Zootaxa 4603 (2): 241–264
https://www.mapress.com/j/zt/

Article

ISSN 1175-5326 (print edition)
ZOOTAXA
ISSN 1175-5334 (online edition)

https://doi.org/10.11646/zootaxa.4603.2.2
http://zoobank.org/urn:lsid:zoobank.org:pub:81DEF6B8-07CE-4ADB-8145-D46516E0A096

A new genus and species of natricine snake from northeast India

VARAD B. GIRI[1,2], DAVID J. GOWER[3], ABHIJIT DAS[4], H.T. LALREMSANGA[5],
SAMUEL LALRONUNGA[6], ASHOK CAPTAIN[7] & V. DEEPAK[3,8,9]
[1]*National Centre for Biological Sciences, Tata Institute of Fundamental Research, GKVK, Bellary Road, Bangalore 560065, India*
[2]*Foundation for Biodiversity Conservation, Shubh Kalyan, A1903, Nanded City, Pune, 411041, Maharashtra, India*
[3]*Department of Life Sciences, The Natural History Museum, London SW7 5BD, UK*
[4]*Wildlife Institute of India, Chandrabani, P.O. 18, Dehradun 248001, India*
[5]*Department of Zoology, Mizoram University, Aizawl 796004, India*
[6]*Department of Zoology, Pachunga University College, Aizawl 796001, India*
[7]*3/1 Boat Club Road, Pune 411001, Maharashtra, India*
[8]*Centre for Ecological Sciences, Indian Institute of Science, Bangalore, 560012, India*
[9]*Corresponding author. E-mail: veerappandeepak@gmail.com*

Abstract

Based on the first molecular phylogenetic analyses of samples from northeast India, specimens referred to *Rhabdops* from this region are more closely related to the southeast and east Asian natricine genera *Opisthotropis* Günther, 1872 and *Sinonatrix* Rossman & Eberle, 1977 (as well as to New World and western Palearctic natricines) than to peninsular Indian (true) *Rhabdops*. Morphologically, these northeast Indian populations differ from other natricines by having a single ('fused' or unpaired) internasal shield and a single prefrontal shield. Given the morphological and phylogenetic distinctiveness of these northeast Indian populations, we refer them to a new genus, *Smithophis* **gen. nov.**, and transfer *Rhabdops bicolor* (Blyth, 1854) to *Smithophis bicolor* **comb. nov.** Based on morphological and molecular variation within our northeast Indian sample, we additionally describe *Smithophis atemporalis* **sp. nov.** from the state of Mizoram.

Keywords: Mizoram, Natricinae, *Opisthotropis*, *Rhabdops*, *Smithophis* **gen. nov.**, taxonomy

Introduction

The colubrid snake genus *Rhabdops* Boulenger, 1893 is conceived currently as comprising three species—the type species, *R. olivaceus* (Beddome, 1863) and recently described *R. aquaticus* Giri, Deepak, Captain & Gower, 2017, both from the Western Ghats region of peninsular India, and *R. bicolor* (Blyth, 1854) from northeast India and adjacent regions of Myanmar and possibly China (Anderson 1879; Dowling & Jenner 1988; Smith 1943; Wallach *et al*. 2014; Giri *et al*. 2017). In addition to describing a new species, Giri *et al.* (2017) recently carried out the first molecular phylogenetic analysis for *Rhabdops* and found support for a very close relationship between the two peninsular Indian species, and for their inclusion within the colubrid subfamily Natricinae. Giri *et al*.'s (2017) taxon sampling for their molecular phylogenetic analyses did not include the northeast Indian *R. bicolor*.

Here we report additional molecular phylogenetic analyses of *Rhabdops*, including samples of multiple populations from northeast India. We find that the northeast samples are more closely related to the southeast and east Asian natricine genus *Opisthotropis* Günther, 1872 than to peninsular Indian (true) *Rhabdops*. Given the morphological and phylogenetic distinctiveness of the northeast Indian populations we assign *R. bicolor* to a new genus. Based on morphological and molecular variation within our northeast Indian sample, we additionally describe a new species from the state of Mizoram that we ascribe to the new genus.

Accepted by T. Nguyen: 4 Mar. 2019; published: 9 May 2019

Methods

Molecular phylogenetics. We generated DNA sequence data for absolute ethanol-fixed muscle tissue of two northeast Indian *Rhabdops* specimens from the state of Mizoram, including one specimen of the new species described here (Appendix 1). We also generated sequences for a specimen of *Macrophisthodon plumbicolor* from Sangli, Maharashtra, India (Appendix 2). Genomic DNA was extracted from liver or tail tissue samples stored in absolute ethanol at –20ºC using DNeasy (Qiagen) blood and tissue kits. We amplified partial sequences of two nuclear (nu) and three mitochondrial (mt) genes. The mt genes that were amplified are 16S rRNA (*16s*), cytochrome b (*cytb*) and NADH dehydrogenase subunit 4 (*nd4*), and the nu markers are the recombination activating gene 1 (*rag1*) and oocyte maturation factor (*cmos*). PCR amplifications were carried out in 26µl aliquots containing 2.5µL of 1X Taq buffer, 2.5µL of 2.5mM dNTP, 2.5µL of 2.5 mM of MgCl2, 0.25 µl each for the forward and reverse primer, 0.33 µl of 2 units of Taq DNA polymerase, 1µl of extracted DNA of the sample and 16.67 µl of PCR grade H_2O. We used a S1000^{TM} Thermal Cycler (Bio-Rad, [USA]) to run the PCR. PCR conditions followed previously reported protocols (*16s*, primers 16Sar-L and 16Sbr-H: Palumbi *et al*. 1991; *nd4*, primers ND4 and Leu: Arévalo *et al*. 1994; *cytb*, primers Gludg: Palumbi 1996 and H16064: Burbrink *et al*. 2000; *cmos*, primers S77 and S78: Lawson *et al*. 2005; *rag1*, primers R13 and R18: Groth & Barrowclough 1999). Contigs were assembled from bidirectional sequence chromatograms and edited using Chromas Lite v. 2.1.1 and protein-coding genes (*cytb, nd4, rag1, cmos*) were checked for stop codons in unexpected regions by translating nucleotide alignments to amino acids.

We used the new mt and nu sequences of northeast Indian *Rhabdops* spp. in an NCBI GenBank BLAST (Altschul *et al.* 1990; Ye *et al.* 2006) search (Megablast default settings). The most similar sequences in the database were all natricines (including Western Ghats *Rhabdops* spp.), though the 90+% similarity BLAST results also included snakes from other colubrid subfamilies including Colubrinae and Dipsadinae. Therefore, to ascertain the higher relationships of northeast Indian *Rhabdops* we assembled a concatenated mt and nu sequence dataset containing 79 species with representatives of all the known families and subfamilies of althenophidian snakes, using scolecophidian snakes as an outgroup (Appendix 1). Subsequently, we assembled a concatenated mt and nu sequence dataset of 55 species to more precisely determine the relationships of northeast Indian *Rhabdops* within Natricinae (using *Sibynophis* as an outgroup based on e.g., Figueroa *et al*. 2016); samples and GenBank accession numbers are given in Appendix 2.

All sequences were aligned using ClustalW (Thompson *et al.* 1994) (default settings: alignments available online from the Natural History Museum data portal (http://data.nhm.ac.uk/dataset/giri-smithophis), and uncorrected genetic distances were calculated using PAUP 4.0a159 (Swofford 2002). For inferring higher level relationships the 79-species dataset (Appendix 1) was concatenated and partitioned by gene, and phylogenetic relationships were estimated using maximum likelihood (ML; Felsenstein 1981) as implemented in RaxML 1.3.1 (Stamatakis *et al*. 2005). For the second, 55-species dataset (Appendix 2) we used PartitionFinder v1.1.1 (Lanfear *et al*. 2012) with default settings to find the best-fit partition scheme for the concatenated dataset and the best-fit model of sequence evolution for each partition. The best-fit scheme comprised five partitions, by gene and by codon position (Table 1). For this dataset we estimated phylogenetic relationships using ML and Bayesian inference (BI; Huelsenbeck *et al*. 2001) as implemented in RaxML 1.3.1 and MrBayes 3.2 (Ronquist *et al*. 2012), respectively. ML analysis in RaxML used the GTRGAMMA model of sequence evolution which is recommended over GTR+G+I because the 25 rate categories account for potentially invariant sites (Stamatakis 2006). The Graphical User Interface (GUI) version of RAxML (Silvestro & Michalak 2012) was used, employing the ML+ rapid bootstrap method to search for best trees, with branch support quantified via 500 non-parametric bootstrap replicates. The BI analysis used two Markov chains initiated from random trees and run for 10,000,000 generations, sampling every 100 generations. When the BI analysis was terminated, the standard deviation of split frequencies was less than 0.005, and convergence was confirmed for all parameters using Tracer v1.6 (Rambaut *et al*. 2014). The first 25% trees were discarded as "burn-in. Support for clades in the BI tree was quantified using posterior probabilities. Stability of terminal taxa (leaves) in phylogenetic trees was assessed using leaf stability (LS: Thorley & Wilkinson 1999; Wilkinson 2006) as implemented on the RogueNaRok server (rnr.h-its.org), and by using the RogueNaRok (Aberer *et al*. 2013) algorithm with a maximum dropset size of 1 (as implemented on the same server).

Morphological analysis. We examined nine specimens (formalin fixed, washed and stored in ca. 70% ethanol) of the new species, which comprised the type series (n = 7) and referred material (n = 2). Comparative material examined directly includes the holotype and 10 additional specimens of *Rhabdops bicolor* (Appendix 3), and the material of *R. olivaceus* and *R. aquaticus* reported by Giri *et al.* (2017: appendix 2). For other natricines, we obtained comparative information from the literature and examined all natricine types in the collections of the Natural History Museum, London. Catalogue numbers for voucher specimens bear the following prefixes: BMNH (The Natural History Museum, London, UK), BNHS (Bombay Natural History Society, Mumbai, India), MZMU (Departmental Museum of Zoology, Mizoram University, Aizawl, India), ZSIK (Zoological Survey of India, Kolkata, India).

Total length, circumference, snout-vent length and tail length were measured with thread and a ruler to the nearest 1 mm. Other dimensions were recorded with dial callipers, to the nearest 0.1 mm. Bilateral scale counts separated by a comma are given in left, right order. Ventrals were counted following Dowling (1951a), and the scale reduction formulae compiled using a modified version of the method presented by Dowling (1951b). Dorsal scale rows were counted in as short (longitudinally) a transverse zig-zag as possible.

TABLE 1. Partitions and models of sequence evolution used in the Maximum Likelihood (ML) and Bayesian Inference (BI) phylogenetic analyses of the 55-species dataset. In the second column, 1st, 2nd and 3rd refer to codon position.

Partitions	Sites	ML	BI
P1	*cmos* 1st, *cmos* 2nd, *rag1* 1st, *rag1* 2nd	GTR+G	HKY+I+G
P2	*cmos* 3rd, *rag1* 3rd	GTR+G	HKY+G
P3	*16s*, *cytb* 1st, *nd4* 1st	GTR+G	GTR+I+G
P4	*cytb* 2nd, *nd4* 2nd	GTR+G	GTR+I+G
P5	*cytb* 3rd, *nd4* 3rd	GTR+G	GTR+G

Results

Molecular phylogenetics. Analysis of the 79-species dataset recovered northeast Indian *Rhabdops* nested within Natricinae with high bootstrap support (Appendix 4). Thus, the rest of the phylogenetic results reported here focus on analysis of the 55-species dataset that attempts to resolve the position of northeast Indian *Rhabdops* within Natricinae.

In the trees recovered from both the ML and BI analyses of the 55-species dataset, the two sampled northeast Indian *Rhabdops* are sister species but they do not form a clade exclusively with the sampled Western Ghats *Rhabdops* (Fig. 1); instead, northeast Indian *Rhabdops* are more closely related to the east and southeast Asian *Sinonatrix* and *Opisthotropis,* the Sri Lankan *Aspidura,* and the sampled European and N American natricines (*Liodytes, Clonophis, Haldea, Storeria, Adelophis, Thamnophis, Tropidoclonion, Nerodia, Natrix*). Based on this phylogenetic result and morphological data (see below), we classify the northeast Indian *Rhabdops* in a new genus, from herein *Smithophis* **gen. nov.**

The monophyly of *Opisthotropis* is not strongly supported in either the ML or BI analysis, and the *Opisthotropis* + *Smithophis* clade is moderately supported in the ML analysis. Based on the RaxML results for the 55-species dataset, *O. maculosa* is the least stable taxon within the *Opisthotropis* + *Smithophis* + *Sinonatrix* clade and the eighth least stable taxon in the dataset overall (LS_{max} score of 0.86 compared with a mean LS_{max} score across all 55 species of 0.90). RogueNaRok identifies *O. maculosa* as the only rogue within the *Opisthotropis* + *Smithophis* + *Sinonatrix* clade, and support for the *Opisthotropis* + *Smithophis* clade ignoring *O. maculosa* (pruning it from the 500 bootstrap trees using PAUP* 4.0a152: Swofford 2000) is 95%, compared with the unpruned value of 85%. The phylogenetic results thus overall support very strongly the monophyly of *Smithophis*, and moderately strongly support the monophyly of *Smithophis* + *Opisthotropis*.

The monophyly of *Opisthotropis* is far from compellingly supported, but ML bootstrap support when the rogue *O. maculosa* is pruned from bootstrap trees is 52% (compared with the unpruned value of 34%; Appendix 5). Analysing the ML bootstrap trees with SplitLogic (Hill & Wilkinson 2017) demonstrates that, ignoring the rogue *O. maculosa*, there are no splits incompatible with the monophyly of *Opisthotropis* that appear in more than 20% of the bootstrap trees, such that there is only very weak signal for the best-supported alternative to *Opisthotropis* monophyly. It might also be borne in mind that only *cytb* sequence data were available for five out of the nine *Opisthotropis* species.

Uncorrected mt *p*-distances between *Smithophis* and *Rhabdops* were high (*16s* 6–7%, *cytb* 25–26%, *nd4* 24–28%). Uncorrected mt *p*-distances between *Smithophis* spp. and *Opisthotropis* spp. were similarly high (*cytb* 20–27%, *nd4* 17–22%). However, we also noticed that within *Opisthotropis* there were high pairwise interspecific genetic differences for the same genes (*cytb* 12–23%, *nd4* 5–19%). The two *Smithophis* species had greater genetic difference (*16s* 2%, *cytb* 13%, *nd4* 12%) than between the two Western Ghats *Rhabdops* species (*16s* 1.5%, *cytb* 7.6–7.7%, *nd4* 4.2–4.9%).

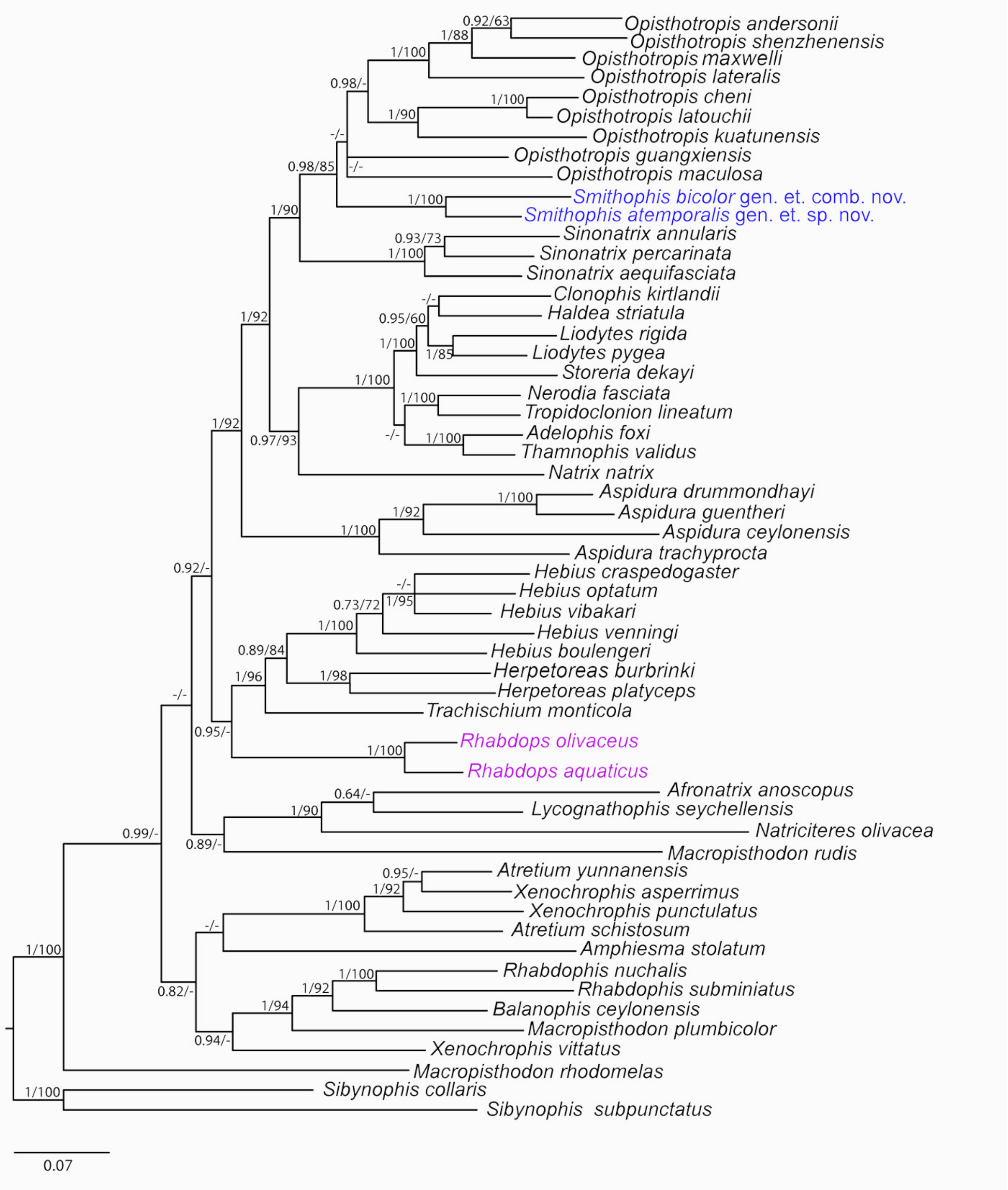


FIGURE 1. Bayesian tree showing phylogenetic relationships of *Smithophis* **gen. nov.** and *Rhabdops* within Natricinae snakes. Bayesian posterior probability and Maximum Likelihood bootstrap support are shown at each internal branch. PP below 0.60 and BS below 60 are not shown.

Systematics

Smithophis gen. nov.

urn:lsid:zoobank.org:act:444965CF-9756-4EF1-83B5-41051AE0F256

Type species. *Smithophis atemporalis* **gen. et. sp. nov.**, by original designation.

Diagnosis. Natricine snakes with the following combination of characters: (1) a single ('fused' or unpaired) internasal shield and a single prefrontal shield, (2) internasal very broad and not or only slightly tapered anteriorly, (3) smooth, unkeeled dorsal scales, (4) fewer than six pairs of supralabial shields, (5) 17 rows of dorsal scales at midbody, (6) C-shaped, valvular external nares, (7) eyes with rounded or elliptical pupils, and (8) eye diameter substantially smaller than distance between eye and naris.

Remarks. The new genus is clearly monophyletic and most closely related to a monophyletic *Opisthotropis* in our molecular phylogenetic trees, and the two genera are similar phenotypically in having a single prefrontal shield (paired in a few species of *Opisthotropis*). Molecular phylogenetic support for *Opisthotropis* monophyly is not yet compelling though clearly stronger than for its non-monophyly, but we have elected to erect a new genus given also that (1) *Smithophis* **gen. nov.** is distinct from *Opisthotropis* in also having a single internasal shield (which, in concert with the single prefrontal, is a unique condition among natricines), in having fewer than 6 supralabial shields on each side, and in having internasal(s) that are not or only slightly anteriorly tapered, and (2) because the phylogenetic relationships of several key taxa remain unclear given incomplete taxon sampling thus far in phylogenetic analyses—in this context we are thinking particularly of the type species of *Opisthotropis* (*O. ater* Günther, 1872), and any representatives of any of the at least superficially similar (David *et al*. 2015) monotypic *Isanophis* David *et al*. 2015, and *Paratapinophis* Angel, 1929 (though it might be noted that the latter three taxa also differ from *Smithophis* **gen. nov.** in having paired internasals that are not notably broad and which taper anteriorly, and in having more than 6 supralabials).

All specimens of *Smithophis* we have observed have a single internasal shield and, to the best of our knowledge, all specimens of *Opisthotropis* have paired internasals. Species of all synonyms of *Opisthotropis* have paired rather than single internasals. Single internasals are derived, providing additional evidence to support the monophyly of the new genus. Wall (1908: 322–323) considered the unusual head shields of *Rhabdops bicolor* distinctive enough that it was "extremely probable that it will have to be separated and relegated to a genus by itself".

Content. Two nominal species; the type species (described below) and *S. bicolor* (Blyth, 1854).

Etymology. Named in honour of Malcolm A. Smith (1875–1958) in recognition of his many contributions to herpetology and especially to the knowledge of Asian snakes.

Distribution. Northeast India, from Meghalaya state, northeast India east to Myanmar and possibly western Yunnan, China (Anderson 1879; Pope 1935; Smith 1943; Dowling & Jenner 1988; Wallach *et al*. 2014).

Smithophis bicolor (Blyth, 1854) comb. nov.

Calamaria bicolor Blyth, 1854: Blyth (1854: 289)
Grotea bicolor (Blyth, 1854): Theobald (1868: 45)
Pseudocylcophis bicolor (Blyth, 1854): Boulenger (1890: 300)
Ablabes bicolor (Blyth, 1854): Günther (1864: 226), Anderson (1879: 809–810)
Rhabdops bicolor (Blyth, 1854): Boulenger (1893: 301), Wall (1908: 322–323, fig. 3), Pope (1935: 176–178, tables LIX, LX, LXIII), Smith (1943: 328–329, fig. 104), Das *et al*. (1998: 146), Wallach *et al*. (2014: 638), Das & Das (2017: 119), Lalremsanga & Lalronunga (2017: 106–107), Giri *et al.* (2017: 27–52)

Diagnosis. A *Smithophis* with temporal shields.

Holotype. ZSI 7030, "Asám" (Blyth 1854).

Distribution. Poorly understood, but at least Khasi and Garo Hills, Meghalaya state, northeast India. Reported to extend eastward to Mizoram state, northeast India and at least into Myanmar and possibly western Yunnan in southern China (Anderson 1879; Pope 1935; Smith 1943; Dowling & Jenner 1988; Das 2012; Wallach *et al*. 2014; Das & Das 2017).

Smithophis atemporalis **gen. et. sp. nov.**

(Figs. 1–7; Table 2)

Rhabdops bicolor (Blyth, 1854): Das (2015: photograph on p. 65), Laltanpuia *et al*. (2008: 119, in part; fig. 16).

Diagnosis. A *Smithophis* lacking temporal shields.

Holotype. BNHS 3523 (Figs. 2, 3), male, collected from Mizoram University Campus, Aizawl, India (23.76338°N, 93.09916°E, 833 m elevation) by H.T. Lalremsanga on 10 July 2014. See map in Fig. 4.

Paratypes (n = 6). BNHS 3524—BNHS 3527, BNHS 3529, males and BNHS 3528, female, collected from Mizoram University Campus, Aizawl on 14 August 2014 by H.T. Lalremsanga.

Referred specimens. BNHS 3530 male, collected from Model Veng, Aizawl, India (23.71083°N, 92.93194°E, 1014 m elevation) on 18 September 2015 and BNHS 3531 male, collected from Luangmual, Aizawl, India (24.45750°N, 92.69953°E, 1025 m elevation) on 20 October 2014 by S. Lalrounga. These are referred rather than paratypic material because we have not generated detailed morphometric and meristic data.

Description of holotype. See Table 2 for morphometric and meristic data. Good condition, slightly dehydrated; ca. 20 mm longitudinal ventral incision into ventral surface of base of tail (through which hemipenis observed).

Body somewhat laterally compressed (1.5 times as high as wide at midbody) with flattened venter and arched dorsum, widest at midbody, tapering posteriorly and more substantially anteriorly. Head elongate, broader than tall, slightly wider than anterior of body. In dorsal view head slightly ovate, sides very slightly convex, gently converging anteriorly. Front of snout not pointed, truncated. In lateral view head tapers very gently from back to prefrontal, more strongly tapered in front of prefrontal. Paired shields on top of head (= parietals only) abutting along midline rather than imbricate/overlapping.

In dorsal view rostral approximately three times broader than long, substantially shorter than distance between it and frontal; projects beyond tip of lower jaw; ventrally with transverse concavity, notched (C-shaped) at margin of mouth. Frontal subpentagonal, lateral edges anteriorly diverging; shorter and smaller than each parietal, shorter than distance between it and snout tip. Internasal single, smaller than single prefrontal. Nasals subquadrangular, squarish, notably larger than squarish loreal. Single supraocular, preocular and postocular each side; supraocular slightly larger than preocular, itself slightly larger than postocular. Pre- and postocular each kidney shaped; supraocular elongate, longer than wide.

External naris on dorsolateral-facing surface, seen as C-shaped slit in front of flap, in broad, shallow depression slightly posterodorsal of centre of nasal. External naris visible anteriorly as well as dorsally and (mostly) laterally. Five supralabials (SLs) on each side; SL 5 largest, longest; SLs 1 and 4 subequal, smallest; SLs 2 and 3 subequal. SL 1 contacts rostral and nasal, SL 2 contacts loreal, SL3 contacts preocular and eye, SL 4 contacts postocular and parietal, SL 5 contacts parietal). Eye contacts third supralabial only. Eye lateral; pupil subcircular, very slightly elliptical (long axis vertical). No temporal shields. Parietals longer than wide, larger than other head scales. Midline interparietal suture a little more than two thirds length of each parietal; parietals barely projecting posterior to suture; each parietal more than twice as long as frontal; each parietal contacts frontal, supraocular, postocular, and fourth and fifth supralabial, plus five other scales. Posterior margin of each parietal rounded, somewhat scalloped.

Mental small, subtriangular, wider than long. Infralabials 7,7; first pair in midline contact; second pair smallest; fourth largest. On right, fourth infralabial longest, on left seventh as long.

Two pairs of genials; first pair largest, longer than broad, in long midline contact; second pair not in contact, separated by one small, midline scale. Anterior genials contact infralabials (ILs) 1–4; posterior genials contact IL 4 and 5 (left) or 4 only (right). Anteriormost ventral separated from each posterior genial by four scales, separated from each posteriormost infralabial by six scales. Teeth largely obscured by gingivae, but estimated as 10 or 11 marginals on each side of upper jaw.

Macroscopically and under low magnification (using a light dissecting microscope) body scales smooth. No keels or apical pits. Vertebral scale row not different from adjacent dorsal scale row. Exposed parts of dorsal body scales generally evenly sized on dorsum and along body except for those involved in dorsal scale row reductions and for lowest dorsal scales level with first few ventrals which are lower, more elongate. Dorsal scales closer to vent slightly smaller than at midbody; those at anterior of body smallest. Dorsal scale rows 17 at level of first ventral, maintained to vent except for loss of third dorsal scale row on left, six ventrals anterior to vent.

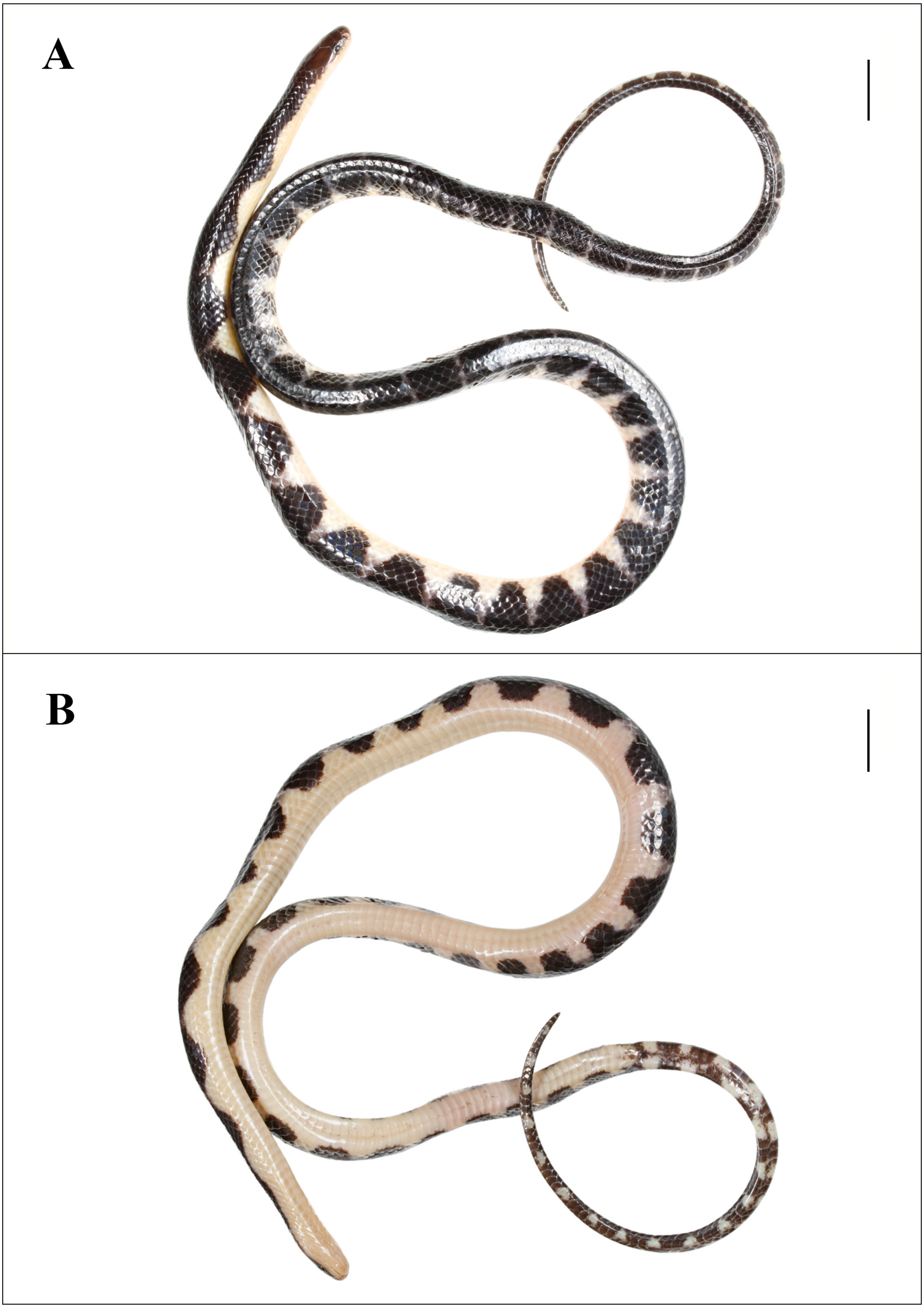


FIGURE 2. Holotype of *Smithophis atemporalis* **gen. et. sp. nov.** (BNHS 3523) whole preserved specimen in A) dorsal and B) ventral views. Scale bars 10 mm.

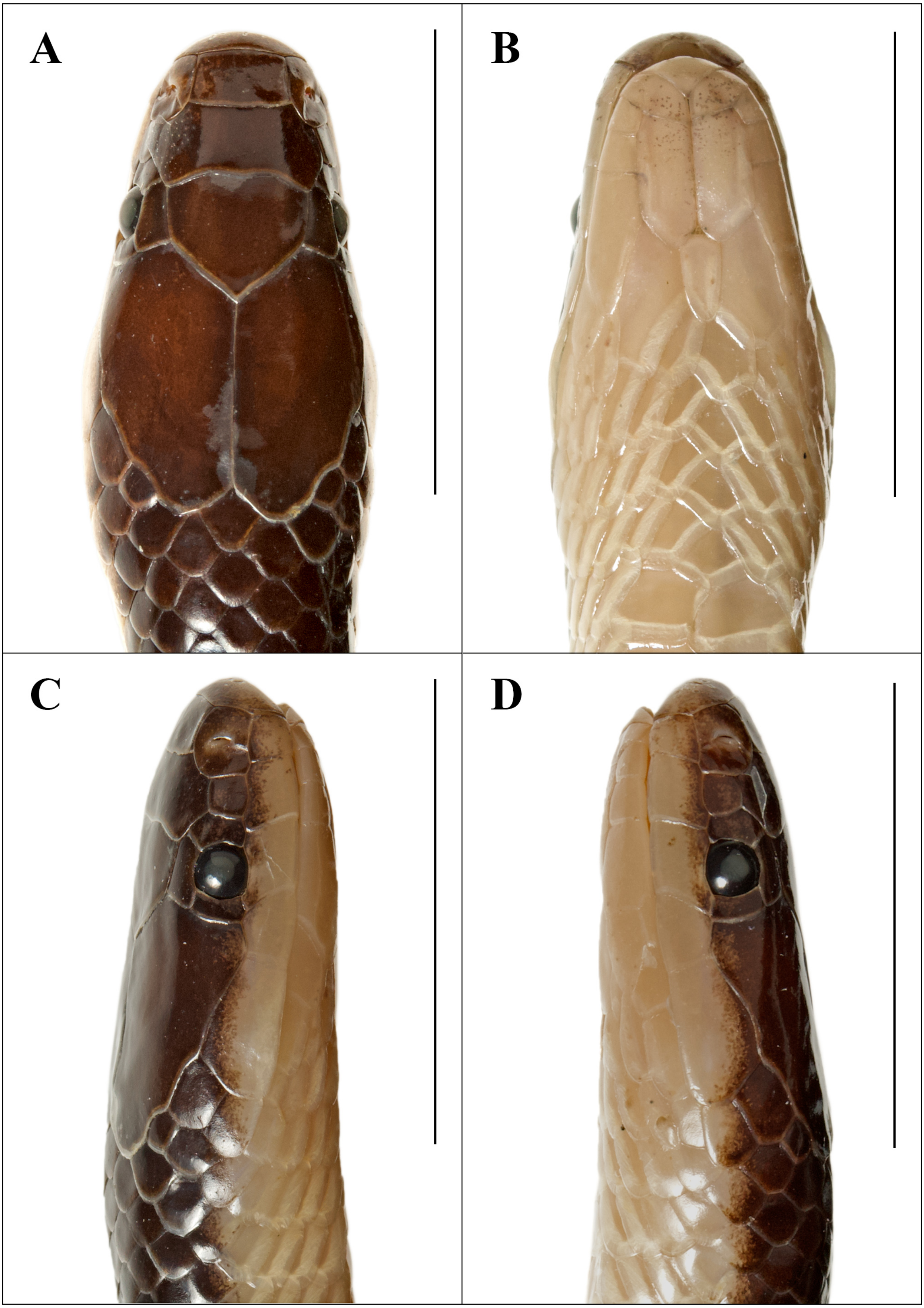


FIGURE 3. Holotype of *Smithophis atemporalis* **gen. et. sp. nov.** (BNHS 3523) head of preserved specimen in A) dorsal, B) ventral, C) right lateral and D) left lateral views. Scale bars 10 mm.

First ventral divided/paired. Posteriormost ventral with slight posteromedial extension. Anals paired (right overlapping left), each slightly larger than posteriormost ventral. Each anal overlaps 6, 7 small scales in addition to first subcaudal. Tail subtriangular in cross section, flattened ventrally. Dorsal tail scales more heterogenous in size than on body, without clear patterns. Subcaudals paired/divided throughout, terminal scale (scute) conical, approximately as wide as long, pointed.

Macroscopically bicoloured, darker black-grey above, whitish below. Body scales iridescent. Dorsum dark. Alternating (at least asymmetric) longer dark and shorter pale markings along body and tail. On body 36, 35 dark 'bands', on tail 20, 16. On last three quarters of body, ventrally projecting dark trapezoids extend onto lateral edges of ventrals (leaving broad, entirely pale band along most of venter), these dark trapezoids anteriorly steadily less ventrally extensive. Anteriormost dark trapezoid (two head lengths behind head) extends onto second dorsal scale row. Whitish inverted-Vs extend dorsally between each dark trapezoid up to the fourth dorsal scale row, though partly continues as mottled pale grey scales up to vertebral scale or even one scale row onto opposite side and often (mostly on posterior half of body) connecting with grey dorsal part of inverted pale Vs from opposite side. Along the first quarter of body the border between pale-dark markings wavy, rapidly becoming increasingly sharply zigzag. Ventrally projecting dark marks extend as far as midventer on tail from behind vent, forming alternating (dark-pale) transverse bands; where pale bands approach midventer (only on anterior half of tail, where they are longer) they remain separated by narrow midventral dark line. Whitish ventrals with fine pale grey speckles on posterior half of body. Anals each with pale grey blotches as well as speckles.

Head dark dorsally, brown-grey, slightly paler than body dorsum, generally uniform, rostral slightly paler. Dark of dorsum extends onto upper margins of SLs, SLs otherwise pale (whitish, as body venter) with very few (more on SL1) pale grey specks. Dark scales on dorsum (including head) are mottled under low power dissecting microscope. First pair of ILs and anterior genials with pale grey speckles (fewer on mental). Underside of head otherwise pale, whitish. Inside of mouth pale.

Variation among paratypes. The heads of the paratypes are illustrated in Fig. 5. See Table 2 for variation in meristic and morphometric features. Paratypes generally in moderate to good condition, with following exceptions. BNHS 3524 dehydrated, contorted, yellowed ventrally with dorsolateral longitudinal incision on posterior half; BNHS 3525 soft posterior half, with 10 mm tail incision and missing terminal scute of tail; BNHS 3526 with couple of breaks along body, distorted mouth, marginal and palatal tooth-bearing bones removed from upper jaw, long tail incision with both hemipenes removed; BNHS 3527 a little dehydrated with two ventral longitudinal incisions on body, ventral tail incision with one hemipenis removed; BNHS 3528 dehydrated in small parts, soft in others, ventral incision in tail; BNHS 3529 a little dehydrated with ventral incision on anterior of tail.

Paratypes typically match holotype description except where noted here. Notch on ventral surface of rostral shield very shallow in BNHS 3524, more U- than C-shaped in BNHS 3526. Posterior margins of parietals not scalloped in BNHS 3524, 3525, 3526 and 3527, and more pointed than rounded in BNHS 3526, 3527, 3528 and 3529. Supraocular and postocular 'fused' on left of BNHS 3524; left pro- and postocular subequal in size in BNHS 3529; six infralabials on left of BNHS 3524; two postoculars on left of BNHS 3524. Each parietal contacts four rather than five scales in addition to head shields in all paratypes except for six on left of BNHS 3526, five on left of BNHS 3527 and 3529. Only first (not first and second) SLs contact nasal shield on each side in BNHS 3524. Fourth IL invariably longest and largest. Only IL 4 contacts posterior genial in BNHS 3527, 3528 and 3529, otherwise IL 5 also makes contact on one side only. Anterior and posterior genials subequal in BNHS 3524, 3526 and 3528; posterior genials slightly larger in BNHS 3529. First ventral entire rather than divided in all paratypes except BNHS 3529. Three rather than four scales between posterior genials and first ventral in BNHS 3526 (and on right of BNHS 3528 and 3529). Upper jaw marginal tooth counts approximately 10 or 11 on each side in all paratypes. Eighteen (rather than 17) dorsal scale rows at level of first ventral in BNHS 3526, though reducing to 17 by fourth ventral; 17 rows maintained to vent in BNHS 3524, 3526, 3527, 3528 and 3529; only BNHS 3525 with reduction to 16 rows (like holotype) shortly anterior to vent (level with third ventral anterior to vent). Each anal overlaps 4–7 small scales in addition to anteriormost subcaudals. Tail with subcircular rather than subtriangular cross section posteriorly in all paratypes except BNHS 3524 and 3528. Terminal scute slightly upturned in BNHS 3527 and 3528.

Dark bands on dorsum of body 27–37, on tail 13–18 (Table 2). Whitish part of inverted Vs on body extend dorsally to third (rather than fourth) dorsal scale row in all paratypes except BNHS 3525 where some reach the fourth. Few of the grey speckled apices of inverted Vs extend beyond midvertebral row or connect with opposite inverted Vs in most paratypes; where they occur, connections typically confined to midbody (BNHS 3528) or posteriorly (BNHS 3524, 3525, 3529). Grey speckles on ventrals sparsely on anterior as well as posterior of BNHS 3525; only at midbody and some of last few ventrals on BNHS 3528; concentrated into very narrow, broken midventral line (as far forwards as second ventral) in BNHS 3529; absent except for single posterior speck in BNHS 3527. Anals variably without grey blotches (BNHS 3527) or speckles (left of BNHS 3526) or both (BNHS 3524). Midventral darker line on posterior of tail absent in BNHS 3526, thick but mostly broken in BNHS 3528, well developed in BNHS 3525 and 3529. Dark bands do not meet midventrally on anterior two thirds of tail in BNHS 3527.

Head blackish dorsally, not paler than anterior of body in BNHS 3525. In addition to rostral, internasal (and to a lesser degree prefrontal, frontal) and anterior half of nasal and internasal paler than rest of head shields dorsally in BNHS 3524 and 3527, respectively. First SL no more speckled than other SLs in BNHS 3525, 3526, 3527 and 3528. Speckles extending beyond first ILs to second (BNHS 3524), fourth (BNHS 3526, 3527) or sixth (BNHS 3525); no speckles on left first IL of BNHS 3529. Mouth with tiny specks of pigment under tongue and posterolaterally in BNHS 3526.

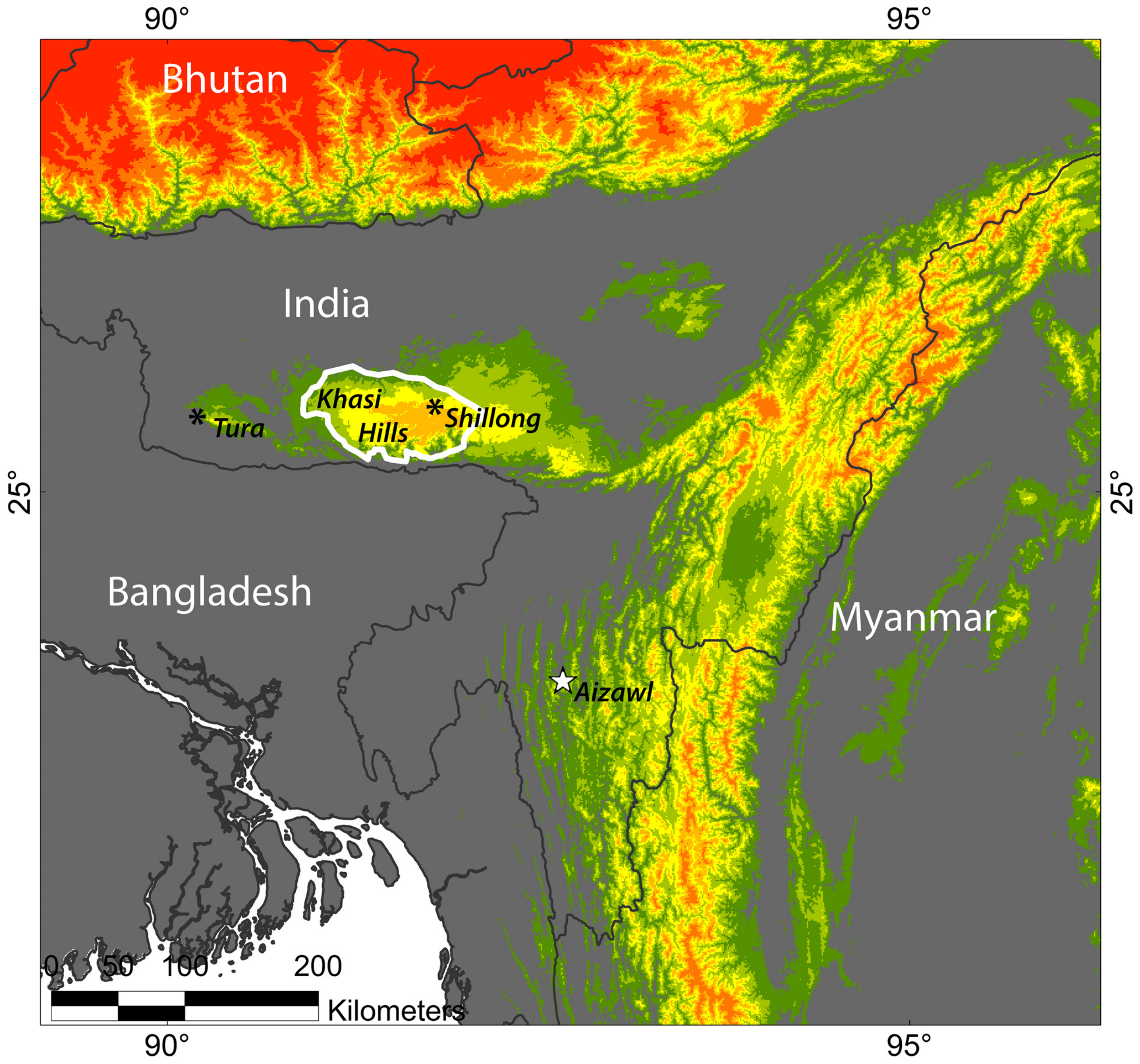


FIGURE 4. Map showing the position (white star) of the type locality of *Smithophis atemporalis* **gen. et. sp. nov.** in Mizoram, India. Examined comparative materials of the only known congener, *S. bicolor* **comb. nov.** (including the type), are from the Khasia (or Khassia or Khasi) Hills, Shillong, Tura or Aizawl, or from unspecified localities in northeast India. See Appendix 3 for locality details.

TABLE 2. Meristic and morphometric (in millimetres) data for examined specimens of *Smithophis atemporalis* **gen. et. sp. nov.** Head length = distance between snout tip and back of lower jaw; bilateral structures given in left, right order; ventral count recorded using Dowling method; subcaudal counts exclude terminal scute; small scales overlapped by anals excludes anteriormost subcaudals. * indicates measure/count incomplete because end of tail missing. The format 'X-Y' is used to denote the shortest distance between features X and Y.

Museum prefix and tag number	BNHS 3523	BNHS 3524	BNHS 3525	BNHS 3526	BNHS 3527	BNHS 3528	BNHS 3529
Sex	M	M	M	M	M	F	M
Tail length	119	145	80*	170	135	135	115
Snout-vent length	321	355	400	455	430	390	330
Total length	440	500	480*	625	565	525	445
Head length	9.3	11.8	10.6	11.5	10	10.8	10
Head width (maximum)	5.3	5.7	5	6.7	5.7	5.2	5.4
Midbody circumference	28	35	32	40	30	32	30
Nostril-nostril	2.5	3.2	2.8	3	2.9	2.9	2.6
Eye-eye	3.8	4.5	4	5	4.3	4	4.3
Eye-snout tip	3.8	4.6	4	4.9	4.1	4.2	4.3
Eye diameter	1.2	1.5	1.5	1.5	1.4	1.3	1.4
Maximum width of rostral	2.6	3.4	3	3.5	3.4	3.1	2.9
Max. length frontal shield	2.8	3.3	2.9	3.5	3.1	3.1	3.1
Max. width frontal shield	3	3.4	3.1	3.5	3.3	3.2	3.1
Max. length parietal	5.8	6.6	6.2	7.2	6.4	6.4	6.1
Ventral scales	199	203	192	201	198	187	197
Subcaudal scales	82, 82	77, 76	51,52*	83, 84	75,75	74,75	77, 77
Small scales overlapped by anals	6,7	5,5	6,6	6,7	7,?	4,5	6,7
Dark Vs on body	36,35	37,36	39,42	36,35	37,36	31,33	32,27
Dark bands on tail	20,16	17,18	13,14	16,18	14,15	13,14	13,13

Colour in life. Based on uncollected specimens (Fig. 6). Head, body and tail predominantly glossy black above, creamish-white below. More precisely: upper scales of head (frontal, prefrontal, internasal, nasals, loreals, preoculars, oculars, supraoculars, postoculars, parietals and all scales bordering posterior margin of parietals) uniform glossy black. Rostral predominantly black, creamish-white on lower portion. Supralabials black above, creamish-white below; the proportions between the two shades vary from about half and half, to almost entirely creamish-white; the border between the two is indistinct and either heavily mottled, or speckled with black. Eye with round pupil; pupil and iris black. Venter creamish-white. Under the head and neck and to approximately three head-lengths behind head, the creamish-white is tinted with yellow (less markedly posteriorly) and this pale region forms an undulating line where it meets the glossy black dorsum on the lower lateral edges of the snake. After approximately three head-lengths, the pale venter colour forms upward-pointing triangles. From approximately midbody the triangles become narrower and taller, sometimes even reaching the uppermost dorsal scale row and forming, or giving the appearance of faint bands.

Etymology. The specific epithet is in reference to the lack of temporal shields, a diagnostic feature of the new species. For nomenclatural purposes, the species epithet is considered a noun in apposition.

Suggested common name. Mizo rain snake or Narrow-headed smithophis (English). Mizo Ruahrul (Mizo).

Distribution, natural history and conservation. *Smithophis atemporalis* **gen. et. sp. nov.** is presently known with certainty only from in and around the type locality of the campus of Mizoram University and some nearby localities. The precise limits of this species' distribution are unclear, partly because the species has sometimes previously been confused with *S. bicolor,* such that anecdotal reports need reassessment. Reassessment of distribution is one of the issues that need to be dealt with before the conservation assessment of this species can be adequately assessed. In Aizawl, *S. atemporalis* **gen. et. sp. nov.** is commonly seen during the monsoons, especially in, or close to streams and other wet places, close to human habitation and after rain showers. Locally this species is called '*ruahlawmrul*', a rain-loving snake. *Smithophis atemporalis* **gen. et. sp. nov.** appears to have a tolerance for human dominated landscapes, though traffic is likely a threat given that these snakes have been seen on paved roads (Fig. 7). Few sightings have been made in forest habitats, though systematic survey data are not available. *Smithophis atemporalis* **gen. et. sp. nov.** have been seen in the wild feeding on earthworms and juvenile skinks, and one individual was observed in captivity eating the eggs of the frog *Fejervarya asmati* (HTL, SL pers. obs.). One other *S. atemporalis* **gen. et. sp. nov.** individual laid three eggs in captivity (HTL, SL pers. obs.).

FIGURE 5. Paratypes of *Smithophis atemporalis* **gen. et. sp. nov.** (specimen numbers given in first row). Heads of preserved specimens in A) dorsal, B) ventral, C) right lateral and D) left lateral views. Scale bars 10 mm.

FIGURE 6. *Smithophis atemporalis* **gen. et. sp. nov.** Colouration in life of: A) specimen from Aizawl, and B) topotypic specimen from Mizoram University Campus, Aizawl. Specimens not collected.

FIGURE 7. Habitat of *Smithophis atemporalis* **gen. et. sp. nov.** A) Stream in Mizoram University Campus, B) Stream in Aizawl, note water pipelines indicating human activity, C) Road near Chawlhhmun, Aizawl, Mizoram,, and D) Road at Tuivamit, Aizawl.

Discussion

Prior to Giri *et al*.'s (2017) description of *Rhabdops aquaticus* and the present study, *Rhabdops* was generally considered Colubridae *incertae sedis* and to comprise only two species with a pronounced disjunct Western Ghats-northeast India distribution (e.g. Smith 1943). We now know that *Rhabdops* is a natricine comprising at least two species confined to the Western Ghats, and that the northeast Indian representatives comprise at least two species representing a distinct natricine genus (*Smithophis*) that is not the closest relative of *Rhabdops,* and that is endemic to northeast India (and possibly extending into adjacent Indochina). Disjunct Western Ghats (and/or Sri Lanka) versus northeast India/southeast Asia distributions have played a prominent role in debates about historical biogeography of India's megadiversity (e.g. Hora 1949; Karanth 2003) but, as with *Rhabdops,* several additional such supposed disjunct distributions for reptiles and amphibians have also not withstood closer scrutiny. For example, the caecilian amphibian genus *Gegeneophis* is now understood to be confined to peninsular India (largely the Western Ghats) while *Chikila* (previously *Gegeneophis*) *fulleri* and closely related species are endemic to northeast India (Kamei *et al*. 2012, 2013), and the caecilian *Ichthyophis sikkimensis* is restricted to the northeast and does not occur also in the Western Ghats as previously claimed (Gower *et al*. 2017). Other similar herpetofaunal examples include the lizard genus *Salea*, previously thought to occur in northeast India as well as the Western Ghats but now, following taxonomic revision, considered restricted to the latter (Mahony 2010); and the skink *Scincella,* the frog *Polypedates*, and the toad *Pedostibes,* for which all Western Ghats (and any Sri Lankan) species have been transferred to new genera, leaving the remaining species restricted to northeast India (and some into Indochina and/or southeast Asia) (Eremchenko & Das, 2004; Zachariah *et al*. 2011; Chandramouli & Amarasinghe 2016). The natricine snake *Atretium* comprises two nominal species considered to have a disjunct, Yunnan versus (largely southern) India and Sri Lanka distribution, but molecular phylogenetic analyses have recovered the genus as non-monophyletic (Figueroa *et al*. 2016; Giri *et al*. 2017; this study). Intact examples of disjunct Western Ghats versus northeast India distributions for amphibians and reptiles include the skink *Sphenomorphus* and frog *Clinotarsus*.

Despite progress in understanding of their phylogenetic relationships, and of their species-level diversity, we know very little about *Smithophis* spp. Almost nothing has been reported of their natural history, and verified distributional data are sparse. In addition, we believe that the taxonomy of *S. bicolor* **comb. nov.** is in need of further assessment, with the variably coloured specimens referred to this taxon from a wide range of locations across northeast India and Indochina (e.g. Wall 1908; Pope 1935; Sanyal & Gayen 2006; Ahmed *et al*. 2009; Das 2012; Lalremsanga & Lalronunga 2017) potentially representing more than one species. Eight of the 25 currently recognised species of *Opisthotropis* have been described since 2007 (Uetz *et al*. 2018), suggesting that basic biodiversity knowledge of the semiaquatic natricine fauna of Indochina and adjacent regions remains in a state of flux. DNA sequence data have been published for little more than one third of the 25 nominal species of *Opisthotropis*, and for most of those data for only a single gene are available; much more work is required to reach a satisfactory understanding of the systematics of the natricine fauna of northeast India and Indochina.

Given our phylogenetic results, in which *Smithophis* + *Opisthotropis* is sister to *Sinonatrix*, parsimony would suggest that *Smithophis* (or a recent ancestor thereof) likely dispersed into northeast India from adjacent Indochina. The Indochinese and northeast Indian *Opisthotropis*, *Sinonatrix,* and *Smithophis* are together sister to New World + western Palearctic natricines, such that the recent recognition of *Rhabdops* and *Smithophis* as natricines, combined with their phylogenetic relationships, does not challenge the hypothesis that natricines dispersed from the Old World to the New World via Beringia during the Cenozoic (perhaps during the Oligocene, Guo *et al*. 2012).

Acknowledgements

We thank Krushnamegh Kunte and Uma Ramakrishnan (NCBS) for support and encouragement, and Praveen Karanth (CES, Indian Institute of Science) for support and lab facilities. We thank the Biodiversity Heritage Library for ready access to historical literature. DV's contribution was supported in part, by a Marie Skłodowska Curie fellowship. DV thanks Krishna Khan for sharing some of the literature. This research was supported in part by awards to DJG from The Royal Society (International Joint Project 2007/R4), The Natural History Museum (Life Sciences DIF), and Leverhulme Trust grant RPG-342, and to VBG from the Ruffords Small Grants programme. HTL thanks Lalbiakzuala, Larinsanga and Jeremy Malsawmhriatzuala (Dept.of Zoology, MZU), and Michael Vanlalchhuana (Dept.of Biotechnology, MZU) for their assistance. HTL thanks financial assistance from DST-SERB, New Delhi, India. AD thanks the Director and Dean of WII and Aaranyak for support. DJG and DV thank Stephen Mahony for discussion and generous provision of information on the distribution of amphibians and reptiles of the Indian subcontinent. SL thanks C. Lalrinchhana, Vanlalhrima, Vanlalhriatzuala Sailo, Lalnunhlua and P.L. Lalsawmliana for their assistance and the Chief Wildlife Warden, Environment, Forest and Climate Change Department, Govt. of Mizoram, India for issuing research and collection permit (A.38011/5/2011-CWLW/338). This paper was improved thanks to constructively critical reviews by Simon Maddock and an anonymous reviewer.

References

Aberer, A.J., Krompa, D. & Stamatakis, A. (2011) RogueNaRok: An efficient and exact algorithm for rogue taxon identification. *Heidelberg Institute for Theoretical Studies*, Heidelberg, 12 pp. [Exelixis-RRDR-2011-10]

Ahmed, M.F., Das, A. & Dutta, S.K. (2009) *Amphibians and Reptiles of Northeast India. A Photographic Guide*. Aaranyak, Guwahati, xiv + 170 pp.

Altschul, S.F., Gish, W., Miller, W., Myers, E.W. & Lipman, D.J. (1990) Basic local alignment search tool. *Journal of Molecular Biology*, 215, 403–410.
https://doi.org/10.1016/S0022-2836(05)80360-2

Anderson, J. (1879) Reptilia and amphibia. *In:* Anderson, J. (Ed.), *Anatomical and zoological researches, comprising an account of the zoological results of the two expeditions to western Yunnan in 1868 and 1875. Vol. 1*. B. Quaritch, London, pp. 809–810.

Arévalo, E., Davis, S.K. & Sites, J.W. (1994) Mitochondrial DNA sequence divergence and phylogenetic relationships among eight chromosome races of *Sceloporus grammicus* complex (Phrynosomatidae) in central Mexico. *Systematic Biology*, 43, 387–418.
https://doi.org/10.1093/sysbio/43.3.387

Blyth, E. (1855) Notices and descriptions of various reptiles, new or little known [part 2]. *Journal of Asiatic Society of Bengal*, 23 (3), 287–302. [1854]

Boulenger, G.A. (1890) *The Fauna of British India, Including Ceylon and Burma. Reptilia and Batrachia*. Taylor & Francis, London, xviii + 541 pp.

Boulenger, G.A. (1893) *Catalogue of the snakes in the British Museum*. Taylor & Francis, London, 448 pp.

Chandramouli, S.R. & Amarasinghe, A.T. (2016) Taxonomic reassessment of the arboreal toad Genus *Pedostibes* Günther 1876 (Anura: Bufonidae) and some allied Oriental bufonid genera. *Herpetologica*, 72 (2), 137–147.
https://doi.org/10.1655/HERPETOLOGICA-D-15-00053

Das, I., Dattagupta, B. & Gayen, N.C. (1998) History and catalogue of reptile types in the collection of the Zoological Survey of India. *Journal of South Asian Natural History*, 3, 121–172.

Das, I. (2012) *A Naturalist's Guide to the Snakes of South-east Asia. Vol. 11.* John Beaufoy Publishing Ltd, Oxford, 160 pp.

Das, I. & Das, A. (2017) *A naturalist's guide to the reptiles of India, Bangladesh, Bhutan, Nepal, Pakistan and Sri Lanka*. John Beaufoy Publishing Ltd, Oxford, 176 pp.

Dowling, H.G. (1951a) A proposed system for counting ventrals in snakes. *British Journal of Herpetology*, 1, 97–99.

Dowling, H.G. (1951b) A proposed method of expressing scale reductions in snakes. *Copeia*, 1951, 131–134.
https://doi.org/10.2307/1437542

Dowling, H.G. & Jenner, J.V. (1988) Snakes of Burma: Checklist of reported species and bibliography. *Smithsonian Herpetological Information Service*, 76, 1–19.

Eremchenko, V.K. & Das, I. (2004) *Kaestlea*: a new genus of scincid lizards (Scincidae: Lygosominae) from the Western Ghats, south-western India. *Hamadryad*, 28, 43–50.

Felsenstein, J. (1981) Evolutionary trees from DNA sequences: a maximum likelihood approach. *Journal of Molecular Evolution*, 17, 368–376.
https://doi.org/10.1007/BF01734359

Figueroa, A., McKelvy, A.D., Grismer, L.L., Bell, C.D. & Lailvaux, S.P. (2016) A species-level phylogeny of extant snakes with description of a new colubrid subfamily and genus. *PLoS One*, 11 (9), p.e0161070.
https://doi.org/10.1371/journal.pone.0161070

Giri, V.B., Deepak, V., Captain, A., Das, A., Das, S., Rajkumar, K.P., Rathish, R.L. & Gower, D.J. (2017) A new species of *Rhabdops* Boulenger, 1893 (Serpentes: Natricinae) from the northern Western Ghats region of India. *Zootaxa*, 4319 (1), 27–52.
https://doi.org/10.11646/zootaxa.4319.1.2

Günther, A.C.L.G. (1864) *The Reptiles of British India*. Taylor & Francis, London, 452 pp.

Guo, P., Liu, Q., Xu, Y., Jiang, K., Hou, M., Ding, L., Pyron, R.A. & Burbrink, F.T. (2012) Out of Asia: natricine snakes support the Cenozoic Beringian dispersal hypothesis. *Molecular Phylogenetics and Evolution*, 63 (3), 825–833.

https://doi.org/10.1016/j.ympev.2012.02.021

Gower, D.J., Giri, V.B., Kamei, R.G., Oommen, O.V., Khot, R. & Wilkinson, M. (2017) On the absence of *Ichthyophis sikkimensis* Taylor, 1960 (Amphibia: Gymnophiona: Ichthyophiidae) in the Western Ghats of peninsular India. *Herpetological Journal*, 27 (2), 181–187.

Groth, J.G. & Barrowclough, G.F. (1999) Basal divergences in birds and the phylogenetic utility of the nuclear RAG-1 Gene. *Molecular Phylogenetics and Evolution*, 12, 115–123.
https://doi.org/10.1006/mpev.1998.0603

Hora, S.L. (1949) Satpura hypothesis of the distribution of the Malayan fauna and flora to Peninsular India. *Proceedings of the National Institute of Science*, 15, 309–314.

Huelsenbeck, J.P., Ronquist, F., Nielsen, R. & Bollback, J.P. (2001) Bayesian inference of phylogeny and its impact on evolutionary biology. *Science*, 294, 2310–2314.
http://doi.org/10.1126/science.1065889

Kamei, R.G., Gower, D.J., Wilkinson, M. & Biju, S.D. (2013) Systematics of the caecilian family Chikilidae (Amphibia: Gymnophiona) with the description of three new species of *Chikila* from northeast India. *Zootaxa*, 3666 (4), 401–435.
https://doi.org/10.11646/zootaxa.3666.4.1

Kamei, R.G., San Mauro, D., Gower, D.J., Van Bocxlaer, I., Sherratt, E., Thomas, A., Babu, S., Bossuyt, F., Wilkinson, M. & Biju, S.D. (2012) Discovery of a new family of amphibians from northeast India with ancient links to Africa. *Proceedings of the Royal Society of London B: Biological Sciences*, 279 (1737), 2396–2401.
https://doi.org/10.1098/rspb.2012.0150

Karanth, K.P. (2003) Evolution of disjunct distributions among wet-zone species of the Indian subcontinent: testing various hypotheses using a phylogenetic approach. *Current Science*, 85 (9), 1276–1283.

Lalremsanga, H.T. & Lalronunga, S. (2017) *Mizoram rul chanchin*. Bhabani Offset Pvt. Ltd., Guwahati, 132 pp.

Laltanpuia, T.C., Lalrinchhana, C., Lalnunsanga, Lalrotluanga, Hmingthansanga, R., Kumari, A., Renthlei, V., Lalrintluangi S. & Lalremsanga, H.T. (2008) Snakes (Reptilia: Serpentes) of Mizoram University Campus, Tanhril, Aizawl with notes on their identification keys. *Science Vision*, 8 (4), 112–127.

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

Lawson, R., Slowinski, J.B., Crother, B.I. & Burbrink, F.T. (2005) Phylogeny of the Colubroidea (Serpentes): new evidence from mitochondrial and nuclear genes. *Molecular Phylogenetics and Evolution*, 37 (2), 581–601.
https://doi.org/10.1016/j.ympev.2005.07.016

Mahony, S. (2010) Systematic and taxomonic revaluation of four little known Asian agamid species, *Calotes kingdonwardi* Smith, 1935, *Japalura kaulbacki* Smith, 1937, *Salea kakhienensis* Anderson, 1879 and the monotypic genus *Mictopholis* Smith, 1935 (Reptilia: Agamidae). *Zootaxa*, 2514, 1–23.
https://doi.org/10.11646/zootaxa.2514.1.1

Palumbi, S.R., Martin, A.P., Romano, S.L., McMillan, W.O., Stice L. & Grabowski, G. (1991) *The Simple Fool's Guide to PCR. Version 2.* University of Hawaii, Honolulu, 15 pp.

Palumbi, S.R. (1996) The polymerase chain reaction. *In*: Hillis, D.M., Moritz, C. & Mable, B.K. (Eds.), *Molecular systematics*. 2nd Edition. Sinauer Associates, Sunderland, MA, pp. 205–247.

Pope, C.H. (1935) The Reptiles of China, Turtles, Crocodilians, Snakes, Lizards. *Natural History of Central Asia*, 10, i–xvii + 1–604, 25 pls., 78 figs.

Pyron, R.A., Burbrink, F.T. & Wiens, J.J. (2013) A phylogeny and revised classification of Squamata, including 4161 species of lizards and snakes. *BMC Evolutionary Biology*, 13, 93.
https://doi.org/10.1186/1471-2148-13-93

Rambaut, A., Suchard, M.A., Xie, D., & Drummond, A.J. (2014) *Tracer. Version 1.6*. Available from: http://beast.bio.ed.ac.uk.Tracer (accessed 27 July 2014)

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

Sanyal, D.P. & Gayen, N.C. (2006) Reptilia. *In*: Alfred, J.R.B. (Ed.), *Fauna of Arunachal Pradesh. State Fauna Series 13. Part 1*. Zoological Survey of India, Kolkata, pp. 247–284.

Stamatakis, A., Ludwig, T. & Meier, H. (2005) RAxML-III: a fast program for maximum likelihood-based inference of large phylogenetic trees. *Bioinformatics*, 21, 456–463.
https://doi.org/10.1093/bioinformatics/bti191

Stamatakis, A., 2006. RAxML-VI-HPC: maximum likelihood-based phylogenetic analyses with thousands of taxa and mixed models. *Bioinformatics*, 22 (21), 2688–2690.
https://doi.org/10.1093/bioinformatics/btl446

Silvestro, D. & Michalak, I. (2012) raxmlGUI: a graphical front-end for RAxML. *Organisms Diversity and Evolution*, 12, 335–337.
https://doi.org/10.1007/s13127-011-0056-0

Smith, M.A. (1943) *The fauna of British India, Ceylon and Burma including the whole of the Indo-Chinese sub-region. Reptilia and Amphibia. Vol. III. Serpentes*. Taylor and Francis, London, xii + 583 pp.

Swofford, D.L. (2002) *PAUP*: phylogenetic analysis using parsimony (* and other methods)*. Sunderland, MA. [program]

Tamura, K., Peterson, D., Peterson, N., Stecher, G., Nei, M. & Kumar, S. (2011) MEGA 5: Molecular Evolutionary Genetics Analysis version 5.1. *Molecular Biology and Evolution*, 30, 2725–2729.
https://doi.org/10.1093/molbev/mst197

Theobald, W.T. (1868) Catalogue of Reptiles in the Museum of the Asiatic Society of Bengal. *Journal of Asiatic Society of Bengal*, 32, 45.

Thorley, J.L. & Wilkinson, M. (1999) Testing the phylogenetic stability of early tetrapods. *Journal of Theoretical Biology*, 200, 343–344.
https://doi.org/10.1006/jtbi.1999.0999

Thompson, J.D., Higgins, D.G. & Gibson, T.J. (1994) ClustalW: improving the sensitivity of progressive multiple sequence alignment through sequence weighting, position-specific gap penalties and weight matrix choice. *Nucleic Acids Research*, 22, 4673–4680.
https://doi.org/10.1093/nar/22.22.4673

Uetz, P., Freed, P. & Hošek, J. (2018) *The Reptile Database*. Available from: http://reptile-database.reptarium.cz (accessed 5 January 2018)

Wall, F. (1908) Notes on a collection of snakes from the Khasi Hills, Assam. *Journal of Bombay Natural History Society*, 18 (2), 312–337.

Wallach, V., Williams, K.L. & Boundy, J. (2014) *Snakes of the World: A catalogue of living and extinct Species*. CRC Press, Taylor & Francis Group, London, 1227 pp.
https://doi.org/10.1201/b16901

Wilkinson, M. (2006) Identifying stable reference taxa for phylogenetic nomenclature. *Zoologica Scripta*, 35, 109–112.
https://doi.org/10.1111/j.1463-6409.2005.00213.x

Ye, J., McGinnis, S. & Madden, T.L. (2006) BLAST: improvements for better sequence analysis. *Nucleic Acids Research*, 34, W6–W9.
https://doi.org/10.1093/nar/gkl164

Zachariah, A., Dinesh, K.P., Radhakrishnan, C., Kunhikrishnan, E., Palot, M.J. & Vishnudas, C.K. (2011) A new species of *Polypedates* Tschudi (Amphibia: Anura: Rhacophoridae) from southern Western Ghats, Kerala, India. *Biosystematica*, 5 (1), 49–53.

APPENDIX 1. GenBank accession and voucher details for gene sequences used in phylogenetic analysis of the 79 species dataset. The voucher specimens for the *Smithophis atemporalis* **gen. et. sp. nov.** and *S. bicolor* **comb. nov.** samples are BNHS 2366 and BNHS 2369, respectively.

	Species	Family (Subfamily)	*cytb*	*16s*	*nd4*	*cmos*	*rag1*
1	*Acrochordus javanicus*	Acrochordidae	_	AF512745	HM234055	HM234058	HM234061
2	*Agkistrodon contortrix*	Viperidae (Crotalinae)	EU483383	AF156566	AF156577	_	EU402833
3	*Ahaetulla pulverulenta*	Colubridae (Ahaetuliinae)	KC347454	KC347339	KC347512	KC347378	KC347416
4	*Anilius scytale*	Aniliidae	U69738	FJ755180	FJ755180	AF544722	AY988072
5	*Anomochilus leonardi*	Cylindrophiidae+ Anomochiliidae	_	AY953431	_	_	_
6	*Aparallactus capensis*	Lamprophiidae (Aparallactinae)	AY188006	AY188045	FJ404331	AY187967	_
7	*Aplopeltura boa*	Pareatidae	JF827673	AF544787	JF827650	JF827696	_
8	*Aspidura ceylonensis*	Colubridae (Natricinae)	KC347477	KC347361	KC347527	KC347400	KC347438
9	*Asthenodipsas malaccanus*	Pareatidae	KX660469	KX660197	KX660597	KX660336	_
10	*Azemiops feae*	Viperidae (Azemiopinae)	AY352747	AF057234	AY352808	AF544695	EU402836
11	*Bitis nasicornis*	Viperidae (Viperinae)	DQ305457	AY188048	DQ305475	AY187970	KC330012
12	*Boa constrictor*	Boidae	AB177354	AB177354	AB177354	AF544676	KC347423
13	*Boaedon fuliginosus*	Lamprophiidae (Lamprophiinae)	AF471060	AY188079	FJ404365	FJ404270	EU402849
14	*Bothrolycus ater*	Lamprophiidae (Lamprophiinae)	AY612041	AY611859	AY611950	FJ404347	_

......*continued on the next page*

APPENDIX 1. (Continued)

	Species	Family (Subfamily)	*cytb*	*16s*	*nd4*	*cmos*	*rag1*
15	*Brachyophidium rhodogaster*	Uropeltidae	_	AY701023	_	_	_
16	*Buhoma depressiceps*	Lamprophiidae *incertae sedis*	AY612042	AY611860	_	AY611951	_
17	*Buhoma procterae*	Lamprophiidae *incertae sedis*	AY612001	AY611818	DQ486328	AY611910	_
18	*Bungarus fasciatus*	Elapidae	EU579523	EU579523	EU579523	AY058924	_
19	*Calabaria reinhardtii*	Calabariidae	AY099985	Z46494	_	AF544682	EU402839
20	*Calamaria pavimentata*	Colubridae (Calamariinae)	AF471081	KX694624	_	AF471103	_
21	*Candoia carinata*	Candoiidae	AY099984	EU419850	_	AY099961	AY988065
22	*Cantoria violacea*	Homalopsidae	EF395897	KX694627	EF395922	_	_
23	*Casarea dussumieri*	Bolyeridae	U69755	AF544827	_	AF544731	EU402840
24	*Charina bottae*	Charinidae (Charininae)	AY099986	AF544816	AF302959	AY099971	AY988076
25	*Chilabothrus striatus*	Boidae	_	_	KC329966	KC329991	KC330027
26	*Contia tenuis*	Colubridae (Dipsadinae)	GU112384	AY577030	GU112419	AF471134	_
27	*Corallus annulatus*	Boidae	KC750012	_	KC750018	KC750007	KC750047
28	*Cylindrophis maculatus*	Cylindrophiidae+ Anomochiliidae	KC347460	KC347355	KC347494	KC347395	KC347433
29	*Cylindrophis ruffus*	Cylindrophiidae+ Anomochiliidae	AB179619	AB179619	AB179619	AF471133	AY988071
30	*Daboia russelii*	Viperidae (Viperinae)	EU913478	EU913478	EU913478	AF471156	EU402843
31	*Ditypophis sp.*	Lamprophiidae	_	_		_	JQ073200
32	*Epicrates cenchria*	Boidae	HQ399501	_	KC329975	KC330008	_
33	*Eryx colubrinus*	Erycidae	U69811	AF544819	_	AF544716	DQ465571
34	*Eryx conicus*	Erycidae	GQ225658	AF512743	GQ225672	_	AY988074
35	*Eunectes notaeus*	Boidae	HQ399499	AM236347	KC329978	HQ399536	HQ399516
36	*Farancia abacura*	Colubridae (Dipsadinae)	U69832	Z46491	U49307	AF471141	KR814740
37	*Gerrhophilus mirus*	Gerrhopiliidae	AM236345	AM236345	AM236345	_	_
38	*Grayia ornata*	Colubridae (Grayinae)	_	AF158503	AF544663	AF544684	_
39	*Grayia smythii*	Colubridae (Grayinae)	DQ112077	_	DQ112080	_	_
40	*Homoroselaps lacteus*	Lamprophiidae (Atractaspidinae)	AY611992	AY611809	FJ404338	AY611901	_
41	*Indotyphlops braminus*	Typhlopidae (Asiatyphlopinae II)	DQ343649	_	_	AF544717	_
42	*Liasis mackloti*	Pythonidae	U69839	EF545051	_	AF544726	_
43	*Liopholidophis sexlineatus*	Lamprophiidae (Pseudoxyrhophiinae)	DQ979985	AY188063	FJ404373	AY187985	_
44	*Liotyphlops albirostris*	Anomalepididae	AF544672	AF366762	_	AF544727	EU402853
45	*Loxocemus bicolor*	Loxocemidae	AY099993	AF544828	_	AY444035	_
46	*Madatyphlops andasibensis*	Typhlopidae (Madatyphlopinae)	_	_	_	_	JQ073249
47	*Malayopython reticulatus*	Pythonidae	U69860	EF545062	_	AF544675	EU624119
48	*Melanophidium punctatum*	Uropeltidae	_	AY701024	_	_	_

......*continued on the next page*

APPENDIX 1. (Continued)

	Species	Family (Subfamily)	*cytb*	*16s*	*nd4*	*cmos*	*rag1*
49	*Micrelaps bicoloratus*	Lamprophiidae *incertae sedis*	DQ486349	_	_	DQ486173	_
50	*Mimophis mahfalensis*	Lamprophiidae (Psammophiinae)	DQ486461	AY188070	_	AY187992	_
51	*Morelia viridis*	Pythonidae	EF545098	EF545048	_	_	_
52	*Naja kaouthia*	Elapidae	FR693728	GQ359757	EU624209	AY058938	EU402857
53	*Namibiana occidentalis*	Leptotyphlopidae (Leptotyphlopinae)	_	GQ469251	_	GQ469074	_
54	*Oligodon arnensis*	Colubridae (Colubrinae)	KC347464	KC347365	KC347504	KC347404	KC347442
55	*Opisthotropis cheni*	Colubridae (Natricinae)	GQ281779	_	JQ687416	JQ687441	_
56	*Oxyrhabdium leporinum*	Lamprophiidae *incertae sedis*	AF471029	_	_	DQ112081	_
57	*Oxyuranus scutellatus*	Elapidae	EU547051	EU547149	EF210827	EU546916	_
58	*Pareas carinatus*	Pareatidae	JF827677	AF544802	JF827653	JF827702	_
59	*Prosymna janii*	Lamprophiidae (Prosymninae)	FJ404319	FJ404222	FJ404389	FJ404293	_
60	*Pseudaspis cana*	Lamprophiidae (Pseudaspidinae)	AY612080	AY611898	DQ486319	DQ486167	_
61	*Pseudoxenodon karlschmidti*	Colubridae (Pseudoxenodontinae)	AF471080	JF697330	_	AF471102	_
62	*Python bivittatus*	Pythonidae	JX401131	KF010492	_	AF435016	_
63	*Rena humilis*	Leptotyphlopidae (Epictinae)	AY099991	AB079597	AB079597	AY099979	_
64	*Rhabdops aquaticus*	Colubridae (Natricinae)	MF352839	MF352832	MF352829	MF352836	_
65	*Rhabdops olivaceus*	Colubridae (Natricinae)	MF352842	MF352834	MF352831	MF352838	MF352843
66	*Rhinophis drummondhayi*	Uropeltidae	AF544673	AY701028	_	AF544719	_
67	*Sanzinia madagascariensis*	Sanziniidae	U69866	AY336066	_	EU403580	AY988067
68	*Sibynophis subpunctatus*	Colubridae (Sibynophiinae)	KC347471	KC347373	KC347516	KC347411	KC347449
69	*Smithophis atemporalis* **gen. nov. et sp. nov.**	Colubridae (Natricinae)	MK350262	MK350255	MK350258	MK350265	MK350257
70	*Smithophis bicolor* **comb. nov.**	Colubridae (Natricinae)	MK350261	MK350254	MK350259	MK350264	MK350256
71	*Trachischium monticola*	Colubridae (Natricinae)	JQ687435		JQ687428	JQ687453	
72	*Tropidophis feicki*	Tropidophiidae	KF811124	AF512733	_	KF811110	_
73	*Typhlops jamaicensis*	Typhlopidae (Typhlopinae)	KF993259	AF366764	_	AF544733	EU402866
74	*Typhlops vermicularis*	Typhlopidae (Asiatyphlopinae I)	JQ910544	_	_	_	_
75	*Ungaliophis continentalis*	Charinidae (Ungaliophiinae)	U69870	AF544833	_	AF544724	EU402867
76	*Xenodermus javanicus*	Xenodermatidae	_	AF544810	U49320	AF544711	EU402869
77	*Xenopeltis unicolor*	Xenopelitidae	AB179620	AB179620	AB179620	AF544689	DQ465564
78	*Xenophidion schaeferi*	Xenophidiidae	AY574279	_	_	_	_
79	*Xenotyphlops grandidieri*	Xenotyphlopidae	KF770844	_	_	_	_

APPENDIX 2. GenBank accession and voucher details for gene sequences used in phylogenetic analyses of the 55-species (Natricinae) dataset.

Species	*nd4*	*cmos*	*16s*	*cytb*	*rag1*
Adelophis foxi	KF258635	_	_	AF420069	_
Afronatrix anoscopus	_	AF471123	_	AF420073	_
Amphiesma stolatum	JQ687425	AF471097	_	AF471030	KJ685610
Aspidura ceylonensis	KC347527	KC347400	KC347361	KC347477	_
Aspidura drummondhayi	KC347519	KC347379	KC347340	KC347455	_
Aspidura guentheri	KC347507	KC347380	KC347341	KC347472	_
Aspidura trachyprocata	KC347523	KC347382	KC347343	KC347473	_
Atretium schistosum	KC347525	KC347383	_	KC347487	_
Atretium yunnanensis	JQ687423	JQ687448	_	GQ281787	_
Balanophis ceylonensis	KC347520	KC347384	KC347344	KC347474	_
Clonophis kirtlandii	KF258630	_	_	AF402908	_
Haldea striatula	KF258640	_	_	AF402933	_
Hebius boulengeri	_	KJ685634	_	KJ685684	_
Herpetoreas burbrinki	JQ687412	JQ687443	_	GQ281781	_
Hebius craspedogaster	_	KJ685653	_	KJ685703	_
Hebius optatum	_	KJ685637	_	KJ685687	_
Hebius venningi	_	KJ685650	_	KJ685700	_
Hebius vibakari	AB989304	KJ685626	_	KJ685676	_
Herpetoreas platyceps	_	KJ685640	_	KJ685690	_
Liodytes pygaea	KF258637	_	_	AF402920	_
Liodytes rigida	KF258642	AF471120	_	AF471052	
Lycognathophis seychellensis	_	FJ387220	_	_	_
Macropisthodon plumbicolor	_	MK350263	MK350253	MK350260	_
Macropisthodon rhodomelas	_	KX660399	KX660258	KX660528	_
Macropisthodon rudis	JQ687427	JQ687452	_	JQ687434	KJ685566
Natriciteres olivacea	_	AF471146	AF544801	AF471058	_
Natrix natrix	AY873710	AF471121	KJ12852	AY866544	_
Nerodia fasciata	KF258631	_	_	AY866529	_
Opisthotropis andersonii	_	_	_	KY594730	_
Opisthotropis cheni	JQ687416	JQ687441	_	GQ281779	_
Opisthotropis guangxiensis	JQ687422	JQ687447	_	GQ281776	_
Ophisthotropis kuatunensis	_	_	_	KY594745	_
Opisthotropis lateralis	JQ687420	JQ687445	_	GQ281782	_
Opisthotropis latouchii	JQ687421	JQ687446	_	GQ281783	_
Opisthotropis maculosa	_	_	_	KY594748	_
Opisthotropis maxwelli	_	_	_	KY594736	_
Opisthotropis shenzhenensis	_	_	_	KY594727	_
Rhabdophis nuchalis	JQ687413	JQ687438	_	GQ281786	_
Rhabdophis subminiatus	JQ687411	KF800918	AF544805	KF800928	KJ685598
Rhabdops aquaticus	MF352839	MF352832	MF352829	MF352836	_
Rhabdops olivaceus	MF352842	MF352834	MF352831	MF352838	MF352843

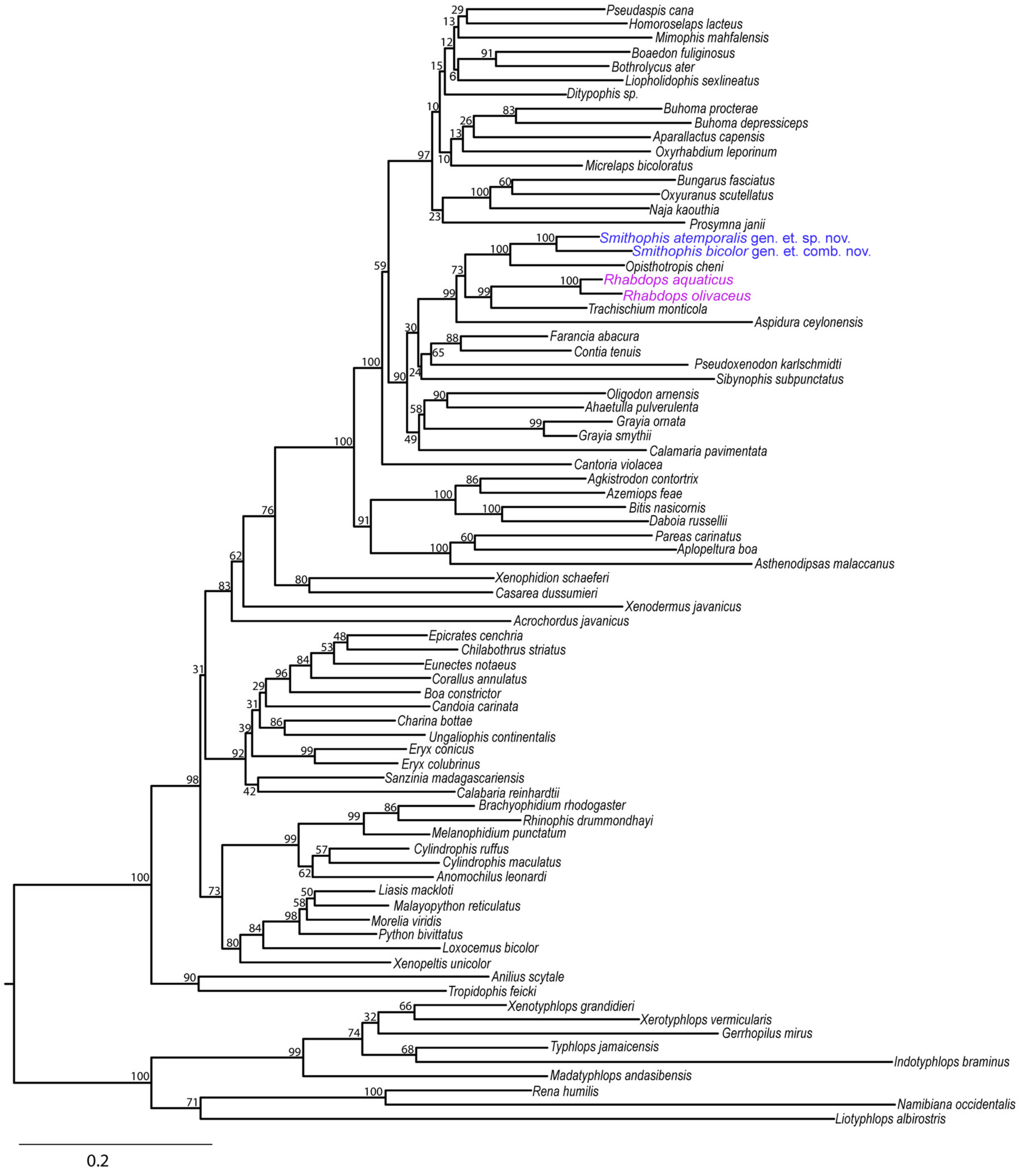
......continued on the next page

APPENDIX 2. (Continued)

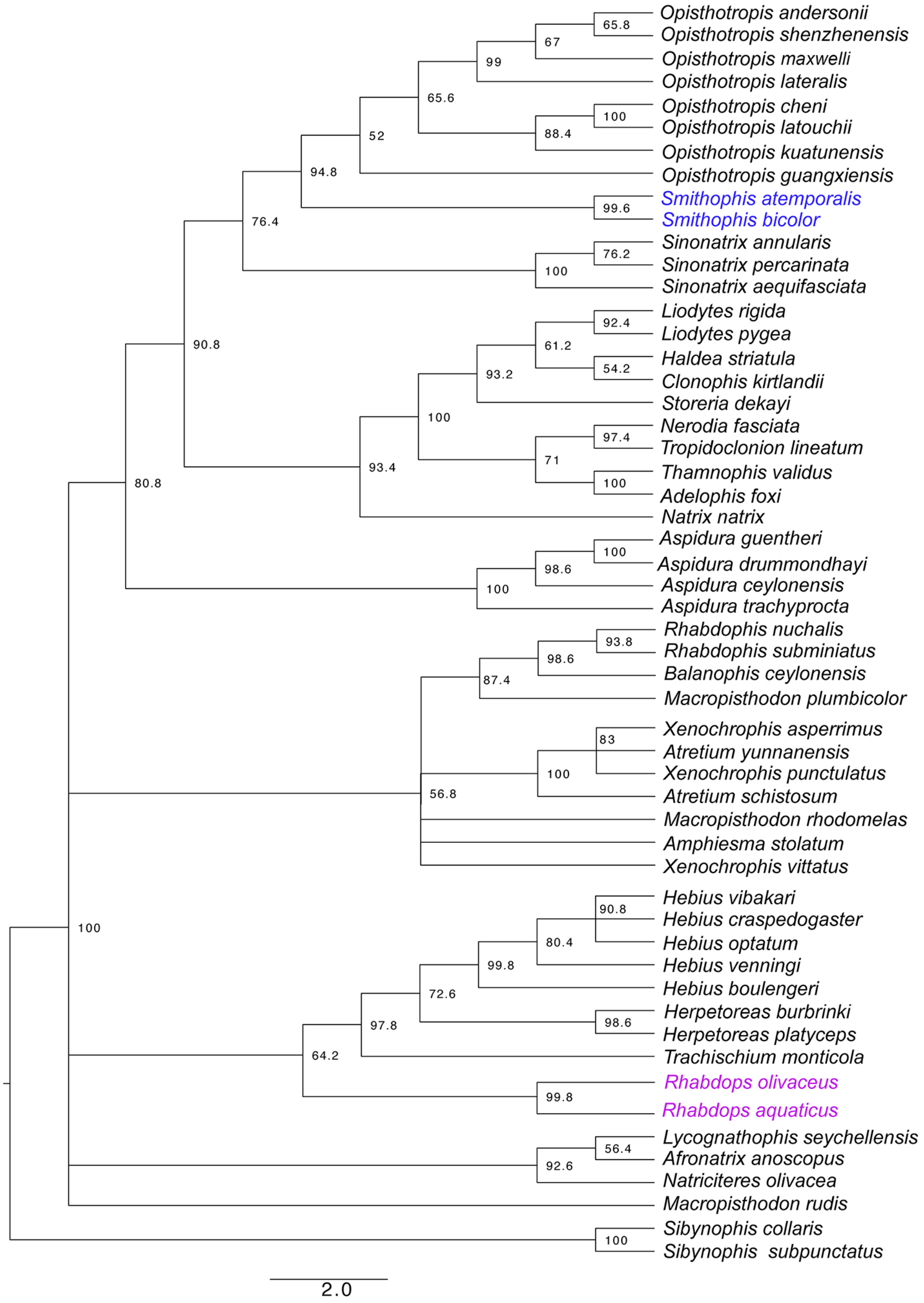
Species	*nd4*	*cmos*	*16s*	*cytb*	*rag1*
Sibynophis subpunctatus	KC347516	KC347411	KC347373	KC347471	_
Sibynophis collaris	NC_016424	_	NC_016424	NC_016424	_
Sinonatrix aequifasciata	JQ687415	JQ687440	_	JQ687430	_
Sinonatrix annularis	JQ687424	JQ687449	AF544807	JQ687431	_
Sinonatrix percarinata	JQ687426	JQ687451	_	JQ687433	_
Smithophis atemporalis **gen. et sp. nov.**	MK350258	MK350265	MK350255	MK350262	MK350257
Smithophis bicolor **comb. nov.**	MK350259	MK350264	MK350254	MK350261	MK350256
Storeria dekayi	EF417365	_	_	AF471050	_
Thamnophis validus	EF417361	_	_	EF417409	_
Trachischium monticola	JQ687428	JQ687453	_	JQ687435	_
Tropidoclonion lineatum	KF258638	_	_	AF402931	KJ685570
Xenochrophis asperrimus	_	KC347413	KC347376	KC347480	_
Xenochrophis punctulatus	AY487074	_	_	_	_
Xenochrophis vittatus	_	_	EF395846	EF395895	_

APPENDIX 3. Comparative material of *Smithophis bicolor* (Blyth, 1854) examined. * indicates holotype.

ZSIK 7030*, “Asám (northeast India: see Das *et al*. 1998: 146)
BNHS 2369, Aizawl, Mizoram, India
MZMU 857, Aizawl, Mizoram, India
BMNH 60.3.19.1270 (male), “Khasia hills [now in Meghalaya state, India]
BMNH 72.4.17.184 (female), “Khasia hills [now in Meghalaya state, India]
BMNH 1908.6.23.5 (female), “Shillong, Assam [now in Meghalaya state, India]
BMNH 1911.30.4 (male), “Shillong, Assam [now in Meghalaya state, India]
BNHS 1730 (two specimens), “Shillong, Assam [now in Meghalaya state, India]
BNHS 1731, “Shilling, Assam [now in Meghalaya state, India]
BNHS 1732, “Tura, Garo Hills [now in Meghalaya state, India]



APPENDIX 4. RaxML tree for 79 taxon dataset showing recovery of Smithophis spp. deeply nested within a well-supported, monophyletic Natricinae. Numbers at internal branches are bootstrap support values.



APPENDIX 5. 50% Majority Rule RaxML tree for 55 taxon dataset showing higher support for the monophyly of *Opisthotropis* and of *Opisthotropis*+*Smithophis* following pruning of the unstable, rogue *O. maculosa* from the ML bootstrap trees (compare with Fig. 1). Numbers at internal branches are bootstrap support values.