

Resolving pitfalls in pit viper systematics – A multi-criteria approach to species delimitation in pit vipers (*Reptilia*, *Viperidae*, *Craspedocephalus*) of Peninsular India reveals cryptic diversity

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Abstract

Asian pit vipers belonging to the genus *Craspedocephalus* are a complex group of vipers, distributed in South and Southeast Asia. Their taxonomy is unresolved in many lineages across their distributional range. Here, we reassess the taxonomy and systematics of pit vipers of the genus *Craspedocephalus* in Peninsular India based on extensive field sampling, in particular in the Western Ghats. We build and expand on the previous findings of genetic relatedness between the peninsular Indian lineages with the Sundaic clade (*C. puniceus* complex) with greater evidence, based on additional taxa sequenced herein. We reconstruct the phylogeny of the group using three mitochondrial genes and delineated lineages using coalescent species delimitation methods. We then used multiple criteria including genetic divergence and separation in morphological and geographic space to designate taxonomic units. Our work revealed the presence of a South Asian radiation of the clade *Craspedocephalus*, with a few Sundaic members. Our study reveals the systematic relationships of four Peninsular Indian species of *Craspedocephalus*, including *Peltopelor macrolepis* and *C. strigatus*, sequenced here for the first time, that are classified or confirmed as members of *Craspedocephalus*. Hence, we place the genus *Peltopelor* in the synonymy of *Craspedocephalus*. Using our multi-criteria approach, we delimit four new cryptic evolutionary lineages within the Western Ghats escarpment of Peninsular India. These cryptic lineages belong to the *C. malabaricus*, *C. gramineus* and *C. macrolepis* complexes and are geographically and/or ecologically (in terms of habitat association) distinct from their sister lineages across their distributional range, while others are separated in morphological space. Our new phylogenetic tree and delimitation analysis thus reveals the presence of multiple clades with several cryptic lineages separated by geographical barriers or habitat association.

Keywords

Craspedocephalus, cryptic species, geographical barriers, phylogenetics

Introduction

Pit vipers are a group of venomous snakes that comprise several genera of vipers with a facial pit; they are terrestrial and arboreal in habit and predominantly found in wet, humid forests and montane habitats as well as in a few dry forest habitats in the Oriental realm. Pit vipers of the genus *Craspedocephalus* Khul & Hasselt, 1822 are a taxonomically complex group of venomous snakes and comprise nine recognized species distributed in South and Southeast Asia, mainly in forested and mountainous tracts (Wallach et al. 2014). These species were, till recently, largely assigned to the genus *Trimeresurus* and continue to be referred to as such in many accounts (David et al. 2011). In Peninsular India, the species level taxonomy of this genus has not been refined since the early 20th century (Rao 1917).

Some of the first members of the group to be named were from the Indian peninsula such as *Coluber gramineus* (now *Craspedocephalus gramineus*) by Shaw (1802). Subsequently, many such nominate descriptions were made across Peninsular India (see Smith, 1943). Three more taxa – *Trimeresurus strigatus* Gray, 1842, *Trigonocophias malabaricus* Jerdon, 1854 and *Trimeresurus macrolepis* Beddome, 1862 – were described. Subjective synonyms and generic reallocations have been provided for these taxa that are currently placed under the genus *Craspedocephalus* (David et al. 2011, Wallach et al. 2014). Of these, *C. gramineus* has, in particular, had a long and convoluted taxonomic and nomenclatural history; in the past it was considered as a single, widespread and variable species from Peninsular India through the Indochina subregion to insular Southeast Asia (see Pope & Pope, 1933).

In a pioneering attempt to reconstruct a molecular phylogeny of the snakes of the *Trimeresurus* radiation, Malhotra & Thorpe (2004) recovered a tree revealing close clustering of southern Indian and Sri Lankan taxa with some Indo-Malayan ones (see their ‘Clade E’). They also established molecular relationships of two Peninsular Indian congeners, *C. gramineus* and *C. malabaricus*. Malhotra & Thorpe (2004) allocated most southern Indian taxa to the genus *Trimeresurus*, with one lineage (*macrolepis*) assigned to the genus *Peltopelor* Günther, 1864, based mainly on scalation and hemipenial characters that were jointly diagnostic of the mitochondrial clades (Malhotra & Thorpe, 2004). This was further reinforced by osteological characterisation of the skull (Guo et al. 2009, 2010).

The following taxa recognized as valid (Wallach et al. 2014) are relevant to the present work: *C. gramineus* (Shaw, 1802) inhabiting the hills of Peninsular India; and *C. strigatus*, *C. malabaricus* and *P. macrolepis* that are endemic to the Western Ghats (Wallach et al. 2014). However, the phylogenetic relationships of *P. macrolepis* and *C. strigatus* are unknown due to the absence of genetic data (Malhotra & Thorpe, 2004, Guo et al. 2010). These taxa not only inhabit multiple discrete ecoregions and habitat patches but also show considerable morpho-

logical variation among populations (Whitaker & Captain 2008, Kanagavel et al. 2012, authors’ personal observations).

Though previous genetic studies on the *Trimeresurus* radiation have included Peninsular Indian taxa, a dedicated study with comprehensive geographic sampling and a robust phylogenetic analysis is still lacking. Prompted by the morphological variations and informed by biogeographic processes, this study approaches the systematics of Peninsular Indian species using a multi-criteria approach. Here, we assess and delimit species boundaries in pit vipers of Peninsular India to reassess species diversity within this group and implement formal nomenclatural changes.

Material and methods

Taxon Sampling and Area of Study

Sampling was carried out in Peninsular India, including in the Western Ghats (WG) and the Eastern Ghats (EG), and in Northeast India as part of Indo-Chinese sub-region. Field surveys and collections were carried out in all possible habitat types, across environmental gradients and at different elevations, as well as type locality locations to maximize the sampling of both rare and range-restricted species, and to capture intra-species variability. Snakes were captured alive and tissue and scale samples were collected by non-intrusive methods and stored in 95% ethanol; snakes were released unharmed after sample collection and measurement. We also collected samples from dead specimens encountered on roads; voucher specimens and samples were collected and preserved in 95% alcohol. The specimens were deposited at Bombay Natural History Society (BNHS). The fieldwork was carried out with the prior written permission from the state forest departments of Maharashtra, Kerala, Karnataka, Tamil Nadu, Odisha, Andhra Pradesh, Arunachal Pradesh and Meghalaya.

Molecular Analysis

DNA Extraction and Amplification

Total genomic DNA was extracted from all available tissue samples stored in 95% absolute alcohol. Genomic DNA was extracted using commercially available DNEasy extraction kit (QIAgen) as well as Phenol-Chloroform-Isoamyl alcohol protocol (Sambrook et al. 1989). To elucidate the phylogenetic relationships between members of the clade, sections of mitochondrial genes including 16S rRNA, Cytochrome-*b* (cyt *b*), and NADH dehydrogenase subunit 4 (ND4) were amplified with previously published primers (see Supplementary File 1: Table S1). The PCR conditions and preparation protocol were the same as in earlier studies; however, modifica-

tions of annealing temperature were applied in a few PCR reactions. PCR amplified products were purified using QIAquick PCR purification kit (Qiagen). The sequencing of purified products was carried out commercially from 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 v5.2 (Tamura et al. 2011). The individual consensus sequences were derived from forward and reverse complements after checking for base miscalls. The sequence alignment was accomplished in MUSCLE (Edgar 2004) algorithm implemented in MEGA v5.2. The protein-coding genes *cyt b* and *ND4* were checked for presence of indels and noncoding sequences to detect possible pseudogene amplification and premature stop codons by translating DNA to protein sequence. The 16S rRNA sequences were aligned against GenBank data submitted by earlier studies (Malhotra & Thorpe 2004) and visually edited; ambiguously aligned regions and gaps were cropped out of the analysis due to the presence of secondary structures in the sequence (Kjer 1995, Parkinson 1999, Gutell 2004). A matrix of 2154 bp was created by combining all three mitochondrial gene datasets. The gaps present in the dataset were treated as missing data. Available sequences for other species of the *Trimeresurus* radiation were downloaded from GenBank (See Supplementary File 2: Table S2).

Phylogenetic Analysis

We reconstructed the phylogeny of pit vipers to understand the relationships of pit vipers of Peninsular India including endemic species (*C. strigatus* and *C. macrolepis*) from the Western Ghats, which had not been included in earlier work (Malhotra & Thorpe 2004). The 2154 bp matrix was analysed with codon partitions where different codon positions of *cyt b* and *ND4* genes were considered as different partitions using PARTITIONFINDER v1.1.1 (Lanfear et al. 2012). A Maximum Likelihood (ML) tree was reconstructed with non-parametric bootstrapping in RAXMLGUI v1.3 (Silvestro et al. 2012, Stamatakis 2006). The RAXML GUI platform implements only GTR substitution model. Therefore, the analysis was carried out with 1000 bootstrap replicates and GTR-GAMMA model was applied to every partition in this analysis. To root the tree, we used *Protobothrops mucrosquamatus*, *Protobothrops jerdonii* and *Protobothrops kaulbacki* as outgroups. The resulting tree was visualized in FIGTREE v1.4.3 (<http://tree.bio.ed.ac.uk/software/figtree>).

Morphological Measurements and Pholidosis

Morphological data were collected from all sampled specimens. Pholidosis analysis was carried out in the field as well as in the laboratory on preserved specimens (See Supplementary File 3: Table S3). Morphometric measure-

ments were carried out with Mitutoyo Vernier calipers (to the nearest to 0.1 mm). We also examined specimens that were morphologically different in scalation or colour as potential ecomorphs. Sampling was carried out in every possible habitat type and along the environmental gradient to scrutinize the possible morphological space shared by individuals with respect to distance and isolation. We recorded the body colouration of individuals belonging to each population and examined both overall colour from head to tail as well as change in colour, if any occurred. Colour variation of ventral scales along with any blotches and speckles present on the ventral shields were also recorded.

Geographical Distribution

We recorded geographic locations for each individual sample collected with the help of a GPS (WGS84) to identify isolation and geographic barriers between lineages if any.

Species Delimitation

For identification of putative species and delimiting species boundaries between clades, we used a multi-criteria approach including phylogeny, coalescent species delimitation (bPTP), genetic distance, morphological characters, and geographic and ecological isolation (Shanker et al., 2017). First, a broad level phylogeny was reconstructed to determine the position of the Peninsular Indian lineages of *Craspedocephalus*. The results showed the presence of a few potentially new lineages distributed in the Western Ghats and Peninsular India. We tested the congruence of these lineages with PTP estimates using three concatenated mitochondrial loci (*cyt b*, *ND4* and 16S) (Zhang et al. 2013). We used the online-based server for bPTP and ran 500000 MCMC iterations to get convergence (<http://species.h-its.org/ptp>). From the bPTP output, the identified lineages on the tree were evaluated carefully using other criteria prior to elevation of evolutionary significant lineages as a putative species.

We calculated genetic p-distance between clades for three mitochondrial loci (*cyt b*, *ND4*, and 16S rRNA) separately in MEGA, and designated deep and shallow divergent lineages. There is shallow genetic divergence (e.g. 1.9 % at *cyt b*, 1.5% at 16S, 2.2 % at *ND4*) between a few closely-related sister species (e.g. *Trimeresurus andersoni* vs. *Tri. purpureomaculatus* and *Tri. erythrurus*) of pit vipers with clear morphological differentiation, which were used as a benchmark for comparison. We considered distances of > 7 % at *cyt b* to be deeply divergent and such lineages were treated as independently evolving and designated as species on the basis of depth of genetic divergence alone. Other lineages were further examined (using additional individuals) along the other axes of morphology and geography to determine whether they should be designated as species. Shallow divergent lineages were designated as species only if they differed in morphology and were geographically isolated.

Results

Phylogenetics

The mitochondrial tree topology derived from Maximum Likelihood analysis of the combined dataset is similar to the tree topology obtained in earlier studies on *Trimeresurus* (Malhotra & Thorpe 2004, Malhotra et al. 2010). The tree has two separate clades (supported by 100 % bootstrap value) (Fig. 1, 2). One clade (clade A) consists predominantly of Peninsular Indian and Sri Lankan taxa as well as two species from Southeast Asia and is referred to as the ‘Peninsular Indian group’. The other clade (clade B) in the tree predominantly comprises *Trimeresurus* species (e.g. *Tri. salazar* and *Tri. erythrurus*) found in the drier parts of Peninsular India (Gowri Shanker, personal communication) and other genera of pit vipers (e.g. *Popeia* and *Viridovipera*) found in the foothills of Himalayas, Indo-Burma sub-region, South China and Southeast Asia.

All Peninsular Indian taxa are clustered within a single clade along with two species from Southeast Asia. Based on our results, we refer to this clade henceforth as the genus *Craspedocephalus*. *Peltopelor* is nested within the *Craspedocephalus* clade and since *Craspedocephalus* Khul & Van Hasselt, 1822 has nomenclatural priority over *Peltopelor* Günther, 1864, the generic name for all Peninsular Indian taxa sampled here should continue to be *Craspedocephalus*.

The two species from Southeast Asia, *C. borneensis* and *C. puniceus* (clade I) are sister to the Peninsular Indian and Sri Lankan group (clade II) consisting of *C. macrolepis*, *C. strigatus*, *C. malabaricus* and *C. gramineus* from Peninsular India and *C. trigonocephalus* from Sri Lanka. Within clade II, the *Craspedocephalus macrolepis* species complex is sister to the other taxa distributed in Peninsular India and Sri Lanka (clade III). Within clade III, clades IV and V share a sister relationship. Clade IV comprises the *C. malabaricus* species complex, which is distributed throughout the Western Ghats and is represented by three separate lineages. Two of these lineages are distributed in the southern Western Ghats; the other is in the northern and central Western Ghats, separated by the Palghat Gap from the two southern lineages. Clade V consists of *C. strigatus* and a clade comprising *C. trigonocephalus* and the *C. gramineus* species complex. The *C. gramineus* group has two separate evolutionary lineages, which are distributed across the Indian peninsula.

Species Delimitation

We delimited species boundaries of the *Craspedocephalus* populations in Peninsular India (Fig. 2, See Supplementary File 4: Fig. S1). Based on a combination of criteria (genetic, geographical and morphological), we inferred a total of seven lineages within the *C. gramineus*, *C. malabaricus* and *C. macrolepis* species complexes in Peninsular India (Figs. 1, 2; See Supplementary File 5: Ta-

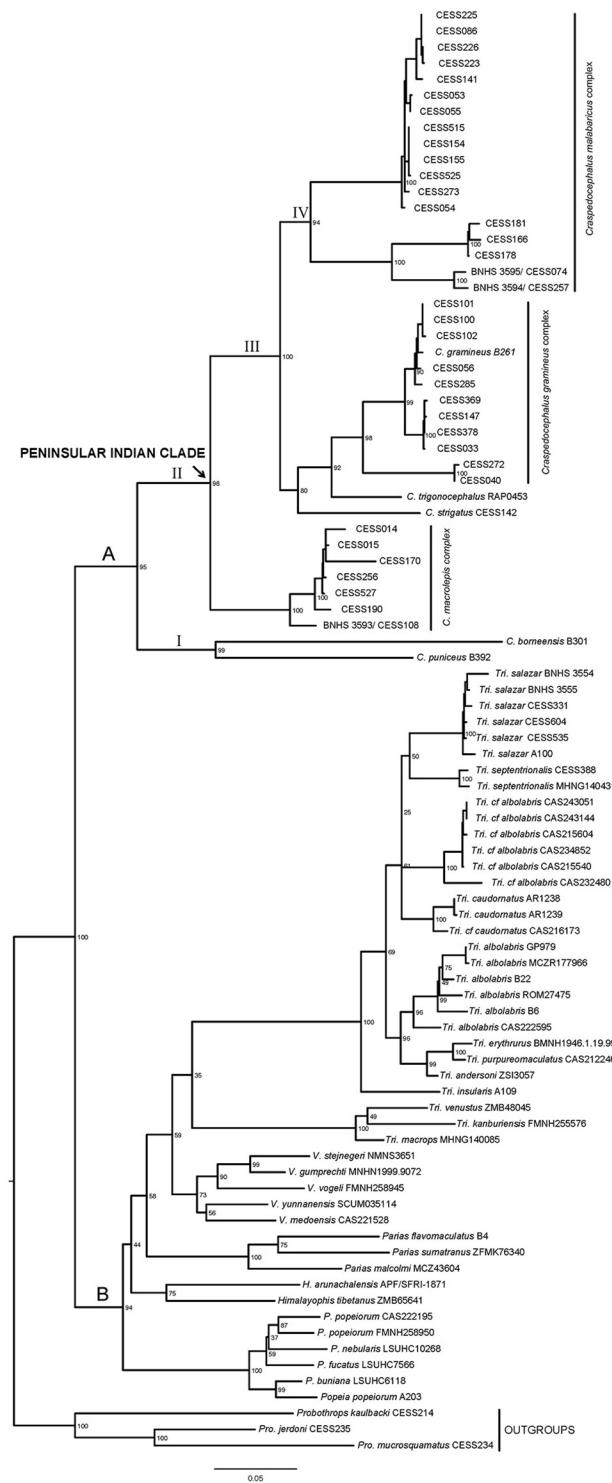


Figure 1. Maximum Likelihood tree reconstructed from a concatenated dataset of three mitochondrial genes (cyt b, ND4 and 16S) for almost all the species of pit vipers found in Peninsular India and the Indo-Burmese sub region. The tree shows two separate major clades (Clade A & B). Clade A includes all peninsular Indian species along with a few taxa from Southeast Asia, while clade B predominantly comprises species from other parts of central India, China and Southeast Asia.

ble S4). *Craspedocephalus malabaricus* comprises three evolutionary lineages whereas *C. gramineus* and *C. macrolepis* comprise two separate lineages each. In addition, an eighth lineage, *C. strigatus*, is part of this clade.

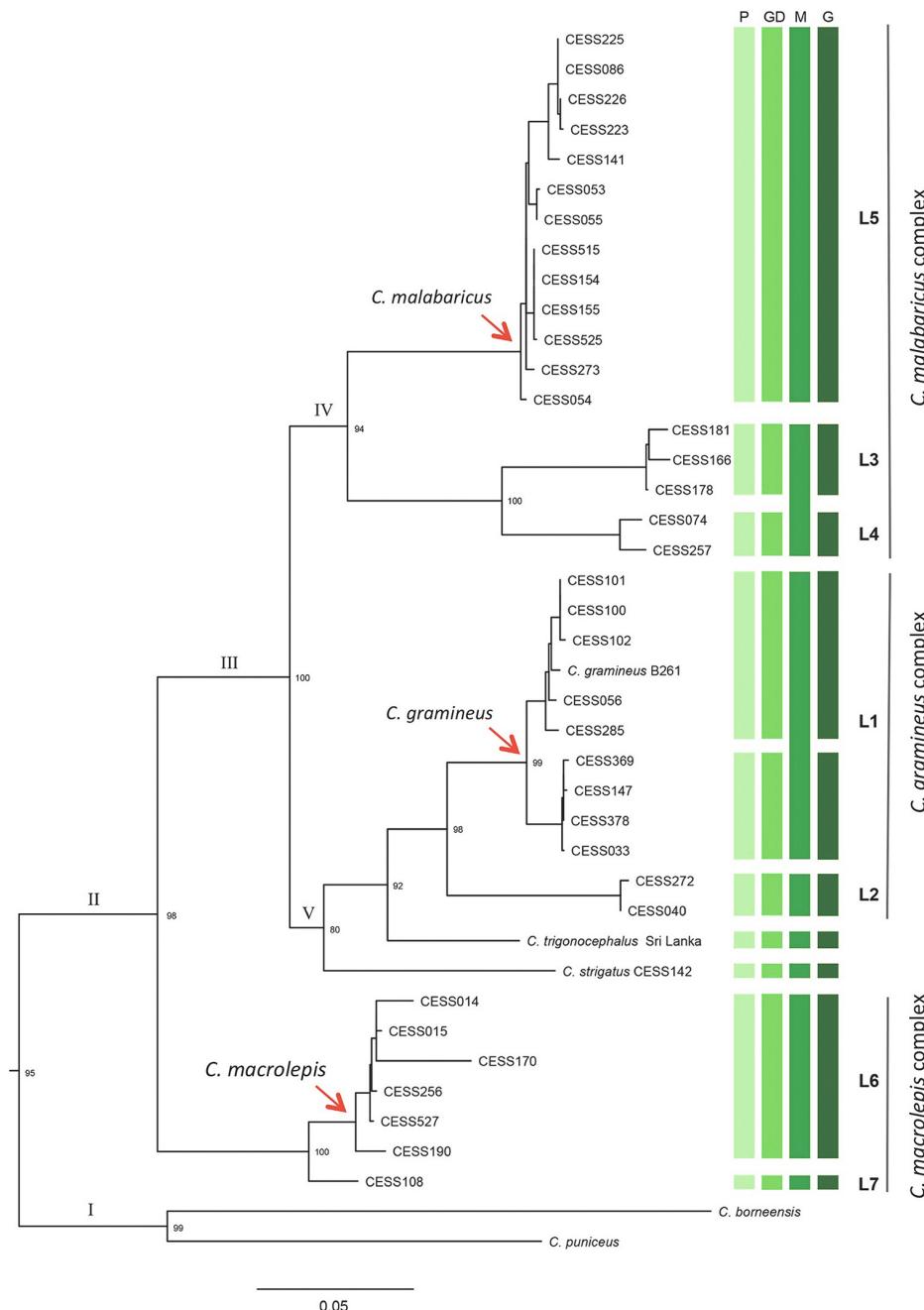


Figure 2. A Maximum Likelihood tree generated from three mitochondrial genes shows the Peninsular Indian, Sri Lankan (I) and Southeast Asian (II) clades. In the Peninsular Indian group (I), the new lineages (L1–L7) are marked with different green bars, which represent the different criteria used to delimit the species boundary. P represents the putative species predicted by bPTP analysis, while GD, M and G represent genetic distance, morphology and geographic isolation. All clades are supported with >70% parametric bootstrap value (see Fig. 1).

The three new lineages in the *C. malabaricus* species complex have low levels of morphological divergence but strong genetic differences due to geographic isolation (Fig. 2, 3). The northern WG group (L5) is isolated from the southern WG group by a geographic barrier, the Palghat gap, which is evident in the genetic divergence between the north-south clades. For the lineages L3 and L4 from the southern WG, the boundary can only be broadly identified as the Periyar Plateau. There was no difference in the quantitative morphological characters between any of the lineages, but the body colour pattern of the southern WG groups (L3 & L4) differentiates them from the

northern population (L5). In addition, there are morphological differences between the females of the southern (L4) and the northern (L5) group. The southern group has a conspicuous post-ocular streak, which is barely visible (or sometimes completely absent) in the northern population. In addition, the southern population has strongly keeled serrated scales on the head compared to the northern population.

Similarly, there is a shallow genetic break, morphological separation and geographical isolation between the populations of *C. macrolepis*. The lineages are divided by the Shencottah gap as a physical barrier. There is a higher

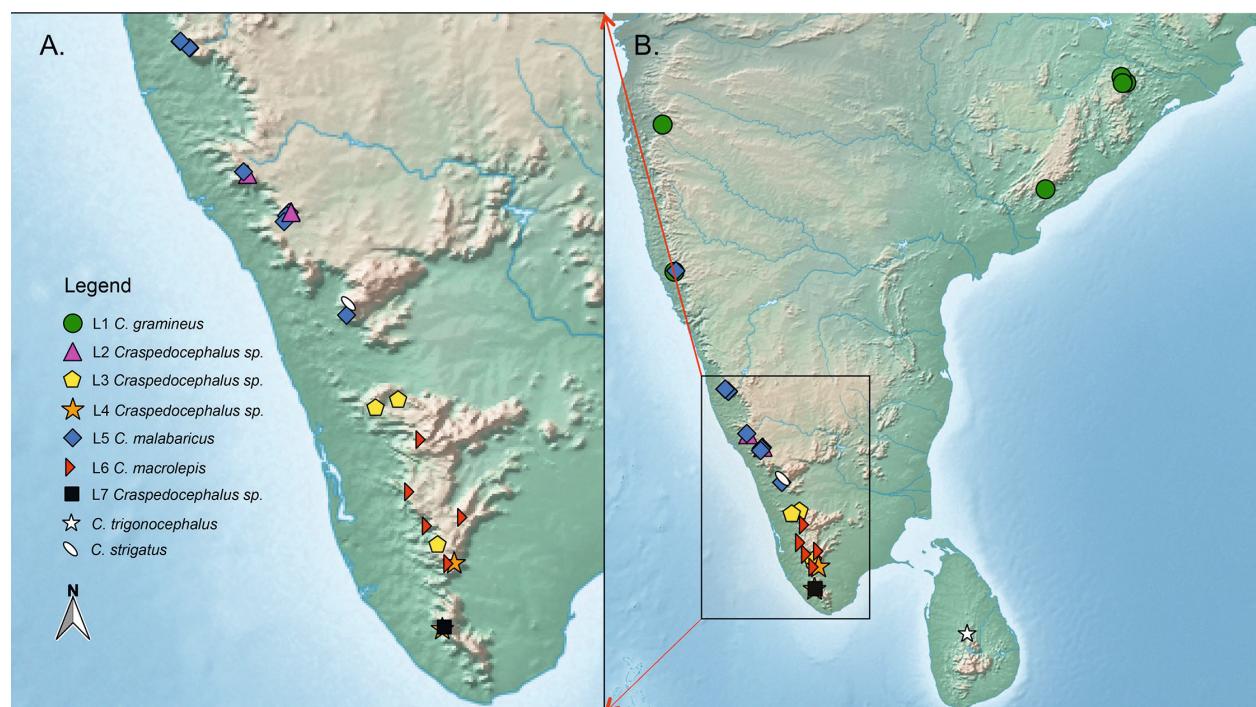


Figure 3. The distribution of *Craspedocephalus* lineages in the Western Ghats (A), in Peninsular India and Sri Lanka (B). L1–L7 the coloured dots indicate the lineages present within the genus *Craspedocephalus* (See Supplementary File 6: Figure S2).

ventral shield count in the southern lineage (L7) than the northern lineage (L6) (Fig. 2). The shallow genetic divergence (3.7% cyt b and 0.7–1.0% 16S rRNA) between lineages L6 and L7 is the lowest genetic break for the lineages inferred here, but is supported by other criteria including bootstrap support on the ML tree, geographical isolation, and morphological data.

Taxonomy

Viperidae Oppel, 1811

Crotalinae Oppel, 1811

Craspedocephalus Khul & Hasselt, 1822

Craspedocephalus macrolepis complex

This species complex can be distinguished from regional congeners as follows: head scales large, shield-like (vs. as small as body scales in the *C. gramineus*, *C. malabaricus* complexes and *C. strigatus*); midbody dorsal scale rows < 19 (vs. 21 or more in the *C. gramineus*, *C. malabaricus* complexes and *C. strigatus*); last rows of costal scales abutting ventrals on either side smaller than rest of the dorsal scale rows (vs. larger in all other congeners throughout the range of the genus); 2nd supralabial bordering the anterior margin of loreal pit (vs. not so in *C. strigatus*); supraoculars undivided (vs. frequently divided in the *C. malabaricus* complex); subcaudals of the tail tip bluish (vs. blackish in the *C. malabaricus* complex).

Craspedocephalus macrolepis (Beddome, 1862)

Figures 4–6

Trimeresurus macrolepis Beddome, 1862

Peltopelor macrolepis (Beddome, 1862) – Günther, 1864; Malhotra & Thorpe, 2004

Trimeresurus macrolepis – Hutton, 1949; Malhotra & Davis, 1991; Vijayakumar et al., 2001; Chandramouli & Ganesh, 2010; Bhupathy & Sathishkumar, 2013

Trimeresurus (*Peltopelor*) *macrolepis* Beddome, 1862 – David et al., 2011

Craspedocephalus macrolepis (Beddome, 1862) (this work)

Taxonomic history. Beddome (1862) described this species from the Anaimalai and Palani hills. The uniqueness of this species resulted in its being assigned to its own genus *Peltopelor* in a subsequent treatment by Günther (1864). Later, Smith (1943) subsumed this genus into *Trimeresurus*. Malhotra and Thorpe (2004) suggested a revised taxonomy for all *Trimeresurus* (sensu lato) groups and assigned them to different genera, reinstating *Peltopelor* as a valid genus (also see Wallach et al. 2014).

Type. Lectotype, NHMUK 1946.1.18.72 (formerly BMNH 1861.12.30.80), a male (R.H. Beddome, 1857–1862), designated by Toriba in Golay et al. (1993: 101).

Material examined. Specimen series: **Lectotype** – NHMUK 1946.1.17.72 from “Anamallay Mountains, at 6000 feet” collected in 1857–62 by R. H. Beddome; CESS014, CESS015 from Vellimala, Periyar and CESS190 from Rajamalai, Kerala, collected in 2011, by Ashok Kumar Mallik; CESS170 from Uppupara, Goodrickal Range-west, Kerala,



Figure 4. *Craspedocephalus macrolepis* comb. nov. in life, showing: (A) juvenile entire view from High Wavy Mountains, (B) close up of hindbody and tail, (C) entire lateral view, (D) head dorsal view, (E) head and forebody lateral view; from Eravikulam, Anaimalai range.

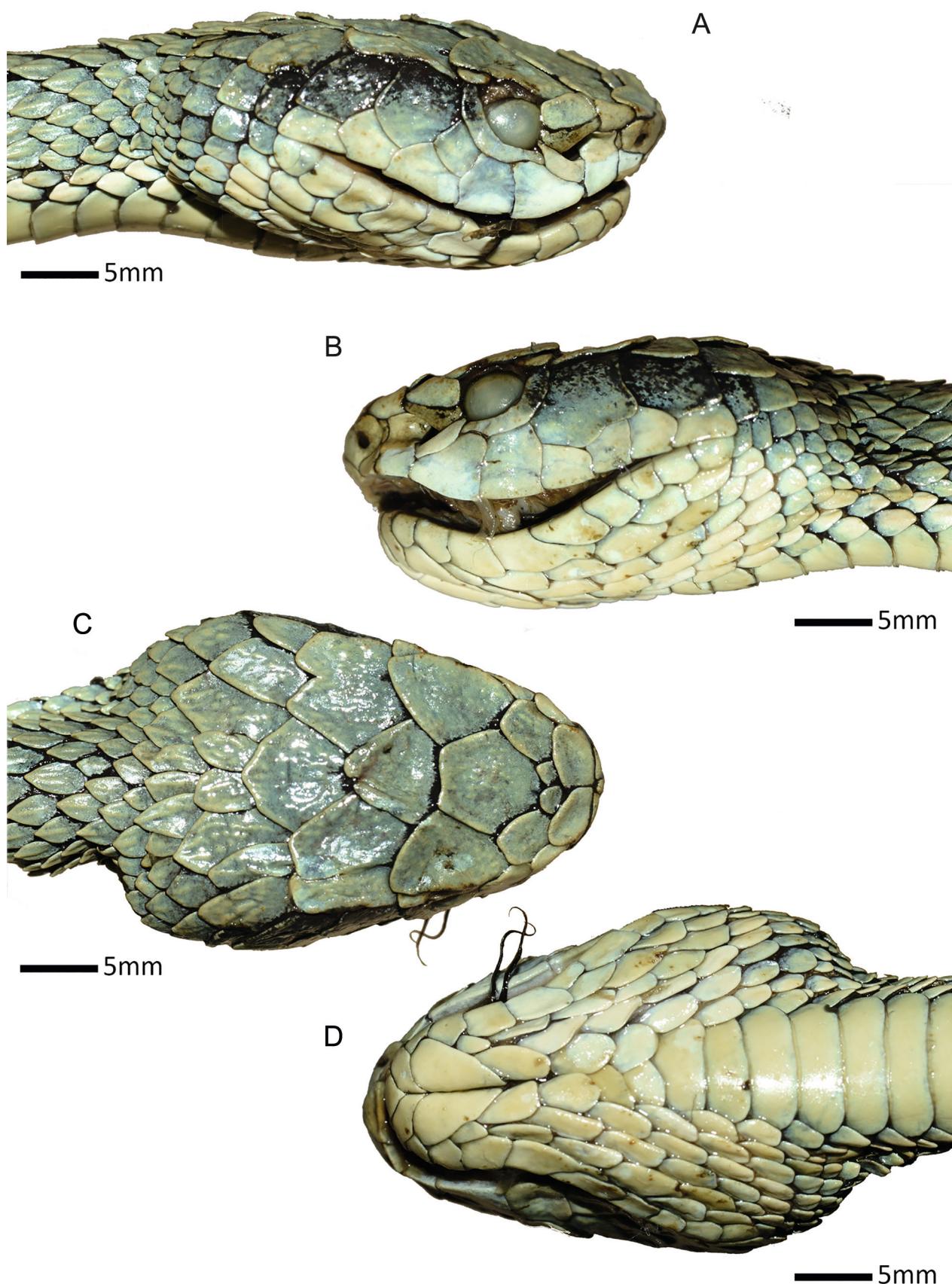


Figure 5. *Craspedocephalus macrolepis* comb. nov. lectotype (NHMUK 1946.1.18.72), in preservation, showing: (A) entire dorsal view, (B) entire ventral view.

CESS256 from Devarmala, Tamil Nadu, collected in 2011, by Saunak P. Pal; BNHS2543 from Shenbaganur, Tamil Nadu and BNHS2545 from Paralai, Valparai collected in 1909, by Maj. Frank Wall.

Type locality. “Anamallay Mountains; at 6,000 feet elevation” [= Anaimalai Hills, Western Ghats India, ca. 10°22’N; 77°08’E] by lectotype designation (Wallach et

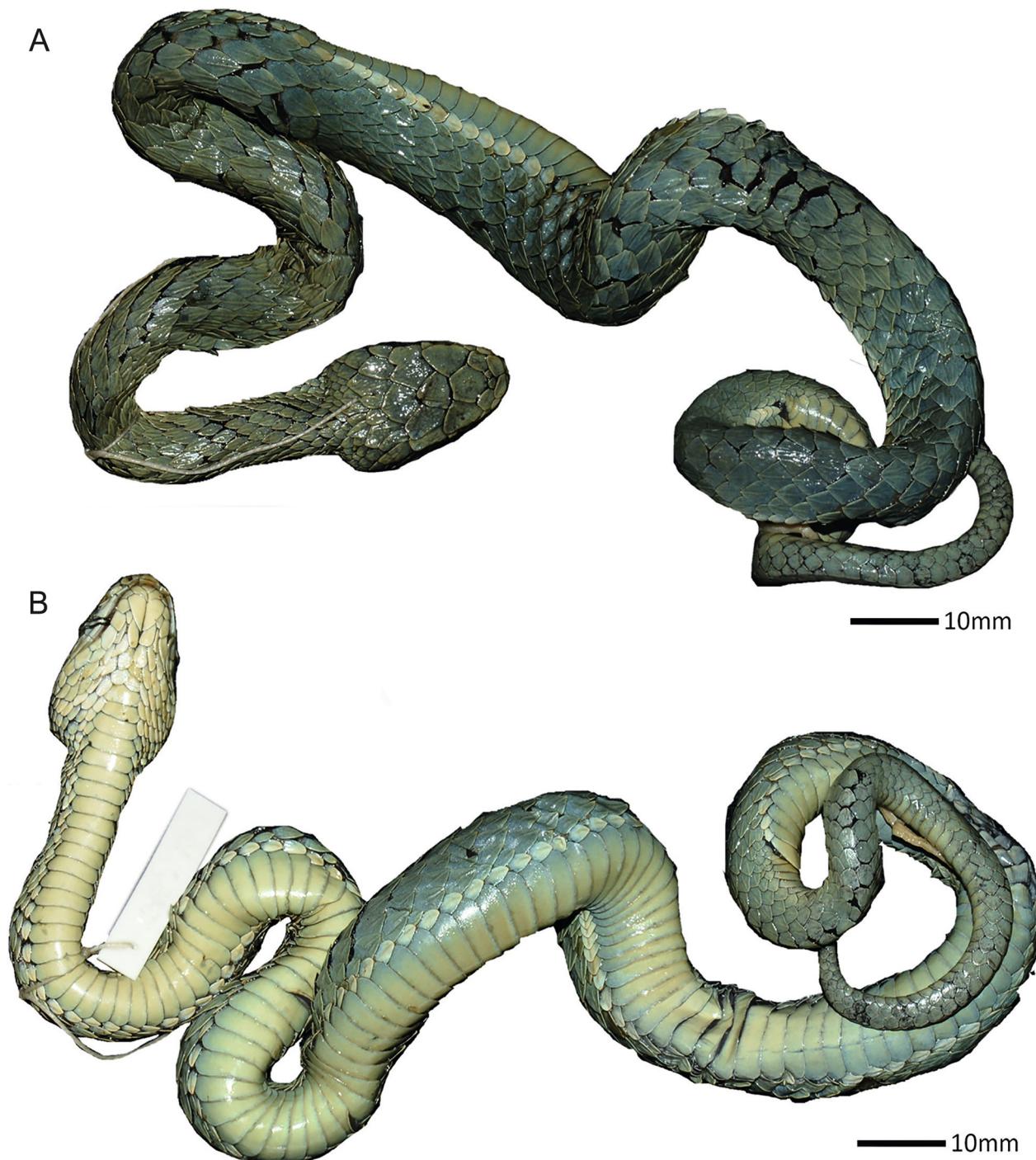


Figure 6. *Craspedocephalus macrolepis* comb. nov. lectotype (NHMUK 1946.1.18.72), in preservation, showing: (A) head lateral left view, (B) head dorsal view, (C) head ventral view, (D) head lateral right view.

al. 2014). The mentioned in the description is “Anamallay mountains at 6000 ft and Pulney Hills at 4000 ft” which is the current day Anamalais, south of the Palghat gap and the Palani hills further east. Here we restrict the nomen *Trimeresurus macrolepis* to the population distributed in mountain ranges north of the Shencottah gap.

Lineage diagnosis (redefined herein). Within the *C. macrolepis* complex, *C. macrolepis* s. str. (L6) can be distinguished as follows: in having higher dorsal scale rows: 13–19 (vs. 10–14 in L7); lower ventral count 133–140 (vs. 150 in L7). *Craspedocephalus macrolepis* (L6) is al-

lomorphic with its sister taxon (L7), from which it has a shallow genetic divergence (3.7% at cyt b and 0.7–1.0% at 16S rRNA). The low level of genetic divergence is the lowest genetic break between any the lineages inferred here (See Supplementary File 5: Table S4). This shallow genetic break coincides with a physical barrier (Shencottah gap) for these lineages.

Description. A medium sized pit viper (recorded till 920mm by Ganesh et al. 2008) with a prehensile tail of length up to 136 mm; a distinct triangular head with large shield-like scales, with 1–3 cephalic scales between the

undivided supraoculars with five scales surrounding the supraoculars, up to two scales between the internasal scales and the tip of the rostral scale visible from above; nasal scale entire, sub-rectangular and encompasses the nostril completely with 2–3 scales between the internasals; 1–2 scales between the nasal and the anterior part of the loreal pit; 8 supralabials and 9–12 infralabials on both sides; 6–8 scales including the last infralabial from the first ventral scale; three preocular scales of which the second and third scale from above constitute to form the posterior shields of the loreal pit; one or two post oculars; temporals smooth; 14–17 NSR (dorsal scale rows at neck), 13–19 MSR (dorsal scale rows at midbody), and 10 PSR (dorsal scale rows before vent), all keeled; Last row of scales on both sides bordered with a slightly larger row of scales, separating the ventral scales from the body; Ventrals 133–140, Anal scale undivided, followed by divided subcaudals 50–57.

Colour in life. Specimens in life are in a uniform dark green throughout the dorsal surface, often with a black post ocular stripe that extends to 2 scale rows; the postocular stripe continues to a white to creamy white lateral stripe that stops at the vent; uniform creamy to light green ventrals with hints of light blue, that continues to the mandibular portion that is either yellow, light green, light blue or creamy white in colour; tail after the vent continues with dark green, feeble blue bands at the end of the tail, the terminal scale black or greyish with feeble white bands.

Colour in preservative. Specimens in preservative show a range of variation in colour depending on the preservative; range from dark to light green on the head and dorsum with hints of or blue black bordering the scales; tail tip banded with grey and white bands, tail darker blue bands with bluish green.

Habitat. A typically arboreal (rarely terrestrial) species (Ganesh et al. 2010) that is found in high elevation shola forests (tropical montane stunted rainforests) and forests bordering high elevation grasslands. Due to anthropogenic changes to the landscape, this species is also sometimes found in cultivated landscapes such as tea estates and cardamom plantations, found at elevations from about 1100 m asl to 2600 m asl.

Distribution. Endemic to the southern Western Ghats. The revised distribution restricts this species to the high elevation landscapes of its range, the northern most limit being south of the Palghat gap, in the Nelliampathi hills, Anaimalai, with Palni hills being the eastern-most end of its distribution, extending southwards across High Wavy's or Meghamalai, Kottaimalai Ranges in the Srivilliputhur-Periyar landscape, to the Sivagiri-Devarmalai range, ending north of the Shencottah gap.

Craspedocephalus peltopelor sp. nov.

Figures 7–9

<http://zoobank.org/E79F04B6-4F5E-4AF5-B1DD-EA0-26B6B936B>

Trimeresurus macrolepis (not of Beddome, 1862) – Ishwar et al., 2001; Seshadri, 2012

Material examined. Specimen series: **Holotype** (BNHS 3593) from Chemunji, Peppara, Agasthyamalai, 08°40.7'N; 77°11.55'E, collected in 2010, by Saunak P. Pal & S.P. Vijayakumar. — **Paratype** (BNHS 2950) from Tirunelveli Hills (Agasthyamalai), collected in 1976 by Romulus Whitaker.

Type locality. Chemmunji, in Peppara Wildlife Sanctuary, a part of Agasthyamalai Hill Complex, Southern Western Ghats.

Etymology. Named after Günther's erstwhile generic nomen that alludes to the shield-like, large scales (*peltē*: shield/scale, *pelor(o)*-: a term meaning monstrous [or literally huge], in Greek).

Lineage diagnosis. A lineage belongs to the *C. macrolepis* complex. Differs from *C. macrolepis* in having lower dorsal scale rows 10–14 (vs. 13–19); higher ventral scale counts 150 (vs. 133–143). The new species is geographically separated from *C. macrolepis* by the Shencottah gap in the Southern Western Ghats. *Craspedocephalus peltopelor* sp. nov. (L7) has a shallow genetic divergence (3.7% at cyt b and 0.7–1.0% at 16S) from *C. macrolepis* (L6).

Description. Holotype in good condition, dissected, with a slender, cylindrical body of snout to vent length (SVL) 263 mm and a prehensile tail of length (TL) 57 mm; dorsal scales keeled with anterior dorsal scale rows (DSR) 17, mid body scale rows (MSR) 15 and posterior scale rows (PSR) 10; head prominent, of length 20.5 mm, clearly distinguished from the neck with large, smooth dorsal shields on the head; rostral scale triangular with the upper side roughly half the size of the lower side with the tip visible from above; supraoculars of length 5.46 mm and frontal separated by pair of scales on both sides and nasal scales separated by three scales from above; five scales other than the pre and post ocular scales bordering the supraoculars on both sides, with three scales between the posterior edge of the supraoculars; canthus rostralis distinct with 3/3 canthal scale; three preoculars, a postocular and a thin elongated crescent shaped subocular, in contact with a small scale, encompassed by the third and fourth supralabial scale; eye with a distinct elliptical pupil, vertical diameter of the eye 2.94 mm and horizontal diameter 3.52 mm; temporal scales smooth; aperture of the nostril completely covered by the nasal scale, undivided and subrectangular; nasal scale bordering the first supralabial; loreal pit present in contact with the second supralabial with two scales between the nasal and the second supralabial; eight supralabials and 12 infralabials,



Figure 7. *Craspedocephalus peltopelor* sp. nov. in life showing: (A) entire lateral view, (B) entire dorsal view, (C) entire dorsolateral view, (D) head and forebody lateral view; from Kalakkad-Mundunthurai, Agasthyamalai, (E) entire front view; from Agasthyakoodam, Agasthyamalai.

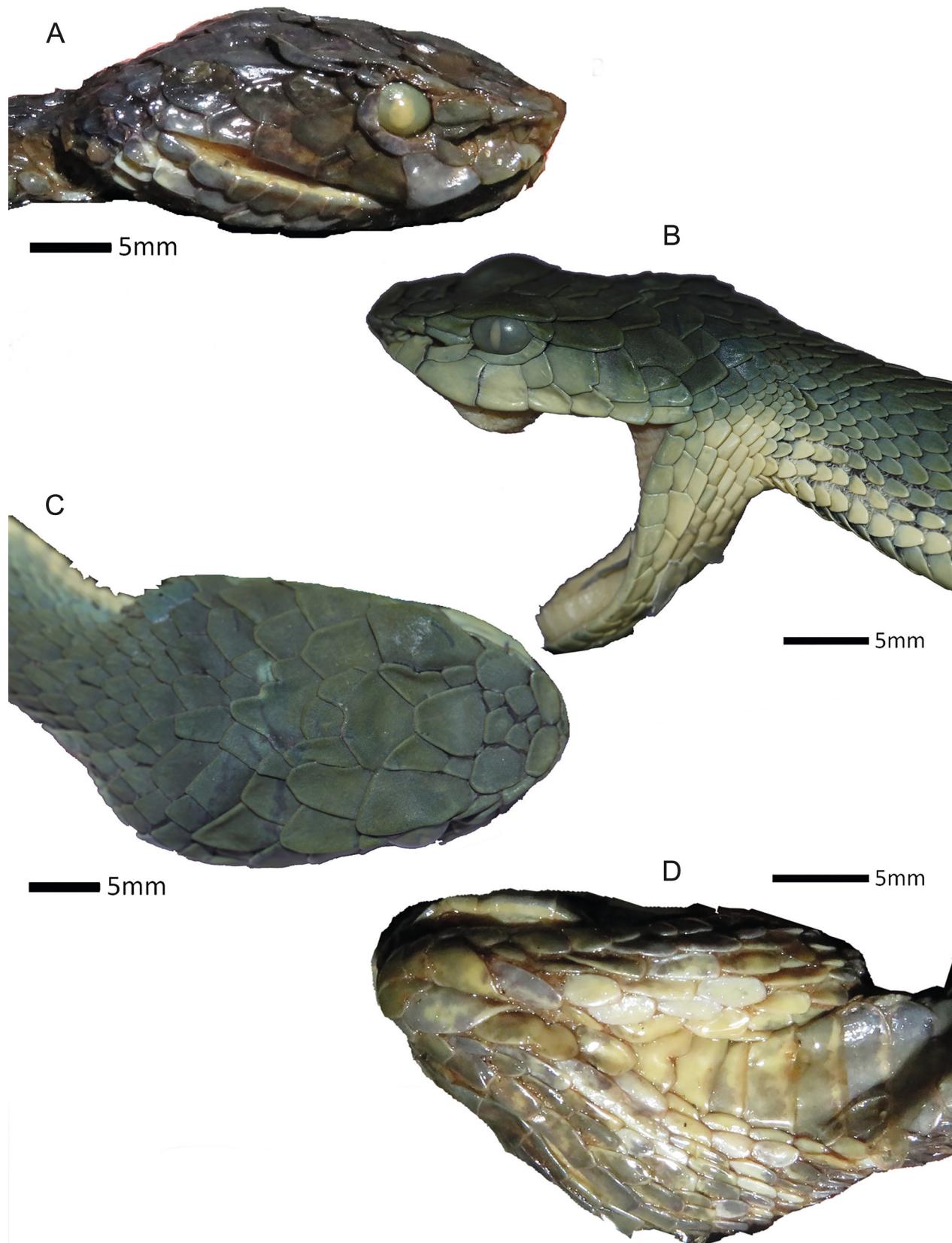


Figure 8. *Craspedocephalus peltopelor* sp. nov. holotype and paratype (BNHS 3593 & BNHS 2950), in preservation, showing: (A) head lateral left view BNHS 3593, (C) head dorsal view BNHS 3593, (D) head ventral view BNHS 2950, (B) head lateral right view BNHS 2950.

with six scales between the last supralabial, including the last supralabial till the start of the ventral scales; 1st, 2nd and 3rd infralabial scale in contact with the first pair of

genials; a gap of four scales including the posterior genials followed by 150 ventrals, laterally separated from the dorsal scale rows by a slightly broader row of dorsal

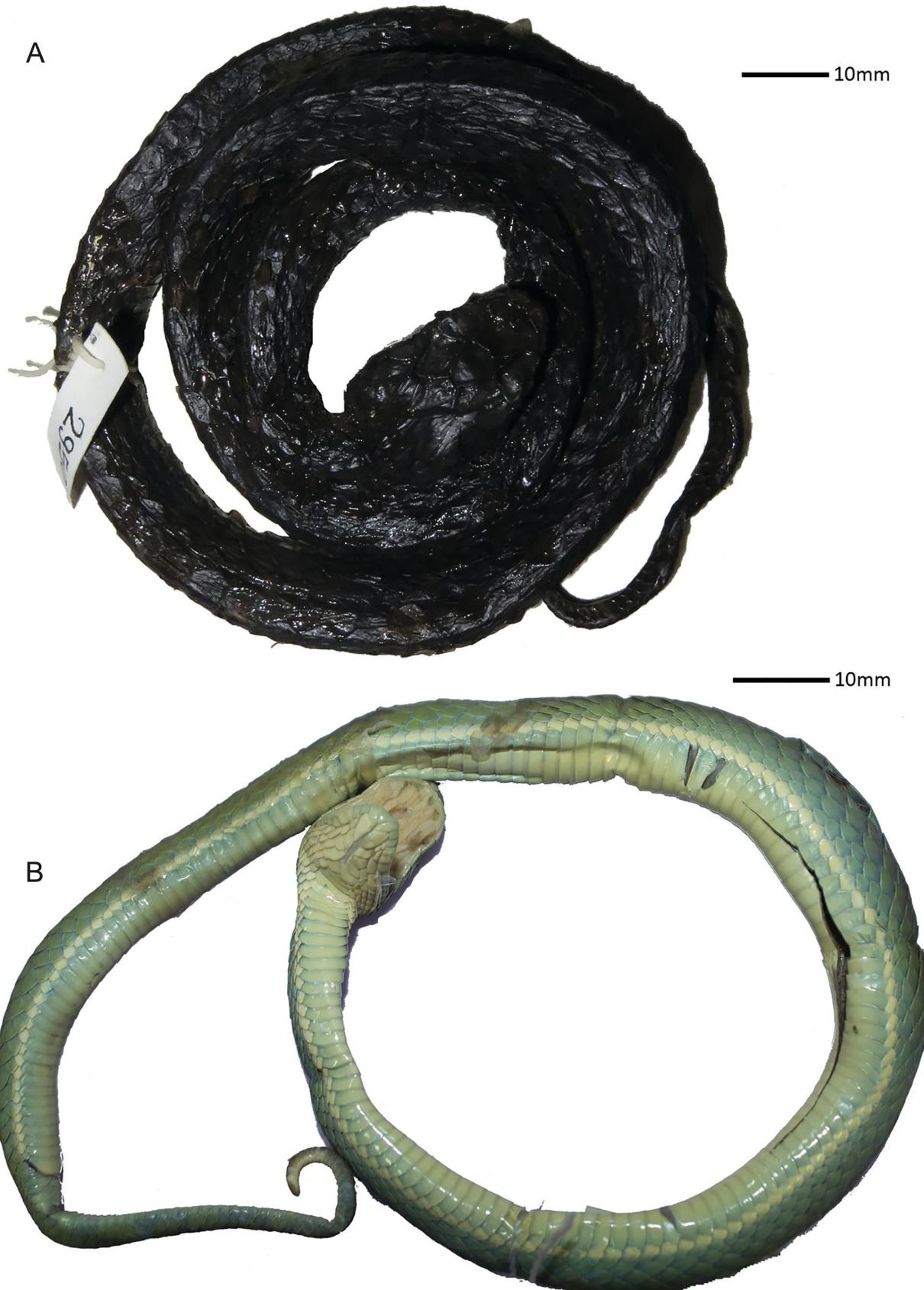


Figure 9. *Craspedocephalus peltopelor* sp. nov. holotype and paratype (BNHS 3593 & BNHS 2950), in preservation, showing: (A) entire dorsal view BNHS 2950, (B) entire ventral view BNHS 3593.

scales; anal scale undivided, followed by 59 divided subcaudals scales; terminal scale on the tail larger than the previous scale, blunt at the tip.

Variation. The paratype, of SVL 504mm and TL 145mm, is discoloured with a uniform dark greenish to black colour throughout the specimen in its current preservation

state. It differs from the holotype with respect to pholidosis by having 14 DSR, 14 MSR, 11 PSR, 150 ventrals and 64 subcaudals; a distinct head of length 27.5 mm with supraoculars that are separated by one scale from above; two canthal scales on the canthus rostralis, and 3 cephalic scales from above; 11 infralabials on both sides.

Colour in life. Dark to verdant green on the dorsal surface of the head that fades into a lighter green throughout the body dorsally up to the tail and along the lateral sides of the body including the head; a prominent, 2-scale wide, white lateral stripe runs from the creamy white mandibular region; small hints and patches of blue visible on the head and dorsal scales, with the tail tip banded with dark blue or sometimes fully covered with dark blue or black; the last 11 scale rows of the tail banded with black to dark blue and white to yellow; creamy white to yellow mentum fades into a light creamy green throughout the ventrals, sometimes separated by the white ventral stripe from the lateral part of the body.

Colour in preservative. Greyish green on the head dorsum that fades into a bluish green shade throughout the body; lateral parts of the head light green to bluish green; mentum creamy yellow that blends with creamy green ventrals, separated by the white lateral stripe; tail tip with grey and white bands, tail bluish green with darker blue bands.

Habitat. A typically arboreal (rarely semi-terrestrial) species (Ishwar et al. 2001, Seshadri, 2012) that is found in high elevation shola forests (tropical montane stunted rainforests) bordering the high elevation grasslands. Due to anthropogenic changes to the landscape, this species is also sometimes found in cultivated landscapes such as tea estates and coffee plantations. Found at elevations from about 1200 m asl to 1868 m asl.

Distribution. Endemic to the southern Western Ghats, south of the Shencottah gap. Geographically separated from its sister species, *C. macrolepis* that inhabits the ranges to the north of the Shencottah gap. Found throughout the high elevations of the Agasthyamalai hills.

***Craspedocephalus malabaricus* complex**

This species complex can be distinguished from regional congeners as follows: head scales as small as body scales (vs. large, shield-like in the *C. macrolepis* complex); midbody dorsal scale rows 21–23 (vs. <19 in the *C. macrolepis* complex); last rows of costal scales abutting ventrals on either sides larger than rest of the dorsal scale rows (vs. smaller in the *C. macrolepis* complex); 2nd supralabial bordering the anterior margin of loreal pit (vs. not so in *C. strigatus*); supraoculars often divided or scale sutures with an indented margin (vs. undivided in the remaining, regional congeners); subcaudals of tail tip blackish (vs. bluish in the *C. gramineus* and *C. macrolepis* complexes). Lineages within *Craspedocephalus mal-*

abaricus group appear to be morphologically cryptic, and do not differ in scalation or external morphological characters, but show geographical separation and are deeply genetically divergent.

***Craspedocephalus malabaricus* (Jerdon, 1854)**

Figures 10–12

Trigonocephalus (Cophias) malabaricus Jerdon, 1854

Trigonocephalus (Cophias) wardii Jerdon, 1854

Lachesis coorgensis Rao, 1917

Trimeresurus malabaricus – Smith, 1943

Lachesis anamallensis (non Günther, 1864) – Wall, 1919, 1924 part

Craspedocephalus malabaricus – Wallach et al., 2014

Taxonomic history. Jerdon (1854) originally described this species as *Trigonocephalus (Cophias) malabaricus* and the type locality of this species was mentioned as the “West Coast of Peninsular India”, restricted to the Western Ghats. The types of this species are currently untraceable (Goley et al. 1993, Gumprecht et al. 2004, Wallach et al. 2014). Other subsequently described nomina of *C. malabaricus*, that are currently recognized as synonyms include *Trigonocephalus (Cophias) wardii* Jerdon 1854, *Trimeresurus anamallensis* Günther, 1864 (now a valid species; see below) and *Lachesis coorgensis* Rao, 1917. Jerdon (1854) in his original descriptions of *Trimeresurus malabaricus* and *Tri. wardii* did not mention any locality names or geographic province. Our perusal of historical collection catalogues (Boulenger, 1896; Das et al. 1998; Slater, 1891; Theobald, 1868, 1876) in two potential repositories associated with Jerdon’s herpetological specimens (the Natural History Museum London and the Zoological Survey of India Kolkata) all reveal that only three precisely-named places have ever been associated with these nomina: Anamalais, Nilgiris and Wayanad (also see Beddome, 1862; Boulenger, 1890).

The specific epithets, mostly toponyms, also suggest the same: *C. malabaricus*: from ‘Malabar’ i.e. north Kerala and Coimbatore / Nilgiris, in the Western Ghats; *C. anamallensis*: from Anamalai hills of the Southern Western Ghats; *Lachesis coorgensis*: from ‘Coorg’ (=Kodagu) a part of Malnad region in Central Western Ghats. The only remaining nomen in its synonymy is *Tri. wardii* of Jerdon, 1854. Our perusal of historical literature reveal that this eponym could only be named after Samuel Neville Ward (18th June 1813 – 31st January 1897). Samuel M. Ward was with the Madras Civil Service (1832–63) and had a final appointment as Judge of Koyambatur (=Coimbatore). He had reportedly been corresponding with naturalists such as Charles Darwin, Edward Blyth, as well as T. C. Jerdon, who described *Tri. wardii*. Ward had been reported to have visited Sirsi, in North Canara for his work on Indian wildlife, mostly butterflies and birds (Pittie, 2016 and references therein). Beddome (1862) explicitly stated that *Tri. wardii* is from the Nilgiris. The earliest reference of this group from Agasthyamalai is



Figure 10. *Craspedocephalus malabaricus* in life, showing: (A) orange morph entire dorsal view (Agumbe), (B) purple morph (Anshi), (C) maroon morph (Agumbe), (D) cream morph (Amboli), (E) green morph (Amboli), (F) yellow morph (Anshi) & (G) brown morph (Anshi).

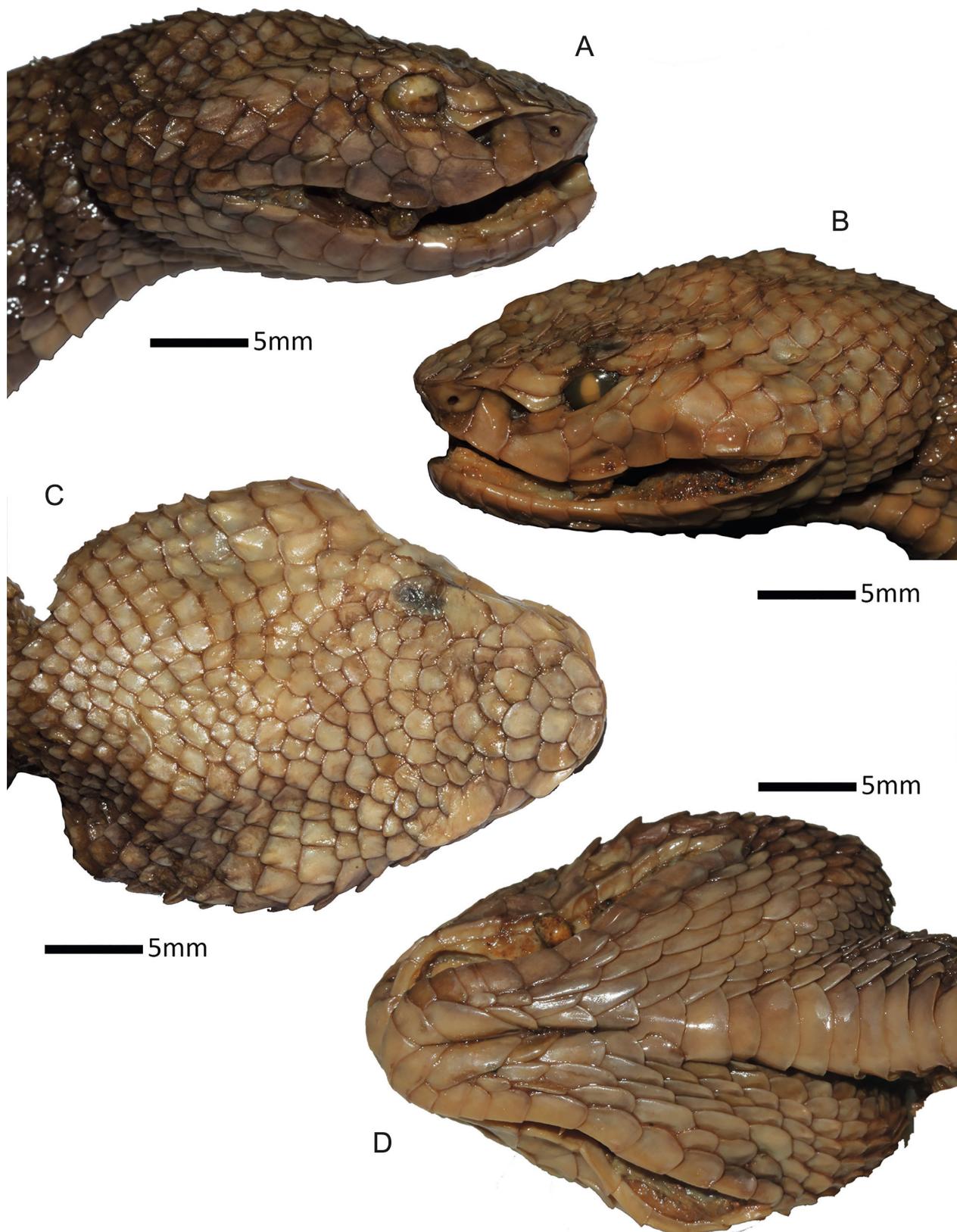


Figure 11. *Craspedocephalus malabaricus* neotype (*Lachesis coorgensis* holotype) (ZSI-18161), in preservation, showing: (A) head dorsal view, (B) head lateral left view, (C) head lateral right view, (D) head ventral view.

that of Ferguson (1895), who used Günther's name (*C. anamallensis*) to refer to it. Thus historical collections prior to typifications (till Rao, 1917) of the *C. malabaricus* complex apparently happened only from Anaimalai, Nilgiris and Wayanad.

Type. Syntypes lost (after Smith, 1943; also see Walach et al. (2014:188), 'Holotype' lost (after Das et al. 1998). Hence, as per Art. 75.3 of the Code (ICZN 1999) since we are revising the taxonomy of this group, we designate as neotype the holotype of its junior synonym

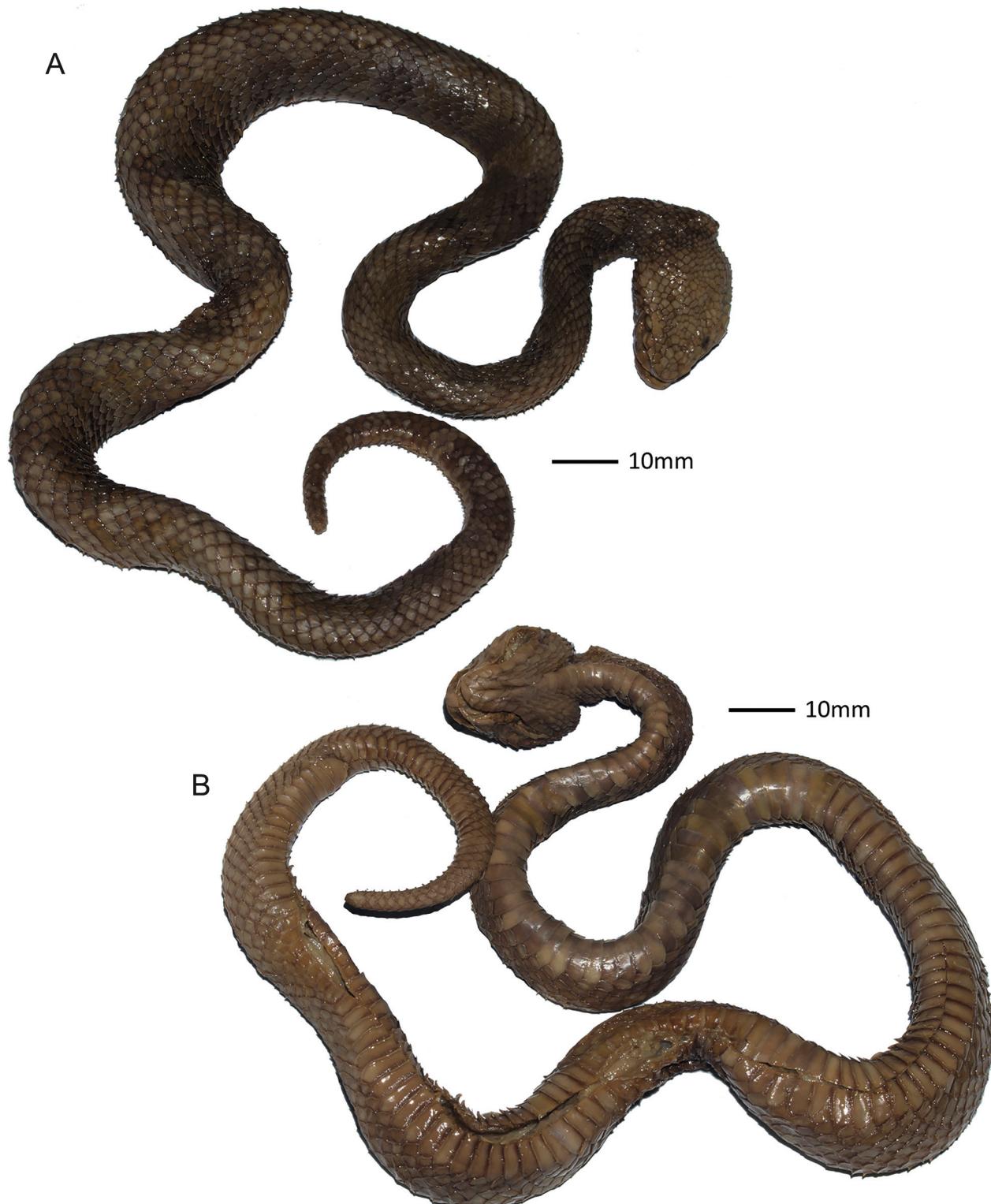


Figure 12. *Craspedocephalus malabaricus* neotype (*Lachesis coorgensis* holotype) (ZSI-18161), in preservation, showing: (A) entire dorsal view, (B) entire ventral view.

Lachesis coorgensis Rao, 1917. The selected neotype (read below) is chosen to clarify the identity of this nominal taxon, a well-preserved adult originating from a precise locality, in conformity with the original description of the conferred nomen and housed in a permanent national repository/museum. Thus *Craspedocephalus malabaricus* and *Lachesis coorgensis* are now objective synonyms.

Materials examined. Specimen series: **Neotype:** ZSI-18161 from Coorg, Karnataka, 12°24.82'N; 75°43.85'E by C.R. Narayan Rao in 1917, the holotype of *Lachesis coorgensis* Rao, 1917. — Other referred material: BNHS 2609-778 from Kotagiri, Tamil Nadu and BNHS 2069-781 from Coonoor, Tamil Nadu by A. M. Kinloch in 1907. Additional comparative material collected for this study - CESS053, CESS055 from Amboli, Maharashtra; CESS063, CESS065 from Saklespura Karnataka; CESS273 from Coorg, Karnataka; CESS086 from Thirunelli, Kerala

by Ashok Kumar Mallik between 2009-11 and CESS141 from Silent valley by Saunak Pal and Mrugank Prabhu in 2010; BNHS 2609A from Kotagiri and BNHS 2609B from Coonor, Nilgiris, Tamil Nadu by A.P Kinloch in 1907; BNHS 2596 from Sirsi, Karnataka by Charles McCann in 1938; BNHS 2599 from Mahabaleshwar, Maharashtra by H. Abdulali in 1953; BNHS 2601 from Castle Rock, Karnataka by Mrs. H. Pearson in 1907.

Type locality. Originally given as “West Coast, Peninsula of India”. Here restricted to Coorg ($12^{\circ}24.82'N$; $75^{\circ}43.85'E$) in Central Western Ghats, by neotype designation.

Etymology. The specific epithet *malabaricus* is a toponym, alluding to its type locality - the Malabar region of the Western Ghats.

Lineage diagnosis (redefined herein). A lineage of the *C. malabaricus* complex, *C. malabaricus* s. str. (L5) is here restricted only to populations north of the Palghat Gap. This nominotypical population is 8.3–9% and 1.2–2.2% divergent at *cyt b* and 16S respectively, from those south of the Palghat Gap (L3 & L4), recognised here as two nominate taxa: *C. anamallensis* (Günther, 1864) and *Craspedocephalus travancoricus* sp. nov. (see below). These taxa are allopatric with respect to each other and *C. malabaricus*.

Description. Neotype in good condition, small lesion near the nape, possibly caused while collecting and euthanizing the individual; specimen with a slender, cylindrical body of snout to vent length (SVL) 481 mm and a prehensile tail of length (TL) 73 mm; dorsal scales keeled with anterior dorsal scale rows (DSR) 21, mid body scale rows (MSR) 21 and posterior scale rows (PSR) 13; head prominent, of length 24.3 mm, clearly distinguished from the neck with small, mildly keeled scales on the head; rostral scale trapezoid, with the lower side roughly more than twice the size of the upper side with the tip visible from above; supraoculars divided, separated by eight cephalic scales between both supraoculars at its posterior border; seven scales bordering each supraocular. Canthus rostralis distinct with four canthal scales; three preoculars, two postoculars and a thin elongated crescent shaped subocular; eye with a distinct elliptical pupil, vertical diameter of the eye 3.31 mm and horizontal diameter 3.68 mm; strongly keeled temporal scales and cephalic scales in the posterior sides above the mandibular joint; aperture of the nostril completely covered by the nasal scale, undivided and sub-pentagonal shaped, in contact with the first two canthal scales and the 1st and 2nd supralabial; loreal pit present in contact with the second supralabial and the 2nd and 3rd preoculars; nine supralabials and 12 infralabials, with eight scales between the last supralabial, including the last supralabial up to the start of the ventral scales; 1st, 2nd and 3rd infralabial scale in contact with the first pair of genials; a gap of four scales including the posterior genials followed by 148 ventrals, laterally separated from the dorsal scale rows by a slightly broader row of dorsal scales; anal scale undivided, followed by 38 divided sub-

caudals scales; Terminal scale on the tail larger than the previous scale, blunt at the tip.

Variation (n=20). The referred materials are of SVL up to 670 mm and TL up to 126 mm with colours varying from dark brownish red to light green throughout the specimens in its current preservation state, differs from the holotype with respect to pholidosis by having 19 to 22 DSR, 19 to 23 MSR, 13 to 15 PSR, 145–149 ventrals and 52–54 subcaudals; head distinct with supralabials ranging between 8–10 and infralabials ranging between 10–13; one to three preocular scales, one to two scales (some specimens showing an absence of these scales) between the 3rd supralabial scale and the suboculars, seven to nine cephalic scales and seven to eight scales surrounding the supraoculars from the dorsum.

Colour in life. A highly variable and polymorphic species, with respect to colour, specimens can be found in a variety of colour morphs - greenish blue-cyan, bright yellow, green, rufous brown, bright orange and red coloured specimens have been encountered during this study; head characterized with a thick dark brown to black postocular stripe till the nape, labials sometimes marked with blotches and a highly variable pattern above the head, sometimes fully dark, some individuals with no markings at all, body with alternating zig-zag saddle shaped markings with the last rows of scales on the tail banded with different colour; these markings vary from brick reddish, dark brown to black, sometimes intermixed with spots of other colours such as green, yellow and blue; the base colour of the body varies from light brown in juveniles, light cream, orange, yellow, brick red, bluish green and sometimes mottled with all or some of the aforementioned colours; ventrals sometimes vary from the colour of the dorsum, complementing the variety of vibrant dorsal colours, but often are coloured similar to the dorsum; colour change is also observed to be seasonal (Kanagavel et al. 2012); juveniles brown with dark brown to black markings, neonates and younger juveniles possess a tail ‘lure’ that is often different from the body’s colouration. Mandibular region and the ventrals in alternating light green, blue, yellow to creamy yellow with speckles, separated from the dorsal scales with a longitudinal lighter irregular stripe, two prominent, labial stripes from the eye and the loreal pit, up to the edge of the lower end of the supralabial region.

Colour in preservative. Fairly faded specimen with a light brown dorsum, ventrals and tail; scales bordered with dark brown; temporal stripe visible on the right side of the specimen in dark brown, left side with no visible temporal stripe; body with barely distinguishable dark brown saddle shaped markings throughout the body; tail with dark brown stripes from the vent up to the tip.

Habitat. An arboreal species, commonly found on bushes and in undergrowth in forests and near streams in evergreen forests to moist deciduous and lowland riparian forests. Due to anthropogenic changes to the landscape,

this species is also abundantly found in agricultural landscapes such as coffee plantations, from 100–1800m MSL.

Distribution. Restricted to the central and northern Western Ghats from Mahabaleshwar – Koyna in Maharashtra to the Nilgiris and Elivalmalai hills, north of the Palghat Gap. Known to occur sympatrically with *C. occidentalis* comb. nov. in Nilgiris and Coorg, with *C. gramineus* in Amboli and may have some overlap with *C. strigatus* in the mid to high elevations of the western slopes of the Nilgiris (at the upper limit of its altitudinal distribution).

Craspedocephalus anamallensis (Günther, 1864)

Figures 13–15

Trimeresurus anamallensis Günther, 1864

Lachesis anamallensis - Boulenger, 1896; Wall, 1919 part

Craspedocephalus anamallensis (Günther, 1864)

Taxonomic history. Günther (1864) described this species as *Trimeresurus anamallensis* based on type specimens from the Anamalai hills collected by Col. R.H. Beddome. Subsequently, Boulenger (1896) transferred this species to the genus *Lachesis*, now attributable to New World crotalids (bushmasters), until Wall (1924) corrected the generic taxonomy. This nomen (*C. anamallensis*) was in prevailing usage for this entire species complex (e.g. see Wall, 1924), until Smith (1943) rightly reinstated Jerdon's senior nomen *C. malabaricus*.

Materials examined. **Lectotype** (here designated): NHMUK 1946.1.19.93 from Anamallay hills (=Anamalai hills) collected by R.H. Beddome. — **Paralectotypes:** NHMUK 1946.1.18.73–74, NHMUK 1946.1.19.82, NHMUK 1946.1.19.89, NHMUK 1946.1.19.94–95, and NHMUK 1946.1.20.3, from Anamallay hills (=Anamalai hills) collected by R.H. Beddome. — Other specimens: CESS178 from Topslip, Anamalai Tiger Reserve, Tamil Nadu, by Ashok Kumar Mallik, 2011; CESS181, Orukomban Range, Parambikulam, Kerala by Ashok Kumar Mallik in 2011; CESS166 from Goodrickal Range, Kakki, Periyar Tiger Reserve, Kerala, by Saunak P. Pal, 2011.

Type locality. Anamalai hills, Southern Western Ghats, Tamil Nadu, India; same type locality for the type series of *C. anamallensis*.

Etymology. The specific epithet *anamallensis* is a toponym, alluding to its type locality - the Anamalai hills of the Southern Western Ghats.

Lineage diagnosis. A cryptic lineage belonging to the *C. malabaricus* complex, this lineage (L3) is genetically divergent from *C. malabaricus* (L5) by 8.3% & 1.2%, and from *C. travancoricus* sp. nov. (L4) by 7.1% and 1.5% at cyt b and 16S respectively. This lineage is geographically isolated from *C. malabaricus* to the North (separated by Palghat Gap) and to the south the boundary broadly lies

in the Periyar Plateau, between Gudrikal range (its southern limit) and Devarmalai (northern limit of its sister lineage *C. travancoricus* sp. nov.).

Description. Lectotype in a generally good condition, entire with a cylindrical body of SVL 505mm and a prehensile tail of TL 87mm; dorsal scales mildly keeled with DSR 21, MSR 21 and PSR 15; head of length 29mm prominent and clearly distinguished from the neck with strongly imbricate small scales; tip of the rostral scale visible from above, with the upper end roughly half the size as the lower; divided supraoculars with nine cephalic scales between both the supraoculars; nine scales surrounding each divided pair of supraoculars on both the sides with nine scales between the posterior border of the supraoculars; distinct canthus rostralis with four scales on the canthal ridge; two preoculars and two postoculars, an elongated crescent shaped subocular; strongly keeled temporals and keels continue to be present in other head scales behind the oculars except the supralabials towards the posterior; eye with a distinct elliptical pupil of vertical diameter 3.3 mm and a horizontal diameter of 3.98 mm; nostril aperture completely covered by the nasal scale, undivided and pentagonal-sub rectangular in shape, in contact with the first three canthal scales, first and second supralabial; nine supralabials and eleven infralabials, with eight scales between the edge of the mouth and the first ventral scale; 1st, 2nd and 3rd infralabial scale in contact with the first pair of genials; a gap of six scales in between the first genial and ventrals; 157 ventrals separated laterally from the body scales by a row of slightly broader dorsal scales; anal scale undivided followed by 55 divided caudals; terminal scale rounded and blunt at the tip, slightly larger than the previous scale.

Variation (n=10). The following characters vary within the specimens of the examined type series. Variations in pholidosis between the specimens were: supralabials 9–10 and infralabials 11–13, preoculars 2–3, ventrals 144–145 and subcaudals 50–62, about 8–12 scales between the edge of the mouth and the ventral scales; 21–22 scale rows around the neck; the post ocular stripe sometimes extends to 2 rows of scales.

Colour in life. Black dorsal head scales with the anterior scales with hints of light green and posterior head scales bordered with yellow, up to the postocular eye stripe, that extends until the nape; light bluish green on the lateral parts of the head that fades into a creamy yellow to white underside, from the mandibular region up to the ventrals; ventral scales creamy yellow scales alternating with light greenish yellow scales, consecutively larger gaps between the lighter scales filled with the greenish yellow scales towards the tail - these correspond to the alternating between creamy yellow and green scales in the column that separates the ventrals and dorsal scales; caudal scales yellow, bordered and often blotched with black scales; black blotches throughout the dorsum with a gap of 3–4 scale rows.

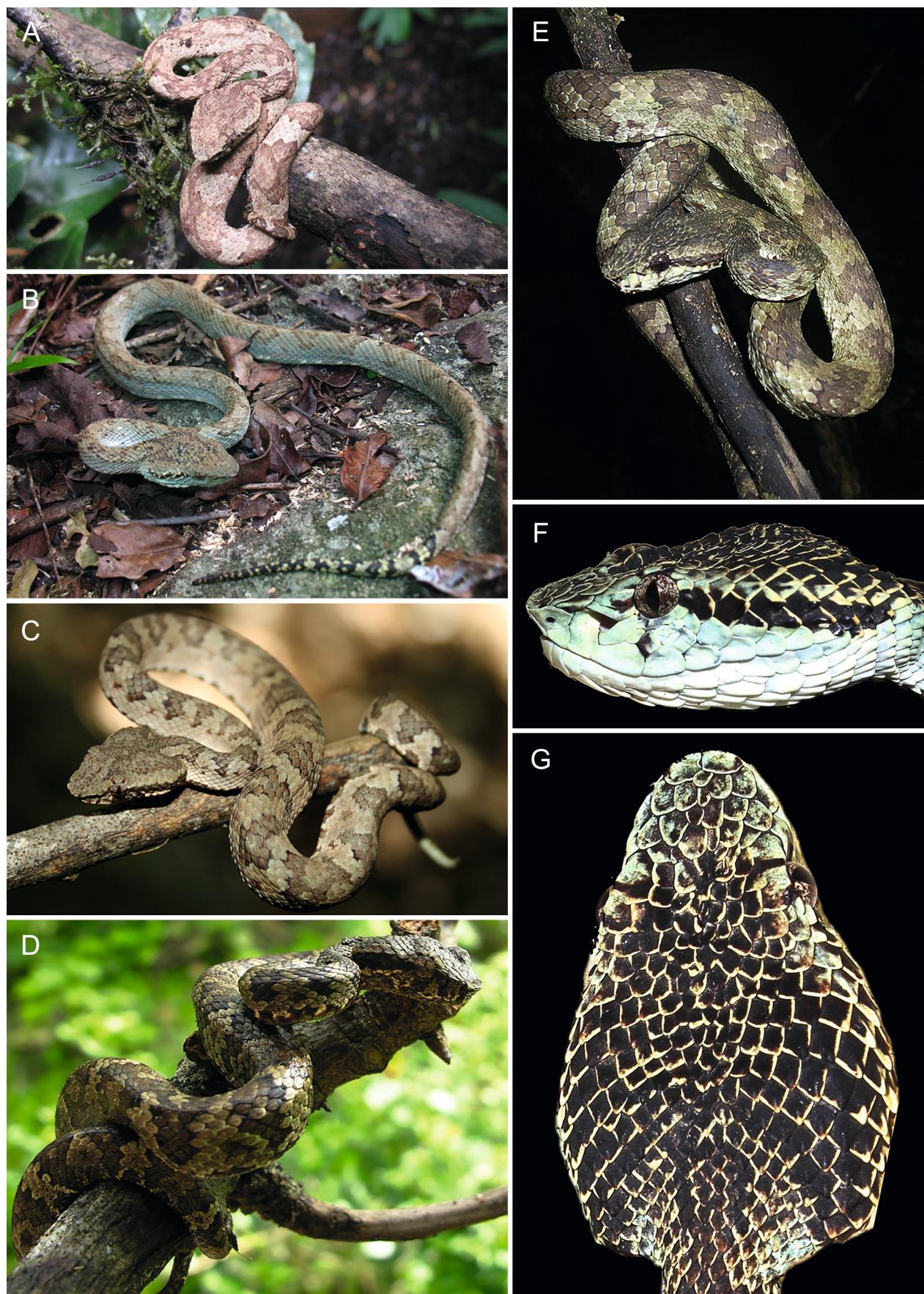


Figure 13. *Craspedocephalus anamallensis* in life, showing: (A) brown morph front view, from Top Slip, (B) green morph, from Kottaimalai, (C) grey morph, from Nelliampathy, (D) & (E) olive morphs from Top Slip; entire dorsolateral views, (F) green morph head lateral view, (G) green morph, head dorsal view; from Parambikulam region.

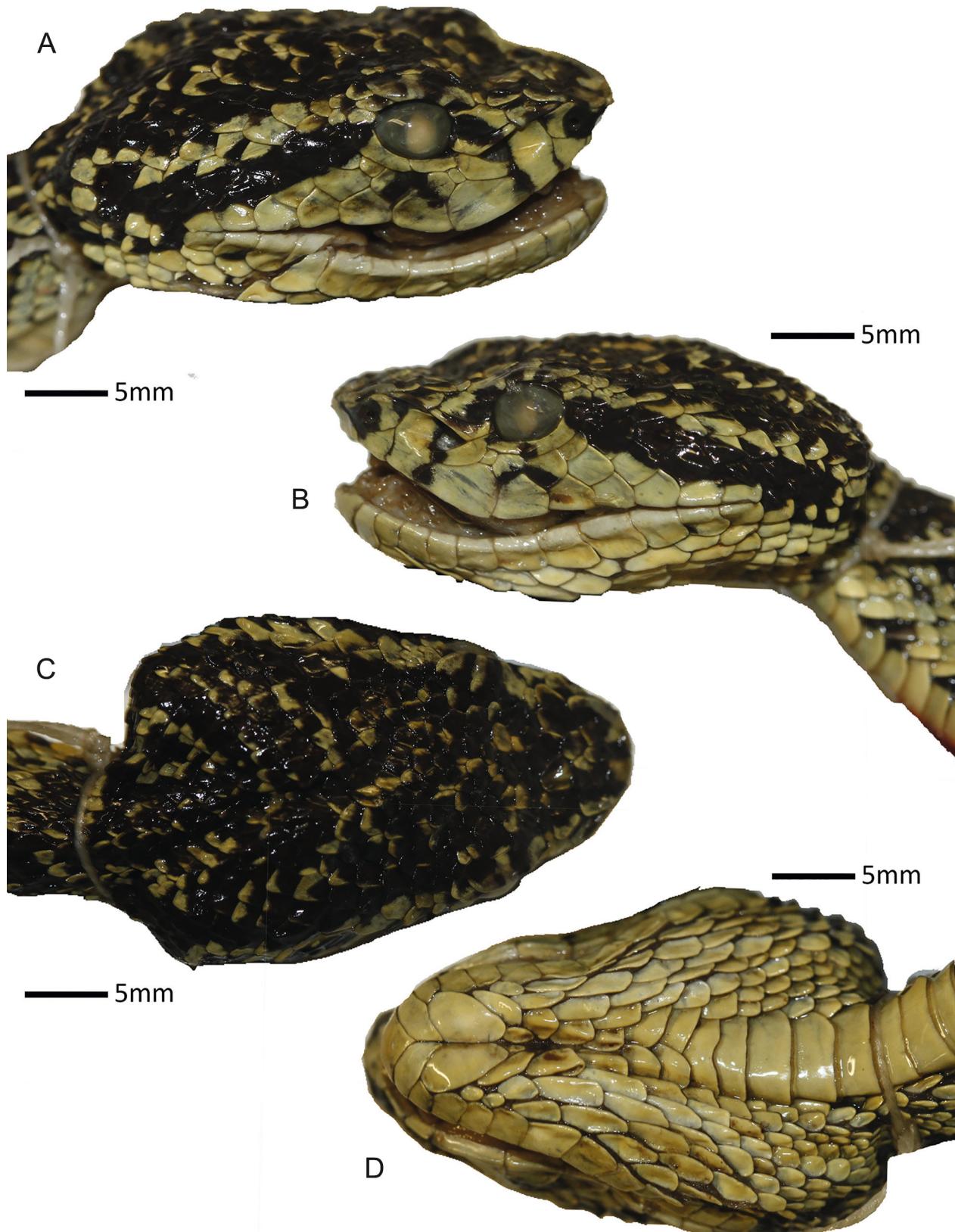


Figure 14. *Craspedocephalus anamallensis* lectotype (NHMUK 1946.1.19.93), in preservation, showing: (A) head lateral left view, (B) head lateral right view, (C) head dorsal view, (D) head ventral view.

Colour in preservative. Head dorsum almost completely covered black to dark brown and scales bordered with light faded green; black/ dark brown postocular stripe about 2 scales wide, a preocular/ temporal stripe that continues to the loreal pit and ends at the supralabials be-

low; black markings on the labials below the suboculars; body in light faded green with black saddle shaped markings, the markings centered with faded brown marbled markings; the row dorsal of scales that meet the ventrals alternate between the dorsal light faded green and dark



Figure 15. *Craspedocephalus anamallensis* lectotype (NHMUK 1946.1.19.93), in preservation, showing: (A) entire dorsal view, (B) entire ventral view.

brown/ black markings with a gap of two to three scales in between them; ventrals plain light creamish yellow; subcaudals in black with yellow blotches.

Habitat. Similar to *C. malabaricus*, an arboreal species, commonly found on bushes and in the undergrowth in forests and near streams in moist evergreen forests to deciduous and lowland riparian forests. Due to anthropogenic changes to the landscape, this species is also often found in cultivated landscapes such as coffee plantations, from 100–1800 m asl.

Distribution. Endemic to the southern Western Ghats, south of the Palghat Gap and north of the Shencottah Gap. We recorded this species in the Nelliampathy, Anamalai and Palni hills, Cardamom hills, and northern sections of the Periyar plateau. *Craspedocephalus anamallensis* has been recorded to be sympatric with *C. macrolepis* at the highest limit of its elevational range (see Malhotra & Davis, 1991).

Craspedocephalus travancoricus sp. nov.

Figures 16–18

<http://zoobank.org/65D10C52-E0F5-4E50-B635-5BF7977EF576>

Trimeresurus anamallensis (not of Günther, 1864) - Ferguson, 1895

Trimeresurus malabaricus (not of Jerdon, 1854) - Inger et al., 1984,
Ishwar et al., 2001

Materials examined. Holotype: BNHS 3595 (CESS074) from Bonnakard, Peppara, Kerala by Saunak Pal and S. P. Vijayakumar in 2010; BNHS 2607 from Thiruvananthapuram, collector and year unknown. — **Paratype:** BNHS 3594 (CESS257) from Devarmalai, Tamil Nadu by Saunak Pal and Mrugank Prabhu in 2011.

Type Locality. Peppara ($8^{\circ}39.7167'N$; $77^{\circ}10.7167'E$), Kerala, a part of the Agasthyamalai Hill complex of the Southern Western Ghats.

Etymology. Toponym, named after its distribution in the far south of the Western Ghats, in the southern parts of the ‘Travancore’ hill ranges.

Remarks. As previously elaborated and clarified (see *C. malabaricus* account), historical collections and typifications (both prevailing and previously synonymized treatments) did not involve the population circumscribed here as a distinct lineage. Therefore, this innominate population, previously cited (see Inger et al. 1984; Ishwar et al. 2001) under the chresomy of *C. malabaricus* s. lat. is here named anew.

Lineage diagnosis. A cryptic lineage belonging to the *C. malabaricus* complex, this lineage (L4) is genetically divergent from *C. malabaricus* (L5) by 9% & 2.2% and from *C. anamallensis* (L3) by 7.1 & 1.5% at cyt b and

16S respectively. This lineage is also allopatric with its related taxa *C. malabaricus* occurring north of the Palghat Gap and is immediately allopatric with *C. anamallensis* distributed just north of its distribution range, north of the Shencottah Gap.

Description. Holotype in good condition, dissected, with a slender, cylindrical body of snout to vent length (SVL) 345 mm and a prehensile tail of length (TL) 61 mm; dorsal scales keeled with anterior dorsal scale rows (DSR) 21, mid body scale rows (MSR) 23 and posterior scale rows (PSR) 14–15; head prominent, of length 20.28 mm, clearly distinguished from the neck with small, juxtaposed dorsal scales on the head; rostral scale sub triangular with the upper side roughly half the size of the lower side with the tip visible from above supraoculars of length 3.64 mm and width 1.0 mm, separated by seven scales, between the posterior edge of the supraocular scales; canthus rostralis distinct with four canthal scales on the ridge; three preoculars, two postoculars and a thin elongated crescent shaped subocular, in contact with a small scale, encompassed by the third and fourth supralabial scale; eye with a distinct elliptical pupil, vertical diameter of the eye 2.6 mm and horizontal diameter 3.4 mm.; temporal scales mildly keeled; aperture of the nostril completely covered by the nasal scale, undivided and subrectangular; nasal scale bordering the first supralabial; loreal pit present in contact with the second supralabial with two scales between the nasal and the second supralabial: nine supralabials and 11 infralabials, with nine scales between the last supralabial, including the last supralabial till the start of the ventral scales; 1st, 2nd and 3rd infralabial scale in contact with the first pair of genials; a gap of three scales including the posterior genials followed by 147 ventrals, laterally separated from the dorsal scale rows by a slightly broader row of dorsal scales; anal scale undivided, followed by 55 to 56 divided subcaudals scales; terminal scale on the tail larger than the previous scale, blunt at the tip.

Variation. The paratypes have SVL upto 282 mm and TL 65 mm, and differ from the holotype with respect to pholidosis by having 20 to 21 DSR, 21 MSR, 14 to 15 PSR, 157 ventrals and 55 subcaudals; three to four canthal scales on the canthus rostralis, and seven to nine cephalic scales from above; 10 to 12 infralabials on both sides.

Colour in life. Head dorsum almost covered with dark brown to purplish brown colour with scales bordered with light yellowish green; postocular and preocular stripe almost indistinguishable from the head dorsum colour, separated with a faded yellowish green stripe; dark brown postocular stripe about 3 scales wide, a preocular/ temporal stripe that continues to the loreal pit and ends at the supralabials below; black border markings on the labials below the suboculars and anterior supralabials; body in light faded green and brown marbled scales with 28 brown saddle shaped markings, the markings centered with faded brown marbled markings; the row dorsal of scales that meet the ventrals alternate between the dorsal marked with faded yellow and dark brown with a gap of two to



Figure 16. *Craspedocephalus travancoricus* sp. nov. in life, showing: (A) brown morph entire front view, (B) green/brown morph entire dorsal view, (C) orange morph front view, (D) green morph lateral view, (E) green morph dorsal view, (F) brown morph lateral view, (G) grey/black morph dorsolateral view; from Ponmudi hills, Kerala.

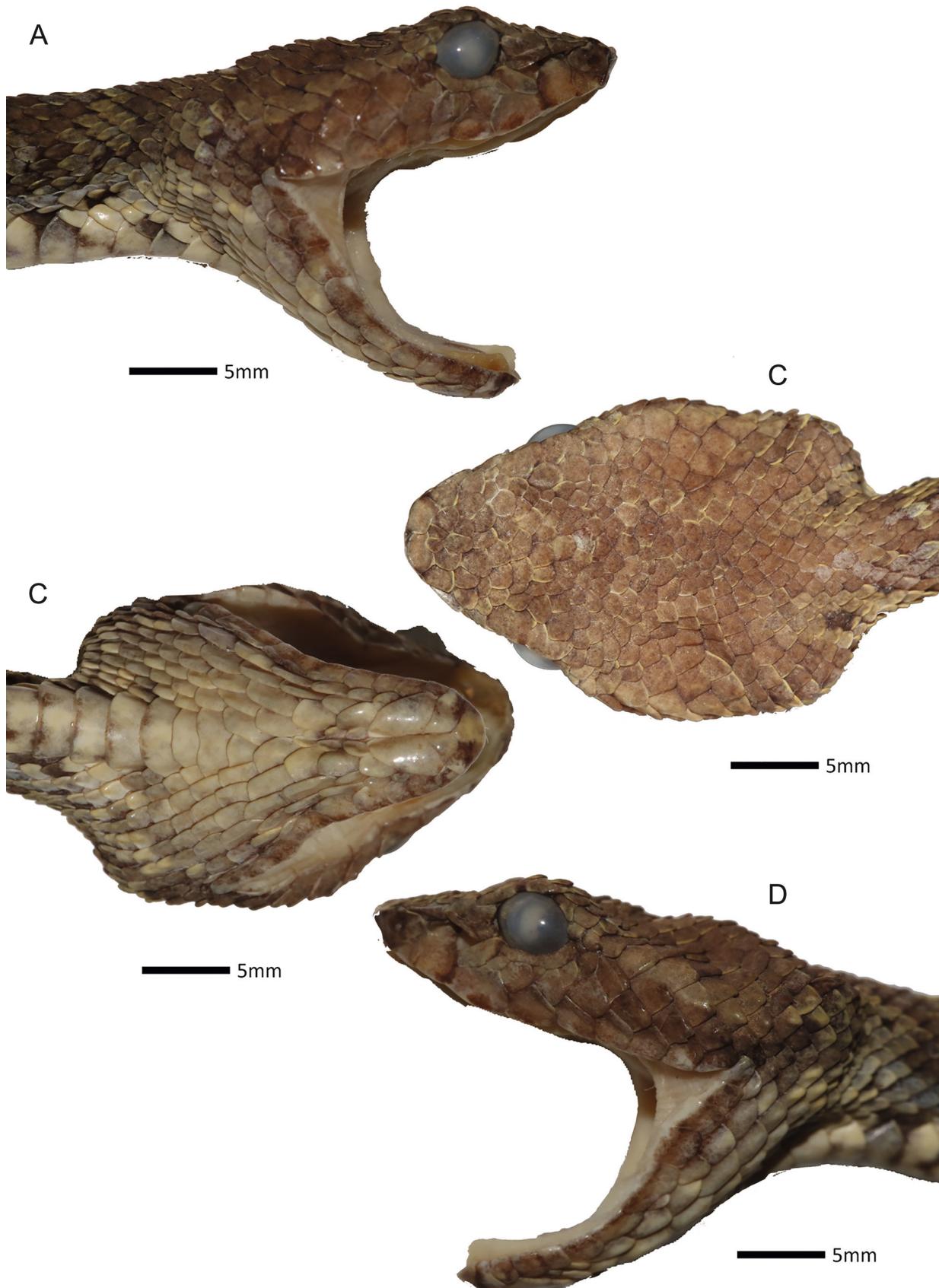


Figure 17. *Craspedocephalus travancoricus* sp. nov. holotype (BNHS 3594), in preservation, showing: (A) head lateral left view, (B) head lateral right view, (C) head dorsal view, (D) head ventral view.

three scales in between them; ventrals plain light creamish yellow; subcaudals in black with yellow blotches; tail with 13 yellowish green bands on dark brown to black;

eyes silverish with a tinge of yellow, rufous red blotches throughout the eye, concentrated towards the middle, perpendicular to the pupil, almost forming a cross.



Figure 18. *Craspedocephalus travancoricus* sp. nov. holotype (BNHS 3594), in preservation, showing: (A) entire dorsal view, (B) entire ventral view.

Colour in preservative. Similar to colouration in life with brighter colours faded dull and yellows throughout the body bleached to a creamish white colour; pupils bluish white, dilated.

Habitat. Similar to other members of the *C. malabaricus* group, an arboreal species, commonly found on bushes and in the undergrowth in forests and near streams in moist evergreen forests to deciduous and lowland riparian forests, from 100–1800 m asl.

Distribution. Recorded mostly from Agasthyamalai with a single isolated record from Devarmalai hills, across the Shencottah gap. This species may occur sympatrically with *C. peltopelor* sp. nov. in the highest elevations of Agasthyamalai.

***Craspedocephalus gramineus* complex**

This species complex can be distinguished from regional congeners as follows: head scales as small as body scales (vs. large, shield-like in the *C. macrolepis* complex); mid-body dorsal scalarows 21–23 (vs. <19 in *C. macrolepis* complex); last rows of costal scales abutting ventrals on either sides larger than rest of the dorsal scale rows (vs. smaller in the *C. macrolepis* complex); 2nd supralabial bordering the anterior margin of loreal pit (vs. not so in *C. strigatus*); supraoculars undivided (vs. often divided or with indented scale in the *C. malabaricus* complex); subcaudals of tail tip bluish (vs. blackish in the *C. malabaricus* complex).

***Craspedocephalus gramineus* (Shaw, 1802)**

Figure 19

Coluber gramineus Shaw, 1802

Coluber viridis (nec *Trimeresurus viridis* Lacépède, 1804) Bechstein, 1802

Vipera viridis (nec *Trimeresurus viridis* Lacépède, 1804) Daudin, 1803

Trigonocephalus fario Jan, 1859 (*nomen nudum*)

Colubar gramineus – Mason, 1860 (*nomen incorrectum*)

Bothrops viridis fario Jan, 1863 (*nomen nudum*)

Bothrops viridis genei Jan, 1863 (*nomen nudum*)

Lachesis graminea – Wall, 1919 part

Trimeresurus gramineus – Whitaker & Captain, 2004 part

Craspedocephalus gramineus – Wallach et al., 2014 part

Taxonomic history. Russell (1796) described ‘*Boodroo Pam*’ based on a specimen from Vizagapatam (now Vishakhapatnam, Andhra Pradesh state, India) in the northern Eastern Ghats. Shaw (1802) provided a nominate description of that taxon as *Coluber gramineus*, based on the specimen depicted by Russell (1796). Bechstein (1802) erected the nomen *Coluber viridis* and Daudin (1803) erected the nomen *Vipera viridis* based on the same specimen depicted in Russell (1796). These nomina are connected by an objective synonymy and

therefore share the same type specimen (see Russell, 1796) and type locality, Vizagapatam. Notwithstanding these, Lacépède (1804) described an Indonesian species as *Trimeresurus viridis*. This nomen *Trimeresurus viridis* Lacépède, 1804 has now been superseded by its junior subjective synonym *Trimeresurus insularis* Kramer, 1977 that is now in prevailing usage (see David et al. 2011). Three unavailable nomina *Trigonocephalus fario* Jan, 1859, *Bothrops viridis fario* Jan, 1863 and *Bothrops viridis genei* Jan, 1863 are present.

Jerdon (1854) discusses this taxon under the nomen *Trigonocephalus (Cophias) viridis* and miscredits it to Merrem. Beddome (1862) discusses this taxon in part (specimen from Condipalli hills) under the nomen *Trimeresurus viridis* (see below). Günther (1864) discusses unrelated East Asian species from Penang, Mergui, Laos, Khasya, Sikkim, Ladakh and Ningpo. Günther (1864) questioned if Andaman and Nicobar populations are conspecific with *Tri. gramineus* s. auct. but concludes that it could not be ascertained based on Blyth’s (1846) brief notes. Theobald (1876) also followed a similar view and refers populations from Sylhet, Burma and Malacca under this name. Subsequently, he maintained the same stance when he mentioned specimens from Sikkim, Khasi hills, Assam, Pegu, Andamans, Bengal and Nepal (Theobald, 1876).

Later Boulenger (1890), perhaps prompted by earlier works (e.g. Theobald), lumped together several S.E. Asian nomina such as *Trimeresurus viridis* Lacépède, 1804 (see David et al. 2011 for its proper explanation), *Trigonocephalus erythrurus* Cantor, 1839, *Trimeresurus albolabris* Gray, 1842, *Trimeresurus elegans* Gray, 1853 and even a non-green taxon *Trimeresurus mutabilis* Stoliczka, 1870 (see Vogel et al. 2014 for its current status). Stejneger (1907) also followed Boulenger (1890). This diluted and over-circumscribed concept of ‘*Tri. gramineus*’ (sic) encompassing almost all green *Trimeresurus* species, gave rise to the false notion that it is a very widespread and variable species.

Remarks. *Coluber viridis* Bechstein, 1802 and *Vipera viridis* Daudin, 1803 are both objective junior synonyms of *Coluber viridis* Shaw, 1802, all being described on the basis of the very same type specimen described and illustrated by Russell (1796) as “*Boodroo Pam*”. *Trimeresurus viridis* Lacépède, 1804 is a nomen oblitum superseded by *Trimeresurus insularis* Kramer, 1977 that is now in prevailing usage for this Indonesian species (Wallach et al. 2014). Two female paratype specimens from the Eastern Ghats and one male specimen from Matheran, northern Western Ghats of a former subjective junior synonym (fide Wallach et al. 2014) *Trimeresurus occidentalis* Pope & Pope, 1933 is herein referred to *Tri. gramineus* (Shaw, 1802) with respect to its phylogenetic and morphological affinities.

Type. Holotype (iconotype), a 762 mm specimen described and illustrated in Russell (1796: 13–14, pl. 9, titled “*Boodroo Pam*”).



Figure 19. *Craspedocephalus gramineus* in life, showing: (A) entire lateral view (Thamini, Pune), (B) head and forebody dorsal view (Belapur, Navi Mumbai), (C) head and forebody lateral view, (D) entire ventrolateral view; from Kharghar, Navi Mumbai, Maharashtra.

Type locality. “hills in the vicinity of Vizagapatam, coast of Coromandel, India” [= Vishakhapatnam, Andhra Pradesh, India, 17°41'N; 83°13'E].

Etymology. *gramineus*, ‘grassy’ in Latin, alluding to its grass-green dorsal colouration.

Material examined. NHMUK 1946.1.19.87 from Cuddapa Hills, Andhra Pradesh, by R.H. Beddome paratype of *Trimeresurus occidentalis* Pope & Pope, 1933; CESS033 from Gandagan, Orissa by Ashok Kumar Mallik; CESS100, CESS101, CESS102 from Naneghat, Maharashtra by Ashok Kumar Mallik in 2010; AFS96.13 from Masinagudi, and AFS96.14 Gingee, Tamil Nadu by Anita Malhotra in 1997; BNHS 2627 from Khandala, Maharashtra by Charles Mc Cann in 1941, BNHS 2764 from Ahwa, Dangs, Gujarat by Dr. E.M. Shull in 1963 and BNHS 3275 from Sirumalai hills, Tamil Nadu by S.P. Vijayakumar, 2001; CESS526 from Shevroy, Tamil Nadu by Achyuthan Srikanthan and M.V. Shreeram in 2019.

Lineage diagnosis. A cryptic lineage (L1) belonging to the *C. gramineus* complex, it is distinguished from *C. occidentalis* (L2) as follows: lower ventral scale count 158–179 (vs. 142–154). It is genetically divergent from *C. occidentalis* by 8.1 % and 1.0 % at cyt b and 16S respectively. This lineage is far more widespread than its parapatric sister taxon *C. occidentalis*, occurring almost throughout peninsular India from Odisha in the east, southern Gujarat to the north-west and as far south as the Srivilliputhur hills.

Description of referred material (n=11). A species with a slender, cylindrical body of snout to vent length (SVL) up to 679 mm and a prehensile tail; dorsal scales keeled with anterior dorsal scale rows (DSR) 19–21, mid body scale rows (MSR) 19–21 and posterior scale rows (PSR) 15; head prominent, clearly distinguished from the neck with small, juxtaposed scales on the head; rostral scale sub triangular with the upper side roughly one fourth the size of the lower side with the tip visible from above; supraoculars separated by 8–11 scales, between the posterior edge of the supraocular scales; canthus rostralis distinct with three to four canthal scales on the ridge; two to three preoculars, two to three postoculars and a thin elongated crescent shaped subocular; eye with a distinct elliptical pupil; temporal scales mildly keeled; aperture of the nostril completely covered by the nasal scale, undivided and subrectangular; nasal scale bordering the first supralabial; loreal pit present in contact with the second supralabial with two scales between the nasal and the second supralabial; 10–12 supralabials and 11–13 infralabials, with 9–13 scales between the last supralabial, including the last supralabial up to the start of the ventral scales; ventrals 158–179, laterally separated from the dorsal scale rows by a slightly broader row of dorsal scales anal scale undivided, divided subcaudals 54–67; terminal scale on the tail larger than the previous scale, blunt at the tip.

Colour in life. Head and dorsum colour from verdant green to leaf green, sometimes bluish green with black, alternating saddle shaped markings on the dorsum; preoc-

ular/ temporal stripe in black, sometimes green fading into black; ventrals with bright yellow, creamish yellow to a dirty white colour; the region where the ventrals meet the dorsum alternating with the ventral colour once every 2–3 scales.

Habitat. A highly arboreal species found in dry scrub, dry deciduous, semi evergreen and lowland riparian forests from 100–1600 m asl.

Distribution. Endemic to Peninsular India. Found in the Eastern Ghats (Simlipal hills, Chota Nagpur plateau southwards upto Sirumalai hills) and hills of Central India (Pachmahri, Seoni hill ranges) as well as the Western Ghats from Surat Dangs, southwards till the Shencottah gap.

Craspedocephalus occidentalis (Pope & Pope, 1933) comb. nov.

Figures 20–22

Trimeresurus occidentalis Pope & Pope, 1933

Trimeresurus viridis (nec *Coluber viridis* Bechstein, 1802) - Beddome, 1862 part

Lachesis graminea – Wall, 1919 part

Craspedocephalus occidentalis (Pope & Pope, 1933)

Taxonomic History. Pope & Pope (1933), in an effort to fix the status of Southeast Asian taxa of superficially similar green *Trimeresurus* species, worked out the systematics of the Indian group. Unfortunately, they were mistaken in allocating the nomen *Coluber gramineus* Shaw, 1802 to the East Asian species (see David et al. 2011). Therefore, thinking that the western population inhabiting India required a new nomen, they thus erected *Trimeresurus occidentalis*. This taxon was described based on a series of specimens (holotype and paratypes) inhabiting both the Western Ghats and the Eastern Ghats.

Remarks. Among the four paratypes attributed to this taxon in its original description (Pope & Pope, 1933), one male from Brahmagiri, Western Ghats is currently attributable to this species based on the phylogenetic position of topotypical samples. The distribution of *C. occidentalis*, as defined here, encompasses the provenance of the holotype (Mudumalai, Wayanad, and the Nilgiri hills in general). We refer three other paratypes, two females originating from the Cuddapa hills and the Shevaroys in the Eastern Ghats and one male from Matheran to *C. gramineus* (Shaw, 1802) based on the phylogenetic placements of topotypical samples. However, as paratypes have no name-bearing function and status, the nomen *Craspedocephalus occidentalis* is available *in toto* for being conferred to this Western Ghats population. Beddome (1862) discusses a specimen from Anamalais under the name *Trimeresurus viridis* and also miscredits the nomen to Gray, instead of Bechstein or Daudin (see Wallach et al. 2014).



Figure 20. *Craspedocephalus occidentalis* comb. nov. in life, showing: (A) entire dorsal view, (B) head dorsal view, (C) head lateral view, (D) entire lateral view; Coorg, Karnataka.

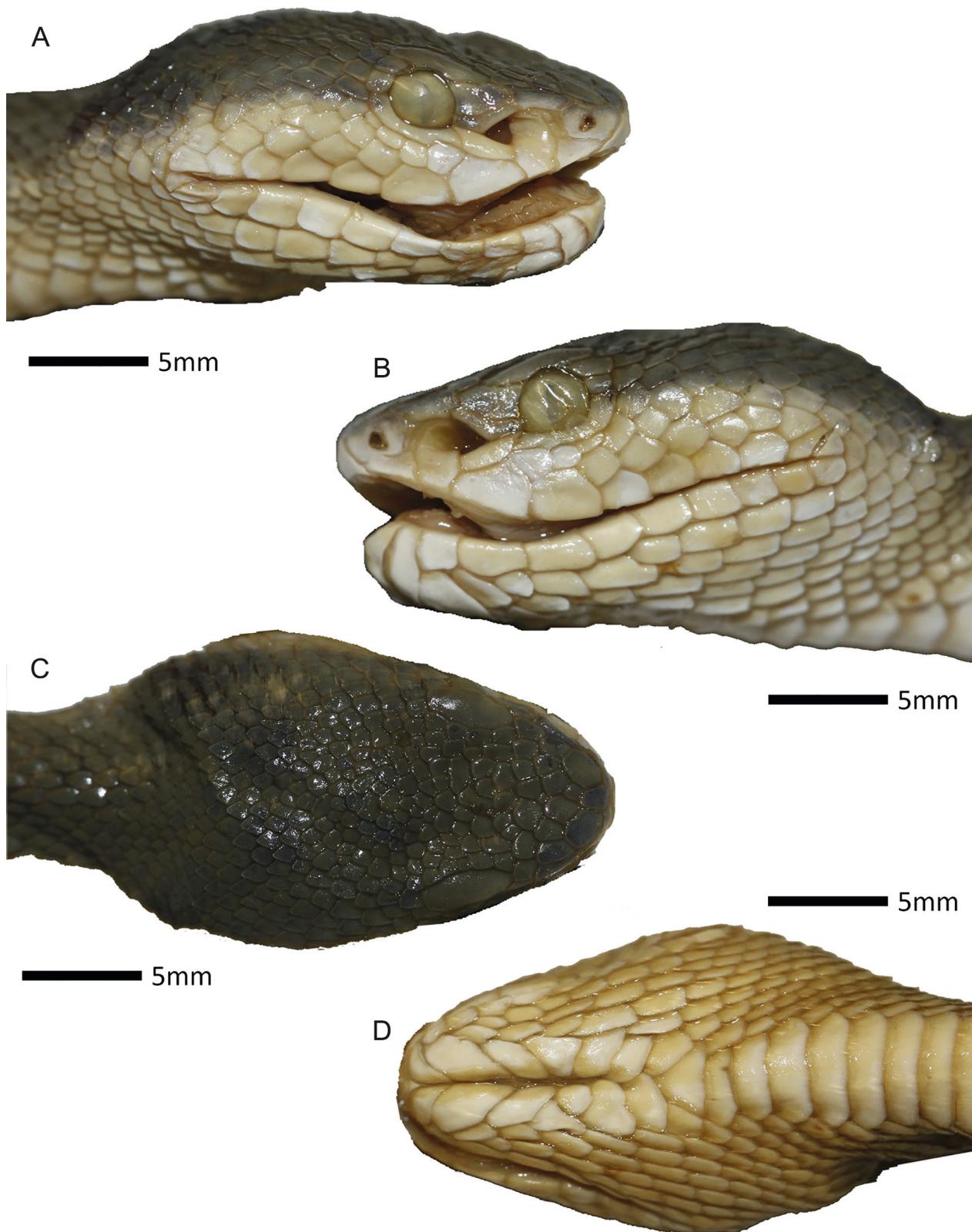


Figure 21. *Craspedocephalus occidentalis* comb. nov. holotype (NHMUK 1982.8.26.40), in preservation, showing: (A) head lateral left view, (B) head dorsal view, (C) head ventral view, (D) head lateral right view.

Type. Holotype, NHMUK 1982.8.26.40, an immature male, collected by R.H. Beddome.

Type locality. Mudumallay, near Wayanad [i.e., Mudumalai hills, in Nilgiris dt., Tamil Nadu, India] in the Western Ghats (*fide* Pope & Pope 1933).

Etymology. Latin, for ‘western’, in allusion to its western distribution range, compared to S.E. Asia.

Material examined. Holotype, NHMUK 1982.8.26.40 from Wayanad, Tamil Nadu by R.H. Beddome; CESS040 from Brahmagiri, Karnataka

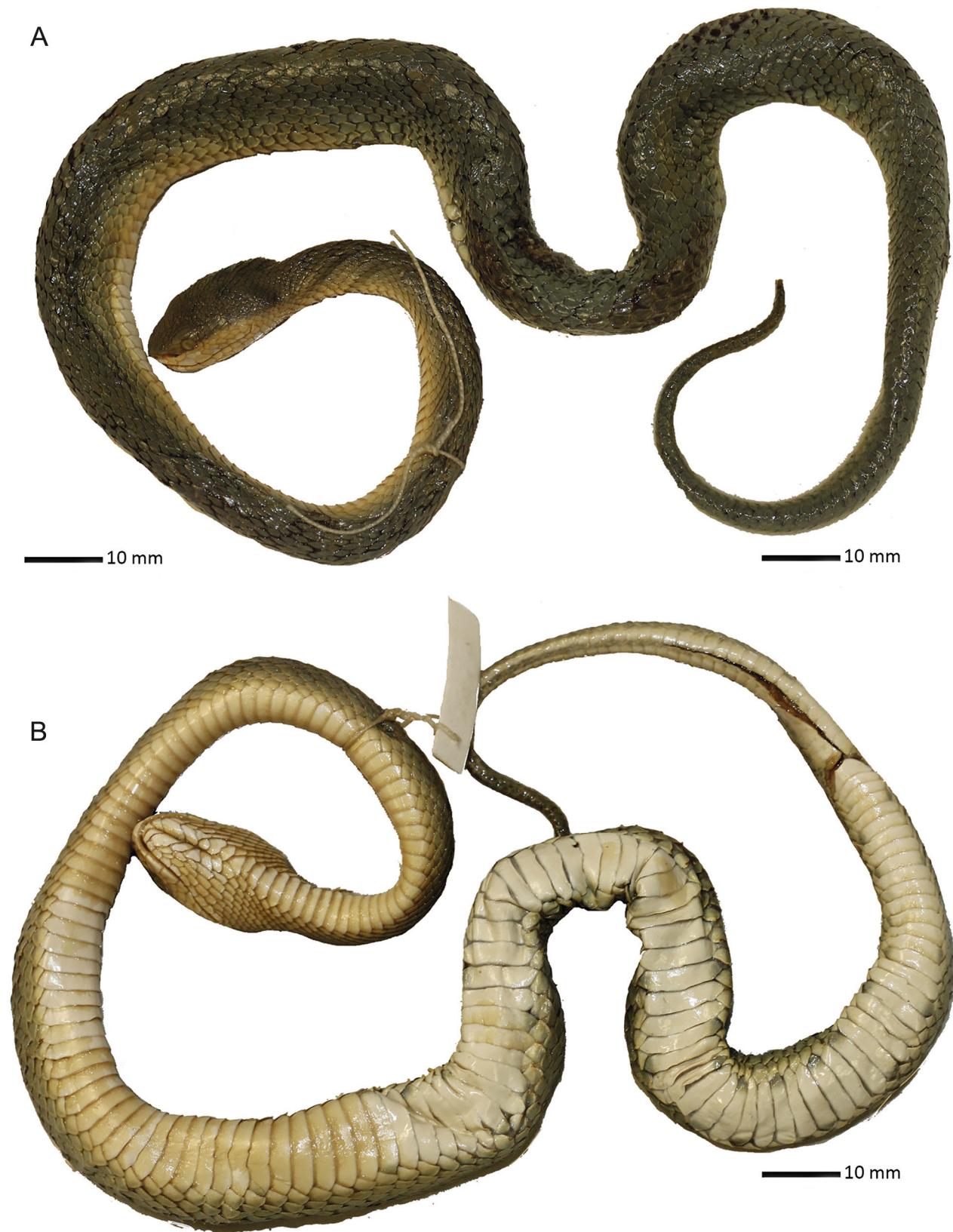


Figure 22. *Craspedocephalus occidentalis* comb. nov. holotype (NHMUK 1982.8.26.40), in preservation, showing: (A) entire dorsal view, (B) entire ventral view.

by S.P. Vijayakumar in 2009; CESS272 from Tadiendamol, Karnataka by Ashok Kumar Mallik in 2011.

Lineage diagnosis. A cryptic lineage (L2) belonging to the *C. gramineus* complex, it can be distinguished from

C. gramineus s. str. (L1) as follows: lower ventral scale count 142–154 (vs. 158–179). L2 is genetically divergent from *C. gramineus* s. str. (L1) by 8.1 % at Cyt b and 1.0 % at 16S. This lineage is possibly parapatric with respect to its far more widespread sister taxon *C. gramineus*, and

is endemic to the Wyanad-Bramagiri-Coorg hill complex of the central Western Ghats, at higher elevations (> 1000 m MSL).

Redescription (also see Pope & Pope 1933). Holotype in good condition, entire, with a slender, cylindrical body of snout to vent length (SVL) 400 mm and a prehensile tail of length (TL) 97 mm; dorsal scales keeled with anterior dorsal scale rows (DSR) 23, mid body scale rows (MSR) 21 and posterior scale rows (PSR) 15; head prominent, of length 21.5 mm, clearly distinguished from the neck with small, juxtaposed dorsal scales on the head; rostral scale sub triangular with the upper side roughly one fourth the size of the lower side with the tip visible from above; supraoculars of length 1.85 mm and width 4.15 mm, separated by eight scales, between the posterior edge of the supraocular scales; canthus rostralis distinct with four canthal scales on the ridge; two preoculars, two postoculars and a thin elongated crescent shaped subocular, in contact with a pair of scales scales that are in contact with the third and fourth supralabial scale; eye with a distinct elliptical pupil, vertical diameter of the eye 2.23 mm and horizontal diameter 2.44 mm; temporal scales mildly keeled; aperture of the nostril completely covered by the nasal scale, undivided and subrectangular; nasal scale bordering the first supralabial; loreal pit present in contact with the second supralabial with two scales between the nasal and the second supralabial; nine supralabials and 10 infralabials, with seven scales between the last supralabial, including the last supralabial up to the start of the first ventral scale; 1st and 2nd infralabial scale in contact with the first pair of genials; a gap of six scales including the posterior genials followed by 155 ventrals, laterally separated from the dorsal scale rows by a slightly broader row of dorsal scales; anal scale undivided, followed by 60 divided subcaudals scales; terminal scale on the tail larger than the previous scale, blunt at the tip.

Colour in life. Head and dorsum colour varies from bright green to faded dull green, with no markings on the dorsum; preocular/temporal stripe absent; ventrals in creamish yellow to dirty white colour; the region where the ventrals meet the dorsum alternating with the ventral colour once every 2–3 scales; the colour of the dorsum and ventrals divides exactly at the pre/postocular stripe area, with an absence of a dark stripe (as opposed to *C. gramineus*).

Colour in preservative. Head and dorsum in light faded green; ventrals creamish to dirty white in colour; some of the dorsum scales with a black interscalar colour, more evident in the front half of the body; the colour of the dorsum and ventrals divides exactly at the pre/postocular stripe area, with an absence of a dark stripe (as opposed to *Tri. gramineus*).

Habitat. A highly arboreal species found in moist evergreen forests from 1000–1900m MSL, sympatric with *C. malabaricus* throughout parts of its range.

Distribution. Endemic to the central Western Ghats, distributed in the Wayanad, Bramagiri, Coorg hills, at higher elevations (> 1000 m asl).

Craspedocephalus strigatus (Gray, 1842)

Figures 23–25

Atropos darwini Duméril, Bibron & Duméril, 1854
Trigonocephalus (Cophias) neelgherriensis Jerdon, 1854
Lachesis strigatus – Boulenger, 1896
Lachesis strigata – Wall, 1919
Trimeresurus strigatus – Smith, 1943
Protobothrops strigatus – Kraus et al., 1996
Craspedocephalus strigatus – Wallach et al., 2014

Type Locality. Originally in error, mentioned as “Cape of Good Hope?” and “Madras” subsequently emended to Madras Presidency (=Tamil Nadu) by Boulenger (1896) (see Wallach et al. 2014).

Etymology. Latinized from its stem word ‘strigate’ alluding to the pattern streaked with colourful, alternate, transverse bars.

Type. Syntypes NHMUK 1946.1.18.79 and NHMUK 1946.1.18.78 from Nilgiris, Tamil Nadu by T.C. Jerdon in 1850.

Material examined. Syntypes NHMUK 1946.1.18.79 and NHMUK 1946.1.18.78 from Nilgiris, Tamil Nadu by T.C. Jerdon in 1850; CESS142 from Silent Valley, Kerala by Saunak Pal and Mrugank Prahu in 2010; BNHS 2617 and BNHS 2618 from Coonor by C. Gray in 1917; BNHS 2619 from Coonor by Maj. Frank Wall in 1911; BNHS 2621 from Ooty by Maj. Frank Wall in 1912.

Lineage diagnosis (also see Whitaker & Captain, 2004). A species of *Craspedocephalus* (L8) endemic to the Western Ghats, characterized by having the following combination of characters: 2nd supralabial (usually) not bordering the anterior margin of loreal pit (vs. always bordering in the *C. malabaricus*, *C. gramineus* complexes); lacking a prehensile tail and green dorsum (vs. having prehensile tail and green dorsum in the *C. gramineus*, *C. macrolepis* complexes); having an undivided supraocular (vs. divided or with indented margins in the *C. malabaricus* complex).

Description. Relatively stout species with a cylindrical body of snout to vent length (SVL) up to 391 mm and a tail of length (TL) up to 64 mm; dorsal scales keeled with anterior dorsal scale rows (DSR) 20 to 22, mid body scale rows (MSR) 19 to 21 and posterior scale rows (PSR) 15 to 17; head prominent, clearly distinguished from the neck with small juxtaposed scales on the dorsal surface of the head; rostral scale sub triangular with the upper side roughly half the size of the lower side with the tip visible from above; supraoculars separated by 9 to 11 scales on the posterior end; canthus rostralis distinct with three can-



Figure 23. *Craspedocephalus strigatus* in life, showing: (A) entire dorsal view, (B) entire lateral view, (C) entire dorsolateral view; from Upper Nilgiris, Tamil Nadu.

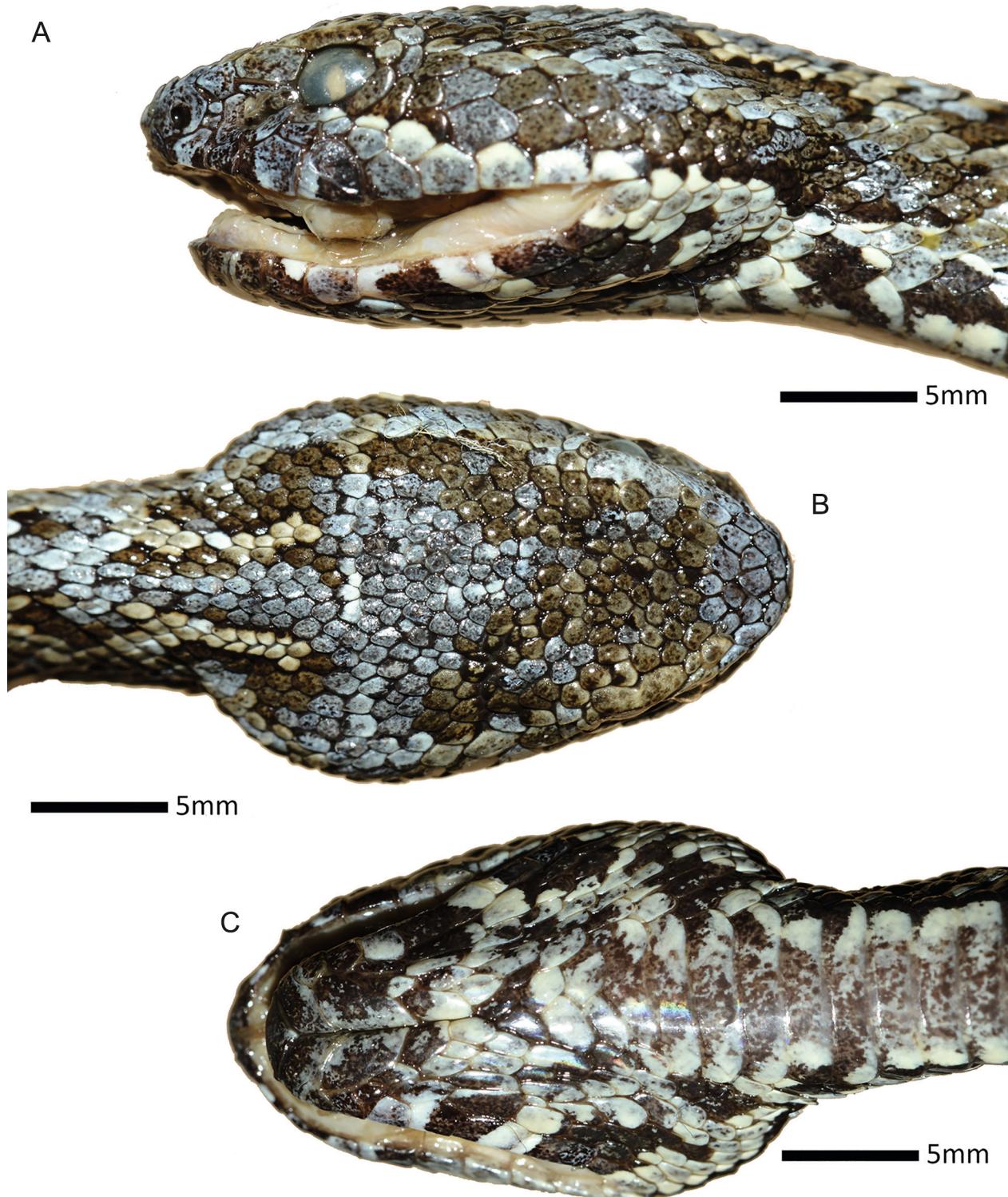


Figure 24. *Craspedocephalus strigatus* syntype (NHMUK 1946.1.18.79), in preservation, showing: (A) head lateral right view, (B) head dorsal view, (C) head ventral view.

thal scales; two to three preoculars, two to three postocular and a thin elongated crescent shaped subocular; eye with a distinct elliptical pupil; temporal scales smooth; aperture of the nostril completely covered by the nasal scale, undivided and subrectangular; nasal scale bordering the first supralabial; loreal pit present in contact with the second supralabial with two scales between the nasal and the second supralabial; nine to 10 supralabials and 10 to 12 infralabials, with six to eight scales between the

last supralabial, including the last supralabial till the start of the ventral scales; 1st, 2nd and 3rd infralabial scale in contact with the first pair of genials; a gap of three scales including the posterior genials followed by 134 to 142 ventrals, laterally separated from the dorsal scale rows by a slightly broader row of dorsal scales; anal scale undivided, followed by 38 to 44 divided subcaudals scales; terminal scale on the tail larger than the previous scale, blunt at the tip.

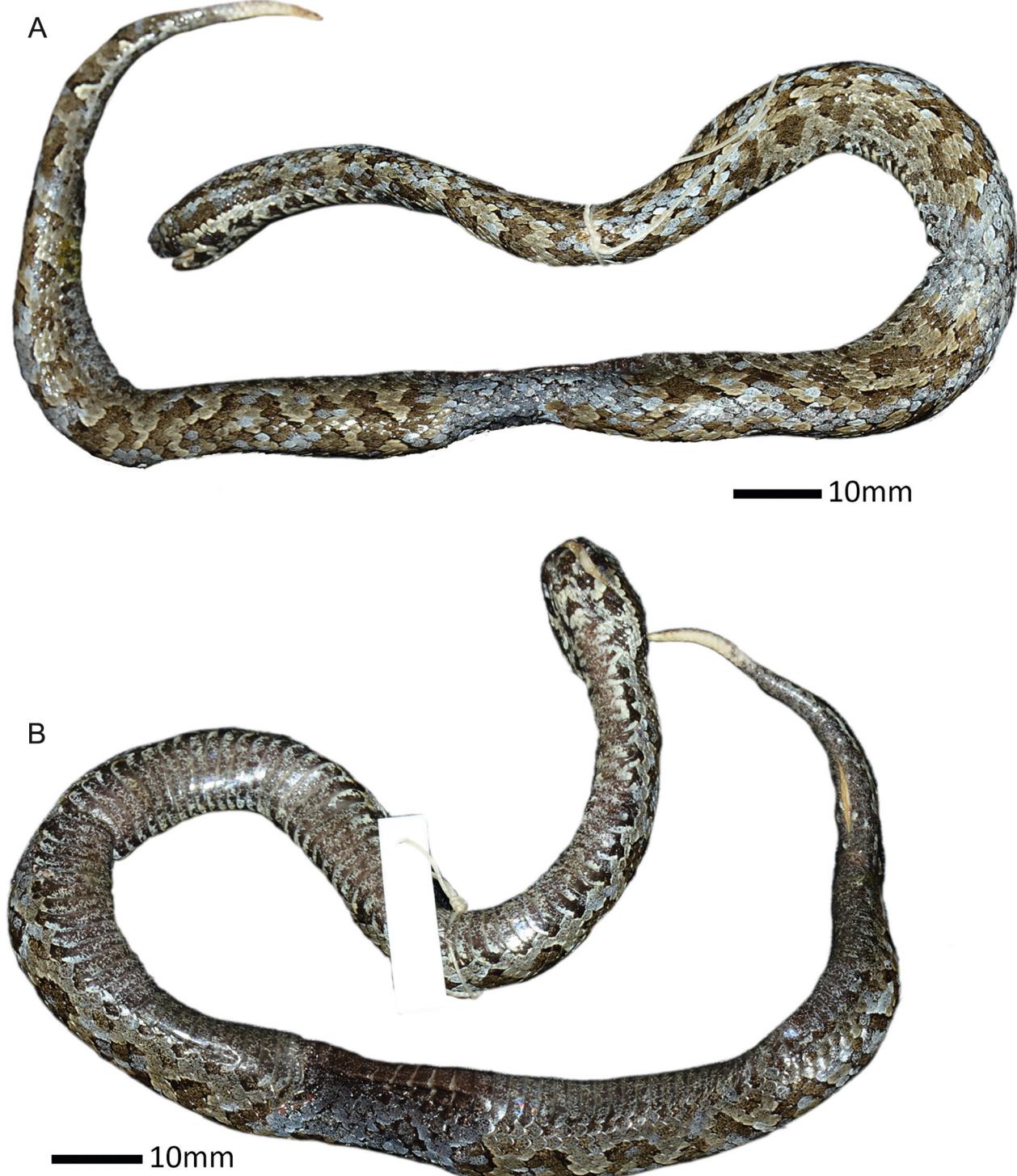


Figure 25. *Craspedocephalus strigatus* syntype (NHMUK 1946.1.18.79), in preservation, showing: (A) entire dorsolateral view, (B) entire ventrolateral view.

Colour in life. Bronze to light brown dorsum blotched with a stark, continuous alternating saddle-shaped pattern in dark brown to black, strikingly similar to the markings on *Vipera berus* or *Gloydius himalayanus*; preocular/temporal stripe in dark brown; post ocular stripe in dirty brown continuing towards the loreal pit and the infralabials; another stripe below the subocular stripe fades into the infralabials followed by another blotch towards the end of the infralabials; base colour of the infralabials and ventrals being light creamish to white in colour, of-

ten dotted with rufous spots in the supralabials the region where the dorsal scales meet the ventrals in alternating dark brown colour and light brown/bronze colour scales; dorsal bronze scales are dotted with darker brown; the nape is characterized with a prominent horse shoe shaped marking hence earning its common name; in juveniles, the bronze colour is replaced with light brown.

Colour in preservative. Brown and cream markings dorsally and laterally, occasionally interrupted with silvery/

grey scales, tail mostly brown and cream coloured with lighter more vivid cream coloured scales making triangular markings vertically along it (four in total); tip of tail fading to a light cream colour.

Habitat. A highly terrestrial species found in montane evergreen, moist evergreen and high elevation grasslands.

Distribution. Endemic to the Nilgiri Massif north of the Palghat Gap, distributed in very high elevations (1700–2600 m asl) (also see Wall, 1919; Bhupathy & Nixon, 2011). This species has the smallest geographic range of all *Craspedocephalus* in Peninsular India (Ganesh & Chandramouli, 2018).

Discussion

The systematics of pit vipers of Peninsular India has been in flux, given their variation in morphology, their distribution in different habitat types and uncertainty of species delimitation criteria (Freitas et al. 2020). We carried out this study to delineate independent evolutionary lineages and evaluate congruence between genetic and morphological variation in the genus *Craspedocephalus* in Peninsular India, using a stepwise multi-criteria approach to delimit species boundaries in this group (Shanker et al. 2017). This study designates four new species in addition to four currently recognized species and confirms the systematic position of two endemic species (*C. strigatus* and *C. macrolepis*) belonging to Peninsular India. There are now a total of eight lineages found in the Western Ghats and Peninsular India (Fig. 26).

The phylogeny generated using three concatenated mitochondrial fragments of almost all the populations and species of *Craspedocephalus* found in Peninsular India is similar to the tree topology published in earlier studies (Malhotra & Thorpe 2004, Alencar et al. 2016), including studies which used nuclear as well as mitochondrial genes (Malhotra et al., 2010). While a combination of nuclear and mitochondrial genes may provide stronger phylogenetic support for deeper relationships of pit vipers within the clade as well as with other clades, there is strong support for the species level divergences that we report here. Our study further supports the systematic position of *C. strigatus* within the *Craspedocephalus* clade. We also found that *C. macrolepis* is nested within *Craspedocephalus*.

The chromatically variable and widely distributed taxon, *C. malabaricus*, was recovered with three divergent lineages, two of which are distributed in the Southern Western Ghats and are sister to each other, with high genetic divergence from a northern Western Ghats lineage. Considering the type locality of *C. malabaricus* as the Western Ghats (all west coast forests in Peninsular India) (Jerdon 1854, Günther 1864), the other two new lineages are recognized as distinct species on the basis of genet-

ic distance, morphological dissimilarity, and geographic barriers between them.

This delineation takes into account the geographic ranges of each of the lineages within the *C. malabaricus* species complex: *C. malabaricus* (Jerdon, 1854), *C. anamallensis* (Günther, 1864) and *C. travancoricus* sp. nov. whose distributions coincide with segments of the Ghats separated by significant gaps. However, there were morphological differences (i.e. strongly keeled dorsal scales) between Jerdon's (1854) *Tri. malabaricus* and Günther's specimen, suggesting that our lineage L3 (*Tri. anamallensis*) is closer to Günther's description. Lineage L5 corresponds to *C. malabaricus* on the basis of morphological similarity, while Lineage L4 is similar to Jerdon's *C. malabaricus* but is geographically disjunct from the former. This historically untypified population, so far cited under the chresonymy of *Tri. malabaricus sensu lato*, is here named as *C. travancoricus* sp. nov.. We found that all species within the *C. malabaricus* group show colour polymorphism and are without much sexual dimorphism.

Similarly, the *C. gramineus* species complex comprises two highly divergent lineages (7 % at ND4 and 8 % at cyt b) with significant morphological variation and strong habitat preference in those lineages (authors' personal observation). Morphologically, they differ in ventral scales and supralabials. Lineage 1 (*C. gramineus*) is distributed in the drier and low-mid elevations of hill ranges (till ca. 1000 m asl) of Peninsular India while Lineage 2 (*C. occidentalis*) is distributed in the wet forests of the Western Ghats. These findings are supported by earlier work (Pope & Pope, 1933).

The endemic *C. macrolepis* was classified as a distinct species with significant morphological differentiation and was found to be nested within the *Craspedocephalus* clade of Peninsular India, as suggested by earlier studies based on morphology alone (Beddome 1862, Guo et al. 2010, David et al. 2011). Genetic support was too low to consider the genus '*Peltopelor*' as different from *Craspedocephalus* despite differences in hemipenial and other morphological characters (Malhotra & Thorpe 2004, Guo et al. 2010). As *Craspedocephalus* Khul & Van Hasselt, 1822 has nomenclatural priority over *Peltopelor* Günther, 1864, the genus name for all Peninsular Indian taxa sampled here remain *Craspedocephalus*. We found two distinct lineages of *C. macrolepis* that were morphologically divergent, geographically separated and with shallow genetic divergence from each other in the southern Western Ghats, that were elevated to species status. In addition, *C. strigatus* was confirmed to be a member of the Indian subcontinent group as earlier suggested by Malhotra & Thorpe (2004) rather than *Protobothrops* as suggested by Kraus et al. (1996).

Our work suggests that there are (at least) eight independent evolutionary lineages in Peninsular India, supported by genetics, morphology, and geography. Besides naming two new lineages, both from the southernmost part of the Western Ghats, this study also clarifies the taxonomic status, distribution and phylogeny of Peninsular Indian *Craspedocephalus* involving both recognized and synonymized taxa. Of the eight species of *Craspedoceph-*

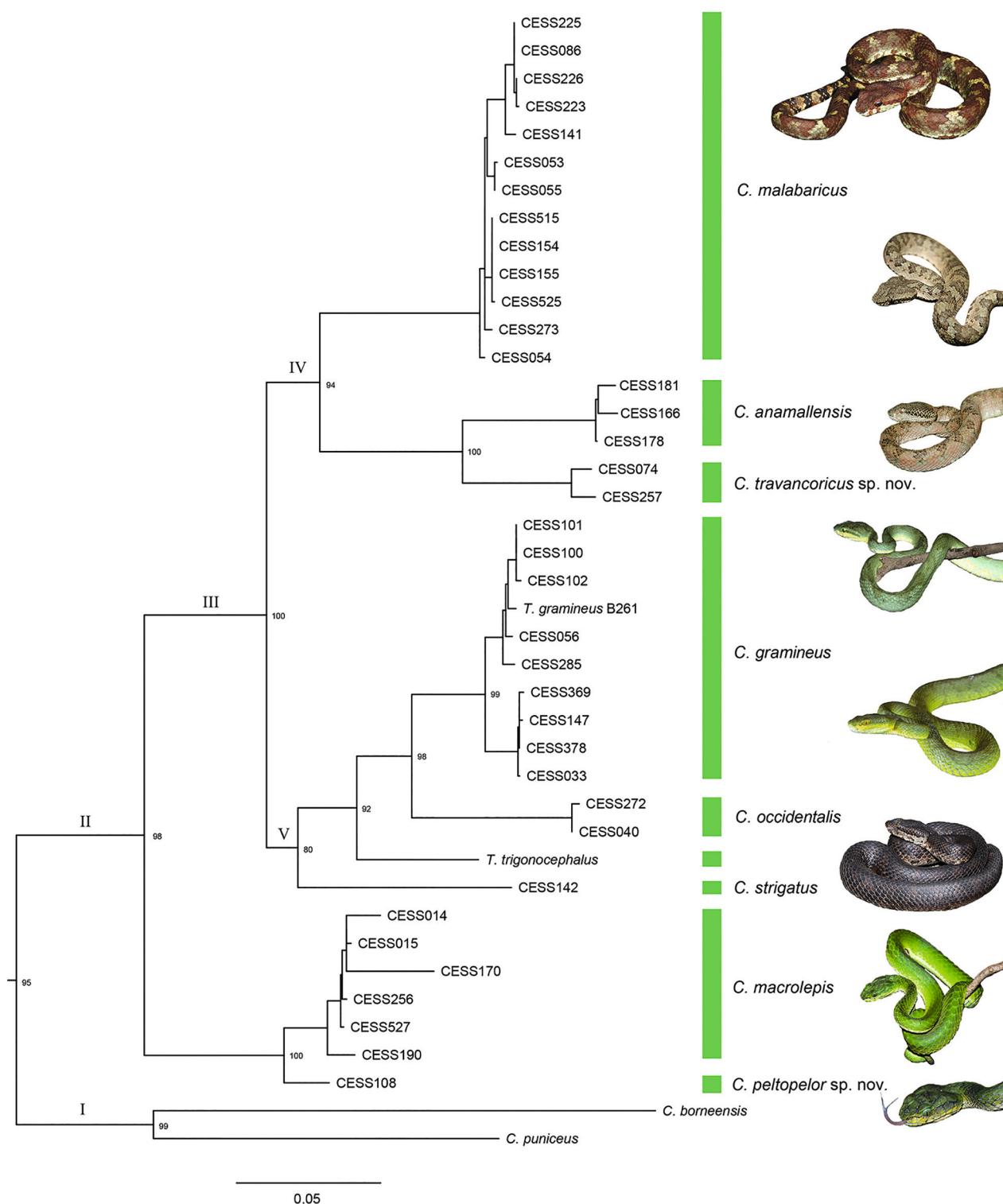


Figure 26. New lineages (green bars) are depicted within *C. gramineus*, *C. malabaricus* and the *C. macrolepis* species complex along with the other species from the Peninsular India. The clade comprising *C. macrolepis* and *C. peltopelor sp. nov.* is sister to the clade comprising all other members of Peninsular Indian *Craspedocephalus* (II). The Western Ghats *C. malabaricus* complex includes *C. malabaricus*, *C. anamallensis* and *C. travancoricus* (IV). *C. trigonocephalus* from Sri Lanka is nested within the Western Ghats sub-clade (III) along with *C. strigatus*, *C. gramineus* and *C. occidentalis* (V). Clade-I comprises species from Southeast Asia.

alus belonging to Peninsular India, seven are restricted to the wet forests of the Western Ghats. The southern Western Ghats stands out in terms of species richness for *Craspedocephalus* in Peninsular India with four endemic species, which is evident in other taxa including frogs

(*Raorchestes* - Vijayakumar et al. 2016, *Mercurana* and *Beddomixalus* – Abraham et al. 2013), lizards (*Hemidactylus* – Srikanthan et al. 2018, *Calotes* – Pal et al. 2018) and snakes (*Calliophis* – Jins et al. 2014, *Ahaetulla* – Mallik et al. 2020, *Boiga* – Ganesh et al. 2021).

The Peninsular Indian clade comprises almost all taxa distributed across South Asia except *Tropidolaemus huttoni*. The phylogenetic relationship of *Tro. huttoni* with *Trimeresurus* is unknown. *Tropidolaemus huttoni* is currently known from two neonate museum specimens, which are underdeveloped sexually. Based on its morphological similarity to *Tropidolaemus wagleri*, David & Vogel (1998) placed *Tro. huttoni* in this genus.

This work underscores the indispensable role of genetic studies that enable us to fully document cryptic diversity including in lineages that have remained taxonomically ‘stable’ for over a century (since Rao, 1917). This study also highlights the profound and untested effect of geographic barriers on this group of snakes. Though there were several synonyms and typifications within, for example, the *C. malabaricus* group between 1854 and 1917, these were primarily driven by morphological variations and not based on geographic rationale. That we uncovered geographically concordant sister lineages within the genus *Craspedocephalus* in the Western Ghats exemplifies the effectiveness of allopatry as a prezygotic reproductive barrier, one that does not instigate morphological changes in lineages, resulting in a high degree of crypsis, but at the same time leading to deep genetic divergence. This pattern is also observed in vine snakes (*Ahaetulla* – Mallik et al 2020) and to a degree, in cat-eyed snakes (*Boiga* – Ganesh et al. 2021). A comparative study with the inclusion of nuclear genes in the future may explain and shed light on gene-flow between these populations over their distribution ranges and across barriers.

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Supplementary material 1

Table S1

Authors: Mallik AK, Srikanthan AN, Ganesh SR, Vijayakumar SP, Campbell PD, Malhotra A, Shanker K (2021)

Data type: .pdf

Explanation note: Details of gene regions amplified and PCR primers used in this study. Table indicates DNA sequence length (in base pairs) and PCR protocols used.

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Link: <https://doi.org/10.3897/vz.71.e66239.suppl1>

Supplementary material 2

Table S2

Authors: Mallik AK, Srikanthan AN, Ganesh SR, Vijayakumar SP, Campbell PD, Malhotra A, Shanker K (2021)

Data type: .cvs

Explanation note: List of tentative species of Asian pit vipers and outgroups used in this study. The table contains the museum voucher numbers, geographic locations and loci used in this study. '*' Indicates non-lethal sampling. Voucher numbers with parentheses indicate the secondary code number.

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Link: <https://doi.org/10.3897/vz.71.e66239.suppl2>

Supplementary material 3

Table S3

Authors: Mallik AK, Srikanthan AN, Ganesh SR, Vijayakumar SP, Campbell PD, Malhotra A, Shanker K (2021)

Data type: .pdf

Explanation note: Morphological characters examined and their abbreviations used to discriminate among species in pit vipers.

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Link: <https://doi.org/10.3897/vz.71.e66239.suppl3>

Supplementary material 4

Figure S1

Authors: Mallik AK, Srikanthan AN, Ganesh SR, Vijayakumar SP, Campbell PD, Malhotra A, Shanker K (2021)

Data type: .jpg

Explanation note: The complete Bayesian Poisson Tree Processes (bPTP) output trees from a concatenated dataset of three mitochondrial loci (cyt b, ND4 and 16S) show predictions of putative species across the clades. The values on clades indicate the posterior probability, monophyly (clade of single species) with 1.00, whereas lower values suggest polyphyly (clade with more than one species). The actual number of putative species in the tree is ascertained with help of other delimiting criteria. Blue colored branches indicate monophyly of that lineage and red color indicates individuals clustered together within a species.

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Link: <https://doi.org/10.3897/vz.71.e66239.suppl4>

Supplementary material 5

Table S4

Authors: Mallik AK, Srikanthan AN, Ganesh SR, Vijayakumar SP, Campbell PD, Malhotra A, Shanker K (2021)

Data type: .pdf

Explanation note: Uncorrected pairwise genetic distances (in per cent) between lineages (L1–L9) for mitochondrial loci ND4, CYTB and 16S.

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Link: <https://doi.org/10.3897/vz.71.e66239.suppl5>

Supplementary material 6

Figure S2

Authors: Mallik AK, Srikanthan AN, Ganesh SR, Vijayakumar SP, Campbell PD, Malhotra A, Shanker K (2021)

Data type: .pdf

Explanation note: Distribution of *Craspedocephalus* lineages in Peninsular India: (A) *Craspedocephalus macrolepis* complex, (B) *Craspedocephalus malabaricus* complex, (C) *Craspedocephalus gramineus* complex.

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Link: <https://doi.org/10.3897/vz.71.e66239.suppl6>