

Research article

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Taxonomic revaluation of the *Ahaetulla prasina* (H. Boie in F. Boie, 1827) complex from Northeast India: resurrection and redescription of *Ahaetulla flavescens* (Wall, 1910) (Reptilia: Serpentes: Colubridae)

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Abstract. The taxonomic status of the nominal taxon *Dryophis prasinus flavescens* Wall, 1910 is reevaluated herein. Based on molecular data generated from fresh collections of *Ahaetulla prasina* (H. Boie in F. Boie, 1827) auctorum from Northeast India and, additionally, morphological data from museum specimens originating from the same areas, we resurrect this taxon as *Ahaetulla flavescens* (Wall, 1910) comb. nov. We clarify the status, identity and locations of its type specimens, rediscover, redescribe and illustrate those specimens and also designate a lectotype in order to effect a proper

taxonomic redefinition of this nominal taxon. We provide further details on the morphology and diagnosis of this species and elucidate its phylogenetic position. We also provide a summary of the natural history and distribution of this species. Adding to the known cryptic diversity and genetic divergence within Southeast Asian populations, this work also hints at the need for a taxonomic revision of the *A. prasina* complex. This work complements a previous study on the *A. prasina* complex focusing on populations in Indonesia. Taken together, these two studies represent phylogenetic reconstructions from different populations of the *A. prasina* complex across its distribution range, on the Asian mainland and the surrounding islands.

Keywords. Assam, Arunachal Pradesh, BNHS, DNA, distribution, scalation, vine snakes.

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Introduction

The Oriental colubrid genus *Ahaetulla* Link, 1807 comprises slender bodied, arboreal, ophisthoglyphous snakes with a characteristic sharp snout, represented by 18 recognized species distributed in South and Southeast Asia (Wallach *et al.* 2014; Mallik *et al.* 2020; Uetz *et al.* 2021). In recent years, Mohapatra *et al.* (2017), Deepak *et al.* (2018) and Mallik *et al.* (2019, 2020) have all further revealed the hidden diversity in this group in Peninsular India, by describing a new genus, several new species and by resurrecting some synonyms as valid taxa. These studies mainly focused on the groups *Ahaetulla nasuta* (Lacépède, 1789) and *Ahaetulla pulverulenta* (Duméril *et al.*, 1854) of South Asia, involving populations inhabiting Peninsular India and the adjacent island of Sri Lanka.

Apart from these groups, the other commonly reported species of *Ahaetulla* inhabiting parts of Northeast India is *Ahaetulla prasina* (H. Boie in F. Boie, 1827) (Das 2002; Whitaker & Captain 2004; Ahmed *et al.* 2009). *Ahaetulla prasina* has been reported to occur over a large and disjunct geographic range, extending from Northeast India, across Indochina up to Indonesia and the Philippines (Smith 1943, as *Dryophis prasinus*). Recently, in line with the unexpected cryptic diversity discovered and resolved in South Asian congeners (see Mallik *et al.* 2020 and references therein), phylogenetic studies on *A. prasina* populations from the Sundas (Indonesia) also revealed cryptic species in this complex. Indahsari *et al.* (2020) sequenced and analysed populations inhabiting the Sundaic islands of Sumatra, Java and Bali. They discovered the presence of up to six cryptic lineages within these populations. However, formal taxonomic descriptions are yet to be completed.

Initially described as *Dryophis prasinus* by H. Boie in F. Boie (1827) from the imprecise locality “Java”, there are currently many subjective junior synonyms recognised for this species. They are: *Tragops prasinus laetus* Cope, 1861 (Philippines), *Dryophis prasinus flavescens* Wall, 1910 (Northeast India), *Dryophis griseus* Taylor, 1922 and *Dryophis praeocularis* Taylor, 1922 (both from the Philippines), *Dryophis prasinus chinensis* Mell, 1931 (South China), *Dryophis prasinus indicus* Mell, 1931 (Northeast India, by implication), *Ahaetulla prasina suluensis* Gaulke, 1994 (Philippines) and *Ahaetulla prasina medioxima* Lazell, 2002 (Shek Kwu Chau Island, China) (see Wallach *et al.* 2014).

Wall (1910) described *Dryophis prasinus flavescens* from Northeast India, as a subspecies based on three syntypes, including one male from Jaipur near Namsang (27.106° N, 95.511° E; Arunachal Pradesh) and two females from North Lakhimpur (26.537° N, 91.907° E; Assam), all from Northeast India. Wall’s nomen at subspecies level has priority over *Dryophis prasinus indicus* Mell, 1931, the other available

nomen from Northeast India. Additionally, Mell's (1931) treatment of the Indian population was by implication (with respect to the Chinese forms) and does not provide details of its provenance in India.

Recently, we collected specimens of the *A. prasina* complex in the field, from the Arunachal Pradesh and Meghalaya states in Northeast India. We also traced and examined two syntypes of *Dryophis prasinus flavescens*, both females from Lakimpur, Assam, presented by Col. Frank Wall (see Wall 1910). In this work, we reevaluate the taxonomic status of the Northeast Indian population of the *A. prasina* group using both morphological and molecular data.

Material and methods

The present study is based on our examination of the syntypes (NMHUK 1908.6.23.58–59) in the Natural History Museum (NHMUK) London, United Kingdom, and other voucher specimens housed in the museum of the Bombay Natural History Society (BNHS), Mumbai, India, and specimens collected for this study from the Arunachal Pradesh and Meghalaya states in Northeast India. Tissue samples were collected prior to the preservation of the specimens in 100% ethanol for molecular studies. Snout to vent length, tail length and total body length were measured with the help of non-elastic thread which was then measured using measuring tape. Photographs were taken with a Canon EOS 6D Mark II camera mounted with a 100 mm macro lens. Geo-coordinates were given in decimal degrees format, correct up to three decimal places, either recorded in the field by a GPS or sourced from Google Earth.

Morphological and meristic data

The following morphological measurements were scored on the left side of the body for symmetrical characters using a MitutoyoTM dial caliper to the nearest 0.1 mm. Total length: measured from tip of the snout to tail tip; snout-vent length: measured from tip of snout to vent; tail length: measured from vent to tip of tail; head length: measured from retroarticular process of jaw to tip of the snout; head width: measured at the widest points of the head; head depth: maximum head depth, measured from tip of crown to lower jaw; horizontal diameter of eye: measured from anterior-most corner to the posterior-most corner of the eye; vertical diameter of eye: measured vertically between uppermost and lowermost point of the orbit; internarial distance: measured between left and right nostrils; interorbital distance: measured between left and right orbits at their midpoint; eye to nostril distance: measured between anterior-most point of eye and nostril; eye to snout tip distance: measured between anterior-most point of eye and snout tip; mid-body width: maximum width of mid body; internasal height: maximum vertical dimension of internasal scale. Meristic characters were counted as follows: supralabials: number of scales bordering the upper jaw up to angle of jaw on both left and right side; infralabials: number of scales bordering the lower lip up to the angle of jaw on both left and right sides; ventral scales: counted as per Dowling (1951) method; dorsal body scale rows: counted around the body from one side of ventral scales to the other side at three positions – anterior scale rows: counted at one head length behind neck, mid-body scale rows: counted at mid-body, and posterior scale rows: counted at one head length before the cloacal opening; subcaudal scales were counted from first postcloacal scale to the scale before the tip of the tail.

Molecular methods

Extraction and amplification

Total genomic DNA was extracted from three tissue samples stored in 95% absolute alcohol. Genomic DNA was extracted using the commercially available DNEasy extraction kit (QIAGEN) as well as the Phenyl-Chloroform-Isoamyl alcohol protocol (Sambrook 2001). To elucidate phylogenetic relationships, three mitochondrial genes, Cytochrome-b (Cytb), NADH dehydrogenase subunit 4 (ND4) and 16S rRNA loci were amplified with previously published primers from different studies (Table 1). The PCR conditions and preparation protocol were the same as earlier studies (Arévalo *et al.* 1994; Palumbi

Table 1. Details of genes amplified, PCR primers used, DNA sequences length (in base pairs) and references for PCR protocols followed in this study.

Gene region	Primer	Sequence 5'-3'	Sequence length (bp)	References
Cytb	Gludg	TGACTTGAARAACCAAYCGTTG	1048	Palumbi 1996
	H16064	CTTTGGTTTACAAGAACAATGCTTTA		Burbrink <i>et al.</i> 2000
16S rRNA	L2510	CGCCTGTTTATCAAAAACAT	472	Palumbi 1996
	H3059	CCGGTCTGAACTCAGATCACGT		
ND4	ND4	CACCTATGACTACCAAAAAGCTCATGTAGA	663	Arévalo <i>et al.</i> 1994
	Leu	AGCCATTACTTTTACTTGGATTTCACCA		

1996; Burbrink *et al.* 2000); however, modifications of annealing temperature were applied in a few PCR reactions. The PCR amplified products were purified using the QIAquick PCR purification kit (Qiagen). The sequencing of purified products was carried out commercially by Amnion Biosciences Pvt. Ltd., Eurofins Biotech Pvt. Ltd. and Centre for Cellular and Molecular Platforms (C-CAMP, NCBS), Bangalore, India.

Sequence alignment

Sequences were edited and visually corrected using MEGA X (Stecher *et al.* 2018). The individual consensus sequences were derived from forward and reverse complements after checking for base miscalls. The sequence alignment was accomplished using the MUSCLE (Edgar 2004) algorithm implemented in MEGA X. The protein coding genes were checked for the presence of indels and examined for possible pseudogene amplification and premature stop codons by translating DNA to protein. No indels were detected in Cytb and ND4. The 16S rRNA sequences were aligned against available data in GenBank submitted by earlier studies and visually edited. Ambiguously aligned regions along with gaps were cropped out of the analysis due to the presence of secondary structures in the sequence (Gutell 1994; Kjer 1995; Parkinson 1999). A sequence matrix of 2183bp was created combining all three mitochondrial genes for 187 sequences of 19 species (Table 2). We downloaded and included *Dendrelaphis schokari* (Kuhl, 1820) and *Chrysopelea taprobanica* Smith, 1943 sequences as outgroup taxa.

Phylogenetic analysis

The 2183 bp matrix was analyzed with data partitions where different codon positions of Cytb & ND4 and 16S rRNA genes were considered as different partitions using PartitionFinder ver. 1.1.1 (Lanfear *et al.* 2012). A maximum likelihood tree was reconstructed with ultrafast bootstrapping in IQTREE ver. 2 for better branch support (Trifinopoulos *et al.* 2016; Minh *et al.* 2020). The analysis was carried out on the web server (iqtree.cibiv.univie.ac.at). Partitions were used from PartitionFinder (Table 3) and we allowed branch support of 5000 ultrafast bootstrapping (Hoang *et al.* 2018). Default settings were retained for all other parameters. To examine the phylogenetic relationships of different members of the *A. prasina* complex belonging to different geographic regions, we then reconstructed a complete phylogeny of genus *Ahaetulla* including all other available mitochondrial DNA sequences from GenBank, with two more available genes (COI and 12S) and the addition of a few more species belonging to genus *Ahaetulla* as well as outgroups. This complete mitochondrial tree provides additional support for revalidating the status of the members of *A. prasina* population in India. The resulting tree was visualized in Figtree ver. 1.4.3 (<http://tree.bio.ed.ac.uk/software/figtree/>).

Table 2 (continued on next five pages). List of species of *Ahaetulla* Link, 1807 and outgroups, their specimen voucher number, geographic locations and GenBank accession numbers for loci used in this study. COI and 12S loci are used to regenerate a complete mitochondrial loci phylogeny of *Ahaetulla*.

Species	Voucher number	Geographic locations	Cytb	ND4	16S	COI	12S
<i>Ahaetulla flavescens</i> comb. nov.	CESS 260	Kheel, Papum Pare, Arunachal Pradesh, India	OK495683	OK495686	OK524310	–	–
<i>Ahaetulla flavescens</i> comb. nov.	CESS 340	Kane, Arunachal Pradesh, India	OK495684	OK495687	OK524311	–	–
<i>Ahaetulla flavescens</i> comb. nov.	CESS 347	Kane, Arunachal Pradesh, India	OK495685	OK495688	OK524312	–	–
<i>Ahaetulla flavescens</i> comb. nov.	ZSI/SHT14_ MZMU1331	Aizawl, Mizoram, India	MN788508	–	–	MN788515	–
<i>Ahaetulla borealis</i>	CESS 057	Amboli, Maharashtra, India	MT363255	MT363303	MT365043	–	–
<i>Ahaetulla borealis</i>	CESS 058	Amboli, Maharashtra, India	MT363256	–	–	–	–
<i>Ahaetulla borealis</i>	CESS 059	Amboli, Maharashtra, India	MT363257	MT363304	MT365044	–	–
<i>Ahaetulla borealis</i>	CESS 103	Matheran, Maharashtra, India	MT363265	MT363312	MT365053	–	–
<i>Ahaetulla borealis</i>	BNHS 3591	Matheran, Maharashtra, India	MT363266	MT363313	MT365054	–	–
<i>Ahaetulla borealis</i>	BNHS 3590	Castlerock, Karnataka, India	MT363294	MT363340	MT365083	–	–
<i>Ahaetulla borealis</i>	CESS 422	Yana, Devimane Ghat, Karnataka, India	MT363295	MT363341	MT365084	–	–
<i>Ahaetulla borealis</i>	CESS 505	Castlerock, Karnataka, India	MT363296	MT363342	MT365085	–	–
<i>Ahaetulla dispar</i>	CESS 187	Anaimudi shola NP, Kerala, India	MT363279	MT363325	MT365068	–	–
<i>Ahaetulla dispar</i>	CESS 189	Anaimudi shola NP, Kerala, India	MT363281	MT363327	MT365070	–	–
<i>Ahaetulla dispar</i>	CESS 188	Anaimudi shola NP, Kerala, India	MT363280	MT363326	MT365069	–	–
<i>Ahaetulla farnsworthi</i>	BNHS 3589	Sakleshpur, Karnataka, India	MT363258	MT363305	MT365045	–	–

Table 2 (continued). List of species of *Ahaetulla* Link, 1807 and outgroups, their specimen voucher number, geographic locations and GenBank accession numbers for loci used in this study. COI and 12S loci are used to regenerate a complete mitochondrial loci phylogeny of *Ahaetulla*.

Species	Voucher number	Geographic locations	Cytb	ND4	16S	COI	12S
<i>Ahaetulla farnsworthi</i>	CESS 070	Kudremukh NP, Karnataka, India	–	MT363306	MT365046	–	–
<i>Ahaetulla farnsworthi</i>	CESS 072	Amboli, Karnataka, India	MT363259	MT363307	MT365047	–	–
<i>Ahaetulla farnsworthi</i>	CESS 111	Agumbe, Karnataka, India	MT363267	MT363314	MT365055	–	–
<i>Ahaetulla farnsworthi</i>	CESS 156	Bhagavathi, Kudremukh NP, Karnataka, India	MT363272	MT363319	MT365060	–	–
<i>Ahaetulla farnsworthi</i>	CESS 158	Bhagavathi, Kudremukh NP, Karnataka, India	MT363273	–	MT365061	–	–
<i>Ahaetulla farnsworthi</i>	CESS 276	Madikeri, Karnataka, India	MT363286	MT363333	MT365075	–	–
<i>Ahaetulla farnsworthi</i>	CESS 277	Near Subramanya, Kodagu, Karnataka, India	MT363287	MT363334	MT365076	–	–
<i>Ahaetulla farnsworthi</i>	BNHS 3588	Bhadra tiger reserve, Karnataka, India	MT363290	MT363337	MT365079	–	–
<i>Ahaetulla farnsworthi</i>	CESS 512	Kadari, Kudremukh FH, Karnataka, India	MT363298	MT363344	MT365087	–	–
<i>Ahaetulla farnsworthi</i>	CESS 513	Kadari, Kudremukh FH, Karnataka, India	MT363299	–	MT365088	–	–
<i>Ahaetulla farnsworthi</i>	CESS 517	SK border, Kudremukh NP, Karnataka, India	MT363300	MT363345	MT365089	–	–
<i>Ahaetulla sahyadrensis</i>	CESS 159	Bhagavathi, Kudremukh NP, Karnataka, India	MT363274	MT363320	MT365062	–	–
<i>Ahaetulla isabellina</i>	CESS 164	Goodrickal, PTR, Kerala, India	MT363275	MT363321	MT365063	–	–
<i>Ahaetulla isabellina</i>	CESS 167	Goodrickal, PTR, Kerala, India	–	–	MT365064	–	–
<i>Ahaetulla isabellina</i>	BNHS 3584	Orukumaban, Parambikulam, Kerala, India	MT363277	MT363323	MT365066	–	–
<i>Ahaetulla isabellina</i>	BNHS 3585	Orukumaban, Parambikulam, Kerala, India	MT363278	MT363324	MT365067	–	–
<i>Ahaetulla isabellina</i>	CESS 261	Achankovil, Devarmala, Kerala, India	MT363283	MT363330	MT365073	–	–

Table 2 (continued). List of species of *Ahaetulla* Link, 1807 and outgroups, their specimen voucher number, geographic locations and GenBank accession numbers for loci used in this study. COI and 12S loci are used to regenerate a complete mitochondrial loci phylogeny of *Ahaetulla*.

Species	Voucher number	Geographic locations	Cytb	ND4	16S	COI	12S
<i>Ahaetulla isabellina</i>	CESS 262	Achalakovil, Devarmala, Kerala, India	MT363284	MT363331	MT365074	–	–
<i>Ahaetulla isabellina</i>	CESS 329	Kakki, Kerala, India	MT363292	–	MT365081	–	–
<i>Ahaetulla isabellina</i>	CESS 404	Idukki WLS, Kerala, India	MT363293	MT363339	MT365082	–	–
<i>Ahaetulla isabellina</i>	CESS 172	Goodrickal, PTR, Kerala, India	MT363276	MT363322	MT365065	–	–
<i>Ahaetulla malabarica</i>	BNHS 3587	Kalpetta, Kerala, India	MT363261	–	MT365049	–	–
<i>Ahaetulla malabarica</i>	CESS 088	Kalpetta, Kerala, India	MT363262	MT363309	MT365050	–	–
<i>Ahaetulla malabarica</i>	CESS 089	Kurchemala, Kerala, India	MT363263	MT363310	MT365051	–	–
<i>Ahaetulla malabarica</i>	BNHS 3586	Thirunelli, Brahmagiri, Karnataka, India	MT363264	MT363311	MT365052	–	–
<i>Ahaetulla malabarica</i>	CESS 114	Siruvani, Silent valley, Kerala, India	MT363268	MT363315	MT365056	–	–
<i>Ahaetulla malabarica</i>	CESS 143	Silent valley, Kerala, India	MT363269	MT363316	MT365057	–	–
<i>Ahaetulla malabarica</i>	CESS 144	Silent valley, Kerala, India	MT363270	MT363317	MT365058	–	–
<i>Ahaetulla malabarica</i>	CESS 145	Silent valley, Poochypara, Kerala, India	MT363271	MT363318	MT365059	–	–
<i>Ahaetulla malabarica</i>	CESS 275	Coorg, Honey valley, Kerala, India	MT363285	MT363332	–	–	–
<i>Ahaetulla malabarica</i>	CESS 311	Iruppu, Coorg, Karnataka, India	MT363291	MT363338	MT365080	–	–
<i>Ahaetulla oxyrhyncha</i>	CESS 211	NCBS campus, Bangalore, Karnataka, India	MT363282	MT363328	MT365071	–	–
<i>Ahaetulla oxyrhyncha</i>	CESS 244	Devanahalli, Karnataka, India	–	MT363329	MT365072	–	–
<i>Ahaetulla oxyrhyncha</i>	CESS 506	Chikbalpur, Karnataka, India	MT363297	MT363343	MT365086	–	–

Table 2 (continued). List of species of *Ahaetulla* Link, 1807 and outgroups, their specimen voucher number, geographic locations and GenBank accession numbers for loci used in this study. COI and 12S loci are used to regenerate a complete mitochondrial loci phylogeny of *Ahaetulla*.

Species	Voucher number	Geographic locations	Cytb	ND4	16S	COI	12S
<i>Ahaetulla perroteti</i>	CESS 286	Upper Bhavani, Mukurthy, Tamil Nadu, India	MT363288	MT363335	MT365077	–	–
<i>Ahaetulla perroteti</i>	CESS 287	Upper Bhavani, Mukurthy, Tamil Nadu, India	MT363289	MT363336	MT365078	–	–
<i>Ahaetulla travancorica</i>	BNHS 3592	Chemunji, Peppara, Agasthyamalai, Kerala, India	MT363260	MT363308	MT365048	–	–
<i>Ahaetulla nasuta</i>	RAP0517	Sri Lanka	KC347453	KC347526	–	–	–
<i>Ahaetulla pulverulenta</i>	RS-C	Sri Lanka	KC347454	KC347512	KC347339	–	KC347304
<i>Ahaetulla fronticincta</i>	CAS204966	Myanmar	AF471072	–	–	–	–
<i>Ahaetulla fronticincta</i>	CAS222635	–	KX660447	KX660576	KX660173	–	–
<i>Ahaetulla fronticincta</i>	CAS245687	Myanmar, Mon State	KX660448	–	KX660174	–	–
<i>Ahaetulla cf. nasuta</i>	FMNH255023	Champasak, Mounlapamok Dist., Laos	KX660467	KX660594	KX660194	–	–
<i>Ahaetulla fasciolata</i>	LSUHC8837	–	KX660478	KX660603	KX660204	–	–
<i>Ahaetulla fasciolata</i>	LSUHC9831	Perlis State Park, West Malaysia	KX660477	KX660602	KX660203	–	–
<i>Ahaetulla mycterizans</i>	LSUHC8913	Gunung Pantli Hutan Lipur, West Malaysia	KX660479	KX660604	KX660205	–	–
<i>Ahaetulla mycterizans</i>	ADM001	–	KX660437	KX660564	KX660161	–	–
<i>Ahaetulla mycterizans</i>	FMNH269042	Borneo	–	KX660595	KX660195	–	–
<i>Ahaetulla mycterizans</i>	USNM:Herp: 587040	Yeybu village, Tanintharyi, Myanmar	–	–	–	MG935417	–
<i>Ahaetulla prasina</i>	LSUHC8586	Vietnam	KX660480	KX660605	KX660206	–	–
<i>Ahaetulla prasina</i>	APR	Bangkok, Thailand	–	–	–	LC075335	–

Table 2 (continued). List of species of *Ahaetulla* Link, 1807 and outgroups, their specimen voucher number, geographic locations and GenBank accession numbers for loci used in this study. COI and 12S loci are used to regenerate a complete mitochondrial loci phylogeny of *Ahaetulla*.

Species	Voucher number	Geographic locations	Cytb	ND4	16S	COI	12S
<i>Ahaetulla prasina</i>	APR1	Chiangrai, Thailand	LC105636	–	–	LC075334	–
<i>Ahaetulla prasina</i>	APR2	Kien Giang Prov., Hon Tre Is., Vietnam	LC105637	–	–	–	–
<i>Ahaetulla prasina</i>	KU:326673	Thailand	KC010339	–	–	–	–
<i>Ahaetulla prasina</i>	KU:302954	Palawan Island, P. Province, Philippines	KC010338	–	–	–	–
<i>Ahaetulla prasina</i>	FMNH269042	Polillo Island, Quezon Province, Philippines	–	KX660595	KX660195	–	–
<i>Ahaetulla prasina</i>	ROM30961	Sarawak, Bintulu Division, Borneo–M	–	–	KX694615	–	KX694556
<i>Ahaetulla prasina</i>	USNM:Herp: 512416	Philippines	–	–	–	MH273124	–
<i>Ahaetulla prasina</i>	USNM:Herp: 512425	Philippines	–	–	–	MH273123	–
<i>Ahaetulla prasina</i>	USNM:Herp: 498921	Philippines	–	–	–	MH273122	–
<i>Ahaetulla prasina</i>	CHS836	China	–	–	–	MK064908	MK065686
<i>Ahaetulla anomala</i>	NCBS–AQ–185	Takatpur, Baripada, Odisha, India	KY769196	–	KY769197	–	–
<i>Ahaetulla anomala</i>	GSCCPPM1288	India	–	–	KY769198.	–	–
<i>Ahaetulla laudankia</i>	ZSI_CZRC_6203	India	MK595796	–	MK595794	–	–
<i>Ahaetulla nasuta</i> cf. <i>isabellina</i>	ZSI_CZRC_2605	India	MK595795	–	MK595793	–	–
<i>Ahaetulla rufusoculara</i>	ITBCZ7504	Vietnam	MW759569	–	–	MW759567	–
<i>Ahaetulla rufusoculara</i>	ITBCZ7505	Vietnam	MW759570	–	–	MW759568	–

Table 2 (continued). List of species of *Ahaetulla* Link, 1807 and outgroups, their specimen voucher number, geographic locations and GenBank accession numbers for loci used in this study. COI and 12S loci are used to regenerate a complete mitochondrial loci phylogeny of *Ahaetulla*.

Species	Voucher number	Geographic locations	Cytb	ND4	16S	COI	12S
<i>Proahaetulla antiqua</i>	BNHS 3572	India	MH779628	MH779629	MH779632	–	–
<i>Proahaetulla antiqua</i>	BNHS 3573	India	MH779633	MH779634	MH779636	–	–
<i>Chrysopelea taprobanica</i>	RAP0538	Sri Lanka	KC347459	KC347508	KC347354	–	KC347319
<i>Dendrelaphis schokari</i>	RAP0477	Sri Lanka	KC347461	KC347497	KC347358	–	–
<i>A. prasina</i>	ENS19730	Andalas, West Sumatra	–	–	–	–	MK691460
<i>A. prasina</i>	ENS16293	Medan, North Sumatra	–	–	–	–	MK691461
<i>A. prasina</i>	ENS16165	Bandung, West Java	–	–	–	–	MK691462
<i>A. prasina</i>	ENS19611	Bukittinggi, West Sumatra	–	–	–	–	MK691464
<i>A. prasina</i>	NK 0812	Banyuwangi, East Java	–	–	–	–	MK691466
<i>A. prasina</i>	NK 0506	Malang, East Java	–	–	–	–	MK691468
<i>A. prasina</i>	ENS13668	Rajabasa, Lampung, South Sumatra	–	–	–	–	MK691469
<i>A. prasina</i>	ENS16926	Rau, North Sumatra	–	–	–	–	MK691470
<i>A. prasina</i>	Nk 1302	Sukawati, Bali	–	–	–	–	MK691472
<i>A. prasina</i>	Nk 1388	Tanah Lot, Bali	–	–	–	–	MK691473
<i>A. prasina</i>	ENS14602	Tanggamus, Lampung, South Sumatra	–	–	–	–	MK691474

Table 3. Partition schemes and best-fit substitution models are selected in PartitionFinder. A total four partitions for three mitochondrial loci and six partitions for five mitochondrial loci with their best fit models are predicted by PartitionFinder. Cp1–cp3 indicates the codon positions of each locus.

Three mitochondrial loci			Five mitochondrial loci	
Partition No.	Partition	Best fit model	Partition	Best fit model
1	Cytb_cp1, ND4_cp1	GTR+I+G	12S, Cytb_cp1, ND4_cp1	GTR+I+G
2	Cytb_cp2, ND4_cp2	TVM+I+G	Cytb_cp2, ND4_cp2	K81uf+I+G
3	Cytb_cp3, ND4_cp3	GTR+G	COI_cp3, Cytb_cp3, ND4_cp3	GTR+G
4	16S	GTR+I+G	16S	GTR+I+G
5			COI_cp1	TIMEf+I
6			COI_cp3	TrN+I

Species delimitation

To delineate the species boundary between lineages, we used Bayesian Poisson Tree Processes (bPTP) (Zhang *et al.* 2013). For bPTP analysis, we used a reconstructed Maximum Likelihood consensus tree (three mitochondrial locus) as the input tree. The analysis was implemented on the bPTP web server (<https://species.h-its.org/ptp/>) with 500 000 MCMC generations and default parameters. The monophyletic clusters predicted by bPTP were considered as putative lineages. In addition, we used support from genetic distance (p-distance) as well as geographic isolation among populations to established them as independent evolutionary lineages.

Results

Molecular phylogenetics

A complete reconstructed phylogeny of almost all members of the genus *Ahaetulla* presents two major clades, which comprise species from the Indo-Chinese sub-region, Southeast Asia and Peninsular India (Fig. 1). Both clades are well supported with 95% SH-aLRT and 98% ultrafast bootstrap support value. Clade I comprises species belonging to South Asia including part of Peninsular India and Sri Lanka as well as a few species from the Indo-Chinese sub-region, whereas Clade II predominantly comprises species from the Indo-Chinese sub-region, Southeast Asia and Northeast India. In addition, the reconstructed five mitochondrial gene tree shows the monophyly of *A. prasina* populations (CESS260, CESS340 and CESS347) belonging to northeast India (see Supp. file 1: Fig. S1).

The *A. prasina* complex is nested within Clade II. This complex represents four separate small clades also including *A. mycterizans* (Linnaeus, 1758) and *A. fasciolata* (Fischer, 1885) within the clade, making *A. prasina* polyphyletic, which has been reported in an earlier study (Figuroa *et al.* 2016). The presence of four sub-clades in the *A. prasina* complex indicates the presence of a few more cryptic species of *Ahaetulla* within its distribution range. Our samples of *A. prasina* from Northeast India are clustered together and are sister to the clade comprising the *A. prasina* population from Thailand, China and Vietnam.

A total of seven lineages are predicted by bPTP in the *A. prasina* species complex (Fig. 2). However, using a multicriteria species delimitation approach (bPTP, genetic divergence and geographical isolation), we inferred five lineages in the *A. prasina* complex. This species complex includes: lineage 1 from

Northeast India, lineage 2 from Thailand and China, lineage 3 from Vietnam, lineage 4 and lineage 5 from Palawan Island and Polillo Island in Philippines. The main clade of interest for the present work, the *A. prasina* Group-A population belonging to the Northeast India, is designated here as a distinct species. We also consider FMNH269042 (labelled as *A. prasina*) from Borneo as *A. cf. mycterizans*, because it is sister to the *A. mycterizans* main clade.

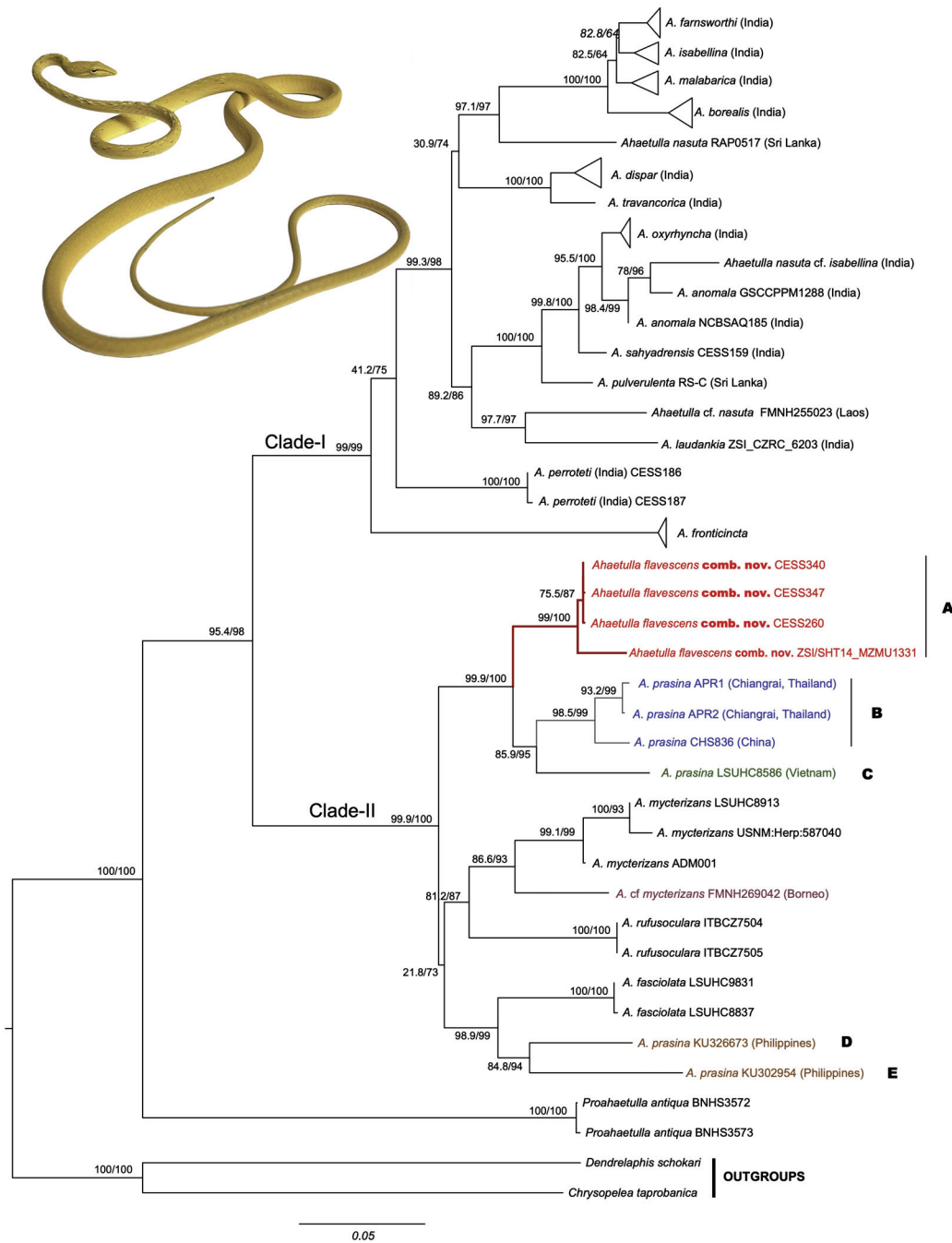


Fig. 1. Maximum Likelihood tree based on Cytb, ND4 and 16S genes, showing the phylogenetic position of *Ahaetulla flavescens* (Wall, 1910) comb. nov. (red), with respect to other congeners, especially the *A. prasina* complex (blue, green, purple and brown).

The populations of *A. prasina* sequenced from its type locality in Java have a genetic distance of 4.86–6.28% (in Cytb) from the Thai population (Indahsari *et al.* 2020). Using this as a bar for comparison, we propose that the Northeast Indian population of *A. prasina* is distinct at the species level from other populations (Table 5). Due to the unavailability in the Genbank dataset of the sequences of Indahsari *et al.* (2020) from the topotypical Javan population of *A. prasina*, we are unable to include the Javan population in our phylogenetic analysis and cannot calculate the genetic distance directly from the Javan population. Nevertheless, the Sundaic population (Indahsari *et al.* 2020) and the Northeast Indian population (current study) are both deeply divergent from the Thai population which lies geographically between the two. We found that the Northeast Indian population differs from the South Chinese population by 6.7%, from the Thai population by 6.3% and from the Vietnamese population by 7.4% at Cytb (Table 5a). At ND4, the sequence divergence between Northeast Indian and the Vietnamese population of *A. prasina* is 8.2% (Table 5b). Usually, 16S rRNA gene shows shallow genetic divergence between lineages as compared to Cytb and ND4 genes, which can be seen between CESS260, CESS340, and CESS347 from Northeast India, and CHS836 from China (Table 5c). The Northeast Indian population (ZSI/SHT14_MZMU1331) was genetically 8.5–11% divergent from Thai and Chinese populations of *A. prasina* at COI gene (Table 5d). In addition, the available 12S genes from Sundaic (Java, Sumatra and Bali) populations have a genetic divergence of 2.5–3.2% from Chinese and Thai population, that further supports Chinese, Thai and Northeast Indian population are distinct lineages (Table 5e). Taken together, these data suggest that the Northeast Indian population is distinct at the species level.

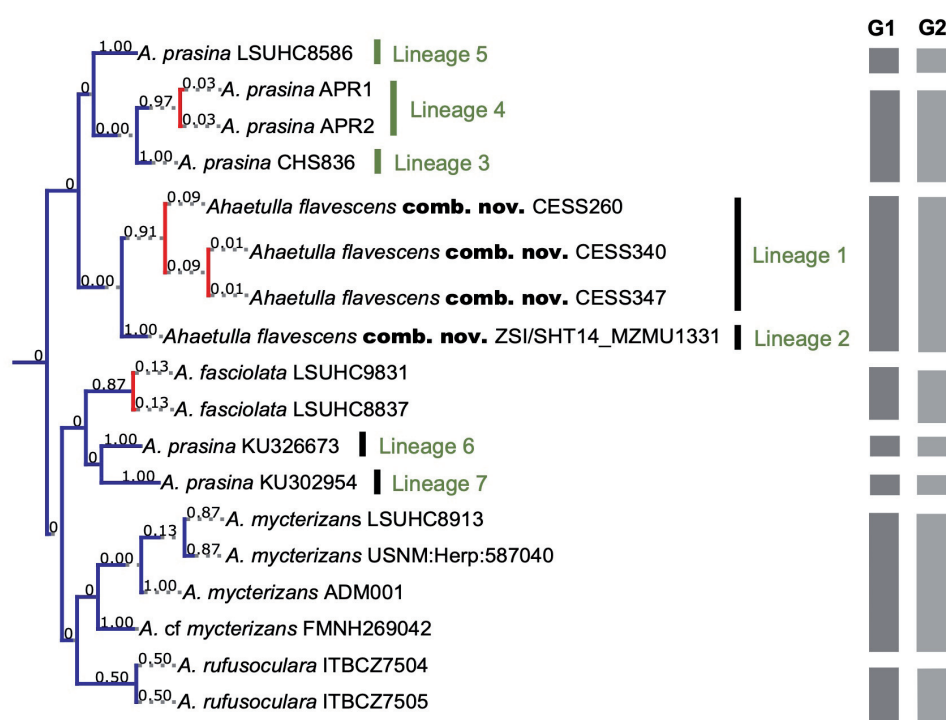


Fig. 2. The bPTP output trees generated from three mitochondrial loci ML trees. Blue coloured branches and black bars indicate monophyly of that lineage, where validity of lineages is further ascertained with genetic divergence (genetic p-distance) and geographic isolation. The grey bars indicate the genetic distance (G1) and geographic isolation (G2) among lineages. The values on clades indicate the posterior probability. The *A. prasina* complex (Lineage 1 and Lineage 2) from northeast India shows a very low genetic divergence with continuous geographic distribution.

Table 4. Main morphological characters of the type and referred materials of *Ahaetulla flavescens* (Wall, 1910) comb. nov.

Measurements (in mm)	NHMUK 1908. 6.23.58.	NHMUK 1908. 6.23.59.	BNHS 1975	BNHS 1976	BNHS 1978	BNHS 1979	Mean $\pm$ std. deviation
Sex	♀	♀	♀	♂	♂	♀	
Total length	1335.0	1006.0	1141.0	678.0	1137.0	1059.0	1059.3 $\pm$ 198.7
Snout-vent length	840.0	631.0	768.0	442.0	758.0	679.0	686.3 $\pm$ 128.0
Tail length	495.0	375.0	373.0	236.0	379.0	380.0	373.0 $\pm$ 75.0
Head length	27.5	28.5	28.1	19.0	29.2	25.6	26.3 $\pm$ 3.5
Head width	13.2	10.9	7.4	7.2	7.4	7.1	8.9 $\pm$ 2.3
Head depth	11.6	10.0	7.1	5.2	7.0	6.3	7.9 $\pm$ 2.2
Horizontal eye diameter	5.1	5.5	4.6	5.3	4.6	4.5	4.9 $\pm$ 0.4
Vertical eye diameter	3.7	4.0	3.1	3.9	3.1	2.4	3.4 $\pm$ 0.6
Internarial distance	5.4	4.8	3.6	3.1	3.7	3.3	4.0 $\pm$ 0.8
Interorbital distance	9.7	9.9	8.5	7.4	8.6	7.9	8.7 $\pm$ 0.9
Eye to nostril distance	8.0	7.2	8.1	5.1	8.3	7.6	7.4 $\pm$ 1.1
Eye to snout tip distance	11.6	10.6	10.5	7.7	10.5	9.5	10.1 $\pm$ 1.2
Mid-body width (Max.)	7.5	7.1	7.5	4.8	7.1	6.4	6.7 $\pm$ 0.9

Taxonomy

Class Reptilia Laurenti, 1768
Order Squamata Oppel, 1811
Suborder Serpentes Linnaeus, 1758
Family Colubridae Oppel, 1811
Subfamily Chrysopelinae Cope, 1893
Genus *Ahaetulla* Link, 1807

Ahaetulla flavescens (Wall, 1910) comb. nov.
Figs 1–9; Tables 2–5

Dryophis prasinus flavescens Wall, 1910: 834.

Dryophis prasinus indicus Mell, 1931: 119–219. (by implication).

Dryophis prasina – Günther 1858: 159 (part).

Tragops prasinus – Günther 1864: 364. — Theobald 1876: 191.

Dryophis prasinus – Boulenger 1890: 369; 1896: 180 (part).

Dryophis prasinus ‘forma typica’ (non H. Boie in F. Boie, 1827) – Wall 1909a: 354; 1909b: 898; 1910: 834.

Dryophis prasinus flavescens (nec Smith, 1914) – Wall 1910: 834.

Table 5a. Interspecific genetic distance (p -distance) estimated from Cytb locus.

SI. No.	SPECIES	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24
1	<i>Ahaetulla flavescens</i> comb. nov. CESS347	7.0																							
2	<i>A. prasina</i> LSUHC586	8.9	9.8																						
3	<i>A. prasina</i> KU32673	9.1	10.7	7.6																					
4	<i>A. prasina</i> KU302954	6.5	7.7	9.1																					
5	<i>A. prasina</i> APR2	6.2	7.7	9.4	10.7																				
6	<i>A. prasina</i> APR1	6.6	8.3	9.0	11.0	0.3																			
7	<i>A. prasina</i> CHS836	13.4	13.4	13.6	14.3	13.6	12.2																		
8	<i>A. nasuta</i> RAP0517	12.2	12.9	12.7	13.0	11.8	11.4	8.1																	
9	<i>A. pulverulenta</i> RS-C	14.4	14.6	14.2	14.0	14.4	14.8	13.1	8.2																
10	<i>A. borealis</i> BNHS3590	13.4	14.6	14.4	15.7	13.4	13.4	12.6	7.9	9.9															
11	<i>A. farnsworthi</i> BNHS3589	13.2	14.1	14.2	14.7	12.9	13.2	11.9	7.0	8.9	4.5														
12	<i>A. malabarica</i> BNHS3586	13.2	14.1	14.2	14.7	12.9	13.2	11.9	7.0	8.9	4.3	2.9													
13	<i>A. sathyadrensis</i> CESS159	13.2	14.1	13.0	13.2	12.9	13.2	11.9	7.2	8.2	3.8	2.7	9.4												
14	<i>A. isabellina</i> BNHS3584	13.2	14.2	14.1	14.3	12.9	13.2	11.9	7.2	8.2	3.8	2.7	9.4	8.7											
15	<i>A. dispar</i> CESS187	14.4	14.8	13.7	13.6	14.1	14.4	12.9	7.2	7.7	9.1	7.5	7.5	8.6	7.5										
16	<i>A. oxyrhyncha</i> CESS211	14.4	14.9	13.2	14.7	13.6	14.1	13.6	12.9	8.9	4.6	10.8	9.3	10.5	9.4	8.9									
17	<i>A. travancorica</i> BNHS3592	14.2	14.8	13.9	14.3	14.8	14.4	14.8	13.6	8.2	7.0	8.7	8.4	8.1	8.1	2.4	8.2								
18	<i>A. perroteti</i> CESS287	13.9	14.8	14.1	14.5	14.4	14.8	13.6	8.2	7.0	8.7	8.4	8.1	8.1	8.1	2.4	8.2	9.4							
19	<i>A. fronticincta</i> CAS204966	14.4	16.0	15.6	16.7	15.1	15.1	14.1	11.8	10.6	13.0	10.3	11.8	11.5	11.7	10.8	11.3	11.3	10.6	12.3					
20	<i>A. cf. nasuta</i> FMNH255023	15.6	16.6	14.8	15.7	16.0	16.3	14.7	9.1	8.7	9.8	9.6	8.6	9.6	9.3	8.6	10.6	8.7	10.6	12.3	16.5				
21	<i>A. fasciolata</i> LSUHC8837	9.4	11.3	8.1	10.5	11.3	11.5	11.0	13.2	13.4	15.4	15.3	15.3	14.1	15.3	14.1	14.6	14.4	15.6	16.3	16.5	14.7			
22	<i>A. mycterizans</i> ADM001	6.7	8.3	7.9	9.1	9.0	9.0	8.1	12.2	11.6	13.4	12.4	12.6	11.9	11.7	12.6	13.1	11.9	12.9	14.5	10.2	10.5			
23	<i>A. anomala</i> NCBSAQ185	14.1	14.6	13.7	15.1	13.4	13.7	12.4	8.7	4.1	11.1	10.1	10.3	3.1	9.8	9.4	1.7	8.2	10.1	11.3	10.1	14.6	13.1		
24	<i>A. laudanka</i> ZSI_CZRC_5203	14.6	14.9	13.7	16.9	13.7	14.1	13.6	8.4	9.4	9.8	9.4	9.3	10.5	9.4	9.1	10.8	8.7	10.3	12.0	8.2	16.1	14.1	10.5	
25	<i>A. rufusculare</i> ITBCZ7504	7.9	9.3	8.7	11.0	10.3	10.3	9.3	11.8	10.8	13.0	12.2	11.7	11.8	11.8	12.9	12.3	13.0	12.9	14.1	13.6	10.8	7.9	12.2	12.5

Table 5b. Interspecific genetic distance (p -distance) estimated from ND4 locus.

Sl. No.	SPECIES	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21
1	<i>Ahaetulla flavescens</i> comb. nov. CESS260																					
2	<i>Ahaetulla flavescens</i> comb. nov. CESS340	0																				
3	<i>Ahaetulla flavescens</i> comb. nov. CESS347	0	0																			
4	<i>A. prasina</i> LSUHC586	8.23	8.23	8.23																		
5	<i>A. prasina</i> FMNH269042	10.9	10.9	10.9	11.6																	
6	<i>A. nasuta</i> RAP0517	17	17	17	16.6	16.1																
7	<i>A. pulverulenta</i>	16	16	16	14.6	14.4	9.89															
8	<i>A. borealis</i> BNHS3590	16.5	16.5	16.5	16.1	15.5	10.8	10.3														
9	<i>A. farnsworthi</i> BNHS3588	16	16	16	15	14.9	9.46	9.18	4.75													
10	<i>A. malabarica</i> BNHS3586	15.8	15.8	15.8	14.7	15	9.89	9.34	4.75	2.69												
11	<i>A. sathyadrensis</i>	16.6	16.6	16.6	16.6	15.2	14.9	10.5	3.8	10.4	8.86	9.18										
12	<i>A. isabellina</i> BNHS3584	16	16	16	14.7	14.6	11.6	7.91	10.9	9.34	9.97	8.7	9.81									
13	<i>A. dispar</i> CESS187	16	16	16	14.7	14.4	11.6	7.91	10.9	9.34	9.97	8.7	9.81									
14	<i>A. oxyrhyncha</i> CESS211	17.1	17.1	17.1	15.3	15.2	12.5	5.54	11.2	9.97	9.49	3.16	8.86	9.65								
15	<i>A. travancorica</i> CESS075	16.3	16.3	16.3	15.3	15	12.3	8.7	11.7	9.49	10.1	9.65	9.97	2.22	10.3							
16	<i>A. perroteti</i> CESS286	15.8	15.8	15.8	14.9	14.6	10.5	10.1	11.7	9.81	10.4	9.65	9.65	10.3	10.1	10.1						
17	<i>A. fronticincta</i> CAS222635	15.8	15.8	15.8	16.5	15.7	15.3	13.5	14.3	14.1	14.4	13	14.4	13	13.6	12.5	10.6					
18	<i>A. cf nasuta</i> FMNH255023	17.2	17.2	17.2	16.3	16	11.2	7.59	11.4	9.97	10.1	6.96	9.49	9.65	7.44	10.3	11.2	13.9				
19	<i>A. fasciolata</i> LSUHC8837	9.81	9.81	9.81	10.1	8.7	14.6	14.1	15	13.4	13.3	13.9	13.1	14.2	13.8	13.9	13.3	15.5	14.7			
20	<i>A. mycterizans</i> LSUHC8913	11.2	11.2	11.2	11.7	4.75	17.4	15.5	15.8	15	15.2	15.7	14.7	15.5	15.5	15.7	16	17.6	16.1	9.65		
21	<i>Prohaetulla antiqua</i> BNHS3573	17.7	17.7	17.7	17.4	16.6	17.8	15.8	16.3	16.3	16.3	15.8	16.1	16.9	15.8	16.9	15.5	17.3	16.5	16.9	17.4	

Table 5c. Interspecific genetic distance (*p*-distance) estimated from 16S locus.

Sl. No.	SPECIES	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23
1	<i>Ahaetulla flavescens</i> comb.nov. CESS260																							
2	<i>Ahaetulla flavescens</i> comb.nov. CESS340	0																						
3	<i>Ahaetulla flavescens</i> comb.nov. CESS347	0.2	0.2																					
4	<i>A. prasina</i> LSUHC8586	1.5	1.5	1.5																				
5	<i>A. prasina</i> FMNH269042	3	3	3.2	3.4																			
6	<i>A. borealis</i> BNHS3590	3	3	3.2	4.1	2.1																		
7	<i>A. farnsworthi</i> BNHS3588	3.6	3.6	3.6	3.6	2.8	1.5																	
8	<i>A. malabarica</i> BNHS3586	3.8	3.8	4.1	3.9	2.8	1.3	1.5																
9	<i>A. sahyadrensis</i> CESS159	3	3	3.2	4.1	2.1	1.7	2.4	2.6															
10	<i>A. pulverulenta</i>	3	3	3.2	4.1	2.1	1.7	2.4	2.1	1.7														
11	<i>A. isabellina</i> BNHS3584	3.4	3.4	3.6	3.4	2.4	0.9	1.1	0.4	2.1	2.1													
12	<i>A. dispar</i> CESS187	2.1	2.1	2.4	3.2	1.5	1.9	2.6	2.8	1.9	1.9	2.4												
13	<i>A. oxyrhyncha</i> CESS211	3.4	3.4	3.6	4.1	2.6	2.1	2.8	3	0.4	2.1	2.6	2.4											
14	<i>A. travancorica</i> CESS075	2.6	2.6	2.8	3.2	1.5	1.9	2.6	2.8	1.5	1.9	2.4	0.9	1.9										
15	<i>A. perroteti</i> CESS286	3.4	3.4	3.6	4.5	2.6	2.1	2.8	3	1.7	2.1	2.6	2.4	2.1	2.4									
16	<i>A. fronticincta</i> CAS222635	4.5	4.5	4.5	4.3	3.4	3.2	3.2	3	3.2	3.6	3	3.9	3.6	3.2	4.1								
17	<i>A. cf nasuta</i> FMNH255023	2.4	2.4	2.4	2.1	3.8	3.6	3.8	4.1	3.2	3.6	3.6	3.6	3.6	3.6	3.6	3.9							
18	<i>A. fasciolata</i> LSUHC8837	1.9	1.9	2.1	2.1	2.8	3	3.6	3.4	3	3	2.8	3.4	2.4	3.4	3.6	1.9							
19	<i>A. mycterizans</i> LSUHC8913	1.7	1.7	1.7	1.9	3.6	3.4	3.6	3.4	3	3.4	3.4	3	3.4	3	3.4	3.6	1.1	1.5					
20	<i>A. anomala</i> NCBS-AQ	3.8	3.8	3.6	3.9	2.8	2.6	3	3	0.9	2.1	2.6	2.8	0.9	2.4	2.6	3.4	3.4	3.4	3.2				
21	<i>A. laudankia</i> ZSI_CZRC_6203	3.9	3.9	3.7	4	2.4	3.1	3.5	3.5	2.2	3.1	3.1	2.9	2.6	2.4	3.1	3.7	4.4	3.5	4.2	2.2			
22	<i>A. prasina</i> CHS836	1.1	1.1	1.1	0.9	3	3.6	3.9	4.1	3.6	3.6	3.6	2.8	4.1	2.8	4.1	4.1	2.1	1.7	1.5	3.9	3.5		
23	<i>Proahaetulla antiqua</i> BNHS3573	5.3	5.3	5.6	6.4	5.3	4.9	5.1	5.8	4.7	5.3	5.3	4.7	5.1	5.3	4.7	6.9	6	6.2	5.8	5.6	5.5	6	

Table 5d. Interspecific genetic distance (*p*-distance) estimated from COI locus.

Sl. No.	SPECIES	1	2	3	4	5	6	7	8	9	10
1	<i>A. prasina</i> APR										
2	<i>A. prasina</i> APR01	4.5									
3	<i>A. prasina</i> CHS836	6.1	3.6								
4	<i>A. prasina</i> USNM:Herp:212416	14.6	12.8	12.1							
5	<i>A. prasina</i> USNM:Herp:212425	14.4	12.6	11.9	0.2						
6	<i>A. prasina</i> USNM:Herp:498921	14.0	12.3	11.3	3.2	3.0					
7	<i>A. prasina</i> ZSI/SHT14_MZMU1331	11.1	9.9	8.5	12.8	12.6	12.1				
8	<i>A. rufusoculara</i> ITBCZ7505	15.4	14.0	13.6	12.1	12.1	11.9	13.2			
9	<i>A. rufusoculara</i> ITBCZ7504	15.4	14.0	13.6	12.1	12.1	11.9	13.2	0.0		
10	<i>A. mycterizans</i> USNM:Herp:587040	16.0	14.4	12.3	11.5	11.5	10.9	13.0	7.9	7.9	

Table 5e. Interspecific genetic distance (*p*-distance) estimated from 12S locus.

	1	2	3	4	5	6	7	8	9	10	11	12	13
1	<i>A. prasina</i> CHS836												
2	<i>A. pulverulenta</i>	0.086											
3	<i>A. prasina</i> ROM30961	0.005	0.092										
4	<i>A. prasina</i> MK691460	0.026	0.082	0.030									
5	<i>A. prasina</i> MK691461	0.026	0.082	0.030	0.012								
6	<i>A. prasina</i> MK691462	0.026	0.080	0.030	0.025	0.022							
7	<i>A. prasina</i> MK691464	0.026	0.082	0.030	0.007	0.005	0.018						
8	<i>A. prasina</i> MK691466	0.026	0.080	0.030	0.034	0.027	0.032	0.027					
9	<i>A. prasina</i> MK691468	0.026	0.084	0.025	0.029	0.022	0.029	0.022	0.007				
10	<i>A. prasina</i> MK691469	0.023	0.080	0.028	0.029	0.025	0.015	0.022	0.027	0.027			
11	<i>A. prasina</i> MK691470	0.026	0.082	0.030	0.010	0.002	0.020	0.003	0.027	0.022	0.024		
12	<i>A. prasina</i> MK691472	0.026	0.082	0.030	0.034	0.027	0.034	0.027	0.017	0.013	0.034	0.027	
13	<i>A. prasina</i> MK691473	0.028	0.087	0.032	0.037	0.034	0.039	0.034	0.022	0.019	0.037	0.034	0.008
14	<i>A. prasina</i> MK691474	0.023	0.080	0.028	0.024	0.020	0.012	0.017	0.027	0.024	0.003	0.018	0.030 0.035

Differential diagnosis

A species of *Ahaetulla* inhabiting Northeast India, defined by the following combination of characters: dorsal scales in 15:15:11–13 smooth rows (vs 13 midbody rows of keeled scales in *Proahaetulla* Link, 1807); rostral appendage absent (vs present in the *A. nasuta* group and *A. pulverulenta* groups); presence of a pair of white ventrolateral stripes throughout the body (vs absence of ventrolateral stripes in the *A. pulverulenta* group); dorsum usually greenish (vs usually brownish in both sexes in the *A. pulverulenta* and *A. laudankia* groups; usually brown in females, in *A. anomala* (Annandale, 1906), *A. perrotetii* (Duméril & Bibron, 1854), *A. dispar* (Günther, 1864) and *A. travancorica* Mallik, Srikanthan, Pal, D'Souza, Shanker & Ganesh, 2020); crown uniform and unpatterned (vs crown with black markings and reticulations in *A. anomala*, *A. laudankia* Deepak, Narayanan, Sarkar, Dutta & Mohapatra, 2019 and *A. fasciolata*); ventrals 194–200 (vs < 190 in *A. nasuta* and *A. pulverulenta* groups); subcaudals 155–168 (vs < 120 in *A. perrotetii*, *A. dispar* and *A. travancorica*); cloacal scale paired (vs entire in *A. mycterizans* and *A. fasciolata*); supralabials entire (vs 3rd–4th supralabials horizontally divided in *A. fronticineta*); nasals not in contact with one another (vs in contact with one another above rostral in *A. fronticineta*); upper snout surface flat to mildly depressed (vs convex in *A. mycterizans*); 8.2–10% divergent in ND4 and 6.5–9.5% in Cytb gene from the SE Asian populations of *A. prasina* sensu lato.

Etymology

A Latin adjective, derived from Latin verb '*flavesco* / *flavesce*', meaning 'turning to yellow' / 'becoming yellow', referring to the yellowish colouration of the type specimens in life (see Wall 1910).

Type material

Lectotype (designated herein)

INDIA • ♀; "Lakimpur, Assam, Northeast India"; 27°13'40.8" N, 94°6'28.8" E; unknown date; Maj. F. Wall leg.; NHMUK (= BMNH) 1908.6.23.58.

Paralectotype

INDIA • ♀; same collection data as for lectotype; NHMUK (= BMNH) 1908.6.23.59.

Other examined material (2 ♂♂, 2 ♀♀)

INDIA – **Meghalaya** • 1 ♀; Shillong; unknown date; maj. F. Wall leg.; BNHS 1975 (green dorsum); BNHS • 1 ♂; Tura, Garo Hills; unknown date; H.W. Wells; BNHS 1978 (green dorsum); BNHS. – **Assam** • 1 ♂; North Lakimpur; unknown date; maj. F. Wall leg.; BNHS 1976 (buff dorsum); BNHS. – **Arunachal Pradesh** • 1 ♀; Janakamukh, Abor Hills; 10 Jun. 1912; 32, Sikh pioneers of Indian Museum; BNHS 1979 (green dorsum); BNHS.

Description

Lectotype (Figs 3, 5)

MEASUREMENTS (in mm). Body elongated, tapering anteriorly and posteriorly, slightly compressed laterally, slightly narrower at mid-body, mid-body width 7.5, flatter on ventral side. Total length 1335.0; snout to vent length 840.0. Head wider than the neck, head length 27.5, elongated anteriorly; slightly wider, head width 13.2; slightly depressed, head depth 11.6. Eyes lateral, circular in shape with oval with horizontal pupil; horizontal eye diameter 5.1 and vertical eye diameter 3.7; interorbital distance 7.4. Snout acuminate, canthus rostralis prominent; eye to snout distance 11.6, sub-equal to head width; eye to nostrils distance 8.0, inter-narial distance 5.4. Tail elongated, complete, tail length 495.0, relative tail length 37.0%.

SCALATION. Dorsal scales smooth, without any keels; dorsal scales are generally even-sized, comparatively smaller which are close to vent and the anterior end of body. Paravertebral scales broader than other

dorsal scale rows, with rounded posterior margin. Anterior scale rows 15 (on neck): mid-body scale rows 15 (at mid-body): posterior scale rows 13 (near vent), arranged in oblique series. Ventrals 206, angulate laterally, pre-ventrals 3; cloacal scales slightly enlarged, paired; subcaudals 168, pairs. Rostral deep and wider at its base; distinctly visible and narrowly grooved in dorsal aspect, without nasal appendage, projects beyond tip of lower jaw when viewed from below. Nasal slightly elongated, laterally oriented, contacting anteriorly with the rostrum on each side. Nostrils distinct, rounded, laterally oriented, situated on posterior surface of the nasal scale on each side. Internasals paired, contacting each other at midline, anteriorly contacting rostral, posteriorly contacting prefrontal and contacting nasal laterally on each side. Loreals two, subequal in size, anterior set of loreals contacting internasals on both sides, posterior loreal contacting anterior on right side. On left side, posterior loreal separated from anterior by 2nd, 3rd supralabials and lower edge of prefrontal contact. Supraocular single, enlarged, broader posteriorly, roughly triangular in dorsal aspect on each side. Preocular single, broad, reaching upper surface of head and contacting prefrontal and frontal on each side; on anterior side contacting the posterior parts of loreals. Fourth supralabial divided horizontally (Fig. 5). Postoculars two, upper one larger in size, contacting supraocular above and lower postocular below; lower postocular contacting 6th supralabial below on each side. Prefrontal paired, roughly rectangular in shape, contacting frontal posteriorly. Frontal single, roughly bell-shaped, situated in middle of two supraoculars, contacting parietal scales posteriorly. Parietal scales paired, large, much wider, roughly pointed posteriorly and sub-equal to supraocular scales in size. Each parietal scale, anteriorly contacting supraocular, fairly touching upper postocular, laterally in contact with upper temporals, posteriorly in contact with three small scales on each side. Temporals 2+2 on both sides; posterior set contacting three comparatively large sized scales on both sides. Supralabials 9 on both sides, 4th–6th contacting the eye and 7th being the largest. Mental small, much wider than long, subtriangular in shape, wedged between 1st pair of infralabials. Two pairs of genials; anterior set sub-equal to posterior set; both longer than broad; both pairs are in long midline contact. Infralabials 9, 11; 1st infralabial on each side elongate compared to the rest, medially contacting each other; 1st–4th infralabials contacting anterior set of genials; 4th and 5th infralabials contacting posterior pair of genials.

COLOURATION IN ETHANOL. Body overall greyish-brown to olive brown, a few small, pale yellowish patches along the trunk. Head mostly faded with grey or bluish grey colour; rostral, upper and lower labials faded grey to off-white, inter-scale colouration on anterior body black white; posteriorly at few places brownish white. Venter cream to light shades of grey; off-white ventrolateral stripe present from neck up to tail tip.

Paralectotype (Fig. 4)

Total length 1006.0; snout to vent length 631.0; tail length 375.0; relative tail length 37.2%; head length 28.5; head width 10.9; head depth 10.0; eye diameter 5.5; eye snout tip distance 10.6; eye nostril distance 7.2; interorbital distance 9.9. Anterior scale rows 15; mid-body scale rows 15; posterior scale rows 13; ventrals 203; pre-ventrals 3; cloacal scale 1; subcaudals 155 pairs; supralabials 9 (4th–5th touching eye); infralabials 9 (1st–5th touching genials); loreal 3; preocular 1; postoculars 2; temporals 2+2; dorsum brownish-green; venter of a lighter shade as dorsum; chin, throat and labials dirty white.

Variation (Table 4; also see Wall 1910)

The examined non-type specimens agree well with the type specimens and show the following intra-specific variations:

MEASUREMENTS (in mm). Total length 1059–1141; snout to vent length 679–768; tail length 373–380; head length 25.6–29.2; head width 9.5–9.6; head depth 7.0–7.1; horizontal eye diameter 4.5–4.6; vertical eye diameter 2.4–3.1; eye to nostrils distance 7.0–8.3; eye to snout tip distance 9.7–10.5; internarial



Fig. 3. *Dryophis prasinus* var. *flavescens* Wall, 1910, lectotype (NHMUK 1908.6.23.58). Entire profile, dorsal and ventral views. Photo: ©The Trustees of the Natural History Museum, London.



Fig. 4. *Dryophis prasinus* var. *flavescens* Wall, 1910, paralectotype (NHMUK 1908.6.23.59). Entire profile, dorsal and ventral views. Photo: ©The Trustees of the Natural History Museum, London.

distance 3.5–5.2; interorbital distance 7.3–9.1; mid-body width 7.1–7.7; internasal length 3.5–3.9; prefrontal length 3.6–5.7; frontal length 6.8–8.7; parietal length 5.3–7.3.

SCALATION. Ventrals 197–200; pre-ventrals 3; supralabials 8 or 9; infralabials 8 or 9; anterior scale row 15; mid-body scale row 15, posterior scale row, 11–13; subcaudals, 155–183. BNHS 1975 has 3 loreals on each side and single pre-subocular, contacting 4th supralabial below and preocular above.

COLOURATION IN LIFE (Figs 6–7). Usually verdant green above, with fluorescent green on the ventral side. A pair of creamy white ventrolateral stripes extends from near neck up to the tip of the tail. Labials, chin and mental region whitish to cream coloured. Inter-scalar skin with alternating black and white ragged bands. Iris yellowish-green with black horizontal pupil. On occasions, body overall yellowish-brown, with minute black dots along the trunk. Venter cream to light brown, flanked on either side by off-white ventrolateral stripes from neck up to tail tip.

Distribution and natural history

Ahaetulla flavescens comb. nov. is currently known from four Northeast Indian states: Arunachal Pradesh, Assam, Mizoram and Meghalaya (Fig. 8) (Wall 1910; Ahmed *et al.* 2009). This species was perhaps first recorded in Northeast India, under the name *A. prasinus* auctorum by Cantor (1847) who mentioned specimens from Bengal and Assam. The following localities were subsequently reported for this taxon, under the name *A. prasina*: Bengal (Günther 1858, 1864), Eastern Himalayas, Sikkim, Katchar, Naga, Jaintea and Khasi hills, (Theobald 1876), Darjeeling, Cherrapunji, Duffla hills, Naga



Fig. 5. *Dryophis prasinus* var. *flavescens* Wall, 1910, lectotype (NHMUK 1908.6.23.58). Head close-up showing the divided 4th supralabial on right side, a unique identifying character in ascertaining its type status. Photo: ©The Trustees of the Natural History Museum, London.

hills, Sibsagar and Cachar (Sclater 1891), Eastern Himalayas, Assam and Bengal (Boulenger 1890, 1896). Wall (1906, 1909a, 1909b) recorded this species from near Darjeeling and Jalpaiguri in Assam.

Judging by the geographic continuity and lack of morphological differences, we hypothesise that populations inhabiting other parts of Northeast India and immediately neighbouring areas of other countries could represent *A. flavescens*. Like other members of this group, *A. flavescens* is a diurnal, arboreal species inhabiting the wet hill forest tracts of Northeast India (Whitaker & Captain 2004; Ahmed *et al.* 2009). It is reported to be live-bearing, as Whitaker & Captain (2004) state “females bear 4-10 live young [in] May-June”, without reference to any country. However, Wall (1910) reported three “eggs” inside a type specimen that was collected in March–April. Given the current knowledge on the reproduction of members of this genus (Das 2002; Whitaker & Captain 2004; Wallach *et al.* 2014), we hypothesise that Wall was probably referring to the caul or outer amniotic layer encapsulating the embryos of viviparous snake species. Wall (1910) also reported the presence of a gecko in its gut content. Based on our primary field observations, *A. flavescens* is somewhat temperamental with some individuals becoming defensive when restrained, displaying their open-mouth gape and striking forwards with a jerky motion.

Comments

Das & Chaturvedi (1998) remarked that *Dryophis prasinus flavescens* Wall, 1910 was described based on six syntypes. We clarify here that Wall only included the three buff-coloured snakes as part of the type series, whereas the green-coloured specimens were termed “forma typica”. Das & Chaturvedi (1998) remarked that BNHM (= BNHS) 1976, a buff-coloured specimen from Lakimpur, Assam is an extant syntype. Wall (1910) reported a ventral range of 200–209 including preventrals and 155–174 subcaudals, whereas the ventral count of BNHS 1976 is 183, clarifying that it is not a syntype. Das & Chaturvedi (1998) commented that other syntypes may in fact exist, without mentioning any repository. Our investigation proved that they are in London, registered as NHMUK (= BMNH) 1908.6.23.58–59 (Fig. 6). Apart from congruence in locality, collector and sex of the snakes, the ventral and subcaudal counts also match well. Wall (1910) reported 205 ventrals for both snakes and 155, 167 subcaudals, whereas we counted 203, 206 ventrals (+ 1 to 3 preventrals) and 155, 168 subcaudals. Wall (1910) gave measurements for only one of his syntypes from Lakhimpur, total length 5'7" (= 1701 mm), tail length 1'7.5" (= 495 mm). The tail length of the lectotype (NHMUK 1908.23.6.58) matched fully, although its total length was only 1335 mm. Above all, Wall (1910) stated that 4th supralabial is divided on the right side, which completely matches with the NHMUK (= BMNH) 1908.23.6.58 specimen. Lastly, Das & Chaturvedi (1998) stated that Smith (1943) erroneously credited the taxon authorship of *Dryophis prasinus flavescens* to Smith (1915; sic, for 1914) and the type locality was given as Trang Pen, Siam. We further add that Smith's treatment and usage of this nomen was only a chresonym, when

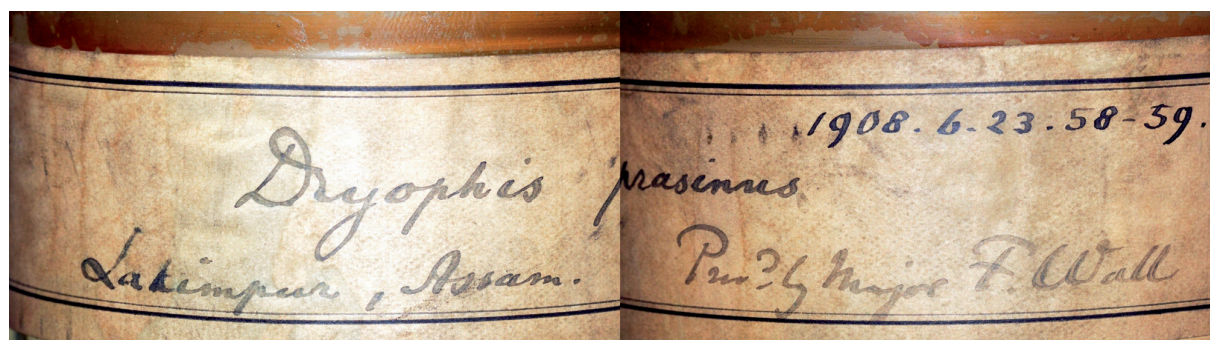


Fig. 6. *Dryophis prasinus* var. *flavescens* Wall, 1910, lectotype (NHMUK 1908.6.23.58) and paralectotype (NHMUK 1908.6.23.59). Jar label. Photo: ©The Trustees of the Natural History Museum, London.

he followed Wall's subspecies arrangement upon finding a buff variety in Siam, i.e., Thailand (see our chresonymy for unambiguity). In essence, we here demonstrate that the first two buff-coloured female snakes Wall dealt with while describing *A. flavescens* are indeed NHMUK (= BMNH) 1908.6.23.58–59.

Here, we clarify the confusions about the identity of the type specimens, rediscover and redescribe the type specimens, prove the specific distinction of this nominal taxon and resurrect it as a valid species. Hence, we evoke Art. 74.7 of the Code (ICZN 1999) and designate NHMUK (= BMNH) 1908.6.23.58 as the lectotype of *Dryophis prasinus flavescens* Wall, 1910. The chosen lectotype is the larger of the two type specimens, has characters that enable its unambiguous recognition, has precise provenance data and is deposited in a scientific institution of permanent record.

Discussion

Recent studies on species complexes in the genus *Ahaetulla* from several countries have revealed gross underestimation of species diversity within the group, which is now being addressed and resolved through molecular phylogenetic studies. Such studies have been conducted on the *A. nasuta*, *A. pulverulenta*,



Fig. 7. *Ahaetulla flavescens* (Wall, 1910) comb. nov. Live uncollected specimens from Arunachal Pradesh, showing the unusual buff or yellowish-brown colouration. Photo: Bharat Bhushan Bhatt.

A. prasina and *A. mycterizans* groups from Peninsular India, Sri Lanka and Indonesia (Mohapatra *et al.* 2017; Deepak *et al.* 2018; Mallik *et al.* 2019, 2020; Indahsari *et al.* 2020; Lam *et al.* 2021). Thus, it is not surprising that the Northeast Indian population of *A. prasina* (sic), once described as a new “variety” (Wall 1910) and then synonymized (Smith 1943), represents a cryptic lineage that is highly divergent and allopatric with respect to the Southeast Asian *A. prasina* complex (Indahsari *et al.* 2020).

A full taxonomic revision of the entire *A. prasina* complex is beyond the scope of the present study. However, using our new phylogenetic and field data as well as data from the old specimens at NHMUK and BNHS, we have resurrected the nomen *Dryophis prasinus flavescens* Wall, 1910. Based on the enormous geographic distance of nearly 1000 km and the known molecular (Indahsari *et al.* 2020) and morphological (Gaulke 1994; Lazell 2002) divergences in the *A. prasina* complex, we are certain that *Ahaetulla flavescens* of Northeast India will not be conspecific with *Tragops prasinus laetus* Cope, 1861 from the Philippines, the only synonym senior to Wall’s nomen. As stated in Mallik *et al.* (2020), the description (Wall 1910) and synonymisation (Smith 1943) of *A. flavescens* by Wall, especially his diagnosis of subspecies, is primarily based on colouration and not on geographic range, which highlights the overarching influence of external morphology and its variation in creating many species descriptions within the complex. For example, Taylor (1922) described two new forms of the *A. prasina* complex, largely prompted by external morphological differences.



Fig. 8. *Ahaetulla flavescens* (Wall, 1910) comb. nov. Live uncollected specimen from Mizoram, showing the usual green colouration which is dominant in this species. Photo: Ajay Karthik.

Wall (1910) was still of the opinion that the green ‘forma typica’ populations in Northeast India represent *A. prasina* (sic) and that it is the colouration that differentiates *A. flavescens*. Wall (1909a, 1909b) recorded this species (as *Dryophis prasinus*) from other parts of Northeast India, but failed to discuss anything about their taxonomy, largely because they were all regular, green-coloured snakes. But sightings of the buff variety prompted Wall to discuss their taxonomy, putting weightage on colour differences. However, based on the current understanding of distributions, it seems that geographic barriers may have prompted the cryptic diversification of the *A. prasina* complex across its range (also see Indahsari *et al.* 2020). Our work on these *A. prasina* populations further emphasizes the underappreciated role of geographic disjunction, coupled with cryptic morphology covering the underlying deep genetic divergence that has rendered the status of the *A. prasina* group, and other similar groups, so challenging.

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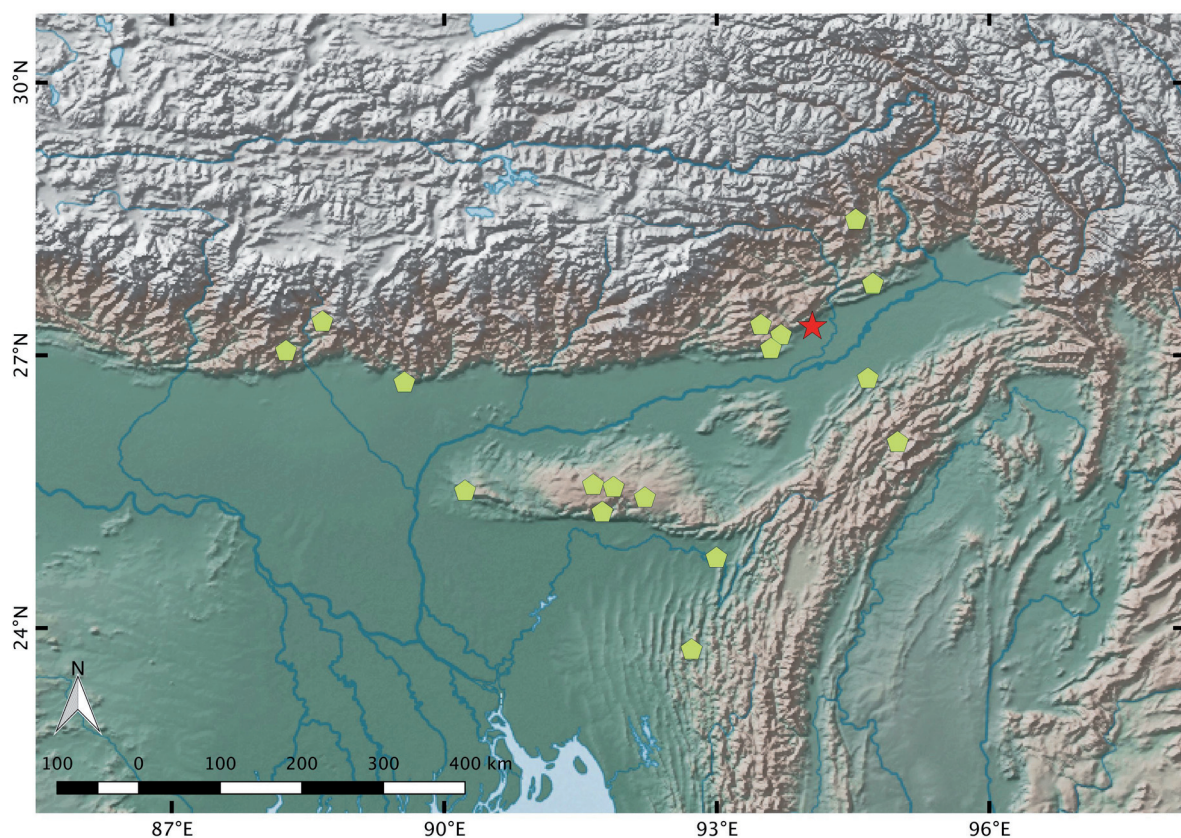


Fig. 9. Map of Northeast India, showing the distribution records of *Ahaetulla flavescens* (Wall, 1910) comb. nov.; red star represents the type locality.

on museum specimens. ODA and ANS thank all the BNHS museum staff: Vithoba Hegde, Vinod Patil, Parshuram Parvate and Shyam Jadhav for their encouragement and assistance during this work. AKM thanks L. Lee Grismer for providing geographic localities of a few species of *Ahaetulla* from Southeast Asia, Romulus Whitaker, Gerry Martin and Toba Tao for their help in the collection of tissue samples and their work in the field. SRG thanks the Executive Chairman and Trustees of the Chennai Snake Park for encouraging his research activities and Ajay Karthik for sharing his photos of *Ahaetulla*. SRG is grateful to Dr Patrick David (MNHN, France) for all his thought-provoking discussions on *Ahaetulla*, for providing important literature and his taxonomic and nomenclatural advice on the genus and Indochinese snake fauna in general.

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Supplementary file

Supp. file 1. Fig. S1. A maximum likelihood tree reconstructed using IQTREE with a concatenated dataset of five genes. The five mitochondrial gene tree also indicates the monophyly of *Ahaetulla flavescens* (Wall, 1910) comb. nov. and the presence of two more lineages (Polillo and Luzon Island, from Philippines, and Borneo) belonging to *Ahaetulla prasina* complex. However, the nodes for the Indonesian *A. prasina* complex are weakly supported as there is inadequate data for 12S or COI genes. <https://doi.org/10.5852/ejt.2022.839.1937.7799>

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