

A catalogue and systematic overview of the shield-tailed snakes (Serpentes: Uropeltidae)

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ABSTRACT

We present a catalogue and systematic overview of Uropeltidae Müller, 1832 based on both new and previously published molecular and morphological data, and a new molecular phylogenetic analysis. We support the monophyly and distinctiveness of *Brachyophidium* Wall, 1921, *Melanophidium* Günther, 1864, *Platyplectrurus* Günther, 1868, *Pseudoplectrurus* Boulenger, 1890, and *Teretrurus* Beddome, 1886. We move *Uropeltis melanogaster* (Gray, 1858), *U. phillipsi* (Nicholls, 1929), and *Pseudotyphlops* Schlegel, 1839 to *Rhinophis* Hemprich, 1820, and re-name *Pseudotyphlops philippinus* (Müller, 1832) as *R. saffragamus* (Kelaart, 1853), and *U. smithi* Gans, 1966 as *U. grandis* (Beddome, 1867). Thanks to these changes, the taxonomy of all these genera is based on monophyletic entities. Diagnoses based on meristic and mensural characters for external and internal anatomy are provided for the family and all genera, and accounts are given for all currently recognized species, summarizing known morphological variation. We note several taxa that continue to be of uncertain phylogenetic affinity, and outline necessary future studies of variation in systematically valuable characters such as rostral and tail morphology. Cryptic variation is likely present in many species, and additional collection of specimens and DNA-sequence data will likely be needed to provide conclusive resolution for remaining taxonomic issues. Numerous questions remain for the systematics of Uropeltidae, and we hope that this study will provide a platform for ongoing research into the group, including the description of cryptic species, clarifying the phylogenetic placement of some remaining taxa, and quantifying the range of intra- and inter-specific variation in crucial morphological characters.

KEY WORDS

Taxonomic revision,
India,
Sri Lanka,
phylogenetics,
shield-tailed snakes,
new synonyms,
new combinations.

RÉSUMÉ

Catalogue et révision systématique des serpents à queue armée (Serpentes: Uropeltidae).

Nous présentons un catalogue et une révision systématique des Uropeltidae Müller, 1832 basés sur des données moléculaires et morphologiques déjà publiées et nouvelles, et sur une nouvelle analyse phylogénétique moléculaire. Nous confirmons la monophylie et la validité de *Brachyophidium* Wall, 1921, *Melanophidium* Günther, 1864, *Platyplectrurus* Günther, 1868, *Pseudoplectrurus* Boulenger, 1890, et *Teretrurus* Beddome, 1886. Nous transférons *Uropeltis melanogaster* (Gray, 1858), *U. phillipsi* (Nicholls, 1929), et *Pseudotyphlops* Schlegel, 1839 dans *Rhinophis* Hemprich, 1820 et nous renommons *Pseudotyphlops philippinus* (Müller, 1832) en *R. saffragamus* (Kelaart, 1853) et *U. smithi* Gans, 1966 en *U. grandis* (Beddome, 1867). Grâce à ces changements, la taxonomie de tous ces genres semble basée sur des entités monophylétiques. Des diagnoses fondées sur des caractères méristiques et métriques de l'anatomie externe et interne sont fournies pour la famille et pour tous les genres, et des descriptions sont données pour toutes les espèces actuellement reconnues, résumant la variation morphologique connue. Nous indiquons plusieurs taxons dont les relations phylogénétiques restent incertaines et mettons en avant les études qui seront nécessaires dans le futur sur la variation de caractères significatifs en systématique, comme la morphologie du rostre et de la queue. Une variation cryptique est probablement présente chez de nombreuses espèces et la collecte supplémentaire de spécimens et de données sur les séquences d'ADN sera certainement nécessaire pour résoudre les problèmes taxonomiques restants. De nombreuses questions subsistent concernant la systématique des Uropeltidae telles que la description d'espèces cryptiques, la clarification du placement phylogénétique des quelques taxons restants, et la quantification de l'extension de la variation intra- et interspécifique des caractères morphologiques déterminants. Nous espérons que ce travail servira de base pour poursuivre la recherche sur ce groupe.

MOTS CLÉS

Révision taxonomique, Inde, Sri Lanka, phylogénie, serpents à queue armée, synonymies nouvelles, combinaisons nouvelles.

INTRODUCTION

The shield-tailed snakes, family Uropeltidae Müller, 1832 (*sensu* Pyron *et al.* 2013a), are a small group (54 species) of poorly studied, fossorial snakes, endemic to peninsular India and Sri Lanka (see Bossuyt *et al.* 2004). Most species were described in a burst of activity in the 19th century. Numerous junior synonyms resulted from this early period of discovery, including *Coloburus* Duméril & Bibron, 1851; *Crealia* Gray, 1858; *Dapatnaya* Kelaart, 1853; *Maudia* Gray, 1858; *Mitylia* Gray, 1858; *Morina* Gray, 1858; *Siluboura* Gray, 1858 (later unjustifiably emended as *Silybura* Peters, 1861); and *Wallia* Werner, 1925 (see Gans 1966; McDiarmid *et al.* 1999 and Wallach *et al.* 2014).

Of the 54 known, extant species, 23 were described by Colonel Richard Henry Beddome (see Wallach *et al.* 2014), a British officer in India who published extensively on South Asian herpetofauna (Ganesh 2010). Beddome (1886) later provided an overview of the known species and numerous subspecies. Beddome's accounts use generic and specific names (e.g., *Silybura* Peters, 1861; *Rhinophis trevelyanus* Kelaart, 1853) that are not in use today, as they were later designated as junior synonyms (see McDiarmid *et al.* 1999).

Building on Beddome (1886), the last comprehensive systematic account of the family that included diagnostic characteristics and distributional data for individual species was that of Malcolm Smith in 1943. Smith was a British herpetologist and physician working primarily in Thailand who published a volume on the serpent fauna of British India, including Sri Lanka and Burma (Smith 1943). This included a key and summary descriptions of the known species, and established the taxonomic framework at the genus level used by most subsequent researchers. In particular, Smith noted that

Fitzinger (1843) had fixed *Uropeltis ceylanica* Cuvier, 1829 as the type species of *Uropeltis* Cuvier, 1829, indicating its priority over *Silybura* Peters, 1861, which was in widespread use in the 19th century (see Beddome 1886; Boulenger 1893a).

However, the characters that Smith (1943) used to characterize individual species were often subjective and potentially ambiguous (e.g., general descriptions of color patterns), and genera such as *Uropeltis* give the appearance of being non-monophyletic. In particular, some species (e.g., *U. melanogaster* [Gray, 1858]; *U. phillipsi* [Nicholls, 1929]) have characters such as the rostral dividing the nasals and enlarged terminal scutes on the tail, that are otherwise more common in species of *Rhinophis* Hemprich, 1820. Smith also did not usually mention or discuss type material, a convention that was not in wide use at the time.

Following the implementation of the Code, taxonomic checklists were later provided by Gans (1966), McDiarmid *et al.* (1999), and Wallach *et al.* (2014), clearing up some nomenclatural issues and consolidating lists of the type material and localities, though they did not otherwise discuss distributions or diagnostic characters at or above the species level. Other research into the biology and interrelationships within the group has been continuous (e.g., Gans *et al.* 1978; Rajendran 1985; Gower 2003; Comeaux *et al.* 2010), but little progress in higher-level taxonomy has been made, other than noting a general disarray in taxonomy (Gans 1966; Rieppel & Zaher 2002; Olori & Bell 2012).

Molecular phylogenies have shown for at least 26 years that the genera *Pseudotyphlops* Schlegel, 1839, *Rhinophis*, and *Uropeltis* are either non-monophyletic, or render other genera paraphyletic (e.g., Cadle *et al.* 1990; Bossuyt *et al.* 2004; Pyron *et al.* 2013a, b). However, a lack of sufficient taxonomic and character sampling precluded confident phylogenetic

resolution and comprehensive taxonomic revision addressing all species and genera in a unified framework. Such a revision, including synonymies, lists of type material, character-based descriptions, observations of potential cryptic diversity, and phylogenetic evidence, would be inordinately beneficial to future workers.

Recent work at the species level highlights numerous problems in defining species boundaries. New species have been described or resurrected from synonymy and subspecies elevated to species rank, showing the high amount of diversity remaining to be described, and highlighting our poor knowledge of species limits and diagnostic characters within most species (Gower *et al.* 2008, 2016; Wickramasinghe *et al.* 2009; Gower & Maduwage 2011; Aengals & Ganesh 2013; Ganesh *et al.* 2014).

Much of the uncertainty surrounding species delimitation stems from continued reliance on a taxonomy that was erected before modern concepts of systematic revision were in place, with few quantifiable diagnostic characters defining and delimiting most taxa (such as in Smith 1943). Additionally, localities given for many (especially historical) specimens (including types) are often imprecise, assigning specimens to known present-day locations is often difficult, and the exact geographic distribution of many taxa is thus unclear (see Ganesh 2015).

However, the situation is not intractable. Recent studies have presented molecular data for some uropeltid species (Cadle *et al.* 1990; Bossuyt *et al.* 2004; Pyron *et al.* 2013b). Additionally, detailed morphological datasets have also been generated containing representatives from all genera (Rieppel & Zaher 2002; Gower 2003; Comeaux *et al.* 2010; Olori 2010; Olori & Bell 2012). Internal and external morphology have been described from museum specimens both in the literature (Gower *et al.* 2008, 2016; Wickramasinghe *et al.* 2009; Ganesh 2011; Gower & Maduwage 2011; Ganesh *et al.* 2014), and in datasets collected by us, presented here. Comparable data are thus available for every currently recognized, extant species, and appear to be sufficient to define, describe, diagnose, and delimit apparently monophyletic genera that are consistent with the results of phylogenetic analyses, to outline a coherent higher-level taxonomy.

The majority of the type material is in London and Paris, with a large number of topotypic specimens sent to Harvard from London in the late 19th century (Constable, 1949). We have examined types for most species (particularly the material held at the Muséum national d'Histoire naturelle, Paris) and hundreds of topotypic specimens ourselves, generated DNA sequence data for some newly discovered populations, and collected several species that had not been encountered for several decades.

These morphological and molecular data now permit us to address many of the known taxonomic issues in the group using molecular phylogenetic analyses and morphological assignment of specimens, and also re-define geographic ranges. The cryptic diversity of the group, their secretive and fossorial nature, and their geographic spread over remote mountain-ranges imposes certain practical research limitations. Nev-

ertheless, informed by our new data, we find a compelling need to consolidate and synthesize current knowledge of the phylogeny, taxonomy, and nomenclature of the currently recognized species of shield-tailed snakes.

Here, we present a catalogue and systematic overview of the family Uropeltidae. We do not generally attempt to present diagnoses at the species level or describe cryptic species, as the characters derived from the examined material are insufficient for this purpose at present. We comment briefly on the applicability of external and internal meristic and mensural characters, coloration in life, and precise distribution data to identify species-level taxa, with suggestions for workers in the field. We provide a robust and hopefully stable classification for uropeltids at the genus level, which can be used by future researchers in unraveling the biology and diversity of the group.

MATERIAL AND METHODS

ABBREVIATIONS

We use a number of nonstandard abbreviations for both morphological characters and institutional codes. From the dissections (see VISCERAL ANATOMY), we scored the following 27 characters as % snout-vent length (SVL) or simple count (Table 2).

Visceral anatomy

AL	length of anterior lobe of right lung;
AVP	length of avascular portion of the lung;
DVP	length of densely vascularized portion of right lung;
GB	length of gallbladder;
GBmp	midpoint of gallbladder;
H-L int	heart-liver interval;
Heart	length of heart;
IPB	length of intrapulmonary bronchus;
JSA	ratio of distance between junction of systemic arches and posterior apex of heart and SVL;
K-V int	kidney-vent interval;
Kol	kidney overlap;
L-GB	int liver-gallbladder interval;
LBrgs	left bronchus;
Liver	length of liver;
Lkid	length of left kidney;
LKmp	midpoint of left kidney;
Llng	length of left lung;
Lmp	midpoint of liver;
Ltori	location of left lung orifice (Ltori);
Rkid	length of right kidney;
RKmp	midpoint of right kidney;
Rlng	length of right lung;
Rltip	posterior tip of right lung;
S-H int	snout-heart interval;
SVL	snout-vent length;
SVP	length of sparsely vascularized portion of right lung;
T	trachea length;
TL	tail length;
Trng	number of cartilaginous rings in trachea.

Collectors

MW Mark Wilkinson field series;
 RAP Alex Pyron field series;
 RS Ruchira Somaweera field series;
 SBH Blair Hedges field series;
 URO1 Zoological Society of India field series;
 U1-U21 & Melkh1 Amit Sayyed field series.

Institutions

AMNH American Museum of Natural History, New York;
 ANSP Academy of Natural Sciences, Philadelphia;
 BMNH British Museum, Natural History, London;
 BNHM Bombay Natural History Museum, Bombay;
 BNHS Bombay Natural History Society, Bombay;
 CAS California Academy of Sciences, San Francisco;
 CM Carnegie Museum, Pittsburgh;
 CSPT Chennai Snake Park Trust, Chennai;
 FMNH Field Museum of Natural History, Chicago;
 KU University of Kansas, Lawrence;
 LSUMNS Louisiana State University Museum of Natural Sciences, Baton Rouge;
 LSUMZ Louisiana State University Museum of Zoology, Baton Rouge;
 MAD Madras Government Museum, Chennai;
 MCZ Museum of Comparative Zoology, Cambridge;
 MNHN Muséum national d'Histoire naturelle, Paris;
 NMSL National Museum of Sri Lanka, Colombo;
 NMW Naturhistorisches Museum Wien, Wien;
 RMNH Rijksmuseum van Natuurlijke Historie, Leiden;
 SDNHM San Diego Natural History Museum, San Diego;
 SDSU San Diego State University, San Diego;
 TCWC Texas Cooperative Wildlife Collection, Texas;
 UIMNH University of Illinois Museum of Natural History, Urbana;
 UMMZ University of Michigan Museum of Zoology, Ann Arbor;
 UMZC University Museum of Zoology, Cambridge;
 WHT Wildlife Heritage Trust, Sri Lanka, Colombo;
 ZMB Museum für Naturkunde, Berlin;
 ZSI/SRC/VRS Zoological Society of India, Chennai.

PHYLOGENY AND TAXONOMY

We recognize 54 valid species (see accounts below; Appendix 1). However, this is complicated by the fact that not all species are present in published phylogenetic analyses or our newly constructed datasets, and those that are do not necessarily all have the same data sources represented. There is thus a mosaic of available characters and taxa. Care must therefore be taken in deciding: 1) how to interpret the results of different phylogenetic analyses; 2) how to combine these results to determine the placement of sampled taxa; and 3) how to use other character data to place taxa not sampled in the phylogeny. We first review previously published phylogenies and discuss their bearing on taxonomic decisions, and derive systematically variable characters for use in subsequent diagnoses.

Secondly, we present a new molecular phylogenetic analysis based on DNA sequence data, and assess the necessary taxonomic changes for the included taxa. Then, we assess the variation and potential phylogenetic informativeness of morphological characters traditionally used to delimit taxa, and determine which are useful for determining taxonomic affinities. We use these characters to place unsampled taxa into genus-level groups. These taxa are placed “provisionally”, with specific hypotheses of phylogenetic affinity based

on the presence of character states shared with a congener in the molecular phylogeny. Finally, we make a preliminary assessment of character variation within genera and to some extent within species, to assist future researchers in further revisions and descriptions of new taxa. We also note when cryptic variation is apparently present within currently recognized nominal species, based either on our observations or previous conclusions from published research.

We follow the methods used in other recent revisions of poorly known and incompletely represented snakes (see below), such as typhlopoid blindsnakes (Pyron & Wallach 2014; Hedges *et al.* 2014). For the family and all genera, we provide explicit diagnoses, based on morphological characters that, in combination, uniquely identify each taxon. For each species, such data are typically not available, and we present descriptions of the external morphology, color pattern, and scalation of each species. We make notes on the applicability of these characters for defining species boundaries, and in some cases present new or previously published morphological evidence that some nominal species contain cryptic variation, possibly representing additional, undescribed species. For some species, we present revised estimates of the type locality, due either to lectotype or neotype designation. We are conservative in revising designations of type material and localities, only doing so when absolutely needed (see Smith 1953), as explained in each instance.

PREVIOUS PHYLOGENETIC ANALYSES

Cadle *et al.* (1990) presented the first quantitative phylogenetic study of some uropeltid species, based in part on a matrix of alleles detected using protein electrophoresis at 27 allozyme loci in 16 representatives of 15 uropeltids, plus the outgroup *Cylindrophis maculatus* (Linnaeus, 1758). Different analytical methods and datasets recovered varying results. They presented evidence that *Uropeltis* and *Rhinophis* were non-monophyletic, as *U. melanogaster* and *U. phillipsi* were typically nested in *Rhinophis* along with *Pseudotyphlops*, while *Brachyophidium* Wall, 1921 was typically the sister lineage to the sampled Indian species of *Uropeltis*, *U. liura* (Günther, 1875) and *U. phipsonii* (Mason, 1888). Thus, the sampled Sri Lankan species form monophyletic groups in most trees, but the relationships of the Indian taxa are less certain, with the indication that *Uropeltis* is non-monophyletic.

Rieppel & Zaher (2002) presented data from 33 characters related to skull osteomorphology for species of *Melanophidium* Günther, 1864; *Platyplectrurus* Günther, 1868, *Uropeltis*, *Brachyophidium*, *Rhinophis*, *Plectrurus* Duméril & Bibron, 1851, and *Pseudotyphlops*, with *Anomochilus* Berg, 1901, *Cylindrophis* Wagler, 1828, and *Anilius* Oken, 1816 as outgroups. Their analysis recovered *Uropeltis woodmasoni* (Theobald, 1876) but not *Pseudotyphlops* nested within *Rhinophis*, and found *Melanophidium* to be paraphyletic, with *M. wynaudense* (Beddome, 1863) more closely related to other uropeltids than to *M. punctatum* Beddome, 1871. Support for their preferred topology was not given, and some of their characters may have been mis-coded (see Gower *et al.* 2016).

Gower (2003) scored six characters describing variation in scale micro-ornamentation for 20 uropeltid species and four outgroups. Gower considered these characters insufficient for an independent phylogenetic analysis, but presented a composite phylogeny based on several sources to reconstruct the history of his scale characters by plotting them on this tree. In his tree, Gower constrained monophyletic groups comprising *Melanophidium*, all Sri Lankan species and the Indian *Rhinophis*, and the Indian *Uropeltis*. The latter two lineages to form a polytomy with the remaining genera *Plectrurus*, *Platyplectrurus*, *Brachyophidium*, and *Teretrurus* Beddome, 1886. Gower's characters generally supported these groups. The species sampled in *Melanophidium*, the Indian *Uropeltis*, and the Sri Lankan species each exhibited a set of characters diagnosing those clades with strong differences, suggesting that they are also diagnostic of more inclusive genus-level taxa.

Olori & Bell (2012) re-evaluated the characters and expanded the matrix of Rieppel & Zaher (2002), scoring more specimens and more species. Olori & Bell found that the best phylogenetic estimate was poorly resolved and supported, beyond supporting monophyly of the family. Their analyses did not support monophyly of *Melanophidium*, with both species in a polytomy at the base of the tree. Additionally, they typically recovered a clade containing *Plectrurus*, *Pseudotyphlops*, *Rhinophis*, and *Uropeltis*, excluding *Brachyophidium* and *Platyplectrurus*. Resolution depended on the type and number of characters they included in each analysis, without a clear pattern of which genera were supported as monophyletic by their results. Olori & Bell (2012) also described 30 additional osteological characters that might be phylogenetically informative across species, but these have not been assessed for consistency among species, and require high-quality skeletal preparations that are still unavailable for most taxa. Olori & Bell (2012) also report ontogenetic or other intraspecific variation in many characters and taxa.

The characters used by Rieppel & Zaher (2002), Gower (2003), and Olori & Bell (2012) do not seem sufficient to generate a resolved and well-supported morphological alone or in combination, since the coverage for various taxa is very uneven and rarely overlapping. However, we referred to their matrices to provide putative diagnostic characters for some genera (see accounts). We did this by examining each matrix to determine whether any character states diagnosed the sampled species of each genus as recovered in our molecular phylogenetic analysis, or as currently recognized in the literature for those genera not included in our molecular phylogenetic analysis. These putative diagnostic characters represent hypotheses to be tested in future examining more taxa, and by morphological phylogenetic analyses of expanded matrices.

Molecular phylogenetic analyses based on DNA-sequence data have also been presented by several authors. Bossuyt *et al.* (2004) presented mitochondrial data showing that *Melanophidium* is the basal uropeltid lineage, that the sampled Indian *Uropeltis* (*U. liura* and several unidentified species) form a monophyletic group, that *Brachyophidium* is the sister lineage of *Rhinophis* to the exclusion of Indian *Uropeltis*, and

that the sampled *Rhinophis* species form a monophyletic group with the Sri Lankan species *U. melanogaster* and *U. phillipsi*.

Pyron *et al.* (2013a, b) built on data (Bossuyt *et al.* 2004) and other published and unpublished sequences from GenBank, adding both nuclear and mitochondrial data and recovered *Uropeltis melanogaster*, *U. phillipsi*, and *Pseudotyphlops* as strongly allied with *Rhinophis*, consistent with the results of Cadle *et al.* (1990) and Bossuyt *et al.* (2004). Pyron *et al.*'s (2013a, b) analyses also suggested non-monophyly of Indian *Uropeltis*, but this was likely due to non-overlapping gene fragments for the sampled species *U. ceylanica* and *U. liura*. Pyron *et al.*'s (2013a, b) analyses also used large-scale matrices including all families and subfamilies of snakes, and were thus sufficient to address the monophyly of Uropeltidae, which was strongly supported in both studies.

In summary, the following taxonomic problems exist at present. First is the monophyly of *Melanophidium*, which has not been re-assessed phylogenetically using non-osteological characters since the results of Olori & Bell (2012) were presented. Gower *et al.* (2016) suggested the genus was monophyletic in their revision, but without presenting an explicit phylogenetic analysis. Second is the placement of *Brachyophidium* based on DNA sequence data, which has been variable among studies, but is often recovered as the sister group of *Rhinophis*. Third are the relationships of the genera *Platyplectrurus*, *Plectrurus*, *Pseudoplectrurus*, and *Teretrurus*, whose monophyly and relationships have not been evaluated using morphological or molecular data. Fourth is the monophyly of Indian *Uropeltis* species, which has been questioned based on allozymes and DNA sequence data. Fifth is the monophyly of the Sri Lankan uropeltids, which has been supported by morphological and molecular analyses for 26 years.

We address these problem below, presenting a new phylogenetic analysis, reinterpreting known morphological character states in a diagnostic framework based on new and previously published data, and arbitrating nomenclatural problems. This allows us to provide a systematic overview and revised taxonomy, in the form of a catalog of the 54 known, extant species of uropeltids. Our analyses are as follows.

MOLECULAR PHYLOGENETIC ANALYSES

Our DNA-sequence dataset consists of six genes (Table 1), two nuclear (CMOS and RAG1) and four mitochondrial (12S, 16S, CYTB, and ND4). Several recent studies have generated a large amount of DNA sequence data for many taxa from most genera (Bossuyt *et al.* 2004; Pyron *et al.* 2013b), many of which are actually from the same samples or populations as the allozyme and morphological datasets (Cadle *et al.* 1990; Olori & Bell 2012). The majority of the data are from 12S and 16S, and the other genes have been sequenced for only five or six species each. We included all available individuals of each species for which sequence data were available. This includes 19 nominal species, and as many as eight unidentified species.

From recent collections by two of the authors (VS and AS), we generated new sequence data for 12S from 16 individuals of at least three species groups, *Uropeltis ellioti* (Gray,

TABLE 1. — GenBank accession numbers for the DNA-sequence dataset. Individuals of the same species in bold face were combined into a single terminal representative for that species. Abbreviations: see Material and methods.

Species	Author	Voucher	12S	16S	ND4	RAG1	CMOS	CYTb
<i>Brachyophidium rhodogaster</i>	Wall, 1921	MW 3804	AY700992	AY701023	—	—	—	—
<i>Cylindrophis maculatus</i>	(Linnaeus, 1758)	MW 1763	AY700991	AY701022	—	—	—	—
<i>Cylindrophis maculatus</i>	(Linnaeus, 1758)	RAP0448	KC347320	KC347355	KC347494	KC347433	KC347395	KC347460
<i>Melanophidium khairi</i>	Gower, Giri, Captain & Melkh1 Wilkinson, 2016		KX898253	KX898254	—	—	—	—
<i>Melanophidium punctatum</i>	Beddome, 1871	MW 2480	AY700993	AY701024	—	—	—	—
<i>Pseudotyphlops philippinus</i>	(Müller, 1832)	RS-140	KC347331	KC347369	KC347492	KC347446	KC347408	—
<i>Rhinophis blythii</i>	Kelaart, 1853	LSUMNS H-5781	AY701018	AY701049	—	—	—	—
<i>Rhinophis blythii</i>	Kelaart, 1853	LSUMNS H-5784	AY700995	AY701026	—	—	—	—
<i>Rhinophis blythii</i>	Kelaart, 1853	RS-N	KC347332	KC347370	KC347517	KC347447	KC347409	—
<i>Rhinophis blythii</i>	Kelaart, 1853	WHT 5221	AY701019	AY701050	—	—	—	—
<i>Rhinophis blythii</i>	Kelaart, 1853	WHT 5223	AY701020	AY701051	—	—	—	—
<i>Rhinophis blythii</i>	Kelaart, 1853	WHT 5227	AY701021	AY701052	—	—	—	—
<i>Rhinophis dorsimaculatus</i>	Deraniyagala, 1941	LSUMNS H-5780	AY701009	AY701040	—	—	—	—
<i>Rhinophis drummondhayi</i>	Wall, 1921	LSUMNS H-5176	AY700997	AY701028	—	—	—	—
<i>Rhinophis drummondhayi</i>	Wall, 1921	LSUMNS H-5177	AY700998	AY701029	—	—	—	—
<i>Rhinophis drummondhayi</i>	Wall, 1921	LSUMNS H-5778	AY700996	AY701027	—	—	—	—
<i>Rhinophis drummondhayi</i>	Wall, 1921	MW 1721	AY700994	AY701025	—	—	—	—
<i>Rhinophis drummondhayi</i>	Wall, 1921	SBH 194102	Z46447	Z46477	—	AY487386	AF544719	AF544673
<i>Rhinophis erangviraji</i>	Wickramasinghe, Vidanapathirana, Wickramasinghe & Ranwella, 2009	RAP0431	KC347333	KC347371	KC347503	KC347448	KC347410	KC347490
<i>Rhinophis homolepis</i>	(Hemprich, 1820)	MW 1787	AY701015	AY701046	—	—	—	—
<i>Rhinophis homolepis</i>	(Hemprich, 1820)	RAP0509	KC347334	KC347372	KC347522	—	—	KC347489
<i>Rhinophis oxyrhynchus</i>	(Schneider, 1801)	LSUMNS H-6131	AY701013	AY701044	—	—	—	—
<i>Rhinophis oxyrhynchus</i>	(Schneider, 1801)	LSUMNS H-6132	AY701014	AY701045	—	—	—	—
<i>Rhinophis philippinus</i>	(Cuvier, 1829)	LSUMNS H-5157	AY701006	AY701037	—	—	—	—
<i>Rhinophis philippinus</i>	(Cuvier, 1829)	LSUMNS H-5158	AY701007	AY701038	—	—	—	—
<i>Rhinophis philippinus</i>	(Cuvier, 1829)	LSUMNS H-6164	AY701016	AY701047	—	—	—	—
<i>Rhinophis philippinus</i>	(Cuvier, 1829)	LSUMNS H-6165	AY701017	AY701048	—	—	—	—
<i>Rhinophis philippinus</i>	(Cuvier, 1829)	LSUMNS H-6179	AF512740	AF512740	—	—	—	—
<i>Rhinophis philippinus</i>	(Cuvier, 1829)	MW 1740	GQ200594	GQ200594	GQ200594	—	—	GQ200594
<i>Rhinophis philippinus</i>	(Cuvier, 1829)	MW 1742	AY701005	AY701036	—	—	—	—
<i>Rhinophis travancoricus</i>	Boulenger, 1893	MW 220	AY701010	AY701041	—	—	—	—
<i>Uropeltis ceylanicus</i>	Cuvier, 1829	URO1	—	—	—	—	—	DQ887823
<i>Uropeltis cf. macrolepis</i>	(Peters, 1861)	U20 3766	KR814610	—	—	—	—	—
<i>Uropeltis cf. macrolepis</i>	(Peters, 1861)	U21 3767	KR814606	—	—	—	—	—
<i>Uropeltis cf. phipsonii</i>	(Mason, 1888)	U11 3302	KR814604	—	—	—	—	—
<i>Uropeltis cf. phipsonii</i>	(Mason, 1888)	U17 3763	KR814605	—	—	—	—	—
<i>Uropeltis cf. phipsonii</i>	(Mason, 1888)	U5 3296	KR814603	—	—	—	—	—
<i>Uropeltis ellioti</i>	(Gray, 1858)	U13 3759	KR814596	—	—	—	—	—
<i>Uropeltis ellioti</i>	(Gray, 1858)	U14 3760	KR814595	—	—	—	—	—
<i>Uropeltis liura</i>	(Günther, 1875)	LSUMNS H-5791	AY701003	AY701034	—	—	—	—
<i>Uropeltis macrolepis</i>	(Peters, 1861)	U1 3292	KR814597	—	—	—	—	—
<i>Uropeltis macrolepis</i>	(Peters, 1861)	U12 3303	KR814599	—	—	—	—	—
<i>Uropeltis macrolepis</i>	(Peters, 1861)	U2 3293	KR814598	—	—	—	—	—
<i>Uropeltis macrolepis</i>	(Peters, 1861)	U3 3294	KR814601	—	—	—	—	—
<i>Uropeltis macrolepis</i>	(Peters, 1861)	U8 3299	KR814600	—	—	—	—	—
<i>Uropeltis macrolepis</i>	(Peters, 1861)	U9 3300	KR814602	—	—	—	—	—
<i>Uropeltis melanogaster</i>	(Gray, 1858)	LSUMNS H-5696	AF512739	AF512739	—	—	—	—
<i>Uropeltis melanogaster</i>	(Gray, 1858)	SBH NV	—	—	—	AY487399	—	—
<i>Uropeltis phillipsi</i>	(Nicholls, 1929)	LSUMNS H-5788	—	—	—	—	AF471100	AF471034
<i>Uropeltis phillipsi</i>	(Nicholls, 1929)	MW 1758	AY701012	AY701043	—	—	—	—
<i>Uropeltis phillipsi</i>	(Nicholls, 1929)	MW 1760	AY701011	AY701042	—	—	—	—
<i>Uropeltis phipsonii</i>	(Mason, 1888)	U19 3765	KR814609	—	—	—	—	—
<i>Uropeltis phipsonii</i>	(Mason, 1888)	U4 3295	KR814607	—	—	—	—	—
<i>Uropeltis phipsonii</i>	(Mason, 1888)	U6 3297	KR814608	—	—	—	—	—
<i>Uropeltis sp.</i>	cf. <i>Uropeltis</i> Cuvier, 1829	LSUMNS H-5795	AY701004	AY701035	—	—	—	—
<i>Uropeltis sp.</i>	cf. <i>Uropeltis</i> Cuvier, 1829	LSUMNS H-9566	AY701001	AY701032	—	—	—	—
<i>Uropeltis sp.</i>	cf. <i>Uropeltis</i> Cuvier, 1829	MW 2173	AY701000	AY701031	—	—	—	—
<i>Uropeltis sp.</i>	cf. <i>Uropeltis</i> Cuvier, 1829	MW 2469	AY701002	AY701033	—	—	—	—
<i>Uropeltis sp.</i>	cf. <i>Uropeltis</i> Cuvier, 1829	MW 2502	AY700999	AY701030	—	—	—	—

1858), *U. macrolepis* (Peters, 1861), and *U. phipsonii* from the northern Western Ghats (Appendix 2). We were also able to obtain and sequence a specimen of the newly described *Melanophidium khairi* (Gower *et al.* 2016), for both 12S and CYTB. These specimens were collected under permission from the relevant Forest Departments of Maharashtra state, and deposited at Modern College Pune (Appendix II). Amplification and sequencing was conducted by geneOmBio Technologies Pvt. Ltd., Pune, Maharashtra. From these specimens, we also collected a suite of morphological characters (see below).

Sequence data from one species (*Uropeltis ceylanica*) do not derive from a vouchered specimen. We were unable to verify the provenance of the animal, but the sequence data was contributed to GenBank by researchers from the Zoological Survey of India working in Maharashtra, in the range of the species *sensu* Ganesh *et al.* (2014), so there is no direct evidence to falsify this identification, but see below for lectotype and type-locality discussion for *U. ceylanica*.

Our molecular dataset contains up to 5249 base pairs from 60 individuals comprising 19 nominal uropeltid species and *Anilius scytale* (Linnaeus, 1758), *Anomochilus leonardi* Smith, 1940, *Cylindrophis maculatus* (Linnaeus, 1758) represented by two individuals, and *C. ruffus* (Laurenti, 1768) as outgroups. We used PartitionFinder (Lanfear *et al.* 2012) to identify the optimal partitioning scheme. For two species (*Uropeltis melanogaster* and *U. phillipsi*), sequence data from two conspecific vouchers were each combined to make composite single terminals (Table 1), because different vouchers were sampled for different loci. As recommended by previous authors (Brown *et al.* 2010), we conducted a preliminary Maximum Likelihood analysis to estimate approximate branch lengths. The mean branch-length was 0.02424591 substitutions per site, and we set the mean of the exponential prior for branch lengths in MrBayes to $-\ln(0.5) / 0.02424591 = 28.58817$. We ran two sets of four chains for 6.666.667 generations, discarding the first 25% as burnin, yielding five million generations, with convergence demonstrated given ESS > 1000 for all parameters (Drummond *et al.* 2006). We summarized trees using all compatible clades.

VISCERAL ANATOMY

We performed 59 dissections on 27 uropeltid species and four outgroups (sample sizes ranging from one to 14 specimens). These data are difficult to measure without full-scale dissection of well-preserved specimens, and may not be immediately valuable to field workers. However, they have been informative in numerous previous studies of snake systematics (Underwood 1967; Rossman 1982; Helfenberger 1989, 2001; Cundall *et al.* 1993; Keogh 1996; Wallach 1998, 2016; Broadley & Wallach 2007; Pyron & Wallach 2014). We include these data to help diagnose the family and genus-level groups (Table 3). We compare the mean and range of the characters among the sampled genera, and present these as a guide for future studies. While the sample sizes are likely insufficient to ensure an adequate range of intraspecific variation to delimit species, we make notes on apparently exceptional features

of some specimens that may prove to be diagnostic within genera or species.

We assessed the magnitude of differences in quantitative visceral characters between families (Aniliidae Stejneger, 1907; Cylindrophiiidae [including *Anomochilus*] Fitzinger, 1843; and Uropeltidae) using a Kruskal-Wallis test, and compared each uropeltid genus to the remaining genera, using the Mann-Whitney U-test. As these tests involve multiple comparisons of small sample-sizes and presumably necessitate significance corrections, which are poorly defined for non-parametric tests, we arbitrarily set a significance threshold of 0.001, much lower than the traditional 0.05. When a character for a genus is significantly different from other genera at a significance level of 0.001, the mean difference is presented as diagnostic (i.e. a putative synapomorphy) for that genus in the diagnosis with respect to the sampled species and specimens in comparison with the other genera.

EXTERNAL MORPHOLOGY

We scored seven objective, unambiguous characters related to scalation for all species, presented in the descriptions. They are condition of: oculars (single ocular shield vs supraocular and postocular), nasal (in contact behind rostral vs separated by rostral), temporal (absent, parietals contact labials vs present, separating parietals and labials), mental (not grooved vs grooved), midbody dorsal scale rows (15, 17, or 19), and the ranges of ventral and subcaudal scale-counts. We also examined two qualitative characters, tail morphology (see below) and snout morphology (see below), that have previously been used to classify uropeltids at the genus level (Smith 1943).

As noted by Gower & Ablett (2006), counting ventral scales in “aniloid” snakes (including *Cylindrophis*, *Anomochilus*, and Uropeltidae) can be ambiguous, since aniloids do not readily follow Dowling’s (1951) transformation. Gower & Ablett (2006) recommended counting all post-mental scales, a convention we assume is followed by subsequent authors and reflected in our new data. However, some older counts reported here may not follow this convention, and may therefore alter the ranges presented (see Wickramasinghe *et al.* 2009 for examples). Thus, care should be taken when using ventral scale-counts from historical literature to delimit species. Additionally, ventral scale counts differ substantially among populations in many species (see Constable 1949; Rajendran 1985), suggesting the presence of cryptic taxa in many nominal species.

Additionally, subcaudal scale counts appear to be sexually dimorphic in the datasets presented by Boulenger (1893a) and Constable (1949) among others, where males have more subcaudal scales than females for nearly all species represented by multiple specimens per sex. Thus, while we report ranges for ventral and subcaudal scales for all species based on the most recent available published sources, it is still nonetheless possible that the true ranges are obscured due to different methods of counting, not accounting for sexual dimorphism, and the presence of cryptic lineages within species.

TABLE 2. — Dissection data in millimeters (SVL, TL), count (Trng, LBrgs), or % SVL (all other characters). Abbreviations: see Material & methods.

Species	Author	Specimen	SVL	TL	T	Rlng	AL	DVP	SVP	AVP	Ritip	IPB
<i>Anilius scytale</i>	(Linnaeus, 1758)	ANSP 3251	363	24.0	26.17	34.44	0.55	4.96	7.16	21.77	60.88	0.28
<i>Anilius scytale</i>	(Linnaeus, 1758)	ANSP 3253	472	21.0	26.48	26.06	0.85	4.66	16.95	3.60	51.91	0.21
<i>Anilius scytale</i>	(Linnaeus, 1758)	ANSP 3255	474	18.0	26.58	24.47	1.27	3.16	11.61	8.44	50.21	0.21
<i>Anilius scytale</i>	(Linnaeus, 1758)	FMNH 74045	396	15.0	25.76	28.28	0.76	5.05	7.32	15.15	53.54	0.13
<i>Anilius scytale</i>	(Linnaeus, 1758)	LSUMZ 11819	858	32.0	25.06	28.32	0.93	6.76	4.66	15.97	52.91	0.35
<i>Anilius scytale</i>	(Linnaeus, 1758)	LSUMZ 41301	980	34.0	23.78	30.61	0.51	7.45	5.51	17.14	54.08	0.41
<i>Anilius scytale</i>	(Linnaeus, 1758)	LSUMZ 46263	882	36.0	24.04	40.59	1.02	4.31	7.14	28.12	64.40	0.34
<i>Anilius scytale</i>	(Linnaeus, 1758)	MCZ 1207	587	13.0	24.70	30.66	0.85	7.50	4.60	17.72	55.36	0.34
<i>Anilius scytale</i>	(Linnaeus, 1758)	MCZ 1207	253	10.0	29.25	33.60	0.79	9.49	6.72	16.60	62.85	0.79
<i>Anilius scytale</i>	(Linnaeus, 1758)	MCZ 2986	441	15.0	25.17	27.21	1.13	6.80	5.90	13.38	51.70	0.45
<i>Anilius scytale</i>	(Linnaeus, 1758)	TCWC 44582	764	30.0	22.64	23.82	0.52	4.58	12.30	6.41	47.51	1.05
<i>Anilius scytale</i>	(Linnaeus, 1758)	UIMNH 54649	446	14.0	25.78	37.67	0.90	5.38	5.83	25.56	63.23	0.22
<i>Anilius scytale</i>	(Linnaeus, 1758)	UMMZ 53923	498	19.0	23.69	28.51	0.80	3.01	6.43	18.27	52.21	0.20
<i>Anilius scytale</i>	(Linnaeus, 1758)	UMMZ 53924	554	17.0	24.37	26.17	0.72	3.79	8.66	13.00	50.54	0.18
<i>Anomochilus weberi</i>	(Lidth de Jeude, 1890)	RMNH 9507	311	9.0	23.15	27.33	0.00	3.86	11.58	11.90	51.13	1.61
<i>Brachyophidium rhodogaster</i>	Wall, 1921	BMNH 1923.10.13.35	188	7.0	29.79	19.15	0.00	3.72	9.04	11.70	50.53	1.06
<i>Brachyophidium rhodogaster</i>	Wall, 1921	CAS 104256	176	6.0	31.25	28.41	0.00	11.36	9.09	7.95	61.36	1.70
<i>Cylindrophis maculatus</i>	(Linnaeus, 1758)	FMNH 121489	281	6.0	25.27	25.27	0.36	11.03	3.20	10.68	51.25	7.83
<i>Cylindrophis maculatus</i>	(Linnaeus, 1758)	MCZ 15797	309	6.0	27.51	26.86	0.00	4.21	13.59	9.06	55.02	5.50
<i>Cylindrophis maculatus</i>	(Linnaeus, 1758)	SDSU Uncat.	318	7.0	29.87	23.58	0.31	8.49	7.55	7.23	45.60	6.39
<i>Cylindrophis ruffus</i>	(Laurenti, 1768)	FMNH 129412	305	6.5	27.54	28.20	0.00	5.57	16.72	5.90	56.07	1.31
<i>Cylindrophis ruffus</i>	(Laurenti, 1768)	FMNH 129415	439	9.0	27.79	33.94	0.91	9.11	18.68	5.24	60.82	1.14
<i>Cylindrophis ruffus</i>	(Laurenti, 1768)	FMNH 129416	400	9.0	27.00	33.25	0.00	10.25	17.00	6.00	59.75	1.00
<i>Cylindrophis ruffus</i>	(Laurenti, 1768)	FMNH 129418	311	7.0	27.65	29.26	1.29	6.75	3.08	13.50	58.20	0.64
<i>Cylindrophis ruffus</i>	(Laurenti, 1768)	LSUMZ 46846	441	11.5	26.76	33.56	0.45	11.11	3.85	18.14	59.86	4.54
<i>Cylindrophis ruffus</i>	(Laurenti, 1768)	LSUMZ 9639	638	17.0	24.14	29.94	4.23	8.31	19.12	0.00	52.82	4.55
<i>Cylindrophis ruffus</i>	(Laurenti, 1768)	MCZ 4076	228	7.0	27.51	28.38	3.49	7.42	9.17	9.61	55.90	4.37
<i>Melanophidium wynaudense</i>	(Beddome, 1863)	CAS 39633	327	19.0	29.36	20.80	2.45	7.95	5.50	7.34	51.38	0.31
<i>Platyplectrurus madurensis</i>	Beddome, 1877	CAS 9114	328	23.0	25.91	20.73	4.27	6.40	9.76	4.57	45.73	0.91
<i>Plectrurus aureus</i>	Beddome, 1880	CAS 17176	342	11.0	27.78	18.13	2.63	8.19	7.60	2.34	47.08	0.29
<i>Plectrurus perrotetii</i>	Duméril & Bibron, 1851	FMNH 171566	173	10.0	31.21	26.59	2.89	8.09	5.20	13.29	58.96	0.87
<i>Plectrurus perrotetii</i>	Duméril & Bibron, 1851	MCZ 3867	197	6.0	31.47	18.27	2.03	7.11	4.57	7.11	51.27	1.02
<i>Pseudoplectrurus canaricus</i>	(Beddome, 1870)	MCZ 24737	314	18.0	31.21	23.57	2.23	5.41	7.01	11.15	56.05	0.80
<i>Rhinophis drummondhayi</i>	Wall, 1921	AMNH 85076	258	7.5	29.46	19.77	1.55	8.14	10.08	0.00	49.61	0.78
<i>Rhinophis homolepis</i>	(Hemprich, 1820)	CM 20484	204	5.0	31.86	23.04	1.47	6.86	16.18	0.00	56.37	0.49
<i>Rhinophis melanogaster</i>	(Gray, 1858)	UMMZ 96275	182	5.0	32.97	19.23	3.30	6.59	12.64	0.00	53.30	1.65
<i>Rhinophis philippinus</i>	(Cuvier, 1829)	SDNHM 25464	99	3.0	37.37	23.23	0.00	10.10	10.10	3.03	61.62	0.76
<i>Rhinophis saffragamus</i>	(Kelaart, 1853)	BMNH 1968.871	284	13.0	27.82	23.24	1.76	10.21	4.23	7.75	51.41	0.88
<i>Rhinophis saffragamus</i>	(Kelaart, 1853)	KU 31249	329	8.0	25.53	29.79	1.52	7.60	9.12	11.55	55.02	1.22
<i>Rhinophis saffragamus</i>	(Kelaart, 1853)	KU 31250	303	5.0	27.39	25.08	1.32	3.30	20.46	0.00	53.80	1.32
<i>Rhinophis saffragamus</i>	(Kelaart, 1853)	KU 31251	302	6.0	27.81	29.14	0.00	9.27	19.87	0.00	59.60	2.65
<i>Teretrurus sanguineus</i>	(Beddome, 1867)	BMNH 1868.8.12.3	198	9.0	29.80	16.67	3.03	5.05	6.57	6.06	47.98	1.01
<i>Teretrurus sanguineus</i>	(Beddome, 1867)	MCZ 6203	183	3.5	31.14	16.39	4.37	8.74	7.65	0.00	48.63	1.09
<i>Uropeltis broughami</i>	(Beddome, 1878)	CAS 9113	256	8.0	34.38	16.02	0.78	4.30	8.20	2.73	51.95	0.39
<i>Uropeltis ceylanica</i>	Cuvier, 1829	MCZ 3868	237	11.0	30.80	28.68	2.53	7.59	21.10	0.00	61.18	1.27
<i>Uropeltis ellioti</i>	(Gray, 1858)	FMNH 16110	158	11.0	29.75	21.52	3.80	5.06	16.46	0.00	53.14	1.27
<i>Uropeltis grandis</i>	(Beddome, 1867)	MCZ 6200	370	16.0	34.05	23.78	0.81	7.30	4.32	12.16	58.65	0.00
<i>Uropeltis liura</i>	(Günther, 1875)	CM 90216	186	9.5	33.87	25.27	3.23	9.68	3.76	11.83	60.22	1.61
<i>Uropeltis macrolepis</i>	(Peters, 1861)	MCZ 28644	177	7.0	27.68	29.94	3.39	6.21	6.78	16.95	59.32	1.13
<i>Uropeltis madurensis</i>	(Beddome, 1878)	FMNH 217697	424	21.0	22.64	28.07	2.59	7.08	6.37	14.62	52.36	2.12
<i>Uropeltis madurensis</i>	(Beddome, 1878)	MCZ 22389	275	14.0	28.73	21.45	1.45	4.73	3.27	13.45	51.64	1.82
<i>Uropeltis myhendrae</i>	(Beddome, 1886)	CAS 39632	300	12.0	31.00	21.67	4.00	4.33	5.67	11.67	54.00	0.67
<i>Uropeltis nitida</i>	(Beddome, 1878)	MCZ 47292	315	13.0	32.06	24.13	2.22	4.76	19.37	0.00	57.46	1.27
<i>Uropeltis ocellata</i>	(Beddome, 1863)	MCZ 3873	304	9.0	36.51	22.37	0.66	6.58	5.92	9.21	58.22	0.13
<i>Uropeltis petersi</i>	(Beddome, 1878)	MCZ 6201	174	11.0	34.48	31.61	3.44	7.47	22.41	0.00	64.37	1.15
<i>Uropeltis phipsonii</i>	(Mason, 1888)	MCZ 47040	189	10.0	30.69	21.69	3.70	4.76	6.88	10.05	53.34	0.79
<i>Uropeltis pulneyensis</i>	(Beddome, 1863)	MCZ 1335	328	11.0	31.71	21.65	0.91	6.71	4.88	9.15	52.13	1.52
<i>Uropeltis rubromaculata</i>	(Beddome, 1867)	MCZ 6199	269	14.0	30.11	21.93	3.71	5.95	10.78	5.58	53.53	0.56
<i>Uropeltis woodmasoni</i>	(Theobald, 1876)	MCZ 18040	201	8.0	36.32	24.38	1.49	7.46	9.45	7.46	61.69	1.74

TABLE 2. — Continuation.

Species	Author	Specimen	Llng	Ltori	S-H int	K-V int	Heart	H-L int	Liver	Lmp	Rkid
<i>Anilius scytale</i>	(Linnaeus, 1758)	ANSP 3251	1.65	27.00	26.17	9.37	3.31	8.82	34.99	52.48	3.58
<i>Anilius scytale</i>	(Linnaeus, 1758)	ANSP 3253	0.64	27.33	26.91	9.75	2.75	8.05	21.19	45.55	3.81
<i>Anilius scytale</i>	(Linnaeus, 1758)	ANSP 3255	1.58	27.64	27.43	9.49	3.59	6.12	21.10	44.09	3.80
<i>Anilius scytale</i>	(Linnaeus, 1758)	FMNH 74045	1.52	26.77	26.01	10.86	2.78	8.33	27.53	48.11	4.04
<i>Anilius scytale</i>	(Linnaeus, 1758)	LSUMZ 11819	1.63	25.99	25.17	8.39	3.85	8.51	24.36	45.86	4.20
<i>Anilius scytale</i>	(Linnaeus, 1758)	LSUMZ 41301	0.92	24.59	24.18	10.20	2.76	6.12	29.69	45.15	4.08
<i>Anilius scytale</i>	(Linnaeus, 1758)	LSUMZ 46263	1.47	25.06	24.60	8.50	3.85	7.48	24.38	44.27	4.20
<i>Anilius scytale</i>	(Linnaeus, 1758)	MCZ 1207	1.36	25.89	25.55	11.07	2.90	8.01	28.45	47.79	4.94
<i>Anilius scytale</i>	(Linnaeus, 1758)	MCZ 1207	0.79	30.44	30.43	8.70	3.56	8.70	29.25	53.75	4.74
<i>Anilius scytale</i>	(Linnaeus, 1758)	MCZ 2986	0.91	26.08	25.17	7.03	2.95	8.16	26.76	46.71	4.08
<i>Anilius scytale</i>	(Linnaeus, 1758)	TCWC 44582	0.00	24.61	23.56	9.03	2.23	8.12	25.65	44.50	4.97
<i>Anilius scytale</i>	(Linnaeus, 1758)	UIMNH 54649	1.12	26.68	26.23	9.19	2.69	6.73	28.03	46.97	4.26
<i>Anilius scytale</i>	(Linnaeus, 1758)	UMMZ 53923	0.80	24.70	24.70	7.83	3.21	7.63	26.31	45.48	3.41
<i>Anilius scytale</i>	(Linnaeus, 1758)	UMMZ 53924	1.44	25.27	25.81	7.94	3.07	7.04	32.67	49.19	2.89
<i>Anomochilus weberi</i>	(Lidth de Jeude, 1890)	RMNH 9507	0.00	0.00	23.79	11.25	2.89	7.07	37.62	49.68	4.18
<i>Brachyophidium rhodogaster</i>	Wall, 1921	BMNH 1923.10.13.35	3.72	31.38	30.32	18.09	4.26	6.91	26.06	50.27	6.91
<i>Brachyophidium rhodogaster</i>	Wall, 1921	CAS 104256	3.41	32.95	31.25	22.73	3.98	10.80	21.02	52.56	6.82
<i>Cylindrophis maculatus</i>	(Linnaeus, 1758)	FMNH 121489	3.56	26.69	26.69	14.23	3.20	9.96	21.00	47.15	4.63
<i>Cylindrophis maculatus</i>	(Linnaeus, 1758)	MCZ 15797	2.27	28.80	26.86	11.00	3.56	8.09	30.74	50.32	4.53
<i>Cylindrophis maculatus</i>	(Linnaeus, 1758)	SDSU Uncat.	2.20	30.50	29.87	11.64	4.50	9.43	24.53	51.57	4.72
<i>Cylindrophis ruffus</i>	(Laurenti, 1768)	FMNH 129412	2.30	28.85	27.54	12.79	2.95	8.85	30.82	51.80	4.26
<i>Cylindrophis ruffus</i>	(Laurenti, 1768)	FMNH 129415	2.05	28.70	28.70	12.30	3.19	9.79	31.21	54.10	5.01
<i>Cylindrophis ruffus</i>	(Laurenti, 1768)	FMNH 129416	2.00	28.25	27.75	11.25	2.75	11.50	31.75	55.13	5.50
<i>Cylindrophis ruffus</i>	(Laurenti, 1768)	FMNH 129418	2.57	28.94	28.62	12.22	2.57	7.07	32.48	51.93	5.79
<i>Cylindrophis ruffus</i>	(Laurenti, 1768)	LSUMZ 46846	3.63	27.89	27.66	12.70	3.63	11.34	29.02	53.51	3.85
<i>Cylindrophis ruffus</i>	(Laurenti, 1768)	LSUMZ 9639	4.23	25.39	25.24	17.08	3.76	9.56	26.65	48.12	7.21
<i>Cylindrophis ruffus</i>	(Laurenti, 1768)	MCZ 4076	3.49	29.69	29.26	14.41	3.95	7.42	27.95	50.66	6.11
<i>Melanophidium wynaudente</i>	(Beddome, 1863)	CAS 39633	1.22	30.58	29.97	21.71	3.98	14.98	17.74	53.82	7.34
<i>Platyplectrurus madurensis</i>	Beddome, 1877	CAS 9114	0.00	0.00	25.91	20.73	3.96	7.93	26.22	46.95	7.93
<i>Plectrurus aureus</i>	Beddome, 1880	CAS 17176	0.88	28.95	28.07	20.18	3.51	5.85	26.90	47.37	6.43
<i>Plectrurus perrotetii</i>	Duméril & Bibron, 1851	FMNH 171566	1.16	32.37	31.79	23.70	4.05	8.09	22.54	51.16	12.72
<i>Plectrurus perrotetii</i>	Duméril & Bibron, 1851	MCZ 3867	0.51	32.99	31.98	20.30	3.55	8.12	22.84	52.03	8.12
<i>Pseudoplectrurus canaricus</i>	(Beddome, 1870)	MCZ 24737	1.59	32.48	31.53	20.06	3.82	7.64	24.52	51.43	8.92
<i>Rhinophis drummondhayi</i>	Wall, 1921	AMNH 85076	0.97	30.62	30.23	18.60	3.10	7.75	23.26	49.61	5.81
<i>Rhinophis homolepis</i>	(Hemprich, 1820)	CM 20484	0.98	33.33	32.84	17.65	4.41	7.84	27.94	54.41	4.90
<i>Rhinophis melanogaster</i>	(Gray, 1858)	UMMZ 96275	1.65	34.07	32.97	14.29	4.40	7.14	25.82	52.75	4.95
<i>Rhinophis philippinus</i>	(Cuvier, 1829)	SDNHM 25464	1.52	39.39	39.39	16.16	6.06	10.10	20.20	59.60	7.07
<i>Rhinophis saffragamus</i>	(Kelaart, 1853)	BMNH 1968.871	3.17	30.28	29.93	23.94	4.58	9.86	16.90	48.24	14.44
<i>Rhinophis saffragamus</i>	(Kelaart, 1853)	KU 31249	4.56	27.66	27.66	14.89	4.86	10.64	24.32	50.46	7.29
<i>Rhinophis saffragamus</i>	(Kelaart, 1853)	KU 31250	4.95	30.36	30.36	20.13	4.62	12.21	18.81	51.98	7.92
<i>Rhinophis saffragamus</i>	(Kelaart, 1853)	KU 31251	5.96	30.79	32.78	15.89	5.30	13.91	20.20	56.79	10.60
<i>Teretrurus sanguineus</i>	(Beddome, 1867)	BMNH 1868.8.12.3	2.02	31.31	30.81	23.23	5.05	8.08	22.22	49.49	7.58
<i>Teretrurus sanguineus</i>	(Beddome, 1867)	MCZ 6203	1.63	32.24	31.15	22.40	3.83	7.10	24.59	50.55	6.56
<i>Uropeltis broughami</i>	(Beddome, 1878)	CAS 9113	3.13	36.72	35.55	18.75	4.69	5.47	14.45	48.24	8.59
<i>Uropeltis ceylanica</i>	Cuvier, 1829	MCZ 3868	2.95	32.44	31.22	22.78	3.80	8.86	26.16	53.16	9.70
<i>Uropeltis ellioti</i>	(Gray, 1858)	FMNH 16110	3.80	31.65	31.65	20.25	5.06	8.23	24.68	52.22	6.96
<i>Uropeltis grandis</i>	(Beddome, 1867)	MCZ 6200	2.97	34.86	34.59	17.30	4.59	6.49	26.22	54.19	7.03
<i>Uropeltis liura</i>	(Günther, 1875)	CM 90216	1.08	34.95	33.33	19.35	3.23	9.68	24.19	54.84	7.53
<i>Uropeltis macrolepis</i>	(Peters, 1861)	MCZ 28644	1.13	29.38	28.81	22.03	3.95	9.60	13.56	45.22	5.65
<i>Uropeltis madurensis</i>	(Beddome, 1878)	FMNH 217697	2.59	24.29	24.53	20.05	4.01	9.91	27.59	48.23	5.90
<i>Uropeltis madurensis</i>	(Beddome, 1878)	MCZ 22389	1.45	30.18	29.45	22.91	3.27	8.36	22.55	49.09	8.73
<i>Uropeltis myhendrae</i>	(Beddome, 1886)	CAS 39632	4.33	32.33	31.33	19.67	4.00	5.67	24.00	48.67	7.00
<i>Uropeltis nitida</i>	(Beddome, 1878)	MCZ 47292	3.17	33.33	32.70	19.37	3.96	8.57	24.44	53.49	6.35
<i>Uropeltis ocellata</i>	(Beddome, 1863)	MCZ 3873	2.30	37.83	36.51	19.41	4.61	6.91	24.67	55.76	7.57
<i>Uropeltis petersi</i>	(Beddome, 1878)	MCZ 6201	2.01	35.63	35.06	18.39	4.60	5.17	23.56	52.01	8.62
<i>Uropeltis phipsonii</i>	(Mason, 1888)	MCZ 47040	5.82	36.75	31.22	21.16	4.76	6.88	25.40	50.79	8.47
<i>Uropeltis pulneyensis</i>	(Beddome, 1863)	MCZ 1335	1.52	32.32	32.01	21.34	5.18	5.49	25.61	50.30	6.71
<i>Uropeltis rubromaculata</i>	(Beddome, 1867)	MCZ 6199	0.93	31.60	30.48	19.70	4.83	7.06	28.25	51.67	8.92
<i>Uropeltis woodmasoni</i>	(Theobald, 1876)	MCZ 18040	2.49	37.31	35.32	20.40	4.98	10.95	19.40	55.97	7.46

TABLE 2. — Continuation.

Species	Author	Specimen	RKmp	Lkid	LKmp	Kol	JSA	GB	GBmp	L.GB		
										int	Trng	LBrgs
<i>Anilius scytale</i>	(Linnaeus, 1758)	ANSP 3251	92.42	4.13	94.08	2.20	0.28	1.38	76.45	5.79	209	1
<i>Anilius scytale</i>	(Linnaeus, 1758)	ANSP 3253	91.10	4.24	94.70	1.48	0.00	1.91	58.79	1.69	250	1
<i>Anilius scytale</i>	(Linnaeus, 1758)	ANSP 3255	92.41	3.59	94.20	1.90	-1.90	1.48	57.49	2.11	252	1
<i>Anilius scytale</i>	(Linnaeus, 1758)	FMNH 74045	91.16	4.04	92.42	2.78	-0.51	1.52	71.72	9.09	224	0
<i>Anilius scytale</i>	(Linnaeus, 1758)	LSUMZ 11819	93.71	3.38	95.16	2.33	-1.40	1.75	70.22	11.31	237	0
<i>Anilius scytale</i>	(Linnaeus, 1758)	LSUMZ 41301	91.84	2.96	93.62	1.73	-1.22	1.43	72.76	12.04	303	1
<i>Anilius scytale</i>	(Linnaeus, 1758)	LSUMZ 46263	93.59	3.63	95.46	2.04	-1.25	1.59	71.09	13.83	-	0
<i>Anilius scytale</i>	(Linnaeus, 1758)	MCZ 1207	91.40	4.09	94.38	1.53	-0.34	1.53	71.98	9.20	265	0
<i>Anilius scytale</i>	(Linnaeus, 1758)	MCZ 1207	93.68	4.35	95.06	3.16	-2.37	1.98	76.48	7.11	247	0
<i>Anilius scytale</i>	(Linnaeus, 1758)	MCZ 2986	95.01	4.08	96.15	2.95	-0.68	1.36	79.37	18.59	289	0
<i>Anilius scytale</i>	(Linnaeus, 1758)	TCWC 44582	93.46	3.66	93.06	4.07	0.39	2.23	68.26	9.82	277	0
<i>Anilius scytale</i>	(Linnaeus, 1758)	UIMNH 54649	92.94	4.26	95.18	2.02	-0.45	1.12	76.79	15.25	276	0
<i>Anilius scytale</i>	(Linnaeus, 1758)	UMMZ 53923	93.88	3.01	94.08	3.01	0.20	1.81	67.77	8.23	236	0
<i>Anilius scytale</i>	(Linnaeus, 1758)	UMMZ 53924	93.50	2.89	95.67	0.90	-0.36	1.26	76.81	10.65	297	0
<i>Anomochilus weberi</i>	(Lidth de Jeude 1890)	RMNH 9507	90.84	4.18	92.44	2.57	-0.96	1.93	80.71	11.25	173	0
<i>Brachyophidium rhodogaster</i>	Wall, 1921	BMNH 1923.10.13.35	85.37	6.38	88.83	3.19	-1.06	-	-	-	-	1
<i>Brachyophidium rhodogaster</i>	Wall, 1921	CAS 104256	80.68	6.25	83.81	3.41	-1.14	-	-	-	165	1
<i>Cylindrophis maculatus</i>	(Linnaeus, 1758)	FMNH 121489	88.08	4.63	91.64	1.07	0.36	2.85	70.46	11.39	225	2
<i>Cylindrophis maculatus</i>	(Linnaeus, 1758)	MCZ 15797	91.26	5.50	93.69	2.59	1.29	1.94	77.35	10.68	255	0
<i>Cylindrophis maculatus</i>	(Linnaeus, 1758)	SDSU Uncat.	90.72	4.40	95.28	0.00	4.09	1.57	73.11	8.49	247	10
<i>Cylindrophis ruffus</i>	(Laurenti, 1768)	FMNH 129412	89.34	2.59	92.46	1.31	0.00	2.62	72.46	1.97	218	1
<i>Cylindrophis ruffus</i>	(Laurenti, 1768)	FMNH 129415	90.21	5.24	92.37	4.26	-0.68	2.05	78.02	7.29	244	1
<i>Cylindrophis ruffus</i>	(Laurenti, 1768)	FMNH 129416	91.50	5.25	92.88	4.00	0.50	2.00	75.25	3.25	216	1
<i>Cylindrophis ruffus</i>	(Laurenti, 1768)	FMNH 129418	90.68	5.47	92.12	4.18	0.00	1.29	71.06	2.25	206	1
<i>Cylindrophis ruffus</i>	(Laurenti, 1768)	LSUMZ 46846	89.23	4.99	92.06	1.59	0.00	1.81	77.32	8.39	236	2
<i>Cylindrophis ruffus</i>	(Laurenti, 1768)	LSUMZ 9639	86.52	6.90	89.34	4.23	0.94	1.72	68.57	6.27	246	6
<i>Cylindrophis ruffus</i>	(Laurenti, 1768)	MCZ 4076	88.65	4.80	90.61	3.49	-1.31	2.00	74.56	8.73	252	1
<i>Melanophidium wynaudente</i>	(Beddome, 1863)	CAS 39633	81.96	4.89	91.13	3.06	-2.14	2.14	64.68	0.92	211	2
<i>Platyplectrurus madurensis</i>	Beddome, 1877	CAS 9114	83.23	8.84	88.57	3.05	-0.91	1.52	65.40	4.57	227	0
<i>Plectrurus aureus</i>	Beddome, 1880	CAS 17176	83.04	5.85	87.43	1.75	-0.29	1.17	65.20	3.80	222	0
<i>Plectrurus perrotetii</i>	Duméril & Bibron, 1851	FMNH 171566	82.66	12.72	88.44	6.94	-1.16	2.31	68.79	5.20	180	0
<i>Plectrurus perrotetii</i>	Duméril & Bibron, 1851	MCZ 3867	83.76	9.14	87.82	4.57	0.00	1.50	67.01	2.54	198	1
<i>Pseudoplectrurus canaricus</i>	(Beddome, 1870)	MCZ 24737	84.39	9.24	87.74	5.73	-0.96	1.91	67.52	2.87	216	1
<i>Rhinophis drummondhayi</i>	Wall, 1921	AMNH 85076	84.30	5.43	87.98	1.94	-2.71	1.94	67.25	5.04	203	2
<i>Rhinophis homolepis</i>	(Hemprich, 1820)	CM 20484	84.80	4.90	88.24	1.47	-4.41	1.96	70.59	0.98	196	0
<i>Rhinophis melanogaster</i>	(Gray, 1858)	UMMZ 96275	88.19	4.40	94.50	1.65	-3.30	-	-	-	180	0
<i>Rhinophis philippinus</i>	(Cuvier, 1829)	SDNHM 25464	87.37	7.07	91.41	3.03	-4.04	2.02	72.73	2.02	173	0
<i>Rhinophis saffragamus</i>	(Kelaart, 1853)	BMNH 1968.871	83.27	12.32	85.74	10.92	-1.41	3.17	65.67	7.39	142	5
<i>Rhinophis saffragamus</i>	(Kelaart, 1853)	KU 31249	88.75	7.90	90.58	5.78	-4.26	1.52	70.06	6.69	168	1
<i>Rhinophis saffragamus</i>	(Kelaart, 1853)	KU 31250	83.83	7.92	86.13	4.62	-2.64	1.98	75.58	13.20	166	7
<i>Rhinophis saffragamus</i>	(Kelaart, 1853)	KU 31251	89.40	10.60	95.03	4.97	-3.64	1.99	75.50	7.62	151	9
<i>Teretrurus sanguineus</i>	(Beddome, 1867)	BMNH 1868.8.12.3	80.56	8.59	84.09	4.55	-1.52	2.02	59.60	-2.02	177	0
<i>Teretrurus sanguineus</i>	(Beddome, 1867)	MCZ 6203	80.87	7.10	83.88	3.83	-2.19	1.09	63.93	0.55	181	1
<i>Uropeltis broughami</i>	(Beddome, 1878)	CAS 9113	85.55	7.03	90.63	2.73	-3.32	1.17	54.88	-1.17	264	3
<i>Uropeltis ceylanica</i>	Cuvier, 1829	MCZ 3868	82.07	10.13	87.34	4.64	-0.38	2.53	69.20	1.69	219	1
<i>Uropeltis ellioti</i>	(Gray, 1858)	FMNH 16110	83.23	7.59	85.44	5.06	-1.90	2.53	68.35	2.53	157	1
<i>Uropeltis grandis</i>	(Beddome, 1867)	MCZ 6200	86.22	7.30	89.05	4.32	-2.97	1.89	70.68	2.43	336	0
<i>Uropeltis liura</i>	(Günther, 1875)	CM 90216	84.41	7.53	88.17	3.76	-1.61	2.69	69.62	1.08	227	1
<i>Uropeltis macrolepis</i>	(Peters, 1861)	MCZ 28644	80.79	6.78	82.49	4.52	0.00	2.82	63.56	10.17	131	0
<i>Uropeltis madurensis</i>	(Beddome, 1878)	FMNH 217697	82.90	6.13	84.67	4.24	-0.71	2.59	71.11	7.78	211	8
<i>Uropeltis madurensis</i>	(Beddome, 1878)	MCZ 22389	81.45	8.73	86.18	4.00	-0.18	1.82	66.73	5.45	158	1
<i>Uropeltis myhendrae</i>	(Beddome, 1886)	CAS 39632	83.83	6.67	87.00	3.67	-1.33	1.33	70.00	8.67	353	0
<i>Uropeltis nitida</i>	(Beddome, 1878)	MCZ 47292	83.81	6.67	87.46	2.86	-1.14	1.90	69.84	3.17	263	4
<i>Uropeltis ocellata</i>	(Beddome, 1863)	MCZ 3873	84.38	7.89	86.51	5.59	-1.32	2.30	69.90	0.66	222	0
<i>Uropeltis petersi</i>	(Beddome, 1878)	MCZ 6201	85.92	7.47	87.64	6.32	-4.02	2.30	65.52	0.57	180	0
<i>Uropeltis phipsonii</i>	(Mason, 1888)	MCZ 47040	83.04	7.41	85.19	5.82	-3.70	2.12	66.67	2.12	155	0
<i>Uropeltis pulneyensis</i>	(Beddome, 1863)	MCZ 1335	82.01	5.79	85.52	2.74	-3.96	1.83	64.02	0.00	166	0
<i>Uropeltis rubromaculata</i>	(Beddome, 1867)	MCZ 6199	84.76	5.58	85.32	6.69	-1.86	2.23	67.66	0.74	203	3
<i>Uropeltis woodmasoni</i>	(Theobald, 1876)	MCZ 18040	83.33	7.46	86.82	3.98	-2.24	1.49	70.90	4.48	243	2

TABLE 3. — Visceral-topology means and ranges for genera in millimeters (SVL, TL), count (Trng, LBrgs), or %SVL (all other characters). Codes are as follows: ANI, *Anilius*; ANO, *Anomochilus*; BRA, *Brachyophidium*; CYL, *Cylindrophis*; MEL, *Melanophidium*; PLA, *Platyplectrurus*; PLE, *Plectrurus*; PSE, *Pseudoplectrurus*; RHI, *Rhinophis*; TER, *Teretrurus*; URO, *Uropeltis*. Sample sizes indicated by “N;” raw data given in Table 2.

	ANI N=14	ANO N=1	BRA N=2	CYL N=10	MEL N=1	PLA N=1	PLE N=3	PSE N=1	RHI N=9	TER N=2	URO N=15
T	25.25 (22.64-29.25)	23.15 –	30.52 (29.79-31.25)	27.1 (24.14-29.87)	29.36 –	25.91 –	30.15 (27.78-31.47)	31.21 –	30.21 (25.53-37.37)	30.47 (29.8-31.14)	31.54 (22.64-36.51)
Rlng	30.03 (23.82-40.59)	27.33 –	23.78 (19.15-28.41)	29.22 (23.58-33.94)	20.8 –	20.73 –	21 (18.13-26.59)	23.57 –	23.8 (19.23-29.79)	16.53 (16.39-16.67)	24.17 (16.02-31.61)
AL	0.83 (0.51-1.27)	0 –	0 –	1.1 (0-4.23)	2.45 –	4.27 –	2.52 (2.03-2.89)	2.23 –	1.31 (0-3.3)	3.7 (3.03-4.37)	2.52 (0.66-4)
DVP	5.49 (3.01-9.49)	3.86 –	7.54 (3.72-11.36)	8.23 (4.21-11.11)	7.95 –	6.4 –	7.8 (7.11-8.19)	5.41 –	7.64 (3.3-10.21)	6.9 (5.05-8.74)	6.22 (4.3-9.68)
SVP	7.91 (4.6-16.95)	11.58 –	9.07 (9.04-9.09)	11.2 (3.08-19.12)	5.5 –	9.76 –	5.79 (4.57-7.6)	7.01 –	11.95 (4.23-20.46)	7.11 (6.57-7.65)	10.05 (3.27-22.41)
AVP	15.8 (3.6-28.12)	11.9 –	9.83 (7.95-11.7)	8.54 (0-18.14)	7.34 –	4.57 –	7.58 (2.34-13.29)	11.15 –	3.5 (0-11.55)	3.03 (0-6.06)	7.71 (0-16.95)
Rltip	55.1 (47.51-64.4)	51.13 –	55.95 (50.53-61.36)	55.53 (45.6-60.82)	51.38 –	45.73 –	52.44 (47.08-58.96)	56.05 –	54.76 (49.61-61.62)	48.31 (47.98-48.63)	56.74 (51.64-64.37)
IPB	0.37 (0.13-1.05)	1.61 –	1.38 (1.06-1.7)	3.73 (0.64-7.83)	0.31 –	0.91 –	0.73 (0.29-1.02)	0.8 –	1.25 (0.49-2.65)	1.05 (1.01-1.09)	1.06 (0-2.12)
Llng	1.13 (0-1.65)	0 –	3.57 (3.41-3.72)	2.83 (2-4.23)	1.22 –	0 –	0.85 (0.51-1.16)	1.59 –	2.81 (0.97-5.96)	1.83 (1.63-2.02)	2.68 (0.93-5.82)
Ltori	26.29 (24.59-30.44)	0 –	32.17 (31.38-32.95)	28.37 (25.39-30.5)	30.58 –	0 –	31.44 (28.95-32.99)	32.48 –	32.09 (27.66-39.39)	31.78 (31.31-32.24)	33.28 (24.29-37.83)
S-H int	25.85 (23.56-30.43)	23.79 –	30.79 (30.32-31.25)	27.82 (25.24-29.87)	29.97 –	25.91 –	30.61 (28.07-31.98)	31.53 –	32.02 (27.66-39.39)	30.98 (30.81-31.15)	32.12 (24.53-36.51)
K-V int	9.1 (7.03-11.07)	11.25 –	20.41 (18.09-22.73)	12.96 (11-17.08)	21.71 –	20.73 –	21.39 (20.18-23.7)	20.06 –	18.1 (14.29-23.94)	22.82 (22.4-23.23)	20.1 (17.3-22.91)
Heart	3.11 (2.23-3.85)	2.89 –	4.12 (3.98-4.26)	3.41 (2.57-4.5)	3.98 –	3.96 –	3.7 (3.51-4.05)	3.82 –	4.72 (3.1-6.06)	4.44 (3.83-5.05)	4.29 (3.23-5.06)
H-L int	7.7 (6.12-8.82)	7.07 –	8.86 (6.91-10.8)	9.3 (7.07-11.5)	14.98 –	7.93 –	7.35 (5.85-8.12)	7.64 –	9.44 (5.49-13.91)	7.59 (7.1-8.08)	7.85 (5.17-10.95)
Liver	27.17 (21.1-34.99)	37.62 –	23.54 (21.02-26.06)	28.62 (21-32.48)	17.74 –	26.22 –	24.09 (22.54-26.9)	24.52 –	22.56 (16.9-27.94)	23.41 (22.22-24.59)	23.27 (13.56-28.25)
Lmp	47.14 (44.09-53.75)	49.68 –	51.42 (50.27-52.56)	51.43 (47.15-55.13)	53.82 –	46.95 –	50.19 (47.37-52.03)	51.43 –	52.68 (48.24-59.6)	50.02 (49.49-50.55)	51.57 (45.22-55.97)
Rkid	4.07 (2.89-4.97)	4.18 –	6.87 (6.82-6.91)	5.16 (3.85-7.21)	7.34 –	7.93 –	9.09 (6.43-12.72)	8.92 –	7.74 (4.9-14.44)	7.07 (6.56-7.58)	7.63 (5.65-9.7)
RKmp	92.86 (91.1-95.01)	90.84 –	83.03 (80.68-85.37)	89.62 (86.52-91.5)	81.96 –	83.23 –	83.15 (82.66-83.76)	84.39 –	85.77 (82.01-89.4)	80.72 (80.56-80.87)	83.71 (80.79-86.22)
Lkid	3.74 (2.89-4.35)	4.18 –	6.32 (6.25-6.38)	4.98 (2.59-6.9)	4.89 –	8.84 –	9.24 (5.85-12.72)	9.24 –	7.37 (4.4-12.32)	7.85 (7.1-8.59)	7.36 (5.58-10.13)
LKmp	94.52 (92.42-96.15)	92.44 –	86.32 (83.81-88.83)	92.25 (89.34-95.28)	91.13 –	88.57 –	87.9 (87.43-88.44)	87.74 –	89.46 (85.52-95.03)	83.99 (83.88-84.09)	86.66 (82.49-90.63)
Kol	2.29 (0.9-4.07)	2.57 –	3.3 (3.19-3.41)	2.67 (0-4.26)	3.06 –	3.05 –	4.42 (1.75-6.94)	5.73 –	4.12 (1.47-10.92)	4.19 (3.83-4.55)	4.55 (2.73-6.69)
JSA	-0.69 (-2.37-0.39)	-0.96 –	-1.1 (-1.14-1.06)	0.52 (-1.31-4.09)	-2.14 –	-0.91 –	-0.48 (-1.16-0)	-0.96 –	-3.37 (-4.41-1.41)	-1.86 (-2.19-1.52)	-1.78 (-4.02-0)
GB	1.6 (1.12-2.23)	1.93 –	– (–)	1.99 (1.29-2.85)	2.14 –	1.52 –	1.66 (1.17-2.31)	1.91 –	2.05 (1.52-3.17)	1.56 (1.09-2.02)	2.11 (1.17-2.82)
GBmp	71.14 (57.49-79.37)	80.71 –	– (–)	73.82 (68.57-78.02)	64.68 –	65.4 –	67 (65.2-68.79)	67.52 –	70.17 (64.02-75.58)	61.76 (59.6-63.93)	67.64 (54.88-71.11)
L-GB int	9.62 (1.69-18.59)	11.25 –	– (–)	6.87 (1.97-11.39)	0.92 –	4.57 –	3.85 (2.54-5.2)	2.87 –	5.37 (0-13.2)	-0.74 (-2.02-0.55)	3.36 (-1.17-10.17)
Trng	258.62 (209-303)	173 –	165 (165-165)	234.5 (206-255)	211 –	227 –	200 (180-222)	216 –	171.67 (142-203)	179 (177-181)	221.47 (131-353)
LBrgg	0.29 (0-1)	0 –	1 (–)	2.5 (0-10)	2 –	0 –	0.33 (0-1)	1 –	2.67 (0-9)	0.5 (0-1)	1.6 (0-8)

SNOUT MORPHOLOGY

The Indian genera other than *Uropeltis* and *Pseudoplectrurus* (*Brachyophidium*, *Melanophidium*, *Plectrurus*, and *Teretrurus*) share a relatively unmodified snout profile, with nasals in broad contact behind the rostral, which is not enlarged, keeled, or strongly projecting rearward. The snout in these taxa is roughly semi-circular when viewed from above, and we

refer to this as “Rounded Rostral”. A similar condition is also shared by many *Uropeltis* species, but with reduced cephalic squamation (e.g., no temporal, mental, or divided ocular), which we refer to as “Alternate Rounded”.

In contrast, all *Rhinophis* species and some *Uropeltis* species have greatly enlarged rostrals that are keeled or ridged, project rearwards to partially or completely separate the nasals, and a

strongly triangular snout-profile, giving a pointed appearance to the head when viewed dorsally and laterally. The rostral gives the appearance of a “boomerang” shape in lateral view, as the upper and lower points project substantially behind the nostril. We refer to this as the “Boomerang Rostral”. Finally, some *Uropeltis* species (e.g., *U. woodmasoni*) and *Pseudoplectrurus* have a snout that is wedge-shaped when viewed from above, but without a significantly enlarged rostral. We refer to this as “Alternate Pointed”. We evaluated the shape of the snout for each species, as reported in the accounts.

TAIL MORPHOLOGY

As a final character for external morphology of uropeltids used by previous researchers (e.g., Smith 1943), we characterized the gross tail-morphology of all species. The tails fall into six somewhat-distinct groups (see Rajendran 1985). First are those species with relatively unmodified, elongated, dorsolaterally compressed tails terminating in a single point (*Brachyophidium*, *Platyplectrurus*, and *Teretrurus*; Type I). Second are those with less elongated, more heavily compressed tails, possibly with lightly-keeled dorsal scales, terminating in a bifid or multi-pointed scute (*Melanophidium*, *Plectrurus*, and *Pseudoplectrurus*; Type II).

In the species currently classified as *Uropeltis*, Smith (1943) identified three tail forms that are re-examined here. In some species, the tail is truncated dorsally, compressed dorsolaterally, and keeled, but still rounded and terminating in a convex cap (our assessment of Smith’s state I). Smith’s state II is a classic “shield” tail, in which the body appears to have been sliced off at a *c.* 45° angle, leaving a flattened disc covered with rugose scales. Smith’s state III is a relatively unmodified, blunt and compressed tail, terminating in a slightly enlarged scute that contains several distinct points. We number these differently, in ascending degree of flattening, from state III (Type III) to state I (Type IV) to state II (Type V). Finally, most *Rhinophis* and *Pseudotyphlops* have a tail terminating in a projecting, rugose, keratinous disc (Type VI), though in some species this disc is small compared to the rounded rear end of the tail, such that the tail as a whole resembles Smith’s (1943) state III (see accounts). The boundaries between these states are often ambiguous, as described in the species accounts.

SYSTEMATICS

DUBIOUS STATUS OF SOME SRI LANKAN UROPELTIDS

Deraniyagala (1954) described two taxa, *Plectrurus rubunae* Deraniyagala, 1954 (holotype NMSL R. S. 51) and *Uropeltis (Siluboura) rubunae* (NMSL R. S. 52), each based on a specimen sent to the Colombo National Museum by Rev. P. Abraham of St. Aloysius’ College in Galle. However, the jar contained specimens from multiple species, not all known, collected in both the Galle district of Sri Lanka, and the Madurai district of India (De Silva 1980). There appears to have been no indication that the *Plectrurus* or *Uropeltis* specimens actually originated in Galle rather than Madurai.

Most authors have treated *Plectrurus rubunae* as a subspecies (Gans 1966), or most recently, as a synonym (Wallach

et al. 2014) of *Platyplectrurus madurensis* Beddome, 1877. We follow Wallach *et al.* (2014) in considering *Ple. rubunae* as a junior synonym of *Pla. madurensis*, considering the specimen likely to have originated from India, and the name not to represent a distinct taxon. We consider this a justifiable conclusion based on the lack of any subsequent published reports of *Platyplectrurus* from Sri Lanka, the great distance from the nearest highland populations of *Platyplectrurus* in India, and the high likelihood of confusion for specimens in that jar.

Having examined the holotype of *Uropeltis rubunae* Deraniyagala, 1954, it is indistinguishable in scutellation, body form, and color pattern from populations currently referred to *U. woodmasoni*. This includes the syntypes of *Silybura nigra* Beddome, 1878 (BMNH 1946.1.1.39 and MNHN-RA-1895.85), a junior subjective synonym of *U. woodmasoni* (see account). In particular, NMSL 52 has 170 ventral scales (Wickramasinghe *et al.* 2009), rather than the 160 originally reported (Deraniyagala 1954), within the range of 157–189 for *U. woodmasoni*, 19 dorsal scale rows at midbody, elongated rostral partially separating the nasals, which meet only at a point behind the rear tip of the rostral, heavily expanded anterior trunk musculature with noticeable diminution of body posteriorly, color in preservative changing from olive-green anteriorly to ruddy posteriorly, terminal scute of tail forming projecting cap with several points, and bands of white or yellow flecks ringing the body. These characters are diagnostic of *U. woodmasoni* in combination. Thus, it seems exceptionally likely that both of the specimens described by Deraniyagala were also among those of Indian origin in the jar. We place *U. rubunae* in the synonymy of *U. woodmasoni*, and suggest that it is a near certainty that neither *Platyplectrurus madurensis* nor *U. woodmasoni* occur in Sri Lanka.

MOLECULAR PHYLOGENY

The molecular analyses quickly converged on a well-resolved, well-supported tree, with estimated sample sizes > 1000 for all parameters (Fig. 1). Values greater than 100 typically indicate good convergence (Drummond *et al.* 2006). As in some previous analyses (Gower *et al.* 2005; Pyron *et al.* 2013a), *Anomochilus* is nested within *Cylindrophis* with strong support (>95%). The family Uropeltidae is strongly supported as monophyletic, with a basal divergence between the sampled species of *Melanophidium* and all other sampled uropeltid taxa. The sampled species of *Melanophidium* are strongly supported as monophyletic.

Several sampled species of *Uropeltis*, including the type species *U. ceylanica*, form a moderately supported clade (81%), which we refer to as *Uropeltis sensu stricto*. The unidentified specimen MW 2502 is strongly allied with *U. ellioti*, while the unidentified specimen LSUMNS H-5795 is strongly allied with *U. liura*. We consider those vouchers to be conspecific with the referenced species for the purposes of further discussion.

Within our newly-sequenced populations from the northern Western Ghats in Maharashtra state, India (data in Appendix II), the specimens identified as *Uropeltis phipsonii* with 17 dorsal scale rows are paraphyletic with respect to the specimens identified as *U. macrolepis* with 15 dorsal

scale rows. Many of these populations have been pictured previously as different color-pattern morphs within their respective nominal species (see Whitaker & Captain 2004). Three specimens (U4, U6, and U19) from Pune and Amboli form a clade that we refer to as *U. phipsonii sensu stricto* based on their color-pattern resemblance to the reported syntypes (Mason 1888), distinct from the remaining *U. cf. phipsonii* + *U. cf. macrolepis* specimens.

Two specimens of *Uropeltis cf. macrolepis* from Amboli (U20 and U21) form the sister lineage of the remaining *U. cf. phipsonii* + *U. cf. macrolepis* specimens. These two specimens have a distinctive color-pattern of thin, incomplete yellow rings, which break into dots on the top of the dorsum, and likely represent a distinct species, on the basis of these color-pattern differences and their genealogical distinctiveness.

The six remaining samples identified as *Uropeltis macrolepis* form a clade with the three remaining *U. cf. phipsonii*. Four of the *U. macrolepis* are from populations and localities previously referred to *U. m. mahableshwarensis* and bear the distinctive color-pattern of broad yellow stripes running dorsolaterally. The other two *U. m. macrolepis* samples from Mahableshwar and Kaas (U1 and U2), have a distinctive all-black dorsal coloration, compared to the striped *mahableshwarensis* form from Mahableshwar.

As Peters' (1861a) type of *Uropeltis macrolepis* has been examined (BMNH 1946.1.15.99) and is clearly what is currently referred to as *U. m. mahableshwarensis* (see account), we treat these six specimens as *U. macrolepis sensu stricto*, exclusive of the *U. cf. macrolepis* samples described above (U20 and U21). However, there are likely additional cryptic species in this complex that are not resolved by the single 12S fragment used here.

The three remaining specimens (U5, U11, and U17) of *Uropeltis cf. phipsonii* from Satara have a distinctive color-pattern of thin, incomplete yellow bands, speckles, and lateral stripes broken posteriorly. These also potentially represent a new species, again on the basis of their unique color-pattern, dorsal scalation, and genealogical distinctiveness. These three specimens are weakly nested within the six individuals of *U. macrolepis*.

In summary, we find populations resembling *Uropeltis phipsonii* from Pune with 17 dorsal scale rows, *U. cf. macrolepis* from Amboli with 15 dorsal scale rows and a color pattern of incomplete thin yellow rings, and a clade comprising *U. macrolepis* ("*mahableshwarensis*" form with 15 dorsal scale rows from Mahableshwar), *U. cf. macrolepis* (all-black form with 15 dorsal scale rows from Mahableshwar), and *U. cf. phipsonii* from Satara with 17 dorsal scale rows and variable color-patterns of yellow bands, stripes, and speckles. Extensive phylogeographic sampling with additional loci will likely be needed to clarify species boundaries and geographic ranges.

The *Uropeltis sensu stricto* group is the sister taxon of a moderately supported clade (Pp = 76%) comprising *Brachyophidium* + (*Rhinophis*, Sri Lankan *Uropeltis*, and *Pseudotyphlops*), as in previous analyses (Pyron *et al.* 2013a, b). This *Rhinophis* group is strongly supported (100%). However, the placement of *Uropeltis melanogaster* + *U. phillipsi* and *Pseudotyphlops* inside the sampled *Rhinophis* species is not strongly supported. Thus,

either or both of those taxa could potentially be sister lineages to a monophyletic *Rhinophis*. One sample of *R. blythii* Kelaart, 1853 (LSUMNS H-5784) is nested within *R. drummondhayi* Wall, 1921, but this perhaps represents a misidentified sample or sequencing error, rather than species-level polyphyly or introgression. We did not examine the voucher, and ignored this sample subsequently.

VISCERAL TOPOLOGY

Statistically significant differences are observed among Aniliidae, Cyliodrophiidae (including *Anomochilus*), and Uropeltidae for: T, Rlng, AL, AVP, IPB, Llng, Ltori, S-H int, K-V int, Heart, Liver, Lmp, Rkid, RKmp, Lkid, LKmp, Kol, JSA, GBmp, L-GB int, and Trng. Thus, the majority of the visceral-topology characters exhibit systematically informative differences among anilioid families, and can thus presumably be used, at least in part, to diagnose genera. We do not explicitly diagnose Cyliodrophiidae + Uropeltidae relative to Aniliidae here due to their phylogenetic distance (see Pyron *et al.* 2013a, b). However, we include these results to show that systematic variation is clearly present in these characters. The particular characters that diagnose Uropeltidae from Cyliodrophiidae (including *Anomochilus*) are given in the family account for Uropeltidae (see below). The particular characters that diagnose each uropeltid genus as recognized here are given in their respective accounts (see below).

SNOUT MORPHOLOGY

Based on our examination, the four conditions for snout morphology seem to be very consistent and relatively well-defined (Fig. 2). The genera *Brachyophidium*, *Melanophidium*, *Platyplectrurus*, *Plectrurus*, *Pseudoplectrurus*, and *Teretrurus* are all characterized by the "Rounded Rostral" form. The species of *Rhinophis*, *Uropeltis melanogaster*, *U. phillipsi*, and *U. pulneyensis* (Beddome, 1863) are all characterized by the "Boomerang Rostral", which projects rearward, separating the nasals. Additionally, *Pseudotyphlops* and *U. macrorhyncha* (Beddome, 1877) exhibit a "Boomerang Rostral" which strongly resembles most *Rhinophis* species in being enlarged, ridged dorsally, and projecting rearward, but does not completely divide the nasals. A similar condition is observed for *U. smithi* Gans, 1966, which Smith (1943) reports occasionally has divided the nasals, though the nasals were in contact for all specimens observed here (Appendix I).

The species *Uropeltis beddomii* (Günther, 1862), *U. broughami* (Beddome, 1878), *U. dindigalensis* (Beddome, 1877), *U. ellioti*, *U. nitida* (Beddome, 1878), *U. ocellata* (Beddome, 1863), *U. rubromaculata* (Beddome, 1867), and *U. woodmasoni* all have a pointed snout and anteriorly projecting rostral that partially separates the nasals, but with tail shields typical of *Uropeltis* species as classified by Smith (1943). The degree of snout narrowing and rostral projection varies among species. We consider these species to exhibit the "Alternate Pointed" form. The remaining *Uropeltis* species all exhibit the "Alternate Rounded" snout form. Finally, we also classify *Pseudoplectrurus* as "Alternate Pointed", as it exhibits a pointed snout and narrowed, recurved rostral that partially separates the nasals.

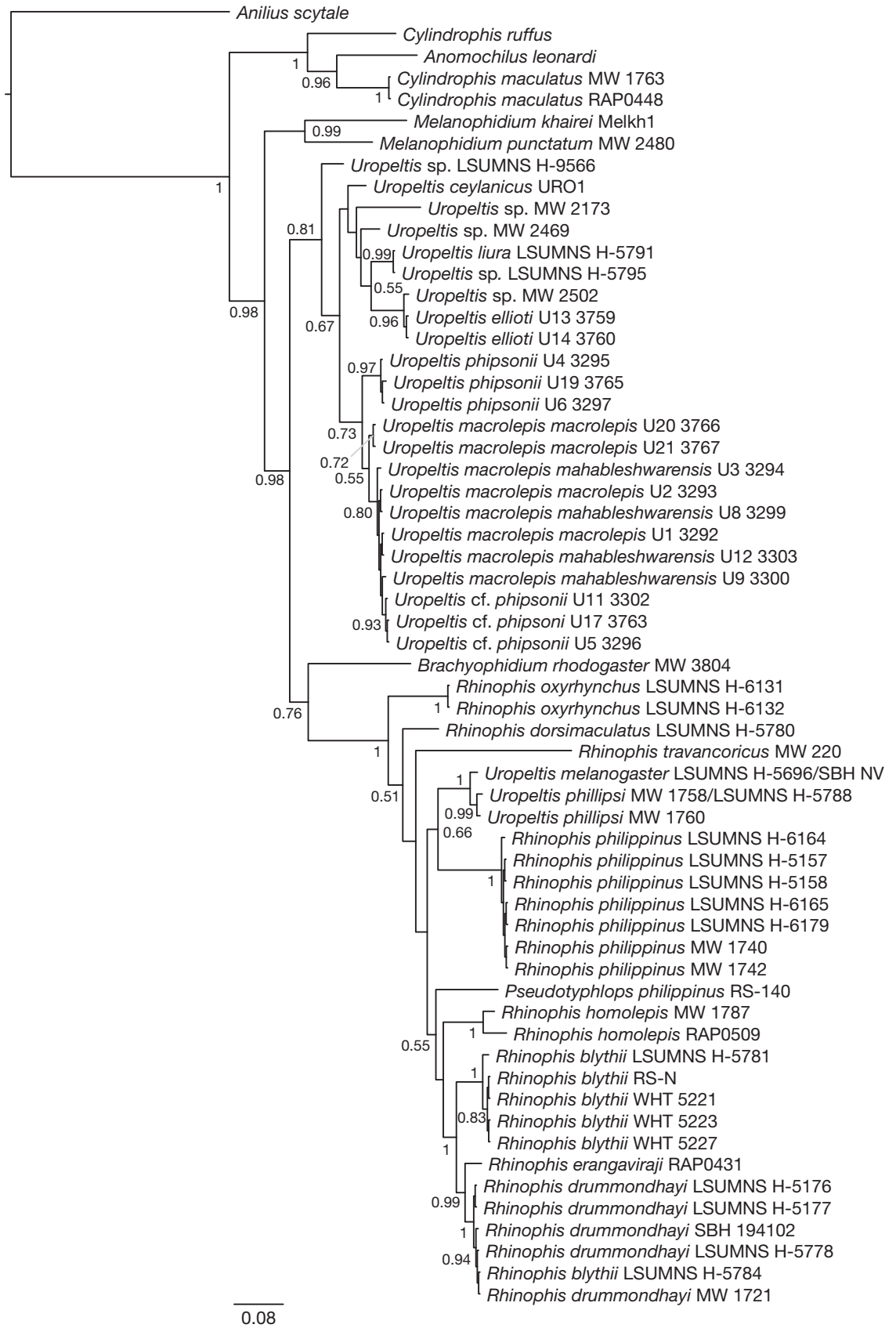


FIG. 1. — Molecular phylogeny of Uropeltidae Müller, 1832 based on Bayesian inference of 5.248bp of DNA-sequence data from 6 genes. Numbers at nodes represent posterior probabilities.

TAIL MORPHOLOGY

Another major character for external morphology of uropeltids, used by previous researchers (e.g., Smith 1943), is the morphology of the tail and tail-shield. The tails can be separated into six fairly distinct groups (see Rajendran 1985; Fig. 3). Examining each species in detail reveals ambiguity about the previous designations of many of these states, as discussed below in the accounts. For instance, Smith (1943) seems to have mis-characterized the shields of *Uropeltis melanogaster*, *U. phillipsi*, and *U. pulneyensis*, which exhibit a more rugose, keratinous disc resembling *Rhinophis* species. There is also ontogenetic development in this disc in some species. For instance, the smaller *U. melanogaster* specimens examined (MNHN-RA-1895.76 and 1999.8055; 220 and 215 mm SVL) barely exhibit a disc, while in the larger specimens (MNHN-RA-1895.69; 430 mm SVL), the disc covers the entire terminus of the tail, approximately the same diameter as the body.

Within the limits that we have established here, Type I tails are exhibited by *Brachyophidium*, *Melanophidium*, *Platyplectrurus*, and *Teretrurus*. Type II tails are exhibited by *Plectrurus* and *Pseudoplectrurus*. Type III tails are exhibited by *Uropeltis liura*, *U. maculata* (Beddome, 1878), *U. petersi* (Beddome, 1878), and *U. smithi*. Type IV tails are exhibited by *U. beddomii*, *U. dindigalensis* (Beddome, 1877), *U. ellioti*, *U. macrorhyncha*, *U. nitida*, *U. ocellata*, and *U. woodmasoni*. Type V tails are exhibited by *U. arcticeps* (Günther, 1875), *U. bicatenata* (Günther, 1864), *U. broughami*, *U. ceylanica*, *U. macrolepis*, *U. madurensis* (Beddome, 1878), *U. myhendrae* (Beddome, 1886), *U. phipsonii*, *U. rubrolineata* (Günther, 1875), *U. rubromaculata*, and *U. shorttii* (Beddome, 1863). Type VI tails are exhibited by *Pseudotyphlops*, *Rhinophis*, *U. melanogaster*, *U. phillipsi*, and possibly *U. pulneyensis* (if not Type III).

TAXONOMIC ASSESSMENT

Our molecular phylogeny, examination of specimens, and literature for morphological characters allows us to resolve some of the aforementioned taxonomic problems in Uropeltidae. We described these resolutions here, before giving revised accounts that detail the diagnostic morphological characters of each genus. Finally, we provide accounts for each species, with an overview of morphological variation.

First, the genus *Melanophidium* appears to be monophyletic and does not require any changes, as numerous morphological characters unite the four recognized species (see accounts), and the two sampled species in our molecular phylogeny are strongly supported as sister taxa. Gower *et al.* (2016) presented new data regarding the presence of palatine teeth in all species. Rieppel & Zaher (2002) had previously suggested that the genus was paraphyletic in part based on the supposed absence of palatine teeth in *M. wynaudente*. However, Gower *et al.* (2016) report that many specimens of that species do, in fact, exhibit palatine teeth. Both Rieppel & Zaher (2002) and Olori & Bell (2012) report variation in some skull characters that do not unambiguously support monophyly, but they did not sample all species, or provide strong support for paraphyly. Thus, we continue to treat *Melanophidium* as monophyletic, pending further evidence.

Secondly, *Brachyophidium* forms a moderately supported clade with *Rhinophis* to the exclusion of *Uropeltis*, but this is not conclusive. Previous studies (e.g., Bossuyt *et al.* 2004; Pyron *et al.* 2013a, b) have recovered it in this or similar positions. Sampling more characters and taxa will hopefully provide decisive support in the future.

Thirdly, we suggest that *Platyplectrurus* and *Plectrurus* are each monophyletic, based on numerous morphological characters described in the accounts below. We continue to recognize the monotypic genera *Pseudoplectrurus* and *Teretrurus* based on apparently apomorphic characters states in each taxon (see accounts). These four genera remain Uropeltidae *incertae sedis*; they share many characteristics (e.g., simple tails and snouts; divided cephalic scales) and may form a clade with *Brachyophidium*, but each also possesses distinctive characteristics and may occupy different phylogenetic positions. Hopefully, their relationships will be resolved in future studies based on sampling DNA sequence data from more species and individuals.

Fourthly, the sampled species of Indian *Uropeltis* form a monophyletic group. This includes species with 15 and 17 scale rows; species with 19 scale rows (*U. broughami*, *U. smithi*, and *U. woodmasoni*) were not sampled, but are retained in this genus to be conservative. Using the proper partitioning strategy for the DNA-sequence data with increased taxon-sampling, the monophyly of sampled Indian *Uropeltis*, including the type species *U. ceylanica*, is moderately supported (Pp = 0.81). We include the species with “Alternate Pointed” snouts, as the sampled species *U. ellioti* is in this group, and the “Alternate Rounded” species, as there is no reason to doubt their affinity.

However, as in many previous analyses (e.g., Cadle *et al.* 1990; Bossuyt *et al.* 2004; Pyron *et al.* 2013a, b), the Sri Lankan *Uropeltis* form a clade with *Rhinophis* and *Pseudotyphlops*. Additionally, the species *U. pulneyensis* might be allied with *Rhinophis* on the basis of the rostral dividing the nasals and the tail-shield having a keratinous, round, rugose disc with a blunt ending. The species *U. macrorhyncha* and *U. smithi* also have *Rhinophis*-type “Boomerang Rostrals”, putatively dividing the nasals on occasion in *U. smithi*, but they do not appear to have a *Rhinophis*-type tail shield (Type VI), but instead Type III (*U. smithi*) or Type IV (*U. macrorhyncha*).

Based directly on our molecular phylogeny, we transfer *Uropeltis melanogaster* and *U. phillipsi* to *Rhinophis* (*U. melanogaster* has been previously placed in this genus by Peters [1861b] and Jan [1863]), yielding *R. melanogaster* (Gray, 1858) and *R. phillipsi* (Nicholls, 1929) n. comb. This action was inadvertently indicated in the appendix of a previous work (Pyron *et al.* 2013b). Also corroborating previous analyses (e.g., Cadle *et al.* 1990; Pyron *et al.* 2013a, b), *Pseudotyphlops philippinus* (Müller, 1832) is nested within *Rhinophis*. We thus synonymize *Pseudotyphlops* with *Rhinophis*.

Because there is already an older species name *Rhinophis philippinus* (Cuvier, 1829), effort is thus needed to resolve the homonymy issue. The next available synonyms for *Pseudotyphlops philippinus* are from Kelaart (1853): *Uropeltis saffragamus* Kelaart, 1853, *U. grandis* Kelaart, 1853 (see below), and *U. pardalis* Kelaart, 1853. These were originally described

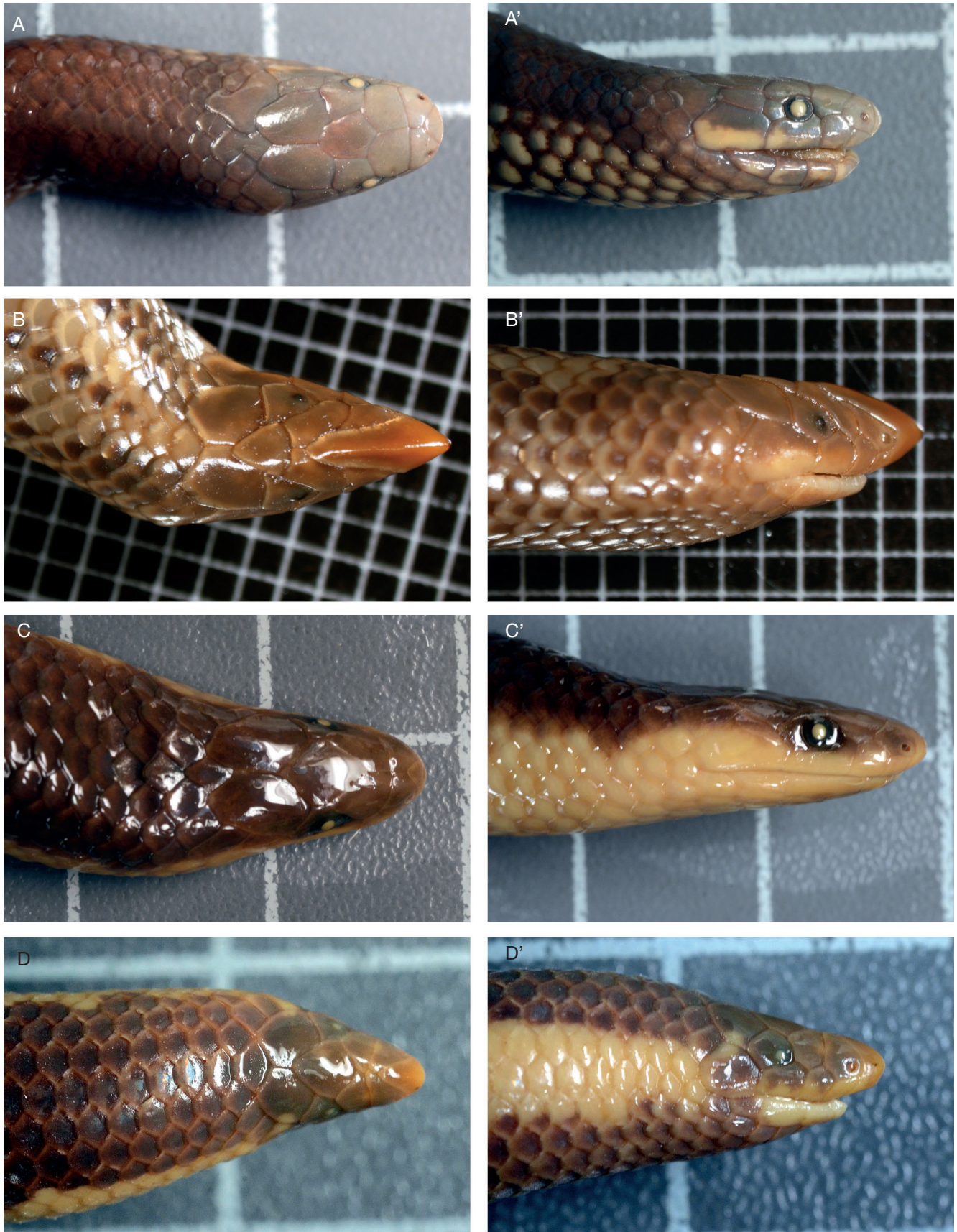


FIG. 2. — Comparison of exemplar rostral characteristics in uropeltids: A, “Rounded Rostral” (*Platyplectrurus madurensis* Beddome, 1877 MNHN-RA-1946.50); B, “Boomerang Rostral” (*Rhinophis punctatus* Müller, 1832 BMNH 1946.1.16.70); C, “Alternate Rounded” (*Uropeltis ceylanica* Cuvier, 1829 MNHN-RA-1897.258); D, “Alternate Pointed” (*U. woodmasoni* [Theobald, 1876] MNHN-RA-1895.85). Scale bars: A, C, D, 1 cm; B, 1 mm. Photos by RAP and RS.



FIG. 3. — Comparison of exemplar tail-shield characteristics of uropeltids: **A**, Type 1 (*Teretrurus sanguineus* [Beddome, 1867] MNHN-RA-1895.118); **B**, Type 2 (*Plectrurus aureus* Beddome, 1880 MNHN-RA-1895.106); **C**, Type 3 (*Uropeltis maculata* [Beddome, 1878] MNHN-RA-1895.81); **D**, Type 4 (*U. nitida* [Beddome, 1878] MNHN-RA-1895.87); **E**, Type 5 (*U. rubromaculata* [Beddome, 1867] MNHN-RA-1895.97); **F**, Type 6 (*Rhinophis philippinus* [Cuvier, 1829] BMNH 1946.1.16.99). Scale bars: A-E, 1 cm; F, 1 mm. Photos by RAP and RS.

as separate species, but are all considered junior subjective synonyms of *Pseudotyphlops philippinus* (see McDiarmid *et al.* 1999), as designated by Tennent (1861).

Under the Principle of the First Reviser (ICZN: article 24), we choose *Uropeltis saffragamus* from among the next available synonyms for *Pseudotyphlops philippinus* (Müller, 1832). Thus, the species *Pseudotyphlops philippinus* becomes *Rhinophis saffragamus* (Kelaart, 1853) n. comb.

The holotype of *U. saffragamus* is lost (*vide* Taylor 1953); thus, we designate MNHN-RA-0.5621 (the holotype of *Pseudotyphlops philippinus* [Müller, 1832]) as the neotype of *Rhinophis saffragamus* (Kelaart, 1853) n. comb., rendering them objective synonyms. Thus, *R. saffragamus* n. comb. is the only *Rhinophis* species in which the rostral does not divide the nasals, but given its nested placement, this may be a reversal.

The genus *Rhinophis* is therefore characterized by the character of the rostral dividing the nasals (possibly reversed in *R. saffragamus* n. comb.; also present in *Uropeltis pulneyensis*), and the projecting, rugose, and keratinous tail shield. Thus, *Rhinophis* also includes species with 15 (*R. sanguineus* Beddome, 1863), 17 (most species), and 19 (*R. saffragamus* n. comb.) dorsal scale rows at midbody, of which species with 17 and 19 are sampled in the molecular phylogeny here. We consider *Rhinophis sanguineus* to be allied with *Rhinophis* on the basis of cell micro-ornamentation (Gower 2003), cranial osteology (Olori & Bell 2012), and head and tail morphology (see accounts).

HOMONYMY ISSUES

Another synonym of *Rhinophis saffragamus* (Kelaart, 1853) n. comb. is *Uropeltis grandis* Kelaart, 1853, which creates a homonymy issue with *U. smithi* Gans, 1966. The name *U. smithi* Gans, 1966 was created as a replacement for *Rhinophis grandis* Beddome, 1867. A possible issue of homonymy was created when *Rhinophis grandis* Beddome, 1867 was transferred to *Uropeltis* by Smith (1943), since *U. grandis* Kelaart, 1853 was a pre-existing name. Gans (1966) thus erected *U. smithi* as a *nomen novum* for *Rhinophis grandis* Beddome, 1867, with the same type series and locality. However, Tennent (1861) had long since relegated *U. grandis* Kelaart, 1853 to the synonymy of *Pseudotyphlops philippinus* (Müller, 1832), which we here rename as *R. saffragamus* (Kelaart, 1853) n. comb.

It does not appear that Gans' creation of *Uropeltis smithi* was correct under article 57 of the ICZN, at least not under the present-day rules, because such a change would only have been necessary if the two taxa, *Rhinophis grandis* Beddome, 1867 and *Pseudotyphlops philippinus* (Müller, 1832), were considered congeneric. Thus, even though *Rhinophis grandis* Beddome, 1867 would be a secondary junior homonym of *Uropeltis grandis* Kelaart, 1853 if they were considered congeneric, there was no need to change the name of *Rhinophis grandis* Beddome, 1867, because Gans (1966) did not consider *Pseudotyphlops philippinus* (Müller, 1832) to be a member of *Uropeltis*, and neither do any other recent authors.

Thus, as *Uropeltis smithi* Gans, 1966 is here retained in *Uropeltis*, it must revert back to *Uropeltis grandis* (Beddome, 1867), as also recognized by Rajendran (1985), under article 59.4 (ICZN), mandating the reinstatement of secondary junior homonyms rejected after 1960 when the two taxa are not considered congeneric. If *Uropeltis grandis* (Beddome, 1867) is ever transferred to *Rhinophis*, it will revert to *R. smithi* (Gans, 1966), as *Uropeltis grandis* Kelaart, 1853 and *Rhinophis grandis* Beddome, 1867 would then be congeneric, and the latter would legitimately be a junior secondary homonym in conflict.

Another problematic issue of junior secondary homonymy exists in the names of the Indian taxon *Silybura melanogaster* Günther, 1875 and the Sri Lankan taxon *Myrtilia (Crealia) melanogaster* Gray, 1858. Peters (1861b) and Jan (1863) recognized the Sri Lankan taxon as *Rhinophis melanogaster*. Beddome (1886) transferred the Sri Lankan *R. melanogaster* to *Silybura*. Beddome (1886) maintained the name *S. melanogaster* for the Sri Lankan taxon, and the Indian taxon was

recognized by him as *Silybura nigra* Beddome, 1878, with Boulenger (1890, 1893a) following the same arrangement. Smith (1943) noted the synonymy of *Silybura* with *Uropeltis*, and followed Beddome (1886) in recognizing the Sri Lankan taxon as *Uropeltis (Silybura) melanogaster*, while also recognizing conspecificity of *U. woodmasoni*, *S. nigra*, and *S. melanogaster*, rather than with *U. pulneyensis* (see Beddome 1886; Boulenger 1890).

We concur with Smith (1943) that *Uropeltis woodmasoni* is distinct from *U. pulneyensis*, because of the number of midbody dorsal-scale rows (19 in *U. woodmasoni* vs 17 in *U. pulneyensis*), and the rostral separating the nasals in *U. pulneyensis* but not in *U. woodmasoni* (Smith 1943). Under article 59.3 (ICZN), a secondary homonym replaced before 1961 (in this case, in 1943 by Smith) is permanently invalid unless the substitute name is not in common use and the relevant taxa are no longer considered congeneric. We do not consider *R. melanogaster* (Gray, 1858) and *U. woodmasoni* (Theobald, 1876) congeneric, but *U. woodmasoni* is a name in common use (e.g., Wall 1928; Smith 1943; Rajendran 1985; McDiarmid *et al.* 1999; Sharma 2004; Whitaker & Captain 2004; Gower *et al.* 2008; Olori 2010; Ganesh *et al.* 2014; Wallach *et al.* 2014), and is thus preserved.

SYSTEMATIC OVERVIEW OF UROPELTIDAE

Our aim is to outline a stable family-level taxonomy that defines, diagnoses, and delimits monophyletic groups with respect to the most inclusive available datasets. As noted by many previous authors, uropeltid taxonomy is clearly in need of revision (Bossuyt *et al.* 2004; Comeaux *et al.* 2010; Olori & Bell 2012; Pyron *et al.* 2013a, b; Ganesh *et al.* 2014). Here, we outline genus-level groups that are supported by the molecular and morphological phylogenies, into which all extant species can be at least tentatively assigned based on the presence of morphological characteristics shared with species placed in our phylogeny. We also provide photographs of 28 species in life.

Maps of some Indian and Sri Lankan localities are also provided, although the type localities in original descriptions were often vague or imprecise, or names have since changed (Figs 4, 5). Accurate geographic information will be particularly important for future studies analyzing variation between populations in different areas in several taxa, such as *Teretrurus sanguineus* (Beddome, 1867), *Plectrurus perrotetii* Duméril & Bibron, 1851, and *Uropeltis ocellata* (see Rajendran 1985). Some type localities are revised to be more specific (*sensu* Smith 1953). For other species, we lack the necessary information (e.g., comparison of specimens from multiple populations) to match type specimens to revised type localities. Examining series of specimens from multiple populations will be needed to identify proper type localities for these taxa, based either on molecular or morphological data.

The following taxonomy can form the basis for future researchers investigating the phylogeny of the group using molecular and morphological data, as well as describing new species, which are likely numerous, and re-delimiting existing taxa, some of which might presently hide cryptic diversity (see

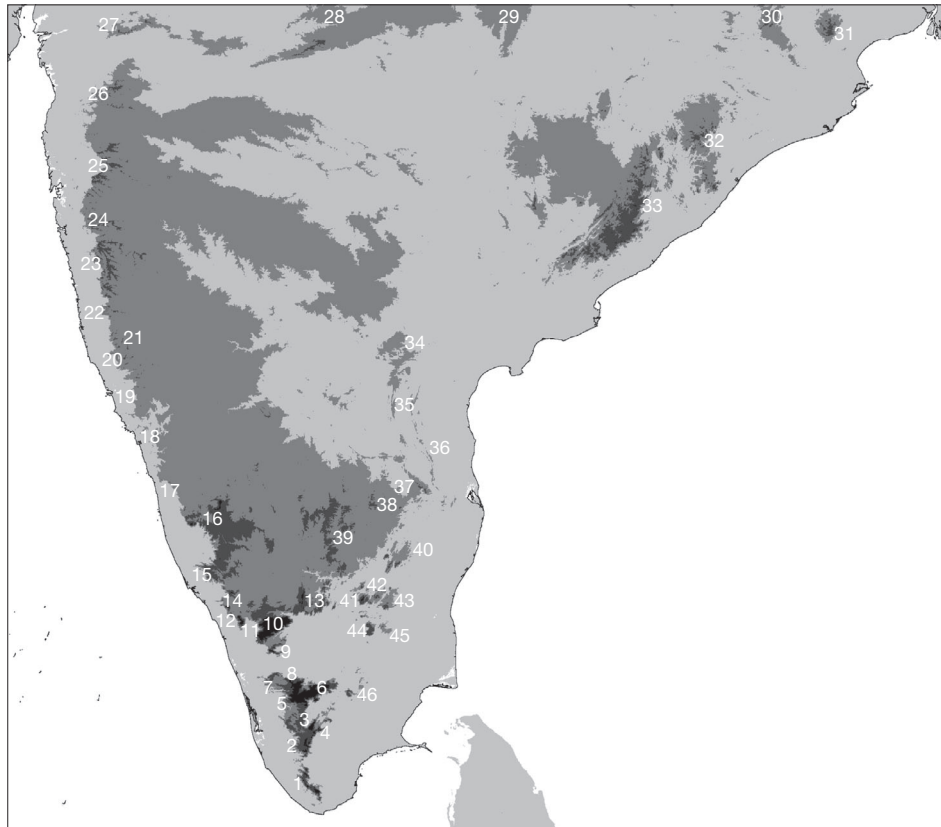


FIG. 4. — Map of the major Indian localities inhabited by uropeltids. Shaded relief indicates elevation at 500, 1000, and 1500 m. Western Ghats: **1**, Agasthyamalais; Sencotta gap; **2**, Kottamalai/Periyar hills; **3**, Meghamalai/High Wavy Mts.; **4**, Srivilliputhur hills; **5**, Munnar/High Range; **6**, Kodaikanal/Palnis; **7**, Nelliampathis; **8**, Anaimalais; Palghat gap; **9**, Sirvani/Muthikulam hills; **10**, Nilgiris; **11**, Wayanad; **12**, Elivalmalai; **13**, Bilgiriangan hills; **14**, Bramagiri-Pushpagiri; **15**, Kodagu/Coorg hills; **16**, Kudramukh hills; **17**, Jog/Canara Ghats; **18**, Castle Rock; Goa gap; **19**, Goa hills; **20**, Amboli hills; **21**, Koyna hills; **22**, Kolhapur; **23**, Ratnagiri hills; **24**, Satara; **25**, Mulsi/Pune hills; **26**, Nasik hills; **27**, Dangs. Central Indian hills: **28**, Pachmarhi hills; **29**, Seoni hills. Eastern Ghats: **30**, Khandadhar hills; **31**, Simlipal hills; **32**, Mahendragiri; **33**, Vizag Ghats; **34**, Srisailem hills; **35**, Nallamalais; **36**, Tirupathi hills; **37**, Tada hills; **38**, Chittoor hills; **39**, Horsely hills; **40**, Yelagiri-Jawadi hills; **41**, Shevaroy's/Yercaud; **42**, Chitteri hills; **43**, Kalrayan hills; **44**, Kolli hills (also Bodamalai); **45**, Pachaimalai; **46**, Sirumalai-Karandmalai.

Rajendran 1985; Gower *et al.* 2008; Ganesh *et al.* 2014). We provide diagnoses for the family and all genera, presenting characters that, in combination, uniquely diagnose each taxon. We also give accounts for every species (see below), with specimen photographs and life illustrations for some taxa when available (Figs 6-9). Except when noted, type localities and type material lists are taken from Gans (1966), McDiarmid *et al.* (1999), and Wallach *et al.* (2014). When localities are given for the distribution, these are mapped in Figure 4 and 5.

UROPELTIDAE Müller, 1832

TYPE GENUS. — *Uropeltis* Cuvier, 1829 by subsequent designation of Fitzinger (1843).

INCLUDED GENERA. — *Brachyophidium*, *Melanophidium*, *Platyplectrurus*, *Plectrurus*, *Pseudoplectrurus*, *Teretrurus*, *Rhinophis*, and *Uropeltis*.

DIAGNOSIS. — Uropeltids are distinguished from all other amniotes by a unique condition of the occipito-vertebral joint (Baumeister 1908; Hoffstetter 1939; Williams 1959). In all species examined thus far (including species from *Melanophidium*, *Platyplectrurus*, *Plectrurus*, *Rhinophis*, *Teretrurus*, and *Uropeltis*), the second vertebra articulates directly with the occipital condyle. These elements exhibit simple

matching convexity and concavity, with no notching or indentation, and there is no intervening odontoid process. The neural arch of the atlas is always present and articulates directly with the neural arch of the second vertebra and the convexity of the occipital condyle. Furthermore, Uropeltidae differs significantly from its sister lineage, *Cylindrophiiidae* + *Anomochilus*, in the following characteristics of visceral anatomy: longer trachea (mean 31% of SVL vs 27%), shorter right lung (23% vs 29%), more posterior orifice of the left lung (32% vs 26%), larger snout-heart interval indicating a more posterior heart (32% vs 27%), larger kidney-vent interval indicating more anterior kidneys (20% vs 13%), larger heart (4.3% vs 3.4%), smaller liver (23% vs 29%), larger right kidney (7.8% vs 5.1%), more anterior right kidney (84% vs 90%), larger left kidney (7.5% vs 4.9%), more anterior left kidney (88% vs 92%), more anterior junction of the systemic arches (−2% vs 0.4%), and more anterior gallbladder (68% vs 74%).

PHYLOGENETIC DEFINITION. — Includes the Most Recent Common Ancestor (MRCA) of *Melanophidium wynaudente* and *Uropeltis ceylanica*, and all descendants thereof, and all species more closely related to *U. ceylanica* than to *Cylindrophis ruffus* (Fig. 1).

DISTRIBUTION. — Peninsular India and Sri Lanka, primarily in the southern Western Ghats of India and southwestern and central Sri Lanka, but with a few species in the Eastern Ghats and northern Western Ghats of India, and northern Sri Lanka (Smith 1943; Rajendran 1985). Many species are highly restricted geographically, and known only from a few specimens and localities.

DESCRIPTION

Uropeltids are small snakes (generally < 500 mm total length), usually fossorial though occasionally surface active, that feed primarily on earthworms and other invertebrates (Smith 1943; Rajendran 1985). Many species of *Rhinophis* and *Uropeltis* have hypertrophied anterior-trunk musculature to facilitate burrowing (occasionally over a meter underground), with associated fusion of the skull elements (see Gans *et al.* 1978; Rieppel & Zaher 2002). Many species (especially of *Rhinophis* and *Uropeltis*) have a highly specialized tail presenting a keratinized disk or plate with keels or projections, generally considered to be of unknown function (Smith 1943; Rajendran 1985). In most species, a polygonal ocular shield covers the eye. In some taxa (*Platyplectrurus*, *Plectrurus*, and *Teretrurus*), the supraocular and postocular scales are separated, and the eye is distinct. As far as is known, all uropeltids are viviparous (Smith 1943; Rajendran 1985). All species have four supralabials, with the second and third in contact with the nasals, no internasals, and no loreal (with rare individual variation; see Constable 1949). A temporal is present in some taxa (*Brachyophidium*, *Platyplectrurus*, and *Teretrurus*), separating the parietal from the fourth supralabial, the latter two of which are in contact in the remaining taxa. The anal and subcaudals are divided, and the tail is short (*c.* 2-8% SVL; see data in Rajendran 1985; Table 2). Little is known about hemipenial morphology (Smith 1943; Constable 1949). The organ in *Melanophidium* is short and thick, lacking spines, with the sulcus spermaticus winding through a series of long, convoluted folds (Smith 1943). In *Uropeltis grandis*, it is longer and more slender, and covered with fine spines (Smith 1943). In *Rhinophis lineatus* Gower & Maduwage, 2011, it is moderately long (*c.* 4 mm), slender, and subcylindrical, with curved spines covering the distal third, with the first two-thirds smooth, and a shallow, smooth sulcus spermaticus (Gower & Maduwage 2011). In *R. dorsimaculatus* Deraniyagala, 1941, it is similarly long, slender, and subcylindrical, with fine spines covering most of the asulcate surface, and a smooth sulcate surface with shallow, smooth sulcus spermaticus (Gower & Wickramasinghe 2016).

REMARKS

Some previous authors considered Uropeltidae to form a clade with Aniliidae, Cyliodrophiidae, and Anomochilidae Cundall, Wallach & Rossman, 1993, called Anilioidea (see Lee & Scanlon 2002; Conrad 2008; Gauthier *et al.* 2012), but this is rejected by most large-scale molecular analyses (see Wilcox *et al.* 2002; Gower *et al.* 2005; Wiens *et al.* 2012; Pyron *et al.* 2013a). From a biogeographic perspective, monophyly of these four families also seems extremely unlikely. The clade would have to be > 150Ma to explain their distribution *via* Gondwanan vicariance. However, Alethinophidia has been dated to *c.* 100Ma (Pyron & Burbrink 2012). Given the relatively young age of the four families, a complex route of dispersal from South America to India during the Cenozoic, with no relicts in intervening areas would be needed to account for their biogeographic distribution if they formed a single clade. Rather, large-scale convergence in aspects of cranial and verte-

bral morphology related to burrowing (see Wiens *et al.* 2010) likely explains the morphological similarities of Aniliidae and Cyliodrophiidae, Anomochilidae and Uropeltidae.

Brachyophidium Wall, 1921

Brachyophidium Wall, 1921: 41.

TYPE SPECIES. — *Brachyophidium rhodogaster* Wall, 1921 by monotypy.

INCLUDED SPECIES. — *Brachyophidium rhodogaster*.

DIAGNOSIS. — *Brachyophidium* can be distinguished from all other amniotes by the characters given above for the family, and from other uropeltids by eye in ocular shield, nasals in contact, a temporal, no mental groove, dorsal scales in 15 rows at midbody, a simple, unmodified tail tapering to a single pointed scale, and interchoanal process of parasphenoid absent (see Olori & Bell 2012).

DISTRIBUTION. — India, in the Anaimalai and Palni hills of the southern Western Ghats (see Wall 1923; Whitaker & Captain 2004; Wallach *et al.* 2014; Ganesh 2015).

REMARK

This genus has occasionally been considered synonymous with *Teretrurus* (Smith 1943; Cadle *et al.* 1990; Rieppel & Zaher 2002), but is diagnosable from that genus by the presence of fused oculars.

Brachyophidium rhodogaster Wall, 1921

(Fig. 6A)

Brachyophidium rhodogaster Wall, 1921a: 41.

TYPE MATERIAL. — Holotype: BMNH 1921.3.4.13 (= 1946.1.15.60).

TYPE LOCALITY. — Designated as Sacred Heart College, Shembaganur, *c.* 5 km North of Kodaikanal, Palani hills, Tamil Nadu state, India by Wall (1922).

DISTRIBUTION. — India, endemic to the Anaimalai-Palni hill complex, at elevations *c.* 1280-2100 m (see Wall 1923; Whitaker & Captain 2004; Wallach *et al.* 2014; Ganesh 2015).

DESCRIPTION

Small even for uropeltids, with a maximum total length of 190-230 mm, dorsum dark brown to black, and red venter (see Rajendran 1985). Tail is slightly compressed laterally, ending in a single point, dorsal scales of tail occasionally weakly bi- or tri-carinate. Ventrals 131-145, subcaudals 6-11 (Wall 1922; Constable 1949; Whitaker & Captain 2004). In the two specimens dissected, there was no anterior lobe of the right lung observed, a condition otherwise seen only in some specimens of *Rhinophis saffragamus* n. comb. and *R. philippinus*. The one specimen for which tracheal rings could be counted had 165, which is less than any specimen of *Melanophidium* (211), *Platyplectrurus* (227), *Plectrurus* (180-222), *Pseudoplectrurus* (216), or *Teretrurus* (177-181), though some specimens of *Rhinophis* and *Uropeltis* have fewer than 165.

REMARKS

The type species of *Brachyophidium* (by original monotypy). This species was reported to be relatively common at several sites by Rajendran (1985).

Melanophidium Günther, 1864

Melanophidium Günther, 1864: 193.

TYPE SPECIES. — *Plectrurus wynaudensis* Beddome, 1863a by original monotypy.

INCLUDED SPECIES. — *Melanophidium bilineatum* Beddome, 1870, *M. khairei*, *M. punctatum*, *M. wynaudense*.

DIAGNOSIS. — *Melanophidium* can be distinguished from all other amniotes by the characters given for the family, and from other uropeltids by a mental groove, dorsal scales in 15 rows at mid-body, eye in ocular shield, and no temporal. At least three species (*M. bilineatum*, *M. punctatum*, and *M. wynaudense*) have a unique micro-ornamentation pattern of dorsal scales at midbody, having large (> 18.5 mm), rounded polygonal *Oberhäutchen* cells with level borders and no denticulations (Gower 2003). These characters separate them from 16 other uropeltid species from all genera except *Pseudoplectrurus*, and are thus likely also diagnostic characters. In recent studies of skull morphology, the following characters are shared by *M. punctatum* and *M. wynaudense*, but not by any sampled representatives of other uropeltid genera (i.e. they are likely, but not definitely, diagnostic of *Melanophidium*; though *Pseudoplectrurus* and *Teretrurus* were not sampled): supraoccipital separate, prootic and opisthotic-exoccipital separate, basisphenoid-basioccipital separate, facial nerve branches into open recess behind the mandibular branch foramen which connects with the posterior opening of the Vidian canal, and posteroventral process of dentary distinct (Rieppel & Zaher 2002; Olori & Bell 2012).

DISTRIBUTION. — India, in the Western Ghats as far North as Amboli (Whitaker & Captain 2004; Gower *et al.* 2016).

DESCRIPTION

Tail is longer (up to 8% SVL; see Rajendran 1985; Table 2) than in most other uropeltids, but not as heavily compressed or modified; caudal scales are unkeeled and terminal scute is small and smooth or terminates in two to four points. In the single specimen of *M. wynaudense* dissected, no aspect of visceral topology is significant in uniquely distinguishing it from other uropeltid genera. However, mean of the heart-liver interval (15% of SVL) is larger than that measured for any other uropeltid genus, the next largest being *Rhinophis* (10% SVL; Table 3). All four species with teeth on the palatine, a condition otherwise absent in Uropeltidae (Rieppel & Zaher 2002; Cundall & Irish 2008; Olori & Bell 2012; Gower *et al.* 2016). However, this condition is variable in *M. wynaudense*, with most examined specimens lacking teeth (Gower *et al.* 2016). All species exhibit a striking blue-green iridescence, which is still noticeable in preservative as it derives from microstructural features in the scales, rather than pigments (see Gower 2003). Few objective and unambiguous external morphological features separate the known species, which are identifiable primarily based on color pattern (Smith 1943; Gower *et al.* 2016). Monophyly of this genus has been questioned in the past (Rieppel & Zaher 2002), but is supported

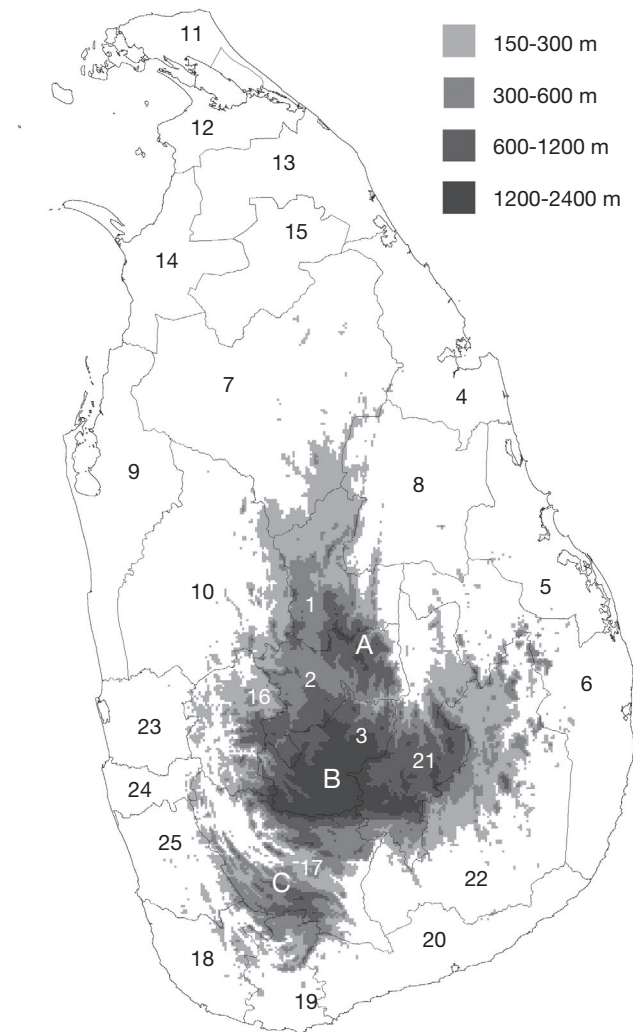


FIG. 5. — Map of the major Sri Lankan localities inhabited by uropeltids, indicating massifs and provinces/districts. Massifs: **A**, Knuckles; **B**, Central; **C**, Rakwana. Central province: 1, Matale; 2, Kandy; 3, Nuwara Eliya. Eastern province: 4, Trincomalee; 5, Batticaloa; 6, Ampara. North Central province: 7, Anuradhapura; 8, Polonnaruwa. North Western province: 9, Puttalam; 10, Kurunegala. Northern province: 11, Jaffna; 12, Kilinochchi; 13, Mullaitivu; 14, Mannar; 15, Vavuniya. Sabaragamuwa province: 16, Kegalle; 17, Ratnapura. Southern province: 18, Galle; 19, Matara; 20, Hambantota. Uva province: 21, Badulla; 22, Moneragala. Western province: 23, Gampaha; 24, Colombo; 25, Kalutara.

by our molecular phylogeny (part), the presence of a mental groove, and the unique features of scale micro-ornamentation and skull morphology (part) given in the diagnosis (Rieppel & Zaher 2002; Gower 2003; Olori & Bell 2012; Gower *et al.* 2016).

REMARKS

A lack of comparative analyses hid the existence of *Melanophidium khairei* for 144 years, disguised as *M. punctatum* (see Gower *et al.* 2016). Extralimital records and confounding character-states exist for each species (see below and Gower *et al.* 2016); there is likely additional cryptic and undiscovered diversity in this group, as with most uropeltid genera.

Melanophidium bilineatum Beddome, 1870

Melanophidium bilineatum Beddome, 1870: 169.

TYPE MATERIAL. — Lectotype: BMNH 1872.1.2.5 (= 1946.1.15.750). Paralectotype: MNHN-RA-1895.111. Both designated by Gower *et al.* (2016).

TYPE LOCALITY. — Lectotype: Periya peak, Wayanad District, Kerala state, India. Paralectotype: possibly Terrihiot peak, Wayanad District, Kerala state, India. Exact localities unclear; see Remarks.

DISTRIBUTION. — India, definitively known only from the type locality, Periya and Tirrihiot peaks in the Wayanad hills, at elevations > 1200 m (Gower *et al.* 2016), but see Remarks).

DESCRIPTION

Maximum total length of *c.* 360 mm, 188–200 ventrals, 14–17 subcaudals, dorsal scales in 15 rows at midbody (see Smith 1943; Gower *et al.* 2016). Color pattern typically a bluish-black venter and dorsum marked by thick light-yellow lines situated dorsoventrally, running from the head to the tail. This character is considered diagnostic (Gower *et al.* 2016).

REMARKS

We concur with Gower *et al.* (2016) in doubting a recent report of this species from the Anaimalai hills South of the Palghat Gap (Vijayakumar *et al.* 2001), as only *M. punctatum* is known from this region. This species is known from a very small number of specimens and sites, possibly restricted to the four specimens from the original collection. Beddome (1870) reported collections at 5000 ft from Periya and Terrihiot peaks, and in 1886 clarified that there were four individuals collected (three adults and one juvenile) at elevations around 4000 ft from those localities. Smith (1943) and Gans (1966) erroneously reported three types, but there are only two, plus two additional specimens from Beddome. Gower *et al.* (2016) report the lectotype as originating from Periya Peak, and two additional BMNH specimens, one adult and one juvenile (together with the lectotype apparently representing three of Beddome's original four), as originating simply from "Wayanad district". Thus, it seems likely that the adult paralectotype from Paris represents the collection from Terrihiot Peak. However, the actual locations of these collections is unclear; there are no peaks > 1200 m in the immediate vicinity of Periya (which is *c.* 800 m), though these elevations can be found *c.* 15 km to the North or the south. Gower *et al.* (2016) also report a specimen (BNHS 3410) from Gurukula, near Periya, at *c.* 800 m. Thus, this species may occur at lower (*c.* 800 m elevations), but apparently only in a small region in the vicinity of Periya, Kerala state, India.

Melanophidium khairei

Gower, Giri, Captain & Wilkinson, 2016

Melanophidium khairei Gower, Giri, Captain & Wilkinson, 2016: 482.

TYPE MATERIAL. — Holotype: BNHS 3452. Paratypes: BNHS 96, 3199, 3253, 3444–3446, 3472.

TYPE LOCALITY. — Holotype: Amboli, Sindudurg district, Maharashtra, India. Paratypes: Patgaon, Kolhapur district, Maharashtra (BNHS 3444–3446); Verle, South Goa, Goa (BNHS 3472); "Jelewadi, Goa Frontier", likely Telewadi, Karnataka (BNHS 96).

DISTRIBUTION. — A small range at elevations *c.* 500–800 m in semi-evergreen forests in the Western Ghats of northern Karnataka, Goa, and southern Maharashtra states, India (Gower *et al.* 2016).

DESCRIPTION

Maximum total length of *c.* 550 mm, 191–200 ventrals, 11–13 subcaudals, dorsal scales in 13–15 rows at midbody, fewer than 13 subcaudal scales, typically exhibiting scale-row reduction to 13 rows (from 15) at midbody (between the 20th and 40th ventral), and having a short, dorsoventrally-compressed terminal scute (Gower *et al.* 2016). Color pattern usually dark brown or black, piebald and punctate (white or yellowish-white markings). These characters are considered diagnostic (Gower *et al.* 2016; but see Remarks).

REMARKS

Reported to be relatively common in recent collections, this species was long considered (see Gower *et al.* 2016) to represent a northern population isolate of *Melanophidium punctatum* (e.g., Srinivasulu *et al.* 2013), but also superficially resembles *M. wynaudense*. Exact relationships remain unclear, pending further molecular sampling in the genus. The specimen identified here as *M. khairei* and included in the molecular phylogeny originates from a topotypic population and generally appears to match the description of *M. khairei* given above (Appendix 2).

Melanophidium punctatum Beddome, 1871

(Fig. 6B)

Melanophidium punctatum Beddome, 1871: 401.

TYPE MATERIAL. — Lectotype: BMNH 1872.1.2.6 (= 1946.1.4.37) and paralectotypes: BMNH 1874.4.29.121–122 (= 1946.1.15.48–49) and MNHN-RA-1895.116. Designated by Gower *et al.* (2016), but see Remarks.

TYPE LOCALITY. — Lectotype: Muthukuzhi Vayal in the Kalakkad-Mundanthurai Tiger Reserve in the Agasthyamalai hills, Kerala state, India. Paralectotypes: Azhutha, Kerala state, India.

DISTRIBUTION. — India, Agasthyamalai hills, at elevations > 1000 m. This is the only *Melanophidium* species occurring South of the Palghat Gap (see Gower *et al.* 2016).

DESCRIPTION

Maximum total length 560 mm but generally *c.* 400 mm, ventrals 180–198, subcaudals 14–18, dorsal scales in 15 rows at midbody, subcaudals typically in 15–17 but occasionally 14–18 pairs, and no dorsal scale-row reduction (Smith 1943; Whitaker & Captain 2004; Gower *et al.* 2016). Color pattern typically characterized by a black venter and dorsum marked dorsoventrally by white edging surrounding the black pigment, giving the appearance of rows of spots running alongside the ventral scales. This character is considered diagnostic (Gower *et al.* 2016).



FIG. 6. — Some uropeltid species photographed in life: **A**, *Brachyophidium rhodogaster* Wall, 1921; **B**, *Melanophidium punctatum* Beddome, 1871; **C**, *M. wynaudense* Beddome, 1863; **D**, *Platyplectrurus madurensis* Beddome, 1877; **E**, *Plectrurus perrotetii* Duméril & Bibron in Duméril & Duméril, 1851; **F**, *Rhinophis blythii* Kelaart, 1853; **G**, *R. erangaviraji* Wickramasinghe, Vidanapathirana, Wickramasinghe & Ranwella, 2009; **H**, *R. goweri* Aengals & Ganesh, 2013. Photos by RAP, RS, SRG, VS, A. Singh, K. Ukuwela, and R. Pethiyagoda.

REMARKS

Beddome (1871) reports one specimen (*c.* 457 mm TL) from ‘Muti-kuli vayal’ (Muthukuzhi Vayal in the Kalakkad-Mundanthurai Tiger Reserve) in the Agasthyamalai (“Asambo” = Ashambu) hills, and two (an adult and a juvenile) from the much more northerly ‘Peermede’ (= Azhutha). The existence of four putative syntypes is thus unclear. The Muthukuzhi Vayal specimen (BMNH 1872.1.2.6 [= 1946.1.4.37]) was erroneously listed as BMNH 1946.1.4.73 by Wallach *et al.* (2014). The MNHN specimen was not specified by Beddome (1871), but was listed by Gans (1966) as a type, and was collected by Beddome. The MNHN specimen is *c.* 400 mm TL, from Peermede, and likely represents one of BMNH 1874.4.29.121-122, later sent to Paris. Welch (1988) listed the type locality only as Agasthyamalai hills. This restriction was cemented by Gower *et al.* (2016). Populations of *M. khairi* were long considered to be *M. punctatum* (e.g., Srinivasulu *et al.* 2013; see Gower *et al.* 2016).

Melanophidium wynaudense (Beddome, 1863)
(Fig. 6C)

Plectrurus wynaudensis Beddome, 1863a: 48.

TYPE MATERIAL. — Lectotype: BMNH 1874.4.29.84 (=1946.1.15.46) and paralectotypes: BMNH 1864.3.9.6 (= 1946.1.15.74) and MNHN-RA-1895.108-109. Designated by Gower *et al.* (2016), but see Remarks.

TYPE LOCALITY. — Cherambadi, Tamil Nadu state, India (see Remarks).

DISTRIBUTION. — India, distributed from the Nilgiri hills to Agumbe, at elevations *c.* 600-2100 m (see Wall 1919; Ganesh *et al.* 2012; Wallach *et al.* 2014; Ganesh 2015).

DESCRIPTION

Maximum total length *c.* 440 mm, ventrals 170-189, subcaudals 11-12 but occasionally 10-18, dorsal scales in 15 rows at midbody (Boulenger 1890; Wall 1919; Smith 1943; Ganesh *et al.* 2012; Gower *et al.* 2016). Color pattern distinguishable by a bluish-black dorsum marked by broad white patches on the venter, which increase in size and irregularity towards the tail. This character is considered diagnostic (Gower *et al.* 2016).

REMARKS

We follow McDiarmid *et al.* (1999) in considering Beddome (1863a) as the original description, supporting the current spelling over *Plectrurus wynandensis* Beddome, 1863 given by Beddome (1863b). However, this is not a settled matter, and may need to be referred to the ICZN. Regarding the type species of *Melanophidium*, the type locality Cherambadi is in Tamil Nadu, not Kerala as stated by Wallach *et al.* (2014). This species was long known from relatively few specimens, with recent reports from new localities (Ganesh *et al.* 2012). Large variation in scale counts among different widespread localities (see Ganesh *et al.* 2012 and discussion therein) may indicate cryptic diversity.

Platyplectrurus Günther, 1868

Platyplectrurus Günther, 1868: 414.

Wallia Werner, 1925: 53. Type species: *Wallia inexpectata* Werner, 1925 by monotypy; designated as a subjective junior synonym of *Platyplectrurus madurensis* Beddome, 1877 by Smith (1928).

TYPE SPECIES. — *Plectrurus trilineatus* Beddome, 1867 by original monotypy.

INCLUDED SPECIES. — *Platyplectrurus madurensis*, *P. trilineatus*.

DIAGNOSIS. — *Platyplectrurus* can be distinguished from all other amniotes by the characters given for the family, and from other uropeltids by divided oculars, nasals in contact, temporal, lack of a mental groove, dorsal scales in 15 rows at midbody, and posteroventral process of dentary reduced in *P. madurensis* (see Olori & Bell 2012).

DISTRIBUTION. — India, in the Western Ghats between the Sencotta and Palghat gaps, from hills including the Anaimalai-Palni hill complex (see Wall 1923; Smith 1943; Ganesh 2011; Wallach *et al.* 2014; Ganesh 2015).

DESCRIPTION

The tail is slightly compressed dorsolaterally, with smooth scales terminating in a scute with a single point. Only a single specimen of *Platyplectrurus madurensis* was dissected, and no characteristic of visceral topology is significant in uniquely diagnosing it from other uropeltid genera. However, a number of characteristics are divergent from other uropeltids. These are a trachea shorter (25% of SVL) than any other uropeltid specimen examined (mean 31%), a more anterior right lung (Rltip 46% of SVL) than any other specimen examined (mean 55%), and left lung absent but present in all other uropeltids examined. These characters should be examined in more specimens to determine if they are indeed diagnostic of the genus.

REMARK

Should not be considered to occur in Sri Lanka (see above).

Platyplectrurus madurensis Beddome, 1877
(Fig. 6D)

Platyplectrurus madurensis Beddome, 1877: 167. Five syntypes: BMNH 1883.1.12.52 (= 1946.1.15.64), BMNH 1883.1.12.56-58 (= 1946.1.15.78-80), and MNHN-RA-1895.115a-b. Type locality: near Kodaikanal, Tamil Nadu state, India.

Wallia inexpectata Werner, 1925: 54. Holotype: NMW 18511. Type locality: Pulney hills, Tamil Nadu state, India. Designated as a junior subjective synonym by Smith (1928).

Plectrurus ruhunae Deraniyagala, 1954: 24. Holotype: NMSL 51. Type locality: Galle District, Sri Lanka. Designated here as a junior subjective synonym.

DISTRIBUTION. — India, distributed in the Palni and Munnar hills at elevations > 1200 m (Wall 1923; Roux 1928; Wallach *et al.* 2014; Ganesh 2015).

DESCRIPTION

Maximum total length *c.* 440 mm, ventrals 149-175, subcaudals 10-16 (see Beddome 1877; Smith 1943; Rajendran 1985). Color pattern typically with dark brown dorsal coloration and somewhat lighter dorsolateral stripes covering a single scale row, and ventral and dorsoventral scales (first 2-3 rows) edged in lighter brown with lighter (white or yellow) centers, giving the appearance of rows of white spots.

REMARKS

This species should not be considered to occur in Sri Lanka (see above). Deraniyagala (1954) diagnosed *Plectrurus rubunae* from *Platyplectrurus madurensis* in part based on the number of ventrals (166), but this is within the range reported by Smith (1943) and Rajendran (1985) of 158-175 for *P. madurensis*. For this and the reasons described above regarding the provenance of Deraniyagala's specimens, we consider *Ple. rubunae* to represent a specimen of *P. madurensis* erroneously referred to Sri Lanka.

Platyplectrurus trilineatus (Beddome, 1867)

Plectrurus trilineatus Beddome, 1867: 14. Three syntypes: BMNH 1866.12.15.10 (= 1946.1.15.72) and MNHN-RA-1895.112-113. Type locality: Pollachi, Anamalai hills, Tamil Nadu state, India.

Platyplectrurus bilineatus Beddome, 1886: 33. Three syntypes: BMNH 1883.1.12.60-61 (= 1946.1.23.54-55), MNHN-RA-1895.114. Type locality: "Madura hills". Designated as a junior subjective synonym by Boulenger (1893a).

DISTRIBUTION. — India, in the Anaimalai and possibly Palni hills, at elevations > 1200 m (see Rajendran 1985; Ganesh 2011, 2015).

DESCRIPTION

Slender, maximum total length *c.* 390 mm, ventrals 163-175, subcaudals 8-16 (Smith 1943; Rajendran 1985; Ganesh 2011). Color pattern typically light brown to reddish-brown dorsal coloration with three rows of dark spots, one down the center of the back, and dorsolaterally on either side of the body (see Ganesh 2011).

REMARK

This species is rarely encountered (see Ganesh 2011). Although reportedly originating from Anaimalais (see Beddome 1867), field studies recorded this species from the Palnis, but surveys in the Anaimalais failed to uncover any specimens (Roux 1928; Rajendran 1985).

Plectrurus Duméril & Bibron
in Duméril & Duméril, 1851

Plectrurus Duméril & Bibron in Duméril & Duméril, 1851: 224.

Maudia Gray, 1858a: 261. It appears that Gray (1858a) intended to place *Plectrurus perrotetii* in *Maudia*, making it the type species

by monotypy, and rendering *Maudia* an objective junior synonym of *Plectrurus*.

TYPE SPECIES. — *Plectrurus perrotetii* Duméril & Bibron in Duméril & Duméril, 1851.

INCLUDED SPECIES. — *Plectrurus aureus* Beddome, 1880, *P. guentheri* Beddome, 1863, *P. perrotetii*.

DISTRIBUTION. — India, Wayanad Plateau and Nilgiri hills (see Beddome 1886; Wallach *et al.* 2014; Ganesh 2015).

DIAGNOSIS. — *Plectrurus* can be distinguished from all other amniotes by the characters given for the family, and oculars divided, nasals in contact, no temporal, no mental groove, dorsal scales in 15 rows at midbody, juxtaspinal process distinctly restricted by approximation of dorsal and ventral margin and fenestra pseudorotunda never exposed in lateral view (*P. perrotetii*) or juxtaspinal process wide open laterally and fenestra pseudorotunda may be exposed in lateral view (*P. aureus*; see Olori & Bell 2012), and *Oberhäutchen* cells 10-20 mm (*P. perrotetii*; Gower 2003).

DESCRIPTION

Tail is slightly compressed with weakly multicarinate scales terminating in a scute with two bifid points. Between the one specimen of *Plectrurus aureus* and two of *P. perrotetii* dissected, no characteristic of visceral topology is significant in uniquely diagnosing the genus from other uropeltid genera. However, a number of characteristics of those specimens appear to be at or near the ranges of other genera. The first is the size of the left lung, which is smaller (mean of 0.85% SVL) compared to the other genera (2.55%). The second is a smaller heart (3.70%) compared to the other genera (4.38%). The third is a more posterior junction of the systemic arches (-0.48%) compared to the other genera (-2.16%). These should be examined in more specimens to determine if they are indeed diagnostic of the genus.

REMARKS

With the exception of *Plectrurus perrotetii*, which is common at several sites throughout its range (Rajendran 1985; SRG pers. obs.), the other species are very rarely encountered and have been collected either not at all (*P. aureus*), or very rarely (*P. guentheri*) since their original description in the late 19th century. Gray (1858a) placed *Plectrurus* in a subgroup *Plecturina*, which is thus a valid name in the family series (e.g., subfamily *Plecturinae* Gray, 1858). We do not recognize any subfamilies of Uropeltidae at present. Two specimens in the BMNH (1964.1678 & 1964.1713) have tags labeled "*Plectrurus* undescribed sp., In bottle A? Ceylon". However, *Plectrurus* was historically much larger and included many species, including *Rhinophis melanogaster* (see Peters 1859). These specimens have a rostral separating the nasals, fused oculars, no temporal, and 17 dorsal scale rows, clearly allying them with Sri Lankan *Rhinophis*, and not *Plectrurus* or other uropeltid genera with nasals in contact, separated oculars or a temporal, and 15 dorsal scale rows. Positive identification of these specimens is difficult, but we suggest that *Plectrurus* should not be considered part of the Sri Lankan snake fauna.

Plectrurus aureus Beddome, 1880

Plectrurus aureus Beddome, 1880: 182.

TYPE MATERIAL. — Two syntypes: BMNH 1883.1.12.53 (= 1946.1.1.54) and MNHN-RA-1895.107.

TYPE LOCALITY. — Chembra Peak, Wayanad hills, Kerala state, India.

DISTRIBUTION. — India, known only from type locality, in the western Nilgiris at elevations *c.* 2050 m (see Beddome 1880; Wallach *et al.* 2014; Ganesh 2015).

DESCRIPTION

Maximum total length *c.* 400 mm, ventrals 164–177, subcaudals 8–12 (see Beddome 1880; Smith 1943). Distinctive color-pattern, with a golden-brown dorsum incompletely ringed with fragmentary purplish-black crossbands or spots.

REMARK

This species has apparently not been collected since the late 19th century based on a lack of recent published reports or accessioned specimens, and is known from only a few specimens collected by Beddome.

Plectrurus guentheri Beddome, 1863

Plectrurus guentheri Beddome, 1863a: 48.

TYPE MATERIAL. — Holotype: BMNH 1883.1.12.54 (= 1946.1.16.32).

TYPE LOCALITY. — Walaghat, Nilgiri hills, Kerala state, India.

DISTRIBUTION. — India, known only from the Nilgiris (Walaghat and Coonoor) at elevations 1065–2250 m (see Rajendran 1985; Wallach *et al.* 2014; Ganesh 2015).

DESCRIPTION

Maximum total length *c.* 375 mm, ventrals 171–175, subcaudals 10–12, and terminal scute of tail with multiple ridges (see Smith 1943; Rajendran 1985). Color-pattern distinctive, with a purplish-black dorsum and golden-yellow venter, which extends onto the dorsum in irregular triangles up the side of the body, running its length.

REMARKS

This species has apparently been collected only once (in 1972) since the late 19th century (see Rajendran 1985). As with many other uropeltid species, we consider Beddome (1863a) to be the original description, rather than Beddome (1863b).

Plectrurus perrotetii Duméril & Bibron
in Duméril & Duméril, 1851
(Fig. 6E)

Plectrurus perrotetii Duméril & Bibron *in* Duméril & Duméril, 1851: 224. Numerous syntypes including BMNH 1886.3.21.6 (= 1946.1.1.41), MNHN-RA-0.170, MNHN-RA-0.190, MNHN-RA-6996, and ZMB 4036; others unknown, possibly *c.* 15–20 (see McDiarmid *et al.* 1999). Type locality: Nilgiri hills, Tamil Nadu state, India.

Plectrurus brevis. *Nomen nudum* from Günther (1875: 230; see McDiarmid *et al.* 1999).

Plectrurus davidsoni Beddome, 1886: 25. Holotype: BMNH 1885.3.21.6 (= 1946.1.1.41). Type locality: Anaimalai hills, Kerala or Tamil Nadu state, India. Designated as a junior subjective synonym by Gans (1966).

DISTRIBUTION. — India, definitively known only from the upper Nilgiris (> 1800 m), including the Ootacamund Plateau, where it is very common (Wall 1919; Whitaker & Captain 2004). Records from Coorg (Whitaker & Captain 2004) would benefit from confirmation in the form of vouchered specimens. Reports South of Palghat Gap including Anaimalai and Meghamalai (Hutton & David 2009) are doubtful, since none was reported from there previously (Wall 1919, 1928; Roux 1928; Chandramouli & Ganesh 2010) or during our fieldwork (Ganesh 2015).

DESCRIPTION

Maximum total length *c.* 440 mm, ventrals 144–180, subcaudals 6–12 (see Wall 1919; Smith 1943; Constable 1949; Rajendran 1985; Whitaker & Captain 2004). Color pattern typically a uniformly dark brown dorsum and lighter venter, and sometimes a reddish-orange stripe on the top of the tail.

REMARKS

The type species of *Plectrurus*. Common at several localities within its range, but records from the Anaimalais (*P. davidsoni*) may represent an undescribed species, based on variation in scale counts (see Rajendran 1985). A lectotype may need to be chosen by future revisers after phylogeographic revision if multiple cryptic species are found; we did not examine the syntypes for such a designation.

Pseudoplectrurus Boulenger, 1890

Pseudoplectrurus Boulenger, 1890: 270.

TYPE SPECIES. — *Silybura canarica* Beddome, 1870 by monotypy.

INCLUDED SPECIES. — *Pseudoplectrurus canaricus* (Beddome, 1870).

DIAGNOSIS. — *Pseudoplectrurus* can be distinguished from all other amniotes by the characters given for the family, and from other uropeltids by oculars united, nasals in contact, no temporal, no mental groove, dorsal scales in 15 rows at midbody, and a slightly compressed, elongate tail with weakly multicarinate scales terminating in a scute with two bifid points. Snout is more pointed than in *Plectrurus*. No continuously varying characteristic of visceral topology measured in the single specimen dissected uniquely diagnoses *Pseudoplectrurus* from other uropeltids, but the viscera are qualitatively unique among uropeltids in having a large saccular lung, an asymmetrical liver with a short right segment, and a distinct left bronchus.

DISTRIBUTION. — India; the distribution of this genus is apparently limited to the type locality of the type species on Mt. Kudremukh, Karnataka state, India (see Beddome 1886; Wallach *et al.* 2014).

REMARKS

Ganesh *et al.* (2013), without discussion, first explicitly re-recognized *Pseudoplectrurus* as a distinct genus, *contra* recent authors such as McDiarmid *et al.* (1999). This was largely because of morphological differences and geographical isola-

tion from *Plectrurus* (see Wallach *et al.* 2014; Ganesh 2015). The original description of this species noted that it was very common c. 6000 ft on “Kudra Mukh” (Beddome 1870). This taxon is allopatric with respect to *Plectrurus*, no species of which are known to occur on Mt. Kudremukh.

Pseudoplectrurus canaricus (Beddome, 1870)

Silybura canarica Beddome, 1870: 170.

TYPE MATERIAL. — Six syntypes: BMNH 1874.4.29.940-943 (= 1946.1.15.95-98), BMNH 1872.1.2.3 (= 1946.1.16.71), and MNHN-RA-1895.102.

TYPE LOCALITY. — Mt. Kudremukh, Karnataka state, India.

DISTRIBUTION. — India; known only from type locality, Mt. Kudremukh in the Kudremuk hills, at elevations > 1800 m (see Beddome 1886; Smith 1943; Wallach *et al.* 2014; Ganesh 2015).

DESCRIPTION

Maximum total length c. 430 mm, ventrals 172-188, subcaudals 6-13 (see Beddome 1886; Smith 1943). Color pattern somewhat similar to *Plectrurus aureus*, with purplish-brown dorsum (scales lighter in the center), and small yellow blotches extending onto the dorsum ventrolaterally (more obvious anteriorly).

REMARK

This species is known only from the syntypes, and has apparently not been collected since 1870, based on a lack of published reports or specimens.

Rhinophis Hemprich, 1820

Rhinophis Hemprich, 1820: 119.

Pseudotyphlops Schlegel, 1839 in Schlegel, 1837-1844: 30. Type species: *Uropeltis philippinus* Müller, 1832 by subsequent designation of Smith (1943); here renamed as *Rhinophis saffragamus* (Kelaart, 1853) n. comb.

Dapatnaya Kelaart, 1853: 104. Type species: *Dapatnaya lankadivana* Kelaart, 1853, a subjective junior synonym of *Anguis oxyrhynchus* Schneider, 1801 as designated by Smith (1943).

Morina Gray, 1858a: 260. *Nomen preoccupatum*; possibly a *lapsus* for *Mitylia* according to Smith (1943). See Gray (1858a).

Mytilia Gray, 1858a: 261. Unjustifiable emendation of *Mitylia* Gray, 1858. Type species: *Mitylia gerrardi* Gray, 1858 by original monotypy; a subjective junior synonym of *Rhinophis homolepis* Hemprich, 1820 as designated by Peters (1861b). See Gray (1858a) for original description of *Mytilia*, and Gray (1858b) for *Mitylia*.

Crealia Gray, 1858b: 264. Type species: *Mytilia (Crealia) melanogaster* Gray, 1858 by original monotypy; here designated as *Rhinophis melanogaster* (Gray, 1858). See Gray (1858a).

TYPE SPECIES. — *Anguis oxyrhynchus* Schneider, 1801 by original designation.

INCLUDED SPECIES. — *Rhinophis blythii*, *R. dorsimaculatus*, *R. drummondhayi*, *R. erangaviraji* Wickramasinghe, Vidanapathirana, Wickramasinghe & Ranwella, 2009, *R. fergusonianus* Boulenger, 1896, *R. goweri* Aengals & Ganesh, 2013, *R. homolepis*, *R. lineatus*, *R. melanogaster*, *R. oxyrhynchus* (Schneider, 1801), *R. philippinus*, *R. phillipsi* n. comb., *R. porrectus* Wall, 1921, *R. punctatus* Müller, 1832, *R. saffragamus* n. comb., *R. sanguineus* Beddome, 1863, *R. travancoricus* Boulenger, 1893, *R. tricoloratus* Deraniyagala, 1975, and *R. zigzag* Gower & Maduwage, 2011.

DISTRIBUTION. — Southern India, in the Western and Eastern Ghats of eastern Kerala, western Karnataka, and southwestern Tamil Nadu states, and Sri Lanka throughout most of the island including the dry zones (see Smith 1943; McDiarmid *et al.* 1999; Somaweera 2006; Wallach *et al.* 2014; Ganesh 2015).

DIAGNOSIS. — *Rhinophis* can be distinguished from all other amniotes by the characters given for the family, and from other uropeltids by united oculars, nasals separated by rostral or barely in contact, no temporal, no mental groove, dorsal scales in 15-19 rows at midbody, *Oberhäutchen* dentitions that are < 1.7 mm and < 50% of the total cell size for all species examined thusfar (*R. saffragamus*, *R. sanguineus*, *R. travancoricus*, *R. drummondhayi*, *R. blythii*, *R. philippinus*, *R. oxyrhynchus*, and *R. homolepis*; Gower 2003), and shortened, dorsally compressed tail that exhibits a distinct, rugose, keratinous disc at the end, clearly separated from the surrounding ventral and dorsal scales, for which the degree of enlargement and rugosity varies among species and ontogenetically, and more anterior junction of systemic arches (mean of -3.37% SVL) compared to other uropeltid genera (mean of -1.52%).

DESCRIPTION

No other examined characteristics of visceral anatomy differ significantly between *Rhinophis* and other uropeltid genera. However, a number of these characteristics differ qualitatively from the other taxa and should be examined in more specimens to determine if they are indeed diagnostic of the genus. They are: smaller anterior lobe of the right lung (mean of 1.3% SVL) compared to the other genera (2.47%), smaller avascular portion of the right lung (3.50% vs 7.50%), smaller kidney-vent interval indicating more posterior kidneys (18% vs 21%), larger heart (4.72% vs 4.17%), more posterior right kidney (86% vs 83%), more posterior left kidney (89% vs 87%), more posterior gallbladder (70% vs 67%), and lower number of tracheal rings (mean of 172 vs 212). In the two species for which it has been observed (*R. dorsimaculatus* and *R. lineatus*), the hemipenis is relatively long (c. 50% of tail length), simple, slender, subcylindrical, tapering slightly, covered to varying degrees in recurved spines (Gower & Maduwage 2011; Gower & Wickramasinghe 2016).

REMARKS

Originally described as a subgenus of the lizard taxon *Anguis* Linnaeus, 1758. These species have the most heavily modified tail shields of uropeltids, though the degree of hypertrophy appears to vary substantially across species and ontogenetic stages. Fitzinger (1843) recognized a subgroup *Rhinophes*, which is thus a valid name in the family group with the type genus *Rhinophis*.

Rhinophis blythii Kelaart, 1853
(Fig. 6F)

Rhinophis blythii Kelaart, 1853: 106. Three syntypes, apparently lost *fade* Gans (1966). Based on the rampant nomenclatural ambiguity and taxonomic uncertainty in uropeltids, we deem it of the utmost importance for an unambiguous type specimen to be associated with each name. The next available synonym for *Rhinophis blythii* is *Mytilia templetonii* Gray, 1858, with two syntypes, BMNH 1946.1.1.45-46. Having examined it and confirmed its identity as Kelaart's *R. blythii*, we designate BMNH 1946.1.1.45 as the neotype of *R. blythii*. Type locality: originally 'mountains of Ceylon'. Neotype locality: 'Ceylon'. This may need to be further restricted by future revisers (see Remarks).

Mytilia templetonii Gray, 1858a: 261. Syntypes: BMNH 1946.1.1.45-46 (3 specimens). Type locality: 'Ceylon' (Sri Lanka). Designated as a junior subjective synonym by Beddome (1886); designated as an objective junior synonym here. See Gray (1858a).

DISTRIBUTION. — This species has a relatively large range in the wet zone of Sri Lanka, *c.* 300-1360 m (Wallach *et al.* 2014). Known from Central, Uva, Sabaragamuwa and Southern provinces (De Silva, 1980; Das & de Silva, 2005; Somaweera, 2006). Earlier records from Southwest Sri Lanka are likely to be *Rhinophis erangaviraji* (Wickramasinghe *et al.* 2009).

DESCRIPTION

Maximum total length *c.* 370 mm, ventrals 148-168, subcaudals 5-9, dorsal scales in 17 rows at midbody (see Smith 1943). Color pattern typically dark brown to black dorsal and ventral coloration, a V-shaped yellow mark on the dorsal surface of the head (apex pointed towards snout) and vertical rows of yellow spots or partial crossbands on the anterior portion of the body, yellow pigment on the ventral scales, and a yellow ring around the base of the tail. Historically confused with *Rhinophis erangaviraji*.

REMARKS

One of the more widely distributed *Rhinophis* species. After the neotype designation, the type locality is 'Ceylon' (Sri Lanka). Given the wide range of this species, its previous confusion with other similar taxa (e.g., *Rhinophis erangaviraji*), revision of this locality is needed to clarify the status of the name *R. blythii*. We did not compare specimens from multiple populations to assign a new locality for the neotype, but such an action will likely be needed in the future after phylogeographic revision.

Rhinophis dorsimaculatus Deraniyagala, 1941

Rhinophis dorsimaculatus Deraniyagala, 1941: 800.

TYPE MATERIAL. — Holotype: NMSL 86. Apparently lost, along with a potential paratype (see Gower & Wickramasinghe 2016).

TYPE LOCALITY. — Marichchukkaddi, North-Western province, Sri Lanka.

DISTRIBUTION. — This species is known from the Northern province, only from the type locality in north-western dry zone of Sri Lanka near sea level (see Deraniyagala 1941), and nearby Sannar (Gower & Wickramasinghe 2016).

DESCRIPTION

The holotype was moderately large, total length *c.* 350 mm, ventrals 238, subcaudals 6, dorsal scales in 17 rows midbody (see Smith 1943). Based on a newly examined collection from the type locality, ventrals 227-250, subcaudals 6-8, maximum total length 415 mm (Gower & Wickramasinghe 2016). Color-pattern distinctive, with a dark brown to black dorsal and ventral coloration, and a large orange vertebral stripe (5-6 scale-rows wide), interrupted posteriorly with mostly discontinuous paravertebral large black blotches.

REMARK

A specimen of *Rhinophis zigzag* was mislabeled as *R. dorsimaculatus* by Somaweera (2006; see Gower & Maduwage 2011).

Rhinophis drummondhayi Wall, 1921

Rhinophis drummondhayi Wall, 1921b: 43.

TYPE MATERIAL. — Thirteen syntypes: BMNH 1920.5.5.1-4 (= 1946.1.16.79-81), MCZ 14348-49 (originally from BMNH), and additional specimens in the BNHM and NMSL.

TYPE LOCALITY. — Lennox and Kalupahana Estates, Uva province, Sri Lanka.

DISTRIBUTION. — This species has a relatively small range in the high elevations of Central and Uva provinces, *c.* 900-1500 m (Das & de Silva 2005; Somaweera 2006; Wallach *et al.* 2014).

DESCRIPTION

Maximum total length *c.* 300 mm, ventrals 173-191, subcaudals 4-8, dorsal scales in 17 rows at midbody (Smith 1943). Color pattern typically uniformly brown dorsum, scales occasionally dappled or with whitish margins, occasionally a series of lighter spots, triangles or bars along the sides of the body, yellow pigment on the ventral scales, and an incomplete light ring around the base of the tail. This species resembles *R. tricoloratus* in color pattern, but is lighter in color and found at different localities (see below).

REMARK

The original description of this species was erroneously cited by Gans (1966) as Wall (1921a), but it is actually Wall (1921b).

Rhinophis erangaviraji

Wickramasinghe, Vidanapathirana,
Wickramasinghe & Ranwella, 2009
(Fig. 6G)

Rhinophis erangaviraji Wickramasinghe, Vidanapathirana, Wickramasinghe & Ranwella, 2009: 6.

TYPE MATERIAL. — Holotype: NMSL 20080601.

TYPE LOCALITY. — Enselwatte Estate, Sinharaja Division (Army Camp Forest), Rakwana hills, Matara District, Southern province, Sri Lanka.

DISTRIBUTION. — Specimens are known from a relatively small range within rainforests of Enselwatte estate and Morningside forest areas of the Southern and Sabaragamuwa provinces of Sri Lanka, *c.* 1000 m (see Wickramasinghe *et al.* 2009; Wallach *et al.* 2014; RAP & RS pers. obs.).

DESCRIPTION

Maximum total length *c.* 300 mm, ventrals 142–154, subcaudals 5–9, dorsal scales in 17 rows at midbody (see Wickramasinghe *et al.* 2009). Color pattern typically back dorsum and lateral surface, yellow stippling on the head shields, a black zigzag pattern on yellow background ventrally, no ring-like pattern at the base of the tail, and a black anal region and underside of tail black. Color pattern similar to *Rhinophis blythii*, differing in having indistinct markings on nape of neck, rather than distinct yellow V-shaped blotch.

REMARK

Resembles *Rhinophis blythii*, for which historical records from southwestern Sri Lanka are likely this species (see Wickramasinghe *et al.* 2009).

Rhinophis fergusonianus Boulenger, 1896

Rhinophis fergusonianus Boulenger, 1896: 236.

TYPE MATERIAL. — Holotype: BMNH 1895.7.29.1 (= 1946.1.16.77).

TYPE LOCALITY. — Cardamom hills, southern Western Ghats, southeastern Kerala state, India.

DISTRIBUTION. — Known only from type locality in the Cardamom hills of India, *c.* 1100 m (see Ferguson 1895, 1902; Wallach *et al.* 2014; Ganesh 2015).

DESCRIPTION

Holotype: total length *c.* 320 mm, 180 ventrals or 196 reported by Gower (2006), subcaudals unknown, dorsal scales in 17 rows at midbody (see Smith 1943). Color-pattern distinctive, with a black dorsum with occasional white speckles, sides yellowish-white and stippled with black, white venter with black blotches forming an irregular zigzag, and yellow edging on the tail shield.

REMARKS

This species is known only from the type specimen. Since *Rhinophis sanguineus* has also been reported (Hutton 1949) from the type locality of *R. fergusonianus*, some authors have doubted its validity (Mahendra 1984). Given the differences in their morphology (see key in Aengals & Ganesh 2013), we suggest that *R. fergusonianus* is distinct from all other sympatric congeners and continue to recognize it as valid.

Rhinophis goweri Aengals & Ganesh, 2013
(Fig. 6H)

Rhinophis goweri Aengals & Ganesh, 2013: 63.

TYPE MATERIAL. — Holotype: ZSI/SRC/VRS 256.

TYPE LOCALITY. — Noolathu Kombai, Bodamalai hills, Tamil Nadu state, India.

DISTRIBUTION. — This species is known only from the type locality at the Bodamalai hills, and the nearby Kolli hills, in the southern Eastern Ghats of India at elevations *c.* 900 m (Aengals & Ganesh 2013; Wallach *et al.* 2014; Ganesh 2015; Ganesh & Arumugam 2016).

DESCRIPTION

Holotype: total length *c.* 270 mm, ventrals 215, subcaudals 5, dorsal scales in 17 rows at midbody. Color pattern unremarkable, uniformly dark-gray or brown ventral coloration, off-white venter with brown stippling, tail with orangish-red blotches underneath, and no discernible pattern otherwise. A collection from the Kolli hills referred to this species has a maximum total length of *c.* 345 mm, 189–192 ventrals, 8–9 subcaudals, and suggests a faint juvenile pattern of ragged, wavy, black bars across the dorsum (Ganesh & Arumugam 2016).

REMARK

This species is known only from the type specimen and five uncollected specimens from the nearby Kolli hills, and represents the only *Rhinophis* species reported from the Eastern Ghats.

Rhinophis homolepis (Hemprich, 1820)
(Fig. 7A)

Anguis (Rhinophis) homolepis Hemprich, 1820: 119. Holotype: ZMB 3827. Type locality: Unknown; designated as Zeylania (Sri Lanka) by Peters (1861b). This may need to be restricted by future revisers (see Remarks).

Dapatnaya trevelyanii Kelaart, 1853: 108. Syntypes lost *vide* Gans 1966. Type locality: Hills near Kandy, Sri Lanka. Designated as a junior subjective synonym by Peters (1861b).

Mitylia gerrardi Gray, 1858b: 58. Three syntypes: BMNH 1946.1.16.66–68. Type locality: ‘Ceylon’ (Sri Lanka). Designated as a junior subjective synonym by Peters (1861b). See Gray (1858b).

DISTRIBUTION. — This species has a moderately large range in the low and mid elevations of the wetzone of Sri Lanka. Records are scattered in the Central, Sabaragamuwa, and Uva provinces, at elevations *c.* 750–950 m (Das & de Silva 2005; Somaweera 2006; Wallach *et al.* 2014).

DESCRIPTION

Maximum total length *c.* 280 mm, ventrals 180–204, subcaudals 3–5, dorsal scales in 17 rows at midbody (see Smith 1943). Color pattern typically uniformly black dorsum, with single row of partial, irregular white or pinkish-white triangular shaped marks along each side of the body, a white rostral, and a white or yellowish-white ring around the base of the tail.

REMARKS

This has a contentious nomenclatural history with respect to the junior synonym *Dapatnaya trevelyanii* Kelaart, 1853, but the name *Anguis homolepis* Hemprich, 1820 is clearly validly associated with this species (see McDiarmid *et al.* 1999). As

with *Rhinophis blythii*, the broad type locality of ‘Sri Lanka’ will likely require subsequent revision after phylogeographic investigation, but we have not examined enough material to identify cryptic species or restrict the locality accurately among the known populations.

Rhinophis lineatus Gower & Maduwage, 2011

Rhinophis lineatus Gower & Maduwage, 2011: 53.

TYPE MATERIAL. — Holotype: CAS 226024. Paratypes: CAS 225806, CAS 226025-226035, and CAS 226042-226044.

TYPE LOCALITY. — Harasbedda, near Ragala, Central province, Sri Lanka.

ETYMOLOGY. — From the Latin *lineatus* for ‘lined’, referring to the dorsal color-pattern.

DISTRIBUTION. — This species is known only from the vicinity of the type locality in the central hills of the wet zone of Sri Lanka, c. 1460 m (Gower & Maduwage 2011; Wallach *et al.* 2014).

DESCRIPTION

Maximum total length c. 290 mm, ventrals 182-195, subcaudals 4-7, dorsal scales in 17 rows at midbody (see Gower & Maduwage 2011). Distinctive color-pattern, with regular, narrow, longitudinal stripes (alternating pale/dark) around and along almost the entire body. It is the only species in the genus characterised by a colour pattern of multiple, narrow longitudinal stripes.

REMARKS

This species was referred to as *Rhinophis* sp. 1 by Cadle *et al.* (1990), who demonstrated its distinctiveness using allozyme data. A specimen of this species was mis-labeled as *R. drummondhayi* by de Silva (1990; see Gower & Maduwage 2011).

Rhinophis melanogaster (Gray, 1858)
(Fig. 7B)

Mytilia (Crealia) melanogaster Gray, 1858a: 261. Four syntypes: BMNH 1946.1.16.94-97. Type locality: Ceylon (Sri Lanka), specified as Meniakanda Group, Mousakanda Estate and Gammaduwa, in the East Matale hills *fide* da Silva (2009). See Gray (1858a).

Plectrurus ceylonicus Peters, 1859: 388. Holotype: ZMB 3872. Type locality: ‘Ceylon’ (Sri Lanka). Designated as a junior subjective synonym by Beddome (1886).

DISTRIBUTION. — This species has a relatively small range in the wet zone of Sri Lanka, Central and Uva provinces, c. 700-1300 m (Somaweera 2006; Wallach *et al.* 2014).

DESCRIPTION

Maximum total length c. 250 mm, ventrals 141-166, subcaudals 6-10, dorsal scales in 17 rows at midbody (see Smith 1943). Typically exhibits non-descript color-pattern, with a dark brown or black dorsal and ventral coloration, and occasionally a yellowish-white wash or stripe down both sides of the

body. The terminal scute of this species is less like the rugose tail plug of most other *Rhinophis* species, instead resembling an enlarged dorsal scale elongated vertically, terminating in a ridge or points.

REMARK

This species was formerly placed in *Uropeltis* (see McDiarmid *et al.* 1999; Wallach *et al.* 2014), but is clearly allied with *Rhinophis* based on phylogenies inferred using allozymes and DNA-sequence data (Fig. 1), rostral dividing the nasals, and enlarged keratinous shield, which exhibits ontogenetic hypertrophy.

Rhinophis oxyrhynchus (Schneider, 1801)
(Fig. 7C)

Anguis oxyrhynchus Schneider, 1801: 341. Two syntypes: ZMB 3825-3826. Type locality: East India, emended to Sri Lanka by Smith (1943).

Dapatnaya lankadivana Kelaart, 1853: 107. Syntypes lost *fide* Gans 1966. Type locality: Trincomalee and Kandy, Sri Lanka. Designated as a junior subjective synonym by Beddome (1886).

Mytilia (Rhinophis) unimaculata Gray, 1858a: 261. Two syntypes: BMNH 1946.1.16.90, BMNH 1946.1.17.1. Type locality: ‘Ceylon’ (Sri Lanka). Designated as a junior objective synonym by Beddome (1886). See Gray (1858a).

DISTRIBUTION. — This species has a relatively large range in the lowland dry zone of Sri Lanka (c. 0-250 m), in the Northern, North-Western, North-Central and Eastern provinces (De Silva 1980; Somaweera 2006; Karunarathna & Amarasinghe 2011; Kumarasinghe *et al.* 2013; Wallach *et al.* 2014).

DESCRIPTION

Maximum total length c. 400 mm, ventrals 211-227, subcaudals 5-7, dorsal scales in 17 or 19 rows at midbody (see Smith 1943). Uniformly dark color-pattern, dark brown dorsal and ventral coloration, a darker base on most scales, and occasional yellowish-white ventrolateral markings near the tail.

REMARKS

This species is the type species of the genus *Rhinophis*, and is one of the few taxa with an extensive range in north-eastern Sri Lanka. This species is also apparently the first named species of any uropeltid. We did not examine the type series; a lectotype and revised type locality should be chosen by future revisers.

Rhinophis philippinus (Cuvier, 1829)
(Fig. 7D)

Typhlops philippinus Cuvier, 1829: 74. Holotype: MNHN-RA-1864.94. Type locality: Philippines, corrected to Zeylania (Sri Lanka) by Peters (1861b). This may need to be restricted by future revisers (see Remarks).

Rhinophis planiceps Peters, 1861b: 17. Holotype: BMNH 1946.1.16.99. Type locality: Sri Lanka. Suggested as a junior subjective synonym by Günther (1864) and formally designated as such by Beddome (1886). See Peters (1861b).



FIG. 7. — Some uropeltid species photographed in life: **A**, *Rhinophis homolepis* Hemprich, 1820; **B**, *R. melanogaster* (Gray, 1858); **C**, *R. oxyrhynchus* (Schneider, 1801); **D**, *R. philippinus* (Cuvier, 1829); **E**, *R. phillipsi* (Nicholls, 1929) n. comb.; **F**, *R. punctatus* Müller, 1832; **G**, *R. saffragamus* (Kelaart, 1853) n. comb.; **H**, *R. sanguineus* Beddome, 1863. Photos by RAP, RS, SRG, VS, A. Dey, R. Pethiyagoda, and S. Kehimkar.

DISTRIBUTION. — This species has a moderately large range in the Central and Sabaragamuwa provinces of Sri Lanka, *c.* 300–900 m (Somaweera 2006; Wickramasinghe *et al.* 2009; Wallach *et al.* 2014).

DESCRIPTION

Maximum total length *c.* 280 mm, ventrals 153–182, subcaudals 3–6, dorsal scales in 17 rows at midbody (see Smith 1943). The single specimen dissected lacks an anterior lobe of the right lung, a condition otherwise only observed in *Brachyophidium rhodogaster* and *R. saffragamus* among examined specimens of sampled uropeltid taxa. Color pattern typically dark brown dorsally and ventrally, usually with a lighter margin on each scale, and occasional yellowish-white blotch near the head and anal scale.

REMARKS

This species has a contentious nomenclatural history with respect to the junior synonym *Rhinophis planiceps* Peters, 1861, but *R. philippinus* is clearly the correct name for this species (see McDiarmid *et al.* 1999). A restricted type locality may need to be designated by future revisers if phylogeographic investigation reveals cryptic species.

Rhinophis phillipsi (Nicholls, 1929) n. comb. (Fig. 7E)

Silybura phillipsi Nicholls, 1929: 153.

TYPE MATERIAL. — Holotype: BMNH 1929.2.5.1 (= 1946.1.17.2).

TYPE LOCALITY. — Meniakanda Group, Gammaduwa, East Matale hills, Central province, Sri Lanka.

DISTRIBUTION. — This species is known only from the the Knuckles massif in the Central province of Sri Lanka, *c.* 360–1115 m (Das & de Silva 2005; de Silva *et al.* 2005; Somaweera 2006; Wallach *et al.* 2014).

DESCRIPTION

Maximum total length *c.* 230 mm, ventrals 197–213, subcaudals 6–9, dorsal scales in 17 rows at midbody (see Smith 1943). As in *Rhinophis melanogaster*, the terminal scute of this species is less like the rugose tail shield of most other *Rhinophis* species, instead resembling an enlarged dorsal scale elongated vertically, terminating in a ridge or points, like *R. melanogaster* and some *Uropeltis* species (*U. grandis* and *U. pulneyensis*). Distinctive color-pattern, with a black dorsal coloration and a yellow stripe down the center of each of the seven mid-dorsal scale rows, and a series of yellow blotches or bars running down each side.

REMARK

This species was formerly placed in *Uropeltis*, but is clearly allied with *Rhinophis* based on DNA-sequence data (Fig. 1), the rostral dividing the nasals, and the keratinous tail-shield.

Rhinophis porrectus Wall, 1921

Rhinophis porrectus Wall, 1921b: 35.

TYPE MATERIAL. — Holotype: BMNH 1920.8.25.1 (= BMNH 1946.1.16.70).

TYPE LOCALITY. — On the road between Puttalam and Chilaw, near Madurankuliya *vide* Willey (1903; the original collector), North-Western province, Sri Lanka.

DISTRIBUTION. — This species is known only from the type specimen collected at Madurankuliya in the lowland dry zone of Sri Lanka (near sea level). Some sources (Smith 1943) record the type locality as Maradankadawala, an area further interior in the lowland dry zone, but this is an error. The original collector (Willey 1903) reports the specimen as originating from Madurankuliya. More recently, Kumarasinghe *et al.* (2013) reported a specimen from Eluwankulama Aruwakkalu Forest, *c.* 35 km North of Puttalam, identified as *Rhinophis* cf. *porrectus*.

DESCRIPTION

The size, scalation, and coloration are indistinguishable from *Rhinophis punctatus* (see below), from which it is distinguishable only by the higher number of ventral scales (281 vs 236–246) and a much thicker body (see Smith 1943). As with *R. punctatus* (see below), color pattern a blackish-brown dorsum with white margins, a white stripe on either side of the body, and a brown vertebral stripe.

REMARKS

It is unclear whether or not this is a distinct species from *Rhinophis punctatus* (Smith 1943; Gans 1966). We continue to treat it as such, given the large difference in ventral-scale count, the largest such count of any known uropeltid species. It is also geographically distinct from *R. punctatus*, being found in the Northwest dry zone vs the central hills in the wet zone (but see Karunarathna & Amarasinghe 2011). More specimens are needed to examine the distinctiveness of these species. See Wall (1921b).

Rhinophis punctatus Müller, 1832 (Fig. 7F)

Rhinophis punctata Müller, 1832: 248.

TYPE MATERIAL. — Holotype lost *vide* Peters (1861b) and Gans (1966). A neotype designation is needed to alleviate potential nomenclatural ambiguity with respect to *Rhinophis porrectus* (see above).

TYPE LOCALITY. — “Guiana”, corrected to Zeylania (Sri Lanka) by Schlegel *in* Peters (1861b).

DISTRIBUTION. — Known from a small range at *c.* 475–600 m elevation in the wet zone of Sri Lanka (De Silva 1980). However, Karunarathna & Amarasinghe (2011) identified a specimen from the dry lowland forests of Nilgala (Uva province) as *Rhinophis* cf. *punctatus*. We did not examine this specimen to confirm its identity.

DESCRIPTION

Maximum total length *c.* 380 mm, ventrals 236–246, subcaudals 7–9, dorsal scales in 17 rows at midbody (Smith 1943). As with *Rhinophis porrectus*, color pattern typically a blackish-brown dorsum with white margins, a white stripe on either side of the body, and a brown vertebral stripe. This coloration is indistinguishable from *R. porrectus* (see above), from which it is distinguishable only by the lower number of ventral scales (236–246 vs 281).

REMARK

This species may be synonymous with *Rhinophis porrectus*, but is morphologically and geographically distinct therefrom, and more specimens are needed to settle this question.

Rhinophis saffragamus (Kelaart, 1853) n. comb.
(Fig. 7G)

Uropeltis saffragamus Kelaart, 1853: 106. Original type lost *vide* Taylor (1953). Type locality: Ratnapura, district of Saffragam (an older name for Sabaragamuwa), near Adam's Peak (Sri Pada), Sabaragamuwa province, Sri Lanka. Designated as a junior subjective synonym by Tennent (1861). The holotype of *Uropeltis philippinus* Müller, 1832, MNHN-RA-0.5621, is here designated as the neotype of *Uropeltis saffragamus* Kelaart 1853, rendering them objective synonyms.

Uropeltis philippinus – Cuvier 1829: 76, *nomen nudum* (Gans 1966; McDiarmid *et al.* 1999).

Uropeltis philippinus Müller, 1832: 252, n. syn. Holotype: MNHN-RA-0.5621 (the specimen of Cuvier 1829 *vide* Gans 1966). Type locality: Philippine islands. Junior homonym of *Typhlops philippinus* Cuvier, 1829, as designated here.

Uropeltis grandis Kelaart, 1853: 106. Holotype: BMNH 1946.1.8.1. Type locality: Kerinday near Matura, Southern province, Sri Lanka. Designated as a junior subjective synonym by Tennent (1861).

Uropeltis pardalis Kelaart, 1853: 107. Holotype: BMNH 1946.1.16.55. Type locality: Matura, Southern province, Sri Lanka. Designated as a junior subjective synonym by Tennent (1861).

DISTRIBUTION. — This species has a relatively large range in the wet, intermediate, and dry zones of Sri Lanka, *c.* 0–1035 m (De Silva 1980; Somaweera 2006; Karunaratna & Amarasinghe 2011; Wallach *et al.* 2014).

DESCRIPTION

Moderately large, maximum total length *c.* 340 mm, ventrals 129–147, subcaudals 6–9, dorsal scales in 19 rows at midbody (see Smith 1943). In the four specimens dissected, we observed a relatively low number of tracheal rings (mean 157), whereas fewer than 160 rings was otherwise only observed in *Uropeltis ellioti* (157), *U. macrolepis* (131), *U. madurensis* (158), and *U. phipsonii* (155). The four specimens also had a relatively large number of left bronchus rings (mean 6), whereas one specimen of *U. madurensis* had 8, and no other uropeltid specimen examined had more than 5. Variable color-pattern, with a brown to blackish-brown dorsal and

ventral coloration, and occasional lighter brown mottling. Tail shield is large and rugose, flatter than most congeners, and rostral does not separate the nasals.

REMARK

This is the only *Rhinophis* species in which the rostral does not separate the nasals, but it is unclear whether this is a reversal or plesiomorphic feature, as the precise placement of the species within *Rhinophis* is unclear (Fig. 1). See above for a detailed discussion of the nomenclatural history of this species.

Rhinophis sanguineus Beddome, 1863
(Fig. 7H)

Rhinophis sanguineus Beddome, 1863a: 47. Beddome (1863a) reports collecting several syntypes, but Boulenger (1893a) reports only one male with 197 ventrals and nine subcaudals. Gans (1966) also states that only one syntype (BMNH 1864.3.9.2 now: 1946.1.16.54), catalogued as “one of the types”, is now known. Wallach *et al.* (2014) also list BMNH 1874.4.29.110 (= 1946.1.16.76) as a syntype, but this specimen is putatively the holotype of *Rhinophis microlepis* Beddome, 1863 (see Gans 1966). We designate BMNH 1946.1.16.54 as the lectotype, to remove any ambiguity. Type locality: Cherambadi, northern Kerala state, India.

Rhinophis microlepis Beddome, 1863a: 47. Holotype: BMNH 1874.4.29.110 (= 1946.1.16.76). Type locality: Minchin estate, Kerala state, India. Designated as a junior subjective synonym by Beddome (1886). See Beddome (1863a).

DISTRIBUTION. — India, known from the Nilgiris northwards to the Agumbe hills, *c.* 750–1065 m (see Ferguson 1895; Wall 1919; Aengals & Ganesh 2013; Wallach *et al.* 2014; Ganesh 2015).

DESCRIPTION

Maximum total length *c.* 460 mm, ventrals 182–218 though Mason (1888) reported 166–183 from putatively conspecific populations in the Wullingy forests near Palghat, subcaudals 5–11, dorsal scales in 15 rows at midbody (see Wall 1919; Smith 1943; Constable 1949). Distinctive color-pattern, with a bluish-black dorsal coloration, bright-red venter with black mottling, and red streaks on the tail.

REMARKS

The original description (Beddome 1863a) reports the collection of several syntypes, but apparently only a few were catalogued, and only one is now known (Gans 1966). Boulenger (1893a) reports a large topotypic series collected by Beddome but does not refer to them as types; either they were collected at a later date, or they weren't catalogued as types initially. The lower ventral count reported by Mason (1888) is of uncertain validity, and may represent a new or cryptic species from the Wullingy forests near Palghat. Records of this species exist from South of Palghat Gap (Hutton 1949), but we did not examine the specimens to determine their validity.

Rhinophis travancoricus Boulenger, 1893

Rhinophis travancoricus Boulenger, 1893b: 318.

TYPE MATERIAL. — Holotype: BMNH 1892.10.5.2.

TYPE LOCALITY. — Vicinity of Thiruvanthapuram (Trivandrum), southern Kerala state (formerly the Kingdom of Travancore), India.

DISTRIBUTION. — India, in the southern Western Ghats from Thattekad to Kanyakumari, typically found mainly on of western slopes < 800 m, but ranging from *c.* 0–1335 m (see Ferguson 1895, 1902; Smith 1943; Rajendran 1985; Wallach *et al.* 2014; Ganesh 2015).

DESCRIPTION

Maximum total length *c.* 240 mm, ventrals 132–148, subcaudals 5–9, dorsal scales in 17 rows at midbody (see Smith 1943; Rajendran 1985). Typically exhibits a non-descript color-pattern, with a purplish-brown dorsal and ventral coloration, dorsoventral and ventral scales with whitish-yellow margins, and underside of tail yellow.

REMARK

Relatively few specimens of this species seem to be known, though it has been recorded at localities other than the type locality since its description (Boulenger 1893b; Rajendran 1985).

Rhinophis tricoloratus Deraniyagala, 1975

Rhinophis tricoloratus Deraniyagala, 1975: 535.

TYPE MATERIAL. — Holotype: NMSL 1978.5.1.

TYPE LOCALITY. — Miyanpalawa in the Sinharaja Forest Reserve, southern Sabaragamuwa province, Sri Lanka.

DISTRIBUTION. — This species is known from a small area of lowland tropical rainforests, *c.* 455 m around Sinharaja World Heritage Site, Kanneliya Forest Reserve, and Beraliya Mukalana Proposed Forest Reserve in the Southern and Sabaragamuwa provinces of Sri Lanka (Somaweera 2006; Karunarathna & Amarasinghe 2012).

DESCRIPTION

The holotype has 163 ventral scales in 17 rows at midbody, contrary to earlier reports (see Wickramasinghe *et al.* 2009), and five subcaudals. Distinctive color-pattern, with a primarily black dorsal coloration, paired white ocellations, mostly anteriorly, occasionally very dark or faded, a yellowish-white wash on the sides and venter, and an incomplete whitish ring around the tail.

REMARK

While this species has been encountered and photographed since its original description, the range of morphological variation has not been well-characterized.

Rhinophis zigzag Gower & Maduwage, 2011
(Fig. 8A)

Rhinophis zigzag Gower & Maduwage, 2011: 59.

TYPE MATERIAL. — Holotype: CAS 226306. Thirteen paratypes: CAS 225690–225691, CAS 225902–225903, CAS 225967–225969, CAS 226014–226016, CAS 226307, WHT 5246, and WHT 5284.

TYPE LOCALITY. — Biblegemma Rd., near Passara, Uva province, Sri Lanka. Distribution. — This species is known only from the vicinity of the type locality in the wet zone of the central hills of Sri Lanka, *c.* 1000 m (see Gower & Maduwage 2011; Wallach *et al.* 2014).

DESCRIPTION

Maximum total length *c.* 390 mm, ventrals 207–221, subcaudals 3–6, dorsal scales in 17 rows at midbody (see Gower & Maduwage 2011). Distinctive color-pattern, with a yellowish-white dorsal coloration on the sides and a purplish-black middorsal stripe that variegates with the yellow to form a chain-like or zig-zag pattern.

REMARKS

This species has been collected multiple times over several years around the type locality (Gower & Maduwage 2011). A photograph of a live specimen was mislabeled as *Rhinophis dorsimaculatus* by Somaweera (2006; see Gower & Maduwage 2011). This species was also referred to as *Rhinophis* sp. 2 by Cadle *et al.* (1990), known specimens having been collected first in the 1970s (Gower & Maduwage 2011).

Teretrurus Beddome, 1886

Teretrurus Beddome, 1886: 28.

TYPE SPECIES. — *Plectrurus sanguineus* Beddome, 1867 by subsequent designation of Smith (1943).

INCLUDED SPECIES. — *Teretrurus sanguineus*.

DIAGNOSIS. — *Teretrurus* can be distinguished from all other amniotes by the characters given for the family, and from other uropeltids by divided oculars, nasals in contact, a temporal, no mental groove, dorsal scales in 15 rows at midbody, *Oberhäutchen* dentitions that are 51–80% of the total cell-size (Gower 2003), and a shortened, slightly compressed tail with weakly multicarinate scales that terminates in a single, pointed scute.

DISTRIBUTION. — The southern Western Ghats of India, in hill ranges South of the Palghat Gap (see Smith 1943; Rajendran 1985; Wallach *et al.* 2014; Ganesh 2015).

DESCRIPTION

For the two specimens dissected, none of the characteristics of visceral topology examined are uniquely diagnostic of the genus at the reduced significance level used. However, several features are near or outside the range of variation seen in the other genera, and larger sample sizes from more taxa may reveal them to be diagnostic. These are smaller right lung (mean of 16% SVL vs 24%), larger anterior lobe of the right lung (3.7% vs 2.1%), more anterior posterior tip of right lung (48% vs 55%), larger kidney-vent interval indicating



FIG. 8. — Some uropeltid species photographed in life: **A**, *Rhinophis zigzag* Gower & Maduwage, 2011; **B**, *Teretrurus sanguineus* (Beddome, 1867); **C**, *Uropeltis bicatenata* (Günther, 1864); **D**, *U. ceylanica* Cuvier, 1829; **E**, *U. dindigalensis* (Beddome, 1877); **F**, *U. ellioti* (Gray, 1858); **G**, *U. liura* (Günther, 1875); **H**, *U. macrolepis* (Peters, 1861). Photos by RAP, RS, SRG, VS, S. Kehimkar, A. Mohan, and D. Raju.

more anterior kidneys (23% vs 20%), more anterior right kidney (81% vs 84%), more anterior left kidney (84% vs 88%), more anterior gallbladder (62% vs 68%), and smaller liver-gallbladder interval (−0.74% vs 3.9%).

REMARKS

This genus has been synonymized with both *Platyplectrurus* and *Plectrurus* (Beddome 1867, 1876; Boulenger 1890, 1893a), but is diagnosable from *Platyplectrurus* by the smaller *Oberhäutchen* dentitions (vs larger), and from *Plectrurus* by the single-pointed tail (vs double-pointed) and the presence of a temporal (vs absence). Smith (1943) included *Brachyophidium rhodogaster* in *Teretrurus*, as did some later authors (e.g., Rieppel & Zaher 2002), but we follow Rajendran (1985), McDiarmid *et al.* (1999) and Wallach *et al.* (2014) in recognizing *Brachyophidium*.

Teretrurus sanguineus (Beddome, 1867)
(Fig. 8B)

Plectrurus sanguineus Beddome, 1867: 14. Putatively twelve syntypes: BMNH 1946.1.16.57-62, MNHN-RA-1895.116a-c, and NMW 2161.1-3 *vide* Wallach *et al.* (2014). The NMW specimens were not listed by Gans (1966). A single specimen was described in the original publication, so the specimen with 144 ventrals and seven subcaudals is actually the holotype. However, none of the six specimens described by Boulenger (1893a) as “types”, presumably BMNH 1946.1.16.57-62, have 144 ventrals or seven subcaudals in his count, suggesting that the holotype is in the MNHN or NMW series, or that ventrals were miscounted by at least one previous researcher (see Gower & Ablett 2006). Type locality: Above Pollachi, Anamalai hills, Tamil Nadu state, India according to the BMNH catalogue *vide* Wallach *et al.* (2014); “Anamallay forests; 4,000 feet elevation” as originally given by Beddome (1867).

Platyplectrurus hewstoni Beddome, 1876: 701. Holotype: BMNH 1946.1.15.77. Type locality: Manantoddy, Kerala state, India. Designated as a junior subjective synonym by Beddome (1886).

Plectrurus scabricauda Theobald, 1876: 136. Holotype reported lost by Gans (1966); reported as ZSI 6996 by McDiarmid *et al.* (1999) based on comments from I. Das. Type locality: Anaimalai hills, Tamil Nadu state, India. Designated as a junior subjective synonym by Boulenger (1893a).

Teretrurus travancoricus Beddome, 1886: 29. Seven syntypes: BMNH 1886.2.1.3-4 & 1886.4.21.5-6 (= 1946.1.2.26-29), and MNHN-RA-1895.117 (3 specimens). Type locality: above Papanasam, Tamil Nadu state, India. Designated as a junior subjective synonym by Boulenger (1893a).

DISTRIBUTION. — This species has an unclear, disjunct distribution in India, including the Anaimalai-Munnar hills at elevations > 1000 m, and the Travancore-Agasthyamalai Hill complex South of the Sencotta Gap (see Ferguson 1895, 1902; Smith 1943; Rajendran 1985; Wallach *et al.* 2014; Ganesh 2015).

DESCRIPTION

Maximum total length *c.* 240 mm, ventrals 120-159, subcaudals 5-11 (see Boulenger 1893a; Smith 1943; Rajendran 1985). Non-descript color-pattern, with purplish- or reddish-brown dorsum, and blood-red ventral coloration with occasional black flecks or bars.

REMARK

We concur with Rajendran (1985) regarding the likely presence of cryptic species in this complex, with populations from Nyamakad North of the Sencotta gap and the Tirunelveli hills South of the gap differing in coloration (unpatterned red vs red with black spots) and ventral scale counts (143-159 vs 121-126).

Uropeltis Cuvier, 1829

Uropeltis Cuvier, 1829: 76.

Siluboura Gray, 1845: 142. Type species: *Uropeltis ceylanica* Cuvier, 1829, by monotypy. The unjustified emendation *Silybura* Peters, 1861 later entered widespread usage (e.g., Beddome 1886; Boulenger 1893a).

Coloburus Duméril in Duméril & Duméril, 1851: 224. Type species: *Uropeltis ceylanica* Cuvier, 1829, by monotypy.

TYPE SPECIES. — *Uropeltis ceylanica* Cuvier, 1829, by subsequent designation of Fitzinger (1843).

INCLUDED SPECIES. — *Uropeltis arcticeps*, *U. beddomii*, *U. bicatenata*, *U. broughami*, *U. ceylanica*, *U. dindigalensis*, *U. ellioti*, *U. grandis*, *U. liura*, *U. macrolepis*, *U. macrorhyncha*, *U. maculata*, *U. madurensis*, *U. myhendrae*, *U. nitida*, *U. ocellata*, *U. petersi*, *U. phipsonii*, *U. pulneyensis*, *U. rubrolineata*, *U. rubromaculata*, *U. shortii*, and *U. woodmasoni*.

DIAGNOSIS. — *Uropeltis* can be distinguished from all other amniotes by the characters given for the family, and from other uropeltids by united oculars, nasals in contact (except *U. pulneyensis* and some *U. grandis*), no temporal, no mental groove, dorsal scales in 15-19 rows at midbody, *Oberhäutchen* dentitions that are > 1.7 mm and 51-80% of the total cell size in all species examined thusfar (*U. phipsonii*, *U. ellioti*, and *U. ceylanica*; Gower 2003), and shortened, compressed tail that is either 1) rounded with keeled dorsal scales terminating in a somewhat enlarged convex cap formed by the terminal scute (Type III), 2) shortened, heavily truncated tail ending in a distinct flattened disc covered in multicarinate scales, with a terminal scute bearing multiple distinct points (Type IV), or 3) shortened, heavily truncated tail ending in a convex disc covered in multicarinate scales with a terminal scute bearing multiple distinct points (Type V; Fig. 3).

DISTRIBUTION. — Peninsular India, mainly in the Western Ghats of eastern Kerala and southwestern Tamil Nadu, with some species extending North as far as Surat, Dangs (*Uropeltis macrolepis*) and into the Central Indian hills and the Eastern Ghats (*U. ellioti* and *U. shortii*; see Smith 1943; Rajendran 1985; McDiarmid *et al.* 1999; Whitaker & Captain 2004; Ganesh *et al.* 2014; Wallach *et al.* 2014; Ganesh 2015).

DESCRIPTION

For the 15 specimens from 14 species dissected, none of the characteristics of visceral topology examined are uniquely diagnostic of the genus at the reduced significance level used (< 0.001). However, several features are near or outside the range of variation seen in the other genera, and larger sample sizes from more taxa may reveal them to be diagnostic. These are smaller densely vascularized portion of the right lung (mean 6.2% SVL vs 7.4%), more posterior tip of the right lung (57% vs 53%), more posterior left lung orifice (33% vs 30%), and larger number of tracheal rings (mean of 222 vs 185).

REMARKS

Following the taxonomic actions taken above, this genus does not occur in Sri Lanka. Some Indian members of this group bearing putative *Rhinophis*-type snout or shield morphologies (but rarely in combination), such as *Uropeltis grandis*, *U. macrorhyncha*, and *U. pulneyensis*, may be re-assigned in future analyses (see below).

Uropeltis arcticeps (Günther, 1875)

Silybura arcticeps Günther, 1875: 229.

TYPE MATERIAL. — Two syntypes: BMNH 1946.1.16.11-12.

TYPE LOCALITY. — Tirunelveli hills, Tamil Nadu state, India.

DISTRIBUTION. — Known from the Agasthyamalai and nearby hills of India South of the Sencotta Gap, at elevations *c.* 1200-1800 m (Whitaker & Captain 2004; Ganesh *et al.* 2014; Wallach *et al.* 2014; Ganesh 2015).

DESCRIPTION

Maximum total size *c.* 290 mm, ventrals 127-128, subcaudals 8 or 9, dorsal scales in 17 rows at midbody (see Smith 1943; Gower *et al.* 2008; Ganesh *et al.* 2014). Type V tail-shield, in accordance with Smith's (1943) state II, the tail is sharply truncated dorsally at a *c.* 45° angle, with the enlarged dorsal scales bi- or tri-carinate. Snout is "Alternate Rounded;" semi-circular when viewed from above. Color pattern typically a brown dorsum with yellow ventral coloration extending irregularly onto the sides.

REMARKS

This species appears to be very rarely collected or reported. The species *Uropeltis madurensis* was once considered a synonym (Smith 1943) or subspecies (Whitaker & Captain 2004) of *U. arcticeps*, but has been resurrected from the synonymy of *U. arcticeps* (see Ganesh *et al.* 2014).

Uropeltis beddomii (Günther, 1862)

Silybura beddomii Günther, 1862: 56.

TYPE MATERIAL. — Putatively four syntypes: BMNH 1946.1.16.13-15, and MNHN-RA-1895.90. The MNHN jar contains two specimens; the actual number of types is unclear.

TYPE LOCALITY. — Anamalai hills, eastern Kerala/western Tamil Nadu state, India.

DISTRIBUTION. — This species has a relatively small distribution in the Anamalai hills of India, *c.* 2000 m (see McDiarmid *et al.* 1999; Wallach *et al.* 2014; Ganesh 2015).

DESCRIPTION

Maximum total length *c.* 250 mm, ventrals 180-188, dorsal scales in 17 rows at midbody. Subcaudals 6-9 *contra* Smith

(1943) who reported 6-7, apparently only examining the BMNH material; both MNHN syntypes have 9. Non-descript color-pattern, with a primarily brown dorsal coloration and a narrow yellow streak on the side of the neck, venter brown and yellow, and a yellow crossband at the base of tail. Tail is partially compressed dorsally as described in Smith's (1943) state I, approaching the "sliced-off" condition of his state II; scales in shield are enlarged and multicarinate, terminal scute is enlarged and has several spines. We classify it as Type IV. The snout is "Alternate Pointed", with an enlarged, pointed, and recurved rostral.

REMARKS

This species has apparently not been reported since the late 19th century (Roux 1928; Wall 1928) based on a lack of recent published reports or accessioned specimens, and is known only from the syntypes and a few later collections. This species was confused with or even treated as conspecific with *U. ellioti* by Beddome (1886), which is likely a complex of multiple species (see below).

Uropeltis bicatenata (Günther, 1864)
(Fig. 8C)

Silybura bicatenata Günther, 1864: 350.

TYPE MATERIAL. — Holotype: BMNH 1860.3.19.1277 (= 1946.1.16.8).

TYPE LOCALITY. — The Deccan Plateau, central India. We revise this by subsequent restriction to the Pune hills, Maharashtra state, based on referred material of known origin, including BNHS S225, 3251, 3252, and 3265-66 from Bhimashankar and Fangul Gauhan (Gower *et al.* 2008).

DISTRIBUTION. — Definitely known only from the Pune hills of India, including Bhimashankar and Fangul Gauhan (Gower *et al.* 2008), and Kalsubai of Igatpuri-Nashik hills (VS & AS, pers. obs.) at elevations *c.* 700-1800 m.

DESCRIPTION

Maximum total length *c.* 260 mm, ventrals 130-141, subcaudals 8-9 (females) or 10-12 (males), dorsal scales in 17 rows at midbody. In accordance with Smith's (1943) state II, the tail is sharply truncated dorsally at a *c.* 45° angle, with the enlarged dorsal scales bi- or tri-carinate. The snout is "Alternate Rounded". Distinctive color-pattern, with a primarily brown dorsal and ventral coloration, with irregular yellow stripes or dots down either side of the dorsum ventrolaterally, giving the appearance of a chain-like pattern.

REMARKS

This species was resurrected from the synonymy of *Uropeltis ceylanica* Cuvier, 1829 by Gower *et al.* (2008), and some existing material referred to *U. ceylanica* may actually be part of this taxon. One of the more northerly ranging species of *Uropeltis*.

Uropeltis broughami (Beddome, 1878)

Silybura broughami Beddome, 1878b: 800. Putatively two syntypes: BMNH 1883.1.12.23 (= 1946.1.16.29) and MNHN-RA-1895.89, as listed by Wallach *et al.* (2014). However, Beddome (1878b) described only a single specimen, and Boulenger (1893a) lists BMNH 1946.1.16.29 as the holotype. Additionally, the MNHN specimen resembles Beddome's (1878b) description of one of the two *Silybura levingii* syntypes, and likely represents one of those specimens (BMNH 1946.1.16.35-36), sent to Paris. We regard BMNH 1946.1.16.29 as the holotype of *Silybura broughami*. Type locality: Sirumalai and Palni hills, Tamil Nadu state, India.

Silybura levingii Beddome, 1878b: 801. Two syntypes: BMNH 1946.1.16.35-36. Type locality: Lower Pulney hills, Tamil Nadu state, India. Designated as a junior subjective synonym by Beddome (1886). The specimen MNHN-RA-1895.89 is listed as a type in the Paris catalogue, and appears to represent one of the two syntypes BMNH 1946.1.16.35-36, likely sent from London at a later date. See Beddome (1878b).

DISTRIBUTION. — Palni hills in the southern Western Ghats of India, *c.* 1230-1680 m (Roux 1928; Ganesh 2015).

DESCRIPTION

Maximum total length *c.* 410 mm, ventrals 195-230, subcaudals 7-10, dorsal scales in 19 rows at midbody (Smith 1943). Smith (1943) also reports one putative specimen with 181 ventrals, and the specimen dissected here has 173. In contrast to the classification of Smith (1943) as state II, the tail appears to match more closely his state I in the specimens examined, being partially compressed dorsally but still somewhat rounded on top, with the expanded dorsal scales multi-carinate. The terminal scute is expanded and terminates in two points. The tail appears more similar to *U. beddomii* or *U. ellioti*, than to *U. macrolepis* as stated by Smith (1943). We classify it as our Type IV. The snout is "Alternate Pointed", with an enlarged, pointed, and recurved rostral. Distinctive color-pattern, with a primarily brown dorsal and ventral coloration, and irregular rows of yellow spots ventrolaterally, and yellow flecking randomly on the other dorsal scales. The single specimen dissected has a much smaller right lung (16% of SVL) than any other *Uropeltis* specimen examined (mean of 25% SVL), as well as a more posterior left kidney (91% vs 85%), and more anterior gallbladder (55% vs 69%).

REMARKS

This is a very rare species that is not frequently sighted or collected, based on a dearth of published records. Roux (1928) recorded this species from Thandikudi in the Palni hills. The specimen dissected here, CAS 9113, was collected by Herre in 1940 at Kodai Kanal in the Palni hills *c.* 6000 ft, a region where *Uropeltis broughami* and *U. woodmasoni* are putatively sympatric (Roux 1928; Wall 1928; Rajendran 1985). The specimen has 173 ventrals, placing it in the range of *U. woodmasoni* (166-183), but strongly resembles the original description of *U. broughami* and the body form and color pattern of MNHN-RA-1895.89 (likely a syntype of *Silybura levingii*) almost exactly, being more slender than *U. woodmasoni* and having irregular black crossbands with yellowish-white spots and yellow blotches on the sides of the body and tail. Given

the small number of specimens known from this area, the status of these species is unclear, but it seems likely that there is much greater taxonomic uncertainty than implied by currently recognized species boundaries, diagnoses, and known geographic distributions. A recent long-term herpetological study in Sirumalai (Ganesh & Arumugam 2016), concluded its absence there based on lack of sightings.

Uropeltis ceylanica Cuvier, 1829
(Fig. 8D)

Uropeltis ceylanica Cuvier, 1829: 76. Lectotype: MNHN-RA-0.39 by subsequent designation of Gans (1966). Type locality: 'Ceylan' (Sri Lanka), in error.

Uropeltis affinis Jerdon, 1854: 527. No type. A *nomen dubium fide* Boulenger (1890). Designated as a junior subjective synonym by Wallach *et al.* (2014). Type locality: Western Coast, peninsular India.

Silybura brevis Günther, 1862: 56. Holotype: BMNH 1946.1.16.42. Type locality: Anaimalai hills, Tamil Nadu state, India. Designated as a junior subjective synonym by Smith (1943). As per McDiarmid *et al.* (1999), NMW 14056 is not a paratype, *contra* Tiedemann & Häupl (1980).

Silybura nilgherriensis Beddome, 1863a: 47. Holotype: BMNH 1874.4.29.88 (= 1946.1.16.41). Type locality: Ooty, Tamil Nadu state, India. Designated as a junior subjective synonym by Günther (1875). See Beddome (1863a).

DISTRIBUTION. — Apparently a widespread species in India, found in the Western Ghats South of the Goa Gap, *c.* 500-1500 m (Wallach *et al.* 2014). One of the most-cited species in local faunal lists, second only perhaps to *U. ellioti*.

DESCRIPTION

Gower *et al.* (2008) did not re-diagnose *U. ceylanica* when they re-described *U. bicatenata*, and the status of much material referred to *U. ceylanica* is thus unclear, as is variation in external morphology. Following Smith (1943), *U. ceylanica* is relatively large, maximum total length *c.* 460 mm, ventrals 119-146, subcaudals 8-12, with dorsal scales in 17 rows mid-body. The tail of specimens examined matches Smith's (1943) state II (our Type V), being sharply truncated dorsally at a *c.* 45° angle, with the enlarged dorsal scales bi- or tri-carinate. Variation in the number of shield scales and their carinations may be helpful in delimiting species in future revisions (Gower *et al.* 2008). Snout is "Alternate Rounded". Color-pattern typically non-descript, with a primarily dark brown or black dorsal and ventral coloration, with irregular yellow blotches extending onto the dorsum ventrolaterally. The single specimen dissected had a larger left kidney (10% SVL) than any other *Uropeltis* specimen examined (mean of 7%).

REMARKS

This is the type species of the genus *Uropeltis*. Two specimens were sent to the MNHN in 1822, which were described in detail and one illustrated by Cocteau (1833). Cocteau also indicates that the specimens seem to have been examined already by Cuvier, thus making it likely that the specimen

illustrated by Cuvier (1829) was one of the two from 1822, possibly the same one illustrated by Cocteau. One specimen was subsequently lost according to Gans (1966), while the second (MNHN-RA-0.39) was designated by Gans (1966: 18) as the lectotype. However, MNHN-RA-0.39 may have been the specimen illustrated by Cuvier (1829), Cocteau (1833), or both, and thus may have already been the holotype. Populations currently referred to *Uropeltis ceylanica* have relatively little dorsal patterning, compared to species such as *U. bicatenata* or *U. shorttii* that have recently been resurrected from the synonymy of *U. ceylanica* (Gower *et al.* 2008; Ganesh *et al.* 2014). There may still be cryptic species in this taxon (see Gower *et al.* 2008; Ganesh *et al.* 2014). Morphologically similar populations exist in southern Eastern Ghats (Boulenger 1893a; Ganesh & Arumugam 2016). A detailed, rangewide comparison of material is needed to determine the true diversity and distribution of species, to assign the lectotype to one of these lineages, and revise the type locality.

Uropeltis dindigalensis (Beddome, 1877)
(Fig. 8E)

Silybura dindigalensis Beddome, 1877: 167.

TYPE MATERIAL. — Four syntypes: BMNH 1883.1.12.5 (= 1946.1.16.2), BMNH 1883.1.12.7 (= 1946.1.16.4), BMNH 1877.8.10.3 (= 1946.1.16.37), and MNHN-RA-1895.88.

TYPE LOCALITY. — Near Dindigul, Sirumalai hills, Eastern Ghats, Tamil Nadu state, India.

DISTRIBUTION. — Endemic to the Sirumalai hills of India in the extreme southern Eastern Ghats at elevations >1000 m (Wallach *et al.* 2014; Ganesh 2015; Ganesh & Arumugam 2016).

DESCRIPTION

Maximum total length *c.* 370 mm, ventrals 155–168, subcaudals 5–12, dorsal scales in 17 rows at midbody (Smith 1943; Rajendran 1985). Distinctive color-pattern, with a primarily dark brown or black dorsal and ventral coloration, with yellowish-white spots or crossbars ringing the body, and yellowish-white triangular markings on the side of the neck and tail. The MNHN specimen examined does not have a yellow streak on the lips, as described by Smith (1943), presumably from the BMNH specimens. Color pattern is somewhat similar to *U. broughami*. Snout is “Alternate Pointed”, with recurved rostral highly reminiscent of *Rhinophis*. The tail generally agrees with Smith’s state I (our Type IV), being slightly compressed dorsally, but not approaching the ‘sliced-off’ state II. The shield scales are enlarged and multicarinate, extending around the tail to the subcaudals. The terminal scute is enlarged and projecting, ending in two points.

REMARKS

This species is apparently rare, having been collected only near the type locality in 1972 (Rajendran 1985), an undated recent collection (Ganesh & Asokan 2010), and a recent

report of nine uncollected specimens from the Sirumalai hills (Ganesh & Arumugam 2016). The taxonomic identity of *Uropeltis cf. dindigalensis* reported by Chandramouli & Ganesh (2010) from the High Wavys is unresolved.

Uropeltis ellioti (Gray, 1858)
(Fig. 8F)

Siloboura ellioti Gray, 1858a: 261. Holotype: BMNH 1946.1.16.6. Type locality: Given only as “Madras”. The phrase probably refers to the Madras Presidency, a colonial province encompassing most of southern and southeastern India, and not the city of Madras (present-day Chennai). Restriction of this locality by subsequent revision will likely be needed in the future, as this is likely a complex of species (see below). See Gray (1858a).

Silybura punctata Günther, 1875: 229. Five syntypes: BMNH 1946.1.16.40, Golcondah hills, Kerala state, India; BMNH 1946.1.16.43–46, Pulney hills, Tamil Nadu state, India. Designated as a subjective junior synonym by Boulenger (1893a).

DISTRIBUTION. — Apparently a widespread Indian species (see Wallach *et al.* 2014; Ganesh 2015), occurring in both the Eastern (Rajendran 1985; Guptha *et al.* 2012; Ganesh & Arumugam 2016) and Western Ghats as far North as Gujarat (VS, pers. obs.); a patched form also occurs in the Satpura hills of Central India at varying elevations (500–1800 m; Wadatar & Chikhale 2010).

DESCRIPTION

Maximum total size *c.* 320 mm, ventrals 144–176, subcaudals 5–11, dorsal scales in 17 rows at midbody (Whitaker & Captain 2004). Ganesh & Arumugam (2016) report 137–153 ventrals from the Jawadi and Shevaroy hills. Smith (1943) classified the tail as state I, but in the MNHN specimens examined, it exhibits his state II, being relatively truncated and compressed dorsally, with clear separation between the bi- or tri-carinate shield scales and the smooth dorsal scales on the side of the tail (see Rajendran 1985). We classify the tail as Type IV. The snout is “Alternate Pointed”, with an enlarged and recurved rostral. Color pattern is variable, with a dark brown or black dorsal coloration with occasional yellowish-white spots, short stripes on the side of the neck and tail, a dark brown venter with small yellow dots, and a transverse yellow bar across the vent connecting the stripes on either side of the tail. The tail and color-pattern clearly varies geographically, in comparison with the specimen pictured by Whitaker & Captain (2004), and those examined here (Appendix I). This is likely a complex of species.

REMARKS

The distribution of this species is not very well-studied, but it is apparently common at several sites throughout its range, with wide geographic variation in meristic characters (particularly ventral-scale counts) and tail morphology suggesting the presence of cryptic species (see Rajendran 1985). Thus, a detailed comparison of multiple populations will be needed to determine the phylogeographic structure and correct geographic assignment of the holotype for the nominal lineage.

Uropeltis grandis (Beddome, 1867)

Rhinophis grandis Beddome, 1867: 15. Three syntypes: BMNH 1946.1.16.82 and MNHN-RA-1895.79 (two specimens). These three specimens are thus the syntypes of both *Rhinophis grandis* erected by Beddome (1867), previously considered a *nomen prae-occupatum* by Gans (1966), and of *Uropeltis smithi* Gans 1966. Type locality: Anaimalai hills, eastern Kerala/western Tamil Nadu state, India.

Uropeltis smithi Gans, 1966: 22. Objective junior synonym (see Remarks).

DISTRIBUTION. — This species has a relatively small range near the type locality in the Anaimalai hills of India, *c.* 1220–2155 m (Wallach *et al.* 2014; Ganesh 2015).

DESCRIPTION

Maximum total size *c.* 470 mm, ventrals 190–218, subcaudals 6–12, dorsal scales in 19 rows at midbody (Smith 1943; Constable 1949). Snout is “Alternate Pointed” with “boomerang” rostral resembling *Rhinophis*, to which the species was originally assigned, but does not divide the nasals in the specimens examined. Smith (1943) classified the tail as state III, a group which contains a great deal of variation in observed tail morphology. In the syntypes examined, the tail is compressed laterally and dorsally, and the expanded multicarinate scales encircle the entire tail. The terminal scute is enlarged, projecting, and rugose, ending in two larger points. We tentatively agree with Smith’s classification (our Type III), but it is also possible that this is a *Rhinophis*-like Type VI tail, masquerading as Type III. Distinctive color-pattern, with a dark violet dorsum and venter, and alternating yellow spots or crossbands on the sides of the body. The single specimen dissected lacks an intrapulmonary bronchus, unlike any other uropeltid specimen examined, and has a large number of tracheal rings (336), of which only *U. myhendrae* (353) also has more than 300 among the examined specimens of sampled uropeltid taxa.

REMARKS

This species bore a replacement name, having originally been described as *Rhinophis grandis* by Beddome (1867), creating an issue of homonymy when transferred to *Uropeltis* by Smith (1943), *U. grandis* Kelaart, 1853 being a pre-existing name, though it had already been relegated to the synonymy of *Pseudotyphlops philippinus* (now *R. saffragamus*). However, this species may actually be a *Rhinophis*, as it bears *Rhinophis*-like rostral and shield morphology, in which case *Rhinophis smithi* (Gans 1966) is the proper name if transferred into that genus. Beddome (1867) stated that it was clearly congeneric with *U. pulneyensis*, which also has *Rhinophis*-like rostral and tail-shield morphology. Further analyses using additional characters such as DNA-sequence data will be needed to resolve the relationships of these species.

Uropeltis liura (Günther, 1875)
(Fig. 8G)

Silybura liura Günther, 1875: 228.

TYPE MATERIAL. — Holotype: BMNH 1874.4.29.1206 (= 1946.1.16.7).

TYPE LOCALITY. — High Wavy Mountains, Madura hills, eastern Kerala and western Tamil Nadu state, India.

DISTRIBUTION. — India, High Wavys or Meghamalai hills, Cardamom hills, and Agasthyamalai or Ashambu hills at elevations > 1200 m (see Rajendran 1985; Wallach *et al.* 2014).

DESCRIPTION

Maximum total size *c.* 320 mm, ventrals 173–188 (but 182–208 reported by Rajendran 1985), subcaudals 8–12, dorsal scales in 17 rows at midbody (Whitaker & Captain 2004). Smith classified the tail as state III, in which the tail is blunt and rounded and the scales are smooth, with an enlarged, projecting terminal scute ending in two points. We tentatively agree with this classification (our Type III). Snout is “Alternate Pointed”, but rostral is less enlarged or recurved than other such species (e.g., *U. beddomii*). Very distinctive color-pattern, with a primarily purplish-black dorsal coloration with small yellowish-white ocelli scattered throughout, and small irregular rectangles of yellow scales extending from the venter onto the dorsum. The single specimen dissected has a larger densely vascularized portion of the right lung (10% of SVL) than any other *Uropeltis* specimen examined (mean of 6%).

REMARKS

This species has a complicated taxonomy; the original name-bearing populations are from the High Wavys and were recently studied *in situ* (Whitaker & Captain 2004; SRG *pers. obs.*). However, Rajendran (1985) assigned populations from Agasthyamalais South of the Sencotta Gap to this taxon, and further work is thus needed to clarify the status of the southern population. There are reports of substantial geographic variation in color pattern and ventral count (Rajendran 1985; Whitaker & Captain 2004; Ganesh 2015).

Uropeltis macrolepis (Peters, 1861)
(Fig. 8H)

Silybura macrolepis Peters, 1861a: 904. Holotype: BMNH 1884.4.20.4 (= 1946.1.15.99). Type locality: Given as “Ceylon?” by Peters (1861a); revised to Bombay hills, Maharashtra, India by Smith (1943). See Peters (1861a).

Uropeltis macrolepis mahableshwarensis Chari, 1955: 901. Holotype: BNHM 1994. Type locality: Mahableshwar, Satara District, Maharashtra state, India.

DISTRIBUTION. — This species has a relatively large distribution in the northern Western Ghats of India, North of the Goa Gap to the Pune hills, and Salsette Island (*c.* 0–1370 m).

DESCRIPTION

Maximum total size *c.* 320 mm, ventrals 120-140, subcaudals 7-13 (Smith 1943; Whitaker & Captain 2004). The only *Uropeltis* with dorsal scales arranged in 15 rows at midbody. Color pattern varies extensively, with numerous drastically different morphs found in different populations (pictured in Whitaker & Captain 2004). Coloration is often black or a dark purplish-brown, with no dorsal pattern or sometimes with lighter edging to scales, or speckles, or yellow ocellations dorsolaterally, or yellow stripes dorsolaterally, a yellow stripe on the lips and side of neck, sometimes breaking up into several large yellow spots ventrolaterally, and a yellow stripe on either side of the tail. The tail is Smith's (1943) state II (our Type V), being sharply truncated dorsally at a *c.* 45° angle, with the enlarged dorsal scales bi- or tri-carinate. Snout is "Alternate Rounded". The single specimen dissected had a larger avascular portion of the right lung (17% of SVL) than any other *Uropeltis* specimen examined (mean of 7%), a larger liver-gallbladder interval (10% vs 3%), and the lowest number of tracheal rings (131) of any examined uropeltid specimen (mean of 204) and any *Uropeltis* species in particular (mean of 228).

REMARKS

This species is not very well-studied, but is apparently common at several sites throughout its range, and exhibits polytypic color-patterns (Whitaker & Captain 2004). One population with thick yellow stripes running down either side of the body was previously described as a separate subspecies *U. m. mahableshwarensis* (see Chari 1952, 1955). Having examined the holotype of *Silybura macrolepis* Peters, 1861 (BMNH 1946.1.15.99), it is clearly this same striped *mahableshwarensis* form, visually similar to the holotype of *U. m. mahableshwarensis* (BNHM 1994). It seems evident that Chari (1952, 1955) did not actually examine Peter's (1861a) type before describing *U. m. mahableshwarensis*. Additionally, there is no genealogical exclusivity between the striped and patternless forms (Fig. 1). Thus, we synonymize *Uropeltis macrolepis mahableshwarensis* Chari, 1955 with *Uropeltis macrolepis* (Peters, 1861). Any subspecific taxon based on the striped form would have to carry the name *U. m. macrolepis* (Peters, 1861) by the Principle of Coordination. We thus revise the type locality of *U. macrolepis* to Mahableshwar, Satara District, Maharashtra state, India. This species is polytypic, with unpatterned, striped, ocellated, speckled and broken-striped populations (see photos in Whitaker & Captain 2004), some of which may also represent additional cryptic species based on our genetic analyses (Fig. 1).

Uropeltis macrorhyncha (Beddome, 1877)

Silybura macrorhyncha Beddome, 1877: 167.

TYPE MATERIAL. — Holotype: BMNH 1883.1.12.24 (= 1946.9.7.45).

TYPE LOCALITY. — Anamalai hills, southern Western Ghats, eastern Kerala and western Tamil Nadu state, India.

DISTRIBUTION. — Restricted to the Anaimalai hills of the southern Western Ghats of India, *c.* 100-1335 m (Roux 1928; Wallach *et al.* 2014; Ganesh 2015).

DESCRIPTION

Ventrals 203-213 or 226 reported by Beddome (1877) for the holotype, subcaudals 6, dorsal scales in 17 rows at midbody (see Smith 1943). Smith (1943) reports the maximum total size as 740 mm; it is unclear if this is a typographical error, or if this species truly does grow exceedingly large compared to all other uropeltid taxa. Beddome (1877) reports the holotype as 546 mm total length. As with *U. ellioti*, the tail was coded as state I by Smith (1943), but approaches state II, with a flattened caudal disk with multicarinate scales in the holotype and specimen examined here. We cannot differentiate it between our Types III and IV if retained in *Uropeltis*. Color-pattern non-descript, with a brown dorsal and ventral coloration mixed diffusely with yellow, a yellow streak along either side of the neck, and a yellow streak on either side of the tail connected by a crossbar over the vent. Rostral strongly keeled, enlarged, and recurved, indistinguishable from most *Rhinophis* species at first glance, but not separating the nasals. We classify it as "Alternate Pointed", but the tail and snout could qualify as Type VI and "Boomerang Rostral", and the species may belong to *Rhinophis*.

REMARKS

This species, along with *Uropeltis grandis* and *U. pulneyensis*, may be allied with *Rhinophis*, as the rostral strongly resembles most *Rhinophis* species in being "boomerang" shaped, significantly enlarged with a dorsal keel that projects rearwards, nearly separating the nasals. Future analyses may result in these species being re-assigned. Reported as very rare by Beddome (1877); only a few specimens seem to exist (Boulenger 1890; Smith 1943; Appendix 1).

Uropeltis maculata (Beddome, 1878)

Silybura maculata Beddome, 1878: 154. See Beddome (1878a).

TYPE MATERIAL. — Putatively eight syntypes: BMNH 1946.1.16.63-65, BMNH 1946.1.16.83-84, MNHN-RA-1895.81a-b, and NMW 21598: 1-2 *vide* Wallach *et al.* (2014). The MNHN jar contains two specimens, possibly representing one of the two BMNH series.

TYPE LOCALITY. — Anamalai hills, southern Western Ghats, eastern Kerala and western Tamil Nadu state, India.

DISTRIBUTION. — Restricted to the Anaimalai hills of India, South of the Palghat Gap, *c.* 1065-2400 m (Ferguson 1895, 1902; Wallach *et al.* 2014; Ganesh 2015).

DESCRIPTION

Moderately large, maximum total size *c.* 390 mm, ventrals 140-165, subcaudals 8-13, dorsal scales in 17 rows at midbody (Smith 1943; Rajendran 1985). The tails of the MNHN syntypes resemble that of *Uropeltis liura*; Smith (1943) coded it as state III (our Type III), and they are relatively blunt and compressed, the scales smooth or very weakly multicarinate,

and an enlarged terminal scute ending in two points. Snout is “Alternate Pointed”, but less acutely pointed than species such as *U. beddomii*. Distinctive color-pattern, with a dark brown or black dorsal and ventral coloration, with dark red blotches on the sides anteriorly, and on the tail.

REMARK

This species has been collected only a few times since its description, around the type locality (see Rajendran 1985).

Uropeltis madurensis (Beddome, 1878)
(Fig. 9A)

Silybura madurensis Beddome, 1878b: 802. See Beddome (1878b).

TYPE MATERIAL. — Two syntypes: BMNH 1882.2.12.11-12 (= 1946.1.16.38-39).

TYPE LOCALITY. — High Wavy Mountains, Theni District, Tamil Nadu state, India.

DISTRIBUTION. — This species is endemic to the High Wavy-Varushanad-Periyar hill complex in Tamil Nadu state, India, *c.* 1300-1600 m (see Ferguson 1895, 1902; Ganesh *et al.* 2014; Ganesh 2015).

DESCRIPTION

Maximum total size *c.* 450 mm, ventrals 144-157, caudals 7-10, dorsal scales in 17 rows at midbody (Smith 1943; Whitaker & Captain 2004; Ganesh *et al.* 2014).

Non-descript color pattern, with a dark brown or black dorsal and ventral coloration, with scales edged in yellow, and yellow blotches on the venter. Tail is firmly Type V and snout is “Alternate Rounded”, as with *Uropeltis arcticeps*. The two specimens dissected differ substantially in the number of left bronchus rings, with one having one and the other having eight, whereas no other *Uropeltis* specimen examined had more than four.

REMARKS

This species was recently resurrected from the synonymy of *Uropeltis arcticeps* by Ganesh *et al.* (2014), the species with which it has historically been synonymised (Smith 1943). We did not examine the type series; a lectotype should be designated by future revisers, given the historical confusion with *U. arcticeps*.

Uropeltis mybendrae (Beddome, 1886)

Silybura nilgherriensis mybendrae Beddome, 1886: 15. Recognized as a full species by Boulenger (1893a).

TYPE MATERIAL. — Two syntypes: BMNH 1883.1.12.49 (= 1946.1.16.9) and MNHN-RA-1895.95.

TYPE LOCALITY. — Mahendragiri, Tamil Nadu state, India.

DISTRIBUTION. — Definitively known only from the Agasthyamalai hills of India, South of the Sencotta Gap, at elevations *c.* 600-1200 m (Ferguson 1895, 1902; Wallach *et al.* 2014; Ganesh 2015).

DESCRIPTION

Maximum total size *c.* 540 mm, ventrals 139-156, subcaudals 6-8, dorsal scales in 17 rows at midbody (Smith 1943; Rajendran 1985). The rostral resembles the *Rhinophis*-type “boomerang” condition and we classify it as “Alternate Pointed”, but the tail is firmly Smith’s (1943) state II (our Type V), resembling that of *U. ceylanica* and others, being sharply truncated at a *c.* 45° angle, with flattened, enlarged, bi- or tricarinate shield scales. Distinctive but variable color-pattern, with a dark brown or black dorsal and ventral coloration, triangular incomplete crossbands of yellow partially ringing the body, with black stippling in the yellow crossbands. The BMNH syntype is relatively patternless. The single specimen dissected had a larger number of tracheal rings (353) than any other uropeltid specimen examined (mean of 197), and any other *Uropeltis* species (mean of 212). Only the specimen of *U. grandis* also had more than 300 (336).

REMARKS

A specimen examined here (MNHN-RA-1897.255) was considered a possible type by McDiarmid *et al.* (1999), but is from another locality in the Punga hills, and has a much stronger color pattern than the relatively patternless syntype BMNH 1946.1.16.9. This is a rarely encountered species that is known only from a few scattered collections (see Rajendran 1985).

Uropeltis nitida (Beddome, 1878)

Silybura nitida Beddome, 1878a: 154. See Beddome (1878a).

TYPE MATERIAL. — Seven syntypes: BMNH 1946.1.16.30-31, BMNH 1946.1.13.95-97, and MNHN-RA-1895.87a-b.

TYPE LOCALITY. — Anamalai hills, around the Nelliampady Estates on the Cochin side, vicinity of western Nelliampathy hills, Palghat District, Kerala state, India.

DISTRIBUTION. — Known only from the type locality, the Anaimalai hill complex of India, South of the Palghat Gap, *c.* 1335-1700 m (Smith 1943; Wallach *et al.* 2014; Ganesh 2015).

DESCRIPTION

Maximum total length *c.* 340 mm, ventrals 184-195 or 197-224 *fide* Constable (1949), subcaudals 5-11, dorsal scales in 17 rows at midbody (see Smith 1943). Distinctive color-pattern, with a black or dark brown dorsal and ventral coloration, and alternating broken crossbands of yellow with offset meetings at the midline, or occasionally intersecting and forming complete rings, and yellow markings on the underside and side of tail. Tail is Smith’s (1943) state I (our Type IV), somewhat compressed dorsally, with scales expanded and multicarinate but no clear separation between shield scales and ordinary dorsal scales, and terminal scute enlarged, projecting, and carinate, ending in two points, similar to *U. liura*. In the juvenile MNHN syntype, tail more closely resembles Smith’s (1943) state III (our Type III), suggesting ontogenetic development. Snout is “Alternate Pointed”, although less acute than some species (e.g., *U. beddomii*).



FIG. 9. — Some uropeltid species photographed in life: **A**, *Uropeltis madurensis* (Beddome, 1878); **B**, *U. phipsonii* (Mason, 1888); **C**, *U. pulneyensis* (Beddome, 1863); **D**, *U. shorttii* (Beddome, 1863). Photos by SRG and S. Ramchandran.

REMARKS

The distinctiveness of this species from *Uropeltis ocellata* has been questioned by several authors (see McDiarmid *et al.* 1999), but we treat it as distinct from that species based on both geographic distribution and color pattern (see Boulenger 1893a). May be part of a species complex with other populations of *U. ocellata* (Constable 1949; see below). Apparently known only from the syntypes, based on a lack of published reports or accessioned specimens.

Uropeltis ocellata (Beddome, 1863)

Silybura ocellata Beddome, 1863a: 46. Lectotype: BMNH 1946.1.15.59 by subsequent designation of Gans (1966). Paralectotypes: MNHN-RA-1895.83-84 (see Remarks). Type locality: Walaghat, on the western slopes of the Nilgherries, Kerala state, India. See Beddome (1863a).

Silybura dupeni Beddome, 1878b: 801. Holotype: BMNH 1883.1.12.25 (= 1946.1.1.42). Type locality: Nelliampathi, Kerala state, India. Designated as a junior subjective synonym of *Silybura ocellata* Beddome, 1863 by Boulenger (1893a). See Beddome (1878b).

Silybura ochracea Beddome, 1878b: 801. Type material of unclear number and status in the ranges BMNH 1946.1.2.30-31, BMNH 1946.1.2.43-45, BMNH 1946.1.15.69-71, and BMNH

1946.1.15.85-86. Type locality: Nelliampathi, Ponachi, and Bolumpetty hills, Kerala state, India. Designated as a junior subjective synonym of *Silybura ochracea* Beddome, 1878 by Beddome (1886). See Beddome (1878b).

DISTRIBUTION. — India; known only from the Nilgiris and nearby hills (Anaimalai, Munnar, Wynaad, and Nelliampathi) North of the Palghat Gap (Wall 1919), at elevations *c.* 610-1980 m, and the Anaimalais South of the gap (see Boulenger 1893a; Ferguson 1895, 1902; Wall 1919; Smith 1943; Constable 1949; Rajendran 1985; Wallach *et al.* 2014; Ganesh 2015).

DESCRIPTION

Relatively large, maximum total length *c.* 530 mm, subcaudals 6-11, dorsal scales in 17 rows at midbody (see Boulenger 1893a; Smith 1943; Constable 1949; Rajendran 1985). Ventral scale-counts represent multiple discontinuous ranges in different populations. Collections from the Munnar hills, Kerala state, India, have 162-174 (Rajendran 1985), which is well outside the range of 196-199 from the Nilgiri and Wynaad hills, and both 184-195 and 214-231 from the Anaimalai hills, the latter representing “*dupeni*” and “*ochracea*” populations (Boulenger 1893a; Constable 1949; Rajendran 1985). Distinctive color-pattern, with a brown or yellowish-brown dorsal coloration banded with transverse rows of four or five yellowish-white spots or blotches, ringed with black.

Smith (1943) classified the tail as state I (our Type IV), but like *U. ellioti*, the tail approaches state II (our Type V) in the specimens examined, being relatively flattened dorsally with multicarinate shield scales distinct from the surrounding dorsals, and an enlarged, projecting terminal scute ending in two points (see also Rajendran 1985). Constable (1949) also reports variation between specimens representing Type IV and Type V tails, but without good locality data. Snout is “Alternate Pointed”, with variation in the acuteness of the rostral (see Constable 1949). This species likely represents a complex, likely including *U. nitida*, in which the “*dupeni*” and “*ochracea*” populations from the Anaimalai hills (see Boulenger 1893a; Constable 1949) and the relatively patternless populations from the Munnar hills (see Rajendran 1985) may all represent distinct species.

REMARKS

The types of *Silybura ocellata* Beddome, 1863, *S. ochracea* Beddome, 1878, and *S. dupeni* Beddome, 1878 are still in a state of confusion (see McDiarmid *et al.* 1999). For *S. dupeni*, Beddome (1878b) reported collecting only a single specimen, believed to be BMNH 1883.1.12.25 (= 1946.1.1.42). Thus, NMW 18695 is not a paratype of *S. dupeni*, *contra* Tiedemann & Häupl (1980). For *S. ochracea*, Beddome (1878b) reports at least three specimens from at least three localities (Nelliampathi, Ponachi, and Bolumpetty hills) in the Anaimalais. Boulenger (1893a) listed five types, and the BMNH collection reportedly contains five jars labeled “types” with 10 specimens, in the ranges BMNH 1946.1.2.30-31; BMNH 1946.1.2.43-45 from Polghat, a locality not reported by Beddome (1878); BMNH 1946.1.15.69-71; and BMNH 1946.1.15.85-86 (Gans 1966). The origin of this confusion (e.g., potential mistakes of Boulenger, the BMNH catalog, or Gans) is unclear; this issue should be resolved and a lectotype chosen by future researchers. For *S. ocellata*, Beddome (1863b) clarifies that he procured three specimens, upon which his (1863a) description was based. These are BMNH 1946.1.15.59, designated by Gans (1966) as the lectotype, and two MNHN specimens, designated by Gans (1966) as the paralectotypes. Gans (1966) listed MNHN “95.83-95.89” as the Paris specimens, which was likely a typographical error. McDiarmid *et al.* (1999) interpreted this to mean MNHN-RA-1895.83 and MNHN-RA-1895.89 were the syntypes, but this is incorrect. Having examined the specimens (see Appendix I) and the Paris catalog, the *S. ocellata* syntypes are MNHN-RA-1895.83-84, while the range from MNHN-RA-1895.85-95 contains a number of other uropeltid species accessioned around the same time. In particular, MNHN-RA-1895.89 is a syntype of *S. levingii* Beddome, 1878, and therefore represents *Uropeltis broughami*. Thus, NMW 13962 is not a paratype of *S. ocellata*, *contra* Tiedemann & Häupl (1980). One extralimital record of *U. ocellata* from Madhya Pradesh (Chandra & Gajbe 2003) was examined by us and found to be *U. ellioti*, with 166 ventrals and seven subcaudals. Although believed to be a common and widespread species, the only records that we deem likely to represent *U. ocellata sensu stricto* are those of Wall (1919), as they are from a topo-

typic population from Wayanad, North of the Palghat Gap. The status of populations from the Anaimalai hills South of the Palghat Gap, bearing the currently synonymised nomina *Silybura ochracea* Beddome, 1878 and *S. dupeni* Beddome, 1878, require re-evaluation. Rajendran (1985) reported differences within his concept of *U. ocellata* from the Munnar hills, also South of the Palghat Gap, with significantly lower ventral-scale counts (162-174). It is thus clear that *U. ocellata* needs a range-wide phylogeographic assessment (see also Constable 1949), and that, at a minimum, populations North and South of the Palghat gap are likely different species.

Uropeltis petersi (Beddome, 1878)

Silybura petersi Beddome, 1878a: 154.

TYPE MATERIAL. — Putatively six syntypes: BMNH 1878.1.11.3a-d (= 1946.1.1.7-9 & 1946.1.16.75), and MNHN-RA-1895.80a-b *vide* Wallach *et al.* (2014). However, only four (the BMNH specimens) are listed by McDiarmid *et al.* (1999); the MNHN catalogue lists their specimens as topotypic, and thus they may be part of the BMNH series, gifted from London (suggested by Wallach *et al.* 2014). See Beddome (1878a).

TYPE LOCALITY. — Forests above Pollachi, Tamil Nadu state, India.

DISTRIBUTION. — India; known with certainty only from the Anaimalai Hill complex South of the Palghat Gap, c. 1220-1700 m (Wallach *et al.* 2014; Ganesh 2015).

DESCRIPTION

Maximum total length c. 190 mm, ventrals 150-180, subcaudals 6-11, dorsal scales in 17 rows at midbody (see Smith 1943; Constable 1949). Smith (1943) classified the tail as state III; we agree (our Type III), the specimen examined here resembles *U. liura* in being slightly compressed, with little distinction of shield scales, being weakly multicarinate, and terminating in an enlarged, projecting, rugose scute. Snout is “Alternate Rounded”. Non-descript color-pattern, with a primarily brown or yellowish-brown dorsum and venter, occasionally with yellowish-white dots, and no tail markings.

REMARK

This species does not seem to have been collected since its description in the late 19th Century based on a lack of published reports, and may be known only from the type series.

Uropeltis phipsonii (Mason, 1888)
(Fig. 9B)

Silybura phipsonii Mason, 1888: 184.

TYPE MATERIAL. — Two syntypes: BMNH 1897.7.19.2-3 (= 1946.1.16.33-34).

TYPE LOCALITY. — Bombay Ghats, “Bombay Presidency”, northern Western Ghats, Maharashtra state, India.

DISTRIBUTION. — India; northern Western Ghats, including the Pune and Mulshi hills, c. 0-500 m (Wallach *et al.* 2014).

DESCRIPTION

Maximum total length *c.* 280 mm, ventrals 138-157, subcaudals 7-12, dorsal scales in 17 rows at midbody. The tail is firmly Smith's (1943) state II (our Type V), resembling that of *U. ceylanica* or *U. macrolepis* in being sharply truncated at a *c.* 45° angle, with thickened, enlarged, multicarinate shield scales, and terminating in an enlarged, rugose scute with two points. Snout is "Alternate Rounded". Highly variable color-pattern, with a primarily dark brown to black dorsum and venter, irregular broken crossbands of yellow dots occurring the length of the body, and yellow striped on either side of the mouth and tail. The single specimen dissected had a larger left lung (5.8% of SVL) than any other *Uropeltis* specimen examined (mean of 2.5%). Among all uropeltids, only *U. myhendrae* (4.3%) and *R. saffragamus* (4.7%) have left lungs larger than 4% of SVL.

REMARKS

Has been considered a synonym of *Uropeltis rubrolineata* (see Wallach *et al.* 2014), but this relationship seems extremely unlikely (see *U. rubrolineata* account). We concur with Whittaker & Captain (2004) that extralimital populations from the southern Western Ghats (Smith 1943; Rajendran 1985) require re-evaluation. Morphologically similar populations exist in southern Eastern Ghats (Boulenger 1893a; Ganesh & Arumugam 2016). We did not examine the type series; a lectotype should be chosen by future revisers. Molecular data suggest that this species as understood here and previously is actually a complex consisting of multiple cryptic lineages, which are closely related or even paraphyletic with respect to the *U. macrolepis* complex (Fig. 1).

Uropeltis pulneyensis (Beddome, 1863)
(Fig. 9C)

Plectrurus pulneyensis Beddome, 1863b: 228. Nine syntypes: BMNH 1946.1.17.6, MNHN-RA-1895.78, and ZSI 4381, 6948, 6950, and 6972-75. Type locality: Palani hills, western Tamil Nadu state, India. See Beddome (1863b).

Silybura guentheri Beddome, 1878b: 801. Holotype: BMNH 1883.1.12.34 (= 1946.1.16.74). Type locality: High Wavy Mountains, Tamil Nadu state, India. Designated as a junior subjective synonym by Boulenger (1893a). See Beddome (1878b).

DISTRIBUTION. — India; Palni hill complex including Kodaikanal and Munnar hills, at elevations > 1200 m (Wall 1923; Roux 1928; Rajendran 1985; Wallach *et al.* 2014; Ganesh 2015).

DESCRIPTION

Maximum total length *c.* 380 mm, ventrals 156-180, subcaudals 6-13, dorsal scales in 17 rows midbody (Smith 1943; Constable 1949). Tail is cylindrical, shortened, and rounded off, with an enlarged terminal scute, Smith's (1943) state III and our Type III. Snout is "Alternate Pointed" but not extremely acute, although rostral divides nasals. Non-descript color-pattern, with a dark brown dorsal and ventral coloration, a yellow stripe beginning on the labials and extending partially down the body, occasional yellow specks on the dorsum, and bright yellow bars or blotches on the venter and tail.

REMARKS

We retain this species in *Uropeltis*, but it may be allied with *Rhinophis* based on the rostral dividing the nasals, and a tail shield resembling *R. melanogaster* and *R. phillipsi* n. comb. (Smith 1943). Theobald (1868) reported a collection of three *U. pulneyensis* from Kelaart, taken near Kandy, which he took to indicate a Sri Lankan origin for the species, which thus also occurred on the Indian mainland. However, we can find no other reference to these specimens or the presence of *U. pulneyensis* in Sri Lanka. It seems likely that these were actually *R. saffragamus*, stated to be highly similar to *U. pulneyensis* by Beddome (1886), or another species, and we suggest that *U. pulneyensis* does not occur in Sri Lanka.

Uropeltis rubrolineata (Günther, 1875)

Silybura rubrolineata Günther, 1875: 228.

TYPE MATERIAL. — Lectotype: BMNH 1874.4.29.804 (= 1946.1.15.53) by subsequent designation of Beddome (1886).

TYPE LOCALITY. — Tirunelveli hills, southwestern Tamil Nadu state, India.

DISTRIBUTION. — Known only from the southern Western Ghats of India, in the Anaimalai and Tirunelveli hills of Kerala and Tamil Nadu states, 0-835 m (Ferguson 1895, 1902; Rajendran 1985; McDiarmid *et al.* 1999; Wallach *et al.* 2014; Ganesh 2015).

DESCRIPTION

Maximum total size *c.* 400 mm, ventrals 165-172, subcaudals 6-9, dorsal scales in 17 rows at midbody (see Smith 1943; Gower *et al.* 2008). Distinctive color-pattern, with a blackish-brown dorsal and ventral coloration, and a bright red stripe along each side, usually *c.* 2.5 scale-rows wide, beginning on the labials. Tail is Smith's (1943) state II (our Type V), resembling that of *U. ceylanica* or *U. macrolepis* in being sharply truncated at a *c.* 45° angle, with thickened, enlarged, bi- or tri-carinate shield scales, and terminating in an enlarged, rugose scute with two points. Snout is ambiguous in specimens examined between "Alternate Rounded" and "Alternate Pointed;" the rostral is somewhat recurved viewed laterally, but the snout is not particularly acute viewed from above.

REMARKS

Previous reports from the northern Western Ghats likely refer to other species such as *Uropeltis bicatenata* (see Gower *et al.* 2008) or *U. phipsonii* (see Wallach *et al.* 2014), based on geographic distribution and color-pattern differences. It is unclear why this species; with 165-172 ventrals, a dark dorsum and distinct red stripe, and geographic range in the southern Western Ghats; has been considered by many authors (e.g., Constable 1949; Gans 1966; Rajendran 1985) to be synonymous with *U. phipsonii*, which has 138-157 ventrals, a color pattern dominated by yellow bands and speckles, and occurs in the northern Western Ghats. The suggestion appears to have been raised by Constable (1949), but his discussion is difficult to follow and does not address these major, obvious

differences. It is possible that *U. phipsonii* and *U. rubrolineata* are closely related, but we suggest that they represent two very distinct species.

Uropeltis rubromaculata (Beddome, 1867)

Silybura rubromaculata Beddome, 1867: 15.

TYPE MATERIAL. — Between five and seven syntypes: BMNH 1946.1.15.51-52, BMNH 1946.1.15.82-84, MNHN-RA-1895.97, and NMW 18932 (see Remarks).

TYPE LOCALITY. — Anaimalai hills of eastern Kerala and western Tamil Nadu states, India.

DISTRIBUTION. — India; restricted to the Anaimalai Hill complex South of the Palghat Gap, at elevations *c.* 1065-1820 m (Wallach *et al.* 2014; Ganesh 2015).

DESCRIPTION

Maximum total size *c.* 380 mm, ventrals 127-136, subcaudals 7-10, dorsal scales in 17 rows at midbody (see Smith 1943). Tail is Smith's (1943) state II (our Type V), resembling that of *U. ceylanica* or *U. macrolepis* in being sharply truncated at a *c.* 45° angle, with thickened, enlarged, bi- or tri-carinate shield scales, and terminating in an enlarged, rugose scute with two points. Snout is "Alternate Pointed", but rostral is not heavily recurved. Distinctive color pattern, with an olive-brown dorsal coloration, dorsal scales two-toned, lighter posteriorly, a small number of red blotches or ocellations on either side of the body anteriorly, one on either side of the tail, and mixed red and yellow pigmentation of the ventral scales. The single specimen dissected had a smaller left lung (0.9% SVL) than any other *Uropeltis* specimen examined (mean of 2.8% SVL), though some *Rhinophis* and *Plectrurus* have similar small left lungs.

REMARKS

The number and location of the type series is unclear. Gans (1966) lists only the five BMNH specimens, while McDiarmid *et al.* (1999) list the same five, plus the NMW specimen, while doubting its validity as a type. Wallach *et al.* (2014) clarify that the MNHN specimen was sent from the BMNH, and the NMW specimen may have been similarly gifted. Thus, the MNHN and NMW specimens may be two of the original five BMNH specimens. We include all seven here as possible syntypes. This situation should be clarified by future researchers, and a lectotype designated.

Uropeltis shorttii (Beddome, 1863) (Fig. 9D)

Silybura shorttii Beddome, 1863a: 45.

TYPE MATERIAL. — Five syntypes: BMNH 1874.4.29.737-739 (= 1946.1.15.91-94), and MNHN-RA-1895.100.

TYPE LOCALITY. — Near Salem, Shevaroy hills, Tamil Nadu state, India.

DISTRIBUTION. — Endemic to the Shevaroy hills (Salem District of Tamil Nadu state, India) in the southern Eastern Ghats, at elevations > 1300 m (see Ganesh *et al.* 2014; Ganesh 2015; Ganesh & Arumugam 2016).

DESCRIPTION

Maximum total length *c.* 360 mm, ventrals 137-156, subcaudals 10-12, dorsal scales in 17 rows at midbody (see Gower 2006; Ganesh *et al.* 2014). Tail is Smith's (1943) state II (our Type V), resembling that of *U. ceylanica* or *U. macrolepis* in being sharply truncated at a *c.* 45° angle, with thickened, enlarged, bi- or tri-carinate shield scales, and terminating in an enlarged, rugose scute with two points. Snout is "Alternate Rounded". Distinctive color-pattern, having a blackish brown dorsum and venter, with irregular partial crossbands of bright yellow down the length of the body.

REMARKS

This species (see Beddome 1863a) was recently resurrected from the synonymy of *Uropeltis ceylanica* (see Ganesh *et al.* 2014), from which it is clearly distinct based on geographic distribution and color pattern. A recent field study (Ganesh & Arumugam 2016) in its type locality yielded further sightings of this point-endemic species. We did not examine the types; a lectotype should be chosen by future revisers.

Uropeltis woodmasoni (Theobald, 1876)

Silybura melanogaster Günther, 1875: 227. Lectotype: BMNH 1874.4.29.1192 (= 1946.1.15.57). Type locality: Anaimalai hills, Tamil Nadu state, India. Junior secondary homonym of *Uropeltis melanogaster* Gray, 1858. Designated as a subjective senior synonym of *Silybura nigra* Beddome, 1878 by Beddome (1886).

Silybura woodmasoni Theobald, 1876: 135. Holotype: ZSI 8760 (erroneously listed as the lectotype *vide* Wallach *et al.* 2014). Type locality: Palni hills, western Tamil Nadu state, India.

Silybura nigra Beddome, 1878a: 154. Five syntypes: BMNH 1883.1.12.17.20 (= 1946.1.1.39), BMNH 1878.1.11.4 (= 1946.1.15.54), BMNH 1878.1.11.5 (= 1946.1.15.56), and MNHN-RA-1895.85 (2 specimens). Type locality: Pulney hills, Tamil Nadu state, India. Designated as a junior subjective synonym by Smith (1943). See Beddome (1878a).

Uropeltis ruhunae Deraniyagala, 1954: 24. Holotype: NMSL R. S. 52. Type locality: Galle District, Sri Lanka. Designated here as a junior subjective synonym.

DISTRIBUTION. — Known from the Palni hills of India, in the Anaimalai-Palni hill complexes, South of the Palghat Gap, *c.* 1860-2100 m (Wall 1923; Wallach *et al.* 2014; Ganesh 2015).

DESCRIPTION

Relatively small, maximum total length *c.* 270 mm, ventrals 157-189, subcaudals 6-11, dorsal scales in 19 rows at midbody (Smith 1943; Constable 1949; Rajendran 1985). Smith (1943) classified the tail as state I, suggesting that it was similar to that of *U. nitida*. We tentatively agree (our Type IV). However, in the specimens examined here, the tail-form is ambiguous; the tail is rather blunt and compressed

with no distinct shield, and the scales are smooth or have weak tubercles, not keels or carinations as in *U. nitida*. The snout is “Alternate Pointed”, with a recurved, angular rostral. Distinctive color-pattern, color changing from olive-green anteriorly to ruddy posteriorly, terminal scute of tail forming projecting cap with several points, and bands of white or yellow flecks ringing the body.

REMARKS

Heavily expanded anterior-trunk musculature and noticeable diminution of body posteriorly. The recurved rostral, blunt tail with expanded terminal scute, and body form with enlarged trunk indicate possible *Rhinophis* affinities, *sensu* Smith (1943) and Rajendran (1985) who suggested conspecificity or close relationships with *U. pulneyensis* and *U. grandis*, respectively. This species was relatively common at a few sites near the type locality, *vide* Rajendran (1985), who also suggested possible conspecificity with *Uropeltis grandis* (Beddome, 1867). The difference in midbody scalerows (19 in *U. woodmasoni* vs 17 in *U. grandis*) is in a very stable, non-plastic character that supports their distinctiveness. Smith (1943) also remarked on suggested conspecificity between *U. woodmasoni* and *U. pulneyensis*, but this is also rejected on the basis of 19 vs 17 dorsal scale rows, and the rostral not dividing the nasals in *U. woodmasoni*.

DISCUSSION

As discussed here and noted by several previous authors (Smith 1943; Rajendran 1985, Gower *et al.* 2008; Gower & Maduwage 2011), there are several conspicuous external characters in uropeltids that appear to have great systematic value, but have not been quantitatively analyzed in terms of both intra- and inter-specific variation across sexes and developmental stages. These include rostral and tail-shield morphology, scale-row reduction, ventral and subcaudal scale counts, cloacal shield overlap (left over right and *vice versa*), visceral topology, and hemipenis morphology.

Diagnoses, particularly of new or re-delimited taxa, should take care to include discussions of as many of these characters as possible. In general, it is difficult to unambiguously diagnose species based on differences in one or two external scalation or color-pattern characters, and most diagnoses are thus composites of multiple, non-exclusive character states. Specifically, color-pattern variation and scale counts alone, the main characters traditionally used to diagnose species, cannot unambiguously separate all populations, particularly similar taxa or cryptic species.

A comparative study of variation in rostral morphology is particularly crucial (Fig. 2). A key question is variation in vertical ridging or keeling of the rostral, which is lower in some species (e.g., *Rhinophis melanogaster*) than in others (e.g., *R. lineatus*). Also seemingly important for distinguishing species is the degree to which the prefrontals and nasals are separated; the nasals are barely touching in some species (e.g., *R. saffragamus*), the nasals are separated but the prefrontals

are barely separated in others (e.g., *R. phillipsi* n. comb.), and in some, the rostral almost completely separates prefrontals, nearly contacting the parietal (e.g., *R. zigzag*). Enlarged rostrals partially or completely separating the nasals also suggest a potential affinity of *Uropeltis grandis*, *U. macrorhyncha*, and *U. pulneyensis* with *Rhinophis*. This remains to be tested with molecular evidence.

Concomitantly, tail-shield morphology appears to be far more complex than the six simple states used here and by previous researchers. In some lineages (e.g., *Brachyophidium*, *Melanophidium*, *Platyplectrurus*, *Plectururus*, *Teretrurus*), tail morphology appears to be highly consistent and easily characterized within and among species, having a compressed tail with either a single or double terminal spine, and without much apparent modification. In contrast, *Rhinophis* and *Uropeltis* exhibit a wide degree of variation that is not well-understood at present. Species of *Rhinophis* exhibit a distinct, rugose, keratinous tail disc that is clearly differentiated from the surrounding caudal scales (Fig. 3). However, this appears to exhibit variation both ontogenetically, and in terms of ultimate hypertrophy. In some species (particularly the Indian species and *R. phillipsi* n. comb.), the disc is less prominent, and resembles that of some *Uropeltis* species.

This ambiguity in characterization can be seen in Smith (1943), who clearly mis-categorized *Uropeltis melanogaster* and *U. phillipsi*, as these species exhibit a distinct, rugose disc. While his state II is fairly consistent, broad variation is seen in his states I and III, as noted in the accounts. Some species of *Uropeltis sensu stricto* appear to exhibit a *Rhinophis*-type “boomerang” rostral, and also potentially exhibit *Rhinophis*-type tail shields. These include, *U. grandis*, *U. macrorhyncha*, *U. pulneyensis*, and *U. woodmasoni*. In these species, the tail is not dorsally compressed or flattened as in *Uropeltis*, but the terminal scute is enlarged and exhibits rugosities or points. This terminal scute is embedded within the typical thickened, multi-carinate scaly area of the ‘tail shield’. In these cases, it is difficult to distinguish between the tail-shield structures of Smith’s (1943) states I and III for *Uropeltis*, and the *Rhinophis*-like Type V.

We suggest that a careful comparative study of a large series of material will be necessary to accurately define these character states, and a new ontological vocabulary for their description. Key features of interest include tail length, degree of flattening/convexity of discs or shields, degree and number of carinations on caudal scales, degree of rugosity or spination on terminal discs, and degree of terminal scute enlargement and projection. These may be particularly helpful in determining species limits and diagnosing new taxa, as noted by many recent authors (e.g., Gower *et al.* 2008; Gower & Maduwage 2011; Aengals & Ganesh 2013; Ganesh *et al.* 2014).

Scale-row reduction formulas and cloacal-shield overlap patterns may also be of interest when differentiating new taxa (Gower *et al.* 2008; Gower & Maduwage 2011; Gower *et al.* 2016). We did not focus on these characters here, as data were not available for large intraspecific series for most taxa, but patterns of scale-row reduction (a loss of 1-2 rows from the

anterior to posterior portion of the body) seem to be common (Gower *et al.* 2008, 2016). This character is important for distinguishing other ecologically similar and morphologically-conservative snakes, such as typhlopids (Pyron & Wallach 2014). The presence and amount of reduction within populations may serve as an important marker of specific distinctiveness. Additionally, whether the right anal-scale overlaps the left or vice versa appears to be important in distinguishing some Sri Lankan *Rhinophis* species (Gower & Maduwage 2011), but this remains to be examined in more Indian taxa.

Additionally, the montane setting of the Indian peninsula and adjacent Sri Lanka where most uropeltids are found is ecologically and geographically heterogenous, with distinct, contrasting, and complex geological and (hence) evolutionary trajectories. The disjunct distribution of wet-zone endemics, as most uropeltids are, presents numerous biogeographic challenges (Ganesh 2015). Given the often imprecise or erroneous historical locality details of many uropeltid specimens, mapping accurate geographic ranges for each species is a must for proper understanding of their diversification (Ganesh 2015).

Ultimately, DNA-sequence data from geographically precise collections will likely be needed to clarify species boundaries, the true geographic distributions of most taxa, and the accurate geographic assignment of available names and delimitation of cryptic species. It is possible that internal anatomical characters related to visceral topology and hemipenis morphology may help in the delimitation of some groups and assignment of preserved material, as in other snake groups (Zaher 1999; Pyron & Wallach 2014). This, too, will require extensive examination of large comparative series. Based on our results and previously published data, it appears that cryptic diversity is similarly high in uropeltids as in other poorly known fossorial snakes such as Typhlopidae (Marin *et al.* 2013), and that numerous species remain to be described.

We hope that this study will provide a platform for the continued study of intra- and inter-specific variation in uropeltids, and a basis for the further clarification of remaining taxonomic and nomenclatural problems, and broader ecological and evolutionary studies, such as biogeographic history and speciation processes in the group. Ironically, the function of the primary defining characteristic of the group, the shield tail, is still somewhat of a mystery.

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APPENDICES

APPENDIX 1. — Material examined.

- Plectrurus*” sp. (BMNH 1964.1678, BMNH 1964.1713);
Anilius scytale (ANSP 3251, ANSP 3253, ANSP 3255, FMNH 74045, LSUMZ 11819, LSUMZ 41301, LSUMZ 46263, MCZ 1207, MCZ 2986, TCWC 44582, UIMNH 54649, UMMZ 53923, UMMZ 53924);
Anomochilus weberi (RMNH 9507);
Brachyophidium rhodogaster (BMNH 1923.10.13.35, CAS 104256, CSPT/S-14a, CSPT/S-14b, MNHN-RA-1946.0049);
Cylindrophis maculatus (FMNH 121489, MCZ 15797, SDSU uncat.);
Cylindrophis ruffus (FMNH 129412, FMNH 129415, FMNH 129416, FMNH 129418, LSUMZ 46846, LSUMZ 9639, MCZ 4076);
Melanophidium bilineatum (MNHN-RA-1895.0111);
Melanophidium khairi (Melkh1);
Melanophidium punctatum (BMNH 1946.1.4.37, CSPT/S-9, MNHN-RA-1895.0110);
Melanophidium wynaudense (CAS 39633, CSPT/S-8, MNHN-RA-895.0108);
Platyplectrurus madurensis (BMNH 1946.1.15.80, CAS 9114, MAD 1929.2, MNHN-RA-1946.0050, MNHN-RA-1946.0052, MNHN-RA-1946.0053);
Platyplectrurus trilineatus (CSPT/S-2a, CSPT/S-2b, CSPT/S-2c, CSPT/S-2d, CSPT/S-2e, MNHN-RA-1897.0264, MNHN-RA-1897.0265);
Plectrurus aureus (CAS 17176, MNHN-RA-1895.0106);
Plectrurus guentheri (MNHN-RA-1895.0105);
Plectrurus perrotetii (CSPT/S-15, FMNH 171566, MAD 1.14.VII.1928, MAD 20.30.V.21, MCZ 3867, MNHN-RA-0000.4229);
Pseudoplectrurus canaricus (MCZ 24737, MNHN-RA-1895.0102);
Rhinophis blythii (BMNH 1903.11.5.1, BMNH 1905.3.25.73-75, BMNH 1930.5.8.65-66, BMNH 1931.5.13.6-22, BMNH 1946.1.1.45-46, BMNH 1964.1.656-59, BMNH 1964.1.688-89, BMNH 1972.2.164, BMNH 63.12.26.8, BMNH 74.4.29.455, BMNH 90.11.8.16-17, MNHN-RA-1895.0072, MNHN-RA-1895.0073, MNHN-RA-1999.8054);
Rhinophis drummondhayi (AMNH 85076, BMNH 1920.7.7.11, BMNH 1920.7.7.12-15, BMNH 1920.7.7.7-10, BMNH 1930.5.8.67, BMNH 1930.5.8.68, BMNH 1946.1.16.79-81, BMNH 1951.1.1.6.22-24, BMNH 1951.1.1.8-12, BMNH 1955.1.19.62-73, MW 1720);
Rhinophis homolepis (BMNH 1930.5.8.63-64, BMNH 1931.5.13.23-24, BMNH 1946.1.16.66-68, BMNH 1964.1.630-31, BMNH 60.3.19.132, BMNH 74.4.29.219, BMNH 80.2.2.117-18, BMNH 89.7.30.1-3, BMNH 97.10.20.17, CM 20484, MNHN-RA-1890.0479, MNHN-RA-1890.0480, MNHN-RA-1895.0071, MNHN-RA-1999.8057, MNHN-RA-1999.8058, WHT 5246);
Rhinophis melanogaster (BMNH 1905.3.25.66-72, BMNH 1946.1.16.94-97, BMNH 1969.2743-2754, BMNH 61.10.12.9-10, BMNH 61.2.21.3, BMNH 61.6.11.1-5, BMNH 62.1.19.5, BMNH 65.5.4.190, BMNH 68.3.17.15-16, BMNH 71.12.14.54, BMNH 98.5.3.12, MNHN-RA-0000.0344, MNHN-RA-1895.0069, MNHN-RA-1895.0076, MNHN-RA-1999.8055, UMMZ 96275);
Rhinophis oxyrhynchus (BMNH 1946.1.16.90, BMNH 1946.1.17.1, BMNH 1975.542, MNHN-RA-0.3237);
Rhinophis philippinus (BMNH 1930.5.8.69, BMNH 1946.1.16.99, BMNH 1964.1.670-77, BMNH 1964.1.690-1712, BMNH 1968.517, BMNH 58.10.19.59, BMNH 61.2.21.2, BMNH 65.5.11.189, BMNH 68.3.17.20, BMNH 98.5.3.11, MNHN-RA-1895.0070, SDNHM 25464, UMZC R5. 7/1);
Rhinophis phillipsi n. comb. (BMNH 1929.2.5.2., BMNH 1936.7.7.27-28, BMNH 1946.1.17.2, BMNH 1972.2.165);
Rhinophis porrectus (BMNH 1946.1.16.70), *Rhinophis punctatus* (BMNH 71.11.13.1-2, BMNH 74.4.29.220-1);
Rhinophis saffragamus (BMNH 1930.5.8.53-54, BMNH 1930.5.8.55-58, BMNH 1946.1.16.55, BMNH 1946.1.8.1, BMNH 1949.1.2.63-65, BMNH 1951.1.1.2-7, BMNH 1951.1.16.17-21, BMNH 1955.1.9.60, BMNH 1955.1.9.61, BMNH 1968.871, BMNH 1978.1092, BMNH 65.5.4.176, BMNH 74.4.29.222, BMNH 92.9.7.1, KU 31249, KU 31250, KU 31251, MNHN-RA-0.5621);
Rhinophis sanguineus (CSPT/S-5a, MAD V. 1937);
Rhinophis travancoricus (CSPT/S-11);
Rhinophis tricoloratus (NMSL 1978.5.1);
Teretrurus sanguineus (BMNH 1868.8.12.3, CSPT/S-10, MAD uncat., MCZ 6203, MNHN-RA-1895.0116, MNHN-RA-1895.0118);
Uropeltis “ruhunae” (NMSL 52);
Uropeltis arcticeps (MNHN-RA-1895.0101);
Uropeltis beddomii (MNHN-RA-1895.0090);
Uropeltis broughami (CAS 9113, MNHN-RA-1895.0089);
Uropeltis ceylanica (BMNH 1946.1.16.1, BMNH 1946.1.16.42, BMNH 1946.1.16.41, MAD uncat., MAD vi. 1938, MCZ 3868, MNHN-RA-1848.0265, MNHN-RA-1848.0266, MNHN-RA-1897.0258, MNHN-RA-1897.0259, MNHN-RA-1946.0266, MNHN-RA-1946.0267);
Uropeltis cf. *macrolepis* (U20 3766, U21 3767);
Uropeltis cf. *phipsonii* (U11 3302, U17 3763, U5 3296);
Uropeltis dindigalensis (MNHN-RA-1895.0077);
Uropeltis ellioti (BMNH 74.4.29.91, BMNH 1946.1.16.40, BMNH 1946.1.16.43-46, CSPT/S-81, FMNH 16110, MNHN-RA-1946.0270, MNHN-RA-1948.0259, MNHN-RA-1989.3842, U13 3759, U14 3760, ZSI-CZRC V/3846);
Uropeltis grandis (BMNH 1946.1.16.82, MCZ 6200, MNHN-RA-1895.0079);
Uropeltis liura (BMNH 1946.1.16.7, CM 90216, CSPT/S-3, MNHN-RA-1895.0082);
Uropeltis macrolepis (BMNH 1946.1.15.99, BMNH 1958.14.62-65, BNHS 177/BNHM 1994, BNHS 186, BNHS 187, BNHS

190, MCZ 28644, MNHN-RA-1897.0260, U1 3292, U12 3303, U2 3293, U3 3294, U8 3299, U9 3300);
Uropeltis macrorhyncha (CAS 39625);
Uropeltis maculata (MNHN-RA-1895.0081);
Uropeltis madurensis (CSPT/S-6, FMNH 217697, MCZ 22389);
Uropeltis mybendrae (BMNH 1946.1.16.9, CAS 39632, CSPT/S-5, MNHN-RA-1897.0255);
Uropeltis nitida (MCZ 47292, MNHN-RA-1895.0087);
Uropeltis ocellata (CSPT/S-7b, MCZ 3873, MNHN-RA-1895.0083);
Uropeltis petersi (CSPT/S-7, MCZ 6201);

Uropeltis phipsonii (BMNH 1946.1.16.33-34, MCZ 47040, U19 3765, U4 3295, U6 3297);
Uropeltis pulneyensis (CSPT/S-4a, MAD 1929, MCZ 1335, MNHN-RA-1948.0253, MNHN-RA-1994.0754, MNHN-RA-1994.0757, MNHN-RA-1994.0758);
Uropeltis rubrolineata (CSPT/S-13, MNHN-RA-1895.0093);
Uropeltis rubromaculata (CSPT/S-7a, MAD uncat., MCZ 6199, MNHN-RA-1895.0097);
Uropeltis shorttii (CSPT/S-80a, CSPT/S-80b);
Uropeltis woodmasoni (BMNH 1946.1.1.39, CSPT/S-4, MCZ 18040, MNHN-RA-1895.0085).

Appendix 2. — Collection data for specimens sequenced from Maharashtra state, India. Vouchers are by permission from AS.

Species	Voucher	Locality	Latitude N	Longitude E	SVL	TL	V	SC	DSR
<i>Melanophidium khairei</i>	Melkh1	Amboli, Maharashtra	15°56'50.55"	74°0'6.22"	368	20	198	11	15-13-14
<i>Uropeltis macrolepis</i>	U1 3292	Mahabaleshwer	17°55'20.258"	73°39'58.222"	217	15	127	10	15-15-15
<i>Uropeltis macrolepis</i>	U2 3293	Kaas	17°43'28.268"	73°50'3.807"	212	18	133	12	15-15-15
<i>Uropeltis macrolepis</i>	U3 3294	Mahabaleshwer	17°55'43.719"	73°39'38.332"	219	16	127	11	17-15-15
<i>Uropeltis phipsonii</i>	U4 3295	Amboli	15°57'27.529"	73°59'42.381"	200	8.5	148	8	17-17-15
<i>Uropeltis cf. phipsonii</i>	U5 3296	Satara	17°40'1.473"	73°59'23.614"	264	14	146	10	19-17-15
<i>Uropeltis phipsonii</i>	U6 3297	Pune	18°30'4.849"	73°51'7.959"	255	14	150	12	19-17-16
<i>Uropeltis macrolepis</i>	U8 3299	Mahabaleshwer	17°55'6.823"	73°40'20.820"	242	14	131	9	17-15-15
<i>Uropeltis macrolepis</i>	U9 3300	Patan, Koyna	17°22'16.053"	73°54'6.904"	243	15	129	10	17-15-15
<i>Uropeltis cf. phipsonii</i>	U11 3302	Kanher, Satara	17°44'16.645"	73°52'44.788"	253	13	150	11	19-17-16
<i>Uropeltis macrolepis</i>	U12 3303	Panchgani, Mahabaleshwer	17°55'0.969"	73°47'17.106"	182	16	126	11	16-15-15
<i>Uropeltis ellioti</i>	U13 3759	Nasik	—	—	200	12	164	11	19-17-15
<i>Uropeltis ellioti</i>	U14 3760	Nasik	—	—	291	11.6	163	7	19-17-15
<i>Uropeltis cf. phipsonii</i>	U17 3763	Satara	17°42'39.592"	73°56'39.004"	218	13	146	11	17-17-15
<i>Uropeltis phipsonii</i>	U19 3765	Amboli	15°57'0.493"	74°0'2.631"	176	8	150	8	18-17-15
<i>Uropeltis cf. macrolepis</i>	U20 3766	Amboli	15°57'43.218"	74°0'11.437"	236	13	129	10	17-15-15
<i>Uropeltis cf. macrolepis</i>	U21 3767	Sawantwadi Amboli	15°54'24.202"	73°49'41.559"	205	10	127	10	17-15-15