		x	x	
Uropeltis grandis	MNHN 1895.79_larger	India		x	x	x	x				x	x
Uropeltis liura	ALB187	India	Oothu, Tamil Nadu	x	x	x	x			x	x	
Uropeltis liura	ALB188	India	Oothu, Tamil Nadu	x	x	x	x	x	x	x	x	x
Uropeltis liura	ALB193	India	Nalumukku, Tamil Nadu	x	x	x	x		x	x	x	
Uropeltis liura	ALB194	India	Nalumukku, Tamil Nadu	x	x	x	x			x	x	
Uropeltis liura	ALB195	India	Nalumukku, Tamil Nadu	x	x	x	x	x	x	x	x	
Uropeltis liura	BMNH 1946.1.16.7	India	can't find in DB	x	x	x	x				x	
Uropeltis liura	LSUMNS H-5791	India	unknown	AY701003	AY701034	x	x	x	x	x	x	
Uropeltis liura	LSUMNS H-5795	India	unknown	AY701004	AY701035	x	x	x	x	x	x	
Uropeltis liura	VPC-001	India	Nalmukku, KMTR	MF775128	MF775166	MF775248		x	x	x	x	
Uropeltis liura	VPC-005	India	Nalmukku, KMTR	x	x	MF775249		MF775207	x	x	x	
Uropeltis macrolepis	MW2518	India	Amboli, Maharashtra	x	x	x	x	x	x	x	x	x
Uropeltis macrolepis	MW2519	India	Amboli, Maharashtra	x	x	x	x		x	x	x	
Uropeltis macrolepis	U1 3292	India		KR814597						x	x	
Uropeltis macrolepis	U12 3303	India		KR814599						x	x	
Uropeltis macrolepis	U2 3293	India		KR814598						x	x	
Uropeltis macrolepis	U20 3766	India		KR814610						x	x	
Uropeltis macrolepis	U21 3767	India		KR814606						x	x	

Species	Sample code	Country	Locality	*12s*	*16s*	*nd4*	*cytb*	*cmos*	*prlr*	Dataset		
										1	2 3.1	3.2
Uropeltis macrolepis	U9 3300	India		KR814602						x	x	
Uropeltis macrolepis	UMAC	India	Matheran, Maharashtra	x	x	x	x	x	x	x	x	x
Uropeltis macrolepis	VPC-047	India	Wai, Satara, Maharashtra	MF775153	x	MF775275		MF775235	x	x	x	
Uropeltis macrolepis	VPC-048	India	Dajipur, Kolhapur, Maharashtra	MF775154	MF775195	MF775276		MF775236	x	x	x	x
Uropeltis macrolepis	VPC-049	India	Barki, Kolhapur, Maharashtra	MF775152	MF775193	MF775273		MF775233	x	x	x	x
Uropeltis macrolepis	VPC-050	India	Barki, Kolhapur, Maharashtra	x	MF775194	MF775274		MF775234	x	x	x	
Uropeltis macrolepis mahableshwarensis	BNHS_Mah	India	Mahableshwar	x	x	x		x	x	x	x	
Uropeltis macrolepis mahableshwarensis	MW2516	India	Amboli, Maharashtra	x	x	x	x		x	x	x	
Uropeltis macrolepis mahableshwarensis	MW2517	India	Mahableshwar, Maharashtra	x	x	x	x			x	x	
Uropeltis macrolepis mahableshwarensis	U3 3294	India		KR814601						x	x	
Uropeltis macrolepis mahableshwarensis	U8 3299	India		KR814600						x	x	
Uropeltis macrorhyncha	BMNH 1946.9.7.45	India	Anamallays	x	x	x	x				x	x
Uropeltis maculata	VPC-002	India	Pettimudi, Eravikulam	MF775129	MF775167	MF775250		MF775208	x	x	x	x
Uropeltis madurensis	MW2469	India	Munnar, Idukki, Kerala	AY701002	AY701033	x	x	x	x	x	x	x
Uropeltis madurensis	MW2472	India	Panniari Estate, Idukki, Kerala	x	x	x	x		x	x	x	
Uropeltis madurensis	MW2476	India	Pallivasal, Munnar, Idukki, Kerala	x	x	x	x	x	x	x	x	
Uropeltis madurensis	MW2478	India	nr. Devikulam, Idukki, Kerala	x	x	x	x	x	x	x	x	
Uropeltis madurensis	VPC-013	India	Tekkady	MF775130	MF775168	MF775251		MF775209	x	x	x	x
Uropeltis madurensis	VPC-019	India	Meghamalai, Tamil Nadu	x	MF775200	MF775281		MF775241	x	x	x	x
Uropeltis madurensis	VPC-028	India	Silent Valley Estate, Munnar	MF775146	MF775187	MF775267		MF775228	x	x	x	

Species	Sample code	Country	Locality	*12s*	*16s*	*nd4*	*cytb*	*cmos*	*prlr*	Dataset		
										1	2 3.1	3.2
Uropeltis myhendrae	LSUMNS H-9566	India		AY701001	AY701032	x	x	x	x	x	x	x
Uropeltis myhendrae	MW1468	India	Aarukani, Kanniyakumari, Tamil Nadu	x	x	x	x	x	x	x	x	
Uropeltis myhendrae	VPC-035	India	Harrison-Malayalam, Konni	MF775155	MF775196	MF775277		MF775237		x	x	
Uropeltis myhendrae	VPC-045	India	Harrison-Malayalam, Konni	MF775156	MF775197	MF775278		MF775238	x	x	x	
Uropeltis myhendrae	VPC-059	India	Ponmudi	x	x	x		x	x	x	x	
Uropeltis nilgherriensis	BMNH 1946.1.16.41	India	Nilgherries	x	x	x	x				x	x
Uropeltis nitida	VPC-040	India	Shekelmudi, Parambikulam TR	MF775157	x	MF775279		MF775239	x	x	x	x
Uropeltis ocellata	BMNH 1946.1.15.59	India	Anamallays	x	x	x	x				x	x
Uropeltis petersi	MNHN 1895.80a	India	Anamallays	x	x	x	x				x	x
Uropeltis petersi	MW2682	India		x	x	x	x	x	x	x	x	x
Uropeltis phipsonii	BNHS 3521	India	Pune	x	x	x		x	x	x	x	
Uropeltis phipsonii	BNHS_Pan	India	Panchgani	x	x	x		x	x	x	x	
Uropeltis phipsonii	MW2513	India	Pune, Maharashtra	x	x	x	x	x	x	x	x	x
Uropeltis phipsonii	MW2520	India	Koyna, Maharashtra	x	x	x	x		x	x	x	
Uropeltis phipsonii	MW2521	India	Koyna, Maharashtra	x	x	x	x	x	x	x	x	
Uropeltis phipsonii	MW2522	India		x	x	x	x		x	x	x	
Uropeltis phipsonii	U19 3765	India		KR814609						x	x	
Uropeltis phipsonii	U4 3295	India		KR814607						x	x	
Uropeltis phipsonii	VPC-046	India	Chalkewadi, Satara, Maharashtra	MF775151	MF775192	MF775272		MF775232	x	x	x	
Uropeltis cf. *phipsonii*	MW248	India	Sulthan Bathery, Wayanad, Kerala	x	x	x		x		x	x	

Species	Sample code	Country	Locality	*12s*	*16s*	*nd4*	*cytb*	*cmos*	*prlr*	Dataset		
										1	2 3.1	3.2
Uropeltis cf. *phipsonii*	MW3440	India		x	x	x	x			x	x	
Uropeltis cf. *phipsonii*	VPC-017	India	Pulpally, Wayanad	MF775131	MF775169	MF775252		MF775210	x	x	x	x
Uropeltis cf. *phipsonii* (Satara)	U11 3302	India		KR814604						x	x	
Uropeltis cf. *phipsonii* (Satara)	U17 3763	India		KR814605						x	x	
Uropeltis cf. *phipsonii* (Satara)	U5 3296	India		KR814603						x	x	
Uropeltis pulneyensis	VPC-026	India	Observatory, Kodaikanal	MF775158	MF775199	MF775280		MF775240		x	x	x
Uropeltis rubrolineata	BMNH 1946.1.15.53	India	Tirunelveli	x	x	x	x				x	x
Uropeltis rubrolineata	VPC-066	India	Oothu, KMTR	x	x	x		x	x	x	x	x
Uropeltis rubromaculata	MNHN 1897.257	India	Anamallays	x	x	x	x				x	x
Uropeltis sp. *(annulata)*	BMNH 1946.1.16.1	India	Wayanad	x	x						x	x
Uropeltis sp. (Munnar)	MW2172	India	Munnar	x	x	x	x	x	x	x	x	x
Uropeltis sp. (Wayanad)	VPC-003	India	Vythiri, Wayanad	MF775124	MF775162	MF775245		MF775204	x	x	x	x
Uropeltis woodmasoni	BMNH 1946.1.15.57	India	Travancore	x	x	x	x				x	
Uropeltis woodmasoni	MNHN 1895.85a	India		x	x	x	x				x	
Uropeltis woodmasoni	MW3802	India	Sacred Heart College, Shembagganur, Kodaikanal, Tamil Nadu	x	x	x	x	x	x	x	x	x

Appendix Table 2-2 Gene, primer name, approximate fragment size in number of base pairs (bp), primer sequence, reference, and PCR cycle conditions for each primer pair. For some primer pairs, touchdown (TD) PCR conditions are also presented, which were employed when regular cycle conditions failed to amplify, or when amplification resulted in multiple bands.

Gene	Primer	bp	Sequence (5'-3')	Reference	PCR cycles
16s	16Sar-L	510	CGCCTGTTTATCAAAAACAT	Palumbi (1996)	92ºC(2'), 30x [92ºC(30"), 48ºC(40"), 72ºC(45")], 72ºC(5')
	16Sbr-H		CCGGTCTGAACTCAGATCACGT	Palumbi (1996)	
12s	12Sa-L1091	380	AAAAAGCTTCAAACTGGGATTAGATACCC CACTAT	Kocher et al. (1989)	92ºC(2'), 30x [92ºC(30"), 48ºC(40"), 72ºC(45")], 72ºC(5')
	12Sb-H1478		TGACTGCAGAGGGTGACGGGCGGTGTGT	Kocher et al. (1989)	
cytb	CB1F	715	CCATCCAACATCTCAGCATGATGAAA	Kocher et al. (1989)	94ºC(3'), 35x [94ºC(30"), 48ºC(30"), 72ºC(1')], 72ºC(5')
	CB3R		GGCAAATAGGAARTATCATTC	Palumbi et al. (1991)	
	GLUDG-L	1000	TGACTTGAARAACCAYCGTTG	Palumbi et al. (1991)	94ºC(3'), 35x [94ºC(40"), 46ºC(30"), 72ºC(1')], 72ºC(7')
	H16064		CTTTGGTTTACAAGAACAATGCTTTA	Burbrink et al. (2000)	(TD) 94ºC(3'), 20x [94ºC(30"), 62ºC(30") ↓0.5ºC/cycle, 72ºC(1')], 20x [94ºC(30"), 52ºC(30"), 72ºC(1')], 72ºC(5')
nd4	ND4	690	TGACTACCAAAAGCTCATGTAGAAGC	Arévalo et al. (1994)	94ºC(3'), 40x [94ºC(30"), 50ºC(30"), 72ºC(45")], 72ºC(5')
	LEU		TACTTTTACTTGGATTTGCACCA	Arévalo et al. (1994)	
cmos	G73	370	GCGGTAAAGCAGGTGAAGAAA	Saint et al. (1998)	
	G74		TGAGCATCCAAAGTCTCCAATC	Saint et al. (1998)	
	S77	570	CAT GGA CTG GGA TCA GTT ATG	Lawson et al. (2005)	94ºC(3'), 40x [94ºC(45"), 47ºC(45"), 72ºC(1')], 72ºC(5')
	S78		CCT TGG GTG TGA TTT TCT CAC CT	Lawson et al. (2005)	(TD) 94ºC(3'), 20x [94ºC(30"), 62ºC(30") ↓0.5ºC/cycle, 72ºC(1')], 20x [94ºC(30"), 52ºC(30"), 72ºC(1')], 72ºC(5')
prlr	PRLR_f1	555	GACARYGARGACCAGCAACTRATGCC	Townsend et al. (2008)	94ºC(2'), 35x [94ºC(30"), 48ºC(30"), 72ºC(45")], 72ºC(5')
	PRLR_r3		GACYTTGTGRACTTCYACRTAATCCAT	Townsend et al. (2008)	(TD) 95ºC(3'), 10x [95ºC(30"), 58ºC(45") ↓1ºC/cycle, 72ºC(1')], 30x [95ºC(30"), 48ºC(45"), 72ºC(1')], 72ºC(5')

Appendix Table 2-3 Information on quality of the libraries used in the shotgun sequencing, tissue weight, type status of each sample, and latest possible collection date of each specimen, according to museum databases records and species descriptions. Libraries concentration was quantified with Broad Range Qubit kit and the ones that failed to give a reading were re-done using a High Sensitivity kit (marked with *). *Rhinophis philippinus* MNHN0.6994 reported seemingly in error as 64.94 by Gans (1966), McDiarmid et al. (1999), and 1864.94 by Pyron et al. (2016).

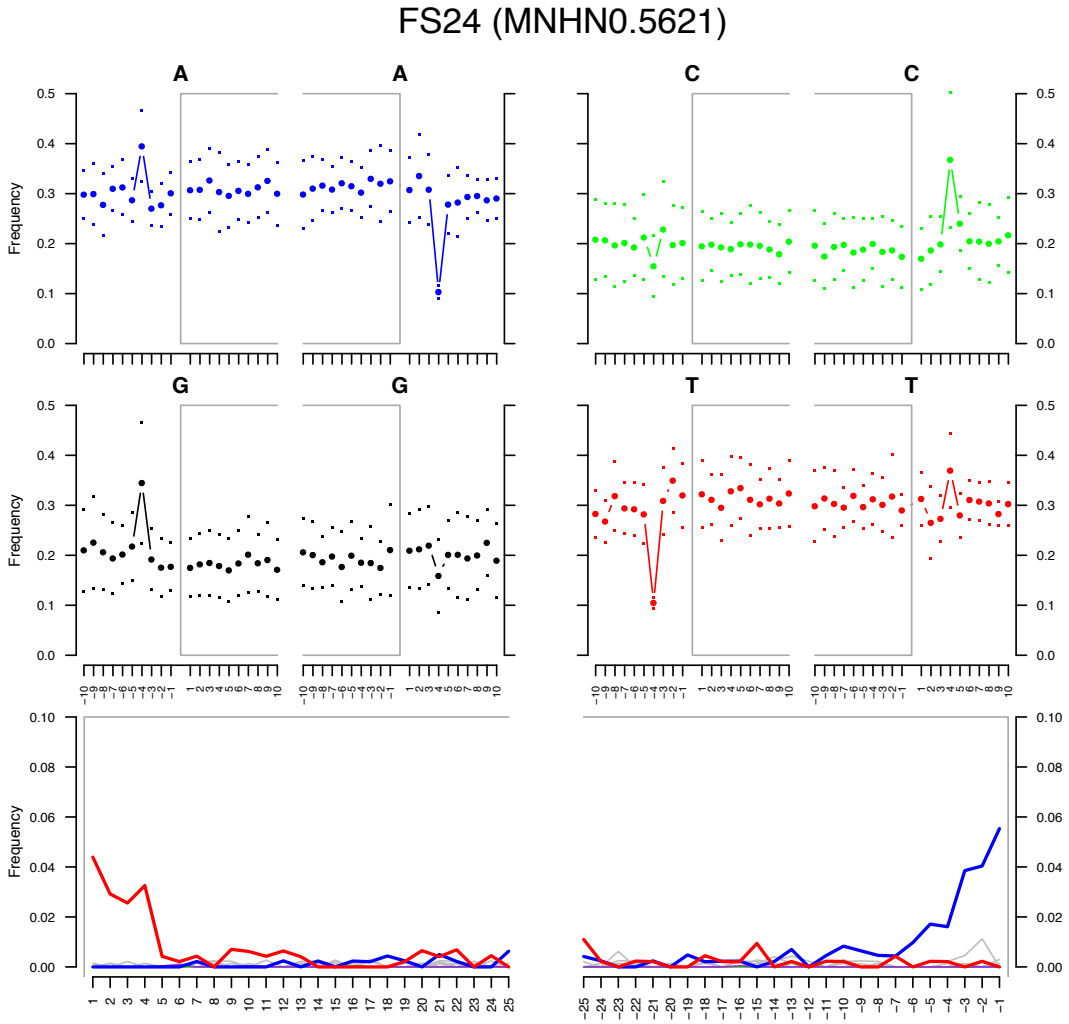
Sample lab ID	Specimen voucher code	Other code	Species	Type	(Latest possible) Collection date	Qubit (ng/μL)	Tissue (mg)
FS24	MNHN0.5621		*Rhinophis saffragamus*	neotype *Uropeltis saffragamus*		1.52	3.27
FS25	MNHN0.6994		*Rhinophis philippinus*	holotype *R. philippinus*	1829	1.94	2.2
FS27	MNHN1897.257		*Uropeltis rubromaculata*		1897	18	4.84
FS31	MNHN1895.107		*Plectrurus aureus*	syntype *P. aureus*	1895	19.7	3.14
FS35	MNHN1895.79 larger		*Uropeltis grandis*	syntype *R. grandis*	1895	11.7	2.63
FS41	MNHN1895.105		*Plectrurus guentheri*		1895	8.89	3.66
FS46	MNHN1895.88		*Uropeltis dindigalensis*	syntype *U. dindigalensis*	1895	18.3	3.09
FS49	MNHN1895.85a		*Uropeltis woodmasoni*	syntype *Silybura nigra*	1895	18.2	1.93
FS54	ZMB3825		*Rhinophis oxyrhynchus*	syntype *R. oxyrhynchus*	1801	1.03	2.63
FS55	ZMB3829		*Rhinophis punctatus*			0.531*	2.26
FS56	ZMB3827		*Rhinophis homolepis*	holotype *R. homolepis*	1820	11.2	2.1
NC1	NA		(Negative control)			0.285*	
FS60	ZMB4034		*Uropeltis ceylanica*			0.668*	5.34

Sample lab ID	Specimen voucher code	Other code	Species	Type	(Latest possible) Collection date	Qubit (ng/μL)	Tissue (mg)
FS61	ZMB3826		*Rhinophis oxyrhynchus*	syntype *R. oxyrhynchus*	1801	0.483*	3.62
FS67	ZMB3872		*Rhinophis melanogaster*	holotype *Plectrurus ceylonicus*	1859	3.95	2.54
FS68	ZMB80290		*Rhinophis* cf. *roshanpererai*			0.43*	2.29
FS69	BMNH1946.1.1.41	BMNH1885.3.21.6	*Plectrurus perrotetii*	syntype *P. perrotetii*; holotype *P. davidsoni*	1851 (*perrotetii* description)	0.693*	2.88
FS70	BMNH1946.1.16.29	BMNH1883.1.12.23	*Uropeltis broughami*	holotype *U. broughami*	1878	1.26	2.48
FS71	BMNH1946.1.16.3	BMNH1883.1.12.6	*Uropeltis dindigalensis*		1883	2.36	4.49
FS72	BMNH89.7.6.7		*Plectrurus aureus*		1889	1.75	4.68
FS73	BMNH1946.1.16.32	BMNH1883.1.12.54	*Plectrurus guentheri*	holotype *P. guentheri*	1863	14.6	7.4
FS74	USNM548131		*Rhinophis erangaviraji*		1977	0.527*	3.14
FS75	MCZ18038		*Rhinophis* sp. nov. 3		1868	11.7	3.6
NC2	NA		(Negative control)			0.299	
FS30	MNHN1895.102		*Pseudoplectrurus canaricus*	syntype *P. canaricus*	1870	9.12	5.21
FS45	MNHN1895.80a		*Uropeltis petersi*	syntype *U. petersi*	1878	10.3	2.9
FS47	MNHN1895.90a		*Uropeltis ellioti*	syntype *U. beddomii*	1862	9.78	3.67
FS87	BMNH1946.1.16.7	BMNH1874.4.29.1206	*Uropeltis liura*	holotype *U. liura*	1874	20.5	3.92
FS88	BMNH1946.1.16.70	BMNH1920.8.25.1	*Rhinophis porrectus*	holotype *R. porrectus*	1920	0.404*	1.94
FS89	BMNH1946.1.16.42		*Uropeltis brevis*	holotype *Silybura brevis*	1862	2.99	3.37
FS90	BMNH1946.1.16.66		*Rhinophis homolepis*	syntype *Mitylia gerrardi*	1858	0.77*	3.51
FS91	BMNH1946.1.15.57	BMNH1874.4.29.1192	*Uropeltis woodmasoni*	lectotype *Silybura melanogaster*	1874	1.96	3.64

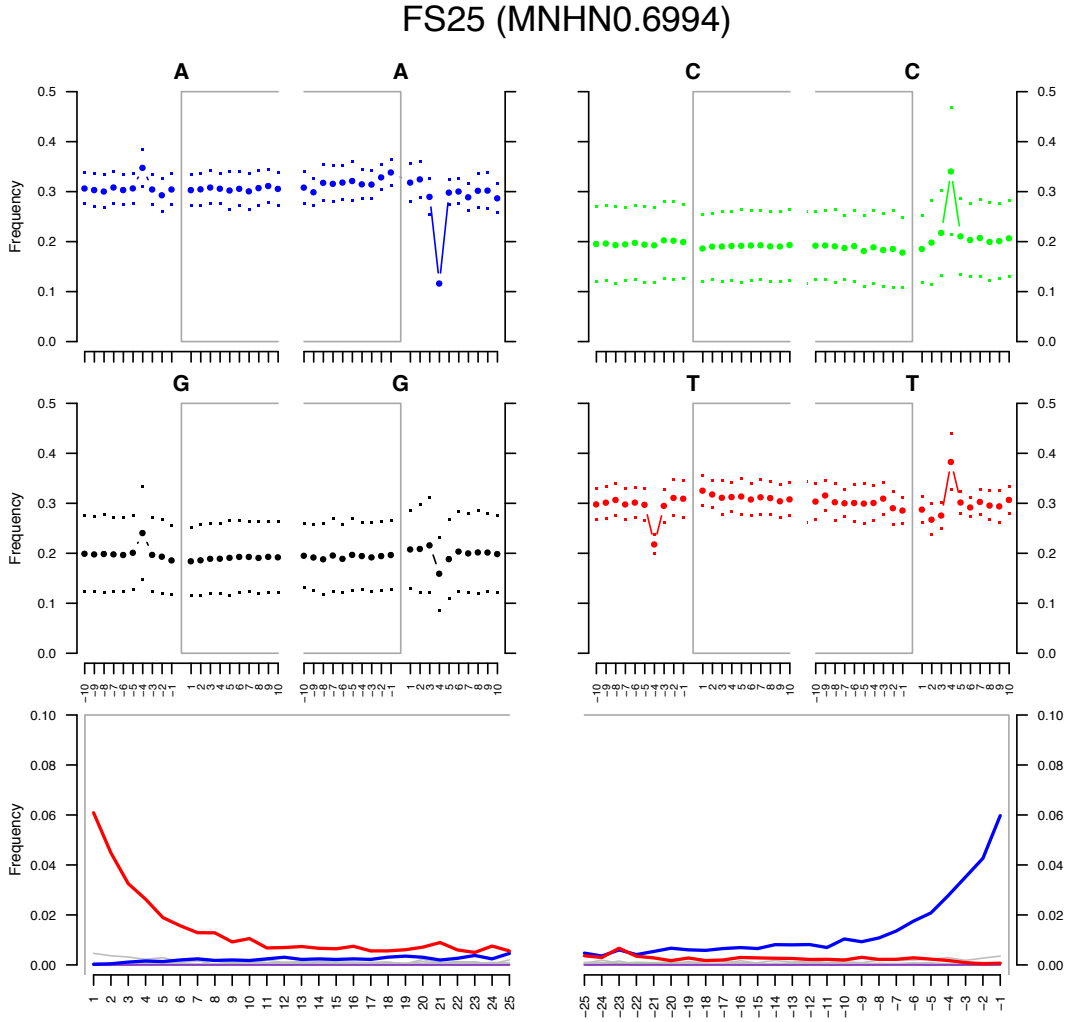
Sample lab ID	Specimen voucher code	Other code	Species	Type	(Latest possible) Collection date	Qubit (ng/μL)	Tissue (mg)
FS92	BMNH1946.1.16.12		*Uropeltis arcticeps*	syntype *U. arcticeps*	1875	2.33	3.02
FS93	CAS226607		*Rhinophis roshanpererai*		1974	0.265*	2.64
FS94	BMNH83.1.12.14		*Uropeltis* cf. *madurensis*	holotype *Silybura nilgherriensis* var. *picta*	1883	0.937*	3.89
NC3	NA		(Negative control)			0.157*	
FS76	BMNH1946.9.7.45	BMNH1883.1.12.24	*Uropeltis macrorhyncha*	holotype *U. macrorhyncha*	1877	22.4	5.08
FS77	BMNH1946.1.16.41	BMNH1874.4.29.88	*Uropeltis nilgherriensis*	holotype *Silybura nilgherriensis*	1863	17.5	6.13
FS78	BMNH1946.1.15.53	BMNH1874.4.29.804	*Uropeltis rubrolineata*	lectotype *U. rubrolineata*	1874	15.4	5.44
FS79	BMNH1946.1.15.59		*Uropeltis ocellata*	lectotype *Silybura ocellata*	pre-1900	17.4	6.35
FS80	BMNH1946.1.16.77	BMNH1895.7.29.1	*Rhinophis fergusonianus*	holotype *R. fergusonianus*	1895	1.39	3.62
FS81	BMNH1946.1.16.6		*Uropeltis ellioti*	holotype *Siloboura ellioti*	1858	1.51	4.61
FS82	USNM548100		*Rhinophis* sp. nov 1		1977	0.502*	4.17
FS83	CAS225856		*Rhinophis* sp. nov 2		1976	0.533*	3.62
FS84	MNHN0039		*Uropeltis ceylanica*	holotype *U. ceylanica*	1829	0.272*	1.65
FS85	BMNH1946.1.16.1		*Uropeltis sp.(annulata)*	holotype *Silybura nilgheriensis* var. *annulata*	1886	1.38	3.59
FS86	BMNH1946.1.1.42	BMNH1883.1.12.25	*Uropeltis dupeni*	holotype *Silybura dupeni*	1878	0.229*	6.39
NC4	NA		(Negative control)			1.73	

Appendix Table 2-4 Mapped reads summary statistics for samples included in the shotgun sequencing run with successful DNA extraction.

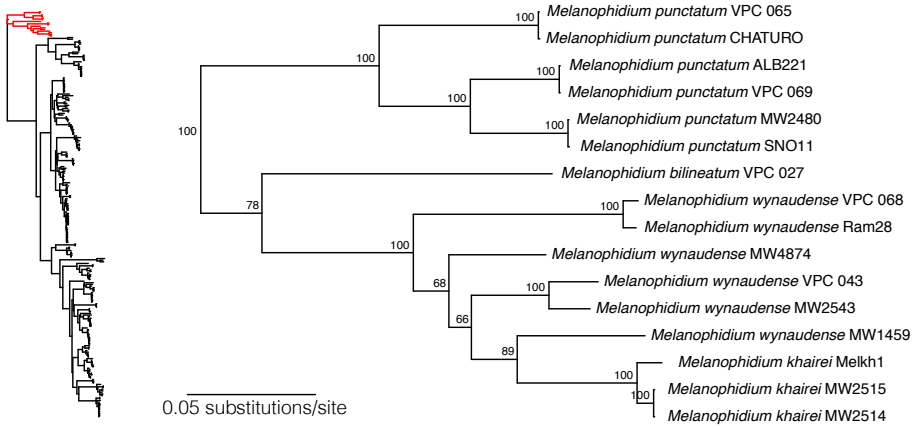
Sample lab ID	Specimen voucher	Total reads	Mapped	% Mapped	Quality filtered (MAPQ30)	Quality filtered & duplicates removed	% Quality filtered & duplicates removed	Mean coverage (X) quality filtered and duplicates removed	Reads mean length (bp)	Reference length (bp)
FS24	MNHN0.5621	3004544	2923	0.1	2879	2336	0.08	5.64	36.76	15,221
FS25	MNHN0.6994	4846309	94157	1.94	93497	23576	0.49	69.88	48.46	16,350
FS27	MNHN1897.257	3454342	31433	0.91	30799	16528	0.48	50.59	49.8	16,270
FS30	MNHN1895.102	2797746	7090	0.25	7038	5775	0.21	14.69	41.47	16,308
FS31	MNHN1895.107	2746864	16034	0.58	15977	10933	0.40	32.62	48.81	16,359
FS35	MNHN1895.79 larger	4694740	27542	0.59	27346	13922	0.30	41.30	48.62	16,390
FS41	MNHN1895.105	3040754	4232	0.14	4156	3498	0.12	8.73	41.35	16,566
FS45	MNHN1895.80a	5285081	3297	0.06	3237	2912	0.06	7.34	38.48	15,273
FS47	MNHN1895.90a	3125186	54188	1.73	52387	20197	0.65	60.95	49.52	16,408
FS49	MNHN1895.85a	3423882	10326	0.3	10203	7861	0.23	22.42	44.05	15,445
FS54	ZMB3825	2438975	18391	0.75	17881	8638	0.35	21.32	39.33	15,933
FS56	ZMB3827	3893121	8321	0.21	8180	6260	0.16	17.38	45.22	16,286
FS70	BMNH1946.1.16.2	1224643	4721	0.39	4630	3989	0.33	9.83	37.58	15,253
FS73	BMNH1946.1.16.3	2934949	13941	0.47	13701	9136	0.31	22.10	39.92	16,499
FS76	BMNH1946.9.7.45	2972070	9914	0.33	9817	7434	0.25	21.09	43.4	15,298
FS77	BMNH1946.1.16.4	2925341	6407	0.22	6364	5292	0.18	15.89	46.31	15,424
FS78	BMNH1946.1.15.5	3394270	89371	2.63	88054	24392	0.72	78.18	52.02	16,232
FS79	BMNH1946.1.15.5	3739596	7570	0.2	7478	6051	0.16	16.89	42.75	15,314
FS85	BMNH1946.1.16.1	1055046	899	0.09	878	825	0.08	2.33	40.02	14,178
FS87	BMNH1946.1.16.7	3830206	7834	0.2	7770	6029	0.16	15.03	38.15	15,306
FS91	BMNH1946.1.15.5	1673969	11128	0.66	10981	8163	0.49	20.88	41.44	16,200
FS92	BMNH1946.1.16.1	3139545	15748	0.5	15615	10061	0.32	27.40	41.74	15,323



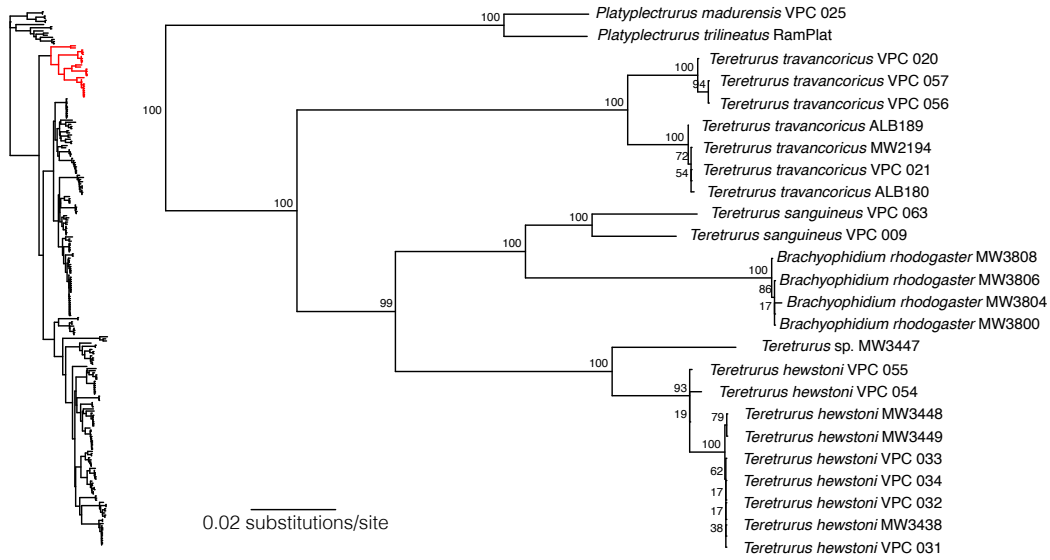
Appendix Figure 2-1 Nucleotide misincorporation plots produced by mapDamage 2.0 for sample FS24 (MNHN0.5621). Top four graphs represent base frequency inside (within the grey brackets) and outside the read. Bottom plots X-axis indicates the specific positions along the DNA fragment of nucleotide misincorporations in the 5' (left) and 3' end (right), where C to T transitions are plotted in red and G to A in blue. Y-axis indicates frequency of sites with nucleotide misincorporation from the reference sequence.



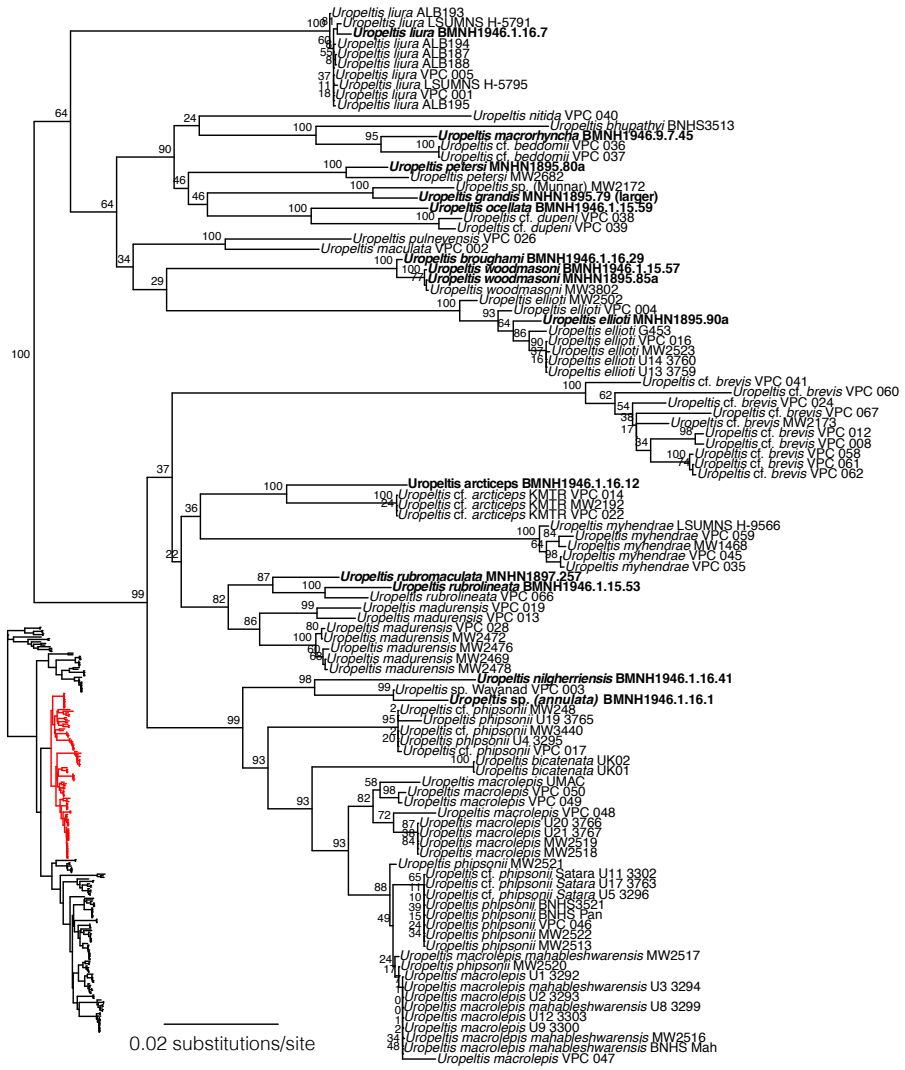
Appendix Figure 2-2 Nucleotide misincorporation plots produced by mapDamage 2.0 for sample FS25 (MNHN0.6994). Top four graphs represent base frequency inside (within the grey brackets) and outside the read. Bottom plots X-axis indicates the specific positions along the DNA fragment of nucleotide misincorporations in the 5' (left) and 3' end (right), where C to T transitions are plotted in red and G to A in blue. Y-axis indicates frequency of sites with nucleotide misincorporation from the reference sequence.



Appendix Figure 2-3 Subset ML phylogeny representing clade A. The whole tree is plotted on the left, with the position of clade A highlighted in red. Tree based on mt (*12s*, *16s*, *nd4* and *cytb*) and nucDNA markers (*cmos* and *prlr*) generated through Sanger and shotgun sequencing. Numbers at internal branches are ML bootstrap probability (BP) values.

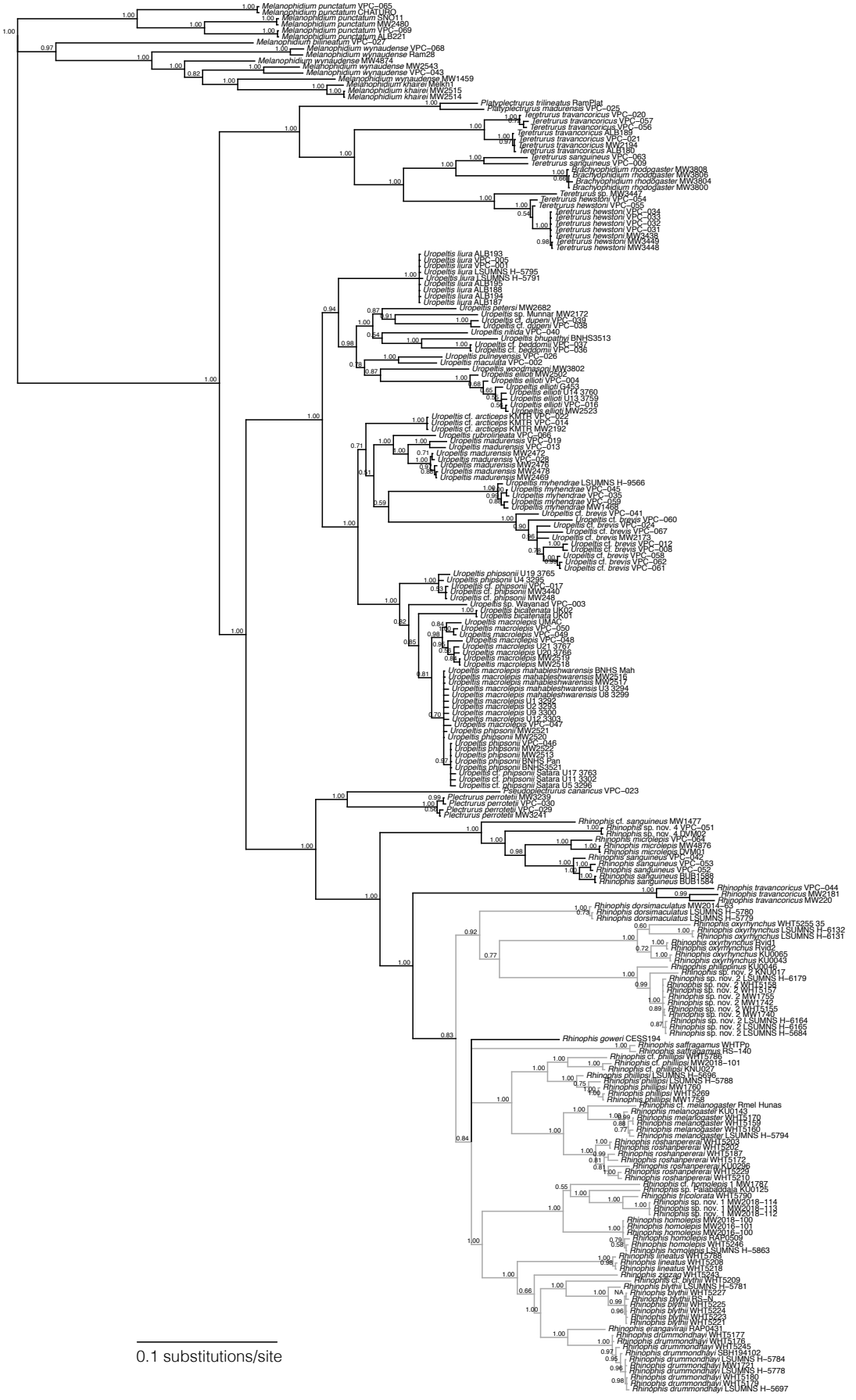


Appendix Figure 2-4 Subset ML phylogeny representing clade B. The whole tree is plotted on the left, with the position of clade B highlighted in red. Tree based on mt (*12s*, *16s*, *nd4* and *cytb*) and nucDNA markers (*cmos* and *prlr*) generated through Sanger and shotgun sequencing. Numbers at internal branches are ML bootstrap probability (BP) values.



Appendix Figure 2-5 Subset ML phylogeny representing clade C. The whole tree is plotted on the left, with the position of clade C highlighted in red. Tree based on mt (*12s*, *16s*, *nd4* and *cytb*) and nucDNA markers (*cmos* and *prlr*) generated through Sanger and shotgun sequencing. Tips in bold indicate ethanol preserved samples obtained through shotgun sequencing. Numbers at internal branches are ML bootstrap probability (BP) values.

Appendix Figure 2-6 Subset ML phylogeny representing clade D. The whole tree is plotted on the left, with the position of clade D highlighted in red. Tree based on mt (*12s*, *16s*, *nd4* and *cytb*) and nucDNA markers (*cmos* and *prlr*) generated through Sanger and shotgun sequencing. Tips in bold indicate ethanol preserved samples obtained through shotgun sequencing. Numbers at internal branches are ML bootstrap probability (BP) values. Indian lineages coloured in black and Sri Lankan in dark grey.



(Figure caption on next page)

Appendix Figure 2-7 BI phylogeny of uropeltid snakes using mtDNA markers *12s*, *16s*, *nd4* and *cytb*, and nucDNA markers cmos and prlr generated through Sanger sequencing. Numbers at the internal branches are Bayesian posterior probability (BPP) values (given to two decimal places). Indian lineages coloured in black and Sri Lankan in grey.

(Figure caption on next page)

Appendix Figure 2-8 ML phylogeny of uropeltid snakes using mtDNA markers *12s*, *16s*, *nd4* and *cytb*, and nucDNA markers *cmos* and *prlr* generated through Sanger sequencing. Numbers at the internal branches are ML bootstrap probability (BP) values. Indian lineages coloured in black and Sri Lankan in grey.

Appendix Table 3-1 Outgroup species used for calibration and associated GenBank accession numbers.

Species	*12s*	*16s*	*nd4*	*cytb*	*cmos*	*prlr*
Acrochordus granulatus	AB177879	AB177879	AB177879	AB177879	AF471124	—
Acrochordus javanicus	AF512745	AF512745	HM234055	KX694897	HM234058	—
Agkistrodon contortrix	KY747498	KY747498	KY747498	KY747498	—	JN880801
Agkistrodon piscivorus	DQ523161	DQ523161	DQ523161	DQ523161	AF471096	—
Ahaetulla pulverulenta	KC347304	KC347339	KC347512	KC347454	KC347378	—
Anilius scytale	FJ755180	FJ755180	FJ755180	U69738	AF544722	JN880805
Anomochilus leonardi	AY953430	AY953431	—	—	—	—
Aparallactus capensis	FJ404129	AY188045	FJ404331	AY188006	AY187967	—
Atractaspis micropholis	AF544740	AY611823	FJ404336	AY612006	AY611915	—
Azemiops feae	KJ872487	KJ872487	KJ872487	KJ872487	AF544695	—
Bitis nasicornis	DQ305411	DQ305434	DQ305475	DQ305457	AY187970	—
Boa constrictor	AB177354	AB177354	AB177354	AB177354	AF544676	JN880812
Calabaria reinhardtii	Z46464	Z46494	AF302943	AY099985	AF544682	JN880815
Candoia carinata	AF544741	EU419850	—	AY099984	AY099961	—
Casarea dussumieri	AF544754	AF544827	—	U69755	AF544731	—
Charina bottae	AF544743	AF544816	AF302959	AY099986	AY099971	—
Coluber constrictor priapus	L01765	L01770	AY487040	AY486913	AY486937	—
Corallus annulatus	JX244286	—	KC750018	KC750012	KC750007	—
Cylindrophis maculatus	KC347320	KC347355	KC347494	KC347460	KC347395	—
Cylindrophis ruffus	AB179619	AB179619	AB179619	AB179619	AF471133	—
Daboia russellii	EU913478	EU913478	EU913478	EU913478	AF471156	JN880826
Epicrates cenchria	AF368059	—	KC329974	KC329949	KC330007	—
Eryx colubrinus	AF544747	AF544819	—	U69811	AF544716	JN880833
Eryx conicus	AF512743	AF512743	—	U69817	GQ225672	—
Eunectes notaeus	AM236347	AM236347	AM236347	AM236347	HQ399536	—
Laticauda colubrina	NC_03605	NC_03605	NC_03605	NC_03605	EU366446	JN880849
Liasis papuana	EF545027	EF545054	—	U69843	AF544720	—
Loxocemus bicolor	AF512737	AF512737	—	AY099993	AY444035	—
Lycophidion capense	FJ404178	AY611893	FJ404376	DQ486344	AY611984	JN880855
Malayopython reticulatus	EF545035	EF545062	—	U69860	AF544675	—
Micrurus fulvius	GU045453	GU045453	GU045453	U69846	AY058935	JN880856
Morelia viridis	EF545021	EF545048	—	EF545098	—	—
Naja naja	DQ343648	DQ343648	DQ343648	DQ343648	EU366445	—
Natrix natrix	AY122682	KJ128952	AY487794	AY487749	AF544697	JN880859
Notechis ater	EU547131	EU547180	EU547034	EU547082	EU546944	—
Oligodon arnensis	KC347327	KC347365	KC347504	KC347464	KC347404	—
Pareas carinatus	AF544773	AF544802	JF827653	JF827677	JF827702	—
Python molurus	NC_01581	NC_01581	NC_01581	JX401131	GQ225667	—
Sanzinia madagascariensis	EU403571	EU403576	—	EU419834	EU403583	—
Tropidophis haetianus	NC_01257	NC_01257	NC_01257	NC_01257	AY099962	—
Ungaliophis continentalis	AF512741	AF512741	—	U69870	AF544724	—
Xylophis captaini	—	MK340909	MK340912	MK340914	MK344195	—
Xenodermus javanicus	AF544781	AF544810	U49320	—	AF544711	JN880896
Xenopeltis unicolor	AB179620	AB179620	AB179620	AB179620	AF544689	JN880897

Appendix Table 3-2 Information on alignment length and number of sequences for each molecular marker, for each BPP analyses dataset. Datasets were divided by clade: A) *Melanophidium*; B) *Platyplectururus* + (*Teretrurus* + *Brachyophidium*); C) *Uropeltis*; D) *Rhinophis* + (*Pseudoplectrurus* + *Plectrurus*).

Clade	Molecular marker	Number of sequences	Alignment length (bp)
A	concatenated mtDNA	16	2294
	cmos	14	570
	prlr	14	556
B	concatenated mtDNA	25	2289
	cmos	23	570
	prlr	24	553
C	concatenated mtDNA	103	2250
	cmos	61	570
	prlr	62	553
D	concatenated mtDNA	108	2289
	cmos	83	570
	prlr	78	553

Appendix Table 3-3 Molecular dating analyses calibration priors settings applied in BEAUti. All six nodes were constrained as monophyletic. Additional monophyletic constraints were implemented in the analyses for Henophidia (not including Aniliidae + Tropidophiinae), Caenophidia, and Henophidia + Caenophidia.

Node	Distribution	Offset	Mean	St. deviation	5% Quantile	95% Quantile	Taxon set	´Use Origin
I) Divergence between (Aniliidae+Tropidophiinae) and all other Alethinophidians	Log-normal	93.9	2	1.25	94	101	all samples	no (root)
II) Divergence between Boinae and Erycinae	Log-normal	58	1.7	1.25	58.1	64.1	*Boa constrictor*; *Corallus annulatus*; *Eunectes notaeus*; *Epicrates cenchria*	yes
III) Divergence between *Corallus* and (*Epicrates*+*Eunectes*))	Log-normal	50.2	4	1.25	50.4	64.5	*Corallus annulatus*	yes
IV) Divergence between *Acrochordus javanicus* and *A. granulatus*	Log-normal	18.05	1.5	1.25	18.1	23.4	*Acrochordus javanicus*	yes
V) Divergence between Crotalinae+Viperinae	Log-normal	20	1	1.25	20.1	23.6	*Bitis nasicornis*; *Daboia russelii*	yes
VI) Divergence between Colubroidea and (*Acrochordus*+Xenodermatidae)	Log-normal	50.5	6	1.25	50.9	72	*Agkistrodon contortrix*; *Agkistrodon piscivorus*; *Ahaetulla pulverulenta*; *Aparallactus capensis*; *Atractaspis micropholis*; *Azemiops feae*; *Bitis nasicornis*; *Coluber constrictor priapus*; *Daboia russellii*; *Laticauda colubrina*; *Lycophidion capense*; *Micrurus fulvius*; *Naja naja*; *Natrix natrix*; *Notechis ater*; *Oligodon arnensis*; *Pareas carinatus*; *Xylophis captaini*	yes

Appendix Table 3-4 Summary of bGMYC (threshold 0.6), PTP and mPTP for mtDNA single-locus species delimitation results and information on samples employed in BEAST2 dating analyses.

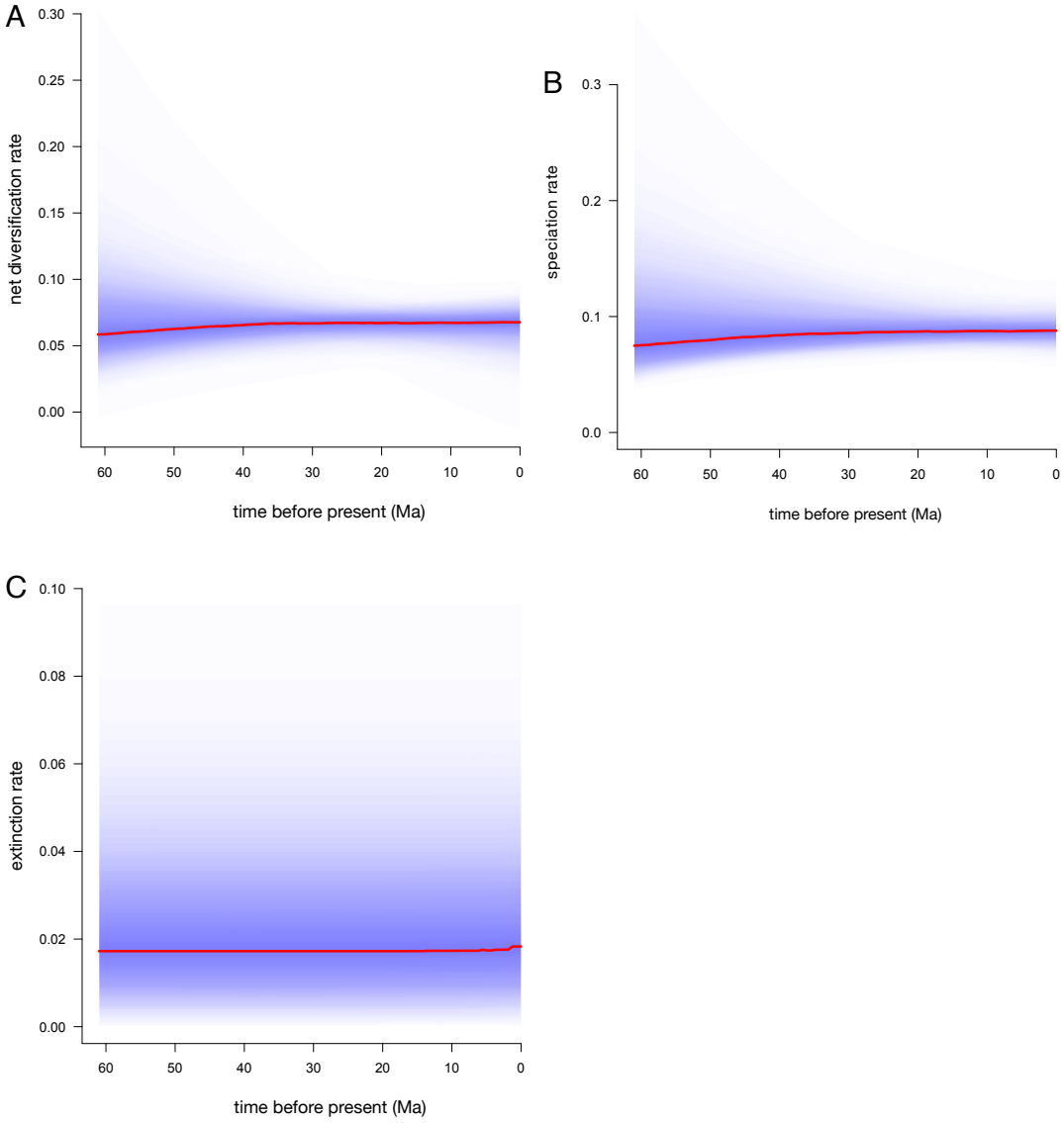
Clade	Sample code	bGMYC 0.6	bPTP	mPTP	BEAST2 sample code
A	*Melanophidium bilineatum* VPC 027	result.1	Species 1	Species 2	*M. bilineatum*
	Melanophidium khairei Melkh1	result.3	Species 10	Species 1	
	Melanophidium khairei MW2514	result.2	Species 9	Species 1	*M. khairei*
	Melanophidium khairei MW2515	result.2	Species 9	Species 1	
	Melanophidium punctatum ALB221	result.4	Species 5	Species 3	*M. punctatum* OTU 1
	Melanophidium punctatum CHATURO	result.5	Species 2	Species 5	*M.* cf. *punctatum*
	Melanophidium punctatum MW2480	result.6	Species 6	Species 4	*M. punctatum* OTU 2
	Melanophidium punctatum SNO11	result.6	Species 6	Species 4	
	Melanophidium punctatum VPC 065	result.5	Species 2	Species 5	
	Melanophidium punctatum VPC 069	result.4	Species 5	Species 3	
	Melanophidium wynaudense MW1459	result.7	Species 3	Species 1	*M. wynaudense* OTU 1
	Melanophidium wynaudense MW2543	result.8	Species 8	Species 1	*M. wynaudense* OTU 2
	Melanophidium wynaudense MW4874	result.9	Species 4	Species 1	*M. wynaudense* OTU 3
	Melanophidium wynaudense Ram28	result.10	Species 11	Species 1	*M. wynaudense* OTU 4
	Melanophidium wynaudense VPC 043	result.11	Species 7	Species 1	*M. wynaudense* OTU 5
	Melanophidium wynaudense VPC 068	result.12	Species 12	Species 1	
B	*Brachyophidium rhodogaster* MW3800	result.1	Species 1	Species 1	*B. rhodogaster*
	Brachyophidium rhodogaster MW3804	result.1	Species 1	Species 1	
	Brachyophidium rhodogaster MW3806	result.1	Species 1	Species 1	
	Brachyophidium rhodogaster MW3808	result.1	Species 1	Species 1	
	Platyplectrurus madurensis VPC 025	result.2	Species 5	Species 7	*P. madurensis*
	Platyplectrurus trilineatus RamPlat	result.3	Species 6	Species 7	*P. trilineatus*
	Teretrurus hewstoni MW3438	result.4	Species 10	Species 3	*T. hewstoni* OTU 1
	Teretrurus hewstoni MW3448	result.4	Species 10	Species 3	
	Teretrurus hewstoni MW3449	result.4	Species 10	Species 3	
	Teretrurus hewstoni VPC 031	result.4	Species 10	Species 3	
	Teretrurus hewstoni VPC 032	result.4	Species 10	Species 3	
	Teretrurus hewstoni VPC 033	result.4	Species 10	Species 3	
	Teretrurus hewstoni VPC 034	result.4	Species 10	Species 3	
	Teretrurus hewstoni VPC 054	result.5	Species 9	Species 3	*T. hewstoni* OTU 2
	Teretrurus hewstoni VPC 055	result.6	Species 11	Species 3	*T. hewstoni* OTU 3
	Teretrurus sanguineus VPC 009	result.7	Species 3	Species 2	*T. sanguineus* OTU 1
	Teretrurus sanguineus VPC 063	result.8	Species 4	Species 2	*T. sanguineus* OTU 2
	Teretrurus sp. MW3447	result.9	Species 2	Species 4	*Teretrurus* sp.
	Teretrurus travancoricus ALB180	result.10	Species 7	Species 5	*T. travancoricus* OTU 1
	Teretrurus travancoricus ALB189	result.10	Species 7	Species 5	
	Teretrurus travancoricus MW2194	result.10	Species 7	Species 5	
	Teretrurus travancoricus VPC 020	result.11	Species 8	Species 6	*T. travancoricus* OTU 2
	Teretrurus travancoricus VPC 021	result.10	Species 7	Species 5	
	Teretrurus travancoricus VPC 056	result.11	Species 8	Species 6	
	Teretrurus travancoricus VPC 057	result.11	Species 8	Species 6	
C	*Uropeltis arcticeps* BMNH1946.1.16.12	result.2	Species 10	Species 12	*U. arcticeps*
	Uropeltis bhupathyi BNHS3513	result.3	Species 5	Species 13	*U. bhupathyi*
	Uropeltis bicatenata UK01	result.4	Species 6	Species 3	*U. bicatenata*
	Uropeltis bicatenata UK02	result.4	Species 6	Species 3	
	Uropeltis broughami BMNH1946.1.16.29	result.5	Species 2	Species 16	*U. broughami*
	Uropeltis cf. *arcticeps* KMTR MW2192	result.6	Species 9	Species 11	*U.* cf. *arcticeps*
	Uropeltis cf. *arcticeps* KMTR VPC 014	result.6	Species 9	Species 11	
	Uropeltis cf. *arcticeps* KMTR VPC 022	result.6	Species 9	Species 11	
	Uropeltis cf. *beddomii* VPC 036	result.7	Species 19	Species 13	*U.* cf. *beddomii*
	Uropeltis cf. *beddomii* VPC 037	result.7	Species 19	Species 13	

Clade	Sample code	bGMYC 0.6	bPTP	mPTP	BEAST2 sample code
	Uropeltis cf. *brevis* MW2173	result.8	Species 33	Species 7	*U.* cf. *brevis* OTU 1
	Uropeltis cf. *brevis* VPC 008	result.9	Species 25	Species 7	*U.* cf. *brevis* OTU 2
	Uropeltis cf. *brevis* VPC 012	result.9	Species 25	Species 7	
	Uropeltis cf. *brevis* VPC 024	result.10	Species 34	Species 7	*U.* cf. *brevis* OTU 3
	Uropeltis cf. *brevis* VPC 041	result.11	Species 12	Species 7	*U.* cf. *brevis* OTU 4
	Uropeltis cf. *brevis* VPC 058	result.12	Species 24	Species 7	*U.* cf. *brevis* OTU 5
	Uropeltis cf. *brevis* VPC 060	result.13	Species 11	Species 7	*U.* cf. *brevis* OTU 6
	Uropeltis cf. *brevis* VPC 061	result.12	Species 24	Species 7	
	Uropeltis cf. *brevis* VPC 062	result.12	Species 24	Species 7	
	Uropeltis cf. *brevis* VPC 067	result.14	Species 15	Species 7	*U.* cf. *brevis* OTU 7
	Uropeltis cf. *dupeni* VPC 038	result.15	Species 43	Species 13	
	Uropeltis cf. *dupeni* VPC 039	result.15	Species 44	Species 13	*U.* cf. *dupeni*
	Uropeltis cf. *phipsonii* MW248	result.16	Species 41	Species 4	
	Uropeltis cf. *phipsonii* MW3440	result.16	Species 41	Species 4	
	Uropeltis cf. *phipsonii* Satara U11 3302	result.17	Species 28	Species 1	
	Uropeltis cf. *phipsonii* Satara U17 3763	result.17	Species 28	Species 1	
	Uropeltis cf. *phipsonii* Satara U5 3296	result.17	Species 28	Species 1	
	Uropeltis cf. *phipsonii* VPC 017	result.16	Species 41	Species 4	*U.* cf. phisonii
	Uropeltis ellioti G453	result.18	Species 39	Species 16	
	Uropeltis ellioti MNHN1895.90a	result.18	Species 39	Species 16	
	Uropeltis ellioti MW2502	result.19	Species 40	Species 16	*U. elliot* OTU 1
	Uropeltis ellioti MW2523	result.18	Species 39	Species 16	*U. elliot* OTU 2
	Uropeltis ellioti U13 3759	result.18	Species 39	Species 16	
	Uropeltis ellioti U14 3760	result.18	Species 39	Species 16	
	Uropeltis ellioti VPC 004	result.20	Species 39	Species 16	
	Uropeltis ellioti VPC 016	result.18	Species 39	Species 16	
	Uropeltis grandis MNHN1895.79 larger	result.21	Species 23	Species 13	*U. grandis*
	Uropeltis liura ALB187	result.22	Species 3	Species 17	
	Uropeltis liura ALB188	result.22	Species 3	Species 17	*U. liura*
	Uropeltis liura ALB193	result.22	Species 3	Species 17	
	Uropeltis liura ALB194	result.22	Species 3	Species 17	
	Uropeltis liura ALB195	result.22	Species 3	Species 17	
	Uropeltis liura BMNH1946.1.16.7	result.22	Species 3	Species 17	
	Uropeltis liura LSUMNS H 5791	result.22	Species 3	Species 17	
	Uropeltis liura LSUMNS H 5795	result.22	Species 3	Species 17	
	Uropeltis liura VPC 001	result.22	Species 3	Species 17	
	Uropeltis liura VPC 005	result.22	Species 3	Species 17	
	Uropeltis macrolepis mahableshwarensis BNHS Mah	result.17	Species 28	Species 1	
	Uropeltis macrolepis mahableshwarensis MW2516	result.17	Species 28	Species 1	
	Uropeltis macrolepis mahableshwarensis MW2517	result.17	Species 28	Species 1	
	Uropeltis macrolepis mahableshwarensis U3 3294	result.17	Species 28	Species 1	
	Uropeltis macrolepis mahableshwarensis U8 3299	result.17	Species 28	Species 1	
	Uropeltis macrolepis MW2518	result.23	Species 31	Species 2	*U. macrolepis* OTU 1
	Uropeltis macrolepis MW2519	result.23	Species 31	Species 2	
	Uropeltis macrolepis U1 3292	result.17	Species 28	Species 1	
	Uropeltis macrolepis U12 3303	result.17	Species 28	Species 1	
	Uropeltis macrolepis U2 3293	result.17	Species 28	Species 1	
	Uropeltis macrolepis U20 3766	result.23	Species 31	Species 2	
	Uropeltis macrolepis U21 3767	result.23	Species 31	Species 2	
	Uropeltis macrolepis U9 3300	result.17	Species 28	Species 1	
	Uropeltis macrolepis UMAC	result.24	Species 36	Species 2	*U. macrolepis* OTU 2
	Uropeltis macrolepis VPC 047	result.17	Species 28	Species 1	
	Uropeltis macrolepis VPC 048	result.25	Species 32	Species 2	*U. macrolepis* OTU 3
	Uropeltis macrolepis VPC 049	result.26	Species 35	Species 2	*U. macrolepis* OTU 4
	Uropeltis macrolepis VPC 050	result.26	Species 35	Species 2	

Clade	Sample code	bGMYC 0.6	bPTP	mPTP	BEAST2 sample code
	Uropeltis macrorhyncha BMNH1946.9.7.45	result.27	Species 20	Species 13	*U. macrorhyncha*
	Uropeltis maculata VPC 002	result.28	Species 13	Species 14	*U. maculata*
	Uropeltis madurensis MW2469	result.29	Species 21	Species 9	*U. madurensis* OTU 1
	Uropeltis madurensis MW2472	result.29	Species 21	Species 9	
	Uropeltis madurensis MW2476	result.29	Species 21	Species 9	
	Uropeltis madurensis MW2478	result.29	Species 21	Species 9	
	Uropeltis madurensis VPC 013	result.30	Species 26	Species 10	*U. madurensis* OTU 2
	Uropeltis madurensis VPC 019	result.31	Species 27	Species 10	*U. madurensis* OTU 3
	Uropeltis madurensis VPC 028	result.29	Species 21	Species 9	
	Uropeltis myhendrae LSUMNS H 9566	result.32	Species 1	Species 6	*U. myhendrae*
	Uropeltis myhendrae MW1468	result.32	Species 1	Species 6	
	Uropeltis myhendrae VPC 035	result.32	Species 1	Species 6	
	Uropeltis myhendrae VPC 045	result.32	Species 1	Species 6	
	Uropeltis myhendrae VPC 059	result.32	Species 1	Species 6	
	Uropeltis nilgherriensis BMNH1946.1.16.41	result.33	Species 7	Species 5	*U. nilgherriensis*
	Uropeltis nitida VPC 040	result.34	Species 4	Species 13	*U. nitida*
	Uropeltis ocellata BMNH1946.1.15.59	result.35	Species 8	Species 13	*U. ocellata*
	Uropeltis petersi MNHN1895.80a	result.36	Species 30	Species 13	*U. petersi* OTU 1
	Uropeltis petersi MW2682	result.37	Species 29	Species 13	*U. petersi* OTU 2
	Uropeltis phipsonii BNHS Pan	result.17	Species 28	Species 1	
	Uropeltis phipsonii BNHS3521	result.17	Species 28	Species 1	
	Uropeltis phipsonii MW2513	result.17	Species 28	Species 1	*U. phipsonii*
	Uropeltis phipsonii MW2520	result.17	Species 28	Species 1	
	Uropeltis phipsonii MW2521	result.17	Species 28	Species 1	
	Uropeltis phipsonii MW2522	result.17	Species 28	Species 1	
	Uropeltis phipsonii U19 3765	result.16	Species 42	Species 4	
	Uropeltis phipsonii U4 3295	result.16	Species 41	Species 4	
	Uropeltis phipsonii VPC 046	result.17	Species 28	Species 1	
	Uropeltis pulneyensis VPC 026	result.38	Species 14	Species 14	*U. pulneyensis*
	Uropeltis rubrolineata BMNH1946.1.15.53	result.39	Species 18	Species 8	*U. rubrolineata* OTU 1
	Uropeltis rubrolineata VPC 066	result.40	Species 17	Species 8	*U. rubrolineata* OTU 2
	Uropeltis rubromaculata MNHN1897.257	result.41	Species 16	Species 8	*U. rubromaculata*
	Uropeltis sp. (*annulata*) BMNH1946.1.16.1	result.1	Species 38	Species 5	*Uropeltis* sp. (*annulata*)
	Uropeltis sp. Munnar MW2172	result.42	Species 22	Species 13	*Uropeltis* sp. (Munnar)
	Uropeltis sp. Wayanad VPC 003	result.43	Species 37	Species 5	*Uropeltis* sp. (Wayanad)
	Uropeltis woodmasoni BMNH1946.1.15.57	result.5	Species 2	Species 16	
	Uropeltis woodmasoni MNHN1895.85a	result.5	Species 2	Species 16	
	Uropeltis woodmasoni MW3802	result.5	Species 2	Species 16	*U. woodmasoni*
D	*Plectrurus aureus* MNHN1895.107	result.1	Species 23	Species 34	*P. aureus*
	Plectrurus guentheri BMNH1946.1.16.32	result.2	Species 24	Species 35	*P. guentheri*
	Plectrurus guentheri MNHN1895.105	result.2	Species 24	Species 35	
	Plectrurus perrotetii MW3239	result.3	Species 22	Species 33	*P. perrotetii*
	Plectrurus perrotetii MW3241	result.3	Species 22	Species 33	
	Plectrurus perrotetii VPC 029	result.3	Species 22	Species 33	
	Plectrurus perrotetii VPC 030	result.3	Species 22	Species 33	
	Pseudoplectrurus canaricus MNHN1895.102	result.4	Species 3	Species 36	
	Pseudoplectrurus canaricus VPC 023	result.4	Species 3	Species 36	*P. canaricus*
	Rhinophis blythii LSUMNS H 5781	result.5	Species 40	Species 15	*R. blythii* OTU 1
	Rhinophis blythii RS N	result.6	Species 39	Species 14	
	Rhinophis blythii WHT5221	result.6	Species 39	Species 14	*R. blythii* OTU 2
	Rhinophis blythii WHT5223	result.6	Species 39	Species 14	
	Rhinophis blythii WHT5224	result.6	Species 39	Species 14	
	Rhinophis blythii WHT5225	result.6	Species 39	Species 14	
	Rhinophis blythii WHT5227	result.6	Species 39	Species 14	

Clade	Sample code	bGMYC 0.6	bPTP	mPTP	BEAST2 sample code
	Rhinophis cf. *blythii* WHT5209	result.7	Species 11	Species 16	*R.* cf. *blythii*
	Rhinophis cf. *homolepis* 1 MW1787	result.8	Species 9	Species 25	*R.* cf. *homolepis*
	Rhinophis cf. *melanogaster* Rmel Hunas	result.9	Species 17	Species 9	*R.* cf. *melanogaster* (Hunas)
	Rhinophis cf. *phillipsi* KNU027	result.10	Species 20	Species 11	*R.* cf. *phillipsi* OTU 1
	Rhinophis cf. *phillipsi* MW2018 101	result.10	Species 20	Species 11	
	Rhinophis cf. *phillipsi* WHT5786	result.11	Species 21	Species 11	*R.* cf. *phillipsi* OTU 2
	Rhinophis cf. *sanguineus* MW1477	result.12	Species 4	Species 32	*R.* cf. *sanguineus*
	Rhinophis dorsimaculatus LSUMNS H 5779	result.13	Species 2	Species 7	
	Rhinophis dorsimaculatus LSUMNS H 5780	result.13	Species 2	Species 7	*R. dorsimaculatus*
	Rhinophis dorsimaculatus MW2014 63	result.13	Species 2	Species 7	
	Rhinophis drummondhayi LSUMNS H 5697	result.14	Species 18	Species 18	
	Rhinophis drummondhayi LSUMNS H 5778	result.14	Species 18	Species 18	*R. drummondhayi*
	Rhinophis drummondhayi LSUMNS H 5784	result.14	Species 18	Species 18	
	Rhinophis drummondhayi MW1721	result.14	Species 18	Species 18	
	Rhinophis drummondhayi SBH194102	result.14	Species 18	Species 18	
	Rhinophis drummondhayi WHT5176	result.14	Species 18	Species 18	
	Rhinophis drummondhayi WHT5177	result.14	Species 18	Species 18	
	Rhinophis drummondhayi WHT5179	result.14	Species 18	Species 18	
	Rhinophis drummondhayi WHT5180	result.14	Species 18	Species 18	
	Rhinophis drummondhayi WHT5245	result.14	Species 18	Species 18	
	Rhinophis erangaviraji RAP0431	result.15	Species 19	Species 19	*R. erangaviraji*
	Rhinophis goweri CESS194	result.16	Species 7	Species 13	*R. goweri*
	Rhinophis homolepis LSUMNS H 5863	result.17	Species 10	Species 21	*R. homolepis*
	Rhinophis homolepis MW2016 100	result.17	Species 10	Species 21	
	Rhinophis homolepis MW2016 101	result.17	Species 10	Species 21	
	Rhinophis homolepis MW2018 100	result.17	Species 10	Species 21	
	Rhinophis homolepis RAP0509	result.17	Species 10	Species 21	
	Rhinophis homolepis WHT5246	result.17	Species 10	Species 21	
	Rhinophis homolepis ZMB3827	result.17	Species 10	Species 21	
	Rhinophis lineatus WHT5208	result.18	Species 6	Species 20	*R. lineatus*
	Rhinophis lineatus WHT5218	result.18	Species 6	Species 20	
	Rhinophis lineatus WHT5788	result.18	Species 6	Species 20	
	Rhinophis melanogaster KU0143	result.19	Species 16	Species 8	*R. melanogaster*
	Rhinophis melanogaster LSUMNS H 5794	result.19	Species 16	Species 8	
	Rhinophis melanogaster WHT5159	result.19	Species 16	Species 8	
	Rhinophis melanogaster WHT5160	result.19	Species 16	Species 8	
	Rhinophis melanogaster WHT5170	result.19	Species 16	Species 8	
	Rhinophis microlepis DVM01	result.20	Species 25	Species 29	
	Rhinophis microlepis MW4876	result.20	Species 25	Species 29	*R. microlepis* OTU 1
	Rhinophis microlepis VPC 064	result.21	Species 26	Species 30	*R. microlepis* OTU 2
	Rhinophis oxyrhynchus KU0043	result.22	Species 34	Species 4	*R. oxyrhynchus* OTU 1
	Rhinophis oxyrhynchus KU0065	result.22	Species 34	Species 4	
	Rhinophis oxyrhynchus LSUMNS H 6131	result.23	Species 14	Species 5	*R. oxyrhynchus* OTU 2
	Rhinophis oxyrhynchus LSUMNS H 6132	result.23	Species 14	Species 5	
	Rhinophis oxyrhynchus Rvid1	result.24	Species 36	Species 4	
	Rhinophis oxyrhynchus Rvid2	result.24	Species 36	Species 4	*R. oxyrhynchus* OTU 3
	Rhinophis oxyrhynchus WHT5255 35	result.25	Species 15	Species 6	*R. oxyrhynchus* OTU 4
	Rhinophis oxyrhynchus ZMB3825	result.26	Species 35	Species 4	*R. oxyrhynchus* OTU 5
	Rhinophis philippinus KU0046	result.27	Species 29	Species 1	*R. philippinus*
	Rhinophis philippinus MNHN0.6994	result.27	Species 29	Species 1	
	Rhinophis phillipsi LSUMNS H 5696	result.28	Species 38	Species 12	
	Rhinophis phillipsi LSUMNS H 5788	result.29	Species 47	Species 12	
	Rhinophis phillipsi MW1758	result.30	Species 46	Species 12	

Clade	Sample code	bGMYC 0.6	bPTP	mPTP	BEAST2 sample code
	Rhinophis phillipsi MW1760	result.30	Species 46	Species 12	*R. phillipsi*
	Rhinophis phillipsi WHT5269	result.30	Species 46	Species 12	
	Rhinophis roshanpererai KU0296	result.31	Species 37	Species 10	*R. roshanpererai* OTU 1
	Rhinophis roshanpererai WHT5172	result.32	Species 48	Species 10	*R. roshanpererai* OTU 2
	Rhinophis roshanpererai WHT5187	result.33	Species 49	Species 10	*R. roshanpererai* OTU 3
	Rhinophis roshanpererai WHT5202	result.34	Species 44	Species 10	*R. roshanpererai* OTU 4
	Rhinophis roshanpererai WHT5203	result.34	Species 44	Species 10	
	Rhinophis roshanpererai WHT5210	result.35	Species 45	Species 10	*R. roshanpererai* OTU 5
	Rhinophis roshanpererai WHT5229	result.35	Species 45	Species 10	
	Rhinophis saffragamus MNHN0.5621	result.36	Species 1	Species 26	
	Rhinophis saffragamus RS 140	result.36	Species 1	Species 26	
	Rhinophis saffragamus WHTPp	result.36	Species 1	Species 26	*R. saffragamus*
	Rhinophis sanguineus BUB1584	result.37	Species 43	Species 31	*R. sanguineus* OTU 1
	Rhinophis sanguineus BUB1588	result.37	Species 43	Species 31	
	Rhinophis sanguineus VPC 042	result.38	Species 42	Species 31	*R. sanguineus* OTU 2
	Rhinophis sanguineus VPC 052	result.39	Species 41	Species 31	*R. sanguineus* OTU 3
	Rhinophis sanguineus VPC 053	result.39	Species 41	Species 31	
	Rhinophis sp. nov. 1 MW2018 112	result.41	Species 32	Species 23	*Rhinophis* sp. nov. 1
	Rhinophis sp. nov. 1 MW2018 113	result.41	Species 32	Species 23	
	Rhinophis sp. nov. 1 MW2018 114	result.41	Species 32	Species 23	
	Rhinophis sp. nov. 2 KNU017	result.42	Species 28	Species 3	*Rhinophis* sp. nov. 2 OTU 1
	Rhinophis sp. nov. 2 LSUMNS H 5684	result.43	Species 27	Species 2	
	Rhinophis sp. nov. 2 LSUMNS H 6164	result.43	Species 27	Species 2	*Rhinophis* sp. nov. 2 OTU 2
	Rhinophis sp. nov. 2 LSUMNS H 6165	result.43	Species 27	Species 2	
	Rhinophis sp. nov. 2 LSUMNS H 6179	result.43	Species 27	Species 2	
	Rhinophis sp. nov. 2 MW1740	result.43	Species 27	Species 2	
	Rhinophis sp. nov. 2 MW1742	result.43	Species 27	Species 2	
	Rhinophis sp. nov. 2 MW1755	result.43	Species 27	Species 2	
	Rhinophis sp. nov. 2 WHT5155	result.43	Species 27	Species 2	
	Rhinophis sp. nov. 2 WHT5157	result.43	Species 27	Species 2	
	Rhinophis sp. nov. 2 WHT5158	result.43	Species 27	Species 2	
	Rhinophis sp. nov. 4 DVM02	result.44	Species 5	Species 28	
	Rhinophis sp. nov. 4 VPC 051	result.44	Species 5	Species 28	*Rhinophis* sp. nov. 4
	Rhinophis sp. Palabaddala KU0125	result.40	Species 12	Species 22	*Rhinophis* sp. (Palabaddala)
	Rhinophis travancoricus MW2181	result.45	Species 31	Species 27	*R. travancoricus* OTU 1
	Rhinophis travancoricus MW220	result.46	Species 30	Species 27	*R. travancoricus* OTU 2
	Rhinophis travancoricus VPC 044	result.47	Species 13	Species 27	*R. travancoricus* OTU 3
	Rhinophis tricolorata WHT5790	result.48	Species 33	Species 24	*R. tricolorata*
	Rhinophis zigzag WHT5243	result.49	Species 8	Species 17	*R. zigzag*



Appendix Figure 3-1 A) Net diversification, B) speciation, and C) extinction rates variation through time plots for Uropeltidae generated in BAMMtools. Mean estimates of rates represented in red lines, and blue shaded areas indicate 95% confidence intervals, with colour density shading denoting confidence of rate reconstructions.

Appendix Table 4-1 List of species, specimens and data collected in this study. Characters' description in Appendix Table 4-2. Collections abbreviations: Natural History Museum, London, UK (BMNH); Muséum national d'Histoire naturelle, Paris, France (MNHN), Museum für Naturkunde, Berlin, Germany (ZMB), Staatliches Museum für Naturkunde, Stuttgart, Germany (SMNS), Muséum d'Histoire naturelle, Geneva, Switzerland (MHNG); American Museum of Natural History, New York, USA (AMNH); Smithsonian Institution National Museum of Natural History, Washington DC, USA (USNM), Museum of Comparative Zoology, Harvard University, USA (MCZ); California Academy of Sciences, San Francisco, USA (CAS), Louisiana Museum of Natural History, USA (LSUMZ), National Centre for Biological Sciences, Bangalore, India (NCBS), Bombay Natural History Society, Mumbai, India (BNHS), IISER Thiruvananthapuram, India (IISER-TVM), Herpetological Foundation of Sri Lanka, Colombo, Sri Lanka (HFSL) National Museum, Colombo, Sri Lanka (NMSL); Centre for Ecological Studies, Indian Institute of Science, Bengaluru, India (CES); Department of Zoology, University of Kerala, Thiruvananthapuram, India (UK); Bangalore University, Bengaluru, India (BU). In addition, the following prefixes are field tags on as yet unaccessioned specimens: MW (specimen to be deposited in BNHS); SDB (SD Biju field tag specimens to be accessioned in BNHS); ALB (A. Rajendran field tag specimen to be accessioned in BNHS) SN (Surya Narayan field tag specimen to be accessioned in BNHS)

Species	Collection	Voucher code	Sex	TL	Mb C	tC	Mb W	tW	tL	SL	SW	HL-SL	HL-P	HH 1-P	HW	MW	IL-M	IL-ST	E	E-N	E-ST	E-SL	RH	E-E	N-N	V	D	SC-L	SC-R
B. rhodogaster	BMNH	1923.10.13.34	M	158	21	18	6.4	4.5	8.2	1.2	0.7	5.8	5.7	3	3.8	3	3.6	4.6	0.6	2	2.8	1	1.8	3	1.1	136	15	11	10
B. rhodogaster	BMNH	1923.10.13.36	F	187	22	19	6.1	4.4	6.2	1.2	0.7	5.8	6	3.3	4	3.5	4.1	4.9	0.6	2.1	2.7	0.9	1.9	2.9	0.9	142	15	7	7
B. rhodogaster	BMNH	1923.10.13.32	F	160	18	17	5.6	4.9	5.8	1.1	0.7	5.7	5.8	3	4.2	3.4	4	4.6	0.6	2	2.7	0.9	1.9	3.1	1.1	142	15	8	8
B. rhodogaster	BMNH	1923.10.13.33	F	119	16	13	4	3.6	4.8	0.9	0.7	4.9	4.9	3.4	3.4	2.8	3.4	4	0.5	1.8	2.4	0.9	1.7	2.5	0.9	145	15	7	7
B. rhodogaster	BMNH	1923.10.13.35	F	198	22	19	6.4	4.7	6.8	1.2	0.7	6.2	6	3.1	4	3.3	3.9	4.7	0.7	2	2.8	1	2	3.1	1	144	15	8	7
B. rhodogaster	BMNH	1923.10.13.37	M	176	23	20	6.5	4.8	9	1.1	0.7	6	6.1	3.6	3.9	3.5	4	5	0.6	2.1	2.7	1	2	3.1	1	141	15	11	11
B. rhodogaster	BMNH	1925.4.2.5	F	137	15	13	4.1	3.4	5.2	1	0.5	5.1	5.1	3	3.3	2.7	3.4	4	0.5	1.8	2.4	0.8	1.6	2.6	0.9	143	15	7	7
B. rhodogaster	BMNH	1946.1.15.60	F	186	25	21	6.4	5	6	1.5	0.7	5.9	5.9	3.3	3.3	2.7	3.5	4.7	0.6	2	2.7	0.9	1.6	2.4	0.9	141	15	7	7
B. rhodogaster	BMNH	1922.3.13.2	F	182	16	14	4.7	3.7	6.6	1.2	0.6	5.6	5.6	2.6	3.3	2.8	3.6	4.5	0.5	2	2.5	0.7	1.7	2.2	0.8	147	15	8	8
B. rhodogaster	BMNH	1936.6.11.3	F	209	26	21	7.1	5.7	7.5	1.3	0.7	6.1	6.1	3.5	4.3	3.1	4.1	5.2	0.7	2.1	2.8	1	1.9	3.2	1.1	143	15	7	7
B. rhodogaster	BMNH	1925.12.22.2	M	188	20	15	5.5	4.4	9.1	1.3	0.7	6.1	6.2	3.1	4	3.1	4	5	0.7	2	2.9	1	1.9	3.1	1.1	139	15	10	11
B. rhodogaster	USNM	217501	F	173	16	13	5.3	3.1	5.8	1.2	0.7	5.8	5.9	2.8	3.5	3.1	3.4	4.5	0.6	2	2.7	0.8	1.8	2.8	1	148	15	8	8
B. rhodogaster	MCZ	18075	M	167	19	16	6.3	4.5	7.9	1.1	0.7	5.6	5.6	3.4	3.8	3.2	3.5	4.4	0.6	1.9	2.5	1	1.8	2.9	1	142	15	11	10
B. rhodogaster	MCZ	18071	F	166	17	15	4.9	3.9	5.3	1.2	0.6	5.5	5.6	3.1	3.8	3.1	3.8	4.4	0.6	2	2.7	0.9	1.9	2.9	1	144	15	7	7
B. rhodogaster	AMNH	77606	M	190	17	14	4.8	3.6	9.7	1.3	0.6	6	5.8	3.3	4	3.3	3.9	4.8	0.6	2.1	2.7	0.8	1.7	2.7	0.9	141	15	10	10
B. rhodogaster	MW	3799	F	172	17	16	5.1	4.3	5.9	1.2	0.8	5.7	5.5	2.9	3.7	2.8	3.1	3	0.6	1.9	2.5	0.8	1.6	2.5	1	145	15	8	7
B. rhodogaster	MW	3805	M	173	17	16	5.3	4.7	9.1	1.3	0.7	6	5.8	2.7	3.6	2.9	3.4	4.2	0.6	2.1	2.8	1.1	1.8	2.7	1.1	141	15	10	9
B. rhodogaster	MW	3803	F	164	18	14	5.2	3.9	6.2	1.2	0.7	5.8	5.8	3.5	3.3	2.9	3.5	4.1	0.5	1.8	2.5	0.9	1.7	2.6	1	142	15	8	7
B. rhodogaster	MW	3807	M	162	20	15	6.2	4.4	8.8	1.3	0.8	5.6	5.5	3.3	4	3	3.6	4.3	0.5	1.8	2.6	1	1.9	2.7	1.1	142	15	9	10
M. bilineatum	MNHN	1895.111	?	346	27	23	7.4	6.5	18.9	1.1	0.9	9.1	8.8	3.7	5	4.3	7.2	7.8	0.5	2.7	3.8	1.2	2.4	3.6	1.5	199	15	16	16
M. bilineatum	BMNH	1946.1.15.75	M	229	17	16	5.5	4.4	12.7	0.9	0.8	6	7	3	4.2	3.9	5.2	5.6	0.4	2.2	3.1	1	2	2.8	1.3	186	15	16	15
M. bilineatum	BMNH	74.4.29.698	F	356	21	20	6.7	6.3	19.4	1.3	1	8.5	9.4	4.3	5.6	5.3	7.2	8	0.5	2.9	4.2	1.3	2.8	4	2	189	15	16	16
M. bilineatum	BMNH	74.4.29.699	F	175	8	7	4	3.4	9.2	0.9	0.6	5.4	6.3	3.2	3.8	3.3	4.6	5.1	0.5	1.8	2.7	0.9	1.9	2.9	1.4	198	15	17	16
M. bilineatum	BNHS	3410	F	357	23	19	7.4	5.4	19.3	1.3	1	7.8	8.7	3.7	3.5	4.9	6.3	7.1	0.6	2.5	3.8	1.5	2.5	3.7	2	200	15	14	15

Species	Collection	Voucher code	Sex	TL	Mb C	tC	Mb W	tW	tL	SL	SW	HL-SL	HL-P	HH 1-P	HW	MW	IL-M	IL-ST	E	E-N	E-ST	E-SL	RH	E-E	N-N	V	D	SC-L	SC-R
M. bilineatum	IISER-TVM	VPMB0915049	?	449	30	24	10.5	6.6	24	1.8	1.3	9.5	10.6	4.6	6.1	4.9	6.3	7.1	0.4	3.2	4.6	1.4	2.7	4.1	1.6	201	15	16	16
M. bilineatum	CES		?	505	NA	NA	10.9	NA	28.7	1.8	1.5	10.7	NA	NA	NA	NA	NA	NA	NA	3.8	5.7	1.5	NA	4.9	2.7	200	15	17	17
M. cf. punctatum	MW	4872	?	199	14	12	4.9	3.5	9.3	0.7	0.6	5.4	6.3	2.8	3.5	3.1	4.3	4.6	0.4	1.7	2.8	1	1.9	2.6	1.3	189	15	16	16
M. cf. punctatum	SDB	CHATURO	?	192	16	15	5.3	4.4	9.9	0.9	0.7	5.4	6.1	3	3.8	3.2	4.2	4.9	0.5	1.7	2.7	1	1.9	2.9	1.3	191	15	16	16
M. cf. punctatum	IISER-TVM	VPMP0618088	M	308	22	17	7.7	5.2	16.6	1.2	0.8	6.4	7.2	3.2	5.1	4.7	5.1	5.6	0.5	2.2	3.4	1.2	2.5	3.3	1.6	192	NA	16	17
M. khairei	UK MW	2691	F	270	19	16	6.4	4.1	12	0.9	1.1	6.1	7.2	3.8	4.4	4	5	5.5	0.3	2.1	3.3	1.1	2.2	3	1.6	196	15	12	12
M. khairei	BNHS	3452	F	550	43	28	11.8	7.9	19.7	1.5	1.8	8.9	9.7	5.8	6.4	5.8	6.7	7.9	NA	3.1	4.6	1.9	3.1	4.8	2.3	192	15	12	11
M. khairei	BNHS	3445	M	312	23	19	6.6	5	15.1	1.7	2.1	6.3	7.3	3.6	4.4	4.1	5.2	5.6	0.3	2.3	3.4	1.1	2.1	3.3	1.6	194	15	13	11
M. khairei	BNHS	3446	F	388	22	17	5.6	4.2	14.1	1.3	1.3	7.4	8.5	3.6	4.8	4.4	6.1	6.5	0.4	2.6	3.7	1.2	2.3	3.4	1.6	199	15	13	11
M. khairei	BNHS	3444	F	409	30	22	10	6.3	14.9	1.2	1.5	7.7	9	4.4	5.5	4.9	6.3	7	0.4	2.8	4.1	1.3	2.5	3.8	1.9	197	15	12	12
M. khairei	BNHS	3199	F	265	17	13	5.3	3.2	10.2	0.9	1	5.7	6.6	3.2	3.9	3.3	4.6	5.2	0.3	2	2.8	0.8	1.8	2.4	1.3	193	15	12	12
M. khairei	BNHS	3253	F	237	19	14	5.5	3.4	9.9	0.9	1	5.8	6.7	4.2	4	3.8	4.8	5.2	0.3	2.1	3	1	1.9	3	1.4	191	15	12	11
M. punctatum	BMNH	83.1.12.62	M	510	42	33	11.1	9.2	33.6	5.4	2	10.9	12.4	7.7	7.3	7.1	8.7	10	0.7	3.8	5.6	2	3.5	5.1	2.8	183	15	16	16
M. punctatum	BMNH	83.1.12.63	M	245	21	16	5.9	4.3	14	2.2	0.9	6.4	7.2	3.7	4.2	3.9	5.1	5.9	0.5	2.3	3.3	1.2	2.3	3.3	1.7	186	15	16	16
M. punctatum	MNHN	1895.11	?	420	36	27	10.5	7.4	27.6	3.2	1.6	7.9	9	5.2	5.4	5	6.4	7.2	0.5	2.8	4.2	1.5	3	4	2	190	15	17	17
M. punctatum	MNHN	1897.263	?	526	50	37	13.9	10.4	35.9	4.3	2	10.5	12	6	7.9	7.5	9	9.6	0.7	3.9	5.4	1.8	3.5	5	2.7	183	15	16	17
M. punctatum	ZMB	10359	?	512	39	31	11.1	8.9	22.4	2.3	1.3	11.1	12.3	6.1	7.2	6.3	9	9.9	0.6	3.9	5.6	2.1	3.3	5	2.6	189	15	16	15
M. punctatum	USNM	204998	?	350	30	23	9	6.8	18	2.1	1.1	7.2	8.1	4.4	5.2	4.8	5.8	6.5	0.6	2.5	3.6	1.4	2.7	3.7	2	189	15	14	14
M. punctatum	USNM	204999	?	309	27	21	8.1	5.4	17.6	2.1	1	7	8.2	4.4	4.8	4.5	5.6	6.4	0.6	2.4	3.6	1.3	2.7	3.6	2	190	15	16	16
M. punctatum	BMNH	1946.1.4.37	M	443	31	25	9.9	6.9	23.2	2.6	1.3	9.7	10.9	5.6	6.9	6.2	8	8.9	0.7	3.6	5.1	1.6	3.5	5.1	2.5	197	15	15	14
M. punctatum	MW	2479	F	473	33	25	9.4	6.3	24.2	3	1.2	9.1	10.2	5	6	5.3	7	7.9	0.7	3.1	4.4	1.4	NA	4.4	2.4	191	15	15	16
M. punctatum	BNHS	97	?	358	23	21	8.5	5.6	23.9	1.4	1.3	7.8	8.7	4.5	5.5	5.1	6	6.7	0.5	2.4	4	1.4	2.7	3.8	2.1	185	15	16	17
M. punctatum	ALB	221	F	364	29	21	8.5	6.7	19.5	2.1	1.2	7.7	8.8	4	5	4.6	5.7	6.7	0.5	2.5	4	1.3	2.7	3.8	2.3	190	15	16	16
M. punctatum	IISER-TVM	VPMP0116078	?	328	27	23	8.3	7	15.9	1.7	1.2	7.8	8.7	3.9	5	4.5	6.3	6.8	0.5	2.7	3.9	1.3	2.8	3.7	2	200	15	15	15

Species	Collection	Voucher code	Sex	TL	Mb C	tC	Mb W	tW	tL	SL	SW	HL-SL	HL-P	HH 1-P	HW	MW	IL-M	IL-ST	E	E-N	E-ST	E-SL	RH	E-E	N-N	V	D	SC-L	SC-R
M. wynaudense	MNHN	1895.108	?	394	34	22	9.3	7.2	15.7	1.7	1.6	7.8	8.9	4.9	5.8	5	6	6.8	0.4	3	3.9	1.5	2.7	3.5	1.6	185	15	11	10
M. wynaudense	MNHN	1895.109	?	304	27	21	7.2	5.5	15.5	1	1.1	7.2	8.5	4.2	5.1	4.7	5.8	6.6	0.4	2.8	3.9	1.4	2.4	3.5	1.6	179	15	12	12
M. wynaudense	BMNH	1946.1.15.74	M	222	16	15	4.3	3.6	10.1	1.1	1	5.9	6.9	3.6	4.2	4.1	4.8	5.5	0.4	2.1	3.1	1	2	2.9	1.2	177	15	11	11
M. wynaudense	MW	2542	F	429	38	31	12.7	9.1	14.4	1.9	1.8	7.9	9.1	4.4	5.9	5.2	6.5	7.8	0.5	3.1	4.2	1.4	2.7	3.9	1.8	192	15	11	11
M. wynaudense	MW	1458	F	206	13	11	4.7	2.6	8.5	0.8	0.7	4.8	5.6	2.8	3.3	2.8	3.7	4.2	0.3	1.8	2.6	0.8	1.6	2.2	1.1	176	15	12	12
M. wynaudense	SMNS	2534	M	381	23	23	8.3	7	17.3	2.3	2.4	7.5	9.1	4.9	5	5	6.3	7.3	0.5	2.8	3.9	1.5	2.6	3.8	1.7	185	15	11	12
M. wynaudense	BMNH	1946.1.15.46	F	438	33	30	10.1	8.9	19.3	1.7	1.7	8.5	9.7	5.5	5.8	5.5	7	8.2	0.5	3.1	4.4	1.7	3	4	1.9	184	15	11	11
M. wynaudense	BMNH	1914.1.26.6	F	402	34	25	10.5	6.9	17.2	1.5	1.6	7.9	9.2	5.6	5.5	4.9	6.5	7.1	0.5	3	4.4	1.5	2.6	3.7	1.7	184	15	11	10
M. wynaudense	BMNH	1914.1.26.7	F	354	28	28	8.7	7.2	14.7	1.4	1.4	7.4	8.9	4.7	5.2	4.7	6.2	7	0.5	2.9	4.1	1.5	2.6	3.8	1.7	182	15	11	11
M. wynaudense	MW	4874	F	273	21	18	6.4	4.5	12.8	1.3	1.1	5.6	6.8	3.4	3.9	3.4	4.3	5.1	NA	2.2	3.2	1.1	1.9	2.7	1.3	169	15	12	12
M. wynaudense	MW	4875	F	249	21	17	6.3	4.7	10.8	0.9	1	5.3	6.3	3.2	3.7	3.2	4.2	4.6	0.3	1.9	2.8	1	1.7	2.4	1.2	169	15	12	10
M. wynaudense	IISER-TVM	VPMW1015066	?	335	21	19	6.2	5	13.5	1.6	2.6	6.5	7.5	3.5	4.5	4.1	5.2	5.7	0.3	2.4	3.5	1.2	2.2	2.9	1.4	197	15	11	12
P. aureus	MNHN	1895.0107	F	413	39	34	11.8	10.4	14.5	2.8	2	9.6	9.6	6.7	6.6	5.6	6.8	7.8	0.7	3.1	4.7	1.9	3.4	4.9	2.2	191	15	8	10
P. aureus	MNHN	1895.0106	M	358	31	27	9.5	7.8	21.1	2.9	2	8.1	8.3	5.6	6	5.2	6	6.9	0.8	2.6	3.8	1.5	3	4.3	2	168	15	13	12
P. aureus	MNHN	1897.262	F	280	26	22	8.2	6.4	10.9	2.1	1.5	6.9	7.1	5.6	4.9	4.2	5.2	6.1	0.7	2.2	3.2	1.3	2.3	3.6	1.5	167	15	8	8
P. aureus	CAS	17176	F	353	31	26	9.3	7.8	12.5	3	2	7.8	8	5.1	5.2	4.6	5.4	6.6	0.7	2.6	3.6	1.4	2.7	3.9	1.9	172	15	10	10
P. aureus	CAS	17177	F	237	18	16	5.6	4.4	8.1	1.8	1.3	6.5	6.9	4.4	4.8	4	4.9	5.6	0.7	2.3	3.1	1.3	2.4	3.5	1.4	172	15	9	8
P. aureus	BMNH	89.7.6.7	M	357	30	28	9.2	7.3	20.3	3	1.8	8.2	8.5	5.3	5.5	4.8	6.1	7.3	0.7	2.7	3.9	1.5	2.9	4.2	1.8	165	15	12	12
P. aureus	BMNH	89.7.6.8	M	224	19	16	5.3	4.6	12.5	1.9	1.1	6.1	6.3	3.9	3.9	3.4	4.4	5.4	0.6	2	2.9	1	2.2	3.2	1.5	161	15	12	11
P. aureus	BMNH	1946.1.1.54	F	398	35	26	10.5	7.6	14	2.8	1.8	8.1	8.2	4.5	5.4	4.5	5.6	6.6	0.8	2.6	3.7	1.3	2.6	4	1.7	176	15	8	9
P. canaricus	MNHN	1895.0102	M	400	32	29	9.9	8.2	19.7	3.2	1.7	9.3	9.4	6.6	6.8	5.9	6.9	8.3	0.9	3.1	4.8	1.8	3.4	4.6	2	181	15	13	13
P. canaricus	MCZ	24737	M	338	26	24	8.2	6.9	17	2.8	1.7	8.6	8.8	5.3	6.1	5.2	6.4	7.5	0.7	3	4.4	1.7	3	4.5	2.3	182	15	12	11
P. canaricus	BMNH	1946.1.16.71	M	336	27	23	8.3	6.5	17.8	2.8	1.5	7.9	8	5.1	5.6	4.6	5.7	6.6	0.6	2.6	3.8	1.4	2.8	3.9	1.7	180	15	11	12
P. canaricus	BMNH	1946.1.15.95	M	430	33	30	9.1	8.3	21.5	3.2	1.6	10	10.2	6.1	6.7	5.9	7.4	8.7	0.8	3.2	4.7	1.6	3.4	4.8	2.1	175	NA	12	13

Species	Collection	Voucher code	Sex	TL	MbC	tC	MbW	tW	tL	SL	SW	HL-SL	HL-P	HH 1-P	HW	MW	IL-M	IL-ST	E	E-N	E-ST	E-SL	RH	E-E	N-N	V	D	SC-L	SC-R
P. canaricus	BMNH	1946.1.15.96	M	232	22	20	6.7	5.7	11.6	2	1	6	6.1	4.3	4.8	4.1	4.8	5.4	0.7	2	2.9	1.2	2.4	3.6	1.6	176	15	12	13
P. canaricus	BMNH	1946.1.15.97	F	302	25	22	7.3	6.2	9.2	2.7	1.6	7.2	7.3	4.5	5.5	4.7	5.5	6.4	0.8	2.4	3.7	1.4	2.5	4	1.7	186	15	8	7
P. canaricus	BMNH	1901.3.8.13	F	366	33	26	10.6	7.9	11.6	3.6	1.8	8.7	8.9	6.1	6.4	5.8	6.5	7.7	0.6	3.2	4.4	1.7	3.3	4.2	2.1	185	15	8	8
P. canaricus	BMNH	79.7.4.6	F	363	25	22	7.6	6.5	10.8	3.5	1.9	8.1	8.4	5.5	5.8	4.9	6	6.9	0.6	2.8	4.1	1.4	2.8	4	1.9	187	15	7	8
P. guentheri	MNHN	1895.0105	M	390	35	29	10.6	8.1	21.3	3.1	1.7	9.3	9.3	6.1	7.1	6	6.9	7.9	0.8	2.9	4.2	1.8	3.3	4.8	1.9	170	15	12	12
P. guentheri	BMNH	1946.1.16.32	M	339	29	26	8.8	6.9	17.1	2.7	1.6	7.9	8.1	5.4	6.3	5.6	5.9	7	0.8	2.8	3.9	1.6	2.9	4.3	1.8	173	15	12	12
P. guentheri	BMNH	64.3.9.8	?	371	28	27	10.2	6.8	18.3	3.2	1.9	8.8	9	5.2	6.2	5.4	6.4	7.5	0.8	2.8	4.1	1.7	3.1	4.5	1.9	171	15	11	10
P. guentheri	BMNH	74.4.29.71	M	341	30	25	8.9	6.6	19.5	2.8	1.7	8.1	8.2	4.8	5.8	5.2	6.1	7.2	0.8	2.6	3.7	1.5	2.9	4.3	1.7	172	15	12	12
P. guentheri	IISER-TVM	VPPG0512003	F	493	38	31	12.2	8.3	16.5	3.2	2	10.9	10.9	6.4	7.6	6.7	7.7	9.1	1	3.6	5	1.9	3.9	5	2.6	187	15	9	9
P. madurensis	MNHN	1895.0115 (no tag) A	F	319	27	24	8.1	6.8	15.6	1.3	1.3	7.4	7.7	4.8	5.6	4.8	5.5	6.3	0.8	2.2	3.4	1.4	2.7	4.2	2	175	15	11	10
P. madurensis	MNHN	1948.252	F	159	17	15	5.5	3.7	7.6	1	0.7	5.8	6	3.6	4.1	3.6	4.2	4.7	0.7	1.6	2.7	1.1	2.3	3.5	1.5	174	15	9	9
P. madurensis	ZMB	10356	F	341	32	26	9.1	6.9	13.7	1.3	1.4	8.4	8.2	4.8	5.6	4.9	6.2	6.7	0.8	2.3	3.7	1.5	3.1	4.3	2	172	15	10	11
P. madurensis	ZMB	30655	M	250	24	21	6.8	5.5	18.4	1.2	1.1	7.1	7.1	4.3	5.6	4.9	5.2	5.8	0.8	1.9	3	1.3	2.5	4.1	1.7	166	15	15	15
P. madurensis	USNM	205000	F	305	27	19	8.1	5.8	12.9	1.3	1.3	7.7	7.5	4.4	5	4.3	NA	5.6	0.7	2.2	3.2	1.3	2.5	3.9	2	172	15	10	10
P. madurensis	USNM	205001	F	334	26	20	8.4	5.1	14.6	1.5	1.5	7.9	7.9	4.2	5	4.7	5.8	6.6	0.8	2.3	3.4	1.3	2.6	4	2	169	15	10	10
P. madurensis	MCZ	18045	F	319	22	17	6.5	4.5	14.9	1.2	1.1	7.8	7.8	4.3	5.4	4.9	5.6	6.6	0.8	2.1	3.4	1.3	2.7	4.2	2	171	15	10	11
P. madurensis	MCZ	18044	F	253	19	16	6	4.9	11.9	1.1	1.1	6.4	6.8	3.8	4.3	3.7	4.9	5.4	0.7	1.8	2.7	1.2	2.4	3.4	1.6	169	15	10	11
P. madurensis	BMNH	77.8.10.4	M	292	22	20	7.1	5.4	22.8	1.3	1.2	7.2	7.3	3.9	5	4.4	5.3	6	0.7	2	3.1	1.3	2.7	3.8	1.7	160	15	15	15
P. madurensis	BMNH	1946.1.15.78	F	350	30	24	9.5	7.9	16	1.5	1.4	7.9	7.8	5.1	5.8	4.9	5.6	6.1	0.7	2.3	3.4	1.3	2.9	4.2	2	172	NA	11	11
P. madurensis	BMNH	1946.1.15.79	F	231	20	16	5.9	4.3	11.4	0.9	0.7	6.8	7	3.8	4.7	4	5.1	5.7	0.7	1.9	3	1.2	2.4	3.6	1.7	165	NA	11	10
P. madurensis	BMNH	1946.1.15.80	F	284	24	21	7.1	6.2	11.5	1.2	1	7.1	6.9	3.7	5	4.4	5.2	5.7	0.7	2	3.1	1.3	2.4	3.7	1.9	175	15	10	10
P. madurensis	CAS	244432	F	352	27	26	9.7	7.6	14.8	1.1	1.1	8.3	8.4	4.8	5.9	5.4	6.1	7.1	0.9	2.4	3.6	1.3	2.9	4.3	2.2	173	15	11	11
P. madurensis	CAS	244431	F	302	26	21	8	5.6	12.7	1.2	1.1	7.9	8	4.1	5.5	4.9	5.7	6.4	0.8	2.2	3.4	1.2	2.9	4.1	2	171	15	12	12
P. madurensis	CAS	244428	M	335	32	25	9.3	7.2	28.3	2	1.7	9	9	5	6.1	5.4	6.3	7	0.9	2.5	3.6	1.4	3.2	4.7	2.3	167	15	15	16

Species	Collection	Voucher code	Sex	TL	Mb C	tC	Mb W	tW	tL	SL	SW	HL-SL	HL-P	HH 1-P	HW	MW	IL-M	IL-ST	E	E-N	E-ST	E-SL	RH	E-E	N-N	V	D	SC-L	SC-R
P. perrotetii	MNHN	0.170.	F	264	26	22	8.1	6	9.3	2.6	1.6	7.9	8.2	5.2	5.8	4.8	5.9	6.8	0.7	2.5	3.6	1.4	2.6	3.7	1.6	158	15	7	7
P. perrotetii	MNHN	1897.0261	F	329	31	25	8.4	6.9	11.2	3	2	8	8.2	5	5.7	4.9	5.9	7.1	0.7	2.5	3.8	1.5	2.7	4	1.9	164	15	6	7
P. perrotetii	ZMB	8077	M	107	13	11	3.2	2.3	6.7	1.1	0.7	4.3	4.6	2.8	2.8	2.3	2.9	3.6	0.5	1.3	1.9	0.7	1.4	2	0.9	145	15	11	11
P. perrotetii	ZMB	4036	F	197	19	17	5.3	3.9	7.7	1.7	0.9	5.9	5.9	3.5	3.8	3.3	4.4	5.2	0.6	1.8	2.7	1	1.8	2.9	1.1	157	15	8	8
P. perrotetii	ZMB	50451	F	247	23	20	7.1	5.2	8.1	2.5	1.3	6.4	6.7	3.5	4.2	3.8	5.1	5.9	0.6	2.3	3.1	0.9	2.1	2.7	1	159	15	7	7
P. perrotetii	USNM	205002	F	189	19	17	5.6	4.8	6.8	2.1	1.2	4.7	4.7	3.6	3.5	2.9	3.1	4	0.4	1.6	2.4	1	1.6	2.2	1.2	166	15	7	8
P. perrotetii	USNM	205003	F	175	18	14	5.6	4.3	7.2	1.7	1	4.7	4.6	2.7	3.3	2.8	3.2	4	0.4	1.3	2.1	0.8	1.6	2.3	1.1	169	15	9	9
P. perrotetii	USNM	205004	F	281	24	23	6.9	6.5	10.7	2.4	1.3	6.9	7.2	3.9	4.4	3.8	4.2	5.1	0.6	2.3	3.1	1.1	2	3	1.8	164	15	8	8
P. perrotetii	USNM	205005	F	216	27	24	8.8	7.7	9.8	2	1.4	6.5	6.6	4	4.9	3.9	4.4	4.9	0.5	2.1	3.1	1.2	2.3	3.1	1.5	156	15	8	9
P. perrotetii	MCZ	6202	M	224	21	18	6.7	4.6	12	2.1	1.1	7.2	7	4.4	5	4.6	5	6.1	0.7	2.3	3.5	1.2	2.4	3.6	1.7	159	15	11	11
P. perrotetii	MCZ	R154138	M	242	23	21	6.4	5.3	12.7	2	1.1	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	158	15	10	11
P. perrotetii	MCZ	3860	F	226	23	21	7.1	5.5	8	2.1	1.2	6.8	7	3.8	4.4	3.6	4.3	5.3	0.5	2.1	3.1	1.2	2.3	2.7	1.3	166	15	8	8
P. perrotetii	MCZ	3867	M	214	18	18	5.5	4.6	13.4	2	1.2	5.7	6	3.7	4.2	3.6	4.2	5.1	0.6	1.8	2.8	1	2	3	1.3	153	15	12	12
P. perrotetii	AMNH	77605	M	161	16	13	5	3.7	9.1	1.4	0.9	5.4	5.6	3.5	3.8	3.2	4	4.7	0.6	1.7	2.6	0.8	1.8	2.7	1	156	15	13	12
P. perrotetii	BMNH	88.1.27.35	M	228	20	17	6	5.1	12.5	2	1.1	6.9	7	4.6	4.9	4.2	4.9	5.9	0.6	2.4	3.4	1.2	2.4	3.6	1.5	157	15	10	10
P. perrotetii	BMNH	88.1.27.36	M	191	18	16	5.5	4.1	11	1.8	1	5.4	5.6	3.2	3.7	3.1	4	4.8	0.5	1.7	2.5	1.1	1.9	2	1.2	153	15	11	11
P. perrotetii	BMNH	88.1.27.37	M	166	18	14	5.1	3.8	8.3	1.4	0.8	5.5	5.6	3.3	3.7	3.1	3.9	4.7	0.5	1.7	2.5	0.9	1.8	2.6	1.1	155	15	11	11
P. perrotetii	BMNH	61.12.30.29	F	264	28	26	9.3	7.6	11.2	2.1	1.5	7.3	7.5	5.1	5.4	4.7	5.3	6.3	0.7	2.1	3.3	1.4	2.5	3.3	1.6	155	15	8	8
P. perrotetii	BMNH	61.12.30.21[or 31?]	F	283	29	24	8.4	7	11.9	2.8	1.5	7.8	8	5.4	5.6	5.2	5.6	7	0.7	2.4	3.7	1.6	2.8	3.9	1.7	160	15	8	8
P. perrotetii	BMNH	1940.1.6.3	F	211	28	22	8.2	6.5	8.6	2.4	1.7	6.2	6.1	3.8	4	3.3	4.2	5.1	0.5	1.9	2.9	1.1	2	3	1.3	158	15	6	6
P. perrotetii	BMNH	97.7.19.8	M	222	20	18	6.7	4.9	11.1	1.9	0.9	6.3	6.2	3.6	4.2	3.7	4.3	5.2	0.7	2.1	2.9	1.2	2.2	3.2	1.3	163	15	11	11
P. perrotetii	BMNH	1922.5.25.9	F	295	22	19	8.6	4.6	7.7	2.5	1.4	8	8.2	4.1	5.1	4.5	5.8	6.8	0.7	2.6	3.6	1.6	2.9	3.6	1.7	172	15	7	7
P. perrotetii	BMNH	1946.1.1.41	F	433	36	30	11.3	8.5	13.7	3.4	2.1	10.5	11	5.9	7.1	6	8	9.3	0.9	3.4	4.8	1.9	3.5	4.5	2.1	178	15	7	8
P. perrotetii	BMNH	88.1.27.33	F	233	22	20	7.1	5.8	9	1.9	1.1	7.2	7.4	4.6	5.1	4.6	5.4	6.2	0.6	2.4	3.5	1.4	2.5	3.5	1.5	161	15	7	8

Species	Collection	Voucher code	Sex	TL	Mb C	tC	Mb W	tW	tL	SL	SW	HL-SL	HL-P	HH 1-P	HW	MW	IL-M	IL-ST	E	E-N	E-ST	E-SL	RH	E-E	N-N	V	D	SC-L	SC-R
P. perrotetii	BMNH	88.1.27.34	M	224	21	19	7.3	5.4	12.4	1.8	1	7.1	7.2	5.1	5.2	4.7	5.2	6.2	0.6	2.3	3.5	1.3	2.5	3.5	1.7	156	15	12	11
P. trilineatus	BMNH	85.3.21.5	F	399	30	24	7.5	6.7	17.5	1.6	1.5	10.5	10.5	5.2	7	6.6	8	8.4	1.1	3.1	4.5	1.8	3.5	5.5	2.4	171	15	9	10
P. trilineatus	BMNH	88.1.27.38	F	388	31	26	8.3	6.8	17.1	NA	NA	10.6	10.3	5.5	7.3	6.6	8.2	9	1.1	3	4.5	1.9	3.7	5.8	2.7	172	15	9	9
P. trilineatus	BMNH	88.1.27.39	M	329	29	26	8.2	7	24.4	1.6	1.5	9.5	9.6	5.1	6.7	6.2	7	7.8	1	2.6	4	1.7	3.3	5.3	2.5	163	15	14	14
P. trilineatus	MNHN	1895.0112	F	350	21	19	6.6	5.5	13.1	1.3	1.2	9.6	9.7	5	6.2	5.4	7.1	8	1	2.7	4.1	1.4	3.2	4.5	2.4	173	15	9	9
P. trilineatus	MNHN	1895.0113	F	419	28	24	9	6.6	14.5	1.5	1.7	10.8	10.7	5.2	7	6.1	7.9	8.6	1	2.9	4.5	1.6	3.4	5.4	2.7	174	15	8	9
P. trilineatus	MNHN	1895.0114	M	163	16	14	4.5	3.3	10.3	1	0.9	5.7	5.9	3.4	4.2	3.6	4.4	4.8	0.6	1.6	2.4	1	2	3.3	1.4	168	15	15	14
P. trilineatus	MNHN	1897.264	F	353	29	24	9	6.8	14.8	1.1	1.1	9.7	9.8	5.5	6.8	6.2	7.5	8.3	0.9	2.6	3.9	1.4	3.2	5	2.4	171	15	10	10
P. trilineatus	MNHN	1897.265	M	352	25	25	8.2	6.7	21	2	1.6	9.7	9.6	5.4	6.7	5.9	7.3	7.9	0.9	2.7	4.2	1.7	3.3	5	2.6	166	15	14	14
P. trilineatus	ZMB	10346	F	149	16	14	4.5	3.3	7.2	0.7	0.6	5.7	6	3.2	4.1	3.7	4.2	4.7	0.7	1.6	2.6	1	1.9	3.4	1.5	169	15	11	11
P. trilineatus	BMNH	1946.1.23.54	M	169	17	14	5	3.8	11.5	0.7	0.6	6.3	6.4	3.5	4.4	4.2	4.8	5.1	0.7	1.7	2.7	1	2.2	3.5	1.6	163	NA	15	15
P. trilineatus	BMNH	1946.1.23.55	M	160	15	13	4.8	3.7	9.9	0.8	0.7	5.9	5.9	3.2	4.1	3.7	4.3	4.9	0.7	1.6	2.5	1	2.1	3.4	1.5	163	15	14	14
R. blythii	BMNH	1972.2164	F	234	25	25	7.1	6.9	6.3	3.7	3	6.4	6.2	4.6	4.8	3.9	4.6	5.6	0.6	2	3.4	1.3	2.5	3.3	1.5	162	17	5	6
R. blythii	BMNH	1863.12.26.8	F	202	25	23	7.3	6.8	5.7	3	2.5	6.3	6	4.4	4.6	3.7	4.4	5.4	0.6	2.1	3.2	1.2	2.3	3.2	1.4	155	17	5	5
R. blythii	BMNH	1905.3.25.73	M	306	28	28	8.9	7.5	11	5.4	3.8	8.3	7.8	5.5	5.9	4.9	5.8	7.3	0.7	2.5	4	1.6	2.8	4.4	1.6	158	17	7	8
R. blythii	BMNH	1905.3.25.74	F	310	25	25	6.9	6.8	6.3	3.6	2.8	7.9	7.6	4.4	6.9	5.9	5.7	7.5	0.7	2.6	4.2	1.4	2.9	4.1	1.6	159	17	6	5
R. blythii	BMNH	1905.3.25.75	F	186	25	24	6.3	5.9	5.1	3.2	2.1	6.2	6	4	4.2	3.7	4.3	5.4	0.6	2	3.3	1.1	2.2	3.2	1.4	157	17	6	6
R. blythii	MNHN	1895.0073	F	324	39	34	11.3	9.7	9.1	4.4	3.5	8.4	8	5.5	5.8	4.9	5.8	7	0.7	2.6	4.1	1.3	2.9	4.1	1.7	156	17	5	6
R. blythii	MNHN	1895.0074	F	346	39	35	12.2	10.5	8.8	5.1	4.2	9.3	8.9	6.7	7	5.7	6.3	7.9	0.7	2.9	4.6	1.6	3	4.5	1.9	156	17	4	4
R. blythii	ZMB	80286	F	262	35	31	10.6	7.8	7.1	4.1	3.4	8.5	8.1	5.6	5.5	5	5.5	7.5	0.7	2.8	4.5	1.5	2.9	4	1.8	159	17	6	5
R. blythii	ZMB	80289	F	238	25	23	7.5	6.9	5.7	3.3	2.7	7.1	6.7	4.4	4.9	4.1	4.9	6.3	0.5	2.2	3.7	1.4	2.6	3.6	1.5	159	17	5	5
R. blythii	ZMB	80288	M	244	28	24	9	8.6	9.9	3.8	2.9	7.9	7.4	5	5.5	4.3	5.4	6.7	0.6	2.6	4.1	1.5	2.9	3.8	1.7	148	17	7	7
R. blythii	ZMB	80287	F	246	30	27	9.4	7.7	6.5	3.4	3	7.4	7.2	4.6	5.2	4.2	5.2	6.7	0.6	2.3	3.9	1.4	2.7	3.6	1.7	163	17	5	5
R. blythii	ZMB	8561	F	363	44	40	13	11.2	10.4	5.2	4.3	10.2	9.8	7.4	7.5	6.4	7.5	9.3	0.8	3.2	5.1	1.9	3.6	4.6	2	159	17	5	6

Species	Collection	Voucher code	Sex	TL	Mb C	tC	Mb W	tW	tL	SL	SW	HL-SL	HL-P	HH 1-P	HW	MW	IL-M	IL-ST	E	E-N	E-ST	E-SL	RH	E-E	N-N	V	D	SC-L	SC-R
R. blythii	ZMB	3833a [b = skin]	M	334	39	34	12.9	13	12.3	5.3	4.4	10.5	10.2	6.7	8.6	7.4	7.7	9.3	0.8	3.4	5.2	2.2	3.9	5	1.9	153	17	7	7
R. blythii	MCZ	34266	M	266	26	23	8.4	7.2	10.4	4.5	3.9	9.2	8.6	5.7	6.2	5.1	6	7.7	0.6	2.9	4.7	1.7	3.2	4	1.7	150	17	7	7
R. blythii	MCZ	34816	F	282	25	24	8	6.6	7.2	4.2	3.3	8.8	8.4	5.4	6.2	5.2	5.9	7.5	0.6	2.9	4.8	1.8	3.4	4.4	2.4	163	17	5	5
R. blythii	MCZ	3172	M	356	40	31	12	8.7	13.4	5.6	4.1	10.9	10.1	6.8	7.8	6.6	7.3	9.2	0.8	3.2	5.4	1.9	3.6	5	2.1	152	17	8	8
R. blythii	AMNH	77604	M	263	30	24	9.9	7.6	10.1	4.1	2.9	8.7	8.2	5.7	6.4	5.1	6.1	7.6	0.6	2.8	4.8	1.6	3.4	4.4	2.2	153	17	6	6
R. blythii	AMNH	94519	M	257	26	22	8.7	6.1	8.7	5	3.4	6.9	6.5	4.2	4.8	4.2	5	6	0.5	2.4	3.5	1.1	2.2	3.2	1.3	149	17	6	6
R. blythii	BMNH	1946.1.1.46	M	368	40	33	12.2	9.3	14.1	5.9	4.7	10.4	9.7	7.8	8.1	6.8	7.1	8.6	0.6	3.3	5.1	2.1	3.7	4.8	2.2	155	17	8	7
R. blythii	BMNH	1946.1.1.45	M	346	42	30	12.4	8.6	13.7	5.9	3.6	11.4	11.2	8.3	9.1	7.6	8	10.1	0.7	3.7	5.9	2.2	4.1	5.2	2.4	148	17	7	7
R. blythii	BMNH	1946.1.1.45&46other	F	331	32	26	9.4	8.8	8.6	4.1	2.8	8.5	8.5	5.7	6.1	5.3	5.9	7.2	NA	2.8	4.3	1.6	3.3	4.2	1.7	167	17	6	5
R. blythii	HFSL	Nuwan: Canon (Maskeliya)	M	245	28	23	9.2	7	9.9	4.5	3.6	8.2	8	5.1	5.9	4.7	5.8	7.1	0.5	2.7	4.4	1.6	3	3.8	1.7	151	17	7	7
R. cf. blythii	NMSL	WHT5209	M	243	29	26	9	7.4	10.1	4.5	3.3	7.6	7.5	5.5	5.4	4.7	5.2	6.7	0.6	2.4	4.1	1.5	2.8	3.6	2.2	148	17	7	7
R. cf. homolepis	NMSL	MW1788	?	193	23	21	6.2	5.9	7.4	5.2	4.5	5.7	5.3	3.7	3.4	2.9	3.7	5	0.3	1.8	3	1	1.9	2.4	1.2	176	17	5	5
R. cf. melanogaster	HFSL	Hunas	?	182	17	16	5.5	4.4	7.4	2.8	1.5	5.7	5.8	3.2	3.6	2.9	3.9	4.6	0.4	1.7	2.7	1	2	2.5	1.2	158	17	10	9
R. cf. phillipsi	HFSL	MW 2018.105	M	287	29	24	9.2	7.4	8.9	4.3	3.2	7.7	7.6	5.4	5.7	4.9	5.3	6.7	0.5	2.3	4.1	1.4	3	3.3	2.2	182	17	7	7
R. cf. phillipsi	HFSL	MW 2018.101	?	156	17	17	5.5	4.8	5.9	2.6	1.8	5.4	5.5	3.5	3.8	3.2	3.6	4.7	0.4	1.7	2.8	1	1.9	2.4	1.4	178	17	8	7
R. cf. phillipsi	HFSL	KNU 027	M	175	19	18	5.9	5.2	6.5	2.9	1.7	5.8	5.9	3.8	4.1	3.3	4	5.2	0.4	2	3.1	1	2	2.6	1.2	178	17	8	8
R. cf. phillipsi	NMSL	WHT5786	F	111	13	13	3.5	3.4	3.3	2.1	1.2	4.7	4.7	3.2	3.1	2.6	3.3	4.2	0.4	1.6	2.4	0.9	1.7	2.2	1.1	180	17	5	5
R. cf. sanguineus	MW	1609	F	236	23	20	6.6	6.2	7.7	6.2	5.4	6.7	6.5	4	4.1	3.3	4.3	6.1	0.4	2	3.9	1.2	2.2	2.9	1.6	186	15	7	6
R. cf. zigzag	HFSL	Galoya	M	286	22	22	6.7	6.5	7	4.8	4.3	7.5	7.1	4.7	4.8	4	4.7	6.3	0.3	2.1	4.1	1.5	2.8	2.9	1.5	214	17	5	5
R. dorsimaculatus	CAS	226077	M	223	16	16	4.4	4.4	7.5	4.5	3.6	5.9	5.7	3.6	3.1	2.8	3.6	5.2	0.3	1.9	3.2	1	2.2	2.3	1.2	227	17	7	7
R. dorsimaculatus	CAS	226078	F	342	22	21	6.9	6	9.3	NA	NA	6.7	6.3	3.2	3.4	2.9	3.9	5.5	0.3	2.1	3.5	1.2	2.5	2.2	1.1	238	17	7	7
R. dorsimaculatus	CAS	244584	M	325	NA	NA	NA	NA	NA	NA	NA	7.2	6.8	3.7	3.4	2.9	4.2	6	0.3	2.2	3.7	1.1	2.5	2.4	1.5	NA	NA	NA	NA
R. dorsimaculatus	CAS	225842	M	374	26	24	6.8	5.8	14	6.8	5.1	7.4	7.4	4	4.2	3.7	4.8	6.7	0.4	2.4	4.1	1.5	2.9	2.8	1.5	230	17	7	8
R. dorsimaculatus	CAS	244583	?	145	10	11	2.5	2.8	5.7	3.8	3	NA	NA	2.5	3	2.4	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	17	6	7

Species	Collection	Voucher code	Sex	TL	Mb C	tC	Mb W	tW	tL	SL	SW	HL-SL	HL-P	HH 1-P	HW	MW	IL-M	IL-ST	E	E-N	E-ST	E-SL	RH	E-E	N-N	V	D	SC-L	SC-R
R. dorsimaculatus	AMNH	85075	?	213	14	14	4.4	3.8	5.7	4.1	3.2	5.6	5.5	3.1	2.9	2.4	3.4	5	0.3	1.8	3	0.9	2.1	2	1.1	247	17	6	6
R. dorsimaculatus	CAS(unsorted)	NMC 4B/C	?	339	22	20	7.3	5.8	10	6.5	5.2	7.3	7.1	4.1	4.1	3.7	4.5	6	0.3	2.2	3.9	1.3	2.9	2.7	1.5	236	17	6	7
R. dorsimaculatus	HFSL	2014.63	?	295	15	13	6.2	NA	10.6	6.2	4.6	7.1	6.6	3.3	3.6	2.8	4.6	6.2	0.3	2.3	3.8	1.1	2.5	2	1.2	225	17	8	7
R. dorsimaculatus	HFSL	2014.64	?	221	12	11	3.7	4.1	8.4	4.9	3.8	5.9	5.8	2.9	3.1	2.5	3.7	5	0.2	1.7	3.2	0.9	2.2	1.8	1	224	17	7	7
R. drummondhayi	USNM	548042	M	205	19	18	5.4	5.3	7.7	3.9	2.4	5.7	5.7	3.7	3.8	3.3	4.1	5.3	0.4	1.9	3.1	1	2	2.8	1.4	177	17	7	8
R. drummondhayi	USNM	548061	F	271	24	24	7.2	7	6.3	3.6	2.6	6.6	6.4	4.3	4.5	4	4.5	5.7	0.4	2.2	3.5	1.3	2.4	3.2	1.6	187	17	5	5
R. drummondhayi	USNM	548067	F	174	18	16	5.6	4.6	4.5	2.5	1.6	5.1	5.1	3	3.5	3	3.4	4.4	0.4	1.7	2.7	1	1.9	2.6	1.2	186	17	5	5
R. drummondhayi	USNM	548068	M	159	16	15	4.5	3.9	5.8	2.8	2	4.9	5	3.3	3.6	3.3	3.3	4.2	0.4	1.7	2.6	1	1.8	2.5	1.2	178	17	6	6
R. drummondhayi	USNM	548075	M	308	30	28	8.9	7.9	10.8	4.5	2.8	7.6	7.6	5.8	5.8	5.2	5.5	7.4	0.5	2.6	4.3	1.6	2.8	3.9	2.1	181	17	7	8
R. drummondhayi	MCZ	14348	M	258	23	22	7.5	6.3	10	4.2	2.9	6.6	6.5	4.5	4.6	3.7	4.7	5.8	0.5	2	3.5	1.3	2.4	3.2	1.7	181	17	6	7
R. drummondhayi	MCZ	14349	M	274	26	25	8	7	8.4	4.6	3	7.3	7.2	4.4	4.8	4	4.9	6.4	0.5	2.5	3.9	1.4	2.6	3.3	1.6	183	17	7	7
R. drummondhayi	BMNH	1946.1.16.79	F	324	26	26	8	7.5	8.1	5	3.5	7.1	7.1	5	5.1	4.4	5.1	6.4	0.5	2.1	3.8	1.5	2.6	3.5	1.8	188	17	4	5
R. drummondhayi	BMNH	1946.1.16.80	F	291	27	24	8.8	7.2	9.4	5.5	3.7	7.7	7.3	5.3	5.4	4.6	5.3	7.1	0.6	2.5	4.2	1.6	2.9	3.7	1.8	180	17	6	5
R. drummondhayi	BMNH	1946.1.16.81	F	283	28	26	8.3	7.7	6.6	5.1	3.4	7.7	7.7	5.3	5.2	4.2	5.1	6.8	0.5	2.7	4.5	1.6	2.9	3.9	2	184	17	4	4
R. drummondhayi	AMNH	85076	M	265	31	26	9.4	6.8	8.3	4.2	3	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	182	17	7	6
R. drummondhayi	AMNH	85077	F	247	23	22	7.3	6.3	5.9	3.7	2.9	6.2	6.1	4.4	4.3	3.4	4	5.4	0.4	2	3.3	1.2	2.2	3.1	1.5	188	17	5	4
R. drummondhayi	AMNH	85493	F	147	15	15	5.1	4	4.1	2.8	2	5.3	5.3	3.7	3.6	3.1	3.4	4.5	0.4	1.8	3	1	1.9	2.8	1.4	190	17	5	5
R. drummondhayi	AMNH	85494	M	163	15	15	5.3	4.1	5.1	3.2	2	5.3	5.4	3.2	3.2	2.8	3.6	4.7	0.4	1.7	2.8	1	1.9	2.5	1.4	184	17	6	7
R. drummondhayi	AMNH	85495	M	248	22	22	8.2	6.8	7.9	4.7	3.2	6.8	6.7	4.5	4.9	3.5	4.4	6	0.5	2.2	3.6	1.2	2.3	3.3	1.6	173	17	7	7
R. erangaviraji	MNHN	1895.0072	F	288	33	27	9.4	8.1	7	4.4	2.8	7.6	7.4	4.9	5.3	4.5	5.4	6.7	0.4	2.6	4.2	1.3	2.5	3.6	1.7	157	17	6	6
R. erangaviraji	MNHN	1895.0072A/1999.8054	F	238	32	30	9.3	8.4	7.1	4.2	2.8	6.9	6.7	4.6	5.3	4.4	4.8	6	0.4	2.2	3.4	1.2	2.3	3.4	1.4	158	17	5	5
R. erangaviraji	USNM	548126	F	275	31	27	9.2	7.2	7.6	4.5	3.6	7.3	7	4.8	5.3	4.4	5	6.3	0.5	2.2	3.7	1.4	2.5	3.3	1.5	156	17	6	5
R. erangaviraji	USNM	548127	M	217	24	20	7.6	5.4	8.7	4.3	3	6.9	6.7	4.3	4.6	4	4.7	5.9	0.5	2.2	3.5	1.2	2.4	2.7	1.4	145	17	7	6
R. erangaviraji	USNM	548129	M	232	30	24	8.4	6.4	9.9	4.8	3.7	7.4	7	4.6	5.3	4.2	5	6.2	0.5	2.4	3.7	1.3	2.6	3.4	1.6	146	17	7	6

Species	Collection	Voucher code	Sex	TL	Mb C	tC	Mb W	tW	tL	SL	SW	HL-SL	HL-P	HH 1-P	HW	MW	IL-M	IL-ST	E	E-N	E-ST	E-SL	RH	E-E	N-N	V	D	SC-L	SC-R
R. erangaviraji	USNM	548130	F	241	26	22	8.6	7.2	7.4	3.5	3.1	6.5	6.3	4.1	5.2	4.1	4.6	5.7	0.5	2	3.2	1.2	2.4	3.2	1.5	159	17	5	6
R. erangaviraji	USNM	548131	F	248	25	24	8.1	6.8	6.4	4.3	3.2	6.9	6.8	4.8	5	4	4.8	5	0.4	2.1	3.4	1.2	2.3	3.3	1.5	159	17	6	5
R. erangaviraji	USNM	548132	M	220	26	20	8	5.7	8.6	4.4	2.9	7.4	6.9	4.9	5.1	4.1	5	6.1	0.4	2.3	3.7	1.2	2.6	3.2	1.5	140	17	6	7
R. erangaviraji	USNM	548133	M	226	27	20	8.1	5.5	8.7	4.3	3.4	6.4	6.2	4.2	4.5	3.7	4.5	5.6	0.4	2.3	3.5	1.1	2.2	3.1	1.4	147	17	7	8
R. erangaviraji	USNM	548134	M	218	26	21	7.2	6.3	8.6	4	2.8	6.5	6.5	4.1	4.5	3.6	4.6	5.7	0.4	2.2	3.4	1.2	2.4	3.2	1.4	144	17	8	7
R. erangaviraji	USNM	548135	M	241	30	24	9.3	6.9	9.8	4.5	3.3	7.2	6.6	4.9	5.9	5	4.7	5.8	0.6	2.2	3.8	1.3	2.7	3.4	1.9	146	17	8	8
R. fergusonianus	BMNH	1946.1.16.77	F	323	23	22	7.2	6.8	9.8	8.4	6.7	7.8	7.5	4.2	4.4	3.6	4.8	6.8	0.4	2.4	4.3	1.2	2.4	3.1	1.7	195	15	5	5
R. homolepis	BMNH	1964.163	F	208	20	21	5.6	5.9	5.1	5.4	4.6	5.3	5.1	3.5	3.6	2.7	3.4	4.6	0.3	1.7	2.8	1	1.8	2.3	1.1	196	17	4	4
R. homolepis	BMNH	1964.1631	F	136	17	16	4.5	3.9	3.4	3.8	3.4	4.7	4.6	3.4	3.6	2.8	3	3.9	0.3	1.6	2.6	0.9	1.8	2.3	1.2	190	17	3	3
R. homolepis	MNHN	1890.0479	M	304	22	23	8.2	8.3	9.9	6.8	6.4	7.1	6.8	4.6	5.1	4.1	4.5	6.3	0.4	2.1	3.9	1.4	2.5	3.1	1.4	200	17	6	5
R. homolepis	MNHN	1890.048	M	196	20	20	5.7	5.8	7.1	5	4.6	5	5.1	3.8	3.9	3.2	3.5	4.6	0.4	1.7	2.9	1.1	1.9	2.5	1	191	17	5	5
R. homolepis	MNHN	173	?	235	21	21	6.5	6.3	5.9	5.8	5.2	5.5	5.6	3.6	3.7	2.9	3.3	5	0.4	1.8	3.2	1.1	1.9	2.5	1.2	202	17	4	4
R. homolepis	MNHN	1999.8058/1895.71B	F	257	21	23	6.3	6.1	6.2	5.9	4.8	5.4	5.7	3.5	3.6	3	3.5	5	0.3	1.8	3.2	1.1	2	2.6	1.1	202	17	4	4
R. homolepis	MNHN	1895.71	?	247	23	23	7.1	6.7	8.6	6	5.2	5.7	6	3.6	4	3.3	3.9	5.2	0.3	2	3.3	0.9	1.9	2.6	1.1	191	17	5	4
R. homolepis	MNHN	1999.8057/1895.71A	F	276	24	25	6.9	7	5.9	5.7	5.1	6	6	3.3	3.8	3.1	3.5	5.4	0.4	1.8	3.4	1	1.9	2.7	1.1	202	17	4	4
R. homolepis	MNHN	1999.8059/1895.71C	M	181	19	17	5.2	4.5	5.9	4.1	3.6	4.8	4.8	2.9	3.2	2.6	3.1	4.4	0.3	1.6	2.6	0.9	1.7	2.4	1	195	17	5	5
R. homolepis	ZMB	3827	M	223	26	26	7.4	7.4	8.1	6	5.8	6.3	6.1	4.4	4.6	3.4	4.1	5.6	0.4	2	3.5	1.2	2.2	2.8	1.2	196	17	5	5
R. homolepis	ZMB	3828	F	261	23	23	7.8	6.8	6.4	6.7	5.5	6.3	6.2	4.5	4.4	3.6	4.2	5.7	0.4	2	3.3	1.2	2.3	2.8	1.3	197	17	4	4
R. homolepis	USNM	548078	?	173	17	18	5.1	4.9	5.8	4.3	4	5	4.9	3.1	3.2	2.5	2.8	4.1	0.3	1.6	2.8	0.9	1.9	2.4	1.4	187	17	4	5
R. homolepis	AMNH	89350	M	176	21	21	6.7	6.3	5.9	4.9	4.3	5	4.8	3.5	3.5	3	3.3	4.5	0.3	1.7	2.9	1	1.9	2.3	1	190	17	5	5
R. homolepis	AMNH	104443	M	136	14	12	4.2	3.3	4.2	3.4	3	4.5	4.3	2.6	2.8	2.5	2.7	3.9	0.4	1.4	2.3	0.7	1.4	1.7	0.8	183	17	5	5
R. homolepis	CAS	226601	F	291	22	25	7.3	7	6.7	6.5	5.6	6.3	6.2	3.7	3.9	3.2	3.8	5.2	0.3	1.9	3.3	1.1	1.9	2.5	1.2	197	17	4	4
R. homolepis	CAS	244608	M	256	25	22	7.7	6.7	8.7	6	5.6	6.5	6.3	4.4	3.9	3.6	3.6	5.7	0.4	2.2	3.7	1.2	2.1	2.8	1.3	180	17	5	5
R. homolepis	CAS	225922	M	247	23	22	7.8	7	7.6	6.3	5.6	6.5	6.3	3.8	4	3.5	4.1	5.7	0.3	2.2	3.6	1.1	2.1	2.6	1.2	192	17	5	6

Species	Collection	Voucher code	Sex	TL	Mb C	tC	Mb W	tW	tL	SL	SW	HL-SL	HL-P	HH 1-P	HW	MW	IL-M	IL-ST	E	E-N	E-ST	E-SL	RH	E-E	N-N	V	D	SC-L	SC-R
R. homolepis	CAS	225924	F	239	18	19	6	5.8	4.5	5.8	4.8	5.7	5.4	3.5	3.6	3	3.5	4.8	0.3	1.8	3.1	1	1.8	2.3	1.1	201	17	3	3
R. homolepis	BMNH	1946.1.16.66	F	286	25	24	7.7	7	6	6.5	5.7	6.2	6	3.8	3.7	3	4	5.3	0.3	2	3.5	1.1	2.2	2.6	1.2	203	17	3	4
R. homolepis	BMNH	1946.1.16.67	M	261	24	20	7.9	6.5	7.5	6.5	5.2	5.5	5.7	3	3.8	3.4	3.8	5	0.3	2.1	3.2	0.9	2	2.3	1	196	17	5	5
R. homolepis	BMNH	1946.1.16.68	F	172	16	16	5	4.9	4.4	4.5	4	5.1	4.9	3.2	3.4	2.6	3.4	4.5	0.3	1.7	2.7	0.9	1.7	2.2	1	202	17	4	4
R. homolepis	HFSL	MW 2016.100	F	160	14	16	4.9	5.1	3.9	4.3	3.7	4.8	4.8	3	3.1	2.8	3.2	4.3	0.3	1.7	2.7	0.8	1.8	2.2	1.2	198	17	4	4
R. homolepis	HFSL	MW 2016.101	M	153	17	17	5.4	5.2	5.2	4.1	4.1	4.8	4.7	3.7	3.6	3	3.2	4.2	0.3	1.7	2.7	0.8	1.8	2.2	1.1	194	17	5	6
R. homolepis	HFSL	MW2018.100	F	253	22	25	7	7	6.1	5.9	5.2	6	5.8	3.7	3.9	3.2	4	5.4	0.4	2	3.3	1	1.8	2.4	1.3	197	17	3	4
R. homolepis	NMSL	WHT5246	M	249	23	21	7.8	6.2	8.3	6.2	5.1	6.2	6.2	3.8	3.6	3.2	4	5.6	0.3	2	3.5	1.1	2.1	2.6	1.2	198	17	6	5
R. lineatus	CAS	226028	F	259	23	21	6.2	5.5	4.7	3.8	3.2	6.1	5.8	3.4	3.8	3.2	4.1	5.3	0.4	1.8	3.2	1	2.1	2.8	1.5	195	17	4	3
R. lineatus	CAS	226042	M	260	28	25	7.9	6.8	8	4.8	4	6.3	6	3.7	3.9	3.5	4.2	5.7	0.4	1.9	3.4	1.1	2.1	2.7	1.4	185	17	6	6
R. lineatus	CAS	226027	M	233	22	19	5.8	5.4	6.9	4	3.4	5.7	5.9	3.5	3.4	2.9	3.9	5.1	0.4	1.9	3.3	1	2	2.6	1.4	195	17	6	6
R. lineatus	CAS	226035	F	254	25	20	6.6	5.4	6	4.9	3.6	6.1	6	3.7	3.7	3.3	4	5.6	0.4	1.9	3.3	1.1	2	2.7	1.3	194	17	4	4
R. lineatus	CAS	226026	M	234	23	22	6	5.7	7.2	5	3.9	6.2	6	3.5	3.8	3.3	4.1	5.5	0.4	2	3.5	1.2	2.2	2.8	1.5	186	17	6	6
R. lineatus	CAS	226043	M	251	27	26	6.8	6.6	6.8	4.4	3.7	6.1	6	3.8	3.8	3.4	4.1	5.6	0.4	1.9	3.4	1.2	2.1	2.9	1.4	180	17	5	6
R. lineatus	CAS	226025	M	236	24	23	6.6	5.6	6.3	4.7	3.8	5.6	5.7	3.5	3.8	3.2	3.8	5.1	0.4	1.8	3.2	1.2	2.2	2.7	1.4	187	17	5	6
R. lineatus	NMSL	WHT5218	M	284	26	25	7.7	7.1	9.8	5.6	3.8	7.3	6.9	4.5	4.5	3.7	4.6	6.4	0.4	2.3	4.1	1.2	2.5	3	1.6	181	17	7	6
R. lineatus	NMSL	WHT5208	M	273	27	25	8.9	7.9	8.3	5.1	3.6	7.1	6.8	4.3	4.5	3.8	4.3	6	0.4	2.2	3.8	1.3	2.5	3	1.6	185	17	6	6
R. melanogaster	BMNH	1905.3.25.66	F	231	24	23	6.8	6.4	6.9	2.8	1.8	6.1	6	3.9	3.9	3.5	4.3	5	0.6	2.2	3.1	1.1	2.2	2.8	1.3	165	17	7	6
R. melanogaster	BMNH	1905.3.25.67	F	228	22	21	5.7	5.3	6.2	2.5	1.9	6.7	6.6	3.8	3.9	3.3	4.4	5.6	0.5	2	3.4	1.2	2.1	2.8	1.5	172	17	6	6
R. melanogaster	BMNH	1905.3.25.68	M	196	20	21	5.6	4.9	9.6	2.2	1.3	6	5.9	3.5	3.9	3.4	4.2	5.3	0.5	1.9	2.9	1.1	2	2.7	1.4	163	17	10	10
R. melanogaster	BMNH	1905.3.25.69	M	184	17	19	5.7	5.2	7.7	2.1	1.4	5.7	5.6	3.8	3.9	3.1	3.9	4.9	0.5	1.9	2.8	1	1.9	2.8	1.3	158	17	11	10
R. melanogaster	BMNH	1905.3.25.70	M	203	20	17	5.8	4.7	8.5	2.4	1.4	5.7	5.7	3.4	3.7	3	3.8	4.9	0.5	2	2.9	1.2	2	2.9	1.3	161	17	9	9
R. melanogaster	BMNH	1905.3.25.71	F	160	17	15	4.5	4.4	4.6	1.7	1.2	4.9	5	3.1	3.3	2.8	3.4	4.3	0.5	1.7	2.6	0.9	1.8	2.4	1.1	162	17	5	5
R. melanogaster	BMNH	1905.3.25.72	F	130	15	13	3.6	3.8	4.2	1.6	1.1	4.6	4.7	3.1	2.9	2.4	3.3	4.2	0.4	1.5	2.4	0.8	1.6	2.3	1	167	17	6	6

Species	Collection	Voucher code	Sex	TL	Mb C	tC	Mb W	tW	tL	SL	SW	HL-SL	HL-P	HH 1-P	HW	MW	IL-M	IL-ST	E	E-N	E-ST	E-SL	RH	E-E	N-N	V	D	SC-L	SC-R
R. melanogaster	BMNH	1946.1.16.94	M	214	22	19	6	4.8	9.3	2.2	1.4	5.9	6.2	3.6	4	3.4	4.2	5.3	0.5	2.1	3.2	1.2	2.1	3	1.4	159	17	10	9
R. melanogaster	BMNH	1946.1.16.95	F	253	25	21	7	5.7	5.7	3	2.1	6.5	6.6	4.4	4.6	3.7	4.6	5.7	0.6	2.3	3.3	1.2	2.2	3	1.4	164	17	4	4
R. melanogaster	BMNH	1946.1.16.96	M	152	19	16	5	4.6	6.9	1.8	1.2	4.8	5	3.4	3.5	2.9	3.3	4.3	0.5	1.6	2.4	1	1.7	2.6	1	156	17	10	10
R. melanogaster	BMNH	1946.1.16.97	F	190	19	18	4.8	5	5.2	2.2	1.4	5.8	5.7	3.3	3.6	2.9	4.1	5.1	0.5	2	2.9	1	1.9	2.7	1.2	167	17	5	5
R. melanogaster	BMNH	98.5.3.12	M	177	24	20	6.4	5.6	7.9	2.2	1.3	5.9	5.8	4.1	4.2	3.4	4	4.9	0.5	1.9	3	1.1	2	2.9	1.3	161	17	9	10
R. melanogaster	BMNH	71.12.14.54	M	115	15	14	4.2	3.3	5.2	1.5	0.9	4.6	4.7	3	3.1	2.7	3.2	4.1	0.5	1.5	2.3	0.9	1.7	2.4	1.2	161	17	9	9
R. melanogaster	BMNH	65.5.4.190	M	178	23	20	6.3	5.2	8.1	2.2	1.2	5.7	5.8	3.6	4.2	3.3	3.9	4.8	0.5	2	2.9	1.1	2.1	2.9	1.3	152	17	9	9
R. melanogaster	BMNH	61.2.21.3	M	235	24	22	6.3	5.3	9.5	2.3	1.3	6.8	6.5	3.8	4.2	3.5	4.8	5.7	0.6	2.2	3.3	1.1	2.2	3.1	1.3	154	17	9	10
R. melanogaster	BMNH	61.6.11.1	M	256	28	25	8.3	6.5	9.6	2.7	1.6	6.8	6.8	4.5	4.5	3.5	5.1	6.2	NA	2.2	3.6	1.3	2.3	3.3	1.4	154	17	8	10
R. melanogaster	BMNH	61.6.11.2	M	227	23	20	6.8	5.5	9.5	2.3	1.1	6.4	6.3	4.4	4.7	4	4.6	5.6	NA	2.3	3.4	1.4	2.3	3.5	1.6	155	17	9	9
R. melanogaster	BMNH	61.6.11.3	F	210	21	20	6.4	5.5	5.5	2.4	1.4	5.7	5.5	3.4	3.8	3.2	4	5	0.6	1.9	2.9	1	2.1	2.9	1.2	163	17	6	6
R. melanogaster	BMNH	61.6.11.4	F	221	24	22	6.7	6.1	5.5	2.4	1.9	6.1	6.2	3.4	4	3.4	4.3	5.3	0.5	2.1	3.2	1	2	2.9	1.1	164	17	6	6
R. melanogaster	BMNH	61.6.11.5	F	300	28	24	6.7	6.5	6.1	2.9	2.3	7.3	7.2	4.8	4.8	4.1	4.7	6	0.7	2.5	3.8	1.4	2.5	3.4	1.4	163	17	6	5
R. melanogaster	BMNH	68.3.17.15.16	M	186	20	19	5.5	5.1	7.7	2.3	1.3	5.2	5.3	3	3.4	2.6	3.7	4.6	0.7	1.9	2.7	0.9	1.6	2.2	0.9	154	17	9	10
R. melanogaster	MNHN	3237	M	223	22	22	6.4	5.8	9.7	2.2	1.3	6.6	6.5	4	4.4	3.7	4.3	5.6	0.5	2.3	3.4	1.3	2.3	3.3	1.3	157	17	10	9
R. melanogaster	ZMB	80283	M	205	20	18	6.4	4.7	9	2.2	1.3	6	6	3.8	3.8	3.3	4.2	5.2	0.5	1.9	2.9	1.1	2.1	2.8	1.3	156	17	9	9
R. melanogaster	ZMB	3873	F	258	27	24	8.2	5.8	5.9	2.9	1.8	6.6	6.5	3.8	4	3.4	4.7	5.7	0.5	2.3	3.4	1.2	2.2	3.1	1.5	166	17	6	6
R. melanogaster	ZMB	4035	F	256	29	26	8.1	5.9	6.9	2.8	1.7	6.7	6.6	4	4.4	3.8	4.7	5.8	0.5	2.2	3.3	1.3	2.2	3.1	1.2	163	17	6	6
R. melanogaster	AMNH	3049	M	210	18	17	5.8	4.8	9.1	2.4	1.3	6.1	6	3.7	3.7	3.3	4.2	5.4	0.5	2.1	3	1.1	2.1	2.9	1.2	158	17	9	10
R. melanogaster	AMNH	3533	M	196	20	19	6	4.8	9.8	2.3	1.3	6.1	6.2	4	4.1	3.4	4.3	5.2	0.4	1.9	3.1	1.1	2.3	2.8	1.5	157	17	8	9
R. melanogaster	HFSL	KU0143	?	240	22	21	7	5.9	8.9	2.8	1.5	7.1	6.7	4.4	4.7	3.9	4.8	6	0.5	2.2	3.6	1.3	2.4	3.1	1.6	161	17	9	9
R. melanogaster	NMSL	WHT5159	F	199	17	16	5.7	4.6	5.3	2	1.3	5.6	5.7	3.2	3.4	2.8	3.8	4.7	0.4	2	3	1	2	2.5	1.2	171	17	6	6
R. melanogaster	NMSL	WHT5160	M	185	18	16	5.7	4.4	7.1	2	1.2	5.6	5.6	3.2	3.6	3	3.5	4.6	0.4	1.9	2.9	1	2	2.6	1.2	167	17	9	9
R. melanogaster	NMSL	WHT5170	M	210	21	19	5.9	5.4	8.3	2	1.4	6.2	6.1	3.7	4	3.4	4.2	5.2	0.4	2.1	3.2	1.1	2.2	2.9	1.4	165	17	9	9

Species	Collection	Voucher code	Sex	TL	Mb C	tC	Mb W	tW	tL	SL	SW	HL-SL	HL-P	HH 1-P	HW	MW	IL-M	IL-ST	E	E-N	E-ST	E-SL	RH	E-E	N-N	V	D	SC-L	SC-R
R. microlepis	MNHN	1895.75	F	280	23	23	6.6	6.7	6.7	6.7	5.8	6.3	6	3.9	4.3	3.4	4.3	5.7	0.4	1.8	3.3	1.1	2.3	2.8	1.3	202	15	4	5
R. microlepis	ZMB	10358	M	257	22	22	7	6.5	10.3	6.5	5.8	6.4	6.1	4.2	4.8	3.5	4.4	5.7	0.4	1.9	3.3	1.2	2.4	2.8	1.3	193	15	8	8
R. microlepis	BMNH	1946.1.16.76	M	158	14	14	4.2	4.2	6.5	4	3.4	5	4.9	3	3.2	2.6	3.2	4.3	0.4	1.6	2.5	0.9	1.5	2.4	1	214	15	10	11
R. microlepis	MW	4842	M	235	20	20	6.4	6.2	9.5	6.1	5.4	6.2	6.2	4.1	3.8	3.1	4	4.9	0.4	1.8	3.3	1.2	2.1	2.6	1.3	181	15	8	8
R. microlepis	MW	4876	F	211	17	17	5.2	5.2	7.3	5.6	4.8	5.6	5.5	3.2	3.5	2.9	3.9	4.9	0.4	1.9	3.1	1.2	2.1	2.5	1.3	190	15	7	7
R. microlepis	MW	4877	M	215	20	18	5.9	5.7	9.4	5.7	5.2	6	5.8	3.2	3.5	3	4.1	5.1	0.4	1.9	3.1	1.1	2	2.4	1.2	189	15	7	6
R. microlepis	IISER-TVM	VPRS0417086	?	201	15	16	4.8	5.3	6.4	5.8	5	5.7	5.5	3.2	3.6	3	4.1	5	0.4	1.6	3	1.6	2.1	2.3	1.2	197	15	4	4
R. oxyrhynchus	BMNH	1946.1.16.90	M	374	29	28	8.7	8.6	13.3	7.7	6.5	8.5	8	5.1	5.9	4.5	5.2	7.4	0.4	2.6	4.7	1.6	3.1	3.6	1.7	218	17	7	7
R. oxyrhynchus	BMNH	1946.1.17.1	F	407	25	29	7.6	8	9.3	7.1	6.5	8.3	8.1	5.7	5.6	3.8	5.1	6.9	0.4	2.6	4.7	1.7	3.1	3.6	1.9	222	17	6	6
R. oxyrhynchus	BMNH	1975.542	?	431	32	33	9.3	10.2	12.9	9	8.6	10	9.5	5.7	6	4.5	5.8	8.9	0.5	3.1	5.6	1.7	3.7	3.5	2.2	225	17	6	7
R. oxyrhynchus	BMNH	95.6.22.1	F	462	31	33	9.2	8.4	9.6	7.7	7.1	8.5	8.5	4.8	5.3	4.6	5.6	7.8	0.4	2.6	4.8	1.6	3	3.4	1.8	244	17	5	5
R. oxyrhynchus	BMNH	1865.5.4.189	F	432	28	32	8.9	9.3	10.5	7.9	7.4	9.2	8.9	5.3	5.6	4.5	5.7	8.3	0.4	2.9	5.3	1.7	3.4	3.8	1.9	225	17	5	5
R. oxyrhynchus	MNHN	1895.69	?	463	36	36	12.2	10.4	12.6	8.8	7.9	9.4	9.4	6.1	6.8	5.7	5.9	8.6	0.4	2.8	5.4	1.9	3.4	3.9	2.1	225	17	6	6
R. oxyrhynchus	ZMB	3825	?	461	39	38	13	11.1	12.3	8.8	7.8	9.5	9.1	6.8	6.9	6	5.1	8.6	0.4	2.6	5.1	1.8	3.5	4	2.1	222	17	6	6
R. oxyrhynchus	ZMB	3826	M	182	18	18	5.1	4.6	7.5	4.4	3.8	6	5.8	3.5	3.8	3.2	4	5.4	0.3	1.8	3.3	1	2.2	2.7	1.3	214	17	7	8
R. oxyrhynchus	USNM	548079	F	608	35	37	11	12.3	16.3	10.4	9.1	10.8	10.2	5.2	6.2	5.1	6.5	9.4	0.4	3.1	6.2	1.9	4.1	4	2.5	233	17	6	6
R. oxyrhynchus	USNM	548080	M	484	30	31	9.6	8.9	16.1	9.1	7.8	8.9	8.5	6.4	5.2	4.9	5.4	8	0.4	2.8	5.5	1.8	3.5	3.7	2.2	230	17	7	7
R. oxyrhynchus	USNM	548081	F	370	24	NA	8.5	NA	NA	NA	NA	8.6	8.1	4.4	4.4	3.5	4.9	7	0.4	2.4	4.9	1.4	3.1	3.1	1.8	236	17	NA	NA
R. oxyrhynchus	USNM	548082	F	359	24	24	8	7.6	9.7	7.3	6.9	9	8.5	4.9	4.9	4.5	4.9	8.1	0.3	2.5	5.3	1.4	2.9	3.3	2.2	214	17	6	6
R. oxyrhynchus	AMNH	85074	F	565	39	38	11.6	11.9	14	10.2	9.3	9.6	9.4	6.8	6	5.9	6.6	9.1	0.6	3.1	5.4	1.9	4	4.2	1.9	244	17	6	6
R. oxyrhynchus	CAS	226074	?	502	37	39	11.7	11.7	13.8	10.6	9.8	10.7	10.1	6.8	6.6	5.1	6	8.9	0.3	3.3	6	1.8	3.9	3.9	2.3	205	17	6	6
R. oxyrhynchus	CAS	226050	?	351	22	23	7.7	7.2	12.1	7.2	6.1	7.9	7.8	4.7	5.1	4.2	5.1	7	0.4	2.4	4.5	1.4	3	3.4	1.7	223	17	7	7
R. oxyrhynchus	CAS	225948	?	431	33	33	10.9	10	16.3	9.3	8.6	10	9.3	7.5	6.9	6.5	5.7	8.9	0.4	2.8	5.5	1.8	3.7	4.1	2.3	203	17	6	6
R. oxyrhynchus	CAS	226018	?	309	23	23	6.8	6.8	8.9	6.8	5.9	7.7	7.6	4.4	4.5	3.6	4.9	6.9	0.3	2.3	4.3	1.3	2.8	3	1.7	198	17	6	6

Species	Collection	Voucher code	Sex	TL	Mb C	tC	Mb W	tW	tL	SL	SW	HL-SL	HL-P	HH 1-P	HW	MW	IL-M	IL-ST	E	E-N	E-ST	E-SL	RH	E-E	N-N	V	D	SC-L	SC-R
R. oxyrhynchus	CAS	226017	?	410	31	29	9.6	8.8	10.4	8.6	7.6	8.5	8.1	5.4	4.8	4.2	5.3	7.6	0.4	2.6	4.9	1.4	2.9	3.4	1.9	216	17	6	6
R. oxyrhynchus	CAS	226019	?	217	16	16	5.6	4.8	7.8	5	4.5	6.3	6	3.5	3.9	3.3	3.8	5.5	NA	1.8	3.5	1.1	2.2	2.7	1.6	209	17	6	6
R. oxyrhynchus	CAS	¬†225815 not 228815	?	543	32	31	10.7	9.5	13.5	9.2	8.1	9.6	9.2	5.9	6.2	4.9	5.4	7.7	0.4	2.8	5.3	1.8	3.7	3.6	2	221	17	6	6
R. oxyrhynchus	CAS	225816	?	349	23	26	7.5	7.7	9.6	7	6.3	8.2	8.2	4.7	4.7	3.6	4.3	6.5	0.3	2.4	4.6	1.6	3	3.3	2	218	17	6	6
R. oxyrhynchus	CAS	225817 not 255817	?	173	13	13	4.1	3.6	5.8	3.8	3.5	5.3	5.2	3.2	2.7	2.2	3.1	4.2	0.3	1.7	2.9	0.9	1.8	1.9	1.1	213	17	7	7
R. oxyrhynchus	CAS	225818 not 255818	?	168	14	13	4.1	4	4.1	4.3	3.8	5.4	5.2	2.6	2.9	2.2	3.1	4.5	0.3	1.6	3.1	0.9	1.9	2.1	1.1	219	17	6	6
R. oxyrhynchus	CAS(unsorted)	NMC 5B/d1	?	307	22	18	6.5	5.6	10.5	5.6	5	6.9	6.7	3.9	3.8	3.3	4	5.9	0.3	2.2	3.9	1.1	2.3	2.3	1.5	219	17	7	7
R. oxyrhynchus	HFSL	R vedi 03	F	341	25	26	7.4	7.6	9.9	8.6	7.2	8.3	7.9	5	5.5	4.3	4.8	7.2	0.4	2.4	4.6	1.5	3	3.9	1.9	206	17	6	7
R. oxyrhynchus	HFSL	R vedi 01	F	351	25	27	8.2	8.3	9.9	8.4	7.4	8.4	8.2	4.6	4.9	4.2	4.9	6.9	0.4	2.6	4.8	1.5	3.2	3.6	1.9	202	17	6	5
R. oxyrhynchus	HFSL	R vedi 02	F	382	25	25	7.8	7.8	9.7	8.7	7.8	8.7	8.5	4.7	5	4.2	5.2	7.2	0.4	2.6	4.8	1.5	3.2	3.7	2	202	17	5	6
R. oxyrhynchus	HFSL	Kabithigollawa	F	451	31	27	10.4	9.6	10.5	8.6	7.6	9.6	9.6	5.5	5.6	4.5	5.8	8.6	0.3	2.7	5.2	1.6	3.3	3.6	1.9	219	17	6	6
R. oxyrhynchus	HFSL	Kabithigollawa or Sannar, Vidattalativu ,Ä¶ ???	?	469	29	26	9.7	8.3	12.3	9.1	8.2	9.4	9.1	5.5	6	4.7	5.6	8	0.4	2.8	5	1.6	3.6	3.5	1.9	219	17	5	5
R. oxyrhynchus	HFSL	180Vs	?	282	19	20	5.7	5	7.9	6.1	5.1	6.7	6.4	4.1	3.6	3.2	4.1	5.8	0.3	2	3.7	1.2	2.4	2.6	1.5	180	17	7	6
R. oxyrhynchus	NMSL	WHT5255	?	406	29	31	9.2	8.9	11.3	8.4	7.4	9.4	9.4	5.9	6.7	5.7	5.5	8.1	0.4	2.7	5.4	1.9	3.7	4.2	2.5	231	17	5	5
R. philippinus	MNHN	6994	F	259	23	25	7.4	7.1	6.4	6.1	5.8	6.5	6.5	4.2	4.4	3.4	4.4	5.7	0.4	2.2	3.4	1.2	2.3	3.1	1.3	173	17	3	4
R. philippinus	MNHN	1895-0070	F	188	24	22	6.8	6.6	5.9	5.4	5.2	5.7	5.8	4	3.7	2.8	3.3	4.5	0.3	1.9	3.1	0.9	2	2.4	1.2	166	17	4	4
R. philippinus	ZMB	80291	F	237	22	23	7	6.5	5.8	5.8	5.6	6.1	6.1	3.8	4	3.3	3.9	5.3	0.4	1.9	3.2	1.1	2.1	2.7	1.4	175	17	3	3
R. philippinus	ZMB	80293	F	153	17	17	5.1	4.7	4	4.2	3.8	4.8	4.7	2.7	3.2	2.5	3.1	4.2	0.3	1.7	2.7	0.8	1.8	2.2	0.9	175	17	3	3
R. philippinus	ZMB	80292	F	181	17	18	5.2	5	4.5	4.7	4.6	5	5	3.2	3.4	2.8	3.1	4.3	0.3	1.7	2.7	0.9	1.8	2.4	1.1	175	17	3	3
R. philippinus	ZMB	7267	F	198	26	24	7.2	6.7	5.5	5.1	5	5.6	5.7	3.3	3.8	2.8	3.8	4.8	0.3	2	3.2	0.9	2.1	2.5	1.1	172	17	4	4
R. philippinus	ZMB	29612	F	149	14	15	4	4	4.5	3.8	3.6	4.8	4.6	2.8	2.8	2.3	3.2	4.2	0.3	1.6	2.5	0.7	1.5	2	1	176	17	4	4
R. philippinus	ZMB	3831	M	154	18	18	5.3	4.5	6.6	6.3	3.9	4.9	4.9	2.9	3.3	2.6	3.3	4.2	0.3	1.6	2.8	1	1.7	2.3	1.2	168	17	6	6
R. philippinus	USNM	548083	F	258	24	23	7.6	7	5.5	5.8	5.5	6	5.9	4.3	4.4	3.5	3.7	5.1	0.3	2	3.4	1.1	2.1	2.8	1.4	171	17	3	3
R. philippinus	USNM	548084	F	190	21	NA	7.2	NA	NA	NA	NA	5	5	2.9	3	2.4	3.3	4.3	0.3	1.7	2.7	0.8	1.8	2.1	1.1	NA	17	NA	NA

Species	Collection	Voucher code	Sex	TL	Mb C	tC	Mb W	tW	tL	SL	SW	HL-SL	HL-P	HH 1-P	HW	MW	IL-M	IL-ST	E	E-N	E-ST	E-SL	RH	E-E	N-N	V	D	SC-L	SC-R
R. philippinus	USNM	548094	M	172	17	16	4.9	4.2	6	5	4.2	4.9	4.7	2.7	3.1	2.5	3.3	4	0.3	1.7	2.5	0.9	1.6	2.1	1.1	162	17	5	6
R. philippinus	USNM	548095	M	174	16	16	5.2	4.5	7	5.1	4.5	5.1	5.1	3	3.3	2.7	3.3	4.4	0.3	1.6	2.8	0.9	1.7	2.4	1.3	159	17	6	6
R. philippinus	BMNH	1946.1.16.99	M	155	18	18	5.9	5.4	6.6	4.9	4.2	5	5	3.4	3.5	3	3.5	4.5	0.3	1.7	2.7	0.9	1.8	2.3	1.1	157	17	6	6
R. philippinus	AMNH	24674	M	158	19	18	5.8	5.7	7.2	4.7	4.3	5.1	5.2	3.3	3.3	2.6	3.4	4.5	0.3	1.8	2.8	0.9	1.8	2.3	1.1	154	17	6	6
R. philippinus	CAS	226621	F	212	20	21	7.2	6.1	4.4	5	4.9	5.5	5.6	3.3	3.4	3	3.6	4.9	0.3	1.7	3	0.9	1.8	2.5	1.3	170	17	3	3
R. philippinus	CAS	226620	F	179	18	18	5.7	5.4	4.4	5	4.6	5.3	5.2	3.3	3.4	2.7	3.5	4.4	0.3	1.7	2.9	0.9	1.8	2.3	1.2	171	17	4	4
R. philippinus	HFSL	KU0046	F	241	19	21	6.8	6.7	6.2	5.4	5.1	7	6.8	4.1	5	4.2	4.3	5.8	0.4	2.1	3.6	1.1	2.3	3.3	1.7	172	17	3	3
R. philippinus	HFSL	KU0085	F	211	22	22	6.8	6.7	4.7	5.9	5.3	6	5.9	3.2	3.5	2.8	4	5.1	0.3	1.9	3.2	0.9	2	2.4	1.2	173	17	3	3
R. phillipsi	BMNH	1972.2165	F	226	25	25	7.7	7.4	5.7	3	1.9	5.7	5.7	4	4.1	3.6	3.9	5.1	0.4	1.7	2.9	1.1	2	2.7	1.4	214	17	6	5
R. phillipsi	BMNH	1946.1.17.2	M	220	23	20	6.5	5.5	8.8	3.3	1.7	6.1	6	3.4	4.3	3.4	3.9	5.2	NA	NA	NA	1	2.3	2.6	1.4	201	17	10	9
R. phillipsi	BMNH	1936.7.7.27	M	226	20	19	5.7	5.4	8.7	3.4	1.7	6.2	6	3.7	3.8	2.9	3.9	5.3	0.4	2.1	3.3	1	2	2.8	1.4	204	17	9	9
R. phillipsi	BMNH	1936.7.7.28	M	218	19	17	4.9	4.5	8.3	3	1.7	5.6	5.7	3.4	3.7	2.9	3.6	4.8	0.3	2	3.1	0.9	1.9	2.5	1.2	197	17	9	9
R. phillipsi	BMNH	1929.2.5.2	F	311	27	26	7.6	7.7	7.7	3.8	2.3	6.7	6.5	3.7	3.7	3.2	4.2	5.7	0.3	2.2	3.5	1.1	1.9	2.3	1.5	211	17	6	6
R. phillipsi	NMSL	WHT5269	M	259	19	18	6.6	5.2	9.7	3.3	1.7	5.8	5.8	3.3	3.7	3	3.9	5	0.3	1.8	3.1	1.1	2	2.6	1.4	201	17	9	9
R. phillipsi	NMSL	WHT7396	F	303	22	25	8.2	7.6	6.4	3.6	2.1	6.6	6.4	4.1	4.3	3.8	4.4	5.6	0.4	2	3.4	1.2	2.1	2.4	1.4	215	17	6	7
R. phillipsi	NMSL	WHT7395	M	248	22	20	7	5.9	9.3	3	1.5	5.5	5.6	3.4	3.4	3.1	3.7	4.9	0.3	1.9	3	1	1.8	2.1	1.2	200	17	9	9
R. phillipsi	NMSL	MW1757	F	319	26	26	8.2	7.6	6.7	4.7	2.3	7.3	7.2	4.8	5.2	4.3	4.5	6.4	NA	2.2	3.9	1.4	2.5	3.2	1.8	213	17	5	5
R. porrectus	BMNH	1946.1.16.70	F	334	17	16	5.5	4.6	6.7	6	4.6	6.8	6.7	3.6	3.9	3.2	4.1	5.9	0.4	2	3.7	1.1	2.6	2.5	1.4	283	17	6	6
R. porrectus	AMNH	96065	F	289	14	14	4.4	4.3	6.5	4.2	3.6	6.2	6	4.3	3.6	3.4	3.2	5.6	0.4	1.8	3.6	1	2.4	2.6	1.7	268	17	7	7
R. porrectus	CAS	225828	M	417	19	20	6.4	6.4	13.5	7.5	5.4	7.7	7.6	3.7	4	3.3	4.8	6.7	0.3	2.3	4.1	1.3	2.9	2.5	1.5	267	NA	8	8
R. porrectus	CAS	244598	F	444	24	24	8.1	7.3	11.5	6.9	5.7	7.5	7.2	5.1	4.7	4.1	4.5	6.6	0.3	2.3	4.1	1.4	3	3	1.7	283	NA	7	7
R. porrectus	CAS	225825	M	366	20	20	6	5.7	11.9	5.5	4.7	7.4	7.1	5.3	4.7	4.5	4.3	6.5	0.3	2.1	4.1	1.4	2.9	3.1	2.1	277	17	8	8
R. porrectus	CAS	225835	F	351	17	20	6	5.5	7.5	6.4	4.9	6.9	6.7	3.5	3.7	3.1	4.3	6.1	0.3	2.3	4	1.1	2.6	2.5	1.6	271	17	7	7
R. porrectus	CAS	225837	F	397	17	19	6	5.6	8.2	6.4	5.3	7.3	7.1	4.3	4	3.6	4.6	6.3	0.3	2.2	4	1.3	2.9	2.6	1.6	276	17	7	7

Species	Collection	Voucher code	Sex	TL	Mb C	tC	Mb W	tW	tL	SL	SW	HL-SL	HL-P	HH 1-P	HW	MW	IL-M	IL-ST	E	E-N	E-ST	E-SL	RH	E-E	N-N	V	D	SC-L	SC-R
R. porrectus	CAS	244599	M	302	19	17	6.3	5.3	10.3	6	4.8	6.7	6.4	4.1	3.5	2.9	4	6	0.3	2.1	3.7	1.1	2.6	2.2	1.3	260	17	8	8
R. porrectus	CAS	225826	M	305	17	18	5.6	5.4	9.7	6	4.7	6.7	6.6	3.3	3.4	2.8	4	5.8	0.3	2.1	3.7	1.1	2.6	2.2	1.4	254	NA	8	8
R. porrectus	CAS	225829	F	294	14	16	4.8	5	7.8	5.4	4.7	6.5	6.3	3.8	3.6	3	3.9	5.4	0.3	1.9	3.5	1	2.6	2.3	1.4	258	NA	6	6
R. porrectus	CAS	225840	M	341	18	17	6	5.7	11.3	6.5	4.9	6.7	6.6	4	3.7	3.1	4	5.8	0.3	2.1	3.7	1.2	2.8	2.5	1.4	261	17	8	9
R. porrectus	CAS	225830	F	249	16	14	5	4.4	6	4.3	3.9	6	5.8	2.9	3.2	2.6	3.4	4.8	0.3	1.7	3.2	0.8	2.2	1.9	1.2	272	17	6	7
R. punctatus	MHNG	524.32	M	347	21	22	6.3	6.3	11.5	6.4	4.9	7.2	7.6	4.3	4.6	3.9	4.8	6.7	0.3	2.3	4.1	1.4	3	3.2	1.7	222	17	9	9
R. punctatus	ZMB	3829	M	361	26	23	8	6.3	11.8	6.4	4.8	6.8	6.7	4	4.1	3.5	4.4	6.2	0.4	2.2	3.9	1.3	2.6	2.9	1.4	229	17	8	8
R. punctatus	USNM	548085	?	515	27	28	8.8	8.5	12.7	8.3	6.8	8.7	8.3	5.1	5.6	4.7	4.8	7.7	0.4	2.5	5.1	1.7	3.4	3.6	2.1	235	17	6	6
R. punctatus	USNM	548086	F	326	18	17	6.1	5.6	8.9	5.3	4.8	6.3	5.9	3.3	3.6	3	3.9	5.6	0.3	1.9	3.5	1	2.4	2.5	1.4	248	17	6	6
R. punctatus	USNM	548087	F	327	16	16	4.7	4.4	8.7	5.4	4.2	6.9	6.2	3.6	3.5	3.1	4.4	6.1	0.3	1.9	3.6	1.1	2.4	2.5	1.4	243	17	8	8
R. punctatus	BMNH	74.4.29.220	F	392	21	23	7.1	6.1	10.7	7.5	5.7	7.3	7.2	4.3	4.1	3.5	4.6	6.6	0.3	2.3	3.9	1.4	2.9	2.9	1.5	240	17	8	9
R. punctatus	BMNH	74.4.29.221	M	304	20	19	5.6	5.3	10.6	5.1	3.8	6	5.9	3.3	3.5	3	3.9	5.4	0.2	2	3.4	1.2	2.4	2.4	1.3	236	17	8	8
R. punctatus	CAS	226070	F	245	14	12	4.5	3.6	6.4	4.3	3.6	5.3	5.3	3.4	3.2	2.7	3.2	4.7	0.2	1.6	2.9	0.9	2.1	2.2	1.2	241	17	7	7
R. punctatus	CAS	226069	M	232	16	14	4.8	4.3	8.3	4.3	3.6	5.7	5.4	3.3	3.4	2.8	3.4	5.1	0.3	1.7	3.2	1	2.1	2.4	1.5	230	17	8	7
R. punctatus	CAS	226067	M	231	14	13	4.2	3.8	6.8	4.4	3.7	5.5	5.2	3.1	3	2.6	3.4	5	0.3	1.6	3	0.9	2.2	2.2	1.1	235	NA	8	7
R. punctatus	CAS	226068	M	244	14	14	4.6	4.2	7.2	4.5	3.6	5.5	5.4	3.2	3.1	2.8	3.4	5	0.2	1.9	3.1	0.9	2.3	2.3	1.2	238	NA	7	8
R. punctatus	CAS	226072	F	263	15	14	5	4	6.4	4.1	3.8	5.6	5.3	3.2	3.3	3	3.5	4.9	0.3	1.9	3.2	1.1	2.3	2.2	1.3	247	17	6	7
R. punctatus	CAS	244605	M	287	19	16	5.7	5.3	9.6	5.3	4.4	6.7	6.5	3.8	3.8	3.3	4.2	6	0.3	2	3.6	1.2	2.7	2.5	1.4	239	NA	8	8
R. punctatus	CAS	226071	M	242	16	13	5	4.3	8.6	4.1	3.5	5.7	5.5	2.8	3.3	2.6	3.5	4.8	0.3	1.8	3	0.8	2.1	2	1	235	17	8	8
R. punctatus	HFSL	Mendis	?	300	17	20	5.3	5.4	8	5.2	4.1	6.5	6.3	3.9	3.7	3.2	4.1	5.7	0.3	2	3.6	1.1	2.5	2.4	1.2	234	17	7	7
R. roshanpererai	BMNH	1969.2743	M	159	16	15	4.4	3.9	8.4	2.1	1.2	5.2	5.2	3	3.1	2.5	3.5	4.5	0.5	1.7	2.6	0.9	1.7	2.5	1.1	173	17	12	12
R. roshanpererai	BMNH	1969.2744	M	187	19	17	5.4	4.3	8.6	2.2	1.3	6.1	6.1	3.7	4.1	3.5	4.2	5.4	NA	2	3.3	1.2	2.2	3	1.6	166	17	10	11
R. roshanpererai	BMNH	1969.2745	M	195	18	17	5	4.3	9.1	2.3	1.2	5.6	5.5	3.3	3.5	3.1	4.2	5	0.5	1.7	2.8	1.1	1.8	2.7	1.3	173	17	11	11
R. roshanpererai	BMNH	1969.2746	M	191	22	18	5.8	4.5	8.6	2.6	1.4	6.2	6	3.6	4	3.4	4.4	5.5	0.5	1.9	3	1.1	2.1	2.9	1.3	170	17	10	10

Species	Collection	Voucher code	Sex	TL	Mb C	tC	Mb W	tW	tL	SL	SW	HL-SL	HL-P	HH 1-P	HW	MW	IL-M	IL-ST	E	E-N	E-ST	E-SL	RH	E-E	N-N	V	D	SC-L	SC-R
R. roshanpererai	BMNH	1969.2747	M	212	18	16	5.1	4	9.7	2.5	1.3	6.5	6.5	4.1	4.3	3.8	4.7	6	0.5	2.2	3.3	1.1	2.2	3.1	1.5	170	17	11	12
R. roshanpererai	BMNH	1969.2748	M	188	19	17	4.9	4.6	8	2.3	1.3	5.4	5.4	3.4	3.5	3.1	3.9	4.8	0.5	1.8	2.8	0.9	1.8	2.7	1.2	165	17	11	11
R. roshanpererai	BMNH	1969.2749	M	184	20	18	5.6	4.8	9	2.3	1.3	5.7	5.8	3.4	3.7	3	4.3	5.1	0.5	1.9	2.9	1.1	1.9	2.8	1.3	164	17	11	10
R. roshanpererai	BMNH	1969.275	F	168	17	16	5	4.5	3.8	2.4	1.2	5.5	5.5	3.3	3.4	2.8	3.8	4.7	0.4	1.8	2.8	0.9	1.8	2.5	1.2	178	17	5	6
R. roshanpererai	BMNH	1969.2751	M	194	20	19	5.8	4.9	8.3	2.4	1.2	6	6.1	3.7	3.7	3.4	4.2	5.3	0.5	1.9	3.1	1.2	2.1	2.9	1.4	169	17	9	10
R. roshanpererai	BMNH	1969.2752	M	182	20	18	5.4	4.2	9.1	2.4	1.3	5.8	5.7	3.5	3.5	3	4.2	5.2	0.5	1.7	2.9	1	2	2.7	1.2	168	17	10	10
R. roshanpererai	BMNH	1969.2753	F	167	17	17	5.2	3.6	4	2.4	1.2	5.6	5.5	3.1	3.3	2.9	3.9	4.9	0.5	1.8	2.8	0.9	1.8	2.8	1.2	175	17	7	7
R. roshanpererai	BMNH	1969.2754	M	194	20	19	5.8	5.1	8.1	2.4	1.2	6.1	6	3.3	3.6	3.1	4.3	5.4	0.5	1.9	2.9	1	2	2.7	1.2	171	17	10	10
R. roshanpererai	ZMB	80290	M	212	21	20	6.6	5.4	7.7	2.2	1.3	6.7	6.6	4.3	4.3	3.3	4.4	5.6	0.4	2.2	3.4	1.2	2.3	3.2	1.6	176	17	10	10
R. roshanpererai	CAS	226606	M	221	20	16	5.6	4.4	11.1	2.2	1.4	6.3	6.2	3.5	3.7	3.1	4.2	5.3	0.4	2.1	3.2	1.1	2.1	2.5	1.3	171	NA	11	11
R. roshanpererai	CAS	226607	M	206	21	19	6.6	5.3	11.1	2.1	1	6	6	3.9	4.1	3.3	4.1	5.1	0.5	2	3.2	1	2.1	2.8	1.3	169	NA	11	10
R. roshanpererai	CAS	225904	F	189	19	17	5.8	4.8	4.2	1.8	1.2	5.6	5.6	3.2	3.8	3.1	3.8	4.8	0.4	1.8	2.9	1	1.9	2.5	1.2	168	17	6	6
R. roshanpererai	CAS	225905	F	205	21	18	6.8	5.2	5.1	1.9	1.3	5.8	5.8	3.4	3.9	3.2	4	5	0.4	2.1	3.1	1	1.9	2.7	1.3	165	17	7	7
R. roshanpererai	CAS	225906	F	230	21	18	7	5.9	5.5	2.3	1.6	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	165	17	7	7
R. roshanpererai	CAS	226269	F	209	20	17	6.5	5.2	5.1	1.9	1.3	5.9	5.8	3.7	3.9	3.2	4	5.1	0.4	2.1	3.1	0.9	1.9	2.7	1.2	168	17	8	7
R. roshanpererai	CAS	226273	F	146	16	14	4.7	4.2	4.6	1.3	0.9	4.7	4.9	3.4	3.1	2.9	3.2	4.7	0.3	1.7	2.5	0.9	1.7	2.3	1.1	165	17	6	6
R. roshanpererai	CAS	39621	F	182	17	15	5.4	4.8	4.5	2.4	1.3	5.9	5.9	3.9	3.8	3.3	4.2	5.1	0.4	2	3.1	1.1	2	2.7	1.3	162	17	5	6
R. roshanpererai	NMSL	WHT5202	F	208	18	19	5.8	5.5	5.8	1.9	1.3	5.7	5.9	3.9	4.1	3.5	4.2	5.2	0.5	1.8	3.1	1.1	2.1	2.7	1.5	169	17	6	6
R. roshanpererai	NMSL	WHT5203	F	170	17	16	4.6	4.4	4.9	1.8	1	5	5.1	3.4	3.4	3	3.7	4.4	0.4	1.6	2.6	1	1.9	2.3	1.2	169	17	7	7
R. roshanpererai	NMSL	WHT5172	M	221	20	18	6.1	4.9	8.4	2.1	1.1	6.9	6.6	3.8	4.2	3.6	4.9	5.7	0.5	2.1	3.3	1.2	2.3	2.9	1.5	165	17	10	10
R. roshanpererai	NMSL	WHT5210	M	212	22	19	6.8	5.6	9.2	2.6	1.3	6.3	6.3	3.8	4	3.4	4.1	5.5	0.5	2.1	3.2	1.2	2.2	2.9	1.4	155	17	10	9
R. roshanpererai	NMSL	WHT5229	F	173	17	17	5.5	4.8	4.5	2.4	1.3	5.6	5.5	3.6	3.8	3.2	3.8	5	0.4	1.8	2.8	1.1	2	2.6	1.2	159	17	5	5
R. roshanpererai	NMSL	WHT5187	F	237	19	19	6.2	6.3	7.4	2.7	1.6	7.3	7.3	4	4.6	3.8	5.2	6.4	0.4	2.4	3.7	1.3	2.4	2.9	1.5	166	17	7	7
R. roshanpererai	NMSL	2016.08.01 NH	F	226	24	21	7.1	6.4	6.7	2.3	1.6	6.3	6.4	3.4	4.3	3.9	4.4	5.4	0.4	2.2	3.3	1.4	2.2	3	1.5	169	17	7	7

Species	Collection	Voucher code	Sex	TL	Mb C	tC	Mb W	tW	tL	SL	SW	HL-SL	HL-P	HH 1-P	HW	MW	IL-M	IL-ST	E	E-N	E-ST	E-SL	RH	E-E	N-N	V	D	SC-L	SC-R
R. saffragamus	BMNH	1955.1.9.60	F	206	25	25	8.3	7	5.2	8.5	7.2	9.7	9.2	5.6	6.3	5.6	7.1	8.5	0.8	3	4.8	1.6	3.2	4.5	2.2	143	19	4	4
R. saffragamus	BMNH	1951.1.6.18	F	520	69	69	22	21.2	14.6	21.5	18.8	19.3	18.5	13.5	12.9	11.5	13.8	15.7	0.9	6.2	10.1	3.3	6	7.6	3.9	151	19	6	6
R. saffragamus	BMNH	1946.1.16.55	?	181	24	22	6.8	6.2	5.4	6.4	5.4	7.8	7.7	4.9	5.4	4.8	5.9	7.3	0.7	2.6	4.3	1.3	3.1	3.9	2	135	19	6	6
R. saffragamus	BMNH	1968.871	M	303	46	45	12	13.4	14.3	15	12.3	12.3	12.1	9.1	8.5	7.9	9.7	12	0.7	4.4	6.4	1.9	4.2	5.2	2	135	19	8	7
R. saffragamus	BMNH	1946.1.8.1	M	479	75	70	23.1	22.4	18.6	21.3	18.8	17.6	16.7	12.3	12.3	9.5	13	15.2	0.9	5.3	8.9	3	5.8	7.2	3.9	140	19	7	6
R. saffragamus	BMNH	1951.1.6.17	F	452	66	65	21.4	21.3	11.2	21.3	19	20.6	20	11.9	13.9	12.8	14.9	16.4	1.5	6.2	10.3	3.4	6.4	8.9	3.9	143	19	5	4
R. saffragamus	BMNH	1951.1.6.19	M	406	51	49	16.8	15.4	20.5	19.5	16.1	16.7	15.8	8.6	10.8	9.4	12.4	14.8	1	5.5	8.6	2.6	5.2	7	3.5	134	19	8	8
R. saffragamus	BMNH	1951.1.6.20	M	366	51	45	14.5	13.6	15.9	17	13.9	15.8	14.5	7.9	9.5	8.6	11.6	14.4	0.8	5.1	8.1	2.3	4.7	6.1	3	138	19	6	7
R. saffragamus	BMNH	1951.1.6.21	F	252	32	33	9.8	9.4	6.4	10.5	9.2	11.7	11.3	7.1	7.9	7.2	8.8	10.6	0.8	3.7	6.1	2	3.8	5.2	2.4	148	19	6	5
R. saffragamus	MNHN	5621	?	222	33	31	9.9	8.7	7.8	9.5	7.4	9.9	9.3	6	6.8	6.5	7.2	8.8	0.7	3.3	5	1.7	3.5	4.8	2.1	139	19	6	6
R. saffragamus	ZMB	11856	F	560	71	73	23	24.5	11.7	21.9	18.1	19.8	18	13.4	13	11.9	15	18.2	1.2	6.5	10.4	3.7	6.4	8	4.2	152	19	5	4
R. saffragamus	MCZ	24738	M	322	44	46	14.4	14.4	13.6	15.2	11.9	13	12.1	9.7	8.7	8.1	10.2	12.3	0.8	4.4	6.9	2.2	4.3	5.4	2.6	144	19	9	9
R. saffragamus	AMNH	94515	M	138	22	20	7.2	6.1	7.4	6.8	5.2	8.1	7.9	4.8	5.2	4.5	6	7	0.7	2.5	3.8	1.4	2.8	3.5	1.7	133	19	7	7
R. saffragamus	CAS	225808, not255808	M	413	46	44	16.4	16	18	16.8	13.3	16	15	10.1	10.7	9.6	10.9	13.9	NA	5.2	8.6	2.7	5.3	6.3	3.4	144	19	7	7
R. saffragamus	CAS	225633	F	328	38	38	11.9	10.1	7.1	12.1	10.5	11.8	10.5	7.6	7.1	6.1	8.3	9.5	NA	3.7	5.9	1.7	3.9	4.6	2.4	154	19	4	5
R. saffragamus	CAS	225809	M	161	22	19	7.1	5.9	6.8	5.6	4.4	7.6	7.2	4.7	4.5	4.1	5	6.6	0.7	2.2	3.9	1.3	2.7	3.6	1.8	144	19	7	6
R. saffragamus	CAS	225635	F	404	57	55	19.8	15.5	10.9	16.3	15.1	16.3	15.5	8.7	10.7	9.3	11.5	14.1	0.9	5.4	8.6	2.4	4.9	5.3	2.9	145	19	5	5
R. saffragamus	CAS	225824	F	421	65	57	20.5	17.5	10.4	17	15.6	16.7	16.1	13.7	13.1	12.1	12.3	14.6	1.1	5.5	8.7	2.9	5.6	6.8	3.4	149	19	5	5
R. saffragamus	CAS	244610	M	460	63	63	19.3	19.6	20.3	20.2	17.4	18.6	17.7	11.4	11.4	9.8	13.8	17.3	0.8	5.9	10	3.3	6.2	7.5	4.3	142	19	7	7
R. saffragamus	CAS	225721	M	269	31	31	9.8	10.6	14.5	11	8.7	12.4	11.7	5.9	7.4	6.7	8.3	10.2	0.8	3.7	6.4	1.9	3.8	5	2.6	NA	19	7	7
R. saffragamus	CAS	225637	M	125	18	16	6.3	4.9	5.7	5.8	4.5	7.7	7.5	4	4.9	4.4	5.8	7	0.5	2.7	4	1.3	2.6	3.4	1.7	142	19	9	9
R. saffragamus	HFSL	Dabana,Albino	?	191	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	140	19	9	8
R. sanguineus	BMNH	74.2.29.695	M	366	26	25	8	7.6	13.1	8.9	7	8.8	8.5	5.3	6.2	4.9	6.1	8.1	0.5	2.8	4.9	1.8	2.9	4.1	1.8	208	15	9	10
R. sanguineus	BMNH	74.4.29.696	M	306	21	20	6	6	12.3	7.3	5.8	7	6.7	4.3	4.5	4	5	6.4	0.4	2.2	3.7	1.3	2.5	3.2	1.3	199	15	9	9

Species	Collection	Voucher code	Sex	TL	Mb C	tC	Mb W	tW	tL	SL	SW	HL-SL	HL-P	HH 1-P	HW	MW	IL-M	IL-ST	E	E-N	E-ST	E-SL	RH	E-E	N-N	V	D	SC-L	SC-R
R. sanguineus	BMNH	74.4.29.697	M	192	17	17	4.8	4.5	7.5	4.9	4.1	5.4	5.2	3.3	3.4	2.7	3.4	4.5	0.4	1.7	2.8	0.9	1.8	2.6	1.2	199	15	9	9
R. sanguineus	MNHN	1897.246	F	337	31	32	9.6	9.5	9.3	8.3	7.8	8.8	8.6	5.2	5.6	4.7	6.1	7.7	0.4	2.9	4.7	1.4	2.7	3.5	1.8	196	15	7	7
R. sanguineus	ZMB	5536	F	306	23	22	6.8	6.2	7.5	7.9	6.1	7.1	6.9	4.3	4.1	3.5	4.7	6.4	0.6	2.2	3.7	1.2	2.3	2.9	1.4	212	15	7	6
R. sanguineus	MCZ	3865	M	257	19	19	5.7	5.6	10.7	6.9	5.7	6.3	6.1	3.7	3.9	3.3	4.1	5.5	0.3	2	3.1	1.1	2.1	2.8	1.2	197	15	9	9
R. sanguineus	MCZ	3854b	F	445	35	35	11.6	11.1	11.7	9.7	8.9	10.4	9.5	6	6.7	5.4	6.7	8.8	0.5	3.4	5.6	1.8	3.4	4.2	2.1	197	15	7	7
R. sanguineus	BMNH	1946.1.16.54	M	309	22	23	7.5	7.1	11.6	7.4	6.2	8.1	7.8	4.7	5.2	4.4	5.6	7.2	0.4	2.6	4.3	1.4	2.6	3.5	1.5	198	15	9	9
R. sanguineus	IISER-TVM	VPRS0918093	M	279	20	19	6.3	6	11.7	6.5	5.7	6.1	6	3.6	4	3.3	4	5	0.4	1.8	3.1	1.1	2.3	2.7	1.3	200	15	9	10
R. sanguineus	IISER-TVM	VPRS0918092	F	290	20	18	6.6	5.8	7.8	6.8	5.8	6.2	6.1	4.2	3.9	3.2	4	5.1	0.4	2	3.2	1.1	2.2	2.6	1.3	210	15	7	6
R. sanguineus	BU	BUS-4	M	239	NA	NA	5.8	NA	8.6	6.1	5.4	6.2	NA	NA	4	NA	NA	NA	NA	1.8	3.1	1.2	NA	2.6	1.3	196	15	9	8
R. sanguineus	BU	BUS-2	F	233	NA	NA	6.3	NA	6.4	6.2	5.1	6.3	NA	NA	4	NA	NA	NA	NA	1.8	3.2	1.2	NA	2.8	1.6	199	15	6	6
R. sanguineus	BU	BUS-15	M	209	NA	NA	6.5	NA	8.1	6.2	5.4	6.2	NA	NA	4.3	NA	NA	NA	NA	1.8	3.3	1.2	NA	2.7	1.5	192	15	9	9
R. sanguineus	BU	BUS-1	M	180	NA	NA	5.8	NA	7	5.4	4.6	5.3	NA	NA	3.6	NA	NA	NA	NA	1.3	2.3	1	NA	1.9	1.3	197	15	8	9
R. sanguineus	BU	BUS-5	F	204	NA	NA	5.7	NA	5.1	5.9	5.3	5.5	NA	NA	3.9	NA	NA	NA	NA	1.7	2.9	1	NA	2.4	1.2	201	15	5	5
R. sanguineus	BU	BUS-3	M	220	NA	NA	5.2	NA	9.2	6	5.3	5.8	NA	NA	3.6	NA	NA	NA	NA	1.8	3.1	1	NA	2.4	1.4	197	15	9	9
R. sp. Bambarabotuwa	HFSL	Bambarabotuwa	?	171	20	20	5.8	5.7	6.5	4.8	4.3	5.1	5.1	3.4	3.5	2.9	3.1	4.3	0.3	1.8	2.7	1	2	2.4	1.2	158	17	5	6
R. sp. nov. 1	USNM	548096	M	229	21	20	7	5.8	9.4	5.2	4.4	6.2	5.9	3.4	3.9	3.4	4	5.4	0.4	1.9	3.3	1.2	2.3	2.7	1.4	177	17	7	6
R. sp. nov. 1	USNM	548097	M	195	22	20	6.9	5.5	8.1	5.1	4.1	6	5.9	3.4	4.1	3	3.6	4.8	0.4	1.8	3.2	1.3	2.2	2.8	1.3	173	17	7	7
R. sp. nov. 1	USNM	548098	M	213	21	20	6.7	5.9	7.8	5.2	4.5	5.7	5.6	3.9	3.7	2.9	3.6	4.8	0.3	1.8	3	1.2	1.9	2.6	1.3	174	17	6	5
R. sp. nov. 1	USNM	548099	F	241	23	22	6.2	6	5.8	5.2	4.6	5.9	5.8	3.6	3.7	2.9	3.6	5.1	0.4	1.8	3.2	1.1	2	2.5	1.2	182	17	4	4
R. sp. nov. 1	USNM	548100	F	226	22	20	7.2	5.8	5.2	5.2	4.3	5.5	5.4	3.1	3.4	2.6	3.6	5	0.4	1.7	3	1.1	1.9	2.4	1.1	180	17	3	3
R. sp. nov. 1	USNM	548101	M	173	15	17	5.9	3.8	6	3.9	3.1	4.9	4.9	2.6	3.3	2.5	3.2	4.2	0.4	1.7	2.6	0.9	1.8	2.3	1.1	177	17	6	6
R. sp. nov. 1	USNM	548103	F	259	21	23	7.4	7.2	5.9	4.8	4.6	5.6	5.6	3.4	3.6	2.8	3.4	4.7	0.4	1.8	3.3	1.1	2.1	2.6	1.3	186	17	4	4
R. sp. nov. 1	USNM	548104	M	242	26	26	8.2	8	9.8	5.9	5.4	6.6	6.4	4.4	4.7	3.8	4.1	5.4	0.4	2.3	3.8	1.3	2.5	3.2	1.7	178	17	6	5
R. sp. nov. 1	USNM	548105	F	199	20	18	5.5	5.2	5.2	4.1	3.6	4.7	4.7	3.4	3.3	2.9	2.9	4.1	0.4	1.5	2.7	0.9	1.9	2.3	1.2	183	17	4	3

Species	Collection	Voucher code	Sex	TL	Mb C	tC	Mb W	tW	tL	SL	SW	HL-SL	HL-P	HH 1-P	HW	MW	IL-M	IL-ST	E	E-N	E-ST	E-SL	RH	E-E	N-N	V	D	SC-L	SC-R
R. sp. nov. 1	USNM	548106	M	228	20	19	6.2	5	8.1	5.6	4.5	5.9	5.8	3.4	3.8	3	3.6	4.8	0.4	1.9	3	1.1	2.1	2.6	1.3	169	17	5	5
R. sp. nov. 1	USNM	548107	F	192	21	19	6	5.3	4.7	4.5	4.1	5	5.1	3.6	3.7	2.9	3.2	4.1	0.4	1.7	2.9	1.2	2	2.6	1.4	185	17	3	2
R. sp. nov. 1	USNM	548108	M	175	18	18	4.9	4.7	7.7	4.4	3.6	4.9	4.9	2.7	3.2	2.7	3	4.3	0.4	1.7	2.8	1	1.8	2.3	1.1	170	17	7	7
R. sp. nov. 1	USNM	548109	F	194	19	18	5.6	5.3	5	4.4	3.9	4.7	4.9	3.1	3.2	2.7	3.2	4.3	0.4	1.7	2.7	1	1.8	2.3	1.1	183	17	4	3
R. sp. nov. 1	USNM	548111	F	258	20	20	6.5	5.9	5.8	5.1	4.7	5.7	5.5	3.4	3.8	2.8	3.7	4.9	0.4	1.9	3.3	1.1	2.1	2.5	1.3	186	17	4	4
R. sp. nov. 1	USNM	548112	M	245	25	20	7.4	6.3	9.1	6.5	4.8	6	5.8	4.3	4.2	3.3	3.7	5.1	0.4	2	3.3	1.1	2.2	2.8	1.2	174	17	6	7
R. sp. nov. 1	USNM	548113	F	223	23	22	6.8	6.9	6.5	5.3	4.5	5.9	5.7	3.9	4.5	3.2	3.6	4.9	0.4	1.8	3.2	1.1	2.2	2.1	1.5	181	17	4	4
R. sp. nov. 1	USNM	548114	F	211	23	20	6.8	6	5.7	4.9	4.6	5.7	5.4	3.3	3.6	2.9	3.5	4.8	0.4	1.8	3	0.9	2	2.5	1.3	182	17	4	3
R. sp. nov. 1	USNM	548115	F	218	23	19	6.7	6.2	6.2	4.4	4.5	5.3	5.3	3.8	3.7	2.9	3.5	4.6	0.4	1.7	2.9	1	2	2.4	1.3	179	17	4	5
R. sp. nov. 1	USNM	548116	F	209	22	18	6.6	5.5	5.5	4.1	4.7	5.3	5.1	3.2	3.5	2.7	3.4	4.6	0.4	1.7	3	1	1.9	2.3	1.2	184	17	4	4
R. sp. nov. 1	USNM	548117	M	172	19	19	5.7	5.7	6.9	4.2	4	4.8	4.8	2.8	3.3	2.5	3.1	4.3	0.3	1.6	2.8	1	1.8	2.3	1.1	172	17	6	6
R. sp. nov. 1	USNM	548118	M	182	19	17	5.6	4.7	7.4	4.4	3.9	5	5	2.7	3.4	2.7	3.1	4.2	0.4	1.7	2.9	1	1.9	2.5	1.1	173	NA	6	6
R. sp. nov. 1	USNM	548119	F	243	25	24	8.6	7	5.7	5.4	4.9	5.7	5.7	3.3	3.9	3.1	3.5	4.8	0.4	1.6	3	1.1	2	2.6	1.2	186	17	3	3
R. sp. nov. 1	USNM	548120	F	220	24	23	7.3	6.9	6.3	5.2	4.8	5.4	5.3	3.2	3.6	3	3.6	4.6	0.4	1.6	2.8	1.1	2	2.5	1.2	178	17	4	4
R. sp. nov. 1	USNM	548121	F	232	24	22	7.9	7.1	6.3	4.8	4.5	5.3	5.2	3.6	4	3.1	3.3	4.1	0.4	1.6	2.8	1.1	2	2.6	1.2	181	17	4	4
R. sp. nov. 1	USNM	548122	M	238	26	25	8.2	7.3	9.9	5.8	4.9	6.1	5.9	3.7	4.4	3.6	3.8	5.2	0.4	1.8	3.2	1.1	2.3	3	1.4	174	17	6	6
R. sp. nov. 1	USNM	548123	M	241	26	23	7.9	7	10	5.8	4.4	6.4	6	4.1	4	3.5	4	5.4	0.4	1.7	3.4	1.2	2.2	2.7	1.2	172	17	7	6
R. sp. nov. 1	USNM	548124	F	221	26	22	7.5	5.7	6.3	5.2	4.5	6.2	6	3.9	4.3	3.5	3.9	5.2	0.4	2.1	3.5	1.1	2.2	3	1.6	181	17	4	4
R. sp. nov. 1	HFSL	Rammale 1	?	194	17	17	5.3	5.1	5.3	4.3	3.7	5.5	5.4	4.1	4.1	3.5	3.4	4.9	0.4	1.7	3.1	1.2	2.2	2.8	1.6	179	17	4	3
R. sp. nov. 1	HFSL	Rammale 2	?	126	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	180	17	4	4
R. sp. nov. 1	HFSL	R2	F	231	25	23	7.8	7.2	6	5.8	4.9	5.7	5.8	4.1	4.4	3.3	3.7	4.9	0.4	1.8	3.1	1.2	2.7	2.5	1.3	175	17	4	4
R. sp. nov. 1	HFSL	R3	M	205	23	20	7.3	6.1	8.5	5.5	4.1	5.7	5.4	4	3.9	3.1	3.4	4.6	0.4	1.7	2.9	1.1	2.1	2.5	1.1	173	17	6	6
R. sp. nov. 1	HFSL	R4	M	186	21	21	6.8	6.2	7.5	5.2	4.3	5.6	5.4	3.7	4	3.3	3.5	4.4	0.4	1.6	2.9	1.2	2.1	2.6	1.2	167	17	5	5
R. sp. nov. 2	USNM	548089	F	265	19	20	6.1	6.3	5.7	5.5	5.2	5.5	5.5	3.4	3.8	3.2	3.8	4.9	0.3	1.7	3	1.1	2.1	2.6	1.3	200	17	4	4

Species	Collection	Voucher code	Sex	TL	Mb C	tC	Mb W	tW	tL	SL	SW	HL-SL	HL-P	HH 1-P	HW	MW	IL-M	IL-ST	E	E-N	E-ST	E-SL	RH	E-E	N-N	V	D	SC-L	SC-R
R. sp. nov. 2	USNM	548090	F	231	22	21	6.4	6.4	5.5	5.4	5.1	5.6	5.7	3.6	4	3.1	3.6	4.8	0.3	1.6	3.2	1	2.1	2.9	1.6	198	17	4	4
R. sp. nov. 2	USNM	548091	F	221	18	17	6.1	5.4	5	4.5	4.5	5.3	5.3	3.2	3.7	3	3.5	4.6	0.4	1.8	3.1	1.1	2	2.8	1.5	197	NA	3	4
R. sp. nov. 2	USNM	548092	M	204	17	17	4.9	5.2	6.9	5.7	4.8	5.3	5.3	3.2	3.5	2.8	3.4	4.8	0.3	1.7	2.9	1	1.9	2.6	1.3	188	17	6	6
R. sp. nov. 2	USNM	548093	M	201	16	16	5.6	4.9	7.6	4.8	4.4	5.2	5.1	2.9	3.5	2.7	3.4	4.7	0.3	1.6	2.9	1	1.8	2.6	1.3	188	17	6	7
R. sp. nov. 2	LSUMZ	39256	M	181	16	15	5.1	5.1	6.8	4.5	4.5	4.7	4.8	3	2.9	2	2.8	3.7	0.4	1.6	2.5	0.7	1.5	1.9	1	181	15	5	6
R. sp. nov. 2	LSUMZ	39255	M	223	16	17	5.1	5.4	7.6	5.6	4.7	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	188	15	7	6
R. sp. nov. 2	AMNH	104444	F	156	14	13	4.3	4	3.5	3.8	3.4	4.7	4.7	2.6	2.8	2.2	3.1	4.1	0.3	1.6	2.5	0.8	1.6	2.1	1.2	189	17	4	4
R. sp. nov. 2	CAS	225856	M	205	20	18	6.3	5.6	7.4	5.2	4.5	4.9	4.9	3.5	3.1	2.7	3.3	4.4	0.2	1.7	2.6	0.9	1.8	2.1	1.1	188	17	6	5
R. sp. nov. 2	CAS	225857	M	170	16	14	5.3	4.7	7	4.2	3.9	4.5	4.6	3.3	3.1	2.8	3.1	4.1	0.2	1.5	2.5	0.8	1.7	2.1	1.1	181	17	6	6
R. sp. nov. 2	CAS	225847	F	224	21	19	6.8	5.5	6.2	5.2	5	4.9	4.9	3.1	3.1	2.6	3.1	4	0.2	1.7	2.7	0.9	1.7	2.2	1.2	199	17	4	4
R. sp. nov. 2	CAS	225862	M	191	17	17	5.4	5.2	7.9	5.1	4.2	4.7	4.8	3	3.3	2.7	2.9	3.8	0.3	1.5	2.6	1	1.6	2.2	1.1	183	17	7	7
R. sp. nov. 2	CAS	225861	F	208	20	20	6.3	6.1	5.3	5.2	4.9	4.9	5	2.9	3.3	2.7	3.1	4.3	0.3	1.6	2.7	0.9	1.8	2.2	1.1	189	17	4	3
R. sp. nov. 2	CAS	225915	M	195	18	17	5.8	5.2	7.6	5	4	4.6	4.7	2.9	3.2	2.6	3	4	0.3	1.5	2.5	0.9	1.8	2.1	1.1	183	17	6	6
R. sp. nov. 2	CAS	226622	F	224	18	18	5.5	5	4.7	4.9	4.4	5.1	5.1	3.1	3.2	2.8	3.3	4.4	0.3	1.7	2.8	0.9	1.8	2.3	1.3	199	17	4	4
R. sp. nov. 2	CAS	226480	M	150	15	16	4.8	4.7	5.8	3.8	3.6	4.5	4.6	2.6	2.8	2.3	2.7	3.7	0.3	1.5	2.5	0.8	1.4	2	1	187	17	6	6
R. sp. nov. 2	HFSL	KNU017	F	182	16	16	4.6	4.6	4.3	4.2	3.8	4.7	4.8	2.7	3	2.7	2.9	3.9	0.3	1.5	2.5	0.9	1.8	2.1	1.1	195	17	3	3
R. sp. nov. 3	MCZ	18037	M	214	29	27	8.5	7.1	8.9	5.9	5.4	6.3	6	4.6	5	4	4.1	5.5	0.3	2.1	3.6	1.1	2.1	2.7	1.2	165	17	4	5
R. sp. nov. 3	MCZ	18034	?	186	24	24	7.2	6.4	7.3	5.8	4.6	5.6	5.5	4	4.2	3.4	3.5	4.9	0.4	1.9	3.2	1	2	2.6	1.1	159	17	5	4
R. sp. nov. 3	MCZ	18038	?	243	31	30	8.7	8.4	9.7	6.4	5.8	6.1	6.1	4.1	4.4	3.9	3.9	5.3	0.4	2.1	3.3	1.1	2.1	2.8	1.2	164	17	5	5
R. sp. nov. 3	MCZ	18035	?	268	33	32	10.2	9.2	10.3	6.5	6.2	6.7	6.8	5.4	4.9	4	4.3	5.8	0.4	2.3	3.8	1.4	2.4	3.1	1.4	169	17	4	5
R. sp. nov. 3	MCZ	194641	F	219	25	25	7.4	7.3	6.7	5.3	5.1	5.3	5.5	4.4	4.2	3.3	3.4	4.8	0.3	2	3.3	1.1	2	2.8	1.4	170	17	4	3
R. sp. nov. 3	MCZ	18036	?	263	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	164	17	4	4
R. sp. nov. 3	CAS	226581	F	192	19	18	5.6	5.2	5	4.1	4	4.7	4.7	3.3	3.3	2.9	3.1	4.1	0.3	1.7	2.8	1	1.8	2.2	1.1	174	17	4	3
R. sp. nov. 3	CAS	226578	F	216	23	22	7.5	6.6	8	6	5	5.9	5.7	3.8	4.2	3.2	3.6	5	0.4	2	3.4	1.1	2	2.4	1.2	170	17	4	4

Species	Collection	Voucher code	Sex	TL	Mb C	tC	Mb W	tW	tL	SL	SW	HL-SL	HL-P	HH 1-P	HW	MW	IL-M	IL-ST	E	E-N	E-ST	E-SL	RH	E-E	N-N	V	D	SC-L	SC-R
R. sp. nov. 3	CAS	226582	F	243	24	23	7.1	6.9	6	5.7	5.3	6.1	6.2	4.2	4.6	3.6	3.7	5.4	0.4	2.2	3.8	1.4	2.4	3.1	1.7	172	17	4	4
R. sp. nov. 3	HFSL	Marathanna, Balangoda MW 2010	M	168	19	18	5.8	5.9	6.5	5.2	4.6	4.8	4.7	2.7	2.9	2.7	3.1	4.1	0.3	1.7	2.7	0.8	1.7	1.8	0.9	168	17	4	4
R. sp. nov. 4	IISER-TVM	VPRS1011001	M	348	22	21	6.9	6.1	9.1	8.1	6.8	8.1	7.7	3.9	4.4	3.3	5	7	0.4	2.4	4.4	1.1	2.5	3.1	1.5	222	15	7	7
R. sp. nov. 4	IISER-TVM	VPRS1014075	M	279	20	19	6.8	6	7.3	7.2	5.7	6.6	6.5	4	5.4	4.7	4.5	5.6	0.4	2	3.5	1.2	2.2	3.1	1.4	218	15	8	8
R. sp. nov. 4	IISER-TVM	VPRS0918091	F	461	22	21	8.1	7	11.2	9.6	7.9	9.1	8.5	4.5	5.4	4.5	6.2	6.9	0.4	2.9	4.9	1.4	3.1	3.5	1.7	231	15	6	6
R. sp. nov. 4	IISER-TVM	VPRS0914020	?	244	21	21	7.4	6.5	5.6	7.4	6	7.1	6.6	4.5	5.7	4.8	4.7	6.2	0.4	2.2	3.9	1.3	2.5	3	1.4	226	15	6	6
R. sp. nov. 4	CES	SNR02	F	357	NA	NA	7.5	NA	9.9	7.6	7	7.6	NA	NA	5.3	NA	NA	NA	NA	2.3	4.2	1.5	NA	3.2	1.6	225	NA	6	6
R. sp. nov. 4	CES	SNR01	M	303	NA	NA	7.7	NA	10.5	6.7	6	6.8	NA	NA	4.4	NA	NA	NA	NA	2.1	3.7	1.2	NA	2.9	1.5	236	NA	8	8
R. sp. nov. 4	IISER-TVM	VPRS0615039	F	293	20	16	6.6	5.7	6.6	6.9	5.5	6.6	6.3	4.1	4.1	3.7	4.4	5.9	0.4	2.1	3.7	1.1	2.3	2.8	1.3	235	15	6	7
R. sp. Palabaddala	HFSL	KU0125	F	242	24	23	7.2	7.4	6	6	5.4	6.7	6	4.1	4.5	3.5	4	5.5	0.3	2.3	3.8	1.2	2.1	2.3	1.4	174	17	3	3
R. travancoricus	BMNH	1903.4.7.1	F	214	20	20	6	5.8	6.2	6.3	5.2	6.3	6.7	4.2	4	3.4	4.2	5.4	0.6	2.2	3.2	1.1	2.3	2.9	1.3	143	17	6	5
R. travancoricus	BMNH	1903.4.7.2	F	186	23	20	6.3	5.6	5.9	5.7	4.8	6	6.2	3.5	3.5	2.8	4.1	5	0.5	2	3	0.9	1.9	2.8	1	142	17	6	6
R. travancoricus	BMNH	99.11.16.1	M	180	22	22	6.6	6.2	8.2	6.2	5	6	6.3	3.8	3.8	3.1	4.2	5.2	0.5	1.9	3	1.1	1.9	2.9	1.3	139	17	6	7
R. travancoricus	BMNH	94.3.15.1	F	191	20	19	5.7	5.4	6.3	6.2	5.2	6.4	6.5	3.4	3.7	2.9	4	5	0.5	2	3.1	1	1.9	2.7	1.1	137	17	5	6
R. travancoricus	BMNH	92.10.5.2	F	178	20	18	5.3	4.9	6	5.3	4.8	5.5	5.6	3.3	3.3	2.4	3.2	4.3	0.5	1.7	2.6	0.9	1.8	2.1	0.9	148	17	5	5
R. travancoricus	UK MW	219	M	180	19	18	6	6.2	7.7	6.4	5.6	5.9	6.3	3.6	3.6	3	3.9	4.9	0.5	1.9	3	1.1	2.2	2.7	1.1	136	17	7	7
R. travancoricus	UK MW	221	?	112	13	12	3.9	4.1	4.2	3.8	3.7	4.5	4.8	2.9	2.6	2.2	3.8	3.7	0.4	1.6	2.4	0.8	1.5	2	0.9	142	17	6	6
R. travancoricus	MW	2182	M	157	20	18	5.5	5.5	6.7	5.3	4.4	5.3	5.5	3.5	3.6	3.2	3.3	4.6	0.4	1.7	2.9	1	1.9	2.6	1.2	127	17	7	7
R. travancoricus	MW	2180	M	171	23	20	5.8	5.1	8.3	5.9	4.8	5.7	5.7	3.8	3.8	3.4	3.7	4.9	0.5	1.7	3	1.1	2.1	2.6	1.3	130	17	7	8
R. travancoricus	MW	2183	M	163	20	18	5.9	5.6	7.2	5.9	4.8	5.9	5.9	4.2	4.1	3.3	3.5	4.6	0.4	1.8	3.1	1.1	2.1	2.7	1.3	132	17	7	7
R. travancoricus	MW	2184	?	104	14	13	4	3.6	4.4	3.7	3.2	4.4	4.6	3	3	2.9	2.7	4	NA	1.6	2.4	1	1.6	2.3	1.1	135	17	6	6
R. travancoricus	IISER-TVM	VPRT1115073	?	132	15	15	4.9	4.3	5.5	4.9	4.1	4.8	5.2	3.6	3.1	2.6	2.9	4.1	0.4	1.6	2.6	0.8	1.7	2.2	1	141	17	7	7
R. tricolorata	HFSL		F	193	15	18	4.8	5.3	5.2	4.6	4	5	5	3.4	4	3.3	3.4	4.4	0.4	1.6	2.8	1.1	2.1	2.3	1.2	183	17	3	4
R. tricolorata	NMSL	WHT5790	?	203	23	20	7.1	5.9	7.6	5.2	4.5	5.6	5.8	3.2	3.4	3	3.8	4.9	0.4	1.9	3.1	1	1.9	2.3	1.1	171	17	5	5

Species	Collection	Voucher code	Sex	TL	Mb C	tC	Mb W	tW	tL	SL	SW	HL-SL	HL-P	HH 1-P	HW	MW	IL-M	IL-ST	E	E-N	E-ST	E-SL	RH	E-E	N-N	V	D	SC-L	SC-R
R. tricolorata	NMSL	1978.5.1	?	262	25	23	7	6.5	6.6	6.8	5.5	6.6	6.5	4.1	4.5	3.6	3.8	5.5	0.5	2.1	3.6	1.3	2.4	2.8	1.4	175	17	3	3
R. zigzag	CAS	226014	M	351	30	28	8.4	8	9.8	6.6	5.2	8.9	8.6	5.9	6	5.2	5.7	8	0.3	2.5	4.8	1.7	3.1	4	2.1	210	17	6	6
R. zigzag	CAS	225691	F	392	29	29	9	8.5	7.6	6.3	5.7	8.6	8	5.3	5.3	4.6	5.5	7.4	0.4	2.7	4.6	1.4	2.9	3.5	1.7	219	17	5	4
R. zigzag	CAS	225967	F	365	29	29	7.8	8.2	6.6	6.8	6	8.1	7.8	4.4	4.8	3.9	5.1	7.1	0.5	2.3	4.3	1.4	2.6	3.2	1.5	217	17	4	3
R. zigzag	CAS	225690	F	329	26	26	7.2	7.7	7.2	6.1	5.1	7.7	7.2	4.2	4.3	3.5	5	6.7	0.4	2.3	4.1	1.4	2.5	3.1	1.5	217	17	4	4
R. zigzag	CAS	226015	F	375	30	28	8.6	8.7	8	7.2	6.2	8.7	8.3	4.9	6.1	4.7	5.7	7.8	0.4	2.6	4.7	1.6	3	3.6	1.8	220	17	5	5
R. zigzag	NMSL	WHT5243	?	384	29	28	9.2	8.5	7.9	6.7	5.9	9.3	8.6	5.5	5.9	5.1	5.7	8	0.4	2.8	5.1	1.9	3.2	3.9	2	217	17	4	3
T. hewstoni	BMNH	1946.1.15.77	F	196	23	18	6.7	5.3	5.6	1.2	0.9	5.3	5.5	3	3.8	3.2	3.5	4.3	0.5	1.9	2.5	0.8	1.6	2.5	1	123	15	5	5
T. hewstoni	BMNH	1891.7.2.13	M	135	17	15	4.5	4	5.7	1	0.9	5	5	2.8	3.4	2.7	3.1	4	0.6	1.6	2.2	0.7	1.6	2.7	1	121	15	8	8
T. hewstoni	BMNH	1946.1.15.64	M	140	17	14	5.1	4.1	5	1.2	0.8	5.1	5.3	3	3.4	2.7	3.3	4.2	0.6	1.7	2.3	0.8	1.7	2.7	1	123	15	7	7
T. hewstoni	IISER-TVM	VPTS0918094	F	139	13	12	4.4	3.5	5	1.1	0.9	5	5	2.5	3.3	2.7	3.3	2.7	0.5	1.6	2.2	0.7	1.6	2.4	0.9	122	15	5	6
T. hewstoni	IISER-TVM	VPTS0918095	F	155	16	13	4.8	4	5.3	1.1	0.9	5.5	5.6	2.6	3.7	2.9	3.7	4.3	0.6	1.9	2.5	0.7	1.6	2.5	0.9	123	15	5	5
T. hewstoni	IISER-TVM	VPTS1015055	?	147	15	14	4.7	4.2	6.2	1.1	0.9	5.4	5.5	2.7	3.1	2.7	3.5	4.1	0.5	1.7	2.4	0.8	1.6	2.5	1	123	15	8	7
T. hewstoni	IISER-TVM	VPTS1015056	?	141	16	14	4.9	4.1	6.1	1.2	0.9	5.3	5.3	3.2	3	2.6	3.3	4.3	0.5	1.8	2.3	0.7	1.6	2.2	1	123	15	8	8
T. sanguineus	BMNH	1868.8.12.3	M	211	19	14	5.5	4.1	9.4	1.2	0.8	6.3	6.4	3.8	4.2	3.4	4	4.8	0.7	2.2	3	0.9	2	3.3	1.1	146	15	10	10
T. sanguineus	BMNH	1883.1.27.40	M	197	24	20	6.2	5	7.8	1.3	0.7	6.6	6.7	4	4.3	3.7	4.4	5.3	0.8	2.4	3.1	1.1	2.1	3.5	1.2	147	15	8	7
T. sanguineus	BMNH	1883.1.27.41	F	200	23	20	6.4	6	6.2	1.1	0.8	6.8	6.9	4.1	4.9	3.8	4.6	5.6	0.8	2.5	3.1	1	2.1	3.5	1.3	146	15	7	6
T. sanguineus	BMNH	1946.1.16.61	?	97	15	13	3.6	2.8	4.6	0.8	0.6	4.6	4.8	2.6	3.2	2.4	3.1	3.7	0.5	1.6	2.3	0.7	1.5	2.7	0.9	146	15	10	9
T. sanguineus	BMNH	1946.1.16.62	M	179	23	18	6.1	5.2	7.6	1.2	0.8	6.2	6.3	3.7	4.5	3.1	3.9	4.7	0.7	2.3	3	0.9	1.9	3.2	1.1	149	15	8	8
T. sanguineus	BMNH	1891.7.2.11	M	211	19	14	5.3	3.8	9.5	1.2	0.8	6.5	6.7	3.6	4	3.2	4.1	5.1	0.7	2.3	3	0.9	1.8	2.8	1	146	15	10	10
T. sanguineus	BMNH	1891.7.2.12	?	132	14	10	3.9	2.4	5.6	0.8	0.5	5.2	5.5	2.9	3.6	2.6	3.2	3.8	0.7	1.7	2.4	0.7	1.5	2.3	0.9	151	15	9	10
T. sanguineus	MNHN	1895.116 (no tag) A	?	183	26	22	6.7	5.8	7.6	1.4	0.9	6.4	6.7	3.8	4.7	3.5	4.2	5.2	0.7	2.3	3	1	2	3.5	1.1	144	15	7	7
T. sanguineus	MNHN	1895.116 (no tag) B	?	184	25	20	7.1	5	5	1	0.7	6.4	6.4	3.5	4.4	3.4	4.2	4.9	0.7	2.1	2.9	0.9	1.9	3.3	1.1	148	15	6	6
T. sanguineus	MNHN	1895.116 (no tag) C	?	110	16	11	3.8	3	4.6	0.8	0.6	4.7	4.8	2.8	3.3	2.5	3.1	3.9	0.5	1.6	2.1	0.8	1.4	2.7	0.9	146	15	9	8

Species	Collection	Voucher code	Sex	TL	Mb C	tC	Mb W	tW	tL	SL	SW	HL-SL	HL-P	HH 1-P	HW	MW	IL-M	IL-ST	E	E-N	E-ST	E-SL	RH	E-E	N-N	V	D	SC-L	SC-R
T. sanguineus	MCZ	6203	?	205	22	21	7.4	5.3	6.1	1.3	0.9	6.9	7.1	4.5	5	4	4.3	5.2	0.8	2.5	3.3	1.1	2.3	3.7	1.2	148	15	7	7
T. sanguineus	MCZ	179586	M	191	23	19	6.4	6.1	8.2	1.1	0.9	6.6	6.7	4.5	4.9	3.9	4.2	5	0.8	2.5	3.2	1.2	2.1	3.6	1.2	148	15	9	8
T. sanguineus	IISER-TVM	VPTS0317085	M	156	18	15	5.3	3.8	7	1.2	0.7	5.7	5.7	3.4	3.7	3	3.7	4.3	0.6	2	2.7	1	1.8	2.8	1.1	151	15	9	9
T. travancoricus	BMNH	1946.1.2.26	F	190	29	23	7.9	6.4	7.9	1.1	0.8	7.3	7.4	5	4.9	4.3	5	6	0.8	2.3	3.3	1.1	2.4	3.9	1.6	131	15	7	7
T. travancoricus	BMNH	1946.1.2.27	M	185	22	19	6.7	4.8	10.5	1.2	0.8	7.4	7.5	4.2	5	4.2	5	6	0.8	2.4	3.4	1.1	2.3	3.9	1.4	131	15	8	9
T. travancoricus	BMNH	1946.1.2.28	F	226	29	23	8.7	6.1	8.2	1.4	0.8	8	8.1	5.1	5.6	4.8	5.7	6.9	0.8	2.6	3.6	1.4	2.5	4	1.7	136	15	7	7
T. travancoricus	BMNH	1946.1.2.29	F	176	26	21	7.5	5.8	6.7	1.2	0.8	6.4	6.1	4.4	4.5	3.4	4.2	5	0.7	2	2.7	1	2.1	3.2	1.3	130	15	7	7
T. travancoricus	BMNH	1946.1.16.57	M	158	22	17	6.4	5	8.1	1.2	0.7	6	6.2	3.3	4	3.5	4.2	4.9	0.6	2	2.8	0.9	2	3.1	1.3	128	15	9	9
T. travancoricus	BMNH	1946.1.16.58	F	210	27	22	7.5	5.8	7.9	1.4	0.9	7	7.2	4.2	4.8	4.3	4.8	5.7	0.7	2.3	3.1	1.1	2.3	3.7	1.4	133	15	6	6
T. travancoricus	BMNH	1946.1.16.59	?	96	16	12	4.6	3.4	4.9	0.9	0.5	4.8	5.2	3.4	3.2	2.6	3.3	3.9	0.6	1.6	2.2	0.8	1.4	2.6	0.9	129	15	9	9
T. travancoricus	BMNH	1946.1.16.60	F	146	22	18	5.4	4.4	5.5	1.1	0.7	5.8	6.1	3.7	3.9	3.2	4.1	4.7	0.6	1.8	2.7	0.9	1.8	3.2	1.3	133	15	6	6
T. travancoricus	MNHN	1895.117_A	?	214	34	23	8.9	6.5	7.7	1.4	0.9	7.8	8.2	5.1	6.1	5.1	5.8	6.5	1.1	2.6	3.8	1.4	2.6	4.3	1.5	134	15	7	7
T. travancoricus	MNHN	1895.117(no tag)_B	?	213	29	22	9.2	6.6	7.3	1.5	1.1	7.6	7.4	5.3	5.1	4.4	5.3	6.1	0.9	2.5	3.2	1.3	2.2	3.7	1.5	137	15	6	6
T. travancoricus	MNHN	1895.117(no tag)_C	?	187	28	17	7.8	5.7	6.7	1.2	0.7	6.6	6.7	3.9	4.4	3.8	4.6	5	0.8	2	2.8	0.9	2	3.3	1.3	133	15	6	6
T. travancoricus	MNHN	1895.118 (no tag) A	?	184	24	18	7.3	5	9.5	1.3	0.9	7	7	4.1	4.6	4.2	5	5.8	0.8	2.2	2.9	1.1	2	3.6	1.2	133	15	8	8
T. travancoricus	MNHN	1895.118 (no tag) B	M	171	22	17	7.2	5	9.5	1.3	0.8	6.9	7.2	4.3	4.5	3.8	4.9	5.7	0.7	2.2	3	1.1	2.1	3.3	1.3	129	15	8	9
T. travancoricus	MNHN	1895.118 (no tag) C	M	170	22	17	6.7	4.7	9.3	1.1	0.8	6.6	6.8	4.1	4.7	3.9	4.8	5.5	0.8	2	2.9	1.1	2.2	3.6	1.3	133	15	9	9
T. travancoricus	MNHN	1895.118 (no tag) D	M	149	21	15	6.3	4.4	8.3	1	0.7	5.8	5.9	3.8	3.8	3.4	4	4.7	0.7	1.9	2.5	0.9	1.8	3	1	129	15	8	9
T. travancoricus	MCZ	47900	?	189	20	16	6.1	4.2	8.6	1.3	0.8	6.4	6.7	4	4.3	3.6	4.5	5.3	0.7	2.1	3	1.1	2.2	3.5	1.4	133	15	8	8
T. travancoricus	ALB	180	F	221	23	21	6.9	6.1	7.9	1.4	0.9	3.4	3.4	4.2	4.7	4.3	5.1	5.7	0.7	2.4	3.2	1.2	2.3	3.6	1.4	134	15	7	7
T. travancoricus	ALB	189	?	202	25	17	7.4	5.2	9.3	1.3	0.8	6.7	7	4.4	4.9	4	4.6	5.2	0.7	2.2	3	1.2	2.2	3.5	1.3	132	15	9	9
T. travancoricus	ALB	185	M	203	25	19	7.4	5.4	8.1	1.3	1	6.7	6.6	4.3	4.7	4	4.5	5.4	0.7	2.2	3	1.3	2.1	3.4	1.3	135	15	7	8
T. travancoricus	ALB	202	M	181	23	15	5.8	4.4	8.6	1.2	1	6.9	6.7	4.2	4.6	3.9	4.9	5.5	0.8	2	3	1.1	2.1	3.3	1.5	131	15	9	9
T. travancoricus	ALB	181	F	208	26	19	7.4	5.1	7.8	1.3	0.9	6.7	6.9	4.3	4.6	4.2	5	5.7	0.7	2.2	3	1.2	2.3	3.4	1.4	134	15	7	7

Species	Collection	Voucher code	Sex	TL	Mb C	tC	Mb W	tW	tL	SL	SW	HL-SL	HL-P	HH 1-P	HW	MW	IL-M	IL-ST	E	E-N	E-ST	E-SL	RH	E-E	N-N	V	D	SC-L	SC-R
T. travancoricus	ALB	204	?	106	15	11	4.1	3.3	5.8	1	0.6	4.9	5.1	2.9	3.2	2.6	3.4	4	0.6	1.5	2.3	0.9	1.7	2.7	1.2	130	15	9	9
T. travancoricus	MW	2193	F	191	23	17	6.5	4.5	7.6	1.5	0.9	6.4	6.4	3.3	4.4	3.6	4	4.8	0.6	2	3	1.2	2.1	3.2	1.4	134	15	7	6
T. travancoricus	IISER-TVM	VPTS1215077	?	220	27	19	7.5	5.2	6.7	1.5	0.9	7.5	7.5	4	4.6	4	5.1	5.8	0.7	2.5	3.3	1.2	2.3	3.3	1.3	141	15	5	6
T. travancoricus	IISER-TVM	VPTS0515035	?	145	19	16	5.9	5	5.1	1.2	0.7	5.8	5.6	3.1	3.9	3.5	4	4.5	0.6	1.9	2.7	0.8	1.7	2.7	1	139	15	7	6
T. travancoricus	IISER-TVM	VPTS0315032	?	153	19	14	5.4	3.9	7.9	1.2	0.8	6.7	6.4	3.2	4	3.3	4.3	5	0.7	2.1	2.9	1	1.9	3.1	1.3	128	15	8	9
U. annulata	BMNH	1946.1.16.1	M	172	21	18	6	5.6	9.5	1.3	2.5	6.4	6.1	4.2	4.2	3.5	4.6	5.2	0.5	1.9	3	1.1	2.2	3.2	1.6	134	17	10	10
U. annulata	MW	2179	F	155	21	18	7.3	5	9.3	1.5	2.4	7	6.7	4.4	4.8	4.3	5	5.8	NA	2	3.4	1.3	2.3	3.9	1.9	124	17	9	9
U. arcticeps	CAS	244718	?	131	15	15	4.3	4.3	5.6	1.5	2.3	4.6	4.6	3	2.9	2.5	3	3.9	0.4	1.7	2.4	0.9	1.6	2.3	1	130	17	6	6
U. arcticeps	CAS	244715	?	142	18	16	5.7	4.8	6.2	1.6	2.4	4.6	4.7	3.1	2.9	2.6	3.9	4.2	0.3	1.7	2.4	0.8	1.6	2.3	1	125	17	6	5
U. arcticeps	CAS	244716	?	152	17	16	5.4	4.7	6.1	1.7	2.8	4.9	5	3.4	3.3	2.8	3.3	4.1	0.4	1.9	2.5	0.9	1.6	2.4	0.9	126	17	6	5
U. arcticeps	CAS	244717	?	157	19	17	6.1	5.3	8	1.9	2.9	5.6	5.5	3.5	3.6	3.3	3.7	4.7	0.4	1.9	2.7	1	1.9	2.7	1.1	126	17	8	7
U. arcticeps	CAS	257377	?	246	21	19	6.4	5.1	6.3	1.8	2.3	5	5	3.4	3.6	3	3.4	4.2	0.4	1.7	2.7	0.9	1.8	2.6	1.2	131	17	6	5
U. arcticeps	CAS	244714	?	140	17	16	5	4.9	5.8	1.7	2.4	4.6	4.6	3.1	3.2	2.9	3.1	3.8	0.4	1.6	2.4	0.9	1.7	2.4	1	130	17	5	6
U. arcticeps	CAS	244713	?	168	21	20	6.3	6	6.8	1.8	2.7	5.3	5.3	3.4	3.4	2.8	3.6	4.5	0.4	2	2.7	0.9	1.8	2.5	1.1	129	17	6	7
U. arcticeps	CAS	39626	?	196	23	18	7.1	5.4	7	2	3.1	7	7	3.9	4.7	4.1	4.8	5.6	0.4	2.4	3.4	1.2	3.4	3.1	1.5	130	17	7	7
U. arcticeps	CAS	39622	?	156	17	17	5.4	4.9	6.3	1.7	2.6	5.3	5.3	3.6	3.5	3	3.5	4.3	0.5	1.8	2.7	0.9	1.8	2.5	1.1	131	17	6	7
U. arcticeps	BMNH	1946.1.16.11	M	157	18	15	5.6	4.7	8.6	1.4	2.2	4.7	4.8	3	3.2	2.7	3.2	3.7	0.3	1.8	2.4	0.9	1.7	2.3	1	127	17	9	9
U. arcticeps	BMNH	1946.1.16.12	M	200	20	18	6.3	5.4	10.3	1.8	2.4	5.9	6.1	3.3	3.8	3.1	3.7	4.7	0.2	2.1	3	1	2	2.8	1.2	127	17	8	8
U. beddomii	ZMB	10350	?	229	24	19	6.6	4.8	9.5	2	1.8	6.1	6	3.3	3.7	3	3.9	5.2	0.5	1.8	3.2	1	2	2.7	1.4	172	17	9	8
U. beddomii	BMNH	1946.1.16.13	?	281	22	20	7.3	6.2	7.6	2.5	2.8	6.3	6.1	3.5	3.8	3.1	3.7	4.9	0.4	1.9	3.2	0.9	2	2.6	1.4	184	17	5	6
U. beddomii	BMNH	1946.1.16.14	F	257	22	20	6.3	5.8	7.8	2.1	2.7	5.9	5.9	3.4	3.8	3.2	3.8	5.1	0.4	1.8	3.2	1	2.1	2.5	1.4	181	17	7	6
U. beddomii	BMNH	1946.1.16.15	?	289	24	20	6.9	6.1	7.2	2.4	3.2	5.8	5.6	3.2	3.5	2.9	3.9	4.8	0.3	2	3.1	0.9	2	2.3	1.2	188	17	6	6
U. bhupathyi	MW	MW 9115	F	366	26	24	8.7	7.2	9.3	2.5	3.4	7.8	7.4	4.4	5.2	4.2	4.9	6.5	0.7	2	4	1.4	2.7	3.3	1.8	217	17	7	7
U. bhupathyi	MW	MW 9112	F	316	22	22	7.3	6.8	9.1	1.9	3	7.1	6.7	3.8	4.6	3.9	4.4	6	0.7	1.9	3.6	1.2	2.5	3.1	1.8	214	17	8	7

Species	Collection	Voucher code	Sex	TL	Mb C	tC	Mb W	tW	tL	SL	SW	HL-SL	HL-P	HH 1-P	HW	MW	IL-M	IL-ST	E	E-N	E-ST	E-SL	RH	E-E	N-N	V	D	SC-L	SC-R
U. bhupathyi	MW	MW 9113	F	346	21	21	7.9	6.7	8.2	2.1	4	7.7	7.4	4.9	5.3	4.4	4.8	6.4	0.6	2.1	4	1.3	2.6	3.2	1.9	219	17	7	7
U. bhupathyi	MW	MW 9114	M	298	24	22	7.9	6.1	11.3	1.7	2.4	7	6.6	3.8	4.6	3.8	4.3	5.8	0.8	1.9	3.5	1.2	2.4	2.9	1.6	206	17	9	9
U. bhupathyi	MW	MW 9116	M	270	21	NA	6.6	4.2	10.3	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	206	17	10	10
U. bhupathyi	MW	MW 9117	F	396	26	NA	9.3	7.8	9.9	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	213	17	8	7
U. bhupathyi	MW	MW 9118	M	313	27	NA	7.9	6.3	12.3	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	205	17	9	9
U. bhupathyi	MW	MW 9119	F	354	23	21	7.3	6.6	8.4	2.6	3.2	8.3	7.9	4.4	5.3	4.6	5	6.9	0.7	2.1	4.2	1.3	2.7	3.4	1.9	214	17	6	7
U. bhupathyi	MW	MW 9120	M	325	23	21	7.6	6	12.8	1.9	2.5	7.8	7.9	4	5.3	4.7	5	6.7	0.8	2	4.1	1.3	2.7	3.3	1.9	202	17	9	9
U. bhupathyi	BNHS	3514	?	330	20	18	6.8	5.7	13.1	2.3	2.4	7.9	7.6	4	5.3	4.4	4.9	6.4	0.5	2.1	4.1	1.1	2.6	3.4	1.8	NA	NA	NA	NA
U. bhupathyi	BNHS	3513	?	312	23	20	6.7	6.2	9.1	2.1	2.8	7	6.8	3.8	4.3	3.7	4.3	5.9	0.5	2	3.7	1	2.3	3	1.7	NA	NA	NA	NA
U. bicatenata	BMNH	1946.1.16.8	M	256	25	20	7.6	5.3	16.7	1.5	2.1	7.4	7.1	4.2	4.7	4.3	5.3	6	0.6	2.5	3.6	1.3	2.6	3.9	1.6	134	17	12	12
U. bicatenata	BNHS	3479	?	211	19	19	6.9	5.3	12.3	1.6	2.2	7.1	7.1	4.7	5.1	4.4	5.1	6	0.7	2.1	3.4	1.3	2.7	3.9	1.8	135	17	11	11
U. bicatenata	BNHS	3480	?	256	22	22	7.5	6.4	11.8	1.6	3	8.1	7.6	5.1	5.5	4.6	5.6	6.4	0.9	2.3	3.7	1.5	3	4.2	2	132	17	8	8
U. bicatenata	BNHS	3477	?	210	20	19	6	5.9	12.5	1.9	2.5	7.4	7.2	4.6	5	4.3	5.4	6.1	0.8	2.4	3.4	1.3	2.6	3.9	1.8	130	17	10	10
U. bicatenata	BNHS	2367	F	244	25	22	7.9	6.4	9.7	1.7	2.8	7.4	7.2	4.9	4.6	4.1	5.2	5.9	0.6	2.1	3.3	1.2	2.5	3.8	1.7	137	17	8	8
U. bicatenata	BNHS	3481	?	177	19	15	5.8	4.6	8.5	1.3	2.2	6.2	6.1	3.9	4.3	3.5	4.5	5.2	0.7	1.8	2.9	1	2.3	3.4	1.5	133	17	9	9
U. bicatenata	BNHS	3476	?	249	23	22	8.1	6.1	11.4	1.9	2.7	7.6	7.1	4.6	5.1	4.4	5.4	6.3	0.8	2	3.4	1.3	2.6	3.8	1.9	141	17	9	8
U. bicatenata	BNHS	3265	M	203	25	21	7.3	6.2	12.4	1.7	2.5	7.3	7.2	5	4.2	4	5.5	6.1	0.6	2.1	3.3	1.3	2.5	3.7	1.7	129	17	12	10
U. bicatenata	BNHS	3266	M	192	21	17	6.8	5.2	13.9	1.5	2.2	7.1	6.6	4.2	4.3	3.9	4.9	5.5	0.7	2.1	3.2	1.1	2.2	3.4	1.8	131	17	12	12
U. brevis	MNHN	1897.258	?	379	52	39	13.7	10.4	13.4	2.3	4.2	11.9	11.5	5.7	7.8	6.8	9.1	10.3	1.1	3.7	5.3	1.8	3.7	5.3	2	140	17	8	8
U. brevis	MNHN	1897.259	?	298	37	32	10.5	9.3	12.2	2.1	4.2	9.1	9.1	5.5	5.8	5	6.2	7	1.1	2.7	4.2	1.5	3	4.3	2	136	17	8	9
U. brevis	MNHN	1895.98	?	294	35	33	11.8	9.7	13.5	1.9	3.6	10.7	9.7	6.8	7.2	6.4	7.8	9	1	2.9	4.7	1.6	3.4	5	2.1	129	17	10	10
U. brevis	MCZ	3916	?	206	25	25	7.3	7.6	8.8	1.6	3.1	7.4	7.2	4.2	5.1	4.3	5.4	6.4	0.8	2.1	3.3	1.3	2.5	3.7	1.7	135	17	8	8
U. brevis	CAS	244479	?	155	17	16	4.6	4.5	6.7	1.2	2.1	6.6	6.4	4	4.1	3.7	4.5	5.4	0.8	1.9	3	1	2.2	3.2	1.5	124	17	10	9
U. brevis	CAS	244788 not 2444788	?	215	24	21	7.8	6.4	11.9	1.6	3.2	8.2	7.7	5.4	5	4.4	5.6	6.6	0.7	2.5	3.7	1.2	2.5	3.7	1.8	127	17	11	11

Species	Collection	Voucher code	Sex	TL	Mb C	tC	Mb W	tW	tL	SL	SW	HL-SL	HL-P	HH 1-P	HW	MW	IL-M	IL-ST	E	E-N	E-ST	E-SL	RH	E-E	N-N	V	D	SC-L	SC-R
U. brevis	CAS	244764	?	227	24	20	7.7	6.2	10	1.5	3	7.3	7	4.4	4.7	4.3	5	5.9	0.9	2.2	3.5	1.3	2.5	3.9	1.7	125	17	8	9
U. brevis	CAS	244765	?	220	26	22	9	6.6	13	2.1	2.7	8.2	7.9	5	5.3	4.9	5.6	6.8	0.9	2.3	3.7	1.5	3	4.2	2	127	17	11	11
U. brevis	CAS	244766	?	135	16	15	5.2	4.1	6.7	1.2	1.7	5.7	5.6	3.8	3.8	3.5	3.8	4.8	0.7	1.6	2.7	1	2	3.2	1.4	125	17	9	9
U. brevis	CAS	244767	?	195	23	19	7.4	6.2	8.9	1.4	2.7	6.6	6.5	4.9	4.7	4.3	4.5	5.7	0.7	1.9	3.2	1.1	2.4	3.7	1.6	129	17	9	10
U. brevis	CAS	244768	?	232	24	22	8.4	5.9	11	1.6	3.2	7.9	7.5	4.9	5.1	4.6	5.8	6.9	0.9	2.3	3.6	1.2	2.6	3.8	1.8	133	17	9	9
U. brevis	CAS	244769	?	107	14	11	4.7	3.5	4.4	1	1.6	5.2	5	3	3.4	3	3.6	4.1	0.6	1.5	2.4	0.8	1.8	2.9	1.3	127	17	9	9
U. brevis	CAS	244770	?	200	22	18	7.1	5.7	10.9	1.4	2.9	7.2	6.9	4.6	4.5	4.1	4.9	5.9	0.8	2.1	3.3	1.2	2.4	3.6	1.5	125	17	10	9
U. brevis	CAS	244489	?	268	37	28	12.8	8.6	16.1	2.3	4.1	10.2	9.5	6.7	7.1	6	6.9	7.9	1	2.9	4.4	1.6	3.2	4.6	2.2	130	17	10	10
U. brevis	CAS	244475	?	224	29	23	9.7	7.5	11.3	1.8	2.6	8.4	7.8	5.7	5.5	4.8	5.6	6.7	0.7	2.5	3.8	1.3	2.7	3.7	1.9	136	17	8	9
U. brevis	CAS	244474	?	222	28	21	9.4	7.6	8.6	1.5	2.8	8.7	8.3	5.3	6	4.9	6.1	7.1	0.7	2.5	3.8	1.4	2.7	4.1	2	135	17	9	9
U. brevis	CAS	244488	?	211	27	21	7.5	7.2	9.1	1.4	2.7	8.2	7.7	5.2	5	4.7	6.1	6.7	0.9	2.3	3.4	1.3	2.7	3.9	1.9	135	17	8	8
U. brevis	CAS	244487	?	166	21	18	6.3	5.4	9.2	1.2	2.2	6.9	6.6	4.5	4.6	3.9	4.8	5.6	0.8	1.9	3.1	1	2.4	3.6	1.6	123	17	10	10
U. brevis	BMNH	1946.1.16.42	?	143	17	14	5.8	4.8	7.7	1.2	2.1	6.4	6.1	3.6	3.9	3.6	4.5	5.2	0.5	1.7	2.7	0.9	2.1	3	1.4	128	17	10	9
U. brevis	BNHS	209a	?	357	47	41	14.7	13.1	14.4	2.5	4.6	12.5	11.9	7.9	7.8	7.2	9.2	10.3	1.2	3.7	5.7	1.8	4	5.3	2.6	133	17	10	10
U. brevis	BNHS	209b	?	238	27	26	8.1	7.2	12.1	1.8	2.3	9.6	9	5.5	6.4	5.8	6.8	8	0.8	2.7	4.3	1.5	3	4.5	2	129	17	10	10
U. brevis	BNHS	201	?	236	28	23	9.2	6.8	12.1	1.6	2.1	9.4	8.9	4.7	5.4	4.9	6.4	7.4	0.8	2.5	4.2	1.3	2.8	3.9	1.8	133	NA	10	10
U. brevis	MW	2266	F	161	18	16	5.9	5	6.7	1.5	2.5	6.8	6.5	3.7	4	3.4	4.8	5.8	0.8	1.9	3.1	1.2	2.2	3.3	1.7	130	17	9	9
U. brevis	IISER-TVM	VPUA1014022	?	144	19	16	6.3	4.6	9.8	1	1.9	6.3	6	3.4	3.9	3.4	4.4	5.3	0.7	1.7	2.1	1	2	3.2	1.4	128	17	11	12
U. brevis	IISER-TVM	VPUC0616082	?	183	21	18	7.5	5.2	11.7	1.3	3.1	7.4	6.9	4.6	4.5	4	4.9	5.9	0.7	2	3.3	1.2	2.4	3.4	1.6	122	17	9	9
U. brevis	IISER-TVM	VPUC0616083	?	235	24	22	7.9	6	15.1	1.5	3.1	7.9	7.5	4.4	5.1	4.6	5.7	6.6	0.8	2.4	3.6	1.2	2.7	3.9	1.8	125	17	10	10
U. brevis	IISER-TVM	VPUA1014023	F	223	29	26	10	6.9	12.7	1.4	3.1	8.2	7.9	NA	6.7	5.1	6.2	NA	NA	2.6	3.9	1.5	2.7	4.4	2	124	17	9	9
U. brevis	IISER-TVM	VPUC1015063	?	231	27	23	8.4	7	12.6	1.5	3	8.6	8	4.6	5.3	4.9	6.1	7.1	0.8	2.5	3.8	1.4	2.8	4	1.9	129	NA	9	10
U. brevis	IISER-TVM	VPUS0216079	F	179	24	20	7.4	6.1	8.3	1.3	2.7	7	6.8	4.2	4.7	4.1	5	5.9	0.6	2	3.2	1.1	2.3	3.4	1.6	136	NA	9	9
U. brevis	IISER-TVM	VPUS0616081	F	344	32	29	11.8	9.2	14.4	1.8	3.9	12.6	11.3	5.7	7.4	6.5	8.5	9.8	1.1	3.7	5.6	1.9	3.9	5.1	2.5	139	NA	9	9

Species	Collection	Voucher code	Sex	TL	Mb C	tC	Mb W	tW	tL	SL	SW	HL-SL	HL-P	HH 1-P	HW	MW	IL-M	IL-ST	E	E-N	E-ST	E-SL	RH	E-E	N-N	V	D	SC-L	SC-R
U. broughami	MHNG	2760.93	F	247	22	21	6.4	5.8	7.5	2.1	2.5	6.2	6.1	3.6	4.3	3.6	3.9	5.3	0.5	2	3.3	1.1	2.3	3	1.6	200	19	8	7
U. broughami	MHNG	2760.96	F	173	18	18	5.6	4.6	5.3	2	1.8	5	4.9	3	3.4	2.7	3.2	4.2	0.4	1.6	2.7	0.9	1.9	2.5	1.2	197	19	5	5
U. broughami	MHNG	¬†2760.95	F	182	18	18	5.5	4.2	5.9	1.7	1.9	5.4	5.4	3.6	3.8	3	3.5	4.5	0.4	1.5	2.8	1	2	2.8	1.4	202	19	7	7
U. broughami	MHNG	2760.94	M	162	18	17	4.6	4.4	7.3	1.4	1.7	4.8	4.7	3.1	3.2	2.7	3.2	3.9	0.4	1.5	2.5	1	1.8	2.4	1.2	187	19	10	9
U. broughami	MNHN	1895.89	M	254	25	21	7.2	5.9	11.5	2.3	2.6	6	6	4	4.3	3.5	3.8	5.4	0.5	2	3.4	1	2.1	2.7	1.2	194	19	9	9
U. broughami	BMNH	1946.1.16.29	F	412	35	29	10.4	8.7	11.5	3	3.8	8.5	8	5.2	5.9	4.8	5.4	7.5	0.5	2.6	4.6	1.4	3	3.6	1.8	222	19	7	7
U. broughami	BMNH	1946.1.16.35	M	206	18	16	5.5	4.2	9.4	1.9	2	5.4	5.2	4.2	4	3.2	3.5	4.6	0.4	1.8	2.9	1	2	2.6	1.1	206	19	11	11
U. broughami	BMNH	1946.1.16.36	F	293	22	19	6.3	5.9	8.8	1.9	2.3	6.4	6.2	4.1	4.5	3.7	4.2	5.5	0.4	2.1	3.4	1.1	2.3	2.8	1.2	233	19	8	7
U. ceylanica	ZMB	4034	?	178	22	20	5.6	5.2	7.1	1.8	2.4	5.3	5.2	3.5	3.6	3.2	3.6	4.4	0.4	1.9	2.6	0.9	1.8	2.6	1	136	17	6	6
U. ceylanica	MNHN	39	?	171	17	14	5.3	4.9	6.9	1.6	2.7	4.9	5.3	3.2	3.4	3.1	4	4.7	0.3	2	2.7	0.8	1.7	2.5	1.1	130	17	6	6
U. cf. arcticeps	CAS	244720	?	155	18	13	4.8	4	7.2	1.1	1.7	5.6	5.7	3.6	3.5	3.2	3.8	5.1	0.5	1.6	2.7	1	2	2.8	1.4	146	17	8	8
U. cf. arcticeps	CAS	244719	?	228	32	27	9.1	8.3	9.9	2.5	3.5	6.7	6.6	5.2	4.4	4	4.3	5.2	0.5	2.2	3.4	1.2	2.3	3.2	1.4	143	17	7	8
U. cf. arcticeps	CAS	244721	?	211	24	20	7.9	6.6	11.9	1.6	2.6	7.1	7.5	4.5	4.5	4	4.9	6	0.4	2.5	3.7	1.3	2.4	3.4	1.6	138	17	9	9
U. cf. arcticeps	CAS	244722	?	150	15	15	4.3	3.6	6	1.5	2.2	5.1	5.1	3	3.1	2.6	3.2	4.1	0.5	1.7	2.5	0.9	1.7	2.3	1.1	138	17	9	9
U. cf. arcticeps	MW	2196	F	197	19	19	6.7	5.2	9.1	1.5	3	6.3	6.2	3.2	3.8	3.3	4.2	5.2	0.5	2.1	3.1	1	2	2.9	1.4	141	17	7	7
U. cf. arcticeps	MW	2191	F	224	21	19	6.4	5.9	9.8	2.1	2.9	7.1	6.9	3.7	4.5	3.9	4.9	6.1	0.4	2.5	3.5	1.2	2.3	3.1	1.6	151	17	7	7
U. cf. arcticeps	IISER-TVM	VPUE1214028	M	169	15	15	5.4	4.8	8.5	1.7	2.7	5.7	5.6	3.4	3.6	3.2	3.9	4.8	0.4	1.9	2.9	1	2	2.7	1.3	141	17	9	8
U. cf. arcticeps	IISER-TVM	VPUS1015064	F	187	20	17	6.1	5.2	8.1	1.6	2.6	6.2	5.8	3.5	4	3.5	4.5	5.4	0.4	2.2	3.1	1.1	2.3	2.7	1.5	142	17	7	7
U. cf. beddomii	IISER-TVM	VPUE1015058	F	235	22	20	6.5	5.8	8.1	1.9	2.7	5.8	5.7	3.6	3.6	2.9	3.6	4.9	0.4	1.8	3.1	1	2.1	2.5	1.2	173	17	7	7
U. cf. beddomii	IISER-TVM	VPUE1015059	M	181	17	15	5.1	3.9	9.2	1.6	1.8	5.8	5.1	2.9	3.4	2.8	3.5	4.6	0.4	1.6	2.8	0.9	1.9	2.2	1.2	164	17	9	9
U. cf. ceylanica	CAS	244382	?	188	23	18	7	5.7	8.1	1.3	2.7	7	7.2	4.2	4.8	4	5	5.8	0.7	1.9	3.3	1.2	2.4	3.4	1.8	133	17	9	9
U. cf. ceylanica	CAS	244381	?	176	21	17	6.7	5.1	9.1	1.3	2.7	6.1	6.1	3.8	4	3.6	4.4	5.2	0.7	1.8	3	1	2.1	3.2	1.6	131	17	10	9
U. cf. ceylanica	CAS	244383	?	226	23	21	8.4	6.7	11.2	1.5	3.3	7.6	7.5	4.5	5	4.8	5.5	6.8	0.8	2.4	3.7	1.2	2.5	3.8	2	132	17	8	7
U. cf. ceylanica	CAS	244380	?	158	20	16	6.1	5	6.9	1.1	2.4	6.1	6.3	3.8	4.1	3.7	4.3	5.3	0.6	1.7	3	1	2.1	3.1	1.7	135	17	8	8

Species	Collection	Voucher code	Sex	TL	Mb C	tC	Mb W	tW	tL	SL	SW	HL-SL	HL-P	HH 1-P	HW	MW	IL-M	IL-ST	E	E-N	E-ST	E-SL	RH	E-E	N-N	V	D	SC-L	SC-R
U. cf. madurensis	MNHN	1897.256	?	281	27	25	7.9	6.7	11.8	1.8	3.2	8.4	7.7	5.1	5.5	5	5.8	7.1	0.6	2.3	3.7	1.4	2.7	4	1.9	155	17	7	7
U. cf. madurensis	MNHN	1895.96	?	312	28	25	8.9	6.8	11.4	1.9	3.3	9.2	8.9	5.2	5.9	4.8	6.7	7.9	0.6	2.9	4.5	1.6	3	4.1	2.1	156	17	8	8
U. cf. madurensis	BMNH	83.1.12.14	F	344	28	29	9.2	8.9	14.2	2.4	3.6	10.8	9.8	6.3	6.5	5.4	6.8	8.5	0.8	3	4.7	1.4	3.1	4.4	2.2	152	17	9	8
U. cf. ocellata	MNHN	1895.84	M	311	25	23	7.3	6	12.1	2.3	2.5	7.3	6.9	4.3	4.6	3.9	4.9	6.4	0.5	2.2	3.7	1.3	2.5	3.2	1.4	219	17	10	10
U. cf. ocellata	MNHN	1895.84[A] (no tag)	F	242	19	18	5.5	5.1	7.4	1.4	2.1	5.3	5.3	2.9	3.8	3.1	3.7	4.6	0.4	1.5	2.7	1	2	2.5	1.3	231	17	7	7
U. cf. ocellata	MNHN	1897.251	?	352	28	25	8.1	7	11	3.1	3.2	7.1	7.2	4.4	5	4.1	5.1	6.2	0.4	2.3	3.7	1.5	2.3	3.2	1.4	223	17	8	8
U. cf. ocellata	NHM	1946.1.15.43	F	505	46	43	14	12.9	16.1	4.8	5.4	12	11.2	7.7	8.8	7.5	8.5	10.5	0.6	3.8	6.1	2.2	4	5.2	2.6	224	17	8	9
U. cf. ocellata	NHM	1946.1.15.45	F	465	37	35	11	10.3	12.2	3.5	4.9	11.1	11	8	8.6	7.1	8.1	9.8	0.6	3.7	5.8	2.4	4	4.9	2.2	228	17	6	6
U. cf. ocellata	NHM	1946.1.2.30	M	296	25	24	8.2	6.9	12.6	2.9	3	7.3	7.1	4.9	5.1	4.5	4.9	6.3	0.4	2.3	3.8	1.4	2.6	3.4	1.5	213	17	11	11
U. cf. ocellata	NHM	1946.1.2.31	F	252	22	21	6.5	5.6	8.1	2.5	3	6.1	6	3.1	3.8	3.1	4.1	4.9	0.4	1.9	3	1	2	2.7	1.3	220	17	8	7
U. cf. ocellata	NHM	1946.1.15.69	F	367	25	25	7.9	7.3	10.8	2.7	3.7	7.9	7.4	5	5	4.2	5.4	6.8	0.4	2.3	3.9	1.5	2.7	3.4	1.7	227	17	8	8
U. cf. ocellata	NHM	1946.1.15.70	F	322	25	22	6.9	6.1	9.4	2.4	3.2	7	6.9	3.9	4.5	3.8	4.9	6	0.4	2.1	3.5	1.3	2.5	3.1	1.5	221	17	7	7
U. cf. ocellata	NHM	1946.1.15.71	F	232	19	16	6.4	4.4	6.6	1.8	2.1	5.8	5.6	3.4	3.6	3	4	4.9	0.4	1.7	2.9	1.1	1.9	2.6	1.2	226	17	6	7
U. cf. ocellata	ZMB	10355	M	307	25	23	7	7	13.3	2.6	2.9	8.1	7.7	4.7	5	4.4	5.4	6.8	0.5	2.6	4.1	1.5	2.8	3.6	1.6	214	17	10	11
U. cf. ocellata	ZMB	10342(a)	M	168	15	15	4.1	3.4	6.5	1.3	1.7	4.4	4.3	2.7	2.8	2.3	3.1	3.7	0.3	1.4	2.1	0.8	1.6	2.2	1	226	17	10	10
U. cf. ocellata	ZMB	10342(b: shorter tail)	F	172	13	14	4.1	4	5.3	1.4	1.5	5	5.2	2.9	3	2.5	3.5	4.4	0.4	1.4	2.3	0.9	1.8	2.3	1.1	231	17	7	7
U. cf. ocellata	MCZ	47291	F	253	20	19	5.9	5.2	7.7	2.1	2.9	6.7	7.5	3.8	4.6	3.8	4.5	5.8	0.4	2.2	3.5	1.3	2.5	3	1.5	219	17	9	8
U. cf. ocellata	MCZ	47292	M	331	27	26	7.7	7.4	13	3.1	3	8.1	7.8	4.5	5.2	4.3	5.2	6.8	0.4	2.5	4	1.4	2.6	3.4	1.8	213	17	10	10
U. cf. ocellata	MCZ	47293	F	282	22	20	6.8	5.3	7.3	2.4	3.6	6.5	6.3	4	4.5	3.7	4.3	5.4	0.4	2	3.3	1.2	2.2	2.9	1.5	226	17	8	8
U. cf. ocellata	CAS	244486	?	247	18	18	6.2	5.1	9	2.7	3.2	5.3	5.2	3.7	3.9	3	3.6	4.5	0.3	1.6	2.7	1.1	2.1	2.6	1.4	222	17	8	7
U. cf. ocellata	CAS	244472	?	265	20	20	6.3	5.9	9.8	2.9	3.3	5.8	5.7	3.7	4.1	3.5	3.8	4.8	0.4	1.8	3.1	1.3	2.2	2.7	1.4	221	17	9	8
U. cf. ocellata	CAS	244821	?	278	25	21	8.4	6.3	8.5	3	3.4	5.8	5.5	3.6	4.1	3.5	3.6	4.8	0.4	1.7	3	1.1	2.1	2.8	1.5	219	17	6	7
U. cf. ocellata	MW	2177	F	230	17	17	5.9	5.3	6.6	2.6	3.2	5.1	5.1	3	3.3	2.6	3.4	4.5	0.3	1.6	2.7	0.9	1.7	2.2	1.2	215	17	6	6
U. cf. ocellata	MW	2171	F	252	17	16	5	4.5	7.1	2.5	2.7	5.5	5.5	3	3.3	2.6	3.6	4.7	0.4	1.6	2.9	1	1.8	2.3	1.3	221	17	7	7

Species	Collection	Voucher code	Sex	TL	Mb C	tC	Mb W	tW	tL	SL	SW	HL-SL	HL-P	HH 1-P	HW	MW	IL-M	IL-ST	E	E-N	E-ST	E-SL	RH	E-E	N-N	V	D	SC-L	SC-R
U. cf. ocellata	MW	2174	M	237	18	16	5.3	4.3	9.6	2.1	2.1	5.8	5.5	3.2	3.6	3	3.4	4.8	0.4	1.5	2.8	1	1.9	2.5	1.4	212	17	9	10
U. cf. ocellata	MW	2175	M	233	18	16	5.3	3.8	9.7	2.3	2.3	5.3	5.2	3.1	3.2	2.7	3.4	4.1	0.3	1.5	2.6	1.1	1.7	2.3	1.4	218	17	10	9
U. cf. ocellata	MW	2176	F	253	20	17	5.9	4.9	6.6	2.3	2.6	5.2	5.1	3.2	3.4	2.9	3.5	4.2	0.3	1.7	2.6	1.1	1.8	2.4	1.2	224	17	6	6
U. cf. ocellata	MW	2178	F	253	16	16	5.3	4.9	7	2.5	2.8	5.1	5	2.8	3.3	2.7	3.3	4.2	0.4	1.5	2.6	1	1.7	2.3	1.3	220	17	6	6
U. cf. ocellata	MW	2265	F	259	23	19	6.4	6	7.2	2.7	2.9	5.6	5.5	3.3	3.5	2.9	3.6	4.3	0.4	1.7	2.9	1.1	1.8	2.4	1.3	227	17	6	6
U. cf. petersi	MNHN	1897.249	?	248	24	22	7.2	5.6	13.1	2.2	1.6	6.3	6.3	4.5	4.9	4	4.4	5.3	0.6	1.8	3.2	1.3	2.3	3.4	1.4	178	17	11	11
U. cf. petersi	BMNH	1946.1.17.8	?	207	16	15	5	4.1	9.1	1.6	1.2	4.8	4.9	3.1	3.4	2.9	3.5	4	0.4	1.7	2.3	1	1.7	2.5	1.2	183	17	10	10
U. cf. petersi	UK MW	2228	M	149	13	11	4.4	3.7	6.8	1.3	1.2	4.3	4.4	2.9	3.1	2.5	2.9	3.4	0.3	1.4	2.2	0.9	1.7	2.3	1.1	177	17	12	12
U. cf. phipsonii	UK MW	247	F	195	20	18	6.5	5.7	7.1	1.7	2.6	6	6	3.5	3.8	3.1	4.2	5	0.5	1.8	2.9	1	2.1	3	1.3	144	17	7	6
U. cf. phipsonii	IISER-TVM	VPU0813007	F	199	21	19	6.9	5.5	7.4	1.4	2.2	6.2	6.1	3.8	4.1	3.6	4.4	5.2	0.5	1.9	2.9	1.1	2.2	3.1	1.4	145	17	8	7
U. cf. phipsonii	IISER-TVM	VPUS0615041	F	227	20	19	6.5	5.6	8.7	1.7	3.1	7.1	6.9	3.8	4.3	3.6	5.2	6	0.5	2.2	3.5	1.2	2.5	3.4	1.6	146	17	7	7
U. cf. phipsonii	IISER-TVM	VPU0813008	F	208	22	19	6.7	5.5	8	1.9	2.6	6.3	6.1	3.9	4.1	3.4	4.4	5.4	0.5	1.9	3.1	1	2.2	3.1	1.6	145	17	7	7
U. dindigalensis	MNHN	1895.88	F	230	19	20	7.1	5.9	8	2	2.8	6	6	4	3.9	3.2	4.1	5.1	0.5	2.1	3.2	1	2	2.8	1.2	168	17	6	6
U. dindigalensis	BMNH	1946.1.16.37	F	353	40	34	11.9	9.7	11.7	3.8	3.7	9.5	8.9	5.5	7.2	5.9	6	7.6	0.6	3	4.9	1.5	2.8	3.8	2	167	17	6	6
U. dindigalensis	BMNH	1946.1.16.4	F	230	22	23	7.1	6.5	8.4	2	2.5	6.2	6.2	3.6	3.9	3.1	3.9	5	0.5	2	3.2	1	2	2.5	1.2	167	17	6	5
U. dindigalensis	BMNH	1946.1.16.3	F	349	35	31	10.2	8.9	12.2	3.1	4.1	9.7	9.2	5.1	6.1	5.1	6.2	7.9	0.6	3	4.8	1.6	2.9	3.8	1.9	168	17	7	6
U. dindigalensis	BMNH	1946.1.16.2	M	186	20	18	6	4.5	10.9	2	2	5.6	5.5	3	3.9	3.2	3.7	5.1	0.4	1.7	2.9	0.9	1.9	2.4	1.3	157	17	11	10
U. dindigalensis	CAS	244757	F	236	21	16	6.6	5.7	8.4	1.8	2.7	5.4	5.3	3.2	3.7	3.4	3.6	4.5	0.4	1.8	2.8	0.9	1.8	2.5	0.9	169	17	7	6
U. dindigalensis	CAS	244758	F	235	25	22	7.5	6	8.3	2.2	2.7	6.3	5.9	3.8	4	3.4	3.9	5.3	0.4	2.1	3.4	1	2	2.5	1.3	166	17	6	6
U. dindigalensis	CAS	244759	M	199	18	16	5.5	NA	11.1	1.8	2.3	5.4	5.5	3.2	3.1	2.5	3.4	4.3	0.4	1.8	2.9	0.9	1.7	2.2	1.1	153	17	9	8
U. dindigalensis	CAS	244760	M	211	18	15	6.5	5.4	12	2	2.4	5.5	5.6	3.8	3.3	2.7	3.5	4.7	0.4	1.9	2.9	0.9	1.9	2.2	1.2	157	17	10	10
U. dindigalensis	CAS	244761	M	213	22	16	7.3	6.8	11.2	2.2	2.4	5.4	5.1	3.3	3.9	3	3.3	4.2	0.4	1.9	2.9	0.9	1.7	2.1	1	151	17	11	11
U. dindigalensis	CAS	244762	M	202	22	19	7.3	5.3	9.9	2.1	2.2	5.4	5.4	3.6	3.6	3.2	3.3	4.5	0.3	1.8	2.9	1	1.8	2.5	1.2	152	17	11	10
U. dindigalensis	CAS	244763	M	156	13	13	4.7	4.6	9.3	1.5	1.6	4.5	4.7	2.5	3.2	2.5	2.6	3.3	0.3	1.5	2.3	0.8	1.4	1.9	1.1	155	17	11	10

Species	Collection	Voucher code	Sex	TL	Mb C	tC	Mb W	tW	tL	SL	SW	HL-SL	HL-P	HH 1-P	HW	MW	IL-M	IL-ST	E	E-N	E-ST	E-SL	RH	E-E	N-N	V	D	SC-L	SC-R
U. dindigalensis	CAS	244756	M	204	20	15	6.9	5.5	12.4	1.8	2.1	5.7	5.5	3	3.4	2.7	3.5	4.7	0.3	1.9	2.9	0.9	1.8	2.4	1.3	158	17	9	10
U. dupeni	NHM	1946.1.1.42	M	301	23	21	7	6.2	10.7	2.4	2.5	6.7	6.4	3.8	4.4	3.7	4.8	5.8	0.5	1.9	3.3	1.2	2.4	3.1	1.6	231	17	10	9
U. dupeni	NHM	1946.1.15.44	F	423	25	24	8.5	7.5	10.4	2.7	3.9	10	9.3	6	6.5	5.4	6.8	8.6	0.4	3.2	5.2	1.6	3.1	3.9	2	221	17	8	8
U. dupeni	NHM	1946.1.15.85	M	263	23	20	6.6	5	10.1	2.4	1.8	6.3	6	3.3	3.9	3.2	4.3	5.6	0.4	1.8	3	1.2	2.2	2.9	1.3	227	17	9	9
U. dupeni	NHM	1946.1.15.86	F	258	21	21	6.2	5.8	7.9	2	2.7	6.1	6	3.6	4.2	3.6	4.3	5.2	0.4	1.8	3	1.1	2.4	2.9	1.3	227	17	7	7
U. dupeni	IISER-TVM	VPUO1015061	?	309	21	22	7	6.5	8.1	2.4	3.2	6.7	6.4	3.6	4.1	3.5	4.4	5.6	0.4	2.1	3.5	1.3	2.3	2.9	1.5	227	17	8	8
U. dupeni	IISER-TVM	VPUO1015060	M	238	17	16	5.5	4.6	9.9	2.2	2.7	6.2	5.8	3.3	3.6	3.2	4.1	5.2	0.3	1.9	3.2	1.2	2.2	2.4	1.4	225	17	9	10
U. ellioti	MNHN	1895.90[a]	?	227	27	21	7.8	5.9	10.8	1.4	1.5	6.9	6.5	3.9	4.7	3.9	4.3	5.7	0.5	1.9	3.3	1.2	2.3	3.1	1.4	166	17	9	9
U. ellioti	MNHN	1895.90[b]	?	211	24	20	6.6	5.1	9.7	1.5	1.7	5.8	5.8	3.7	4	3.1	3.8	4.7	0.4	1.9	2.9	1	1.8	2.7	1.2	163	17	9	9
U. ellioti	MNHN	1895.91[a]	?	242	26	25	7.8	6.5	8.5	1.8	2.2	6.2	5.9	3.6	4	3.2	4	4.9	0.4	2	3	1.1	2	2.8	1.3	157	17	8	7
U. ellioti	MNHN	1895.91[b]	?	225	21	20	6.5	5.5	8.7	1.9	2.7	5.8	5.6	3.2	3.9	3.1	3.6	4.7	0.4	1.7	2.9	1	2.1	2.6	1.4	175	17	7	7
U. ellioti	MNHN	1895.91[c]	?	215	24	23	7.2	6.4	8.6	1.8	2	5.7	5.5	3.7	4	3.3	3.7	4.6	0.3	1.9	2.9	1	2	2.5	1.3	150	17	8	7
U. ellioti	MNHN	1895.91[d]	?	170	18	14	4.7	3.8	9.3	1.7	1.4	5.1	5	3.1	3.3	2.6	3.5	4.4	0.4	1.7	2.6	0.8	1.7	2.4	1	165	17	10	9
U. ellioti	MNHN	1895.92[a]longtai	?	250	23	20	6.8	4.6	13.2	1.7	1.8	7	7	3.9	4.4	3.5	4.7	5.8	0.5	2.2	3.6	1	2.3	3.2	1.6	168	17	10	9
U. ellioti	MNHN	1895.92[b]shorttai l	?	249	21	21	6.6	5.8	6.7	1.8	2.2	6.5	6.1	3.5	3.8	3.2	4.2	5.4	0.4	2	3.3	1	2	2.8	1.3	178	17	7	7
U. ellioti	MNHN	1946.270.	?	233	24	24	7.3	6.3	8.2	2.3	2.7	6.5	6.5	4.2	4.8	4	4.3	5.6	0.5	1.9	3.4	1.4	2.4	3.3	1.7	163	17	6	5
U. ellioti	MNHN	1948.257	?	188	19	17	5	4.3	6.6	1.5	1.7	5	4.9	3.1	3.4	2.6	3.1	4	0.3	1.5	2.6	0.8	1.7	2.3	1	167	17	7	7
U. ellioti	MNHN	1948.259	?	181	17	17	4.8	4.3	6.1	1.6	1.8	5	4.8	3	3.2	2.5	3.1	4	0.4	1.6	2.4	0.8	1.6	2.3	1	168	17	7	7
U. ellioti	MNHN	1948.260.	?	192	20	19	5.2	4.1	9.6	1.2	1.3	5.2	5.1	3.3	3.3	2.6	3.4	4.4	0.4	1.6	2.7	0.9	1.7	2.4	1.1	156	17	10	9
U. ellioti	MNHN	1948.261	?	197	18	17	5.4	4.1	10.2	1.2	1.5	5.4	5.4	3.1	3.6	2.8	3.5	4.6	0.3	1.6	2.8	1	1.7	2.4	1.2	161	17	9	10
U. ellioti	MNHN	1989.3840.	?	142	15	14	4.4	3.9	5.8	1.4	1.6	4.6	4.7	2.8	3.2	2.7	3	4.1	0.4	1.3	2.4	0.8	1.6	2.4	1.1	160	17	7	6
U. ellioti	MNHN	1989.3842	?	168	17	17	5.2	4.3	9.7	1.4	1.6	5.4	5.3	3.2	3.6	3.1	3.5	4.7	0.4	1.7	2.8	1	1.8	2.6	1.2	159	17	10	11
U. ellioti	MNHN	1989.3845	?	116	13	12	3.6	2.9	5.7	1.1	1.2	4.1	4.2	2.2	2.5	1.9	2.6	3.4	0.3	1.3	2	0.7	1.4	1.9	0.7	156	17	10	10
U. ellioti	ZMB	10340	?	246	23	21	7	5.3	11.4	1.3	1.5	6.2	5.8	3.4	4	3.2	4.1	5.1	0.5	2	3.2	1.1	2.1	2.7	1.3	169	17	11	11

Species	Collection	Voucher code	Sex	TL	Mb C	tC	Mb W	tW	tL	SL	SW	HL-SL	HL-P	HH 1-P	HW	MW	IL-M	IL-ST	E	E-N	E-ST	E-SL	RH	E-E	N-N	V	D	SC-L	SC-R
U. ellioti	ZMB	5542b	?	144	17	13	4.7	3.9	5.7	1.1	1.3	4.4	4.2	2.5	2.8	2.4	3	3.8	0.4	1.6	2.5	0.9	1.6	2.3	1.1	167	17	6	5
U. ellioti	MCZ	47037	M	164	20	18	5.6	4.4	7.4	1.5	1.5	4.9	4.9	3.4	3.3	2.9	3.2	4.1	0.4	1.6	2.5	0.9	1.8	2.5	1.2	140	17	8	9
U. ellioti	MCZ	47038	F	213	17	17	4.9	4.8	6.4	1.5	2.4	5.5	5.4	3.2	3.3	2.7	3.3	4.4	0.4	1.6	2.7	0.9	1.9	2.4	1.3	168	17	7	7
U. ellioti	MCZ	47036	M	156	17	16	4.9	4.1	8.7	1.2	1.5	4.7	4.6	2.9	3.1	2.6	3.1	4.1	0.4	1.3	2.1	0.8	1.6	2.4	1.2	146	17	11	10
U. ellioti	MCZ	47039	F	186	20	18	5.9	4.9	6.9	1.8	2.1	5.4	5.3	3.8	3.7	3.1	3.8	4.8	0.4	1.8	2.8	1.1	1.8	2.7	1.2	143	17	7	7
U. ellioti	MCZ	3880	F	194	20	18	6.1	5.8	8.7	1.3	2	6	6.1	3.5	3.6	3.1	4.2	5.1	0.6	1.7	2.7	0.9	1.9	3	1.4	145	17	7	7
U. ellioti	MCZ	3881	F	153	19	17	5.7	5.3	5.8	1.7	2.2	5.5	5.4	3.3	3.6	3.1	3.5	4.7	0.4	1.6	2.6	0.9	1.8	2.7	1.3	149	17	6	7
U. ellioti	MCZ	3850	F	232	20	19	6.9	5.7	7.9	1.7	2.3	5.5	5.3	3.5	3.8	3.3	3.8	4.9	0.4	1.6	2.7	1	2	2.7	1.3	176	17	6	6
U. ellioti	MCZ	3911	M	212	19	16	5.7	4.1	9.2	1.4	1.6	5.5	5.6	3.2	3.7	2.9	3.6	4.8	0.4	1.7	2.9	1	1.8	2.5	1.2	161	17	10	10
U. ellioti	MCZ	47040	M	203	21	17	6	4.8	9.3	1.5	1.6	5	5.1	3.4	3.7	3.2	3.7	4.4	0.5	2	2.7	0.9	2	2.6	1.2	145	17	9	9
U. ellioti	AMNH	46307	?	113	15	14	4.5	3.6	6.4	1.1	1.3	4.9	4.8	3.8	3.7	3.2	3.4	4.4	0.5	1.5	2.4	0.8	1.7	2.8	1.2	145	17	10	10
U. ellioti	BMNH	1946.1.16.40	F	194	24	20	7.6	5.5	7.5	1.9	2	5.2	5.3	3.5	3.6	3.1	3	4	0.4	1.7	2.6	0.9	1.8	2.7	1.3	144	17	7	6
U. ellioti	UK MW	2501	M	199	16	14	5.5	3.5	9	1.5	2.2	5.5	5.3	2.8	3.6	2.8	3.6	4.4	0.4	1.6	2.8	0.9	1.9	2.4	1.3	177	17	10	11
U. ellioti	UK MW	2503	?	157	17	15	5.4	5.1	8	1.4	2	5.8	5.7	3	3.8	3.1	4.2	4.6	0.5	1.7	2.7	1	1.8	2.7	1.4	152	17	9	9
U. ellioti	BMNH	1946.1.16.43	F	204	19	18	6.5	5.3	7.2	1.9	2.7	6.2	6.1	3.7	4.2	3.3	4.1	5.1	0.4	1.9	3	1	2.1	2.8	1.4	158	17	6	7
U. ellioti	BMNH	1946.1.16.44	?	132	14	13	4.4	3.8	4.9	1.5	1.7	4.6	4.7	2.8	3.2	2.7	3.1	3.7	0.3	1.4	2.2	0.8	1.7	2.4	1.1	157	17	7	6
U. ellioti	BMNH	1946.1.16.45	F	166	18	18	6	5.1	5.7	1.5	2.3	5.7	5.4	3.7	4.2	3.3	3.7	4.4	0.4	1.8	2.7	0.8	2	2.8	1.3	155	17	7	7
U. ellioti	BMNH	1946.1.16.46	M	204	21	18	6.8	5.3	10.2	1.9	2.1	6.2	6	4.2	4.3	3.5	4.3	5	0.4	2.1	3.1	1.1	2.3	3.1	1.4	151	17	9	9
U. ellioti	BMNH	1946.1.16.6	M	243	21	18	6.9	5.2	11.7	1.6	2	6.1	6	4	4.1	3.4	4	4.9	0.4	2	3.1	1.1	2.1	2.9	1.3	167	17	9	10
U. ellioti	BNHS	3486	?	170	19	16	6.2	4.7	10.6	1.5	1.2	4.7	4.6	3.6	3.3	2.8	3.1	4	0.4	1.5	2.4	0.9	1.7	2.3	1.1	146	17	11	11
U. ellioti	BNHS	3487	?	183	21	15	6.5	4.4	11	1.5	1.4	5.2	5.1	3.4	3.5	3	3.4	4.4	0.3	1.7	2.8	1	2	2.5	1.3	146	17	11	10
U. ellioti	BNHS	3488	M	199	22	18	6.3	5.4	12	1.7	1.6	5.7	5.7	3.4	3.8	3.2	3.6	4.8	0.4	1.8	3	0.9	1.9	2.8	1.5	148	17	11	10
U. ellioti	BNHS	3489	M	179	21	14	6.4	4.8	11	1.5	1.3	5	4.9	2.8	3.1	2.6	3.2	4.1	0.4	1.6	2.6	1	1.8	2.3	1.2	148	17	11	10
U. ellioti	IISER-TVM	VPUE0713005	F	226	20	15	5.8	4.8	8.2	2	1.9	6.2	5.9	3.9	4.2	3.4	4	5	NA	1.9	3.2	1.1	2.2	2.8	1.6	164	17	7	7

Species	Collection	Voucher code	Sex	TL	Mb C	tC	Mb W	tW	tL	SL	SW	HL-SL	HL-P	HH 1-P	HW	MW	IL-M	IL-ST	E	E-N	E-ST	E-SL	RH	E-E	N-N	V	D	SC-L	SC-R
U. ellioti	IISER-TVM	VPUE1214030	F	232	19	17	5.8	4.9	6.9	1.8	2.2	6.2	6	3.9	3.9	3.4	4.1	5.2	0.4	2	3.3	1.1	2.2	2.7	1.4	162	17	7	7
U. ellioti	IISER-TVM	VPUE0713006	F	183	17	16	5	4.3	6.3	1.8	2	5	4.8	2.7	3.1	2.6	3.2	4	0.3	1.7	2.6	0.9	1.8	2.3	1.2	163	17	7	7
U. grandis	MNHN	1895.79	M	386	32	29	9.3	7.8	14.2	2.4	2.1	9.6	9.5	5.8	7.3	6.2	7	8.4	0.5	3.3	4.9	1.9	3.2	4.4	2.2	211	19	10	11
U. grandis	MNHN	1895.79[a]	F	199	17	16	5.3	4.2	6.2	1.2	1.3	5.1	5.1	3.2	3.7	3.1	3.5	4.5	0.4	1.7	2.8	1	2	2.8	1.3	214	19	8	6
U. grandis	MNHN	1897.266	M	238	20	19	6.3	5.2	9	1.5	1.5	5.8	5.9	4.3	4.5	3.8	4.2	4.9	0.5	1.9	3.2	1.2	2.3	3.3	1.6	200	19	10	10
U. grandis	ZMB	10347	F	345	34	27	8.3	7.5	9.6	2.3	2.2	8.2	7.8	6.2	6.3	5.5	5.5	6.9	0.5	2.5	4.2	1.7	3	3.8	1.6	217	19	8	7
U. grandis	ZMB	5540	M	395	32	29	10.4	7.2	15.3	2.8	2.2	10	9.4	6.2	6.2	5.1	6.9	8.4	0.6	3.2	4.9	1.6	3.1	4.2	1.9	211	19	11	11
U. grandis	MCZ	6200	M	385	30	26	9.8	7.1	16.3	2.8	2	9.2	8.9	5.7	6.3	5.5	6.1	7.5	0.5	3.2	4.7	1.8	3.2	4.2	1.9	203	19	12	12
U. grandis	MCZ	179589	M	247	21	20	6.2	5.8	9.4	1.7	1.7	6	6.2	4.4	4.4	3.8	4.2	5.3	0.4	1.8	3.2	1.2	2.3	3.1	1.4	195	19	9	9
U. grandis	MCZ	179590	?	139	15	12	4.1	3.4	4.2	1.2	1.2	4.5	4.6	3.1	3.2	2.8	3	3.8	0.3	1.3	2.3	0.9	1.7	2.3	1.1	197	19	7	6
U. liura	CAS	244860	M	212	19	18	6.2	5.2	10.8	1.3	1.2	5.3	5.2	3.7	3.5	3.2	3.5	4.5	0.4	1.5	2.6	1	2	2.7	1.2	186	17	11	12
U. liura	CAS	244861	F	280	22	22	6.6	6.3	8.3	1.7	2	6.1	6	3.7	4.5	3.7	4	4.9	0.4	1.8	3	1.2	2.3	3.1	1.6	201	17	9	8
U. liura	CAS	244863	M	237	20	18	6.9	5.5	11.5	1.5	1.3	6	5.8	3.8	4.2	3.7	4.1	4.8	0.4	1.9	3	1.1	2.1	3	1.4	186	17	12	11
U. liura	CAS	244862	M	206	19	16	6.2	5	9.2	1.5	1.2	5.2	5.1	2.8	3.7	3	3.7	4.4	0.3	1.7	2.6	1.1	1.8	2.5	1.2	183	17	13	13
U. liura	CAS	244376	F	243	20	19	7.1	5.8	7.4	1.7	1.6	5.8	5.6	3.5	3.9	3.4	4	4.8	0.4	1.7	2.8	1	2	2.7	1.2	197	17	8	7
U. liura	CAS	244378	F	299	24	23	7.4	7.1	9.5	2.3	1.9	6.7	6.5	5.3	5.5	5	4.6	5.9	0.5	2	3.2	1.2	2.4	3.3	1.6	187	17	8	8
U. liura	BMNH	1946.1.16.7	M	265	19	19	6.8	5.8	12.2	1.6	1.4	6.2	6.2	4	4.4	3.8	4.4	5.3	0.5	2	3.2	1.1	2.2	3	1.6	183	17	13	12
U. liura	BMNH	83.1.12.35	F	321	29	25	8.6	8.1	9.6	1.5	1.7	7	6.8	4.6	4.9	4.1	4.8	5.9	0.5	2.3	3.6	1.3	2.6	3.4	1.7	189	17	9	8
U. liura	BMNH	83.1.12.36	M	245	21	18	6.3	5.2	12.9	1.5	1.3	6.1	6.3	4.2	4.4	3.7	4.5	5.2	0.5	1.9	3	1.2	2.4	3.1	1.5	173	17	12	12
U. liura	BMNH	83.1.12.37	M	263	21	19	6.9	5.4	13	1.7	1.4	6.2	6.2	3.9	4.7	3.9	4.6	5.3	0.5	2.1	3.2	1.2	2.4	3	1.5	178	17	11	12
U. liura	ALB	193	?	245	19	19	6	5.2	7.5	1.5	1.6	5.8	5.7	3.6	3.6	3.3	3.9	4.7	0.4	1.8	2.9	1.1	2.1	2.7	1.4	197	17	9	8
U. liura	ALB	187	?	256	23	22	6.7	6.1	12.6	1.7	1.5	6.3	6	4	4.7	4	4.4	5.3	0.5	1.8	3.1	1.4	2.4	3.3	1.6	187	17	13	12
U. liura	ALB	206	M	233	20	20	6.5	5.2	10	1.6	1.5	5.3	5.5	3.2	3.8	3.1	3.7	4.6	0.4	1.6	2.7	1	1.8	2.6	1.3	194	17	11	11
U. liura	ALB	188	?	244	21	20	6.2	5.4	11.5	1.2	1.4	5.9	5.8	3.7	4.3	3.7	4	4.8	0.5	1.8	2.9	1.2	2.1	3	1.4	188	17	12	12

Species	Collection	Voucher code	Sex	TL	Mb C	tC	Mb W	tW	tL	SL	SW	HL-SL	HL-P	HH 1-P	HW	MW	IL-M	IL-ST	E	E-N	E-ST	E-SL	RH	E-E	N-N	V	D	SC-L	SC-R
U. liura	ALB	208	M	208	18	17	5.6	4.7	9.4	1.3	1.3	4.9	5.1	3.1	3.9	3.4	3.3	4.1	NA	1.7	3.8	1.1	2.2	2.7	1.4	187	17	12	12
U. liura	ALB	194	?	253	21	20	6.5	5.2	8.7	1.7	1.7	5.8	5.9	3.5	3.8	3.4	4.1	4.9	0.5	1.8	2.9	1.2	2.2	2.8	1.4	193	17	8	8
U. liura	ALB	186	?	234	23	21	6.9	6	10.9	1.7	1.4	5.9	5.8	4	4.5	3.8	4	5	NA	1.9	3.2	1.2	2.3	3.1	1.7	185	17	11	11
U. liura	ALB	ALB no tag	?	274	24	21	7.8	5.9	7.6	2	2	6.4	6.1	3.7	4.4	3.6	4.3	5.3	0.4	1.9	3	1.2	2.2	2.9	1.5	198	17	9	9
U. liura	ALB	210	?	248	22	21	6.2	5.8	7.3	1.6	1.5	5.6	5.6	3.7	4.3	3.5	3.9	4.7	0.4	1.6	2.7	1.2	1.9	2.7	1.3	194	17	8	8
U. liura	ALB	205	F	236	21	20	6.7	5.7	7.7	1.5	1.4	5.5	5.4	3.3	3.7	3	4	4.6	0.5	1.7	2.7	1.1	2	2.8	1.3	195	17	9	9
U. liura	ALB	195	?	241	20	19	5.4	5.3	8.2	1.3	1.5	5.4	5.5	3.1	3.6	3	3.7	4.6	0.5	1.6	2.7	1.1	1.9	2.7	1.3	201	17	9	9
U. liura	ALB	209	?	251	21	19	6.7	6.6	11.4	1.7	1.3	5.8	5.7	3.5	4.4	3.5	3.9	4.8	0.4	1.8	3	1.1	2.1	2.8	1.3	185	17	13	12
U. macrolepis	MNHN	1897.26	?	162	22	19	6.3	5.2	7	1	2.1	6.5	6.2	3.9	4.4	3.6	4.7	5.7	0.8	2	3.1	1	2.2	3.6	1.5	132	15	9	9
U. macrolepis	MCZ	28644	F	183	21	20	6.2	5.8	7.7	1.3	2.3	7	6.8	3.7	4.6	3.8	5	6	0.7	2.2	3.2	1.1	2.4	3.6	1.6	136	15	8	9
U. macrolepis	BMNH	97.10.9.1-3 a	F	201	22	19	6.5	5.7	9.3	1.3	2.3	7.1	6.9	4	4.6	3.9	5	5.7	0.6	2.1	3.2	1.2	2.4	3.6	1.7	136	15	9	8
U. macrolepis	BMNH	97.10.9.1-3 b	F	215	27	23	8.8	7.1	9.8	1.2	2.6	7.8	7.3	5.2	5.7	4.9	5.6	6.3	0.8	2.4	3.5	1.4	2.9	4.1	1.8	132	15	8	8
U. macrolepis	BMNH	1946.1.15.99	F	260	30	27	9.7	8	13.4	1.6	3.4	9.6	9.1	5.4	6.2	5.4	6.9	7.8	0.6	2.8	4.3	1.6	3.1	4.4	2	130	15	8	8
U. macrolepis	BMNH	97.7.19.6	?	217	18	19	6.9	5.9	14	1.6	2.9	8.3	7.1	5.3	4.9	4.5	5.5	6.8	0.8	2.4	3.6	1.1	2.6	3.8	1.8	134	15	13	12
U. macrolepis	BMNH	97.7.19.7	?	273	25	23	8.1	6.9	11.9	1.6	3.1	8.7	8.6	5.3	5.8	5.1	6.7	7.6	0.9	2.5	3.9	1.4	2.9	4.4	2.1	138	15	9	9
U. macrolepis	BNHS	3221	?	176	21	19	6.4	5.9	7	1.3	1.9	6.9	6.3	4.1	4.3	3.5	4.7	5.4	0.8	2.1	3.1	1.1	2.3	3.4	1.5	130	15	9	9
U. macrolepis	BNHS	3511	?	321	42	32	13.1	9.8	15	2.5	5.7	13	12.5	10.3	9.7	8.9	9.1	10	1.3	3.6	5.5	2.1	4.1	6.4	3.1	130	15	10	10
U. macrolepis	BNHS	179	M	230	27	23	7.3	6.4	16.3	1.7	2.7	9	8.7	5.2	5.8	5.1	6.6	7.4	1	2.6	4	1.4	2.8	4.6	2	126	15	11	12
U. macrolepis	BNHS	180	M	244	26	23	8.1	7.4	16.7	1.8	3.2	10.1	9.2	5.6	6.2	5.3	6.8	8.2	1.1	2.9	4.3	1.4	3.2	5	2.4	125	15	12	11
U. macrolepis	BNHS	3104	?	322	40	33	13.7	10.3	15.5	2.2	4.3	10.6	10.1	6.2	6.9	6	7.4	8.4	1	3.1	4.8	1.7	3.3	5.1	2.4	140	15	9	9
U. macrolepis	BNHS	181	M	243	27	23	8.1	6.5	16.3	1.6	2.8	9.4	8.8	6.2	6.6	5.8	6.8	7.7	1	2.7	4.3	1.6	3	4.9	2.1	130	15	12	12
U. macrolepis	BNHS	3167	M	298	37	33	12.1	10.1	11	2.2	4.4	10.1	9.2	7	7.7	6.4	7.1	7.6	1.1	2.8	4.5	1.5	3.3	4.9	2.5	129	15	10	9
U. macrolepis	IISER-TVM	VPUM1015069	F	290	31	31	10.6	9.7	12.5	1.9	4.6	10.3	9.5	6.4	7.1	6.2	7.1	8.3	0.8	2.9	4.6	1.7	3.2	4.8	2.4	129	15	9	9
U. macrolepis	IISER-TVM	VPUM1015070	M	234	26	23	8.2	7.6	12	1.7	3.1	8.4	7.8	4.8	6.5	5.5	6.4	7	0.6	2.6	3.9	1.4	2.8	3.9	2	127	15	10	10

Species	Collection	Voucher code	Sex	TL	Mb C	tC	Mb W	tW	tL	SL	SW	HL-SL	HL-P	HH 1-P	HW	MW	IL-M	IL-ST	E	E-N	E-ST	E-SL	RH	E-E	N-N	V	D	SC-L	SC-R
U. macrolepis	IISER-TVM	VPUM1015071/72a	M	258	29	24	9.1	7.2	17.9	1.9	3.7	8.9	8.3	6.8	5.7	5.4	6.1	7.5	0.9	2.7	3.9	1.2	2.7	4.3	2	129	15	11	12
U. macrolepis	IISER-TVM	VPUM1015071/72b	M	278	27	25	8.5	7.6	17.4	2	3.8	9.7	9.3	6.8	6.5	5.6	7	8.3	1	3	4.3	1.2	3	4.7	2.2	127	15	11	11
U. macrolepis mahableshwarensis	BMNH	1958.14.62	M	254	28	23	8.8	7.2	17.2	1.8	3.2	9	8.8	6	5.5	4.7	6.4	7.4	1	2.8	4.2	1.4	2.9	4.3	2.2	127	15	12	12
U. macrolepis mahableshwarensis	BMNH	1958.14.63	M	242	27	24	8.8	7.4	17.2	2.1	2.5	8	7.5	5	5.8	5	5.9	6.5	0.8	2.2	3.5	1.3	2.9	4.3	1.9	126	15	13	13
U. macrolepis mahableshwarensis	BMNH	1958.14.64	M	231	27	24	9.2	7.8	16.5	1.6	3	9	8.3	4.9	5.9	4.8	6.4	7.5	0.8	2.6	4.2	1.2	2.8	4.8	2	123	15	11	12
U. macrolepis mahableshwarensis	BNHS	177	?	226	24	22	7.9	7	12	2	2.5	9	8.6	5.2	5.7	4.6	6.1	7.2	0.8	2.7	4.2	1.5	2.9	4.6	1.9	125	15	12	13
U. macrolepis mahableshwarensis	BNHS	Mah	M	278	28	27	9.3	8.1	18.5	2.1	3.2	9.4	8.6	5.5	6.7	5.6	6.6	7.6	1	2.7	4	1.6	3.2	4.8	2.2	127	15	11	12
U. macrorhyncha	MHNG	845.13	F	386	36	34	9.9	9.3	9.4	3.2	4.1	8.5	7.9	5.2	5.8	4.3	5.2	7	0.5	2.5	4.6	1.3	2.6	3.4	1.8	204	17	7	7
U. macrorhyncha	NHM	1946.9.7.45	F	551	48	42	13.8	10.1	15.6	5.6	6.1	11.5	10.6	5.6	6.6	5.2	6.8	9.9	0.5	3	6.1	1.6	3.8	4.2	2.2	214	17	6	5
U. macrorhyncha	CAS	39625	?	414	26	24	8.9	7.5	12.2	3.2	3.4	8.5	7.8	4.8	5.6	4.5	5.2	7.3	0.4	2.7	4.8	1.5	3	3.4	1.7	203	17	7	7
U. maculata	MNHN	1895.81	M	351	30	28	10.1	8	17.6	2.3	1.8	9	8.9	5.7	6.8	5.6	6.6	7.5	0.7	2.7	4.2	1.5	3.2	4.6	2.1	159	17	12	11
U. maculata	MNHN	1895.81 [a] no tag	F	245	22	17	6.5	5	8.4	1.9	1.7	6.4	6.3	4.2	5	4.2	4.6	5.3	0.5	1.9	3.1	1.2	2.5	3.4	2.4	171	17	8	7
U. maculata	MNHN	1897.250.	?	333	31	28	9.2	7.6	16.2	1.9	1.9	8.8	8.5	5.9	6.5	5.6	5.8	7.3	0.7	2.7	4.6	1.8	3.4	4.9	2.4	163	17	12	12
U. maculata	ZMB	10344(a)	M	362	35	31	10.7	8.1	21.1	2.5	2	9.9	9.6	6.7	6.8	6.2	6.9	8.1	1	2.9	4.8	1.7	3.8	5.5	2.4	157	17	13	13
U. maculata	ZMB	10344(b)	M	186	20	18	5.8	4	10.1	1.3	1.2	6	6.2	4	4.6	3.7	4	5.1	0.6	1.9	2.9	1.1	2.3	3.4	1.7	154	17	12	11
U. maculata	CAS	244457	F	302	29	24	9.2	7.6	11.8	1.9	1.7	6.9	6.8	4.4	4.9	4.2	4.7	5.6	0.6	2.2	3.5	1.3	2.6	3.7	1.8	165	17	8	8
U. maculata	CAS	244459	F	299	29	26	9.3	8	11.1	2.1	2.1	7.3	7.2	5.1	5.8	4.4	4.9	5.9	0.6	2.2	3.6	1.4	2.7	3.7	1.8	164	17	7	7
U. maculata	CAS	244458	F	347	20	27	10.1	8	13.7	2.5	2.2	8	7.8	5.8	6	5.4	5.6	6.6	0.6	2.5	3.8	1.6	3.1	4.1	2.1	163	17	8	7
U. maculata	CAS	244463	M	282	32	27	9.1	8.2	18.1	1.8	1.7	7.5	7.3	5.2	5.9	5	5.1	6	0.6	2.2	3.3	1.4	2.9	3.8	1.9	161	17	12	12
U. maculata	BMNH	1946.1.16.83	M	194	18	16	5.7	4.2	10.5	1.4	1.3	5.8	5.9	3.8	4.3	3.6	4.1	4.8	0.5	1.7	2.8	1.1	2.3	3.1	1.4	154	17	11	11
U. maculata	BMNH	1946.1.16.84	M	352	32	26	10.5	8	20.6	2.2	2.1	9.3	9.3	6.4	6.7	6.1	6.5	7.9	0.6	3.1	4.7	1.7	3.6	4.6	2.3	155	17	13	13
U. maculata	BMNH	1946.1.16.63	M	379	35	30	10.6	8.5	19.9	2.6	2	9.8	9.5	6.2	6.9	6	6.8	7.8	0.7	3.1	4.8	1.8	3.8	4.9	2.6	158	17	11	12
U. maculata	BMNH	1946.1.16.64	F	308	32	26	9.8	8.1	12.2	1.9	2.2	8.4	8.5	6.6	6.8	5.6	6	6.9	NA	2.8	4.2	1.6	3.3	4.5	2.3	164	17	9	8

Species	Collection	Voucher code	Sex	TL	Mb C	tC	Mb W	tW	tL	SL	SW	HL-SL	HL-P	HH 1-P	HW	MW	IL-M	IL-ST	E	E-N	E-ST	E-SL	RH	E-E	N-N	V	D	SC-L	SC-R
U. maculata	BMNH	1946.1.16.65	M	269	25	23	8	6.1	14.2	2	1.7	7.6	7.3	5.4	6	5.2	5.3	6.3	0.7	2.3	3.7	1.5	3	4.2	2.2	154	17	11	12
U. madurensis	MNHN	1895.101[a]	?	233	25	21	7.6	6.1	10.5	1.4	2.2	7.1	7	4.6	4.8	4.1	4.9	5.9	0.6	2	3.4	1.2	2.3	3.8	1.7	142	17	8	9
U. madurensis	MNHN	1895.101[b]	?	225	25	23	7.9	6.4	8.4	1.7	2.1	6.9	6.5	4.7	4.8	3.9	4.8	5.6	0.6	1.9	3.1	1.1	2.4	3.6	1.7	147	17	8	8
U. madurensis	USNM	257684	?	312	40	29	12.7	9.2	10.9	2.2	3.5	12.3	11.8	7.7	8.9	7.8	9.1	10.6	1.1	3.7	5.6	2.3	4.1	5.3	2.7	144	17	7	7
U. madurensis	USNM	257685	?	249	25	22	8	5.7	11	1.7	2.3	8.6	8	5.7	5.5	4.9	6.3	7.4	0.9	2.6	4	1.4	3	4.3	1.9	144	17	8	9
U. madurensis	MCZ	22389	?	284	26	22	8.1	6.4	14	2.8	1.9	8.8	8.4	4.6	5.7	5.1	6.1	6.9	0.7	2.5	3.7	1.3	2.7	4.1	1.8	152	17	9	8
U. madurensis	CAS	244446	?	274	32	29	9.5	7.9	13.7	1.9	3.1	8	7.6	5.6	5.4	4.8	5.1	6.5	NA	2.3	4.1	1.4	2.9	4.1	2.3	149	17	8	8
U. madurensis	CAS	244469	?	199	22	18	6.5	5.2	10.1	1.4	2.4	6.2	6.1	3.9	3.9	3.4	4.1	4.9	0.6	1.7	2.7	1.1	2.2	3.1	1.4	145	17	9	9
U. madurensis	CAS	244470	?	258	29	26	10.11	8.5	11.9	2.3	3.5	7.5	7.3	5.1	6	4.7	5.3	6.4	0.8	2.2	3.5	1.3	2.4	3.5	1.8	151	17	8	8
U. madurensis	CAS	244471	?	253	25	23	9.4	7	11.4	2.1	3	7.4	7.1	5.2	5.6	5.4	5.2	5.9	NA	2	3.3	1.2	2.5	3.8	1.6	152	17	7	7
U. madurensis	CAS	244435	?	271	28	25	8.9	8	12.1	2.2	3.8	7.9	7.4	4.6	5.2	4.5	5.3	6.4	0.7	2.1	3.7	1.3	2.7	3.8	2	148	17	7	7
U. madurensis	CAS	244433	?	264	29	21	9.3	6.6	12.6	2	3.1	7.9	7.4	4.5	5.5	4.1	5.2	6.3	0.7	2.3	3.5	1.3	2.4	3.5	1.9	146	17	8	8
U. madurensis	CAS	244434	?	265	27	21	8.7	6.7	14.4	1.6	3.1	7.9	7.4	4.4	5.3	4.3	5.4	6.4	0.7	2.3	3.7	1.3	2.6	3.8	1.8	149	17	9	9
U. madurensis	UK MW	2477	?	282	29	25	9.4	7.3	11.3	2.1	3.1	7.8	7.2	4.7	4.8	4	5.5	6.5	0.6	2.1	3.5	1.3	2.5	3.6	1.9	152	17	8	8
U. madurensis	UK MW	2499	?	292	31	27	9.8	8.2	10.3	2.9	3.4	7.4	7.3	4.9	5.1	4.3	5.1	6	0.6	2.2	3.6	1.2	2.6	3.6	1.9	155	17	7	7
U. madurensis	IISER-TVM	VPUM0515036	M	242	23	20	7.2	5.8	10.9	1.5	2.3	8.1	7.9	4.5	4.9	4	5.8	6.6	0.7	2.2	3.6	1.5	2.7	3.7	1.8	142	17	8	8
U. madurensis	IISER-TVM	VPUM1014024	F	290	27	25	8.7	7.7	12	1.9	3.8	7.8	7.5	4.9	4.8	4.3	5.5	6.5	0.5	2.1	3.5	1.5	2.8	3.5	1.8	153	17	8	8
U. madurensis	IISER-TVM	VPUS0915050	M	205	17	15	6.1	4.2	9.4	1.4	1.9	6.6	6.5	3.7	3.7	3.4	4.8	5.6	0.6	1.8	3.1	1.2	2.2	3.2	1.7	151	17	10	9
U. myhendrae	MNHN	1897.0255	?	364	34	28	9.6	8.2	13	2.3	4.1	12	11	6.5	7.3	6.1	8.3	10.1	1	3.3	5.4	1.8	3.5	5.2	2.6	148	17	7	7
U. myhendrae	MNHN	1895.95	?	182	21	19	6.7	5.4	8.6	1.4	2.3	7.4	7.2	4.3	4.9	4.3	5.5	6.5	0.7	2.1	3.7	1.3	2.5	3.6	1.9	145	17	9	9
U. myhendrae	BMNH	1946.1.16.9	F	337	35	32	11.4	9.6	13.5	2.4	5.1	11.1	10.7	6.7	7	6	8	9.3	0.7	3.3	5.5	1.9	3.7	5.1	2.6	140	17	7	7
U. myhendrae	BMNH	93.4.18.8	F	352	32	29	9.8	8.8	13.7	1.9	4.4	10.7	10.2	6.4	7	6.3	7.4	8.8	0.7	3	5.4	1.8	3.7	4.6	2.6	151	17	7	8
U. myhendrae	BMNH	1914.1.26.1	F	295	26	26	8.3	7.4	11.8	1.8	4.2	10.6	10.4	6.1	6.8	6.1	7.8	9.5	0.7	2.9	5.2	1.6	3.3	4.5	2.3	149	17	7	7
U. myhendrae	BMNH	1914.1.26.2	F	137	15	15	4.5	4.5	7	1.2	2.3	6.9	6.9	4.2	4.7	4.3	4.9	6	0.6	1.9	3.3	1.1	2.3	3.4	1.8	149	17	8	8

Species	Collection	Voucher code	Sex	TL	Mb C	tC	Mb W	tW	tL	SL	SW	HL-SL	HL-P	HH 1-P	HW	MW	IL-M	IL-ST	E	E-N	E-ST	E-SL	RH	E-E	N-N	V	D	SC-L	SC-R
U. myhendrae	BMNH	97.7.19.4	F	543	56	44	17.1	15.7	20.3	4.3	7.7	15.8	14.9	10.4	10.9	9.9	11.3	13.3	1	4.3	7.7	2.7	5.5	6.6	3.8	153	17	6	6
U. myhendrae	IISER-TVM	VPUM0616080	F	469	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	153	NA	8	8
U. myhendrae	IISER-TVM	1015057	?	411	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	148	17	9	9
U. myhendrae	IISER-TVM	1115074	M	390	41	40	12.4	11.9	15	2.4	5.2	13.4	12.7	7.5	9.1	NA	9.3	13.1	0.7	3.4	6.4	1.9	3.8	5.6	2.4	150	17	9	9
U. myhendrae	IISER-TVM	618087	F	400	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	159	17	8	8
U. nilgherriensis	MNHN	1895.99	?	333	39	36	12.5	10.6	12.9	1.9	4.9	11.2	10.5	7.4	7.3	6.6	8.7	9.6	1.1	3.4	4.7	1.8	3.5	5.3	2.2	135	17	10	10
U. nilgherriensis	ZMB	5541	?	316	34	33	10.7	8.5	13.3	2.1	4.5	10.4	9.8	6.5	7	5.5	7.3	8.7	0.9	2.8	4.1	1.8	3	4.6	1.8	142	17	9	9
U. nilgherriensis	CAS	39631	?	251	31	26	11.2	8.6	11.2	1.7	3.7	9	8.4	5.4	6.2	5.6	6.4	7.3	0.8	2.8	3.9	1.5	2.9	4.3	1.6	144	17	8	9
U. nilgherriensis	BMNH	1946.1.16.41	M	424	36	28	13.5	9	16.4	2.3	4.6	12.4	11.2	7.1	8.9	7.9	9	9.7	0.8	3.9	5.2	2	3.7	5.4	2.1	139	17	10	11
U. nilgherriensis	IISER-TVM	VPUC1113011	M	440	52	38	16.9	11.3	20	2.2	4.8	15.3	13.9	9.9	11.1	9.7	11.7	12.8	1.2	4.4	6.4	2.5	4.6	6.2	2.4	140	17	10	10
U. nitida	MNHN	1895.87[a]	M	270	26	22	6.9	5.7	13	2.6	2.9	6.7	6.4	3.7	4.3	3.5	4.5	5.3	0.5	1.8	3.2	1	2.2	3.1	1.5	196	17	10	10
U. nitida	BMNH	1946.1.13.96	F	291	30	28	9.3	8.2	9.1	2.9	2.9	6.8	6.3	3.8	4.2	3.5	4.7	5.9	0.5	1.9	3.3	1.2	2.3	3.3	1.5	189	17	6	7
U. nitida	BMNH	1946.1.13.95	F	345	32	28	8.8	7.5	11.7	3.6	3.8	7.7	7.2	4.4	4.7	3.9	5.3	6.5	0.5	2.2	3.8	1.3	2.4	3.6	1.6	186	17	7	6
U. nitida	BMNH	1946.1.13.97	F	246	22	20	6.9	5.8	6.9	2.5	2.8	6.2	6.2	3.4	3.9	3.2	4.5	5.5	0.5	1.8	3	1.1	2.1	3	1.4	190	17	5	6
U. nitida	BMNH	1946.1.16.30	M	299	26	22	8.9	6.2	15.8	2.8	3	7	6.6	3.8	4.4	3.9	5	6	0.5	1.9	3.4	1.3	2.4	3.4	1.5	196	17	11	11
U. nitida	BMNH	1946.1.16.31	M	287	26	24	8	6.4	15.5	3.1	3	6.7	6.7	3.9	4.8	4	4.4	5.5	0.5	1.9	3.3	1	2.2	3.3	1.5	191	17	10	11
U. nitida	ZMB	10351	M	241	26	22	8.4	6.4	13.7	2.2	2.5	6.3	6.1	3.8	4.4	3.8	4.4	5.2	0.5	1.8	3	1.1	2.2	3.1	1.5	182	17	10	10
U. ocellata	NHM	1946.1.15.59	F	358	30	27	9	7.5	10.5	3	3.5	8.5	8.5	5	5.5	4.6	6	7.1	0.5	2.6	4	1.4	2.9	3.6	1.8	201	17	8	8
U. ocellata	ZMB	5543a	M	289	26	24	8.4	6.6	12.4	2.3	2.7	7.2	7.2	4.8	4.9	4.1	4.8	6.1	0.5	2.2	3.6	1.5	2.7	3.4	1.6	194	17	10	10
U. ocellata	MCZ	47288	M	294	25	22	7.1	6.3	13	2.4	2.6	6.9	7	5.1	5.9	5.1	5	5.9	0.5	2.3	5.6	1.5	2.8	3.7	1.8	198	17	11	11
U. ocellata	MCZ	3884(18921)	M	303	27	23	8.2	6.2	14.2	2.8	2.5	7.3	7	4.2	5	4.3	4.8	6.1	0.5	2.2	3.6	1.3	2.5	3.3	1.5	196	17	10	10
U. ocellata	MCZ	3873	M	319	27	25	7.8	6.9	13.5	2.5	2.7	7.7	7.5	5	5.4	4.5	5	6.4	0.6	2.4	3.8	1.4	2.7	3.6	1.8	193	17	10	10
U. ocellata	MCZ	47289	F	243	23	21	6.8	6.1	8.9	2.6	2.7	5.6	5.6	3.6	3.9	3.5	3.9	4.8	0.4	1.7	2.6	1.1	2.1	2.6	1.3	201	17	8	8
U. ocellata	AMNH	77608	?	255	21	20	6.1	5.3	9.6	2.2	2.5	6.3	6.7	3.9	4	3.4	4.3	5.3	0.4	1.8	3.2	1.1	2.2	2.8	1.4	199	17	9	9

Species	Collection	Voucher code	Sex	TL	Mb C	tC	Mb W	tW	tL	SL	SW	HL-SL	HL-P	HH 1-P	HW	MW	IL-M	IL-ST	E	E-N	E-ST	E-SL	RH	E-E	N-N	V	D	SC-L	SC-R
U. petersi	MNHN	1895.80[a]	M	165	19	17	5.5	4.9	5.6	1.8	1.7	4.9	5	3	3.5	2.9	3.2	4.2	0.4	1.6	2.5	1	1.7	2.4	1.1	161	17	6	6
U. petersi	MNHN	1895.80[b]	?	159	18	17	5.1	4.3	5.6	1.7	1.5	4.5	4.7	2.9	3.3	2.5	3.1	3.8	0.4	1.4	2.3	0.9	1.6	2.3	1	159	17	6	6
U. petersi	MCZ	6201	M	187	22	19	6.8	5.3	11.2	1.7	1.5	5.5	5.5	3.8	4.1	3.5	3.7	4.4	0.4	1.8	2.6	1.2	1.9	2.8	1.2	157	17	10	10
U. petersi	MCZ	6201.3	F	170	19	17	5.4	4.8	5.6	1.8	1.7	4.8	4.9	3.6	3.8	3.1	3.2	4	0.4	1.5	2.3	1	1.8	2.6	1.2	162	17	6	5
U. petersi	MCZ	string but no tag (jar 6201)	F	171	20	17	5.9	4.7	6.4	1.7	1.4	4.9	5	3.2	3.5	3	3.3	4	0.4	1.6	2.5	1	1.8	2.5	1.1	160	17	5	6
U. petersi	MCZ	no string or tag (jar 6201)	F	176	22	18	6.1	5	6.5	1.8	1.7	4.9	4.9	3.4	3.5	3	3.4	4.2	0.4	1.6	2.4	1	1.7	2.4	1.1	159	17	6	6
U. petersi	BMNH	1946.1.17.7	?	180	17	16	5.9	5	6.1	2	1.5	4.8	4.9	2.8	3.3	2.6	3.2	3.8	0.3	1.6	2.4	0.9	1.6	2.2	1.1	163	17	6	5
U. petersi	BMNH	1946.1.17.9	?	149	14	13	4.3	3.5	8.1	1.7	1.3	4.5	4.7	3.3	2.9	2.4	3.3	3.7	0.3	1.4	2.3	0.9	1.6	2.2	1.1	156	17	10	10
U. phipsonii	MNHN	1895.93[a]	?	272	28	25	8.2	7.5	10.8	2.2	3.7	6.8	6.6	4.1	4.6	3.7	4.8	5.5	0.6	2.1	3.3	1	2.3	3.5	1.6	148	17	9	8
U. phipsonii	MNHN	1895.93[b]	?	186	21	18	6.4	5	8.4	1.7	2.5	6.4	6.5	3.7	4.1	3.3	4.2	5.3	0.6	1.9	3.1	1.1	2.2	3.3	1.4	143	17	7	7
U. phipsonii	MNHN	1897.254	?	233	23	22	7.1	5.9	10.8	1.7	2.8	6.3	6.2	3.5	4.3	3.4	4.2	5.4	0.6	1.8	3.1	0.9	2	3.3	1.4	151	17	8	8
U. phipsonii	MCZ	22381	F	272	26	23	7.1	6.6	10.3	2.2	3.6	6.5	6.4	4.2	4.8	4	4.7	5.6	0.7	2	3.1	1.1	2.3	3.5	1.5	151	17	8	8
U. phipsonii	AMNH	R46309	?	228	23	22	7.7	6.5	13.9	2.3	2.8	7.4	6.9	4.5	4.9	4.2	5.4	6.4	0.7	2.3	3.5	1.3	2.5	3.5	1.7	145	17	11	11
U. phipsonii	AMNH	46309	?	223	22	22	7.1	6.5	13.1	2	2.7	7.3	6.9	4.5	4.8	4.3	5.5	6.4	0.7	2.2	3.4	1.2	2.5	3.6	1.6	145	17	11	12
U. phipsonii	AMNH	46308	?	145	12	11	4.1	3.1	8	1.3	1.6	5.3	5.2	3.5	3.2	2.9	3.8	4.7	0.6	1.6	2.5	0.8	1.8	2.7	1.2	146	17	11	11
U. phipsonii	BMNH	1946.1.16.33	F	221	28	23	8.9	6.6	11.9	2	2.2	6.7	6.3	4	4.6	3.8	4.8	5.5	0.6	2.1	3.1	1	2.2	3.3	1.4	143	17	11	12
U. phipsonii	BMNH	1946.1.16.34	F	274	30	24	8.2	7	14.1	3.2	3.5	8.2	7.3	4.8	5.3	4.7	5.8	7	0.7	2.3	3.6	1.1	2.7	3.8	1.7	146	17	11	11
U. phipsonii	BMNH	1956.1.12.54	F	297	33	27	10.3	8.5	16.2	2.4	3.1	8.3	7.6	4.9	4.8	4.2	5.9	7	0.6	2.4	3.9	1.4	2.8	3.5	2.1	146	17	11	11
U. phipsonii	BMNH	60.3.19.1213	F	279	27	24	8.2	7.2	14.6	2.6	3.1	7.6	7.2	4.7	4.8	4.1	5.5	6.2	0.6	2.2	3.5	1.3	2.6	3.6	1.6	148	17	11	11
U. phipsonii	BNHS	228	?	194	21	20	6.9	5.7	9.1	1.8	2.4	5.5	5.7	3.6	3.7	3.2	3.7	4.6	0.5	1.7	2.7	1.1	1.8	2.8	1.3	149	17	8	8
U. phipsonii	BNHS	231	?	266	21	18	6.7	7.1	14.8	1.9	2.8	8.2	7.8	4.3	4.7	3.9	5.3	6.9	0.6	2.6	3.8	1.1	2.4	3.3	1.8	147	17	11	11
U. phipsonii	BNHS	233	?	234	25	26	7.8	7.7	10.9	2.6	2.9	7.6	7	5.5	5.3	4.9	5.4	6.4	0.7	2.3	3.5	1.4	2.6	3.7	1.8	146	17	11	11
U. phipsonii	BNHS	234	?	238	22	21	7.5	6	12.9	1.8	2.3	7.1	6.7	4.3	4.9	4.3	5	5.8	0.6	2.1	3.3	1.2	2.5	3.6	1.7	143	17	11	11
U. phipsonii	BNHS	232	?	298	24	23	8.2	6.4	13.2	2.1	3.1	7.3	6.9	4.2	4.2	3.4	5.1	6	0.6	2.3	3.4	1.2	2.4	3.1	1.7	138	17	10	11

Species	Collection	Voucher code	Sex	TL	Mb C	tC	Mb W	tW	tL	SL	SW	HL-SL	HL-P	HH 1-P	HW	MW	IL-M	IL-ST	E	E-N	E-ST	E-SL	RH	E-E	N-N	V	D	SC-L	SC-R
U. phipsonii	BNHS	235	?	228	19	19	6.3	5.5	10.5	1.8	2.9	6.1	6	3.8	4.1	3.6	3.8	4.9	0.5	1.8	3	1.1	1.9	3.1	1.4	138	17	8	8
U. phipsonii	BNHS	Pan	F	185	18	18	5.5	5.2	9.8	1.8	1.9	5.7	5.4	3.1	4	3.4	4.1	4.8	0.5	1.7	2.7	1	2.1	2.9	1.4	145	17	10	11
U. pulneyensis	MNHN	1895.78	?	356	35	29	11	8.6	17.5	2	1.8	9.2	9	6.5	6.5	5.3	6.3	7.8	0.7	2.9	4.5	1.6	3.3	4.5	2.2	175	17	12	11
U. pulneyensis	MNHN	1946.44	?	244	21	21	6.7	6.2	13.2	2.1	1.9	6.1	6.2	4	4.4	3.4	4	5	0.6	1.7	2.9	1.2	2.1	3.2	1.6	166	17	11	11
U. pulneyensis	MNHN	1946.46	?	218	20	18	5.8	5.1	7.3	1.6	1.6	5.6	5.5	3.7	4	3.3	3.8	4.7	0.5	1.8	2.6	1.1	2	3	1.3	177	17	9	9
U. pulneyensis	MNHN	1946.47	?	238	24	21	6.5	5.4	7.8	1.8	1.9	6.3	6.4	4	4.5	3.6	4.2	4.8	0.6	1.9	3	1.1	2.3	3.2	1.5	177	17	7	8
U. pulneyensis	MNHN	1946.268	?	250	21	18	6.5	5.1	13.4	1.8	1.8	6.4	6.3	3.9	4.5	3.5	4.2	4.9	0.6	1.9	3.1	1.1	2.3	3.4	1.6	162	17	12	12
U. pulneyensis	MNHN	1946.269	?	247	23	21	6.8	6	8.2	1.7	1.8	6.1	6.2	4.2	4.7	4.2	4.1	5	0.5	1.9	3.2	1.1	2.2	3.2	1.6	169	17	8	8
U. pulneyensis	MNHN	1948.253	?	239	NA	NA	NA	NA	7.9	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	179	17	7	8
U. pulneyensis	MNHN	1948.255	?	244	NA	NA	NA	NA	8.8	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	181	17	9	9
U. pulneyensis	MNHN	1948.256	?	187	NA	NA	NA	NA	10.9	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	167	17	13	14
U. pulneyensis	MNHN	1994.751	?	190	NA	NA	NA	NA	7.5	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	169	17	8	8
U. pulneyensis	MNHN	1994.752	?	252	NA	NA	NA	NA	8.1	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	180	17	8	8
U. pulneyensis	MNHN	1994.753	?	149	17	15	4.4	3.6	7.6	1.2	1.3	4.5	4.5	3.3	3.5	2.9	3.1	3.8	0.4	1.4	2.3	0.8	1.8	2.6	1.3	173	17	11	12
U. pulneyensis	MNHN	1994.754	?	239	NA	NA	NA	NA	12.5	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	156	17	11	11
U. pulneyensis	MNHN	1994.757	?	256	22	22	7.5	6.6	7.5	2	2.1	6.6	6.6	4.2	4.3	3.4	4.3	5.3	0.6	1.8	3.2	1	2.3	3.3	1.7	171	17	7	7
U. pulneyensis	MNHN	1994.758	?	204	NA	NA	NA	NA	7.4	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	174	17	7	8
U. pulneyensis	ZMB	10357	?	300	29	24	9.2	6.1	14.1	1.7	1.6	7.6	7.4	4.7	5.7	4.5	5.3	6.6	0.6	2.3	3.7	1.4	2.8	4	1.8	167	17	13	13
U. pulneyensis	ZMB	5538	?	231	23	22	7	5.9	8.2	2	1.7	5.8	5.9	3.9	4.2	3.4	4	4.8	0.5	1.8	2.9	1.1	2.2	2.9	1.5	177	17	7	7
U. pulneyensis	ZMB	5537	?	259	22	20	6.9	5.6	9.8	1.8	1.7	5.7	5.7	3.7	4.2	3.6	3.8	4.9	0.5	1.7	2.9	1	2.1	2.9	1.4	182	17	8	9
U. rubrolineata	MNHN	1895.94	?	374	30	28	10.2	7.9	11.2	2.1	3.4	10.3	9.9	5.3	6.1	5.6	7.5	8.8	0.8	3	4.7	1.7	3.2	4.6	2.2	170	17	8	7
U. rubrolineata	CAS	244347	?	391	36	28	12.9	7.4	12.7	1.9	3.9	13.1	12.2	6.6	8.2	7.5	9	10.5	0.8	3.7	5.9	2.3	4	4.8	2.8	150	17	7	7
U. rubrolineata	CAS	244377	?	351	36	28	9.7	8.8	13	2	4	11.7	10.7	6.3	7.6	6.7	8.9	10.2	0.9	3.2	5.3	2	3.9	5	2.5	152	17	8	8
U. rubrolineata	BMNH	1946.1.16.26	?	284	21	20	7.9	6.1	7.1	1.9	3.7	9.6	9.5	5.1	5.1	4.9	6.5	8.3	0.7	2.9	4.6	1.4	2.9	3.3	1.9	NA	15	NA	NA

Species	Collection	Voucher code	Sex	TL	Mb C	tC	Mb W	tW	tL	SL	SW	HL-SL	HL-P	HH 1-P	HW	MW	IL-M	IL-ST	E	E-N	E-ST	E-SL	RH	E-E	N-N	V	D	SC-L	SC-R
U. rubrolineata	BMNH	1946.1.15.63	?	176	18	16	5.8	4.8	6.3	1.4	2	6.3	6	3.9	4.2	3.9	4.7	5.2	0.5	1.9	3	1.2	2.3	3	1.6	166	17	7	6
U. rubrolineata	BMNH	1946.1.15.53	F	403	38	31	12.4	8.7	12.5	2.4	4.5	13	12.3	7.5	8.5	7.9	9.7	10.9	0.8	3.7	5.9	2.1	4.1	5.6	2.8	165	17	6	6
U. rubrolineata	IISER-TVM	VPUS0716090	M	258	23	21	7.3	6.1	9.9	1.6	2.7	9.3	8.8	5.1	6	5.3	6.7	7.7	0.7	2.6	4.2	1.7	3	4.2	2.1	149	17	8	9
U. rubromaculata	MNHN	1895.97	?	281	34	29	10.4	8.4	12.1	1.7	2.8	9.9	9.4	7	7.4	6.5	7.2	8.3	0.8	2.8	4.5	1.7	3.3	5.1	2	130	17	10	10
U. rubromaculata	MNHN	1897.257	?	355	40	36	12.4	10.7	12.5	2.4	4.3	11.3	10.6	7.1	7.9	6.6	7.8	9.2	1	3.1	5.1	1.8	3.6	5.5	2.6	137	17	8	8
U. rubromaculata	ZMB	10348	?	238	22	22	7	6.7	10.4	1.7	2.7	7.9	7.7	5.2	5.4	4.7	5.7	6.4	1	2.2	3.6	1.4	2.8	4.2	1.8	131	17	9	8
U. rubromaculata	MCZ	6199	M	285	33	26	10.4	8.6	14.4	3.3	1.9	9.5	9	6.3	6.7	5.9	6.5	7.5	0.8	2.6	4.3	1.7	3.3	4.6	2.3	133	17	10	9
U. rubromaculata	BMNH	1946.1.15.51	F	358	37	34	12.1	10.6	13.7	2.1	3.8	12.9	12.4	10	10.5	9.4	9.6	10.2	1.1	3.2	5.4	2.1	4.2	6.1	3	135	17	9	8
U. rubromaculata	BMNH	1946.1.15.52	F	371	33	32	10.7	9.7	16.2	2.5	4	12.9	12	6.5	8.8	7.3	9.4	10.5	0.9	3.8	5.9	1.9	3.9	5.9	2.9	130	17	8	8
U. rubromaculata	BMNH	1946.1.15.82	F	343	31	31	10.2	8.9	14.9	2.4	4.3	11.1	11.9	6.3	7.8	7	8.6	9.6	0.7	3.3	5.2	1.6	3.5	5.3	2.6	133	17	9	8
U. rubromaculata	BMNH	1946.1.15.83	M	339	34	29	10.7	8.9	17.7	2.4	3.7	12.3	11.8	6.7	7.9	7	8.6	10	0.8	3.4	5.5	1.9	4	5.7	2.7	131	17	10	9
U. rubromaculata	BMNH	1946.1.15.84	M	263	29	25	8.6	7.7	14.2	1.6	3.3	9.3	8.9	5.5	6.3	5.6	6.8	7.6	0.7	2.6	4.1	1.4	3	4.4	2.3	127	17	10	10
U. shorttii	MNHN	1895.0100.	?	287	32	32	10.2	9.8	10.5	2.3	4.1	10.6	9.8	5.7	7.3	6.4	8.1	9.1	1.1	3.2	4.7	1.7	3.3	5	2	128	17	8	8
U. shorttii	MNHN	1848.265	M	252	28	23	8.5	6.5	14.7	1.5	2.6	7.6	7.5	4.4	5.3	4.7	5.4	6.2	0.7	2.2	3.3	1.2	2.7	4.1	1.6	139	17	11	10
U. shorttii	MNHN	1848.266	?	194	22	20	7.4	5.9	10.7	1.3	2.5	6.4	6.1	4.1	4.6	3.9	4.7	5.4	0.6	1.8	2.7	1	2.3	3.5	1.2	139	17	11	9
U. shorttii	MNHN	1848.268	?	260	NA	NA	NA	NA	8.4	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	146	17	8	8
U. shorttii	MNHN	1848.269	?	115	NA	NA	NA	NA	5	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	147	17	9	9
U. shorttii	MNHN	1846.266	?	222	19	18	6.2	4.6	12.3	1.3	2.8	7.2	7.3	4.8	4.6	4	5.4	6.4	0.7	2	3	1.2	2.4	3.8	1.5	140	17	10	10
U. shorttii	MNHN	1846.267	?	221	22	19	7.1	5.1	11.9	1.3	2.4	7.5	7.1	4.3	4.6	4	5	5.9	0.6	2	3	1.1	2.5	3.7	1.4	142	17	10	9
U. shorttii	ZMB	10352	M	231	35	30	11	8.5	10.6	1.9	3.3	8.8	8.4	5.2	5.7	5	6.5	7.2	0.9	2.6	3.9	1.4	2.9	4.4	1.8	128	17	9	8
U. shorttii	ZMB	10354	?	335	38	33	11	10.2	14.9	2.2	4.1	10.5	10.2	6.3	6.8	6.1	8.3	9.1	1.2	3.1	4.8	1.8	3.3	5.1	2.4	136	17	8	8
U. shorttii	AMNH	43345	F	351	36	33	11.4	10.1	16.1	2.2	4.8	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	148	17	9	9
U. shorttii	AMNH	58527	M	339	37	33	10.6	10	17.2	3	5.1	9.8	9.4	6.6	5.8	5.2	6.9	7.9	1	2.8	4.2	1.5	3.1	4.5	2.2	146	17	9	8
U. shorttii	AMNH	58528	F	328	39	31	11.3	9.2	14.6	2.4	5.1	9.5	9.1	5.5	6.1	5.6	7.1	8	1	2.5	4	1.4	3.1	4.5	2.2	145	17	7	7

Species	Collection	Voucher code	Sex	TL	Mb C	tC	Mb W	tW	tL	SL	SW	HL-SL	HL-P	HH 1-P	HW	MW	IL-M	IL-ST	E	E-N	E-ST	E-SL	RH	E-E	N-N	V	D	SC-L	SC-R
U. shorttii	AMNH	58547	?	89	11	10	3.6	3.6	5.5	0.9	1.5	5.1	5.5	3.8	3.1	2.9	3.3	4.2	0.6	1.5	2.3	0.8	1.8	2.7	1.3	144	17	10	10
U. shorttii	AMNH	58548	?	92	12	10	4.3	3	5.5	0.8	1.4	5.1	5.3	2.9	3.2	2.6	3.5	4.3	0.5	1.5	2.4	0.8	1.7	2.6	1.3	140	17	10	9
U. shorttii	AMNH	58549	?	93	11	10	3.5	3.9	5.7	0.9	1.4	5	5.2	2.5	3.2	2.8	3.7	4.3	0.5	1.5	2.4	0.8	1.8	2.7	1.3	144	17	9	10
U. shorttii	AMNH	58550	?	91	12	11	3.5	2.8	5.7	0.8	1.6	5.2	5.2	2.4	3.4	2.8	3.8	4.3	0.5	1.4	2.3	0.8	1.7	2.7	1.2	143	17	10	9
U. shorttii	BMNH	1946.1.15.91	M	246	24	21	7.3	6.3	14.6	1.8	2.5	7.7	7.4	5.2	NA	NA	5.8	6.5	0.5	2.5	3.6	1.3	2.8	4	1.8	140	17	11	11
U. shorttii	BMNH	1946.1.15.92	M	235	23	19	7	5.7	14.5	1.4	2.7	7.8	7.3	5	5.2	4.5	5.5	6.2	0.5	2.4	3.4	1.3	2.8	3.8	1.7	142	17	10	10
U. shorttii	BMNH	1946.1.15.93	F	196	20	17	6.4	5.8	10.8	1.4	3	7	6.7	3.5	4.4	3.6	5.2	5.7	0.5	2	2.9	1	2.2	3.2	1.3	135	17	9	9
U. shorttii	BMNH	1946.1.15.94	F	315	38	30	11.4	9.9	15	2.5	4.1	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	147	NA	10	10
U. woodmasoni	MNHN	1895.77	?	255	28	22	8.7	6.2	12	2.1	1.8	6.4	6.1	4	4.1	3.3	3.8	5	0.5	2.1	3.4	1.1	2.3	3.1	1.4	173	19	10	10
U. woodmasoni	MNHN	1895.85[a]	M	219	28	22	8	6.3	9.8	1.9	1.6	6	5.9	3.8	4.2	3.4	3.9	5.2	0.5	1.9	3	1.1	1.9	2.9	1.4	163	19	9	10
U. woodmasoni	MNHN	1895.85[b]	F	193	20	19	6.5	5.4	5.1	1.7	1.7	5.4	5.3	3.4	3.8	3	3.5	4.5	0.4	1.6	2.8	0.9	1.8	2.6	1.2	178	19	6	7
U. woodmasoni	ZMB	10353	F	258	25	21	7.5	5.8	7.7	2.5	2.3	6.3	6.1	3.8	4.4	3.3	3.7	5.1	0.5	2.1	3.2	1.1	2.3	2.9	1.4	176	19	6	7
U. woodmasoni	USNM	129695	M	317	40	28	11.1	8.5	14.1	2.8	2.2	7.9	7.7	4.9	5.3	4.6	4.8	6.5	0.6	2.7	4.2	1.5	2.8	3.6	1.9	166	19	10	10
U. woodmasoni	USNM	129696	F	214	21	20	7.1	5.6	6.7	2.1	1.9	5.8	5.8	3.4	3.9	3.2	3.5	4.7	0.4	2.1	3.1	1	2	2.7	1.3	179	19	7	7
U. woodmasoni	MCZ	18040	M	212	22	19	6.6	5.3	8.6	1.9	1.6	5.8	5.7	3.5	3.6	3	3.4	4.6	0.4	1.8	3	1	2	2.7	1.2	168	19	9	10
U. woodmasoni	MCZ	18042	M	189	20	17	6.2	4.9	9.5	2	1.5	5.7	5.7	3.5	3.8	3.1	3.7	4.7	0.4	1.7	2.9	1	2	2.6	1.3	165	19	9	9
U. woodmasoni	MCZ	18039	F	162	18	16	5.3	4.6	5.7	1.8	1.8	4.6	4.7	2.8	3.2	2.6	3	3.8	0.4	1.5	2.5	0.8	1.7	2.3	1.1	179	19	6	6
U. woodmasoni	MCZ	18041	F	214	21	19	7	5.5	7.3	2.5	2.3	5.9	6.1	4.1	4.3	3.6	3.9	5	0.5	1.8	3.2	1.3	2.3	2.9	1.6	178	19	7	7
U. woodmasoni	BMNH	1946.1.15.57	M	287	32	24	10.8	6.7	13.2	2.4	2.1	7.5	7.1	4.4	5.3	4.2	4.8	5.9	0.5	2.3	3.7	1.4	2.8	3.6	1.5	167	19	9	10
U. woodmasoni	MW	3801	M	229	26	20	7.5	5.6	11.5	2.5	2.1	6.3	6	3.6	4.4	3.2	4	4.9	0.4	2	3.2	1.1	2.1	2.7	1.4	166	19	9	9

Appendix Table 4-2 Morphological character names, abbreviations, and descriptions.

Character	Abbreviation	Description
Total length	TL	Distance between anteriormost tip of rostral shield to posterior end of tail, measured gently but firmly straightening the specimen along a metric tape. Coiled specimens were measured by rolling them along a flat tape.
Midbody circumference	MbC	Distance measured around midbody, approximately halfway along the specimen length (depending on the preservation/condition of the specimen, some measurements were taken in an area slightly anterior or posterior of midbody)
Tail circumference	tC	Distance measured close to the anterior base of the tail, immediately anterior to the anal scales.
Midbody width	MbW	Distance measured approximately at midbody. See MbC.
Tail width	tW	Distance measured at the anterior base of the tail, immediately anterior to the anal scales.
Tail length	tL	Distance between vent (gently pressing over the anal scales covering the vent to find the opening) and posteriormost tip of the tail.
Terminal scute base length	SL	Maximum length of the base of the terminal scute.
Terminal scute base width	SW	Maximum width of the base of the terminal scute.
Head length 1	HL-SL	Distance measured from anteriormost tip of rostral to posteriormost edge of last supralabial shield.
Head length 2	HL-P	Distance between tip of rostral and posteriormost edge of parietal shield.
Head height	HH1.P	Vertical distance measured by a straight line between posterior end of parietal shields and the ventral surface of the body.
Head width	HW	Distance between posteriormost edges of last pair of supralabial shields.
Mouth width	MW	Distance between posteriormost edges of last pair of infralabial shields.
Lower jaw length 1	IL-M	Distance between posteriormost edge of last infralabial and anteriormost tip of mental shield.
Lower jaw length 2	IL-ST	Distance between posterior edge of last infralabial and tip of snout (tip of rostral shield)
Eye diameter	E	Distance measured around the eye

Character	Abbreviation	Description
Eye-naris distance	E-N	Shortest distance between eye and naris, measured between the anterior margin of eye and posterior margin of naris.
Eye-snout distance	E-ST	Shortest distance between anterior margin of eye and snout tip (tip of rostral shield)
Eye-supralabial distance	E-SL	Vertical distance measured by a straight line between centre of the eye and lower edge of third supralabial shield (immediately under the eye centre)
Anterior partial head height	RH	Distance between anterior end of frontal shield and bottom of posteriormost edge of second supralabial shield
Inter-ocular distance	E-E	Distance between centres of the eyes
Nares distance	N-N	Shortest distance between nares, measured between interior margins of nares
Ventral scales	V	Number of ventral scales including all midventral scales between the mental scale and the pair of anal scales, following Gower & Ablett (2006).
Subcaudal scales	SC	number of scales between vent and terminal scute of tail, counted on the left and right sides

Appendix Table 4-3 Standard PCA variable loadings, and variance explained by each axis.

	PC1	PC2	PC3	PC4	PC5	PC6	PC7	PC8	PC9	PC10	PC11	PC12	PC13	PC14	PC15	PC16	PC17	PC18
MbW	-0.245	0.058	0.569	-0.034	-0.146	-0.219	0.198	-0.126	0.095	-0.396	0.13	-0.008	0.448	-0.286	0.051	-0.128	0.056	0.004
tW	-0.209	0.291	0.486	0.029	-0.081	-0.141	0.02	-0.032	0.151	0.096	0.145	-0.191	-0.636	0.314	-0.007	0.117	0.002	-0.022
SL	0.038	0.495	-0.057	-0.003	-0.283	0.495	-0.223	-0.582	-0.049	-0.011	-0.079	-0.104	0.062	-0.116	-0.002	0.009	0.01	0.011
SW	-0.023	0.499	-0.025	0.259	-0.233	-0.291	-0.455	0.438	-0.113	0.031	-0.077	0.267	0.182	0.074	-0.022	-0.115	-0.049	0.001
HL2.P	-0.27	-0.078	-0.222	-0.235	-0.095	-0.097	-0.16	-0.049	0.08	-0.023	-0.046	-0.243	0.001	0.237	0.614	-0.505	0.108	-0.041
HH1.P	-0.271	0.088	0.099	0.096	0.056	0.195	0.185	0.185	-0.496	0.406	0.197	-0.117	0.198	-0.075	0.401	0.331	0.099	0.046
HW	-0.277	-0.055	0.155	0.002	0.03	0.156	0.067	0.127	-0.098	0.036	-0.587	-0.19	0.016	-0.031	-0.073	-0.093	-0.663	-0.071
MW.IL.IL	-0.276	-0.097	0.036	0.044	-0.092	0.097	0.042	0.065	-0.065	0.116	-0.337	-0.209	0.189	0.295	-0.475	-0.089	0.596	0.007
IL.M	-0.27	-0.115	-0.188	-0.042	-0.204	-0.108	-0.172	0.026	0.235	0.168	0.21	-0.254	0.037	-0.198	-0.184	0.099	-0.166	0.699
IL.ST	-0.272	0.075	-0.245	-0.125	0.012	-0.157	-0.118	0.024	0.255	0.192	0.197	-0.246	0.082	-0.288	-0.19	0.174	-0.042	-0.668
E	-0.233	-0.203	0.248	-0.074	0.429	0.212	-0.596	-0.086	0.2	-0.051	0.003	0.235	0.167	0.194	0.085	0.274	0.008	0.014
E.N	-0.258	-0.011	-0.086	-0.575	-0.22	0.027	0.083	-0.055	-0.337	-0.039	0.266	0.406	0	0.276	-0.261	-0.038	-0.198	-0.038
E.ST	-0.238	0.238	-0.26	-0.207	0.044	-0.255	0.21	-0.07	0.127	-0.194	-0.469	0.238	-0.113	-0.108	0.201	0.462	0.187	0.13
E.SL	-0.26	0.076	-0.125	0.28	-0.104	0.45	0.353	0.209	0.519	0.036	0.139	0.353	0.038	0.111	0.065	-0.125	-0.039	-0.027
RH	-0.264	0.077	-0.245	0.202	0.218	0.193	-0.064	0.193	-0.275	-0.683	0.206	-0.233	-0.212	-0.049	-0.101	0.005	0.026	0.014
E.E	-0.267	-0.157	0.095	0.068	0.046	0.041	-0.148	-0.064	-0.167	0.192	-0.086	0.358	-0.408	-0.575	-0.04	-0.344	0.209	0
N.N	-0.249	-0.051	-0.189	0.529	0.175	-0.363	0.106	-0.542	-0.142	0.095	0.068	0.129	0.092	0.238	-0.061	-0.059	-0.169	-0.016
RP	0.02	0.486	-0.012	-0.254	0.67	-0.021	0.161	0.021	0.067	0.179	0.061	-0.055	0.108	-0.037	-0.151	-0.33	0.002	0.188
Standard deviation	3.513	1.855	0.7819	0.6468	0.5687	0.4861	0.4389	0.3595	0.2563	0.24	0.222	0.1953	0.1827	0.1583	0.1282	0.1125	0.0749	0.0501
Proportion of Variance	0.6856	0.1912	0.034	0.0232	0.018	0.0131	0.0107	0.0072	0.0037	0.0032	0.0027	0.0021	0.0019	0.0014	0.0009	0.0007	0.0003	0.0001
Cumulative Proportion	0.6856	0.8768	0.9108	0.934	0.952	0.9651	0.9758	0.983	0.9866	0.9898	0.9926	0.9947	0.9965	0.9979	0.9989	0.9996	0.9999	1

Appendix Table 4-4 Phylogenetic PCA variables' loadings, and variance explained by each axis.

	PC1	PC2	PC3	PC4	PC5	PC6	PC7	PC8	PC9	PC10	PC11	PC12	PC13	PC14	PC15	PC16	PC17	PC18
MbW	-0.231	-0.055	-0.495	0.305	-0.006	0.186	-0.156	0.015	0.372	-0.419	-0.004	-0.331	-0.049	0.333	-0.058	-0.033	0.07	-0.008
tW	-0.219	-0.235	-0.422	0.313	-0.054	0.138	-0.107	0.151	0.052	0.39	0.237	0.293	0.209	-0.452	0.114	0.078	-0.019	0.025
SL	-0.036	-0.549	-0.237	-0.333	-0.158	0.032	0.219	-0.627	-0.059	0.035	0.094	0.103	-0.138	0.139	-0.011	0.026	0.004	0.016
SW	-0.063	-0.549	-0.091	-0.339	-0.003	-0.373	-0.136	0.55	-0.052	-0.085	-0.261	-0.15	0.037	-0.036	0.022	-0.081	-0.02	-0.014
HL2.P	-0.275	0.018	0.106	-0.058	0.188	-0.178	-0.145	-0.102	0.076	-0.031	0.295	0.087	-0.09	-0.165	-0.395	-0.685	0.217	0.039
HH1.P	-0.272	-0.003	-0.027	0.014	-0.055	0.263	0.174	0.186	-0.503	0.252	0.115	-0.411	-0.184	0.052	-0.463	0.179	0.057	-0.063
HW	-0.274	0.08	-0.086	0.001	0.032	0.081	0.178	0.163	-0.276	-0.316	0.05	0.411	-0.086	0.16	0.02	-0.164	-0.661	0.028
MW.IL.IL	-0.274	0.107	-0.041	-0.065	0.041	0.022	0.092	0.147	-0.224	-0.158	0.064	0.21	-0.42	0.027	0.503	0.052	0.565	0.027
IL.M	-0.271	0.08	0.054	-0.15	0.203	-0.193	-0.214	-0.042	0.176	0.29	0.211	-0.009	-0.066	0.266	0.139	0.161	-0.16	-0.68
IL.ST	-0.271	-0.056	0.215	0.002	0.163	-0.167	-0.187	0.004	0.155	0.243	0.173	0.001	-0.049	0.326	0.024	0.268	-0.103	0.695
E	-0.228	0.197	-0.122	0.248	-0.299	-0.693	0.368	-0.109	0.092	-0.027	-0.125	-0.02	-0.105	-0.154	-0.151	0.181	-0.013	-0.013
E.N	-0.259	-0.033	0.001	0.132	0.514	-0.007	-0.042	-0.342	-0.191	0.015	-0.414	-0.331	-0.026	-0.324	0.262	-0.072	-0.181	0.047
E.ST	-0.256	-0.167	0.273	0.033	0.133	0.107	-0.178	-0.087	0.017	-0.369	-0.201	0.363	0.174	-0.13	-0.377	0.456	0.196	-0.136
E.SL	-0.258	0.042	0.111	-0.227	-0.006	0.345	0.434	0.159	0.546	0.252	-0.368	0.075	-0.121	-0.054	-0.054	-0.107	-0.006	0.009
RH	-0.264	0.021	0.201	-0.243	-0.093	0.047	0.283	0.008	0.074	-0.296	0.436	-0.329	0.491	-0.207	0.244	0.067	-0.018	0.02
E.E	-0.265	0.15	-0.083	-0.01	-0.195	-0.025	-0.045	-0.095	-0.253	0.206	-0.34	0.112	0.591	0.399	0.063	-0.234	0.222	0.007
N.N	-0.237	0.075	0.2	-0.097	-0.654	0.138	-0.502	-0.121	0.008	-0.02	-0.124	-0.112	-0.231	-0.214	0.113	-0.059	-0.175	0.017
RP	-0.023	-0.461	0.503	0.594	-0.131	0.024	0.185	0.036	-0.002	0.032	0.034	-0.035	-0.042	0.186	0.162	-0.193	0.007	-0.156
Standard deviation	3.5098	1.598	0.9537	0.7543	0.6405	0.5355	0.4846	0.4323	0.3387	0.3032	0.2767	0.2548	0.2501	0.2376	0.1732	0.1419	0.0989	0.0574
Proportion Variance	0.6844	0.1419	0.0505	0.0316	0.0228	0.0159	0.013	0.0104	0.0064	0.0051	0.0043	0.0036	0.0035	0.0031	0.0017	0.0011	0.0005	0.0002
Cumulative Proportion	0.6844	0.8262	0.8768	0.9084	0.9312	0.9471	0.9601	0.9705	0.9769	0.982	0.9863	0.9899	0.9934	0.9965	0.9982	0.9993	0.9998	1

Appendix Table 4-5 Summary of phylogenetic signal tests for standard PCA axes.

PC axis	K	p-value	lambda	logL	logL0	p-value
PC1	0.551439	0.001	0.9688002	-186.6952	-205.5037	8.61E-10
PC2	3.200896	0.001	1.013476	-91.86826	-156.3325	7.03E-30
PC3	0.3880598	0.002	0.7782133	-81.19796	-89.81045	3.32E-05
PC4	0.5672116	0.001	0.8971253	-58.43581	-75.1993	7.03E-09
PC5	0.4745251	0.001	0.8186754	-53.97268	-65.30033	1.94E-06
	k_{mult}	p-value				
PC1-5	0.721	0.001				
PC1-18	0.6838	0.001				

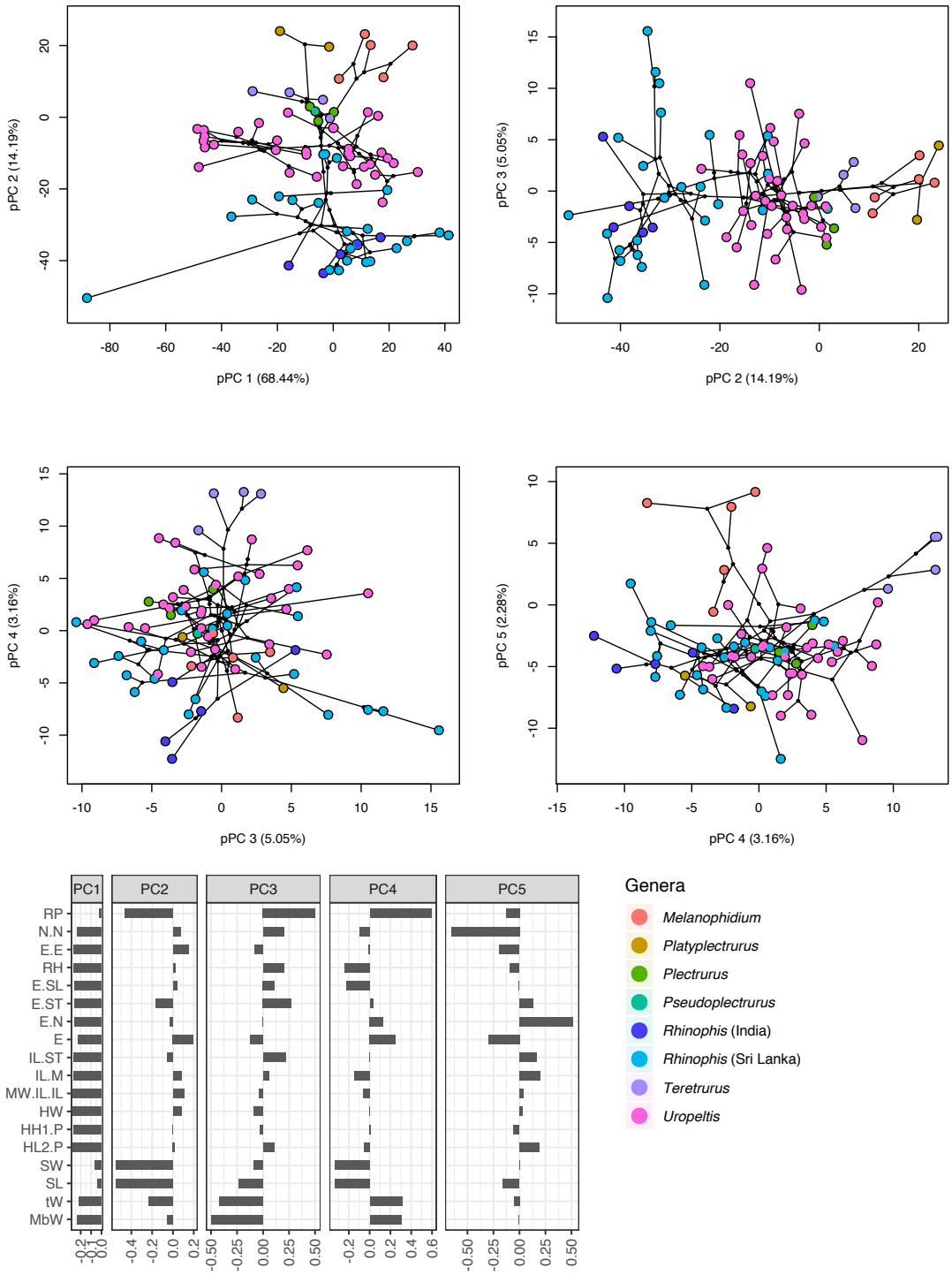
Appendix Table 4-6 Summary of phylogenetic signal tests for single trait residual values from PGLS.

	K	p-value	lambda	logL	logL0	p-value
MbW	0.5008892	0.001	0.9207864	116.1768	99.68321	9.28E-09
tW	0.8689642	0.001	0.9575712	120.3872	96.31163	3.95E-12
SL	3.399216	0.001	1.011826	75.81886	-0.9321044	2.98E-35
SW	3.079796	0.001	1.006473	61.8247	-1.135336	3.20E-29
HL2.P	0.5588157	0.001	0.9569795	127.8555	110.057	2.43E-09
HH1.P	0.5952192	0.001	0.9594637	111.1321	93.69695	3.52E-09
HW	0.5236049	0.001	0.9453357	111.0399	93.65519	3.71E-09
MW.IL.IL	0.5477546	0.001	0.96388	107.1358	88.53617	1.07E-09
IL.M	0.6475701	0.001	0.9899823	111.2583	88.05908	9.65E-12
IL.ST	0.5029652	0.001	0.9512724	123.4684	107.8823	2.36E-08
E	0.7571436	0.001	0.9894237	74.34051	44.2499	8.65E-15
E.N	0.5109874	0.001	0.9572509	123.8097	108.2711	2.48E-08
E.ST	0.4805528	0.001	0.9273438	132.8381	121.7401	2.46E-06
E.SL	0.4763667	0.001	0.9290425	125.3654	112.5299	4.05E-07
RH	0.4714769	0.001	0.8704391	128.0205	114.6597	2.35E-07
E.E	0.6745029	0.001	0.9638398	111.0771	84.67755	3.69E-13
N.N	0.4912355	0.001	0.9591784	108.4884	94.11687	8.26E-08
RP	1.677149	0.001	0.9692208	86.26868	47.18624	9.48E-19

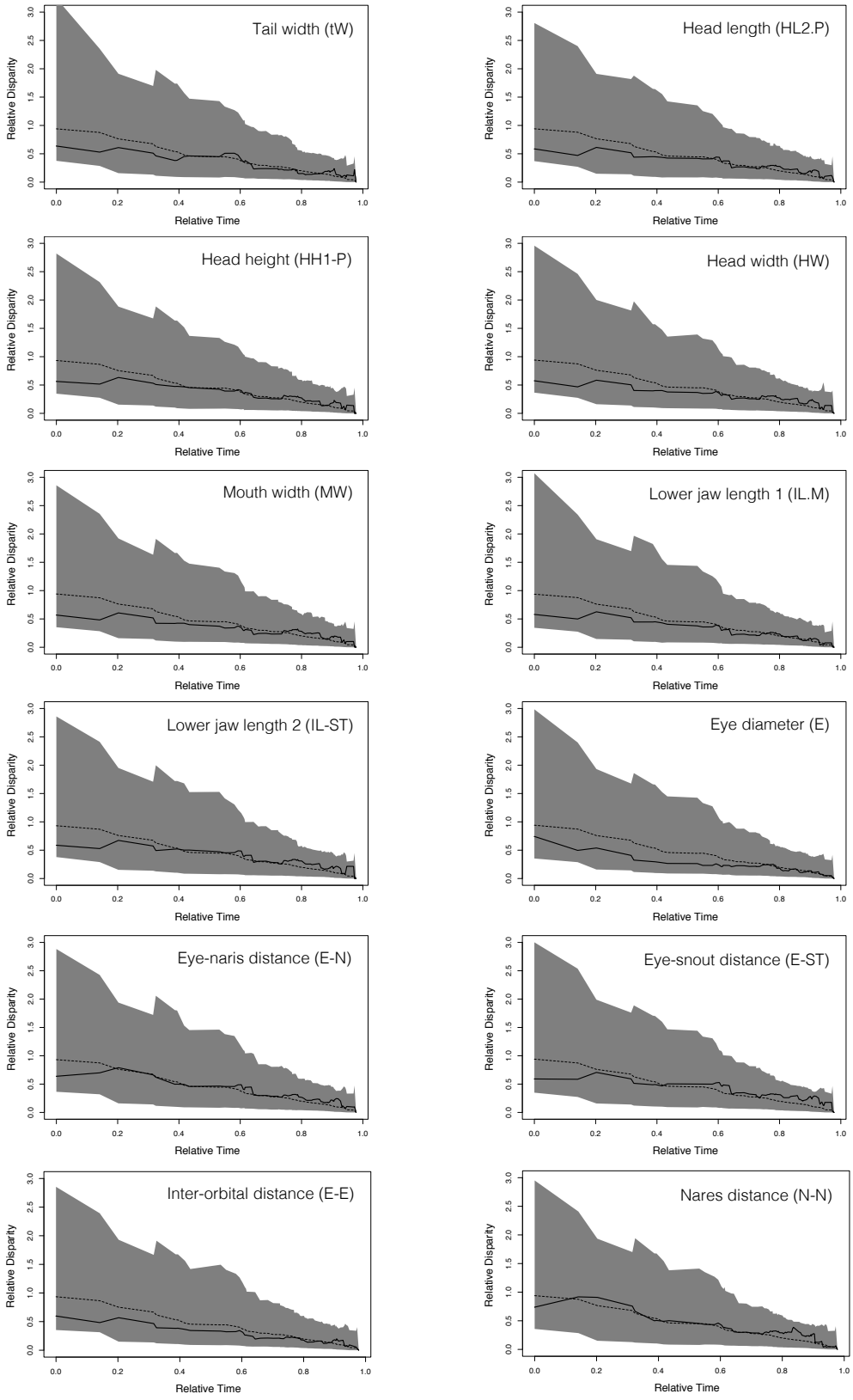
Appendix Table 4-7 AICc scores and weights for Brownian motion (BM), Ornstein-Uhlenbeck (OU) and early burst (EB) models of evolution, fitted to individual traits residuals.

PGSL residuals	Model	log-likelihood	AICc	deltaAICc	weight AICc
MbW	BM	111.438458	-218.71475	3.723038	0.128668
	OU	**114.38328**	**-222.43779**	**0**	**0.82778577**
	EB	111.438348	-216.54793	5.889862	0.04354623
tW	BM	118.882337	-233.60251	0	0.5462227
	OU	119.256962	-232.18516	1.417355	0.2689026
	EB	118.882292	-231.43582	2.166696	0.1848748
SL	BM	75.193855	-146.22555	13.3803	1.24E-03
	OU	75.193855	-144.05894	15.5469	4.20E-04
	EB	**82.967306**	**-159.60584**	**0**	**9.98E-01**
SW	BM	61.622241	-119.08232	14.40084	0.00074553
	OU	61.622241	-116.91571	16.56745	0.00025234
	EB	**69.905965**	**-133.48316**	**0**	**0.99900213**
HL2.P	BM	127.003097	-249.84403	1.534926	0.28630796
	OU	128.853862	-251.37896	0	0.61679136
	EB	127.003018	-247.67727	3.701689	0.09690067
HH1.P	BM	110.394319	-216.62648	0.608109	0.3712237
	OU	111.781676	-217.23459	0	0.5031355
	EB	110.394244	-214.45972	2.774865	0.1256408
HW	BM	109.9571	-215.75204	1.423525	0.2962062
	OU	111.752165	-217.17556	0	0.6035437
	EB	109.957015	-213.58526	3.590301	0.1002501
MW.IL.IL	BM	106.606835	-209.05151	1.353355	0.3025006
	OU	108.366815	-210.40486	0	0.5951185
	EB	106.606755	-206.88474	3.52012	0.1023809
IL.M	BM	111.186702	-218.21124	0	0.4508478
	OU	112.141702	-217.95464	0.2566065	0.3965597
	EB	111.186646	-216.04453	2.1667178	0.1525925
IL.ST	BM	122.338415	-240.51467	2.12343	0.2364193
	OU	124.483432	-242.6381	0	0.6835651
	EB	122.338332	-238.3479	4.290201	0.0800156
E	BM	74.262947	-144.36373	0	0.5707725
	OU	74.463266	-142.59777	1.765967	0.2360414
	EB	74.262913	-142.19706	2.166673	0.1931861
E.N	BM	122.933774	-241.70539	1.229427	0.3137179
	OU	124.63179	-242.93481	0	0.5801042
	EB	122.933699	-239.53863	3.396183	0.1061779
E.ST	BM	131.324865	-258.48757	2.560302	0.20260846
	OU	133.688318	-261.04787	0	0.72881955
	EB	131.324776	-256.32079	4.727084	0.06857199
E.SL	BM	122.779163	-241.39616	4.412644	0.09596295
	OU	**126.068787**	**-245.80881**	**0**	**0.87155937**
	EB	122.779056	-239.22935	6.579462	0.03247768
RH	BM	123.524624	-242.88709	5.30642	0.06435841
	OU	**127.261137**	**-248.19351**	**0**	**0.91386043**
	EB	123.524504	-240.72024	7.473266	0.02178115
E.E	BM	110.284735	-216.40731	0	0.4486645
	OU	111.251934	-216.1751	0.2322069	0.3994833
	EB	110.284669	-214.24057	2.1667368	0.1518521
N.N	BM	108.10762	-212.05308	3.486695	0.14174565
	OU	110.93427	-215.53977	0	0.81028137
	EB	108.107526	-209.88629	5.653487	0.04797298
RP	BM	85.508296	-166.85443	0	0.5955997
	OU	85.508296	-164.68783	2.166605	0.2015961
	EB	85.514271	-164.69978	2.154655	0.2028042

Appendix Figure 4-1 Calibrated molecular phylogenetic tree integrated in the analyses of shape evolution. Phylogeny generated in Chapter 3 of this thesis. Lines coloured by genera (*Rhinophis* in different shades of blue according to geographical area), with the same colours used in phylomorphospace plots.



Appendix Figure 4-2 Phylomorphospace occupation of the phylogenetic PCA scores (PC1 vs. PC2, PC2 vs. PC3, PC3 vs. PC4, PC4 vs. PC5), with species coloured according to genus. Graphical representation of loadings for axes 1 to 5.



Appendix Figure 4-3 DTT plot with curves for individual traits residuals. Dashed line represents the median curve representing the null model under BM evolution based on 5000 simulations. Grey shaded area represents the 95% confidence envelope.

Jins, V. J., Sampaio, F. L., & Gower, D. J. (2018). A new species of *Uropeltis* Cuvier, 1829 (Serpentes: Uropeltidae) from the Anaikatty Hills of the Western Ghats of India. Zootaxa, 4415(3), 401-422.

(https://www.mapress.com/j/zt)

I conducted the morphometric and molecular phylogenetic analyses, drafted methods analyses section and prepared figures with analyses results.

Cyriac, V. P., Narayanan, S., Sampaio, F. L., Umesh, P., & Gower, D.J. (Zootaxa – accepted pending minor revisions). A new species of *Rhinophis* Hemprich, 1820 (Serpentes: Uropeltidae) from the Wayanad region of peninsular India.

(https://www.mapress.com/j/zt)

I recorded morphometric data for type specimens and comparative material, co-wrote the holotype description, and generated and analysed DNA sequence data that in combination with the morphological material helped identify and diagnose the new species.