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Genus-level phylogeny of snakes reveals the origins of species richness in Sri Lanka

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ABSTRACT

Snake diversity in the island of Sri Lanka is extremely high, hosting at least 89 inland (i.e., non-marine) snake species, of which at least 49 are endemic. This includes the endemic genera *Aspidura*, *Balanophis*, *Cercaspis*, *Haplocercus*, and *Pseudotyphlops*, which are of uncertain phylogenetic affinity. We present phylogenetic evidence from nuclear and mitochondrial loci showing the relationships of 40 snake species from Sri Lanka (22 endemics) to the remaining global snake fauna. To determine the phylogenetic placement of these species, we create a molecular dataset containing 10 genes for all global snake genera, while also sampling all available species for genera with endemic species occurring in Sri Lanka. Our sampling comprises five mitochondrial genes (12S, 16S, cyt-*b*, ND2, and ND4) and five nuclear genes (BDNF, c-mos, NT3 RAG-1, and RAG-2), for a total of up to 9582 bp per taxon. We find that the five endemic genera represent portions of four independent colonizations of Sri Lanka, with *Cercaspis* nested within Colubrinae, *Balanophis* in Natricinae, *Pseudotyphlops* in Uropeltidae, and that *Aspidura* + *Haplocercus* represents a distinct, ancient lineage within Natricinae. We synonymize two endemic genera that render other genera paraphyletic (*Haplocercus* with *Aspidura*, and *Cercaspis* with *Lycodon*), and discover that further endemic radiations may be present on the island, including a new taxon from the blindsnake family Typhlopidae, suggesting a large endemic radiation. Despite its small size relative to other islands such as New Guinea, Borneo, and Madagascar, Sri Lanka has one of the most phylogenetically diverse island snake faunas in the world, and more research is needed to characterize the island's biodiversity, with numerous undescribed species in multiple lineages.

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1. Introduction

Studies of the evolutionary origins of island diversity have typically focused on large islands or island groups with diverse endemic faunas arising from autochthonous (*in situ*) diversification, such as Madagascar (Nagy et al., 2003; Raxworthy et al., 2002; Vieites et al., 2009) or the West Indies (Burbrink et al., 2012; Heinicke et al., 2007; Losos et al., 1998). Other large islands have very diverse faunas derived primarily from colonization by mainland forms, with relatively low (i.e., <25%) endemism for many groups such as snakes (e.g., New Guinea (O'Shea, 1996); Borneo (Stuebing and Inger, 1999)). However, large oceanic islands with faunas derived from a mixture of recent colonization by mainland species and long-term autochthonous diversification have rarely been studied, and may offer new perspectives on processes

generating island biodiversity. A key example of this type is Sri Lanka, a moderately sized (64,742 km² of land) tropical island located off the southern tip of the Indian subcontinent, separated by the narrow and shallow (<20 km wide with a minimum depth of ∼10 m) Gulf of Mannar and Palk Strait. Despite its proximity to the continent, the island hosts a very distinct fauna assemblage with high levels of endemism, especially in its herpetofauna (Bossuyt et al., 2004; Meegaskumbura et al., 2002), with new species being discovered continually (Gower and Maduwage, 2011; Maduwage et al., 2009; Meegaskumbura et al., 2010; Smith et al., 2008; Somaweera, 2006, 2011; Somaweera and Somaweera, 2009; Wickramasinghe et al., 2009).

The inland snake fauna (including all terrestrial, fossorial and freshwater species but not the true marine or estuarine forms) of Sri Lanka is diverse, represented by at least 89 species from 11 families, at least 49 of which are endemic (>50%), including five endemic genera (*Aspidura*, *Balanophis*, *Cercaspis*, *Haplocercus*, and *Pseudotyphlops*) (Somaweera, 2011). Many other species have

recently been discovered and are awaiting description. A great deal of this fauna is of uncertain phylogenetic affinity, as few of these taxa have been included in phylogenetic analyses. Indeed, only one Sri Lankan endemic was included in the most recent revision of colubroid snake taxonomy (the most species-rich group of snakes both globally and in Sri Lanka), in a molecular dataset containing 761 of ~2500 (~30%) colubroids (Pyron et al., 2011).

The only in-depth examination of endemic Sri Lankan snakes focused on a single lineage (Uropeltidae), and sampled only eight of the 14 described fossorial species (Bossuyt et al., 2004). None of the endemic genera have ever been included in a molecular phylogeny based on DNA sequence data. Thus, it is unknown whether (i) endemic Sri Lankan species generally represent autochthonous diversification or multiple colonizations, (ii) how many radiations are represented by the five endemic genera, and (iii) whether any endemic taxa represent previously unknown lineages.

To answer these questions, it is desirable to sample as many Sri Lankan species as possible for both nuclear and mitochondrial data, as well as to include as many known snake taxa as possible in phylogenetic analyses. This is due to both the known beneficial effects of increased taxon sampling for phylogenetic inference (Graybeal, 1998; Zwickl and Hillis, 2002), and due to the negative effects that omitting crucial lineages can have on determining the phylogenetic affinities of enigmatic groups (Pyron et al., 2011; Vidal et al., 2010). Because the Sri Lankan snake fauna includes members from all major snake lineages (i.e., Scolecophidia, Henophidia, and Caenophidia), it is necessary to include all of these in a phylogenetic analysis of Sri Lankan snakes. Similarly, since there are multiple genera of uncertain placement, it is also advantageous to include all currently described genera of extant snakes.

Many snake taxa have no representative DNA sequence, and while the remaining that have sequences are represented in existing databases (Gower et al., 2005; Lawson et al., 2004; Pyron et al., 2011). Relatively few taxa have been sampled extensively for multiple independent nuclear loci (Pyron and Burbrink, 2012). Therefore, supermatrix strategies (de Queiroz and Gatesy, 2007; Sanderson, 2007) are still necessary for large-scale phylogenetic reconstruction of large, diverse groups with heterogeneous genetic sampling. This strategy has proven robust and apparently successful in the past for snakes and other groups (McMahon and Sanderson, 2006; Pyron et al., 2011; Pyron and Wiens, 2011; Thomson and Shaffer, 2010). Thus, a combination of DNA sequencing and the utilization of existing databases to create a supermatrix allows us to answer many preliminary questions about the Sri Lankan snake fauna.

Here, we present molecular sequence data for 40 species of snake occurring in Sri Lanka, including 22 endemics and representatives from all five endemic genera, with both nuclear and mitochondrial sequences for the first time for these taxa. We combined these with existing data for all other available snake genera, as well as for all available species for genera which are represented in Sri Lanka by endemic species. We analyze these data using Maximum Likelihood (ML) to (i) infer a large-scale genus-level phylogeny of snakes, and (ii) estimate the placement of the Sri Lankan fauna, paying particular attention to endemic species and genera. We find relatively high concordance with previous studies for the higher-level relationships within snakes, though the addition of taxa and genes for the Sri Lankan species clarifies both the relationships among some groups, and the origins of Sri Lankan diversity. Excitingly, we find a new, undescribed taxon from the family Typhlopidae, suggesting the presence of a diverse, endemic radiation of blindsnakes on the island. These results suggest that the Sri Lankan snake fauna is much more diverse than previously suspected, and that conservation and exploration should be priorities for future research. Sri Lanka represents an ideal model system for studying the interplay between ecological and evolutionary processes generating high diversity in island systems (Losos and Schluter, 2000; MacArthur and Wilson, 1967).

2. Materials and methods

2.1. Baseline taxonomy

We based our generic (and where appropriate, species-level) taxonomy on the January 2012 update of the Reptile Database (Uetz, 2011), which recognizes 510 extant snake genera. We classified these into families and subfamilies using recent revisions of snake taxonomy (Noonan and Chippindale, 2006; Pyron et al., 2011; Vidal et al., 2010), conforming to Pyron and Burbrink (2012). Note that other recent revisions differ in their assignment of Linnaean ranks to these groups, but recover very similar topologies (Vidal et al., 2007; Zaher et al., 2009). Also, our taxonomic changes are made based on phylogenetic evidence from molecular sequence data, and not detailed morphological datasets. Thus, changes made such as the congeneric reclassification of morphologically distinct taxa invite morphological re-evaluation for supporting evidence in the form of trait-based synapomorphies.

2.2. Sequence acquisition

Tissues from 60 Sri Lankan snake species were acquired through salvage or non-lethal methods (scute and tail clips) during fieldwork by R.A.P., H.K.D.K., V.P., R.S., and others (see Acknowledgments) during June and July, 2011, collected and exported under Sri Lankan Department of Wildlife Conservation permit WL/3/2/1/7, and Forest Department permit R&E/RES/NFSRC/10. Species were identified by group consultation with the existing literature on Sri Lankan snake diversity (Somaweera, 2006), led by the resident experts (R.S. and H.K.D.K.). Specimens were collected opportunistically at sites throughout the country, both on roads and on foot, as well as in public lands (e.g., national parks) under the supervision of local authorities. In general, our collecting permits prohibited vouchering of live animals, so the majority of animals were identified, sampled, photographed (photo vouchered; Fig. 1), and released. An exception is an undescribed taxon from the blindsnake family Typhlopidae (see below), which was vouchered and accessioned at the National Museum of Sri Lanka (2012.01.01.NH), and is currently awaiting description.

Of the 60 taxa collected, we sequenced 40 species, including 22 endemics, all of which are represented by both nuclear and mitochondrial data for the first time, though a few were represented by mitochondrial fragments (e.g., 12S/16S) in previous studies. For these species, we sequenced four mitochondrial genes (12S, 16S, cyt-*b*, and ND4) and two nuclear genes (c-mos and RAG1) using existing primers and protocols (Pyron and Burbrink, 2009; Pyron et al., 2011). GenBank and voucher accession numbers are given in Table 1. For these same genes, we searched by genus through GenBank and gathered all available sequences for the species with the most data available. In addition to the 40 species sequenced for this project, there were existing data for 22 other Sri Lankan species (though the sequenced individuals were not necessarily from Sri Lanka), so our dataset includes a total of 62 of the 89 currently described inland Sri Lankan snakes (70%), including 29 of the 49 endemics (60%) (Somaweera, 2011).

If multiple species within a genus provided nearly the full complement of genes, and the genus was not represented in Sri Lanka, we combined the species into a single chimeric terminal. This approach should influence neither the higher-level relationships of snakes (provided the combined species from the genus are monophyletic), nor the placement of the Sri Lankan taxa, and has proven

Typhlopidae sp.

Cylindrophis maculatus

Rhinophis erangaviraji

Hypnale zara

Trimeresurus trigonocephalus
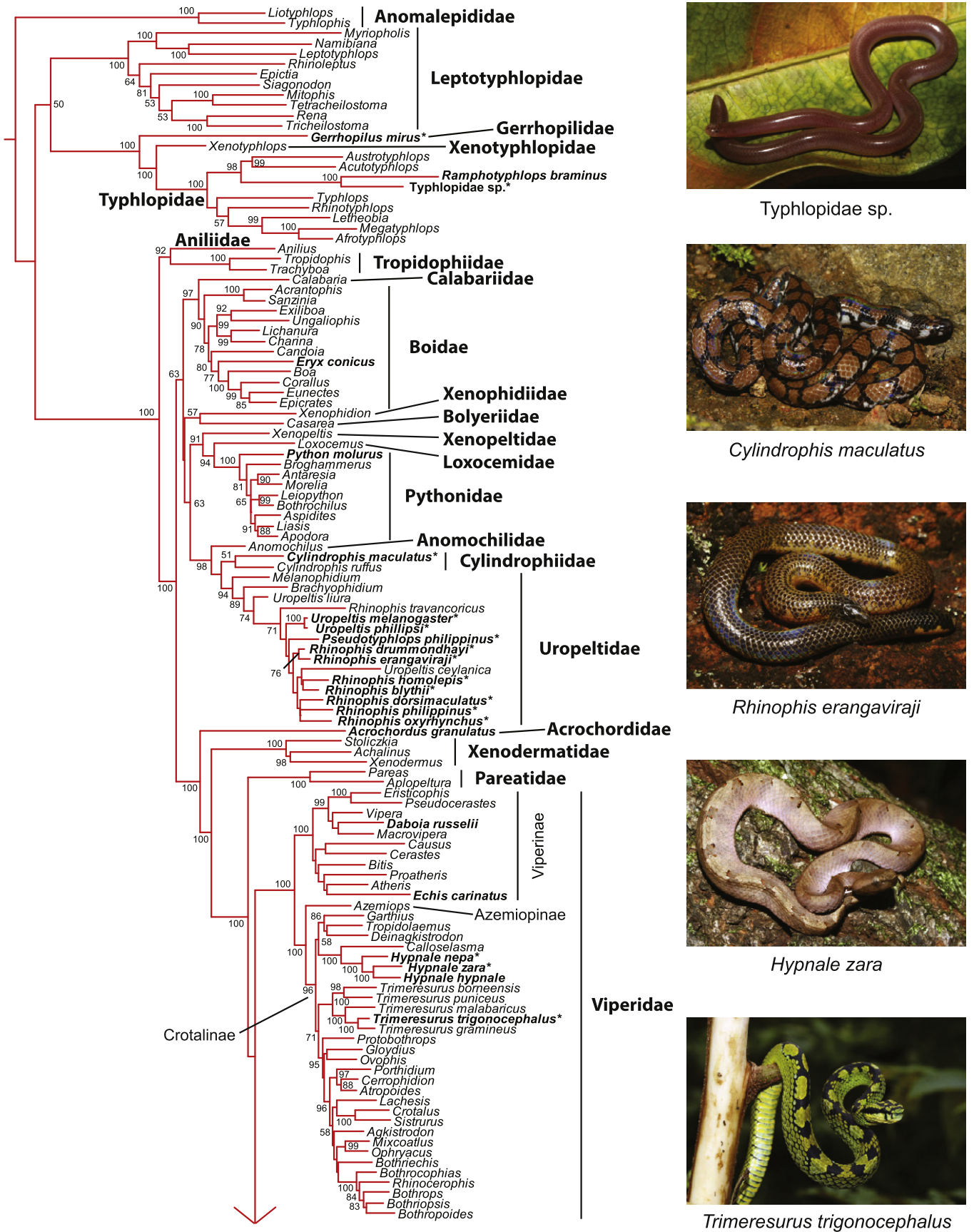
Fig. 1. Genus-level estimate of snake phylogeny, based on 478 ingroup taxa from 395 of the 510 known, extant genera, plus 81 additional species from genera occurring in Sri Lanka. Inland Sri Lankan species are indicated in bold, and endemics with an asterisk (*). Support values at nodes are bootstrap proportions >50% from 1000 replicates generated in RAxMLv7.2.8. Snakes pictured are Sri Lankan endemics, and the photographed specimens are the ones sequenced (Table 1), with the exception of *Balanophis ceylonensis* and *Haplocercus ceylonensis*.

Homalopsidae

Lamprophiidae

Elapidae

Myron
Enhydris enhydris
Homalopsis
Cerberus rynchops
Erpeton
Bitia
Cantoria
Fordonia
Gerarda prevostiana
Prosymna
Rhamphiophis
Malpolon
Psammophis
Dipsina
Mimophis
Psammophylax
Hemirhagerrhis
Pseudaspis
Pythonodipsas
Psammodynastes
Buhoma
Atractaspis
Homoroselaps
Polemon
Aparallactus
Macrelaps
Amblyodipsas
Xenocalamus
Gonionotophis
Hormonotus
Inyoka
Lycophidion
Pseudoboodon
Lycodonomorphus
Bothrophthalmus
Bothrolycus
Boaedon
Lamprophis
Ditypophis
Compsophis
Duberria
Amplorhinus
Dromicodryas
Liophidium
Pseudoxyrhopus
Heteroliodon
Liopholidophis
Exallodontophis
Thamnosophis
Alluaudina
Leioheterodon
Parastenophis
Langaha
Ithycyphus
Micropisthodon
Madagascarophis
Lycodryas
Phisalixella
Micrelaps
Oxyrhabdium
Calliophis melanurus
Sinomicrurus
Micrurus
Micruroides
Ophiophagus
Hemibungarus
Dendroaspis
Naja naja
Walterinnesia
Hemachatus
Aspidelaps
Bungarus flaviceps
Bungarus bungaroides
Bungarus slowinskii
Bungarus fasciatus
Bungarus candidus
Bungarus multicinctus
Bungarus caeruleus
Bungarus ceylonicus*
Elapsoidea
Laticauda
Acanthophis
Micropechis
Pseudechis
Toxicocalamus
Simoselaps
Demansia
Furina
Aspidomorphus
Cacophis
Suta
Elapognathus
Rhinoplocephalus
Cryptophis
Vermicella
Denisonia
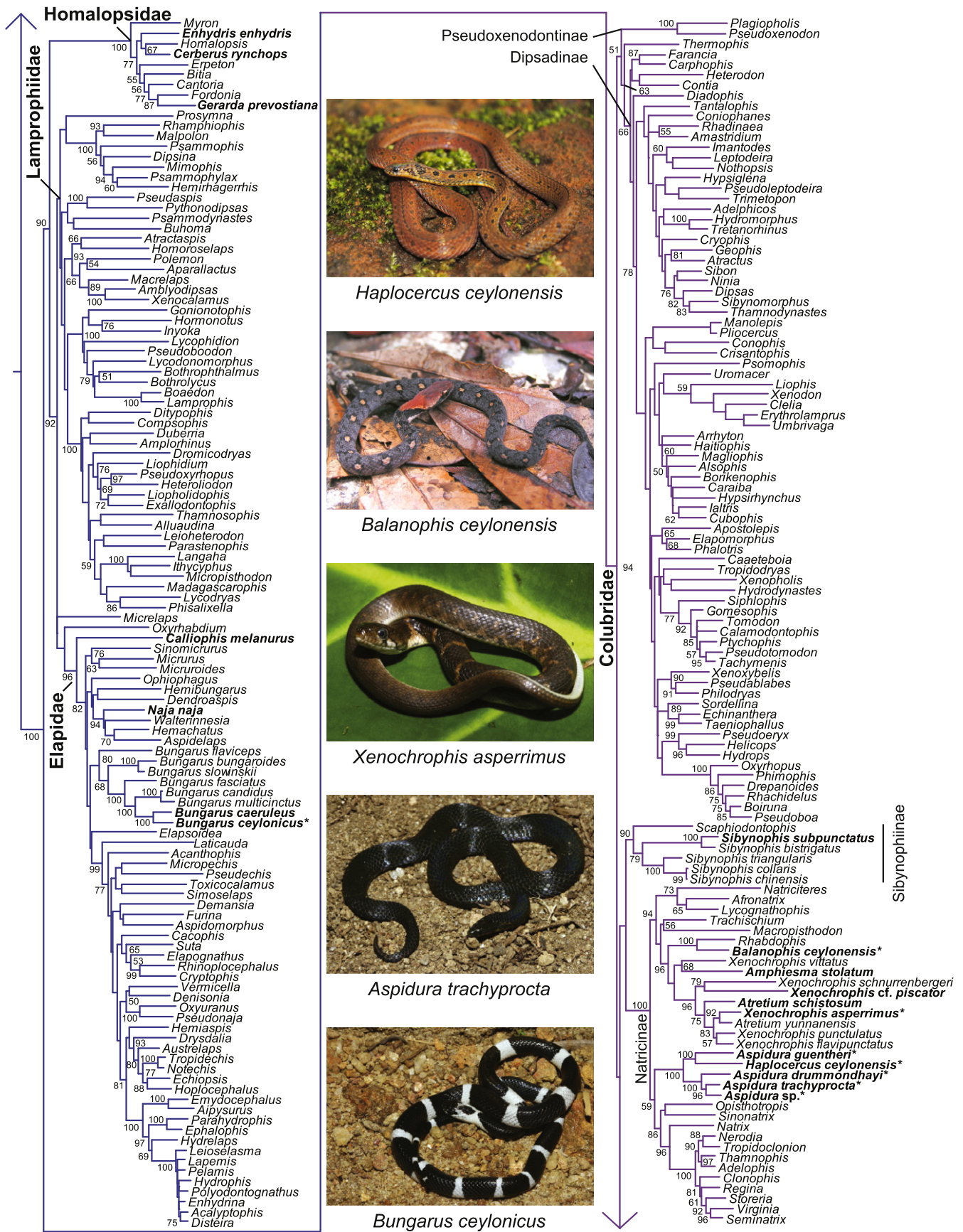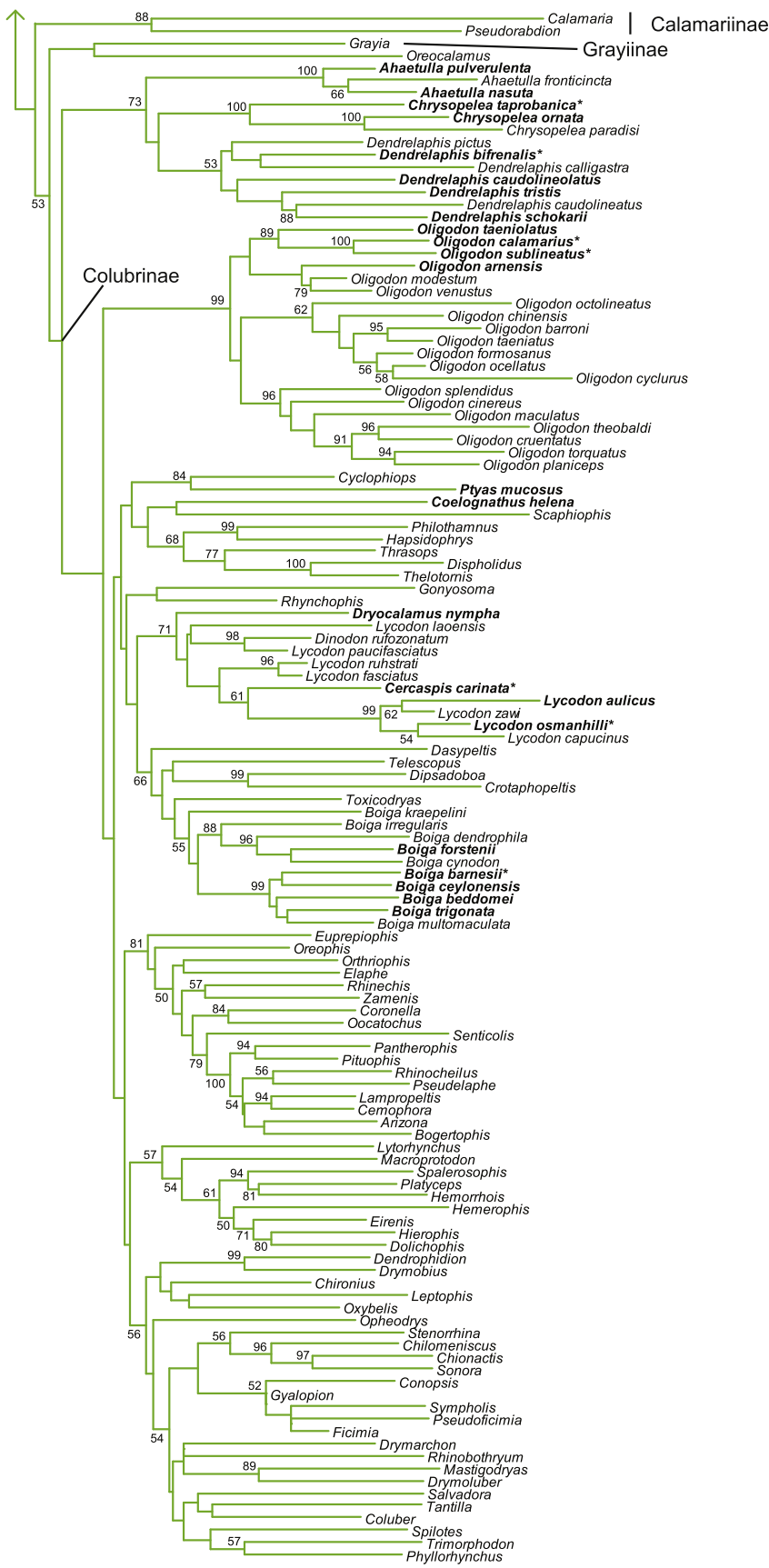*Oxyuranus*
Pseudonaja
Hemiaspis
Drysdalia
Austrelaps
Tropidechis
Notechis
Echiopsis
Hoplocephalus
Emydocephalus
Aipysurus
Parahydrophis
Ephalophis
Hydrelaps
Leioselasma
Lapemis
Pelamis
Hydrophis
Polyodontognathus
Enhydrina
Acalyptophis
Disteira

Haplocercus ceylonensis

Balanophis ceylonensis

Xenochrophis asperrimus

Aspidura trachyprocta

Bungarus ceylonicus

Pseudoxenodontinae
Dipsadinae

Colubridae

Sibynophiinae

Natricinae

Plagiopholis
Pseudoxenodon
Thermophis
Farancia
Carphophis
Heterodon
Contia
Diadophis
Tantalophis
Coniophanes
Rhadinaea
Amastridium
Imantodes
Leptodeira
Nothopsis
Hypsiglena
Pseudoleptodeira
Trimetopon
Adelphicos
Hydromorphus
Tretanorhinus
Cryophis
Geophis
Atractus
Sibon
Ninia
Dipsas
Sibynomorphus
Thamnodynastes
Manolepis
Pliocercus
Conophis
Crisantophis
Psomophis
Uromacer
Liophis
Xenodon
Clelia
Erythrolamprus
Umbrivaga
Arrhyton
Haitiophis
Magliophis
Alsophis
Borikenophis
Caraiba
Hypsirhynchus
Ialtris
Cubophis
Apostolepis
Elapomorphus
Phalotris
Caaeteboia
Tropidodryas
Xenopholis
Hydrodynastes
Siphlophis
Gomesophis
Tomodon
Calamodontophis
Ptychophis
Pseudotomodon
Tachymenis
Xenoxybelis
Pseudablabes
Philodryas
Sordellina
Echinanthera
Taeniophallus
Pseudoeryx
Helicops
Hydrops
Oxyrhopus
Phimophis
Drepanoides
Rhachidelus
Boiruna
Pseudoboa
Scaphiodontophis
Sibynophis subpunctatus
Sibynophis bistrigatus
Sibynophis triangularis
Sibynophis collaris
Sibynophis chinensis
Natriciteres
Afronatrix
Lycognathophis
Trachischium
Macropisthodon
Rhabdophis
Balanophis ceylonensis*
Xenochrophis vittatus
Amphiesma stolatum
Xenochrophis schnurrenbergeri
Xenochrophis cf. **piscator**
Atretium schistosum
Xenochrophis asperrimus*
Atretium yunnanensis
Xenochrophis punctulatus
Xenochrophis flavipunctatus
Aspidura guntheri*
Haplocercus ceylonensis*
Aspidura drummondhayi*
Aspidura trachyprocta*
Aspidura sp.*
Opisthotropis
Sinonatrix
Natrix
Nerodia
Tropidoclonion
Thamnophis
Adelophis
Clonophis
Regina
Storeria
Virginia
Seminatrix

Fig. 1. (*continued*)

Calamaria — Calamariinae
Pseudorabdion
88

Grayia — Grayiinae
Oreocalamus
73
100 Ahaetulla pulverulenta
Ahaetulla fronticincta
66 Ahaetulla nasuta
100 Chrysopelea taprobanica*
100 Chrysopelea ornata
Chrysopelea paradisi
Dendrelaphis pictus
Dendrelaphis bifrenalis*
53 Dendrelaphis calligastra
Dendrelaphis caudolineolatus
Dendrelaphis tristis
Dendrelaphis caudolineatus
88 Dendrelaphis schokarii
89 Oligodon taeniolatus
100 Oligodon calamarius*
Oligodon sublineatus*
Oligodon arnensis
Oligodon modestum
79 Oligodon venustus
62 Oligodon octolineatus
Oligodon chinensis
95 Oligodon barroni
Oligodon taeniatus
Oligodon formosanus
56 Oligodon ocellatus
58 Oligodon cyclurus
96 Oligodon splendidus
Oligodon cinereus
Oligodon maculatus
96 Oligodon theobaldi
91 Oligodon cruentatus
94 Oligodon torquatus
Oligodon planiceps
99
53
Colubrinae
84 Cyclophiops
Ptyas mucosus
Coelognathus helena
Scaphiophis
99 Philothamnus
68 Hapsidophrys
77 Thrasops
100 Dispholidus
Thelotornis
Gonyosoma
Rhynchophis
Dryocalamus nympha
71 Lycodon laoensis
98 Dinodon rufozonatum
Lycodon paucifasciatus
96 Lycodon ruhstrati
Lycodon fasciatus
61 Cercaspis carinata* — Lycodon aulicus
99 62 Lycodon zawi
Lycodon osmanhilli*
54 Lycodon capucinus
Dasypeltis
Telescopus
99 Dipsadoboa
Crotaphopeltis
66 Toxicodryas
Boiga kraepelini
Boiga irregularis
88 96 Boiga dendrophila
Boiga forstenii
55 Boiga cynodon
Boiga barnesii*
99 Boiga ceylonensis
Boiga beddomei
Boiga trigonata
Boiga multomaculata
Euprepiophis
81 Oreophis
Orthriophis
Elaphe
57 Rhinechis
Zamenis
84 Coronella
Oocatochus
50 Senticolis
94 Pantherophis
Pituophis
79 56 Rhinocheilus
100 Pseudelaphe
94 Lampropeltis
54 Cemophora
Arizona
Bogertophis
57 Lytorhynchus
Macroprotodon
94 Spalerosophis
54 Platyceps
61 81 Hemorrhois
Hemerophis
50 Eirenis
71 Hierophis
80 Dolichophis
99 Dendrophidion
Drymobius
Chironius
Leptophis
Oxybelis
Opheodrys
56 Stenorrhina
56 96 Chilomeniscus
97 Chionactis
Sonora
Conopsis
52 Gyalopion
Symphulis
Pseudoficimia
Ficimia
Drymarchon
Rhinobothryum
89 Mastigodryas
Drymoluber
Salvadora
Tantilla
Coluber
Spilotes
57 Trimorphodon
Phyllorhynchus
56
54

Chrysopelea taprobanica

Dendrelaphis bifrenalis

Lycodon osmanhilli

Cercaspis carinata

Boiga barnesii

Fig. 1. (*continued*)

Table 1
GenBank accession numbers for DNA sequence data generated for 40 Sri Lankan taxa, including 22 endemics indicated with an asterisk (*). Some sequence fragments less than 200bp were not accepted by GenBank, and are provided in Appendix S1.

Species	12S	16S	cytb	ND4	cmos	RAG1	Field Number	Locality
Ahaetulla nasuta	Appendix S1	–	KC347453	KC347491	KC347377	KC347415	RAP0517	1
Ahaetulla pulverulenta	KC347304	KC347339	KC347454	KC347492	KC347378	KC347416	RS-C	2
Aspidura drummondhayi*	KC347305	KC347340	KC347455	KC347493	KC347379	KC347417	RS-M	3
Aspidura guentheri*	KC347306	KC347341	KC347456	KC347494	KC347380	KC347418	RAP0437	4
Aspidura sp.*	KC347307	KC347342	KC347457	KC347495	KC347381	KC347419	RS-U	5
Aspidura trachyprocta*	KC347308	KC347343	KC347458	KC347496	KC347382	KC347420	RS-134	6
Atretium schistosum	KC347309	Appendix S1	KC347459	KC347497	KC347383	KC347421	RS-R	1
Balanophis ceylonensis*	KC347310	KC347344	KC347460	KC347498	KC347384	KC347422	RS-D	4
Boiga barnesii*	KC347311	KC347345	KC347461	KC347499	KC347385	KC347423	RAP0452	4
Boiga beddomei	KC347312	KC347346	KC347462	KC347500	KC347386	KC347424	RAP0450	4
Boiga ceylonensis	KC347313	KC347347	KC347463	KC347501	KC347387	KC347425	RS-Y	5
Boiga forstenii	KC347314	KC347348	KC347464	KC347502	KC347388	KC347426	RAP0540	7
Boiga trigonata	KC347315	KC347349	KC347465	KC347503	KC347389	KC347427	RS-143	8
Bungarus ceylonicus*	KC347316	KC347350	KC347466	KC347504	KC347390	KC347428	RS-135	9
Calliophis melanurus	KC347317	KC347351	KC347467	KC347505	KC347391	KC347429	RS-148	10
Cercaspis carinata*	–	KC347352	KC347468	–	KC347392	KC347430	RAP0447	4
Chrysopelea ornata	KC347318	KC347353	KC347469	KC347506	KC347393	KC347431	RAP0433	4
Chrysopelea taprobanica*	KC347319	KC347354	KC347470	KC347507	KC347394	KC347432	RAP0538	7
Cylindrophis maculatus*	KC347320	KC347355	KC347472	KC347508	KC347396	KC347433	RAP0448	4
Dendrelaphis bifrenalis*	KC347321	KC347356	KC347473	KC347509	KC347397	KC347434	RAP0455	4
Dendrelaphis caudolineolatus	–	KC347357	KC347474	KC347510	–	–	RAP0508	11
Dendrelaphis schokarii	–	KC347358	KC347475	KC347511	KC347398	KC347435	RAP0477	12
Dendrelaphis tristis	KC347322	KC347359	KC347476	KC347512	KC347399	KC347436	RAP0492	13
Dryocalamus nympha	KC347323	KC347360	KC347477	KC347513	KC347400	KC347437	RAP0536	7
Haplocercus ceylonensis*	KC347324	KC347361	KC347478	KC347514	KC347401	KC347438	RS-145	14
Hypnale nepa*	KC347325	KC347362	KC347479	KC347515	KC347402	KC347439	RS-S	5
Hypnale zara*	KC347326	KC347363	KC347480	KC347516	KC347403	KC347440	RAP0552	15
Lycodon osmanhilli*	–	KC347364	–	KC347517	KC347404	KC347441	RAP0528	16
Oligodon arnensis	KC347327	KC347365	KC347481	KC347518	KC347405	KC347442	RAP0483	17
Oligodon calamarius*	KC347328	KC347366	KC347482	KC347519	KC347406	KC347443	RS-OC	18
Oligodon sublineatus*	KC347329	KC347367	KC347483	KC347520	KC347407	KC347444	RAP0504	11
Oligodon taeniolatus	KC347330	KC347368	KC347484	KC347521	KC347408	KC347445	RS-136	8
Pseudotyphlops philippinus*	KC347331	KC347369	–	KC347522	KC347409	KC347446	RS-140	19
Rhinophis blythii*	KC347332	KC347370	–	KC347523	KC347410	KC347447	RS-N	3
Rhinophis erangaviraji*	KC347333	KC347371	KC347485	KC347524	KC347411	KC347448	RAP0431	20
Rhinophis homolepis*	KC347334	KC347372	KC347486	KC347525	–	–	RAP0509	11
Sibynophis subpunctatus	KC347335	KC347373	KC347487	KC347526	KC347412	KC347449	RAP0491	17
Trimeresurus trigonocephalus*	KC347336	KC347374	KC347488	–	KC347413	–	RAP0453	4
Typhlopidae sp.*	KC347337	KC347375	KC347489	KC347527	–	KC347450	RAP0534	16
Xenochrophis asperrimus*	KC347338	KC347376	KC347490	Appendix S1	KC347414	KC347451	RS-J	18

Localities 1: Nuwara Eliya Dist., Norton Bridge; 2: Matale Dist., Sigiriya; 3: Nuwara Eliya Dist., Maskeliya; 4: Galle Dist., Kanneliya Forest Reserve; 5: Ratnapura Dist., Sri Pada; 6: Nuwara Eliya Dist., Horton Plains Natl. Park; 7: Matale Dist., Kandalama Resort; 8: Polonnaruwa Dist., Bakamuna; 9: Kandy Dist., Kandy; 10: Matale Dist., Dambulla; 11: Kandy Dist., Rambukpitiya; 12: Galle Dist., Kottawa, Hiyare Forest Reserve; 13: Hambantota Dist., Bundala Natl. Park; 14: No locality given; 15: Kandy Dist., Gonnaruwa; 16: Puttalam Dist., Kalpitiya; 17: Hambantota Dist., Yala Natl. Park; 18: Kandy Dist., Nawalapitiya; 19: Badulla Dist., Badulla; 20: Ratnapura Dist., Sinharaja Forest Reserve.

advantageous for phylogenetic inference in the past (Campbell and Lapointe, 2009). Additional mitochondrial (ND2) and nuclear (BDNF) genes have proven informative in past studies (Noonan and Chippindale, 2006; Pyron et al., 2011) and were also included. This yielded representatives from 395 of the 510 snake genera (77%), and an additional 81 taxa from genera represented in the Sri Lankan fauna. This includes representatives from all known, extant families and subfamilies of snakes, with both nuclear and mitochondrial data for most.

Sequences were aligned using the default, high-accuracy settings in MUSCLE (Edgar, 2004). Protein-coding genes were translated to amino acids to confirm a lack of stop codons indicative of pseudogenes. The individual alignments were then concatenated to build the final matrix for analysis. The final matrix as 10852 bp in length for 478 taxa and one outgroup (*Heloderma suspectum*). Sequence data were available from 373 taxa for 12S (1127 bp), 368 for 16S (1388 bp), 125 for BDNF (676 bp), 357 for c-mos (722 bp), 414 for cyt-*b* (1134 bp), 90 for ND2 (1038 bp), 281 for ND4 (700 bp), 73 for NT3 (516 bp), 159 for RAG1 (2834 bp), and 93 for RAG-2 (717 bp). The mean concatenated sequence-length was 3343 bp (31% of the total length), ranging from 322 bp (3%) to 9582 bp (88%). GenBank accession numbers for the non-Sri Lankan taxa are given in Appendix S1.

2.3. Phylogenetic inference

We performed phylogenetic inference using ML and assessed support using non-parametric bootstrapping in the program RAx-MLv7.2.8 (Stamatakis, 2006) with the ten-gene concatenated matrix. We used the GTRGAMMA model for all genes and partitions because GTR is the only substitution model implemented in RAx-ML. Previous phylogenetic analyses of snakes suggest that GTR + Γ + I is the best-fitting model for these genes, and that these genes should be partitioned by codon positions (Noonan and Chippindale, 2006; Pyron et al., 2011; Vidal et al., 2010). Further, the GTRGAMMA model in RAxML is recommended over the GTR + G + I because the 25 rate categories account for potentially invariant sites (Stamatakis, 2006). We used the rapid-bootstrapping algorithm (1000 non-parametric bootstrap replicates) with the thorough ML search option (200 independent searches, starting from every fifth bootstrap replicate). Given that BS values generally appear to be biased but conservative (Felsenstein, 2004), we considered clades with values of 70% or greater to be well-supported (Hillis and Bull, 1993; Taylor and Piel, 2004), and report values >50% ("moderate" support).

We also tested the robustness of our supermatrix approach in three ways. First, we determined if support for the placement of

terminal taxa was related to the proportion of data missing for those taxa, using the approach of Pyron et al. (2011). Second, we determined if node support was related to the rank of a node (e.g., distance from the root), to test if nodes towards the tips had higher or lower support than nodes towards the root. Third, we tested whether or not terminal branch lengths were related to the proportion of missing data in the terminals, to determine if missing data was related to bias in ML parameter estimates. These correlations were tested using Spearman's rank correlation coefficient. While a large body of literature suggests that missing data are not likely to be problematic for phylogenetic inference under most empirical conditions (Wiens and Morrill, 2011), some simulation studies have suggested the opposite (Lemmon et al., 2009). The analyses presented here represent at least a preliminary check of the consistency of large-scale estimates based on sparse supermatrices.

3. Results

The ML tree from RAxMLv7.2.8 ($-\ln L = -446355.98$) is presented in Fig. 1. The tree is moderately well-supported (46% of nodes have BS > 70), though nearly all higher-level relationships receive strong support, as do the placement of most Sri Lankan taxa (Fig. 1a–c). The higher-level relationships of snakes are similar in most respects to previous estimates of serpent phylogeny (Burbrink and Pyron, 2008; Heise et al., 1995; Lawson et al., 2004; Slowinski and Lawson, 2002; Vidal and Hedges, 2002), including two recent multi-locus estimates (Pyron and Burbrink, 2012; Wiens et al., 2008). Here, we detail concordances and discordances between our tree and recent studies as needed to clarify the relationships among higher-level snake groups, and resolve taxonomic problems revealed by our sampling of Sri Lankan species.

We find weak support for the paraphyly of Scolecophidia (Anomalepididae, Gerrhopilidae, Leptotyphlopidae, Typhlopidae, and Xenotyphlopidae). However, in our tree, Anomalepididae is the sister group to all other snakes, as opposed to sister to all snakes exclusive of the remaining "scolecophidians" (Pyron and Burbrink, 2012; Wiens et al., 2008). Within the remaining "scolecophidians," relationships among the families and genera are similar to recent revisions (Adalsteinsson et al., 2009; Vidal et al., 2010). These two groups of "scolecophidians" are weakly supported, respectively, to a strongly supported Alethinophidia (Fig. 1a).

Within Typhlopidae, a new Sri Lankan taxon, Typhlopidae sp., is found to be the sister-group to *Ramphotyphlops* (Fig. 1a). This form is likely allied with the several other endemic Sri Lankan species currently placed in *Typhlops, T. lankaensis, T. leucomelas, T. malcolmi, T. tenebrarum, T. veddae,* and *T. violaceus,* on the basis of general morphological similarity (Taylor, 1947). While material for these species was unavailable to us, these taxa cannot remain in *Typhlops* without expanding that genus to include all typhlopid species (given the placement of other *Typhlops* in a distant clade in Typhlopidae; Fig. 1a); they bear several distinguishing characters from the other typhlopoid genera on the island (*Ramphotyphlops*, also paraphyletic; and *Gerrhopilus*; see (Vidal et al., 2010)), and thus likely should not be placed in those genera either, but in a new genus. A revision of Sri Lankan blindsnakes currently in progress suggests that numerous additional species remain to be described (L.J.M. Wickramasinghe, pers. comm., 2012). The wide-ranging (outside of Sri Lanka) and morphologically distinct species *T. porrectus* is allied with a different South and East Asian species group (Wallach, 1999; Wallach and Pauwels, 2004), but will likely also require generic reassignment (Vidal et al., 2010).

The relationships within Alethinophidia that are strongly supported in this tree (Fig. 1) are similar to those found in recent studies (Pyron and Burbrink, 2012; Wiens et al., 2008). We find a strongly supported sister-group relationship between Anilioidea (Aniliidae + Tropidophiidae) and a strongly supported clade consisting of Booidea + Caenophidia (Acrochordoidea + Colubroidea). The booid clade (Anomochilidae, Boidae, Bolyeriidae, Calabariidae, Cylindrophiidae, Loxocemidae, Pythonidae, Uropeltidae, Xenophiidae, and Xenopeltidae) remains weakly supported as in recent studies (Pyron and Burbrink, 2012). Subfamilies in Boidae and Lamprophiidae are also of uncertain monophyly, and are not addressed here (Fig. 1a,b), as they do not contain endemic Sri Lankan taxa.

Increased sampling within Cylindrophiidae and Uropeltidae reveals that Anomochilidae, Cylindrophiidae, and Uropeltidae form a strongly supported clade, though Cylindrophiidae is not strongly supported (Fig. 1a). In contrast to previous studies, Anomochilidae is the sister-group to a poorly supported clade consisting of Cylindrophiidae + Uropeltidae (Fig. 1a), rather than nested within Cylindrophiidae (Gower et al., 2005), suggesting that it is indeed a valid family level taxon. We find strong support for *Melanophidium* as the sister-group to all other uropeltids, and *Brachyophidium* as the sister-group to all remaining uropeltids (Fig. 1a). As in previous studies (Bossuyt et al., 2004; Cadle et al., 1990; Gower et al., 2005), we find strong support for paraphyly of *Rhinophis* and *Uropeltis* with respect to each other and *Pseudotyphlops*. There is weak support for a sister-group relationship between *U. liura*, and a strongly supported clade containing *Rhinophis, Pseudotyphlops, U. ceylanica,* and *U. melanogaster + U. phillipsi* (Fig. 1a). Paraphyly of these genera has been supported for over 20 years based on allozymes, albumin immunology, and DNA sequence data, and obviously requires taxonomic revision. However, based on our incomplete taxon sampling and lack of strong support for all relevant branches, we refrain from addressing this here. The genus *Platyplectrurus* also occurs in Sri Lanka, but its affinities in Uropeltidae are still unknown. Numerous newly discovered uropeltids exist in Sri Lanka, and are currently being described (L.J.M. Wickramasinghe, pers. comm., 2012).

Within Caenophidia (Acrochordoidea + Colubroidea), our results here are congruent in most respects with previous revisions of the group (Pyron et al., 2011). A primary exception is weak support for paraphyly of Lamprophiidae with respect to Elapidae, as also found in other recent studies (Kelly et al., 2009; Pyron and Burbrink, 2012). We find that *Oxyrhabdium* and *Micrelaps*, respectively, represent the sister groups to Elapidae (Fig. 1b), though Lamprophiidae is monophyletic to the exclusion of these taxa (Fig. 1b) and Lamprophiidae + Elapidae is strongly supported (Fig. 1)(Vidal et al., 2008). Other relationships, such as among the subfamilies of Colubridae, remain poorly supported (Pyron et al., 2011; Zaher et al., 2009). Monophyly of all families other than Lamprophiidae is strongly supported, as are most previously defined subfamilies (Fig. 1a–c; but see below).

With respect to the endemic Sri Lankan colubroid species, the crotaline viperid genus *Hypnale* is strongly supported as the monophyletic sister-group to *Calloselasma*, as part of a larger basal crotaline lineage including *Tropidolaemus, Garthius,* and *Deinagkistrodon* (Fig. 1a). Additionally, *Trimeresurus trigonocephalus* is strongly supported as a member of the South Asian *Trimeresurus* group, as in previous studies (Malhotra and Thorpe, 2004). Within Elapidae, the endemic krait *Bungarus ceylonicus* is strongly nested within the genus *Bungarus* (Fig. 1b).

Within Colubridae, the endemic genus *Balanophis* is strongly supported as the sister-group to *Rhabdophis* in the colubrid subfamily Natricinae. The endemic genus *Haplocercus* (Günther, 1858) is strongly nested within the endemic genus *Aspidura* (Wagler, 1830)(Fig. 1b); thus, we synonymize *Haplocercus* with *Aspidura*. This clade forms the weakly supported sister-group to several OW and NW natricine lineages (Fig. 1b; the "Clade A" of (Guo et al., 2012)), representing a previously unknown, but very ancient

(>25 Ma) and distinct lineage within Natricinae. Sri Lankan endemics in the genera *Chrysopelea* and *Dendrelaphis* are allied with mainland forms, and these genera form a strongly supported group with *Ahaetulla*. This clade represents the weakly supported sister-group to all other colubrines (Fig. 1c).

The four Sri Lankan *Oligodon*, including the endemics *O. calamarius* and *O. sublineatus*, are part of a weakly supported clade weakly placed sister to all other *Oligodon* (Fig. 1c). The colubrine genera *Cercaspis* (a Sri Lankan endemic), *Dinodon, Dryocalamus* (included here in a molecular phylogeny for the first time), and *Lycodon* (including the Sri Lankan endemic *L. osmanhilli*) form a strongly supported clade, with *Dinodon* and *Cercaspis* nested within *Lycodon*, and *Dryocalamus* as the sister taxon to this group (Fig. 1c). These taxa are morphologically similar, and all have been classified as *Lycodon* in the past (Uetz, 2011), and we thus synonymize *Cercaspis* (Wagler, 1830) with *Lycodon* (Fitzinger, 1826). We retain *Dryocalamus* (Günther, 1858), though it too may be nested within *Lycodon,* while *Dinodon* and other *Lycodon* species are currently being assessed in greater detail by other authors (C. Siler et al., pers. comm.). The Sri Lankan endemic *Boiga barnesii* is part of a strongly supported clade containing several other South Asian *Boiga* species, which is part of a weakly supported *Boiga* (excluding *Toxicodryas*) containing other Sri Lankan taxa and Asian species (Fig. 1c).

Our phylogeny also has implications for non-endemic Sri Lankan species. The genus *Calliophis,* which includes a Sri Lankan endemic not sampled, *C. haematoetron* (Smith et al., 2008), is included in a molecular phylogeny here for the first time, forming the strongly supported sister-group to all other elapid species, and is not part of the coral snake clade containing *Sinomicrurus, Micruroides,* and *Micrurus* (Fig. 1b). The natricine genus *Xenochrophis* (Günther, 1864), including the type species *X. vittatus* (Linnaeus, 1758), is rendered paraphyletic with strong support by *Atretium* (Cope, 1861) and weakly by *Amphiesma* (Dumeril et al., 1854) as in previous studies (Guo et al., 2012), corroborated here by the addition of the type species *A. schistosum* (Daudin, 1803)(Fig. 1b). The genus *Amphiesma* is also known to be paraphyletic with respect to *Xenochrophis* (see Guo et al., 2012). Given this uncertainty over the resolution of these species, we refrain from making any changes at present. The South Asian species *Sibynophis subpunctatus* is part of a strongly supported Sibynophiinae (Fig. 1b). We also generated sequence data (ND2, cyt-*b*, and c-mos from specimen FTB2310 from Sichuan Province, China; GenBank: KC347452, KC347471, and KC347395; combined with existing BDNF sequences; Appendix S1) for the Asian *Cyclophiops*, which is weakly placed as the sister-group to *Ptyas* in Colubrinae (Fig. 1c).

With respect to the robustness of this supermatrix estimate of snake phylogeny, we find no relationship between the completeness of terminal taxa and support for their placement ($\rho = 0.08$, $P = 0.17$). There is, however, a significantly negative relationship between support and node rank ($\rho = -0.22$, $P = <0.00001$), indicating that nodes closer to the root have greater support than those near the tips. Finally, there is no relationship between terminal branch-length and the proportion of missing data for terminal species ($\rho = 0.03$, $P = 0.56$).

4. Discussion

4.1. Sri Lankan serpent diversity

The inland snake fauna of Sri Lanka comprises at least 89 species (49 endemic) in 11 families and 38 genera (Appendix 1), and shows a high degree of distinctness from that of the Western Ghats despite the proximity and frequent historical connections to India (Bossuyt et al., 2004; Meegaskumbura et al., 2002). This is also ex-

tremely high relative to its size (64,742 km^2), as compared to other much larger and very diverse tropical islands such as New Guinea (786,000 km^2, 86 species, 8 families, 32 genera, 20 endemics), Borneo (743,330 km^2, 144 species, 14 families, 60 genera, 35 endemics), and Madagascar (587,041 km^2, 91 endemic species, 4 families, 22 genera)(Uetz, 2011).

Indeed, the exceptional and mostly undescribed diversity of the smaller forms (i.e., *Aspidura, Rhinophis*, and the typhlopid presented here) suggest that the Sri Lankan snake fauna may rival its amphibians as a global center of endemism and diversity (Bossuyt et al., 2004; Meegaskumbura et al., 2002). As with many large islands, a substantial proportion of this diversity has been generated through within-island diversification (Losos and Schluter, 2000). We find evidence for autochthonous speciation (i.e., clades consisting of multiple endemic species) in at least three lineages of endemic genera: Uropeltidae (*Rhinophis* + *Pseudotyhlops* + *Uropeltis*; 14 spp.), Natricinae (*Aspidura* + *Haplocercus*; 7 spp.), and Typhlopidae (~7 spp. including the new form presented here), though the actual diversity of these lineages is likely much higher. We also find evidence for autochthonous speciation (i.e., endemic sister-species) in *Oligodon* and *Hypnale* (Fig. 1), and there are at least 2 endemic species (not sampled here) each in *Dendrelaphis* and *Xenochrophis* (Somaweera, 2011).

Some of the endemic diversity instead results from allopatric speciation from mainland lineages (i.e., sister-group relationships between endemic and mainland taxa) in the genera *Balanophis, Boiga, Bungarus, Calliophis, Cercaspis, Chrysopelea, Cylindrophis, Lycodon,* and *Trimeresurus*. Indeed, the most widespread in Sri Lanka are the most broadly distributed globally (e.g., *Coelognathus, Naja, Ptyas, Python,* etc.). Thus, the high diversity of the Sri Lankan snake fauna appears to be fairly well-explained by a mixture of the ecological (i.e., dispersal and colonization) and evolutionary (i.e., *in situ* diversification) models of island biogeography (Losos et al., 2010; Losos and Schluter, 2000; MacArthur and Wilson, 1967; Rosenzweig, 1995). This is a mixture of processes that has rarely been examined in the context of island biodiversity (see Bossuyt et al., 2004 for an example). With high richness and endemism in frogs, lizards, and snakes, Sri Lanka represents an ideal model for future studies examining the interplay and relative contribution of ecological and evolutionary drivers of high local and regional diversity (Ricklefs, 1987, 2004; Wiens et al., 2011).

4.2. Snake phylogeny and the supermatrix approach

Somewhat ironically, the basic structure of higher-level snake phylogeny has not changed much after nearly 20 years of investigation, from a few mitochondrial fragments (Heise et al., 1995; Lawson et al., 2004; Slowinski and Lawson, 2002), to the addition of hundreds of taxa and tens of independent loci (Noonan and Chippindale, 2006; Pyron and Burbrink, 2012; Pyron et al., 2011; Wiens et al., 2008; Zaher et al., 2009). Perhaps even more ironically, resolution and support for the most contentious nodes in the serpent tree (e.g., monophyly of Booidea and Lamprophiidae, relationships between the colubrid subfamilies, and placement of taxa such as Bolyeriidae) have not changed much either through the addition of those taxa or genes (Fig. 1). Nonetheless, support for the placement and monophyly of the majority of families and subfamilies, as well as for the monophyly of most genera, is high (Fig. 1). Additionally, we find stronger support for nodes near the root, indicating that the higher-level relationships of snakes are stable and well-supported. This suggests that overall, the supermatrix approach is fulfilling its intended purpose in providing a robust large-scale tree based on heterogeneous existing data sources, to inform both taxonomy and phylogenetic analyses (de Queiroz and Gatesy, 2007; Heath et al., 2008a, 2008b; Pyron et al., 2011; Pyron and Wiens, 2011; Thomson and Shaffer, 2010).

In terms of the effects of missing data, we find no obvious impact of incomplete sequences on either node support or parameter estimation, consistent with most empirical evidence (Wiens and Morrill, 2012), but contrary to some simulation studies (Lemmon et al., 2009). Thus, heterogeneous data sources do not appear to be significantly impacting our estimates of snake phylogeny. However, missing data are clearly suboptimal, and both the limited gene sampling (10 genes out of thousands in the genome) and the missing data within the sampled genes may be perpetuating the regions of the tree with poor support (e.g., monophyly of Lamprophiidae and Booidea, relationships within Colubridae). It remains to be seen if strategies such as phylogenomic estimates from next-generation sequencing technologies producing hundreds or thousands of loci will allow us to resolve these nodes with higher confidence.

Acknowledgments

Appendix A. Appendices

Appendix 1. A revised classification of the 89 currently known inland snake species found in Sri Lanka. The 49 described endemic species are indicated with an asterisk (*).

Acrochordidae: *Acrochordus granulatus*; **Boidae**: Erycinae (*Eryx conicus*); **Colubridae**: Colubrinae (*Ahaetulla nasuta*, *Ahaetulla pulverulenta*, *Argyrogena fasciolata*, *Boiga barnesii**, *Boiga beddomei*, *Boiga ceylonensis*, *Boiga forsteni*, *Boiga trigonata*, *Chrysopelea ornata*, *Chrysopelea taprobanica**, *Coelognathus helena*, *Dendrelaphis bifrenalis**, *Dendrelaphis caudolineatus*, *Dendrelaphis oliveri**, *Dendrelaphis schokari*, *Dendrelaphis tristis*, *Dryocalamus gracilis*, *Dryocalamus nympha*, *Liopeltis calamaria*, *Lycodon aulicus*, *Lycodon carinatus**, *Lycodon osmanhilli**, *Lycodon striatus*, *Oligodon arnensis*, *Oligodon calamarius**, *Oligodon sublineatus**, *Oligodon taeniolatus*, *Ptyas mucosus*), Natricinae (*Amphiesma stolatum*, *Aspidura brachyorrhos**, *Aspidura ceylonensis**, *Aspidura copei**, *Aspidura deraniyagalae**, *Aspidura drummondhayi**, *Aspidura guentheri**, *Aspidura trachyprocta**, *Atretium schistosum*, *Balanophis ceylonensis**, *Macropisthodon plumbicolor*, *Xenochrophis asperrimus**, *Xenochrophis* cf. *piscator*), Sibynophiinae (*Sibynophis subpunctatus*); **Cylindrophiidae**: *Cylindrophis maculatus**; **Elapidae**: *Bungarus caeruleus*, *Bungarus ceylonicus**, *Calliophis haematoetron**, *Calliophis melanurus*, *Naja naja*; **Gerrhopilidae**: *Gerrhopilus ceylonicus**, *Gerrhopilus mirus**; **Homalopsidae**: *Cerberus rhynchops*, *Enhydris enhydris*, *Gerarda prevostiana*; **Pythonidae**: *Python molurus*; **Typhlopidae**: *incertae sedis* (Typhlopidae *sp.**), *Ramphotyphlops braminus*, *Typhlops lankaensis**, *Typhlops leucomelas**, *Typhlops malcolmi**, *Typhlops porrectus*, *Typhlops tenebrarum**, *Typhlops veddae**, *Typhlops violaceus**; **Uropeltidae**: *Platyplectrurus madurensis*, *Rhinophis blythii**, *Rhinophis dorsimaculatus**, *Rhinophis drummondhayi**, *Rhinophis erangaviraji**, *Rhinophis homolepis**, *Rhinophis lineatus**, *Rhinophis melanogaster**, *Rhinophis oxyrhynchus**, *Rhinophis philippinus**, *Rhinophis phillipsi**, *Rhinophis porrectus**, *Rhinophis punctatus**, *Rhinophis ruhunae**, *Rhinophis saffragamus**, *Rhinophis tricoloratus**, *Rhinophis zigzag**; **Viperidae**: Crotalinae (*Hypnale hypnale*, *Hypnale nepa**, *Hypnale* sp. 'amal'*, *Hypnale zara**, *Trimeresurus trigonocephalus**), Viperinae (*Daboia russelii*, *Echis carinatus*).

Appendix B. Supplementary material

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