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A NEW FOSSORIAL REED SNAKE (SQUAMATA: CALAMARIIDAE: *Calamaria*) FROM NORTHEAST INDIA, WITH A NOMENCLATURAL SYNOPSIS OF THE *Calamaria pavimentata* COMPLEX

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Abstract
The fossorial reed snakes of the genus *Calamaria* are morphologically conservative, geographically structured, and frequently misidentified across broad regions, especially where historical names have been applied without explicit synonymy audits. During surveys in the Garo Hills, Meghalaya, Northeast India, we collected a series of *Calamaria* specimens referable to the "*Calamaria pavimentata*" concept historically used for the region. We evaluate these specimens using a morphology-first framework complemented by mitochondrial cytochrome *b* phylogenetic placement. Maximum-likelihood inference recovers the Meghalaya lineage as the strongly supported sister to *C. mizoramensis*, with an uncorrected *p*-distance of 6.3%; these mitochondrial values are treated as descriptive support rather than as threshold-based evidence. Morphologically, the Meghalaya lineage is diagnosable by a unique combination of scalation, tail morphology, and coloration, including a short tail that is not gradually tapering, an obtusely pointed tail tip, and a broad median black stripe on the tail venter. To stabilize name usage around the new taxon, we summarize the historical names associated with the *C. pavimentata* complex, emphasizing type localities and type material where known.

Keywords: Cytochrome *b*, Garo Hills, Meghalaya, morphology, phylogeny, taxonomy

Introduction

The reed snakes of the genus *Calamaria* H. Boie in F. Boie, 1827 are small, secretive, largely semi-fossorial colubroids that occupy a broad latitudinal and ecological span from northeastern India through Indochina and southern China to Taiwan and the southern Ryukyus, and southward into Sundaland and the Philippines (Inger & Marx 1965, Poyarkov *et al*. 2019, Yeung *et al*. 2022). Despite their geographic sweep, *Calamaria* species tend to converge on a conservative external phenotype with typically smooth dorsal scales in 13 rows, reduced head scalation (including absence of a loreal), and compact bodies adapted for life beneath leaf litter and soil (Inger & Marx 1965, Poyarkov *et al*. 2019, Yeung *et al*. 2022).

This combination of morphological conservatism and low detectability has repeatedly produced the same outcome: lineages remain "hidden in plain sight" until targeted sampling and close-scale scrutiny of scalation and colour pattern bring them to the surface (Inger & Marx 1965, Yeung *et al*. 2022, Cai *et al*. 2023, Liang *et al*. 2024). The net result is a genus whose recognized diversity continues to rise; the Reptile Database currently lists 71 species of *Calamaria* (Uetz *et al*. 2025).

Over the past decade, the systematics of *Calamaria* has shifted from broad, morphology-led descriptions toward a more explicitly integrative approach that combines classical scalation/colour pattern diagnoses with phylogenetic placement (Poyarkov *et al*. 2019, Yeung *et al*. 2022, Cai *et al*. 2023, Liang *et al*. 2024, Zhang *et al*. 2025). That pivot was necessary, but it also comes with a conceptual pitfall: integrative does not mean "mtDNA decides." Single-locus mitochondrial datasets can efficiently flag candidate lineages. Still, they do not, by themselves, test evolutionary independence and are vulnerable to cytonuclear discordance and misleading histories (e.g., introgression/mitochondrial capture; Wüster 2025). In other words, mtDNA should be treated as a decision-support signal, not the sole decision maker, especially in groups where subtle morphology and limited sampling can inflate confidence without reducing uncertainty (Wüster 2025).

Nowhere is the cost of historical name recycling clearer than in the long-standing, pan-regional application of *Calamaria pavimentata* Duméril, Bibron & Duméril, 1854. This name has been used for "collared reed snakes" across a vast mainland and island arc, yet the taxon is burdened by a complicated synonymy and a type locality problem that directly affects how the name should be applied (Duméril *et al*. 1854, Marx & Inger 1955, Inger & Marx 1965). Current syntheses list multiple nominal forms historically associated with *C. pavimentata* and explicitly note that the original Javan type locality is erroneous ("not on Java"; Inger & Marx 1965). Critically, synonyms and geographically structured populations across East and Southeast Asia mean that any attempt to restrict *C. pavimentata* to a particular mainland lineage without an explicit audit of available names, type localities, and name-bearing types risks trading one instability for another (Inger & Marx 1965).

Northeastern India represents the westernmost limit of *Calamaria* and a biogeographic junction where landscape complexity and low vagility can promote narrow geographic range endemism in semi-fossorial snakes. Regional syntheses continue to list historical "*C. pavimentata*" records for multiple northeastern Indian states, including Meghalaya, reflecting the legacy of broad name application in the absence of detailed systematic revision (Basfore *et al*. 2024). Within *Calamaria* specifically, the recent description of *C. mizoramensis* from Mizoram underscores that "*pavimentata*" in northeastern India is not a single homogeneous entity and that lineages in the region require reassessment with modern comparative frameworks (Lalremsanga *et al*. 2026).

During recent surveys in the Garo Hills of Meghalaya, we obtained a series of *Calamaria* specimens consistent with the historical "*pavimentata*" concept used in northeastern India. Here we evaluate these specimens using a morphology-first diagnostic framework, complemented by mitochondrial cytochrome *b* phylogenetic placement as an additional line of evidence, and a quantitative assessment of morphometric differentiation using an allometry-corrected PCA.

We describe the Garo Hills population as a new species and provide a comparative diagnosis against congeners from the Indo-Burma region and adjacent parts of East and Southeast Asia. We also frame our taxonomic decision within the broader *C. pavimentata* complex problem and provide a synopsis of putative synonyms historically associated with *C. pavimentata* (with type localities) so that regional lineages can be evaluated against the correct available names.

Materials and Methods

Sampling and voucher information. The focal specimen of *Calamaria* (ADBUSB150) was collected from Oragitok, Rongram Block, West Garo Hills, Meghalaya, India. Four additional specimens (VR/ERS/ZSI/358, 39036, 338, 365) that had already been deposited at the Zoological Survey of India, Shillong, were examined. For molecular analyses, we assembled a comparative dataset of 46 *Calamaria* sequences representing mainland East Asia, Indochina, Sundaland, and the Philippines (Sup. Table 1). Three Colubroid taxa (*Orientocoluber spinalis*, *Elaphe quatuorlineata*, *Lycodon rufozonatus*) were included as outgroups. All voucher numbers and GenBank accession numbers are listed in Sup. Table 1.

DNA extraction, amplification, and sequencing. Genomic DNA was extracted from ethanol-preserved liver tissue of the holotype using a Qiagen DNeasy Tissue Kit following the manufacturer's protocol. A fragment of the mitochondrial cytochrome *b* (cyt *b*) gene was amplified using primers L14910 and H16064 (Burbrink *et al*. 2000). PCR reactions were performed under standard cycling conditions with an annealing temperature of 48–50°C. Amplified products were purified and sequenced bidirectionally using an ABI automated sequencer. Chromatograms were examined and edited in Chromas and Sequence Scanner v1.0. Consensus sequences were assembled and checked manually to ensure the absence of stop codons and frame shifts. The final alignment comprised 1,117 base pairs, consistent across all included taxa. The new sequence has been deposited in GenBank (Sup. Table 1).

Sequence alignment and phylogenetic analyses. Comparative cyt *b* sequences were downloaded from GenBank (Sup. Table 1). Alignment was performed using MUSCLE (Edgar 2004) implemented in MEGA7 (Kumar *et al*. 2016) under default parameters. The alignment was inspected visually and trimmed to equal length.

Phylogenetic relationships were inferred using Maximum Likelihood (ML) in IQ-TREE v1.6 (Nguyen *et al*. 2015). The best-fitting nucleotide substitution model (TIM2+F+I+G4) was selected using ModelFinder under the Bayesian Information Criterion (Kalyaanamoorthy *et al*. 2017). Nodal support was assessed with 1,000 ultrafast bootstrap replicates (Minh *et al*. 2013). Ultrafast bootstrap (UFBoot) values ≥95 were considered strongly supported. Tree visualization and editing were performed in FigTree v1.4.4. Sister relationships were inferred strictly from tree topology and bootstrap support values (i.e., not from pairwise distances).

Uncorrected pairwise genetic distances (*p*-distances) were calculated in MEGA7 using pairwise deletion of gaps and missing data (Sup. Table 2). *P*-distances are presented as descriptive measures of sequence divergence and were not interpreted using fixed threshold criteria.

Assessment of mitochondrial divergence context. To contextualize the divergence of the Meghalaya lineage, we examined the full pairwise distance matrix (Sup. Table 2). Intraspecific divergences among sampled congeners generally ranged from 0–3.5% in most taxa (except for *C. gervaisii* and *C. lumbricoidea*), whereas interspecific divergences ranged broadly from approximately 3.5% to >30%, with several deeply divergent lineages exceeding 20%. No discrete barcode gap was observed across the dataset. Accordingly, mitochondrial divergence was treated as one line of evidence supporting lineage distinctiveness, rather than as a diagnostic indicator. We acknowledge that single-locus mitochondrial data cannot alone establish evolutionary independence and may be influenced by incomplete lineage sorting or introgression.

Morphological examination. Morphological terminology follows Inger & Marx (1965) and Poyarkov *et al*. (2019). Measurements were taken using digital calipers to the nearest 0.1 mm; head length (HL; snout tip to jaw angles), head width (HW), interorbital distance (IOD), eye–nostril distance (EN; from anterior margin of orbit to posterior margin of nostril), eye diameter (ED; horizontal diameter), snout length (SnL; tip of rostral to anterior margin of eye), frontal length (FT-l), frontal width (FT-w), rostral width (RT-w), and rostral height (RT-h). Snout–vent length (SVL) was measured to the nearest 1 mm with a measuring tape, and tail length (TaL) to the nearest 0.1 mm (short tails were measured using calipers where feasible). Total length (TL) and the ratio TaL/TL were calculated from SVL and TaL.

Ventrals (VEN) follow Dowling (1951). Dorsal scale rows were recorded one head-length posterior to the head (ASR), at midbody (MSR), and one head-length anterior to the vent (PSR). Subcaudals (SC) were counted as paired. Asymmetrical characters are presented as left/right. The following variables were also recorded: supralabials (SL), supralabials entering the orbit (SLE), infralabials (IL), preoculars (PrO), and postoculars (PoO). Sex was determined by inspection of gonads where possible; otherwise, secondary sexual characters (tail length and shape) were used. Maxillary teeth were counted on both maxillae using a dissecting pin under a binocular microscope before preservation. Because of the small sample size for the Meghalaya lineage (*n*=5), multivariate analyses were treated as exploratory and not used as primary evidence for species delimitation. Comparative morphological data of the examined specimens were compared with those of other *Calamaria* species from mainland China and the Indo-Burma region. Comparative data were obtained from published sources (e.g., Cai *et al*. 2023; Darevsky & Orlov 1992; Duméril *et al*. 1854; Inger & Marx 1965; Lee 2021; Liang *et al*. 2024; Nguyen *et al*. 2010; Nguyen *et al*. 2025; Orlov 2009; Orlov *et al*. 2010; Poyarkov *et al*. 2019; Stuart & Heatwole 2008; Yang & Zheng 2018; Yeung *et al*. 2022; Ziegler & Le 2005; Ziegler *et al*. 2007, 2008, 2019; Zhang *et al*. 2025; Lalremsanga *et al*. 2026).

Sexual dimorphism screening and morphometric PCA. Because sexual dimorphism can bias multivariate morphometric comparisons in snakes (particularly via tail proportion), we screened for dimorphism in the comparative dataset using TaL/SVL in *C. mizoramensis* (as the best-sampled close relative available for this purpose). Given strong dimorphism in that taxon (see Results), we conducted two PCA analyses: (i) females only (primary analysis) and (ii) all specimens combined (exploratory).

Allometric size correction followed Chan & Grismer (2022) using the GroupStruct framework (Thorpe-type allometric adjustment). Morphometric variables were log10-transformed and adjusted using species-specific allometric slopes with SVL as the body-length proxy; SVL was used only for size correction, not as an ordination variable. PCA was then conducted on centered, scaled (unit-variance) size-corrected variables. PCA outputs (scores, loadings, variance explained) are reported in the Results and provided as supplementary spreadsheets.

Nomenclatural review. To address historical ambiguity surrounding the *Calamaria pavimentata* complex, we reviewed original descriptions and subsequent taxonomic treatments (Duméril *et al*. 1854; Marx & Inger 1955; Inger & Marx 1965; and later revisions cited in the Discussion). Available names, type localities, and reported type repositories were compiled from primary literature and current catalogues. This review was undertaken to reduce the risk that the Meghalaya lineage corresponds to an existing available name, and to frame the taxonomic decision explicitly within the documented synonymy and name-bearing type framework for the *pavimentata* complex.

Results

Phylogenetic relationships. The aligned mitochondrial cytochrome *b* dataset comprised 1,117 bp for 46 terminals, including 43 ingroup *Calamaria* samples and three outgroup taxa (Sup. Table 1). The Maximum Likelihood (ML) analysis recovered a well-resolved topology (Fig. 1); numbers on nodes represent ultrafast bootstrap support values (UFBoot). Most major nodes within *Calamaria* were strongly supported (UFBoot ≥95), and all taxa represented by multiple samples were recovered as monophyletic. The Meghalaya specimen (ADBUSB150), herein described as *Calamaria garoensis* sp. nov., forms a strongly supported clade with *C. mizoramensis* (UFBoot = 100). These two taxa together constitute a distinct northeastern Indian lineage within the genus.

The *C. garoensis* sp. nov. + *C. mizoramensis* clade is recovered as sister to a broader assemblage comprising mainland East and Southeast Asian taxa, including species from China and Laos. This assemblage, in turn, is placed sister to a more inclusive clade containing Sundaland and Philippines representatives (Fig. 1). Sister relationships reported here are inferred strictly from tree topology and bootstrap support, not from pairwise genetic distances.

Genetic divergence. Uncorrected pairwise distances (p-distances) based on cytochrome *b* are summarised in Sup. Table 2. The smallest interspecific divergence involving the Meghalaya lineage is observed between *C. garoensis* sp. nov. and *C. mizoramensis* (6.3%). Divergences between *C. garoensis* sp. nov. and other sampled congeners range from 14.7% (e.g., *C. jinggangensis*) to 23.3% (the Guangxi population identified as *C. pavimentata*).

Across the full dataset, within-nominal-taxon divergences were low in most multi-sampled taxa (commonly 0–3%), but several nominal taxa show markedly higher values (e.g., up to 16.4% in *C. lumbricoidea* and 9.7% in *C. gervaisii*). Between-nominal-taxon divergences span 3.5–29.4%. Accordingly, no discrete "barcode gap" separating all within- from among-taxon distances is evident. P-distances are presented here as descriptive measures of mitochondrial differentiation and are not interpreted using fixed distance thresholds.

Sexual dimorphism screening. In *C. mizoramensis* (*n*=11; 7 ♂, 4 ♀), tail proportion shows strong sexual dimorphism: males have substantially higher TaL/SVL than females (Welch t-test $p = 8.0 \times 10^{-6}$; Mann–Whitney U $p = 0.0061$). Given this, the female-only PCA is treated as the primary morphometric analysis for interspecific comparison.

Allometry-corrected PCA of morphometrics. Female-only PCA (*n*=8; 4 *C. garoensis* sp. nov. + 4 *C. mizoramensis*) shows complete separation of the two taxa along PC1 (51.8% of variance; PC2 = 26%; Fig. 2; Sup. Table 3), with no overlap in PC1 scores. Variables with the highest absolute loadings on PC1 include rostral dimensions (RT-h, RT-w), snout length (SnL), frontal width (FT-w), and interorbital distance (IOD), reflecting consistent head-shape differences after allometric size correction.

The exploratory PCA including males and females (*n*=16; 5 *C. garoensis* sp. nov. + 11 *C. mizoramensis*) explains 48.8% (PC1) and 24.4.0% (PC2) of variance (Fig. 2; Sup. Table 3). In this combined-sex dataset, separation between species remains pronounced along PC1, but within-species dispersion increases and PC2 is influenced strongly by sex-associated variation (notably tail proportion), underscoring the value of sex-stratified morphometric comparisons where possible.

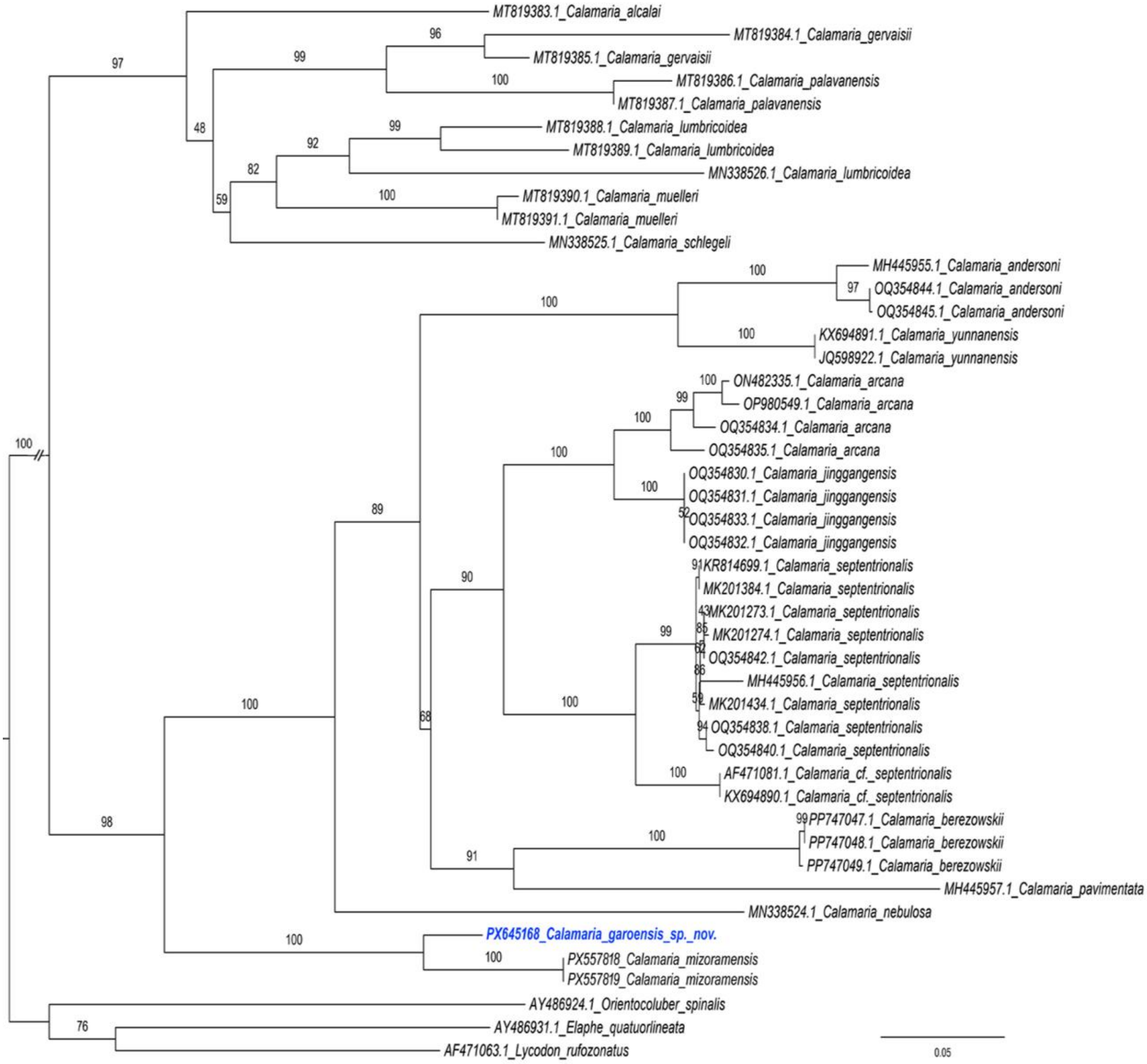

Figure 1. Maximum-likelihood phylogeny depicting relationships among species of the genus *Calamaria* based on mitochondrial cytochrome b gene sequences.

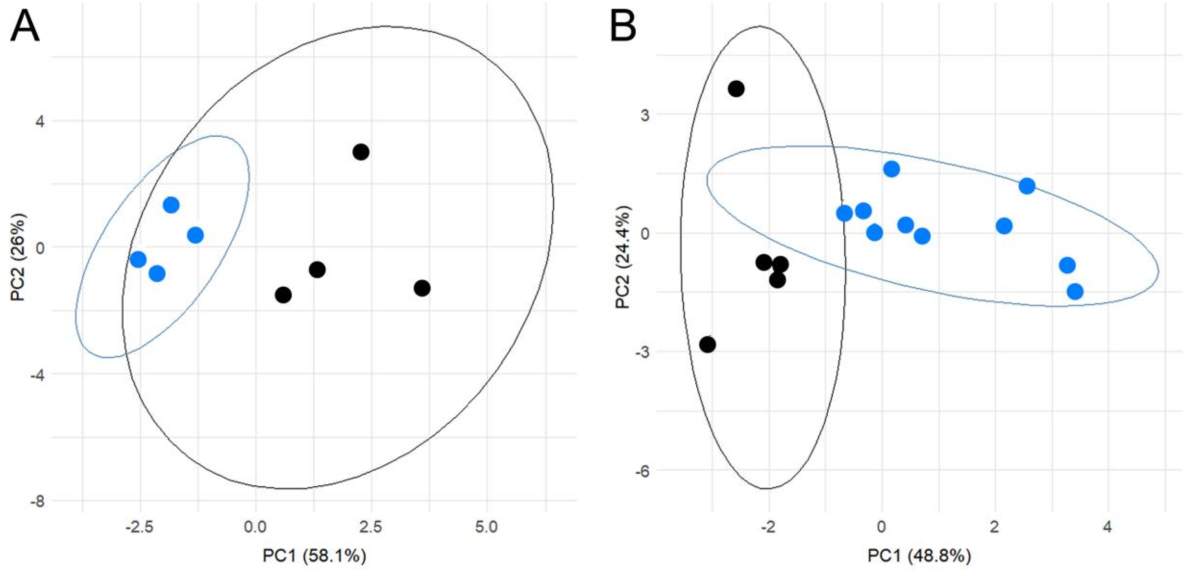

Figure 2. Principal Component Analysis (PCA) of allometry-corrected morphometric variables comparing *Calamaria garoensis* sp. nov. and *C. mizoramensis*. **(A)** Female-only analysis (*n*=8); **(B)** Pooled female and male analysis (*n*=16). Black dots represent *C. garoensis* sp. nov., and blue dots represent *C. mizoramensis*. Ellipses indicate 95% confidence intervals for each taxon.

Taxonomy. An integrative taxonomic assessment demonstrates that the Meghalaya population possesses a distinct combination of diagnostic characters separating it from all sampled congeners. Consequently, we recognize and describe it here as a new species endemic to Meghalaya, India.

Calamaria ***garoensis*** Bharali, Sangma,
Amarasinghe, Lalremsanga, Hazarika, Bohra &
Purkayastha, **sp. nov.**
[urn:lsid:zoobank.org:act:497CCB87-7FBE-4DD1-B4E5-CC7F02BE5A00]
(Figs. 3–7; Sup. Table 4)

Calamaria pavimentata — Ranade (2022); Basfore *et al.* (2024: 26133, *partim*).

***Holotype*.** ADBUSB150, adult male, collected from Oragitok (25.5460° N, 90.3240° E; alt. 783 m a.s.l. Fig. 8) Rongram Block, West Garo Hills, Meghalaya, India on 6 May 2025, ca. 1830 h by S. Bohra, P. Swargiary, C.M. Sangma, G.C. Marak, and M. Bharali.

***Paratypes*.** (*n*=4; all females): VR/ERS/ZSI/358, VR/ERS/ZSI/39036, VR/ERS/ZSI/338 and VR/ERS/ZSI/365, deposited by R. Mathew & Party in the North Eastern Regional Centre, Zoological Survey of India, Shillong.

***Diagnosis*.** *Calamaria garoensis* sp. nov. can be distinguished from all congeners by the following combination of characters: 8–9 enlarged maxillary teeth; rostral broader than high; prefrontal shorter than the frontal and contacting the first two supralabials; mental not contacting the anterior chin shields; dorsal scales in 13–13–13 rows, smooth throughout; one preocular and one postocular; four supralabials, the second and third entering the orbit; five infralabials; six scales surrounding the paraparietal; 165–187 ventrals; 12–27 paired subcaudals; a short tail (TaL/TL 4.7–14.2%), not gradually tapering and terminating in an obtuse tip; dorsum dark brown to blackish brown with six narrow longitudinal stripes and a faint pale nuchal ring; ventral surface yellow with dark outer corners on the ventral scales; and a broad, distinct median black stripe on the tail venter.

Description of holotype. The holotype (ADBUSB150), an adult male, is in good condition. Body slender and cylindrical (SVL 193 mm); tail short and thinner than the body, uniformly cylindrical anteriorly and abruptly tapering toward the tip, which is obtusely pointed (TaL 32 mm; TaL/TL 14.2%). Head small and elliptical in dorsal view (HL 6.1 mm; HW 3.8 mm). Eye small and round (ED 1.0 mm), smaller than the eye–nostril distance (EN 1.2 mm).

Rostral broader than high (RT-w 1.4 mm; RT-h 1.0 mm), its dorsal portion visible from above for more than half the length of the prefrontal suture. Prefrontal shorter than the frontal, not entering the orbit, in contact with the first and second supralabials. Frontal hexagonal, longer than wide (FT-l 2.4 mm; FT-w 2.0 mm). Paraparietal surrounded by six scales. One preocular on each side, higher than wide. One postocular on each side. Nasals small, completely surrounding the nostril, bordered by the rostral, prefrontal and first supralabial. Four supralabials on each side; the second and third enter the orbit; the fourth is the largest (4 > 2 > 1 > 3). Five infralabials on each side; the first three pairs contact the anterior chin shields; the first pair meets at the midline; the third is the longest. Anterior chin shields longer than wide, pentagonal, meeting at the midline. Posterior chin shields shorter, meeting anteriorly and separated posteriorly by the first gular scale. Mental triangular, not contacting the anterior chin shields.

Dorsal scale rows 13–13–13 throughout, all smooth. Dorsal rows reduce to 11 at the level of the second subcaudal, to six rows at the level of the seventh to ninth subcaudals, remaining at six rows to the twenty-eighth subcaudal, and reducing to four rows above the last six subcaudals. Ventrals 165 including two preventrals; subcaudals 27, all paired.

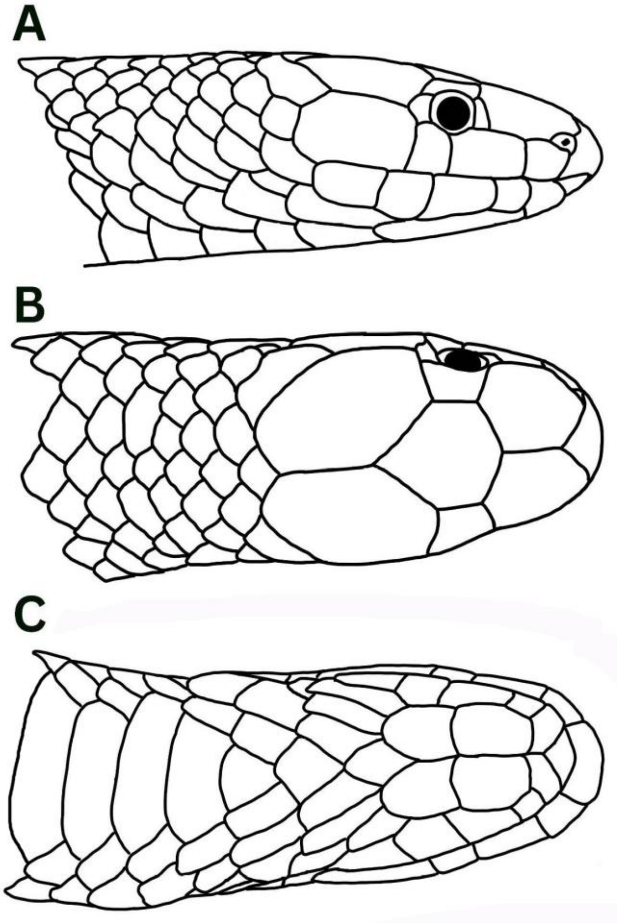

Figure 3. Head scalation of the holotype of *Calamaria garoensis* sp. nov. (ADBUSB150, adult male): **(A)** lateral, **(B)** dorsal, and **(C)** ventral views of the head (not to scale).

Dentition. Nine enlarged maxillary teeth on each side (9/9).

Coloration. In life, the dorsal surface of the head, body and tail is blackish brown, bearing six narrow and slightly distinct longitudinal stripes formed by alternating pale and dark dorsal scale margins, most prominently expressed on the dorsolateral rows (Fig. 4, 7). Immediately posterior to the parietal margin a darker patch extends across approximately four dorsal scale rows, followed by a pale-yellow nuchal ring that broadens laterally and tapers along the mid-dorsal line. The eye is uniformly black. The supralabials have dark brown upper edges adjacent to the parietals, whereas their lower margins are suffused with light yellow and white. The infralabials and anterior chin shields are yellow with scattered dark speckling. All dorsal scales exhibit a distinct iridescent lustre. The ventral surface of the body is uniformly yellow, with dark pigmentation restricted to the outer margins of the ventral scales, forming a narrow lateral line. The tail venter is yellow with a prominent median dark stripe that begins at the fourth subcaudal, is briefly absent on the fifth, and then continues uninterrupted to the tail tip.

In preservative, the overall coloration becomes slightly faded, although the dorsal striping pattern and the nuchal ring remain clearly discernible.

Variation. Variation of the type series is summarised in Sup. Table 4 (Fig. 5). The holotype (ADBUSB150), the only male examined, has a total length of 225 mm, whereas the largest specimen in the series is a female paratype (VR/ERS/ZSI/338) with a total length of 276.8 mm. Sexual dimorphism is evident in several characters. Females exhibit higher ventral counts (185–187) than males (165), but markedly fewer subcaudals (12–16 in females vs. 27 in the male). Tail proportions also differ distinctly: the male has a longer tail relative to total length (TaL/TL 14.2%), whereas adult females have shorter tails (TaL/TL 4.7–5.5%).

Comparison. Comparative morphological data for *Calamaria garoensis* sp. nov. and congeners from mainland China and the Indo-Burma region are summarised below. *Calamaria garoensis* sp. nov. differs from *C. mizoramensis* in having more ventrals in males (165 vs. 147–155) and females (185–187 vs. 166–175), a shorter maximum total length in males (225 mm vs. 251 mm), a longer maximum total length in females (276.8 mm vs. 258 mm), and a slightly longer relative tail length in males (TaL/TL

14.2% vs. 10.3–13.1%); from *C. abramovi* Orlov 2009 in having more ventrals (males 165 vs. 159; females 185–187 vs. 174), slightly more subcaudals in males (27 vs. 26) but fewer in females (12–16 vs. 20), a longer relative tail length in males (14.2% vs. 13.3%) and a shorter relative tail length in females (4.7–5.5% vs. 7.1%); from *C. andersoni* Yang & Zheng 2018 in having more subcaudals in males (27 vs. 20–23), a longer relative tail length in males (14.2% vs. 8.8–9.2%) and a slightly shorter relative tail length in females (4.7–5.5% vs. 5.8%); from *C. arcana* Yeung, Lau & Yang 2022 in having fewer ventrals (males 165 vs. 170–176; females 185–187 vs. 192), more subcaudals in males (27 vs. 20–22) and a longer relative tail length in males (14.2% vs. 7.2–11.8%); from *C. berezowskii* Günther 1896 in having more ventrals in both sexes (males 165 vs. 149–155; females 185–187 vs. 153–171), more subcaudals in males (27 vs. 22–25), a longer relative tail length in males (14.2% vs. 6.6–10.5%) and a shorter relative tail length in females (4.7–5.5% vs. 6.5–6.9%); from *C. buchi* Marx & Inger 1955 in having six shields surrounding the paraparietal (vs. five), the mental not contacting the chin shields (vs. contacting), fewer female ventrals (185–187 vs. 221–236), and a longer relative tail length in females (4.7–5.5% vs. 3.9–4.1%); from *C. concolor* Orlov, Truong, Tao *et al.,* 2010, in having six shields around the paraparietal (vs. five), the mental not contacting the chin shields (vs. contacting), fewer supralabials (4 vs. 5), fewer male ventrals (165 vs. 209), more male subcaudals (27 vs. 19), and a longer relative tail length in males (14.2% vs. 7.2%); from *C. dominici* Ziegler, Tran & Nguyen 2019 in Ziegler *et al*. (2019) in having more female ventrals (185–187 vs. 174), fewer female subcaudals (12–16 vs. 17–18) and a shorter female relative tail length (4.7–5.5% vs. 6.2%); from *C. gialaiensis* Ziegler, Sang & Truong 2008 in Ziegler *et al.* (2008) in having six shields around the paraparietal (vs. five), the mental not contacting the chin shields (vs. contacting), fewer male ventrals (165 vs. 191), more male subcaudals (27 vs. 23) and a longer relative tail length in males (14.2% vs. 8.1%); from *C. jinggangensis* in having more ventrals (males 165 vs. 157–158; females 185–187 vs. 179), more male subcaudals (27 vs. 20), a slightly shorter relative tail length in males (14.2% vs. 15%) and a longer relative tail length in females (4.7–5.5% vs. 3.6%); from *C. lovii* Boulenger 1887 in having a preocular (vs. absent), the mental not contacting the chin shields (vs. contacting), fewer male ventrals (165 vs. 205), more male subcaudals (27 vs. 23) and a longer relative tail length in males (14.2% vs. 7.4%); from *C. lumbricoidea* Boie 1827 in having six shields surrounding the paraparietal (vs. four or five), the mental not contacting the chin shields (vs. contacting) and a longer relative tail length in males (14.2% vs. 6.3–11.4%); from *C. nebulosa* Lee 2021 in having a preocular (vs. absent), more female ventrals (185–187 vs. 179), fewer female subcaudals (12–16 vs. 22) and a shorter relative tail length in females (4.7–5.5% vs. 7.9%); from *C. sangi* Nguyen, Koch & Ziegler 2009 in having the mental not contacting the chin shields (vs. contacting), more male ventrals (165 vs. 190), more male subcaudals (27 vs. 19) and a longer relative tail length in males (14.2% vs. 6.2%); from *C. schlegeli* Duméril, Bibron & Duméril 1854 in having fewer supralabials (4 vs. 5), more ventrals in both sexes (males 165 vs. 129–161; females 185–187 vs. 136–180), fewer female subcaudals (12–16 vs. 19–37) and a shorter relative tail length in females (4.7–5.5% vs. 7.3–14.4%); from *C. septentrionalis* Boulenger 1890 in having more subcaudals in males (27 vs. 15–19) and females (12–16 vs. 6–11), and longer relative tail lengths in both sexes (males 14.2% vs. 6.3–8.6%; females 4.7–5.5% vs. 2.6–4.3%); from *C. strigventris* Poyarkov, Nguyen, Orlov *et al.,* 2019 in having more female ventrals (185–187 vs. 176–183), fewer male (27 vs. 29–31) and female subcaudals (12–16 vs. 20–22) and a shorter relative tail length in females (4.7–5.5% vs. 8.4–8.6%); from *C. thanhi* Ziegler & Quyet, 2005 in having a preocular (vs. absent), fewer ventrals (males 165 vs. 184; females 185–187 vs. 198), slightly fewer subcaudals (males 27 vs. 28; females 12–16 vs. 21) and a longer relative tail length in males (14.2% vs. 9.9%) and shorter in females (4.7–5.5% vs. 6.8%); from *C. yunnanensis* Chernov 1962 in having a preocular (vs. absent), fewer ventrals (males 165 vs. 167–184; females 185–187 vs. 199), more male subcaudals (27 vs. 15–20), fewer female subcaudals (12–16 vs. 19) and a longer relative tail length in males (14.2% vs. 8.2–8.8%); and from *C. synergis* by having six shields surrounding the paraparietal (vs. five); a greater number of subcaudal scales in males (27 vs. 20-23); a longer relative tail length in males (ratio TaL/TL 14.2% vs. 6.6-9.2%).

Comparisons with nominal taxa historically treated as synonyms of Calamaria pavimentata. Because *C. pavimentata* has a complicated nomenclatural history and has been broadly applied across East and Southeast Asia, we summarize here the principal nominal taxa historically placed in the "*pavimentata* complex," including type localities and known type repositories, and compare *C. garoensis* sp. nov. against the diagnoses associated with each name. These comparisons are based on published descriptions and subsequent taxonomic syntheses; they do not substitute for direct examination of name-bearing types. Comparison with the original description of *Calamaria pavimentata* Duméril, Bibron & Duméril, 1854 indicates that the species possesses 151 ventrals and 27 subcaudals, and a relatively long tail (TaL/TL vs. 12.1%); in contrast, *C. garoensis* sp. nov. has more ventrals in males (165 vs. 151) and females (185–187 vs. 151), and a shorter relative tail length in females (TaL/TL 4.7–5.5% vs. 12.1% in *C. pavimentata*) and a slightly longer relative tail length in males (14.2% vs. 12.1%), the latter value in *C. pavimentata* being derived from a single type specimen of unknown sex. These differences, particularly in ventral counts and tail morphology, preclude assignment of the Meghalaya lineage to *C. pavimentata* as originally described.

Calamaria garoensis sp. nov. differs from the Guangxi lineage currently identified as '*C. pavimentata*' in recent phylogenetic studies, in having a short tail that is not gradually tapering and terminates in an obtuse tip (vs. gradually tapering, sharply tipped), lacking pale dorsal spots at the base of the tail (vs. present), and possessing a broad, distinct median black stripe on the tail venter (vs. absent) (Fig. 7). Because *C. pavimentata* sensu lato has accumulated several geographically disparate nominal taxa that have been treated as junior synonyms, *C. garoensis* sp. nov. is further compared with each available name historically subsumed under *C. pavimentata* (see Table 1).

Table 1. Nominal taxa historically associated with the *Calamaria pavimentata* complex. Type localities and repositories follow original descriptions and subsequent catalogues; where ambiguity exists, this is noted in the Discussion.

Name (original combination) Author, year	Type locality as published	Type repository as published	Notes on current usage
C. pavimentata Duméril, Bibron & Duméril, 1854	"Java" [Indonesia]	MNHN-RA 3298 (Paris)	Type locality problem; name historically applied widely
C. quadrimaculata Duméril, Bibron & Duméril, 1854	"Java" [Indonesia]	MNHN (Paris)	Has long been treated as a synonym within the complex
C. siamensis Günther, 1864	"Siam" [Thailand]	NHMUK (London)	Historically linked to the *C. pavimentata* complex in older treatments
C. pavimentata semidoliata Werner, 1896	"Java" [Indonesia]	NHMW (Vienna)	Described as a color variant, currently treated as a junior synonym of *C. pavimentata*
C. pavimentata var. *uniformis* Smith, 1921	Langbian Plateau, southern Annam [Vietnam]	NHMUK (London)	Described as a uniform-vaulted form, frequently synonymized
C. pavimentata formosana Maki, 1931	Taiwan (Formosa)	NSMT H02352 (Tokyo)	Requires topotypic genetic sampling for placement
C. pavimentata banaensis Bourret, 1934	Ba Na, Central Vietnam	MNHN (Paris)	Nominal taxon associated with Annamite populations
C. pavimentata annamensis Bourret, 1937	Truong Son Range, Central Vietnam	MNHN (Paris)	Revalidated recently as *C. annamensis* (Korolev *et al.* 2026)
C. pavimentata miyarai Takara, 1962	Yonaguni-jima, southern Ryukyus	URJ No. 1 (Japan)	Island form; historically treated within a complex

Plate 4

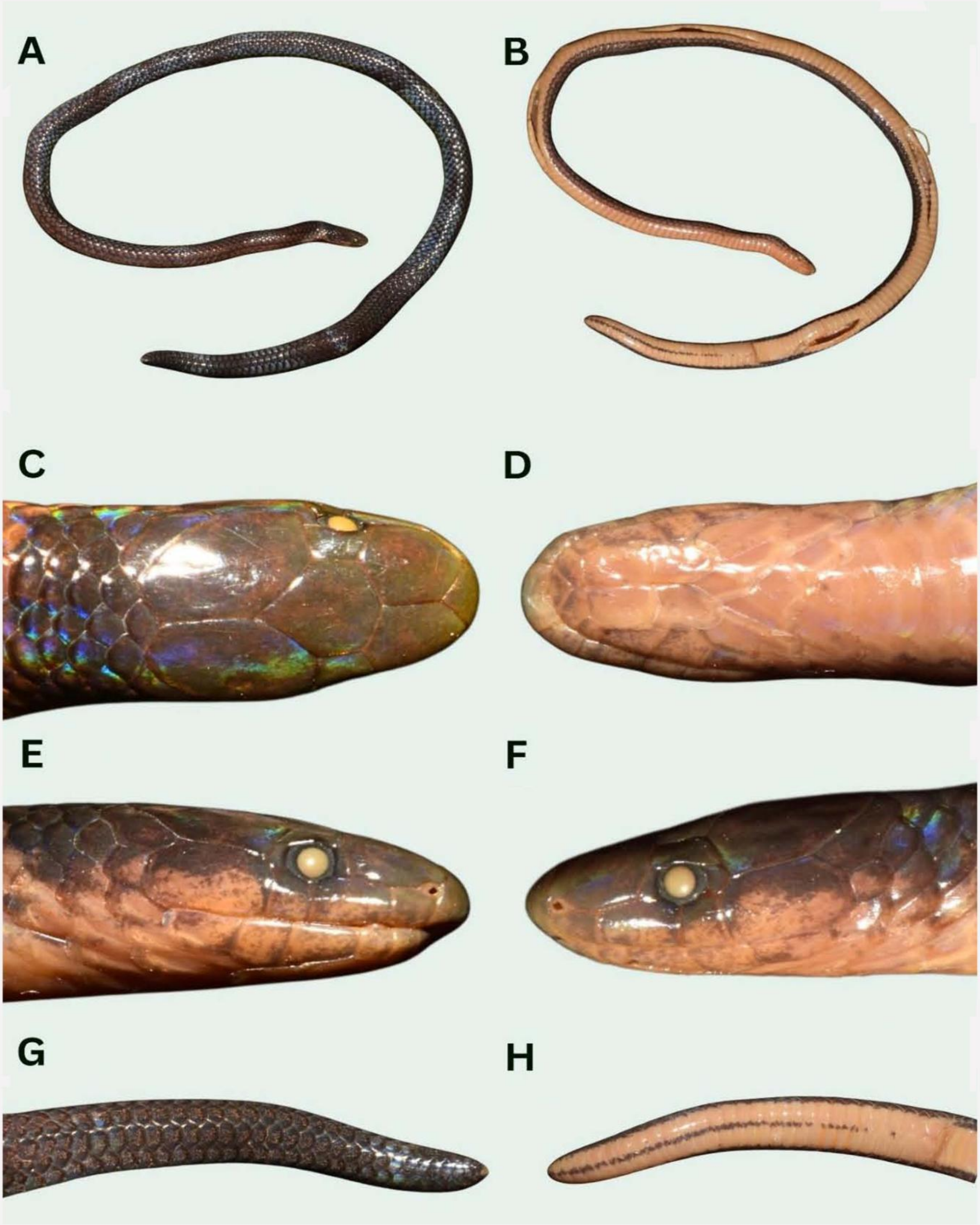

Figure 4. *Calamaria garoensis* sp. nov. holotype (adult male; ADBUSB150): **(A)** dorsal and **(B)** ventral views of the full body; **(C)** dorsal, **(D)** ventral, **(E)** lateral (right side), **(F)** lateral (left side) of the head; **(G)** dorsal and **(H)** ventral views of the tail; © Photo: J. Purkayastha

Plate 5

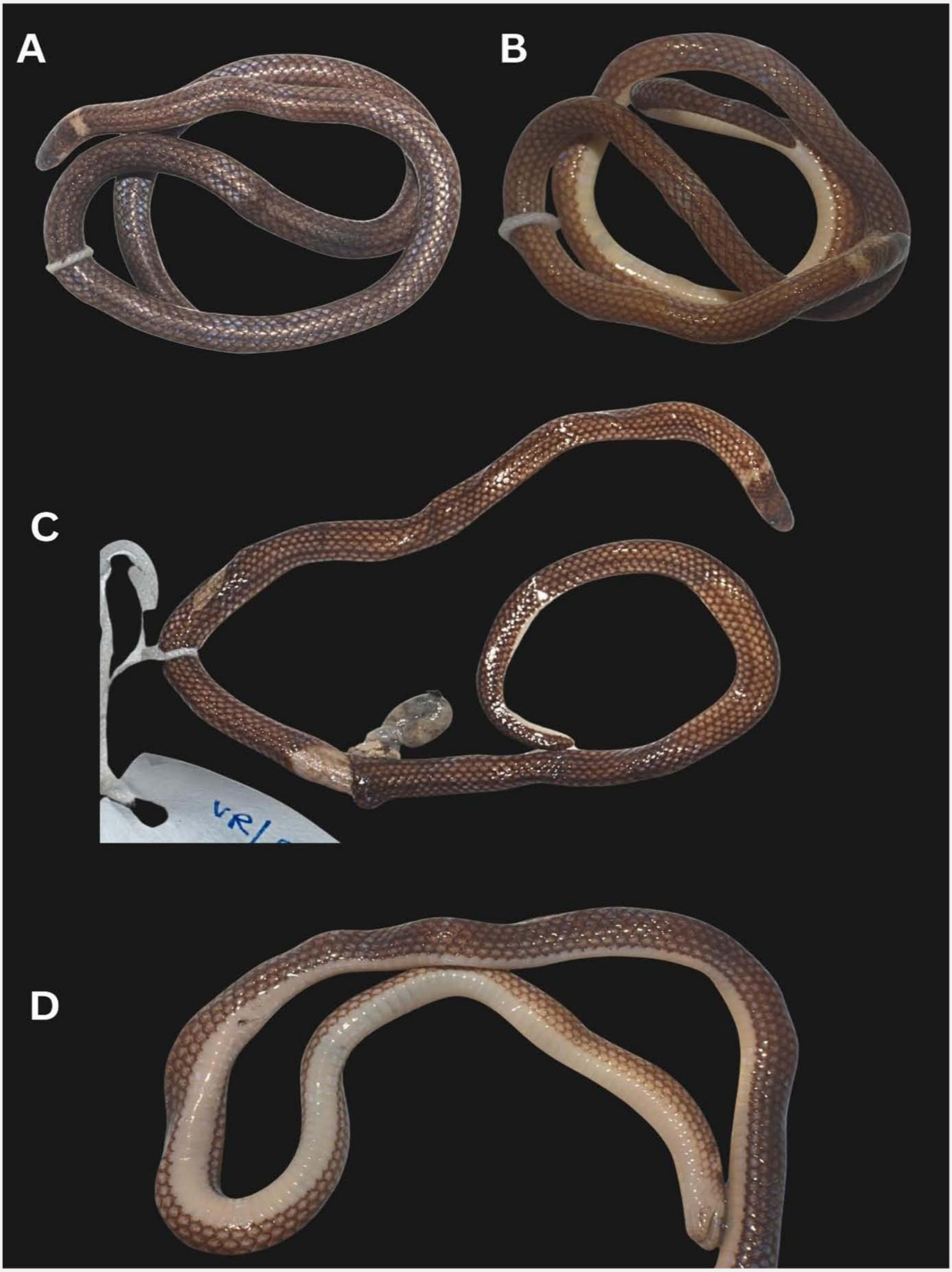

Figure 5. *Calamaria garoensis* sp. nov. adult female paratypes: **(A)** VR/ERS/ZSI/338, **(B)** VR/ERS/ZSI/365, **(C)** VR /ERS/ZSI/358), and **(D)** VR/ERS/ZSI/39036

Plate 6

Figure 6. *Calamaria garoensis* sp. nov. holotype (ADBUSB150, adult male) in life, collected from Oragitok, West Garo Hills, Meghalaya, India

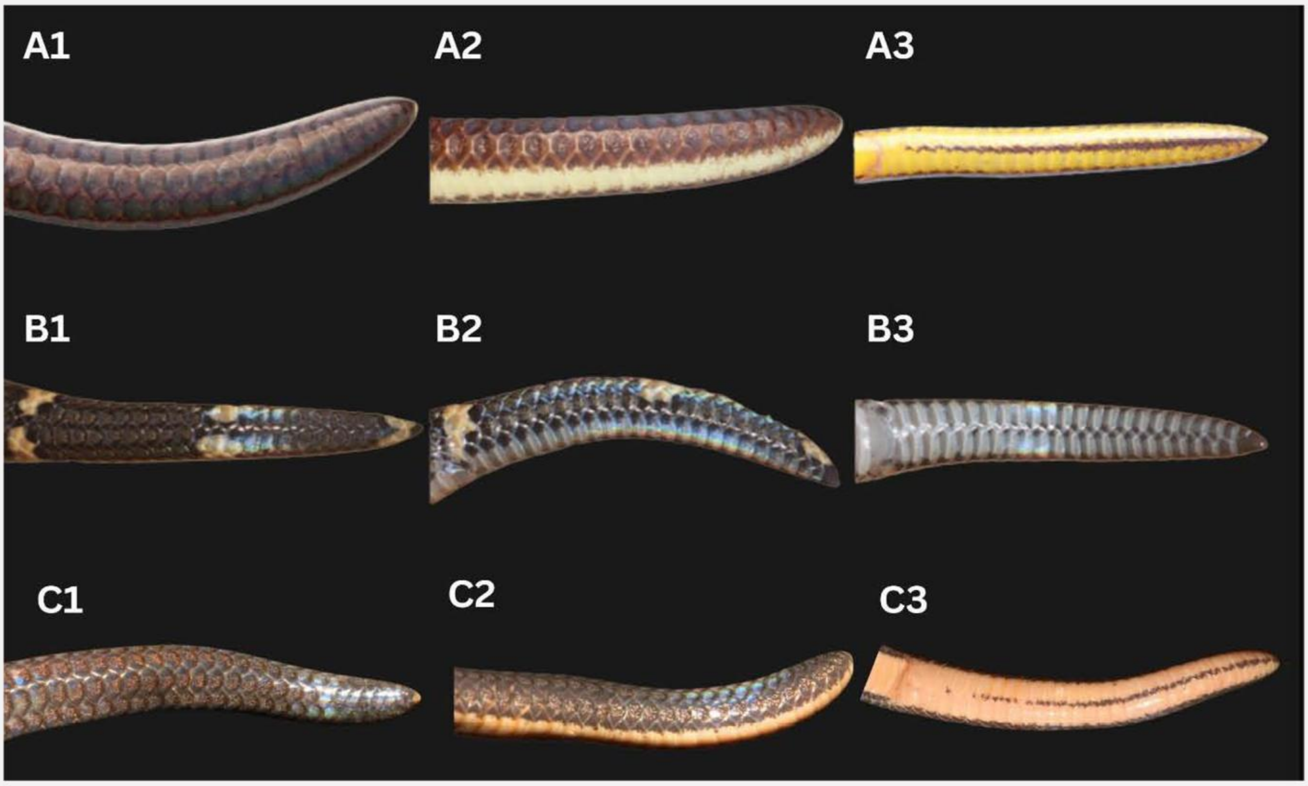

Figure 7. Comparative tail morphology and coloration among **(A)** *Calamaria mizoramensis* (MZMU 3744; © Photo: H.T. Lalremsanga); **(B)** *C. pavimentata* (KFBG 14507; © Photo: Yeung *et al*. (2022); and **(C)** *C. garoensis* sp. nov. (ADBUSB150; © Photo: J. Purkayastha): Panels 1–3 illustrate the dorsal, lateral, and ventral views of the tail

Plate 7

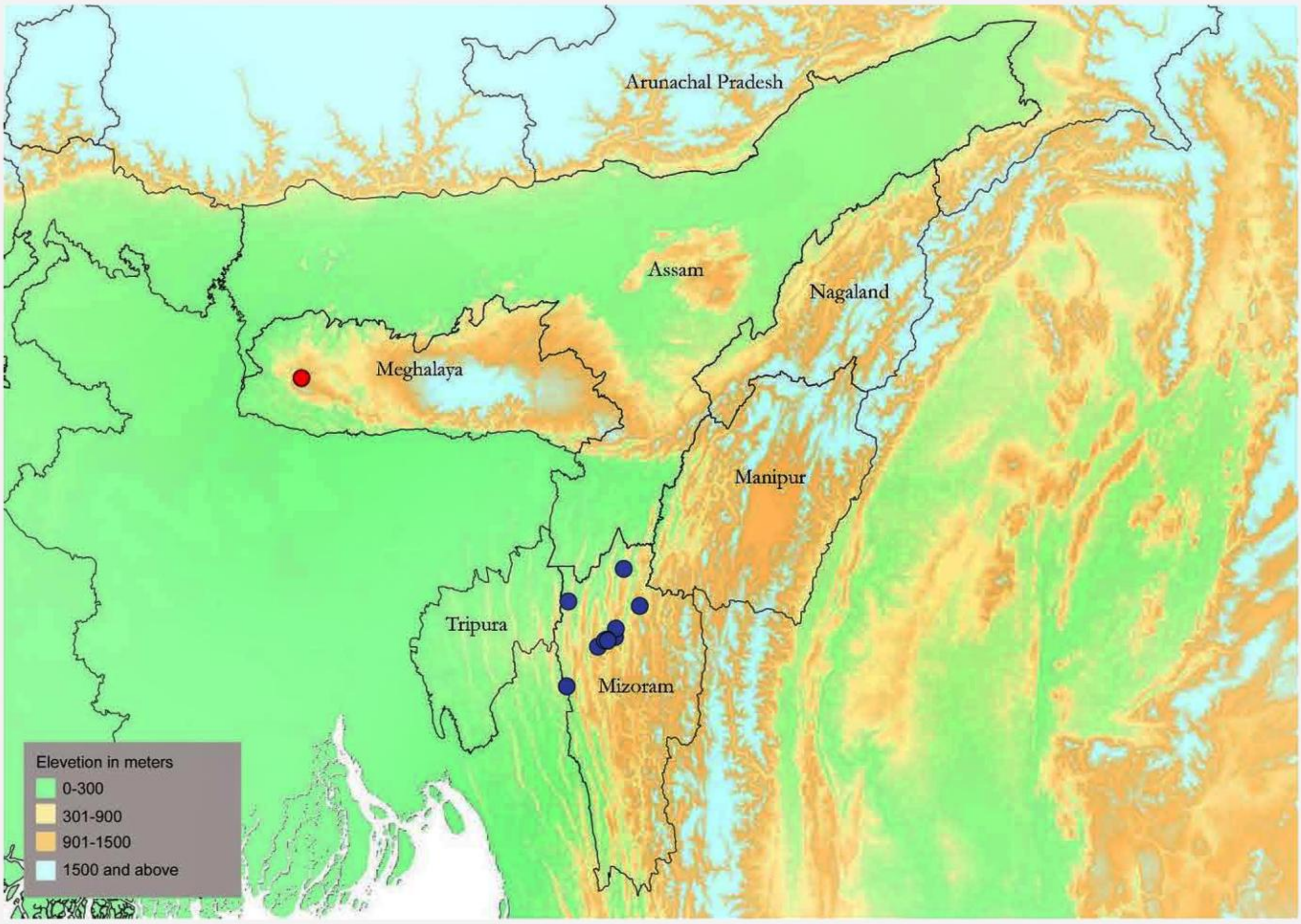

Figure 8. An elevation map of Northeast India showing locality records of *Calamaria garoensis* sp. nov. (red circle) from Meghalaya, India and *Calamaria mizoramensis* (blue circles) from Mizoram, India

Figure 9. Microhabitat of *Calamaria garoensis* sp. nov. at Oragitok, West Garo Hills, Meghalaya, India

Calamaria garoensis sp. nov. differs from *C. quadrimaculata* Duméril, Bibron & Duméril, 1854 (type locality reported as Java) in having much higher ventral counts (♂ 165; ♀ 185–187 vs. 136–145) and a different ventral pattern (yellow venter with dark outer corners and a broad median black stripe restricted to the subcaudals, vs. lower parts described as uniform white with only a faint subcaudal line) (Günther 1864).

Calamaria garoensis sp. nov. differs from *C. siamensis* Günther, 1864 (southern Siam and Lao Mountains/Cochinchina) in dorsal and caudal coloration, including the absence of white/pale tail spots (vs. 2–3 pairs of pale tail spots), in ventral coloration (yellow with dark outer corners vs. ventrals/subcaudals whitish and densely punctulated with brown, with hind margins immaculate) (Günther 1864), and in having a distinctly striped dorsum with six narrow longitudinal stripes and a faint pale nuchal ring (vs. dorsum described as uniform brownish or with indistinct lines) (Günther 1864).

Calamaria garoensis sp. nov. differs from *C. pavimentata semidoliata* Werner, 1896, which was described as a color variant within the *pavimentata* complex. In the original account, *semidoliata* is characterized by a darker dorsal ground color with reduced or partially interrupted pale striping, and a comparatively slender, gradually tapering tail terminating in a pointed tip. Ventral counts reported in Werner (1896) fall within the lower range typical of historical *pavimentata* material (female ventrals approximately in the mid-130s), and subcaudals correspond to the low paired counts reported for the complex (female ca. 13). In contrast, *Calamaria garoensis* sp. nov. has substantially higher female ventral counts (185–187), a short tail that is not gradually tapering and terminates in an obtuse tip, and a conspicuous broad median black stripe on the tail venter. The combination of markedly elevated ventral counts and distinct tail morphology excludes conspecificity of the Meghalaya lineage with *C. pavimentata semidoliata* as originally described.

Calamaria garoensis sp. nov. differs from *C. pavimentata* var. uniformis Smith, 1921 (type locality: Langbian Peaks, Vietnam) by its striped dorsum and faint nuchal ring (vs. uniform olive-brown, explicitly lacking longitudinal lines or collar), higher ventral counts (♂ 165 vs. 143–149; ♀ 185–187 vs. 166–167), and lower female subcaudal counts (♀ 12–16 vs. 18–19). It further differs in ventral pattern by lacking a dark median line along the belly (often present in var. *uniformis*) and in having a broad median black stripe confined to the subcaudals rather than a narrow midline extending onto the venter (Smith 1921).

Calamaria garoensis sp. nov. differs from *C. pavimentata formosana* Maki, 1931 (Taiwan) in having higher female ventral counts (♀ 185–187 vs. 172–175) and lower female subcaudal counts (♀ 12–16 vs. 17–18) (Maki 1931; data summarized in Takara 1962).

Calamaria garoensis sp. nov. differs from *C. pavimentata miyarai* Takara, 1962 (Yonaguni-jima, Yaeyama Islands, southern Ryukyus) by possessing a faint pale nuchal ring (reported absent in *miyarai*) and in ventral coloration (venter yellow with dark outer corners vs. orange with dark cross-bands/basal markings associated with the ventrals), and by markedly lower female subcaudal counts (♀ 12–16 vs. 21–27 in *miyarai*) (Takara 1962).

Calamaria garoensis sp. nov. differs from *C. pavimentata banaensis* Bourret, 1934 (type locality: Ba Na–Nui Chua area, central Vietnam) by lacking a dark midventral stripe along the belly (reported present in *banaensis*) and by higher ventral counts (♂ 165 vs. 157–160; ♀ 185–187 vs. 178–179) (Bourret 1934; comparative data summarized in Korolev *et al*. 2026).

Calamaria garoensis sp. nov. differs from *C. pavimentata annamensis* Bourret, 1937 (Truong Son Range, central Vietnam) by having a striped dorsum with six narrow longitudinal stripes (vs. dorsum reported as uniform dark brown to olive-brown without longitudinal lines), and by lower ventral counts (♂ 165 vs. 182; ♀ 185–187 vs. 196–205) (Bourret 1937; Korolev *et al*. 2026).

Etymology. The specific epithet ***garoensis*** is derived from *Garo*, referring to the Garo Hills of Meghalaya, and the Latin suffix *–ensis* signifies the species' occurrence within the traditional homeland of the Garo Hills region of Northeast India. It is to be treated as an adjective. Suggested common name: Garo Hills Reed Snake

Natural history. The holotype, an adult male, was encountered at approximately 1830 h, following rainfall that had ended 2–3 hours earlier. The individual was observed emerging from loose soil, presumably from its burrow. The circumstances of its appearance suggest that the snake may have been responding either to the availability of prey or to the ingress of water into its subterranean retreat after the rain (Fig. 9). Upon detection, the specimen attempted to retreat rapidly into the burrow; however, it was captured before fully disappearing underground.

Discussion

Taxonomic implications within the Calamaria pavimentata complex. The discovery of *Calamaria garoensis* sp. nov. reinforces the growing evidence that northeastern Indian populations historically referred to *C. pavimentata* represent a heterogeneous assemblage of geographically structured lineages rather than a single widespread taxon. The taxonomic instability of *C. pavimentata* can be traced to its original description by Duméril, Bibron & Duméril (1854), in which multiple congeners were described with poorly substantiated or erroneous locality data. Subsequent re-examination by Marx & Inger (1955) and Inger & Marx (1965) demonstrated that the reported Javan provenance of *C. pavimentata* was almost certainly incorrect (“not on Java”), and that later usage of the name across a mainland–island arc outpaced any stable link to name-bearing types.

The long-standing application of the name *C. pavimentata* across mainland East and Southeast Asia therefore reflects historical inertia rather than demonstrated conspecificity. Multiple nominal forms historically associated with the species have been synonymized, revalidated, or reassessed over time (Marx & Inger 1955; Inger & Marx 1965; Liang *et al.* 2024). Recent molecular and morphological studies have further revealed that populations previously assigned to *C. pavimentata* comprise distinct evolutionary lineages (Yang & Zheng 2018; Yeung *et al.* 2022; Cai *et al.* 2023; Liang *et al.* 2024; Zhang *et al.* 2025).

The Guangxi population of southern China has been widely used in recent phylogenetic studies as the operational representation of “*C. pavimentata*” (Yang & Zheng 2018; Yeung *et al.* 2022; Cai *et al.* 2023). Recent integrative work in northeastern India demonstrated that the only genetically corroborated Indian population previously assigned to *C. pavimentata* (from Mizoram) represents a distinct species, *C. mizoramensis*, and recommended provisionally removing *C. pavimentata* from the snake fauna of India pending broader revision of the complex (Lalremsanga *et al.* 2026). At the same time, because the name-bearing type of *C. pavimentata* is associated with an erroneous type locality and predates modern phylogenetic sampling, the definitive application of the name cannot be resolved by “operational” mainland lineages alone. This uncertainty also affects how available names historically subsumed under *pavimentata* should be treated, including geographically relevant taxa such as *C. pavimentata formosana* Maki, 1931 (Taiwan), which may ultimately prove applicable to some East Asian lineages currently treated under “*pavimentata*”.

We emphasize that the recognition of *Calamaria garoensis* sp. nov. does not depend on any assumption regarding the precise geographic origin of the name-bearing type of *C. pavimentata*. Our taxonomic decision is based on direct comparison with all available nominal taxa historically associated with the *pavimentata* complex (Table 1), rather than on equating any modern population (e.g., from Guangxi or Taiwan) with *C. pavimentata* sensu stricto. Even if future work demonstrates that the name *C. pavimentata* applies to a lineage other than the Guangxi population currently used in phylogenetic studies, the Meghalaya lineage remains morphologically diagnosable and incompatible with the original descriptions and subsequent diagnoses of the available names reviewed herein. Accordingly, the description of *C. garoensis* sp. nov. does not pre-empt or depend upon the resolution of the type locality problem of *C. pavimentata*.

In this context, the present study does not rely on a nomenclatural restriction of *C. pavimentata* to any particular mainland lineage to justify recognition of the Meghalaya lineage. Instead, *C. garoensis* sp. nov. is diagnosed independently based on a unique combination of meristic characters, tail morphology, and coloration that distinguish it from all examined congeners, including the Guangxi lineage currently treated as *C. pavimentata*. To address the core nomenclatural risk explicitly, we provide a synopsis of the nominal taxa historically associated with *C. pavimentata* sensu lato (see Table 1), including their type localities, documented type repositories, and salient diagnostic information, and we explain why none can be applied confidently to the Meghalaya lineage under current evidence. This approach avoids circular reasoning and does not assume resolution of outstanding synonymy problems within the complex.

Molecular differentiation and its limitations. The mitochondrial phylogeny recovers *C. garoensis* sp. nov. as sister to *C. mizoramensis* with strong bootstrap support (UFBoot = 100; Fig. 1). The uncorrected cyt *b* divergence between the two species (6.3%) exceeds typical within-lineage variation observed in the dataset and falls within the range of interspecific divergences reported among other *Calamaria* taxa (Sup. Table 2). However, no universal barcode gap separates intra- from interspecific divergences across the genus, as pairwise distances span a wide continuum. The very high divergences (>20%) among some congeners are plausibly consistent with deep lineage ages and/or heterogeneous historical sampling (e.g., uneven taxon coverage, varying fragments, and the possibility of misidentifications in public databases), and therefore further argue against simplistic distance-cutoff interpretations.

Recent syntheses in herpetological systematics emphasize that single-locus mitochondrial data alone cannot test evolutionary independence and may be influenced by incomplete lineage sorting, introgression, or demographic history (Wüster 2025). Accordingly, mitochondrial divergence is interpreted here as one line of supportive evidence rather than a standalone diagnostic threshold. The congruence between mitochondrial distinctiveness and consistent morphological differentiation strengthens the species hypothesis for *C. garoensis* sp. nov. Nevertheless, future work incorporating nuclear loci and broader geographic sampling across northeastern India and adjacent regions will be essential to refine relationships within the western clade of *Calamaria* and to test for potential cytonuclear discordance.

Morphological differentiation and species diagnosis. Species of *Calamaria* are often externally conservative, and diagnostic characters may involve subtle but stable differences in scale counts, head scalation, and tail morphology (Inger & Marx 1965; Poyarkov *et al*. 2019; Yeung *et al*. 2022). The Meghalaya population differs from *C. mizoramensis* in higher ventral counts in both sexes and proportionally longer male tail length, and from the Guangxi lineage in tail shape, absence of pale dorsal tail spots, and presence of a distinct median ventral tail stripe. In addition to the Guangxi lineage, we compared *C. garoensis* sp. nov. with each putative synonym historically placed under *C. pavimentata* sensu lato (see Comparisons; Table 1), rather than treating "Guangxi *pavimentata*" as a sufficient proxy for the entire complex.

The quantitative morphometric results add a transparent layer to these qualitative diagnoses. In particular, the allometry-corrected, female-only PCA shows non-overlapping morphometric space between *C. garoensis* sp. nov. and *C. mizoramensis* along PC1, whereas the combined-sex analysis is less clean due to strong sexual dimorphism in tail proportion and correlated measurements. This pattern underlines the importance of sex-stratified morphometric comparisons in small-bodied fossorial snakes and supports interpreting the PCA as corroborative rather than primary delimitation evidence, given sample sizes.

Biogeographic considerations. Northeastern India represents the westernmost extent of *Calamaria* distribution and lies within a complex biogeographic transition zone between Indo-Burman and Himalayan elements. The recovery of a distinct Meghalaya lineage sister to *C. mizoramensis* suggests that the western clade of *Calamaria* comprises geographically structured, narrow-range taxa rather than a single broadly distributed species, matching expectations for low-vagility, semi-fossorial snakes in topographically complex landscapes.

The Garo Hills are characterized by mid-elevation evergreen forests and fragmented hill systems that may promote genetic isolation in semi-fossorial snakes with limited dispersal capacity. The apparent restriction of *C. garoensis* sp. nov. to this region underscores the likelihood that additional diversity remains undetected in northeastern India and that historical "*pavimentata*" records in the region should be treated as hypotheses requiring re-evaluation with modern comparative frameworks.

Future directions and nomenclatural stability. Resolving the *C. pavimentata* complex requires a comprehensive reassessment of historical synonymies, including direct examination of name-bearing types and expanded molecular sampling from Taiwan, Indochina, southern China, and northeastern India. Critically, such a revision should explicitly evaluate the available names historically associated with *pavimentata* sensu lato (e.g., *C. quadrimaculata*, *C. siamensis*, *C. pavimentata* var. *uniformis*, *C. pavimentata formosana*, *C. pavimentata banaensis*, *C. pavimentata annamensis*, *C. pavimentata miyarai*) against geographically structured clades identified in phylogenetic studies, ideally including nuclear loci and careful vetting of voucher identifications.

Until such a revision is completed, the recognition of *C. garoensis* sp. nov. reflects a conservative and evidence-based approach: the Meghalaya lineage is morphologically diagnosable, quantitatively distinct in multivariate morphometric space, genetically differentiated, and geographically structured, and is not assignable with confidence to any currently available name based on our synopsis of the *pavimentata* complex. At the same time, because the provenance and identity of *C. pavimentata* sensu stricto remain unresolved, we explicitly acknowledge that future work on name-bearing types and topotypic sampling could still reshape name application within the complex, including in northeastern India.

Author contributions

All the authors contributed equally.

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Supplemental data

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