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Trimeresurus arunachalensis sp. nov.

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A NEW SPECIES OF PITVIPER (SERPENTES: VIPERIDAE: *Trimeresurus* LACEPÈDE, 1804) FROM WEST KAMENG DISTRICT, ARUNACHAL PRADESH, INDIA

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A new species of pitviper, *Trimeresurus arunachalensis* sp. nov., is described based on a single specimen. It differs from all known congeners by the following combination of characters — 19:17:15 acutely keeled dorsal scale rows (except first row — keeled or smooth); overall reddish-brown coloration; white dorsolateral stripe on outer posterior edges of ventrals and sometimes first dorsal scale row; 7 supralabials; 6 – 7 scales between supraoculars; 145 ventrals; 51 paired subcaudals (excluding the terminal scale); single anal; a sharply defined canthus rostralis with the margin overhanging the loreal region; a distinctly concave rostral scale with the upper edge projecting well beyond its lower margin; an unforked, attenuate hemipenis that extends to the 8th subcaudal scale, and has no visible spines. DNA phylogenetic analysis indicates that the new species is distinct from congeners and nested well within the *Trimeresurus* clade. The closest relative based on available DNA data is *T. tibetanus*. The new species is presently known from a single locality — Ramda, West Kameng, Arunachal Pradesh, northeastern India.

Keywords: Crotalinae; snake; taxonomy; *Trimeresurus arunachalensis* sp. nov.; viper.

INTRODUCTION

Of the eight genera of pitvipers found in Asia (*Calloselasma* Cope, 1860; *Deinagkistrodon* Gloyd, 1979; *Gloydius* Hoge et Romano-Hoge, 1981; *Hypnale* Fitzinger, 1843; *Ovophis* Burger in Hoge et Romano-Hoge, 1981; *Tropidolaemus* Wagler, 1830; *Protobothrops* Hoge et Romano-Hoge, 1983 and *Trimeresurus* Lacepède,

1804) comprising more than 90 species in total, *Trimeresurus* is the most diverse group with 50 known species distributed across south and south-east Asia (e.g., Uetz et al., 2018). Notable new descriptions from the Indo-Chinese region include *Trimeresurus tibetanus* Huang, 1982; *Protobothrops maolanensis* Yang et al., 2011 and *Protobothrops himalayanus* Pan et al., 2013. Although China and Nepal have been extensively surveyed for snakes since the early part of the 21st Century (Zhao and Adler, 1993; Schleich and Kästle, 2002), north-eastern India has more or less remained neglected. The region has yielded several new species descriptions over the last two decades including herpetofauna, birds and mammals (Gumprecht et al., 2004; Slowinski et al., 2001; Sinha et al., 2005; Athreya, 2006; Sondhi and Ohler, 2011).

During an ongoing biodiversity survey in Arunachal Pradesh, India being conducted by our team, a brown pitviper visually distinct from the other brown pitvipers of the region (*Ovophis monticola* and *Protobothrops mucrosquamatus*) was encountered in West Kameng district. Closer examination showed that it was a hitherto undescribed species. We here describe this specimen and assign it to a new taxon. The specimen is referable to the family Viperidae on the basis of its folding fangs and to

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the genus *Trimeresurus* due to the presence of loreal pits and its phylogenetic relationship based on DNA sequence data. It can be distinguished from sympatric members of the *Trimeresurus* species complex by a combination of scalation, color pattern, distinctive hemipenes; and DNA sequence data.

MATERIAL AND METHODS

Specimen preservation and morphology. The snake was euthanized using chloroform. After euthanizing, muscle tissue samples were stored in absolute ethanol at -20°C for DNA analyses. Then, the digestive system was removed and the specimen fixed in 10% formalin for 48 h. After two changes of water over two days the specimen was transferred to 70% ethyl alcohol, which was changed thrice. Scalation data were recorded after preservation. We made morphometric measurements using ‘Aerospace’ digital callipers. A mean of five readings was taken for each trait. Snout-vent length was recorded using a non-stretchable twine along the mid-vertebral line from snout-tip to the posterior edge of the anal scale. The length of the twine was measured to the nearest millimeter using a steel tape measure. The tail was measured directly against an etched, acrylic ruler. One hemipenis was everted from the formalin preserved specimen. The right hemipenis was detached from the body by cutting the retractor muscle at the 9th subcaudal and by making an incision along its circumference in the cloacal region. It was everted by gently pushing the organ from the distal to the proximal end with the help of fine, rounded-end forceps, and a dental flossing pick, while also being periodically softened in warm water (50°C). After eversion, the organ was inflated using petroleum jelly and dipped in a low concentration solution of alizarin red in 70% ethanol for 6 hours. DNA PCR amplification and Sanger sequencing used previously reported primers.

Molecular techniques and phylogeny. Genomic DNA was extracted from the stored muscle tissue sample using the DNeasy (Qiagen™) Blood and Tissue Kit. We amplified partial sequences of two mitochondrial (mt) genes, cytochrome b (*cytb* primers: *GluDG* and H16064 described in Palumbi, 1996; Burbrink et al., 2000) and 16S rRNA (*16s* primers: 16Sar-L and 16Sbr-H described in Palumbi, 1991). PCR amplifications were carried out in 26 µl aliquots containing 2.5 µl of 1X Taq buffer, 2.5 µl of 2.5 mM dNTP, 2.5 µl of 2.5 mM of MgCl₂, 0.25 µl each of the forward and reverse primers, 0.33 µl of 2 units of Taq DNA polymerase, 1 µl of extracted DNA of the sample and 16.67 µl of PCR grade H₂O. We used S1000 TM Thermal Cycler (Bio-Rad, [USA]) to run the PCR. The PCR conditions are as follows: initial denaturation at 94°C for 50 sec; denaturation for 35 cy-

cles at 94°C for 50 sec; annealing (at 45°C for 16s and 53°C for *cytb* and extension at 72°C for 40 sec. The final extension was at 4°C for 30 min. Amplified PCR products were run on 2% agarose gel, viewed in an Essential V4 (UVITEC Cambridge, [UK]) gel documentation system, and purified using a QIAquick PCR Purification Kit (Qiagen®, [Germany]). PCR products were Sanger sequenced for the forward and reverse strand at Medauxin Sequencing Services (Bangalore, India). Sequence chromatograms were checked and edited using the program Chromas LITE ver. 2.1.1.

The two sequences generated in this study have been submitted to NCBI GenBank (Table 1). We assembled a dataset of *cytb* and *16s* data for 48 species for comparison and phylogenetic analysis, including 35 of the 50 known *Trimeresurus* species (Table 1; Uetz et al. 2018), other viperids from the GenBank. Sequences of Pareids (Figueroa et al., 2016) were used as an outgroup to root the tree.

The sequences were aligned using ClustalW (default settings) (Thompson et al., 1994), and the *cytb* alignment was checked to confirm the absence of unexpected stop codons that might indicate amplification of pseudogenes in MEGA v5 (Tamura et al., 2011). Uncorrected p-distances were calculated using MEGA ver. 5 (Tamura et al., 2011). PartitionFinder ver. 1.1.1 (Lanfear et al., 2012) was used (default MrBayes settings) to find the best-fit partition scheme for the concatenated data set and the optimal model of sequence evolution for each partition. The best-fit scheme comprised three partitions viz. (1) GTR + I + G: *16s* + *cytb* 1st, (2) HKY + I + G: *cytb* 2nd, and (3) GTR + G: *cytb* 3rd. We estimated phylogenetic relationships using Maximum likelihood (ML) (Felsenstein, 1981) and Bayesian inference (BI) (Huelsenbeck and Ronquist, 2001) methods as implemented in RaxML v1.3. 1 (Stamatakis et al., 2005) and MrBayes v3.2 (Ronquist et al., 2012), respectively. ML analysis in RaxML 1.3. 1 accepts only one model (GTR) of sequence evolution, and PartitionFinder suggested Gamma (G) correction for all the partitions, therefore, we used GTR + G. We employed the ML + rapid bootstrap method in the Graphical User Interface (GUI) version of RAxML (Silvestro and Michalak, 2012) to search for the best trees, with branch support quantified via 1000 non-parametric bootstrap replicates. The BI analysis used four Markov chains initiated from random trees and run for 10 million generations sampling every 100 generations. When the BI analysis was terminated, the standard deviation of split frequencies was less than 0.005, the first 25% trees were discarded as “burn-in,” and trees were constructed under 50% majority consensus rule. Convergence for all parameters was confirmed using Tracer v1.6

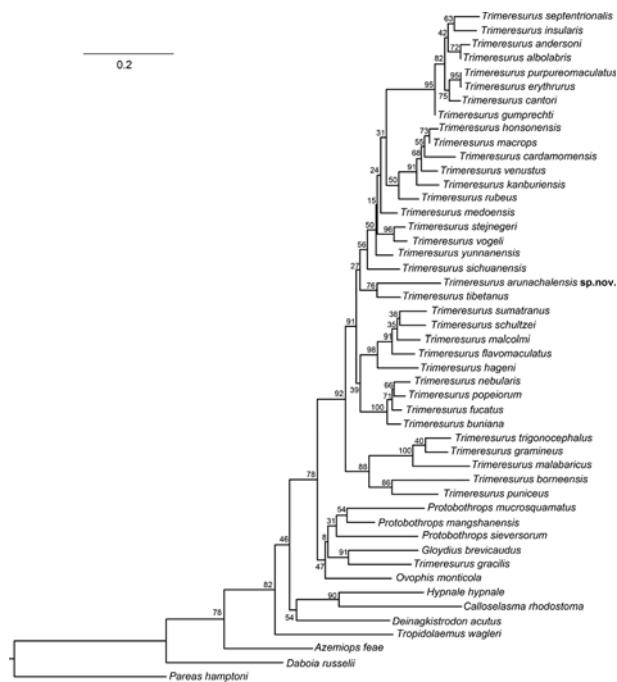


Fig. 1. Maximum likelihood tree showing inferred phylogenetic relationships of *Trimeresurus arunachalensis* sp. nov. Numbers at internal branches represent bootstrap support. Scale bar indicates substitutions per site.

(Rambaut et al., 2014). Support for clades in the BI tree was quantified using posterior probabilities.

RESULTS

Phylogenetic relationship. The ML and BI phylogenetic trees are shown in Figs. 1 and 2, respectively. All species in the genus *Trimeresurus* except *T. gracilis* formed a well-supported monophyletic clade. Though ML phylogeny showed moderate support, Bayesian analyses yielded a well-supported sister relationship between our specimen from Arunachal Pradesh and *T. tibetanus*. These two species are nested within the *Trimeresurus* clade. Therefore, we assign our specimen to a new species of *Trimeresurus*.

SYSTEMATICS

Arunachal pitviper

Trimeresurus arunachalensis sp. nov. (Fig. 3)

Holotype. APF/SFRI-1871, male. Deposited in the collection of the State Forest Research Institute, Van Vihar, Itanagar, Arunachal Pradesh, India; collected from near Ramda, West Kameng, Arunachal Pradesh, north-eastern India ($27^{\circ}15' N$ $92^{\circ}46' E$; 1876 m elevation) by

TABLE 1. Dataset of 16s and cytb DNA Sequences (with GenBank accession codes) for 48 Snake Species, Including 35 of the 50 Currently Recognized *Trimeresurus* Species (including *T. arunachalensis* sp. nov.), Other Viperids, and the Outgroup Pareids

Taxa	16s	cytb
1 <i>Azemiops feae</i>	AY352713.1	KF997881.1
2 <i>Calloselasma rhodostoma</i>	AY352718.1	AY223562.1
3 <i>Daboia russelii</i>	AY352712.1	AF471076.1
4 <i>Deinagkistrodon acutus</i>	AY352716.1	KX694847.1
5 <i>Gloydius brevicaudus</i>	AY352720.1	JX661198.1
6 <i>Hypnale hypnale</i>	AY352717.1	AY352750.1
7 <i>Ovophis monticola</i>	AY059561.1	HQ325127.1
8 <i>Pareas hamptoni</i>	KX694656.1	KJ642150.1
9 <i>Protobothrops (Zhaoermia) mangshanensis</i>	AY352726.1	HM567537.1
10 <i>Protobothrops mucrosquamatus</i>	AY294271.1	KT220318.1
11 <i>Protobothrops sieversorum</i>	AY352721.1	KT220320.1
12 <i>Trimeresurus albolabris</i>	AY059560.1	AY352770.1
13 <i>Trimeresurus andersoni</i>	AY352740.1	—
14 <i>Trimeresurus arunachalensis</i>	MK722155	MK720609
15 <i>Trimeresurus borneensis</i>	AY352722.1	AY352754.1
16 <i>Trimeresurus buniana</i>	KX660234.1	KX660503.1
17 <i>Trimeresurus cantori</i>	AY352741.1	AF171899.1
18 <i>Trimeresurus cardamomensis</i>	KR021138.1	—
19 <i>Trimeresurus erythrurus</i>	AY352739.1	AF171900.1
20 <i>Trimeresurus flavomaculatus</i>	AY059551.1	AY352764.1
21 <i>Trimeresurus fucatus</i>	KX660235.1	KX660505.1
22 <i>Trimeresurus gracilis</i>	AY352728.1	AF171913.1
23 <i>Trimeresurus gramineus</i>	AY352732.1	AY352762.1
24 <i>Trimeresurus gumprechtii</i>	AY352736.1	AY059566.1
25 <i>Trimeresurus puniceus</i>	AY059552.1	AY059567.1
26 <i>Trimeresurus honsonensis</i>	KX660221.1	—
27 <i>Trimeresurus insularis</i>	AY059550.1	AY059568.1
28 <i>Trimeresurus kanburiensis</i>	AY352737.1	AY289225.1
29 <i>Trimeresurus macrops</i>	AF517176.1	KP999371.1
30 <i>Trimeresurus malabaricus</i>	AY059564.1	AY059569.1
31 <i>Trimeresurus malcolmi</i>	AY371793.1	AY371832.1
32 <i>Trimeresurus medoensis</i>	AY352735.1	AY352765.1
33 <i>Trimeresurus nebulosus</i>	KX660236.1	KX660506.1
34 <i>Trimeresurus popeiorum</i>	AY059558.1	AY059571.1
35 <i>Trimeresurus puniceus</i>	AF517177.1	AY352757.1
36 <i>Trimeresurus purpureomaculatus</i>	AY352746.1	AY352772.1
37 <i>Trimeresurus rubeus</i>	KR021140.1	—
38 <i>Trimeresurus schultzei</i>	AY352725.1	AY352756.1
39 <i>Trimeresurus septentrionalis</i>	AY059559.1	AY352755.1
40 <i>Trimeresurus sichuanensis</i>	HQ850446.1	HQ850448.1
41 <i>Trimeresurus stejnegeri</i>	AY059562.1	AF171903.1
42 <i>Trimeresurus sumatranus</i>	AY371792.1	AY371824.1
43 <i>Trimeresurus tibetanus</i>	AY352715.1	AY352749.1
44 <i>Trimeresurus trigonocephalus</i>	AY059565.1	KC347479.1
45 <i>Trimeresurus venustus</i>	AY352723.1	AF171914.1
46 <i>Trimeresurus vogeli</i>	AF517183.1	AY059574.1
47 <i>Trimeresurus yunnanensis</i>	EU443812.1	EF597522.1
48 <i>Tropidolaemus wagleri</i>	AF517180.1	GQ428472.1

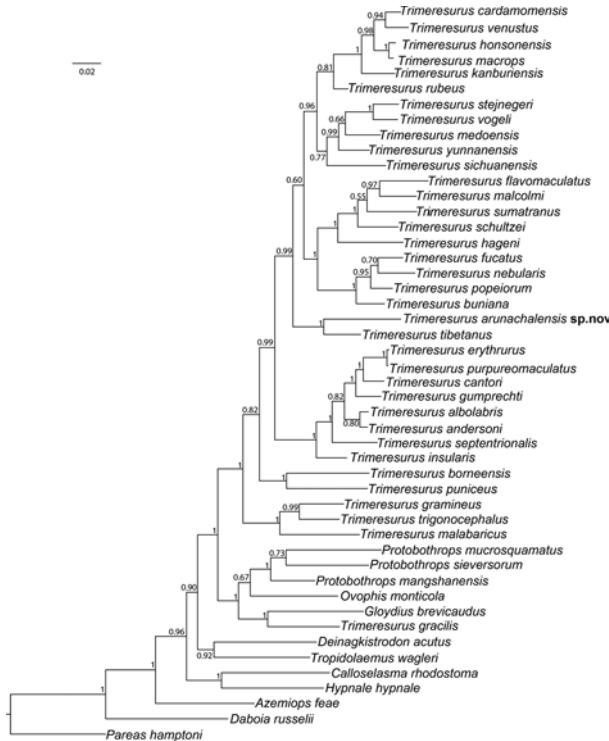


Fig. 2. Bayesian inference tree showing inferred phylogenetic relationships of *Trimeresurus arunachalensis* sp. nov. with *Trimeresurus* spp. and other viperids. Numbers at internal branches represent Bayesian posterior probability. Scale bar indicates substitutions per site.

Wangchu Phiang and Rohan Pandit under permit CWL/G/13(95)/2011-12/Pt.V/1596-607 issued by the Chief Wildlife Warden, Government of Arunachal Pradesh, India.

Diagnosis. *Trimeresurus arunachalensis* sp. nov. differs from all mainland Asian pitvipers of northeastern India and adjacent China except *T. medoensis* (i.e., from *Ovophis monticola*, *Protobothrops himalayanus*, *P. jerdonii*, *P. kaulbacki*, *P. mucrosquamatus*, *Trimeresurus albolabris*, *T. erythrurus*, *T. gumprechtii*, *T. popeiorum*, *T. stejnegeri*, *T. tibetanus*, and *T. vogeli*) in having 17 dorsal scale rows at midbody.

Trimeresurus arunachalensis sp. nov. can be distinguished from *T. medoensis* by its distinctive hemipenis — unforked, slender, attenuate and with no spines visible to the naked eye (vs forked, spinose hemipenis with large spines); by its scales being acutely keeled (vs obtuse keels which are like ‘loose folds of skin’ — David et al., 2001); by its overall coloration being reddish-brown (vs. green); by having a white lateral stripe on the outer posterior edges of ventrals or sometimes the first dorsal scale row (vs. lateral stripe — red below, white above on first dorsal scale row); and by a reddish-brown

eye (vs. green). *Trimeresurus arunachalensis*, though phylogenetically very close to *T. tibetanus*, differs from it morphologically in having midbody scales in 17 longitudinal rows (vs. 21, 19, or 20) and an unforked hemipenis with no spines visible to the naked eye (vs. forked, with large spines).

Description of the holotype. In life, a reddish-brown, slender-bodied pitviper; upon preservation, though the reddish tinge has faded, it is still visible (Fig. 3).

Head distinctly broader than neck. Pupil vertical. Snout broadly rounded when viewed from above. Tail is 0.17 of total body length. Dorsal body scales acutely keeled. Only some of the scales in the first dorsal row at midbody faintly keeled.

Scales on dorsal surface of head smooth, not imbricate; scales of the temporal region with small knob-like protuberances arranged in a line towards the posterior edges of the scales. Dorsal scales on head, body and tail dull, not glossy. Ventrals, subcaudals and rostral glossy. Ventrals though visible on sides of body, are not angulate laterally. A white ventro-lateral line starts immediately behind the head and ends 13 scales before the terminal scale; it is well-defined on the fore-body till the 45th ventral after which it becomes irregular. Top of head uniform brown, the same shade as the ground color of the body. Dorsum with blotches of various shades of brown, with irregular dark margins, alternating and zig-zagging along the entire length. Blotches more distinct dorsally, fading towards lateral edges of body. Venter glossy reddish-brown. Ventrals pale creamish-brown and heavily mottled with dark reddish-brown; so much so, that the latter predominates and appears to be the ground color of the venter. Gular region scales similar but with more pronounced mottling. Subcaudals proximal to anal are dark brown while the last 13 and terminal scale are pale cream. The specimen has a mid-ventral cut from the 70th to the 129th ventral. Hemipenis: unforked, slender, attenuate and with no spines visible to the naked eye (Fig. 3), extends to the 8th caudal shield. To remove the hemipenis we made a mid-ventral incision from the subcaudal adjacent to the anal to the 13th subcaudal.

Measurements. Snout-vent length: 548 mm; tail: 110 mm; head length: 29 mm; head width: 20 mm; eye diameter: 4.0 mm; snout tip to anterior border of ocular (left): 9.4 mm; snout tip to anterior border of ocular (right): 9.6 mm; snout tip to anterior border of left pit: 7.0 mm; snout tip to anterior border of right pit: 7.1 mm; snout tip to left nare: 3.1 mm; snout tip to right nare: 3.2 mm; distance between supraoculars: 6.6 mm.

Scalation. Dorsal scales in 19:17:15 rows, acutely keeled at midbody, except the first row which has faint keels. Ventrals 145; subcaudals 51 (excluding terminal

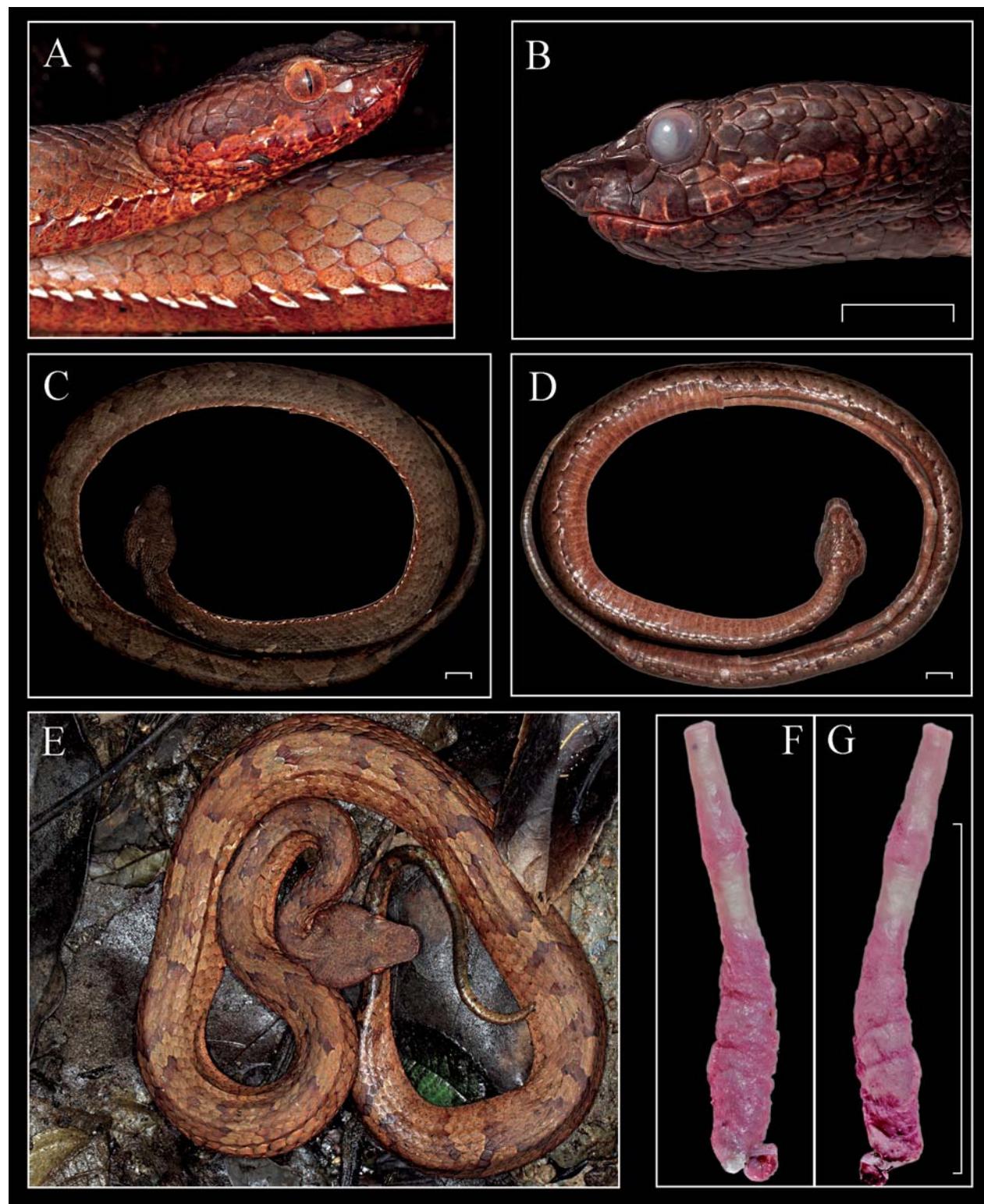


Fig. 3. Holotype of *Trimeresurus arunachalensis* sp. nov. (APF/SFRI-1871, TBL 658 mm): A, right lateral view of head and forebody in life, note white lateral stripe on outer edges of ventrals; B, Left lateral view of head after preservation, note sharply defined canthus rostralis overhanging the loreal region; C, Dorsal view after preservation; D, Ventral view after preservation; E, Dorsal view in life; F and G, Dorsal and ventral views of right hemipenis; note it is unpaired, attenuate and without large spines. Scale bars are 10 mm.

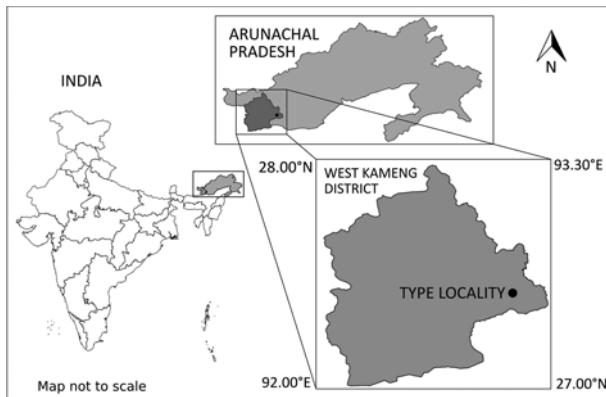


Fig. 4. Map of West Kameng, Arunachal Pradesh, India showing the type (and only currently known) locality of *Trimeresurus arunachalensis* sp. nov. (solid black dot).

scale); anal single. Nostril in an undivided nasal; supralabials 7, 1st completely separated from nasal, 2nd forms anterior border of pit and could be called a lacunal, 3rd largest and separated from eye by a postocular that curves below the eye and could well be termed a postsubocular. Preoculars 3, the middle and lowermost form the posterior border of the pit. Two squarish loreal scales, the upper larger than the lower; these scales are bordered anteriorly by the nasal, below by the 1st supralabial; behind by the 2nd supralabial/lacunal and above by scales of the canthus rostralis. The canthus ridge extends from the upper margin of the nasal, continues onto the lower edge of the scale immediately behind it and runs along the entire length of the lower margin of the middle preocular. Scales between supraoculars 6. Infralabials 8; anterior genials smaller than posterior.

The DNA sequence data provide strong supporting evidence that *Trimeresurus arunachalensis* sp. nov. is indeed a distinct species. Both ML and BI trees suggest that the closest sister species of *T. arunachalensis* sp. nov. is *T. tibetanus*. The uncorrected p-distance between *T. arunachalensis* sp. nov. and *T. tibetanus* are 2% for 16s and 9% for cytb. *Trimeresurus arunachalensis* sp. nov. has an uncorrected p-distance from *T. medoensis* (which has the same number of dorsal scale rows at midbody) of 3% for 16s and 11% for cytb. The lowest uncorrected p-distance between any two *Trimeresurus* species in the analysed data set are 0% for 16s (*T. purpureomaculatus* and *T. erythrurus*) and 0.2% for cytb (*T. purpureomaculatus* and *T. erythrurus*), and the highest are 7% for 16s (*T. trigonoccephalus* and *T. hageni*) and 21% for cytb (*T. hageni* and *T. gramineus*) (Appendix 1 and 2).

Etymology. Named after Arunachal Pradesh, India, a state that has yielded many notable herpetological discoveries. The type and only known locality is in Aruna-

chal Pradesh, India. This is the first snake to be named after the state.

Suggested common name: Arunachal pitviper (English).

Distribution and natural history. As of now, known from a single locality 27°15' N 92°46' E; 1876 m (nearest settlement Ramda) in West Kameng district, Arunachal Pradesh, northeastern India (Fig. 4). The holotype of *Trimeresurus arunachalensis* sp. nov. was found on the forest floor during the day. The snake was well camouflaged in leaf litter on a very steep slope and was detected only because it moved. When disturbed, it formed a flat coil with the head angled upwards.

DISCUSSION

Though preferable to describe a new species based on a series of individuals, there have been cases where species that are clearly taxonomically unique have been described based on a single specimen, including snakes such as *Oligodon erythrorhachis* Wall, 1910, *O. nikhili* Whitaker et Dattatri, 1983, and *Bitis harenna* Gower et al., 2016.

The sister relationship between *T. tibetanus* and *T. arunachalensis* sp. nov. is noteworthy because the former is known only from the western Himalayas, while the latter, described here, is from the eastern Himalayas. The analysis of Malhotra and Thorpe (2004) recovered *T. tibetanus* as sister to *T. popeiorum* with reasonable support (BI probability of 0.93), but this relationship was not recovered by Figueroa et al. (2016) who instead show that *T. tibetanus* was sister to 32 other *Trimeresurus* species including *T. popeiorum*. In our phylogenies *T. tibetanus* together with *T. arunachalensis* sp. nov. is sister to 19 other *Trimeresurus* excluding *T. popeiorum* which is recovered in a sister clade instead. The relationship between *T. tibetanus* and *T. popeiorum* in our analyses is similar to that recovered by Figueroa et al. (2016); and in our phylogenies *T. arunachalensis* sp. nov. is well separated from *T. popeiorum*. We emphasise that our objective in carrying out the DNA phylogeny was not to construct a fully resolved, robust tree but primarily to help establish the generic assignment of the new species and test its distinctiveness from congeners.

Trimeresurus arunachalensis sp. nov. is unique in the *Trimeresurus* group in having an unforked hemipenis with no spines visible to the naked eye. Given that *T. arunachalensis* sp. nov. and *T. tibetanus* are phylogenetically very close and have extremely different hemipenes, differences in hemipenes may not always reflect taxonomic relatedness within a genus.

The addition of *Trimeresurus arunachalensis* sp. nov. to the Indian snake fauna brings the number of pitvipers

APPENDIX 1. Uncorrected Pairwise Genetic Distances for the Samples Used in This Study for the *16s* Gene

No.	Species	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16
1	<i>Trimeresurus albolabris</i>	—															
2	<i>Trimeresurus andersoni</i>	0.003	—														
3	<i>Trimeresurus arunachalensis</i> sp. nov.	0.039	0.042	—													
4	<i>Trimeresurus borneensis</i>	0.045	0.042	0.045	—												
5	<i>Trimeresurus bannana</i>	0.042	0.045	0.043	0.054	—											
6	<i>Trimeresurus cantori</i>	0.008	0.011	0.048	0.042	0.045	—										
7	<i>Trimeresurus cardamomensis</i>	0.028	0.025	0.048	0.039	0.051	0.025	—									
8	<i>Trimeresurus erythrurus</i>	0.008	0.005	0.048	0.042	0.045	0.005	0.025	—								
9	<i>Trimeresurus flavomaculatus</i>	0.036	0.039	0.028	0.033	0.042	0.039	0.039	0.045	—							
10	<i>Trimeresurus fuscatus</i>	0.034	0.036	0.034	0.045	0.014	0.036	0.042	0.036	0.034	—						
11	<i>Trimeresurus gracilis</i>	0.037	0.034	0.043	0.036	0.054	0.045	0.049	0.039	0.043	0.045	—					
12	<i>Trimeresurus gramineus</i>	0.039	0.037	0.046	0.051	0.061	0.048	0.043	0.042	0.051	0.057	0.043	—				
13	<i>Trimeresurus gumprechtii</i>	0.022	0.025	0.028	0.033	0.031	0.019	0.025	0.019	0.025	0.022	0.037	0.046	—			
14	<i>Trimeresurus hageni</i>	0.054	0.056	0.039	0.051	0.060	0.056	0.057	0.062	0.028	0.051	0.060	0.063	0.042	—		
15	<i>Trimeresurus honsonensis</i>	0.033	0.036	0.039	0.045	0.045	0.031	0.014	0.036	0.040	0.055	0.051	0.022	0.054	—		
16	<i>Trimeresurus insularis</i>	0.011	0.014	0.039	0.051	0.042	0.014	0.036	0.014	0.036	0.034	0.042	0.045	0.016	0.048	0.039	—
17	<i>Trimeresurus kanburiensis</i>	0.028	0.031	0.034	0.033	0.037	0.025	0.019	0.031	0.025	0.028	0.042	0.040	0.011	0.042	0.017	0.028
18	<i>Trimeresurus macrops</i>	0.031	0.033	0.036	0.042	0.045	0.028	0.011	0.033	0.033	0.037	0.051	0.048	0.019	0.051	0.003	0.036
19	<i>Trimeresurus malabaricus</i>	0.031	0.028	0.042	0.042	0.057	0.039	0.036	0.034	0.048	0.048	0.040	0.017	0.042	0.060	0.048	0.042
20	<i>Trimeresurus maccolimi</i>	0.033	0.036	0.025	0.036	0.045	0.036	0.036	0.042	0.008	0.036	0.040	0.043	0.022	0.025	0.034	0.033
21	<i>Trimeresurus medoensis</i>	0.028	0.031	0.031	0.031	0.031	0.031	0.031	0.019	0.022	0.034	0.049	0.011	0.042	0.028	0.028	0.028
22	<i>Trimeresurus nebularis</i>	0.034	0.037	0.034	0.039	0.014	0.037	0.042	0.037	0.034	0.005	0.045	0.057	0.022	0.051	0.040	0.034
23	<i>Trimeresurus popeiorum</i>	0.034	0.037	0.034	0.045	0.014	0.037	0.042	0.037	0.034	0.005	0.045	0.057	0.022	0.051	0.040	0.034
24	<i>Trimeresurus puniceus</i>	0.034	0.031	0.034	0.033	0.048	0.042	0.037	0.037	0.039	0.039	0.037	0.037	0.028	0.057	0.045	0.034
25	<i>Trimeresurus purpureomaculatus</i>	0.008	0.005	0.048	0.042	0.045	0.005	0.025	0.000	0.045	0.036	0.039	0.042	0.019	0.062	0.036	0.014
26	<i>Trimeresurus rubens</i>	0.025	0.028	0.037	0.036	0.039	0.028	0.031	0.028	0.033	0.025	0.040	0.055	0.014	0.051	0.031	0.031
27	<i>Trimeresurus schultzei</i>	0.039	0.042	0.031	0.048	0.048	0.051	0.048	0.019	0.037	0.046	0.052	0.033	0.036	0.045	0.045	0.045
28	<i>Trimeresurus septentrionalis</i>	0.014	0.011	0.048	0.048	0.039	0.016	0.036	0.011	0.045	0.042	0.040	0.042	0.025	0.062	0.039	0.019
29	<i>Trimeresurus sichuanensis</i>	0.017	0.019	0.037	0.048	0.040	0.025	0.028	0.025	0.034	0.031	0.034	0.037	0.019	0.051	0.025	0.022
30	<i>Trimeresurus stejnegeri</i>	0.028	0.031	0.031	0.042	0.037	0.025	0.034	0.025	0.034	0.028	0.046	0.055	0.008	0.051	0.031	0.022
31	<i>Trimeresurus sumatrana</i>	0.045	0.048	0.031	0.048	0.051	0.042	0.048	0.014	0.036	0.051	0.054	0.028	0.031	0.045	0.039	—
32	<i>Trimeresurus tibetanus</i>	0.022	0.025	0.022	0.033	0.036	0.031	0.034	0.028	0.028	0.031	0.045	0.017	0.045	0.034	0.028	0.028
33	<i>Trimeresurus trigonocephalus</i>	0.034	0.031	0.051	0.045	0.048	0.043	0.040	0.037	0.051	0.045	0.043	0.028	0.039	0.069	0.051	0.040
34	<i>Trimeresurus venustus</i>	0.031	0.033	0.048	0.042	0.051	0.028	0.017	0.033	0.039	0.042	0.057	0.048	0.025	0.051	0.019	0.036
35	<i>Trimeresurus vogeli</i>	0.033	0.031	0.034	0.039	0.042	0.031	0.025	0.036	0.034	0.043	0.052	0.011	0.054	0.034	0.028	—
36	<i>Trimeresurus yunnanensis</i>	0.025	0.028	0.031	0.031	0.034	0.028	0.028	0.028	0.025	0.040	0.049	0.008	0.045	0.025	0.025	—
37	<i>Tropidolaemus wagleri</i>	0.079	0.082	0.073	0.058	0.089	0.082	0.085	0.070	0.079	0.070	0.073	0.076	0.083	0.089	0.082	—
38	<i>Azemias feae</i>	0.080	0.083	0.089	0.076	0.096	0.083	0.099	0.089	0.074	0.086	0.089	0.109	0.086	0.096	0.099	0.086
39	<i>Calloselasma rhodostoma</i>	0.082	0.079	0.098	0.082	0.089	0.073	0.076	0.073	0.088	0.095	0.095	0.105	0.073	0.095	0.089	0.073

APPENDIX 1 (continued)

No.	Species	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16
40	<i>Daboia russelii</i>	0.102	0.106	0.110	0.106	0.119	0.106	0.112	0.107	0.116	0.109	0.096	0.109	0.129	0.096	0.109	
41	<i>Deinagkistrodon acutus</i>	0.077	0.074	0.075	0.045	0.081	0.074	0.078	0.074	0.057	0.075	0.066	0.082	0.065	0.063	0.084	0.077
42	<i>Gloydius brevicaudus</i>	0.037	0.040	0.046	0.048	0.063	0.046	0.061	0.046	0.049	0.061	0.034	0.049	0.049	0.067	0.061	0.043
43	<i>Hypnale hypnale</i>	0.061	0.064	0.055	0.046	0.070	0.064	0.063	0.070	0.049	0.055	0.048	0.067	0.054	0.073	0.061	0.064
44	<i>Ovophis monticola</i>	0.063	0.066	0.058	0.057	0.057	0.066	0.070	0.066	0.055	0.054	0.057	0.064	0.049	0.070	0.067	0.063
45	<i>Pareas hamptoni</i>	0.119	0.116	0.120	0.106	0.143	0.122	0.126	0.122	0.113	0.126	0.116	0.129	0.119	0.123	0.130	0.125
46	<i>Protobothrops mangshanensis</i>	0.028	0.031	0.048	0.042	0.051	0.036	0.048	0.036	0.039	0.037	0.039	0.048	0.033	0.063	0.051	0.028
47	<i>Protobothrops mucrosquamatus</i>	0.045	0.048	0.051	0.042	0.057	0.042	0.046	0.048	0.048	0.043	0.048	0.057	0.037	0.066	0.049	0.045
48	<i>Protobothrops sieversorum</i>	0.054	0.057	0.057	0.037	0.067	0.051	0.054	0.057	0.051	0.051	0.054	0.069	0.045	0.075	0.052	0.057
No.	Species	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32
17	<i>Trimeresurus kanburiensis</i>	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
18	<i>Trimeresurus macrops</i>	0.014	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
19	<i>Trimeresurus malabaricus</i>	0.036	0.045	—	—	—	—	—	—	—	—	—	—	—	—	—	—
20	<i>Trimeresurus malcolmi</i>	0.022	0.031	0.039	—	—	—	—	—	—	—	—	—	—	—	—	—
21	<i>Trimeresurus medoensis</i>	0.017	0.025	0.045	0.022	—	—	—	—	—	—	—	—	—	—	—	—
22	<i>Trimeresurus nebularis</i>	0.028	0.037	0.048	0.037	0.022	0.005	—	—	—	—	—	—	—	—	—	—
23	<i>Trimeresurus popeiorum</i>	0.028	0.037	0.048	0.037	0.022	0.005	—	—	—	—	—	—	—	—	—	—
24	<i>Trimeresurus puniceus</i>	0.034	0.042	0.031	0.037	0.031	0.039	0.039	—	—	—	—	—	—	—	—	—
25	<i>Trimeresurus purpureomaculatus</i>	0.031	0.033	0.034	0.042	0.031	0.037	0.037	0.037	—	—	—	—	—	—	—	—
26	<i>Trimeresurus rubens</i>	0.019	0.028	0.045	0.031	0.019	0.031	0.031	0.037	0.028	0.028	—	—	—	—	—	—
27	<i>Trimeresurus schultzei</i>	0.039	0.048	0.039	0.016	0.033	0.042	0.042	0.042	0.048	0.048	0.048	0.048	0.031	0.045	—	—
28	<i>Trimeresurus septentrionalis</i>	0.036	0.039	0.039	0.042	0.036	0.042	0.042	0.042	0.042	0.042	0.042	0.042	0.042	0.042	0.036	—
29	<i>Trimeresurus sichuanensis</i>	0.019	0.022	0.037	0.031	0.019	0.031	0.031	0.037	0.025	0.028	0.042	0.042	0.025	—	—	—
30	<i>Trimeresurus stejnegeri</i>	0.019	0.028	0.048	0.031	0.019	0.028	0.028	0.031	0.025	0.022	0.042	0.031	0.022	—	—	—
31	<i>Trimeresurus sumatrana</i>	0.033	0.042	0.051	0.011	0.033	0.042	0.042	0.048	0.048	0.036	0.016	0.048	0.042	0.042	0.036	—
32	<i>Trimeresurus tibetanus</i>	0.022	0.031	0.036	0.025	0.019	0.028	0.028	0.028	0.031	0.019	0.031	0.031	0.025	0.025	0.036	—
33	<i>Trimeresurus trigonocephalus</i>	0.039	0.048	0.028	0.048	0.042	0.045	0.045	0.031	0.037	0.043	0.051	0.037	0.040	0.046	0.060	0.034
34	<i>Trimeresurus venustus</i>	0.019	0.017	0.045	0.036	0.031	0.042	0.042	0.042	0.033	0.034	0.054	0.045	0.028	0.034	0.048	0.036
35	<i>Trimeresurus vogeli</i>	0.022	0.031	0.048	0.033	0.022	0.034	0.034	0.028	0.025	0.025	0.045	0.031	0.031	0.031	0.039	0.028
36	<i>Trimeresurus yunnanensis</i>	0.014	0.022	0.045	0.025	0.014	0.019	0.025	0.031	0.028	0.017	0.036	0.034	0.022	0.017	0.036	0.019
37	<i>Tropidolaemus wagleri</i>	0.076	0.086	0.079	0.067	0.070	0.085	0.085	0.079	0.088	0.077	0.077	0.082	0.077	0.086	0.073	0.070
38	<i>Azemiops feae</i>	0.086	0.096	0.089	0.083	0.083	0.086	0.086	0.089	0.086	0.086	0.083	0.090	0.093	0.089	0.089	0.073
39	<i>Calloselasma rhodostoma</i>	0.079	0.086	0.092	0.088	0.076	0.089	0.086	0.073	0.079	0.101	0.086	0.092	0.080	0.095	0.085	—
40	<i>Daboia russelii</i>	0.097	0.097	0.092	0.107	0.107	0.117	0.117	0.116	0.112	0.116	0.122	0.109	0.097	0.113	0.119	0.109
41	<i>Deinagkistrodon acutus</i>	0.071	0.081	0.078	0.066	0.065	0.081	0.081	0.069	0.074	0.068	0.066	0.069	0.081	0.075	0.060	0.069
42	<i>Gloydius brevicaudus</i>	0.055	0.064	0.046	0.046	0.046	0.061	0.061	0.049	0.046	0.052	0.046	0.049	0.052	0.058	0.058	0.043
43	<i>Hypnale hypnale</i>	0.055	0.057	0.061	0.052	0.046	0.061	0.061	0.057	0.070	0.055	0.058	0.070	0.052	0.058	0.058	0.051
44	<i>Ovophis monticola</i>	0.049	0.064	0.064	0.058	0.043	0.054	0.054	0.067	0.066	0.058	0.070	0.072	0.058	0.058	0.070	0.048
45	<i>Pareas hamptoni</i>	0.119	0.126	0.119	0.107	0.122	0.129	0.133	0.122	0.116	0.113	0.122	0.119	0.115	0.113	0.112	—

APPENDIX 1 (continued)

No.	Species	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32
46	<i>Protobothrops mangshanensis</i>	0.039	0.048	0.045	0.042	0.031	0.042	0.042	0.031	0.036	0.037	0.048	0.042	0.034	0.040	0.048	0.036
47	<i>Protobothrops mucrosquamatus</i>	0.037	0.046	0.057	0.046	0.040	0.048	0.048	0.037	0.048	0.040	0.057	0.060	0.049	0.046	0.051	0.039
48	<i>Protobothrops stevensorum</i>	0.046	0.048	0.063	0.055	0.043	0.057	0.057	0.045	0.057	0.046	0.058	0.063	0.058	0.055	0.060	0.048
No.	Species	33	34	35	36	37	38	39	40	41	42	43	44	45	46	47	48
33	<i>Trimeresurus trigonocephalus</i>	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
34	<i>Trimeresurus venustus</i>	0.042	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
35	<i>Trimeresurus vogeli</i>	0.039	0.031	—	—	—	—	—	—	—	—	—	—	—	—	—	—
36	<i>Trimeresurus yumanensis</i>	0.043	0.022	0.019	—	—	—	—	—	—	—	—	—	—	—	—	—
37	<i>Tropidolaemus wagleri</i>	0.089	0.086	0.089	0.080	—	—	—	—	—	—	—	—	—	—	—	—
38	<i>Azemiops feei</i>	0.083	0.099	0.099	0.089	0.093	—	—	—	—	—	—	—	—	—	—	—
39	<i>Calloselasma rhodostoma</i>	0.089	0.082	0.073	0.079	0.115	0.126	—	—	—	—	—	—	—	—	—	—
40	<i>Daboia russelii</i>	0.116	0.106	0.120	0.113	0.103	0.099	0.135	—	—	—	—	—	—	—	—	—
41	<i>Deinagkistrodon acutus</i>	0.075	0.081	0.069	0.074	0.061	0.095	0.098	0.119	—	—	—	—	—	—	—	—
42	<i>Gloydius brevicaudus</i>	0.055	0.064	0.061	0.052	0.070	0.083	0.099	0.095	0.079	—	—	—	—	—	—	—
43	<i>Hypnale hypnale</i>	0.060	0.067	0.067	0.055	0.061	0.080	0.088	0.111	0.063	0.061	—	—	—	—	—	—
44	<i>Ophisophis monticola</i>	0.076	0.064	0.057	0.052	0.073	0.095	0.092	0.113	0.085	0.061	0.073	—	—	—	—	—
45	<i>Pareas hamponi</i>	0.126	0.129	0.123	0.112	0.131	0.127	0.151	0.130	0.110	0.126	0.117	0.143	—	—	—	—
46	<i>Protobothrops mangshanensis</i>	0.042	0.048	0.045	0.037	0.052	0.082	0.079	0.093	0.057	0.040	0.048	0.060	0.115	—	—	—
47	<i>Protobothrops mucrosquamatus</i>	0.054	0.046	0.049	0.040	0.067	0.085	0.092	0.102	0.066	0.048	0.058	0.054	0.105	0.031	—	—
48	<i>Protobothrops stevensorum</i>	0.063	0.061	0.058	0.049	0.058	0.074	0.089	0.096	0.060	0.058	0.040	0.067	0.120	0.034	0.037	—

APPENDIX 2. Uncorrected Pairwise Genetic Distances for the Samples Used in This Study for the *cytb* Gene

No.	Species	1	2	3	4	5	6	7	8	9	10	11	12	13	14
1	<i>Trimeresurus albolabris</i>	—	—	—	—	—	—	—	—	—	—	—	—	—	—
2	<i>Trimeresurus arunachalensis</i> sp. nov.	0.138	—	—	—	—	—	—	—	—	—	—	—	—	—
3	<i>Trimeresurus borneensis</i>	0.170	0.159	—	—	—	—	—	—	—	—	—	—	—	—
4	<i>Trimeresurus buniana</i>	0.142	0.116	0.178	—	—	—	—	—	—	—	—	—	—	—
5	<i>Trimeresurus cantori</i>	0.066	0.136	0.176	0.143	0.045	—	—	—	—	—	—	—	—	—
6	<i>Trimeresurus erythrolamprus</i>	0.070	0.127	0.179	0.143	0.045	—	—	—	—	—	—	—	—	—
7	<i>Trimeresurus flavomaculatus</i>	0.168	0.160	0.201	0.130	0.161	0.168	—	—	—	—	—	—	—	—
8	<i>Trimeresurus fuscatus</i>	0.131	0.125	0.188	0.062	0.139	0.141	0.151	—	—	—	—	—	—	—
9	<i>Trimeresurus gracilis</i>	0.175	0.161	0.193	0.186	0.187	0.178	0.204	0.160	—	—	—	—	—	—
10	<i>Trimeresurus gramineus</i>	0.152	0.183	0.170	0.180	0.157	0.168	0.208	0.175	0.194	—	—	—	—	—
11	<i>Trimeresurus gumprechtii</i>	0.042	0.138	0.186	0.157	0.047	0.056	0.176	0.140	0.178	0.170	—	—	—	—
12	<i>Trimeresurus hageni</i>	0.140	0.143	0.178	0.125	0.128	0.145	0.115	0.123	0.190	0.210	0.152	—	—	—
13	<i>Trimeresurus insularis</i>	0.077	0.131	0.158	0.138	0.077	0.091	0.157	0.136	0.156	0.149	0.066	0.138	—	—
14	<i>Trimeresurus kanburiensis</i>	0.146	0.115	0.178	0.128	0.136	0.143	0.141	0.139	0.174	0.170	0.137	0.169	0.135	—

APPENDIX 2 (continued)

No.	Species	15	16	17	18	19	20	21	22	23	24	25	26	27	28		
23	<i>Trimeresurus schultzei</i>	0.134	0.178	0.094	0.129	0.113	0.109	0.160	0.149	—	0.159	—	—	—	—		
24	<i>Trimeresurus septentrionalis</i>	0.137	0.162	0.168	0.125	0.121	0.150	0.167	0.077	0.159	—	0.155	—	—	—		
25	<i>Trimeresurus sichuanensis</i>	0.129	0.172	0.130	0.092	0.130	0.112	0.159	0.161	0.146	0.155	—	—	—	—		
26	<i>Trimeresurus stejnegeri</i>	0.115	0.149	0.133	0.070	0.122	0.124	0.176	0.153	0.137	0.149	0.104	—	—	—		
27	<i>Trimeresurus sumatranaus</i>	0.140	0.152	0.106	0.140	0.128	0.133	0.170	0.151	0.103	0.148	0.161	0.141	—	—		
28	<i>Trimeresurus tibetanus</i>	0.122	0.170	0.150	0.119	0.132	0.115	0.155	0.128	0.123	0.136	0.115	0.124	0.149	—		
29	<i>Trimeresurus trigonoccephalus</i>	0.141	0.100	0.200	0.163	0.137	0.159	0.156	0.157	0.197	0.164	0.176	0.159	0.175	0.167		
30	<i>Trimeresurus venustus</i>	0.059	0.149	0.117	0.105	0.138	0.114	0.139	0.160	0.141	0.148	0.115	0.128	0.152	0.127		
31	<i>Trimeresurus vogeli</i>	0.119	0.154	0.146	0.085	0.114	0.124	0.173	0.146	0.134	0.149	0.108	0.047	0.145	0.119		
32	<i>Trimeresurus yunnanensis</i>	0.108	0.140	0.116	0.063	0.120	0.108	0.166	0.122	0.125	0.138	0.099	0.081	0.146	0.107		
33	<i>Tropidolaemus wagleri</i>	0.191	0.189	0.208	0.153	0.162	0.196	0.242	0.170	0.205	0.160	0.207	0.184	0.212	0.212		
34	<i>Azemiops feae</i>	0.184	0.181	0.162	0.177	0.180	0.164	0.211	0.200	0.174	0.203	0.188	0.178	0.186	0.199		
35	<i>Calloselasma rhodostoma</i>	0.228	0.196	0.211	0.207	0.203	0.210	0.239	0.201	0.197	0.220	0.216	0.203	0.209	0.217		
36	<i>Daboia russelii</i>	0.216	0.230	0.190	0.211	0.214	0.241	0.229	0.246	0.233	0.235	0.229	0.222	0.215	0.244		
37	<i>Deinagkistrodon acutus</i>	0.218	0.195	0.200	0.191	0.193	0.189	0.209	0.217	0.215	0.198	0.206	0.211	0.200	0.208		
38	<i>Gloydius brevicaudatus</i>	0.197	0.213	0.228	0.203	0.192	0.205	0.227	0.202	0.218	0.203	0.209	0.227	0.228	0.226		
39	<i>Hypnale hypnale</i>	0.249	0.219	0.191	0.214	0.198	0.234	0.255	0.251	0.209	0.222	0.211	0.210	0.205	0.254		
40	<i>Ovophis monticola</i>	0.151	0.199	0.166	0.137	0.165	0.148	0.175	0.163	0.188	0.167	0.147	0.174	0.169	0.157		
41	<i>Pareas hamptoni</i>	0.292	0.272	0.276	0.284	0.251	0.279	0.303	0.278	0.246	0.283	0.300	0.292	0.275	0.311		
42	<i>Protobothrops mangshanensis</i>	0.139	0.148	0.159	0.137	0.114	0.143	0.183	0.147	0.151	0.137	0.157	0.145	0.157	0.136		
43	<i>Protobothrops mucrosquamatus</i>	0.205	0.169	0.182	0.178	0.198	0.207	0.227	0.193	0.183	0.189	0.190	0.175	0.204	0.200		
44	<i>Protobothrops siersvorum</i>	0.166	0.176	0.184	0.172	0.164	0.172	0.192	0.187	0.185	0.187	0.182	0.179	0.186	0.196		
No.	Species	29	30	31	32	33	34	35	36	37	38	39	40	41	42	43	44
30	<i>Trimeresurus venustus</i>	0.156	—	—	—	—	—	—	—	—	—	—	—	—	—	—	
31	<i>Trimeresurus vogeli</i>	0.156	0.128	—	—	—	—	—	—	—	—	—	—	—	—	—	
32	<i>Trimeresurus yunnanensis</i>	0.157	0.115	0.079	—	—	—	—	—	—	—	—	—	—	—	—	
33	<i>Tropidolaemus wagleri</i>	0.185	0.204	0.191	0.185	—	—	—	—	—	—	—	—	—	—	—	
34	<i>Azemiops feae</i>	0.207	0.185	0.170	0.178	0.186	—	—	—	—	—	—	—	—	—	—	
35	<i>Calloselasma rhodostoma</i>	0.213	0.239	0.203	0.195	0.188	0.206	—	—	—	—	—	—	—	—	—	
36	<i>Daboia russelii</i>	0.226	0.222	0.226	0.212	0.230	0.230	0.275	—	—	—	—	—	—	—	—	
37	<i>Deinagkistrodon acutus</i>	0.189	0.217	0.215	0.200	0.174	0.214	0.194	0.220	—	—	—	—	—	—	—	
38	<i>Gloydius brevicaudatus</i>	0.222	0.216	0.223	0.213	0.205	0.255	0.252	0.259	0.200	—	—	—	—	—	—	
39	<i>Hypnale hypnale</i>	0.219	0.222	0.226	0.229	0.211	0.242	0.210	0.225	0.223	0.252	—	—	—	—	—	
40	<i>Ovophis monticola</i>	0.183	0.168	0.161	0.162	0.227	0.209	0.217	0.234	0.174	0.194	0.245	—	—	—	—	
41	<i>Pareas hamptoni</i>	0.277	0.310	0.282	0.298	0.280	0.290	0.252	0.289	0.274	0.301	0.321	—	—	—	—	
42	<i>Protobothrops mangshanensis</i>	0.146	0.175	0.132	0.136	0.163	0.188	0.195	0.224	0.172	0.166	0.212	0.124	0.267	—	—	
43	<i>Protobothrops mucrosquamatus</i>	0.211	0.213	0.178	0.186	0.196	0.200	0.218	0.237	0.212	0.214	0.249	0.169	0.290	0.146	—	
44	<i>Protobothrops siersvorum</i>	0.185	0.180	0.179	0.182	0.197	0.191	0.200	0.243	0.186	0.190	0.246	0.161	0.278	0.114	0.181	

to 24 (Uetz et al., 2018). Further surveys are needed to determine the range and natural history of this species.

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