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A NEW DAY GECKO OF THE *Cnemaspis podihuna* (REPTILIA: GEKKONIDAE) CLADE FROM NORTHEAST INDIA

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Abstract

We describe a new species of *Cnemaspis* from Assam, a valley of an antecedent river, the Brahmaputra, in northeastern India that belongs to the *C. podihuna* species group. The new species is the second *Cnemaspis* reported from the mainland Indian subcontinent, representing the entire *podihuna* clade. It is small (SVL 30.8–35.7 mm) and diurnal. The new species is genetically and morphologically allied to *C. assamensis* in northeast India, and also morphologically allied to the members of the *C. podihuna* group in Sri Lanka, especially to *C. molligodai* and *C. manoae*, but is distinguished by its larger body size but with lower number of midbody scale rows, higher number of miventrals and ventral scale rows across the belly, no tubercles on lower flanks, three enlarged rows of thigh scales parallel to the enlarged femoral scale row, and fewer poreless scales separating precloacal and femoral pore scales in males. The new species is also genetically divergent from *C. assamensis* by *p*-distances of 6.0–7.2% and from Sri Lankan congeners by 21.2–24.8% in the mitochondrial ND2 gene. With this new species, only two species of *Cnemaspis* are now known from the *podihuna* clade in India, but additional species likely remain unrecognized.

Keywords: phylogeny, saxicoline geckos, species complex, systematics, taxonomy

Introduction

The polyphyletic gekkonid genus, *Cnemaspis* Strauch, 1887, consists of two distantly related assemblages; one primarily from South Asia with some members in Southeast Asia (*i.e.*, diminutive *Cnemaspis*), and the other exclusively from Southeast Asia (Bauer *et al*. 2007, Grismer *et al*. 2014). Interestingly, both diminutive South Asian and augmentative Southeast Asian assemblages of *Cnemaspis* occur on Sumatra

(Amarasinghe *et al*. 2015, Iskandar *et al*. 2017). This large disjunction in the geographic range of the diminutive *Cnemaspis* suggested the possibility that this South Asian assemblage spread into Sumatra by independent overwater dispersal from Sri Lanka along the Andaman and Nicobar island chains (Iskandar *et al*. 2017). On the other hand, most of the northeast Indian reptile species are considered to have a stronger affinity to Southeast Asia, dispersed through the gateway of Assam, rather than Peninsular Indian fauna (e.g., Amarasinghe *et al*. 2018, 2021a). However, the deeply divergent (Oligocene) member of the South Asian *Cnemaspis* radiation—*Cnemaspis assamensis* Das & Sengupta, 2000—belongs to the *podihuna* clade (Agarwal *et al*. 2021).

Sri Lankan species of *Cnemaspis*—all endemic—fall into two broad divergent clades among the South Asian assemblage: the *podihuna* and *kandiana* clades (Agarwal *et al*. 2017, Karunarathna *et al*. 2019a). The identity of the holotype of *C. podihuna* Deraniyagala, 1944 has long been disputed (Manamendra-Arachchi *et al*. 2007) and was later resolved by Amarasinghe & Bauer (2009), Amarasinghe *et al*. (2009), and Amarasinghe & Campbell (2016). Amarasinghe & Karunarathna (2020) defined three species groups within the *podihuna* clade concerning their morphology and biogeographic distribution: *C. podihuna* group, *C. scalpensis* group, and *C. alwisi* group. *Cnemaspis rammalensis* and *C. rajakarunai* were tentatively placed within the *C. alwisi* group. Amarasinghe & Karunarathna (2020) included four species in the *C. podihuna* group: *C. podihuna*; *C. molligodai* Wickramasinghe & Munindradasa, 2007; *C. kandambyi* Batuwita & Udugampala, 2017; and *C. manoae* Amarasinghe & Karunarathna, 2020.

Currently, there are 21 members in the *podihuna* clade (Amarasinghe & Karunarathna 2020, Agarwal *et al*. 2021, Amarasinghe *et al*. 2021b, Karunarathna *et al*. 2023) with a sole representative from the mainland Indian subcontinent—*Cnemaspis assamensis,* a species described from the Mayeng Reserved Forest in Assam, Northeast India—originally described as both a precloacal and femoral poreless gecko. Das & Ahmed (2007) reported the species from Kaziranga National Park, a locality 200 km northeast of the type locality. Das *et al*. (2016) extended the distribution of this species, reporting from Zemgang District in Bhutan. Recently, *Cnemaspis assamensis* has been extensively studied for its unique phylogenetic placement and morphological characteristics (Agarwal *et al*. 2017, Sengupta *et al*. 2021). The type specimen was re-diagnosed based on new morphological and genetic data, revealing the presence of both precloacal and femoral pores (Sengupta *et al*. 2021). The distribution between Sri Lankan members of *C. podihuna* clade and *C. assamensis* is highly disjunct and isolated from each congener by approximately 1,450 km (Agarwal *et al*. 2021). On the other hand, the historical connections between the wet forests of Northeast India and those of the Western Ghats and Sri Lanka during the Paleogene period facilitated numerous faunal exchanges, allowing species to disperse across these regions (Karanth 2003).

Materials and methods

In January 2023, a few of us visited the Dirgheswari Temple (Fig. 1) in Guwahati, Assam, India. We collected a series of four unknown *Cnemaspis* specimens, which were superficially similar to the Sri Lankan endemic *C. molligodai*.

Figure 1. The distribution map of the *Cnemaspis assamensis* group (after Sengupta *et al*. 2021; for the distribution of the *podihuna* clade in Sri Lanka see Amarasinghe & Karunarathna 2020; Karunarathna *et al*. 2023): *C. assamensis* sensu stricto (green circles); the new species (red triangle); *C.* cf. *assamensis* (yellow squares) from ^{1}Bhutan, ^{2}Meghalaya, ^{3}Kaziranga NP, ^{4}Mayeng RF, ^{5}Nongpoh, ^{6}Garbhanga, ^{7}Nilachal Hills, ^{8}Basistha, ^{9}Geetanagar, ^{10}Maligaon, ^{11}Kamakhya, ^{12}Amchang RF, ^{13}Hengrabari RF, ^{14}Jalukbari RF, ^{15}Deeporbeel WS, and ^{16}Dirgheswari Temple. Type localities are with a middle dot.

Specimens were collected by hand, euthanized with halothane, and fixed in 4% buffered formalin prior to storage in 70% ethanol. We preserved tail tissue samples for DNA analysis in 95% ethanol. The latitude, longitude, and elevation of the localities where specimens were collected were recorded using a Garmin GPSmap 60CSx with the WGS84 map datum. All the specimens are permanently deposited at the Assam Don Bonso University (ADBU), Guwahati, Assam, India. Additional comparative material examined for morphological comparisons is listed in Appendix I. Specimens were examined at the Natural History Museum, London, UK (NHMUK); National Museum of Sri Lanka, Colombo, Sri Lanka (NMSL); and Wildlife Heritage Trust, Colombo, Sri Lanka (WHT). The WHT collection has now been deposited at NMSL, but is currently uncatalogued.

As it was peculiar to find a Sri Lankan endemic from far northeastern India, we sought to analyze its phylogenetic relationships. New sequences generated in this work were deposited in GenBank, and additional genetic data were downloaded from GenBank (Sup. Table 1). As noted above, following Agarwal (2021) and Karunarathna *et al*. (2023), we consider DNA sequences from specimens of the Dirgheswari Temple, Guwahati, to represent a member of the *C. podihuna* clade, superficially similar to *C. assamensis* (hereafter referred to as *Cnemaspis* cf. *assamensis*). Following Karunarathna *et al*. (2023), *Calodactylodes illingworthorum* was used as an outgroup. We extracted genomic DNA from ethanol (100%) preserved tail tissue using a Qiagen Tissue Kit following the manufacturer's instructions. Partial sequences for the mitochondrial ND2 gene were generated using the primer pair MetF1 and H5934 (Macey *et al.* 1997, 1354 nucleotides). Sequence chromatograms were quality-checked, edited, and assembled into contigs using Sequence Scanner v1.0 (Applied Biosystems). We assembled and aligned DNA sequences with available data from GenBank (Sup. Table 1) using MUSCLE (Edgar 2004) in MEGA7 (Tamura & Nei 1993, Kumar *et al.* 2016) with default parameter settings. The uncorrected *p*-distance (sequence divergence) was calculated in MEGA X, and all ambiguous positions were removed for each sequence pair (pairwise deletion option).

We estimated phylogenetic relationships using a final alignment of 1,354 base pairs (bp) of the ND2 gene and its flanking tRNAs, employing Maximum Likelihood (ML) on IQ-TREE (Nguyen *et al*., 2015). Molecular substitution model TIM+F+G4 was selected based on the BIC scores by ModelFinder (Kalyaanamoorthy *et al.* 2017). We ran 1000 iterations to assess clade support using the ultrafast bootstrap option (Minh *et al.* 2013). Nodes with bootstrap values above 95 were considered highly supported (Minh *et al*. 2013). We conducted our BI analysis using MrBayes v3.2.6 (Ronquist & Huelsenbeck 2003) under GTR+Gamma as the best-fitting model, for 10 million generations with parameter and topology sampling every 1000 generations and Markov Chain Monte Carlo (MCMC) diagnosis frequency of 100,000, and later discarded 25% of the first analysis as burn-in.

For morphological analyses, we made comparisons with specimens (Appendix I) and published descriptions of *Cnemaspis* from India and Sri Lanka. We scored specimens for the same morphological and morphometric characters used in recent descriptions of the *C. podihuna* clade (e.g., Manamendra-Arachchi *et al.* 2007, Amarasinghe & Campbell 2016, Amarasinghe & Karunarathna 2020, Amarasinghe *et al*. 2021b, Karunarathna *et al*. 2023). Measurements were taken with Mitutoyo digital calipers to the nearest 0.1 mm under an AmScope SM-1BZ-RL dissecting microscope on the right side of the body. We took the following measurements: snout–vent length (SVL, from tip of snout to anterior margin of vent), axilla–groin length (AG, from the posterior margin of the forelimb at its insertion point on the body to the anterior margin of the hind limb at its insertion point on the body), head length (HL, from posterior edge of mandible to tip of snout); head width (HW, maximum width of head at the angle of the jaws); head depth (HD, maximum height of head between occiput and throat); orbit diameter (the greatest diameter of the orbit); tympanum–eye length (from posterior border of orbit to anterior border of tympanum), snout length (from anterior border of orbit to tip of snout), eye–nostril length (EN, from anterior border of orbit to posterior border of nostril), interorbital width (shortest distance between dorso-medial margins of orbits), tympanum diameter (greatest diameter of tympanum), internarial length (IN, shortest distance between dorsal margins of nostrils), brachium length (on the dorsal surface from the axilla to the inflection of the flexed elbow), forearm length (LAL, on the dorsal surface from the posterior margin of the elbow while flexed to the inflection of the dorsiflexed wrist), finger lengths I–V (from tip of claw to the nearest fork), thigh length (from the anterior margin of the hind limb at its insertion point on the body to the knee while flexed), shank length (TBL, from the posterior surface of the knee while flexed to the base of the heel), toe lengths I–V (from tip of claw to the nearest fork), and tail length (TAL, from tip of tail to posterior margin of vent).

We counted supralabial and infralabial scales (from the gape of mouth to the rostral and mental scales, respectively), paravertebral scales (the dorsal granules between pelvic and pectoral limb insertion points along a straight line immediately left of the vertebral column); midventral (all the scales from the postmental to the last scale bordering the vent along the midventral line), ventral scale rows across the belly (the number of longitudinal ventral scale rows at midbody), midbody scale rows (total number of longitudinal scale rows around the midbody including both dorsal and ventral sides). We counted subdigital lamellae on each finger and toe I–V, from the first proximal enlarged scansor wider than the width of the largest palm scale to the distal-most lamella (excluding the claw sheath) at the base of the claw. We also counted the total number of precloacal and femoral pores and assessed their orientation. The number of non-pored scales (poreless scales) counted between pore-bearing precloacal and femoral scales.

We measured the degree and arrangement of body and tail tuberculation texture (homogeneous or heterogeneous), spinous scales on flanks, and the relative size and morphology of the subcaudal scales. We evaluated the texture of the scales on the ventral surface of the brachium and antebrachium. We sexed specimens by examining everted hemipenes or hemipenial bulges at the tail base. To view some small characters, such as keeling of the ventrals, we applied the reversible stain methylene blue in 70% ethanol, following Amarasinghe *et al.* (2015).

To assess the morphometric variation between the new species (*C.* cf. *assamensis*) and its closest congeners (*C. assamensis* sensu stricto from Mayeng, *C. molligodai*, and *C. manoae* from Sri Lanka), we performed a separate Kruskal–Wallis one-way analysis of variance test because of the small sample size (Zar 2010). A total of 19 adult specimens (seven specimens of *C. assamensis* (including holotype), five specimens of *C. molligodai*, three specimens of *C. manoae*, and four specimens of the new species) were used for the statistical analysis. Juveniles were excluded to avoid confounding allometry in the statistical analysis. Statistically informative tests could not be performed on separate sexes due to the smaller sample sizes of each sex.

Univariate and multivariate analyses were conducted on eight morphometrics: SVL, HL, HD, HW, IN, EN, LAL, and TBL. Additionally, variation in adult size was normalized using the following equation: $\log X_{adj} = \log(X) - \beta[\log(SVL) - \log(SVL_{mean})]$, where X_{adj} = adjusted value; X = measured value; β = unstandardized regression coefficient for each population; and SVL_{mean} = overall average SVL of all populations (Lleonart *et al.* 2000, Chan & Grismer 2022). The scaled morphometric data were treated as the dependent variables and the population as the predictor variable. A multivariate analysis was conducted using Principal Component Analysis (PCA) on the scaled morphometrics above to reduce the highly correlated multidimensional data matrix into a few uncorrelated variables [i.e., principal components (PC)]. We used the *princomp* function in the R statistical software program (v4.0.4; R Core Team 2021). Biplots of the first three principal component scores were used to examine the morphometric differentiation between the species. All statistical analyses were conducted using the R statistical software program (v4.0.4; R Core Team 2021).

Results

Morphologically and genetically, we confirm that the populations of the true *C. assamensis* (also based on its holotype) are distributed on the south bank of the Brahmaputra River basin in Assam, India. Although we could not discover any live population in the exact type locality of *C. assamensis* at Mayeng Reserve Forest, we did find the closest matching population around 50 km south of the type locality, at Basistha (26.100713°N, 91.782606°E), where the same population was mentioned in Sengupta *et al.* (2001). The molecular analysis based on the mitochondrial ND2 gene using Maximum Likelihood (ML; Fig. 2) indicated that the *C.* cf. *assamensis* sample from the north bank of the Brahmaputra River basin in Assam is sister to *C. assamensis* sensu stricto (uncorrected *p*-distance 6.0–7.2%; Table 1) and nested within the *podihuna* clade.

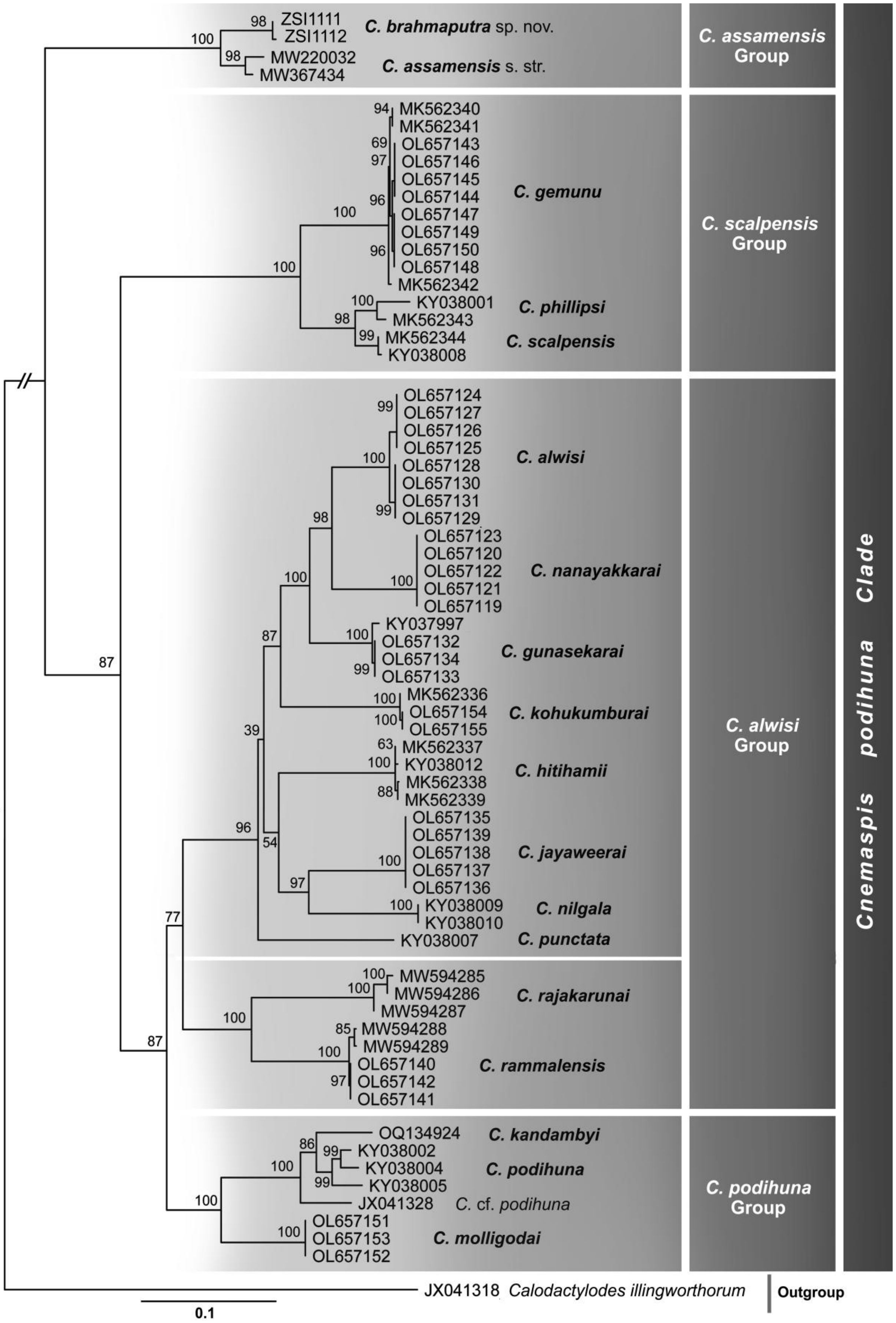

Figure 2. Phylogenetic affinities of the members of the *Cnemaspis podihuna* clade using a Maximum Likelihood (ML) analysis of the ND2 region.

Table 1. Uncorrected pairwise sequence divergence (%) for the ND2 protein-coding mitochondrial gene among the members of *Cnemaspis podihuna* group (*C. kandambyi*, *C. podihuna*, *C. molligodai*) and *C. assamensis* group (the new species and *C. assamensis*).

No	Species	1	2	3	4	5
1	*C. brahmaputra* sp. nov.	0.0–0.2%				
2	*C. assamensis* s.str.	6.0–7.2%	0.0–1.9%			
3	*C. kandambyi*	22.5–24.1%	20.6%	0.0%		
4	*C. podihuna*	21.8–23.2%	19.6–19.9%	5.7–6.8%	2.0–3.8%	
5	*C. molligodai*	18.7–19.7%	18.3–18.9%	12.5%	11.4–12.2%	0.0%

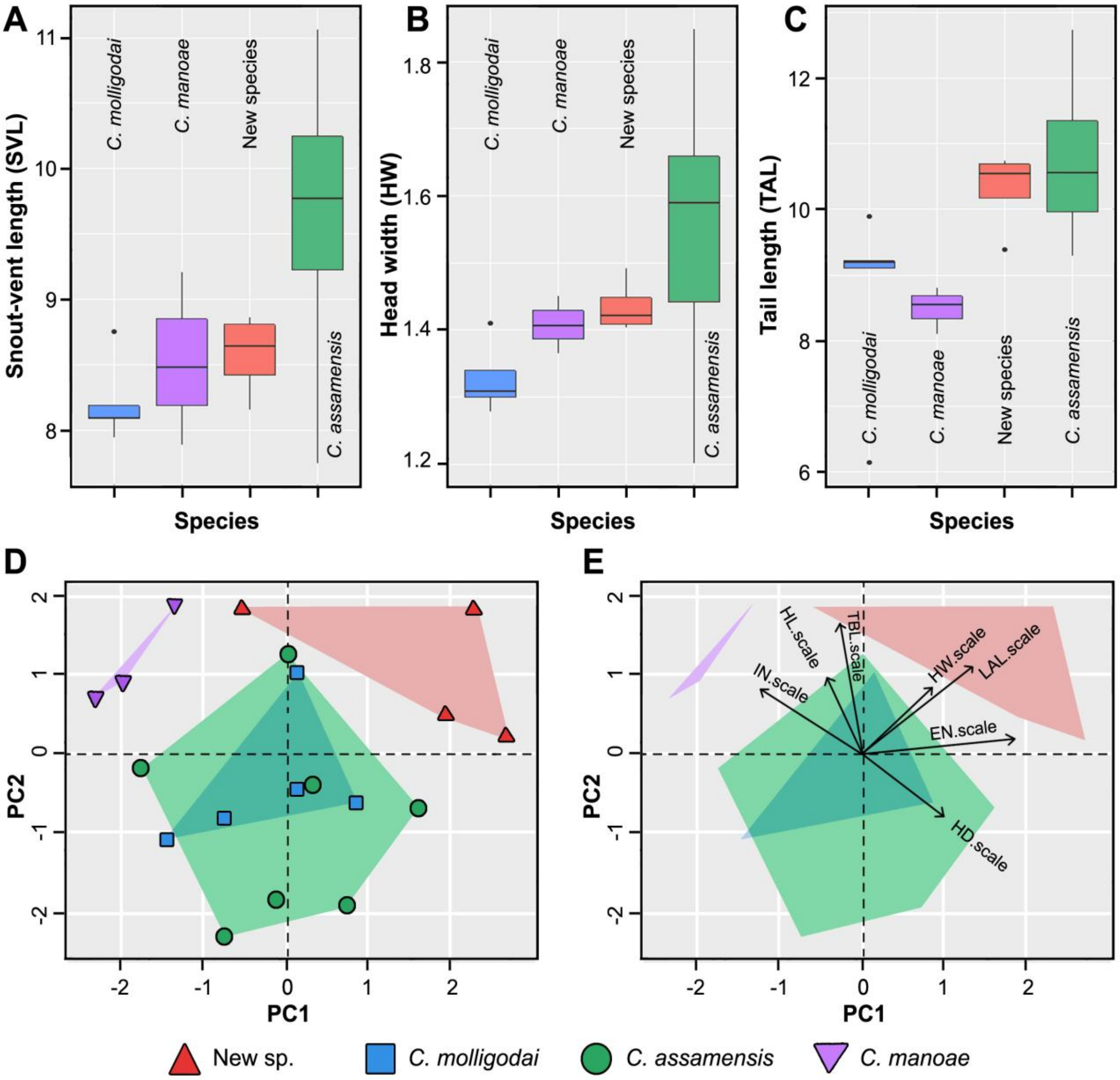

Figure 3. Boxplots of (A) snout–vent length, (B) head width, and (C) tail length indicating differences among *Cnemaspis* cf. *assamensis* (new species) and its Indian congener, *C. assamensis* sensu stricto, and their closely allied taxa from Sri Lanka: *C. molligodai* and *C. manoae*; (D) Principal Component Analysis (PCA) biplot of morphometric variation among the above species, clearly shows the morphological distinctiveness of the new species. Each point represents an individual specimen, and the relative distance between two points is equivalent to the amount of dissimilarity; (E) the same base biplot with vectors associated with population clusters. SVL = snout–vent length; HL = head length; HW = head width; HD = head depth; IN = internarial length; EN = eye–nostril length; LAL = forearm length; TBL = tibia length; PC = principal component.

However, it was deeply divergent (uncorrected *p*-distance 18.7–24.1%; Sup. Table 2) from their sampled relatives from Sri Lanka. The basal position of the *podihuna* clade represents a single group consisting of *C. assamensis* and *C.* cf. *assamensis* (hereafter *C. assamensis* group), sister to Sri Lankan members of the *podihuna* clade. Among them, the *C. assamensis group* is genetically more similar to the *C. podihuna* group than other groups within the clade (Sup. Table 2). The molecular analysis using Bayesian Inference (BI; Sup. Fig. 1) yielded trees with similar topology.

Among the morphometric characteristics, three morphometric mean comparisons of the Kruskal–Wallis test showed significant separation between *C.* cf. *assamensis* and *C. assamensis* sensu stricto and two closely similar species from Sri Lanka: TAL (χ^2 = 12.04, P = 0.007), IN (χ^2 = 16.57, P = 0.0009), and HD (χ^2 = 11.36, P = 0.009), indicating the new population has a relatively longer tail and wider snout compared to the Sri Lankan members of the clade (Fig. 3A–C), and slightly shorter tail and slightly narrower snout compared to its Indian sister species. Furthermore, these characteristics are demonstrated by the new species with its medium-sized head and body compared to *C. assamensis* sensu stricto, which is larger, and two Sri Lankan members, *C. molligodai* and *C. manoae*, which are smaller (Fig. 3A–C). Multivariate analysis by Principal Component Analysis (PCA) also showed other differences in morphometric characters between these four species, as well as *C.* cf. *assamensis* (new species) with a non-overlapping cluster (Fig. 3D–E). Principal Components 1 and 2 collectively explained 54.0% of the variation in the morphometric data matrix (Sup. Table 2). Scaled HL, IN, and TBL loaded negatively on the first principal components, while only scaled HD loaded positively on the second principal component. After considering genetic divergence, morphometric distinctiveness, as well as biogeographical isolation (separation) from *C. assamensis* sensu stricto by the Brahmaputra River, we believe that the population of *C.* cf. *assamensis* is a new species requiring a new name, which is described below.

Taxonomy

Cnemaspis ***brahmaputra*** sp. nov.

(Tables 2, S4; Figs. 4, 5)

[urn:lsid:zoobank.org:act:38C93425-2186-4345-947B-F24CAAACAB51]

Holotype. Adult male (ADBU 1111), near Dirgheswari Temple (26.244854°N, 91.746809°E, datum = WGS84; 134 m above sea level), North Guwahati, Assam, India, collected on 9 January 2023 by A. Sayyed.

***Paratypes* (*n*=3).** Adult males (ADBU 1112, 1113) and an adult female (ADBU 1114) from the same holotype locality by J. Purkayastha and A. Sayyed on the same date.

Diagnosis. A diminutive, rupicolous *Cnemaspis* with adult SVL 30.8–35.7 mm; dorsal scales homogeneous, small granular scales, intermixed with slightly large, randomly arranged smooth scales; enlarged tubercles absent on dorsum; scales on gular, throat, pectoral, and abdomen smooth; median subcaudals smooth, enlarged, slightly semicircular, subimbricate; 26–27 interorbital scales; 7–9 supralabials up to midorbital position, 11–13 up to the angle of jaw; 8–12 infralabials; two pairs of postmentals, inner pair larger, separated by single hexagonal intermediate scale; 83–87 scale rows at midbody, 21–25 ventral scales rows across the belly; 127–131 paravertebral granules, 130–138 midventral scales; similar scales on flanks; four or five spine-like tubercles on lateral body, but absent in lower flanks; 19 subdigital lamellae under fourth toe; males with six or seven precloacal pores and 12 femoral pores (on each thigh) separated by four enlarged poreless scales; dorsal scales on brachium and forearm smooth, granular; ventral scales of thigh with three rows of enlarged scales parallel to femoral scales; ventral scales on tail base not enlarged; a single pair of postcloacal spur on tail base.

Description of holotype. An adult male, SVL 30.85 mm; head moderately large, elongate, narrow, distinct from neck, its length 26% of SVL; head width 66% of head length; snout elongate, its length 47% of head length and greater than eye diameter; interorbital region relatively broad, 27 interorbital scales; eye large, pupil rounded; ear-opening deep, eye to ear distance greater than diameter of eyes (eye diameter 50.5% of eye–ear distance; scales on snout smooth, round, much larger than those of occipital region; scales of interorbital, superciliary, and gular regions granular; occipital and temporal region with slightly larger, smooth, granular scales; loreal region slightly inflated, canthus rostralis not prominent, blunt-edged; rostral scale partially divided by a medial groove, posteroventrally in contact with first supralabial, contacted posteriorly by a nasal, supranasal, and an internasal; nostrils small, oval, bordered by postnasals, supranasal, and rostral.

Mental subtriangular, elongate, but not pointed posteriorly; posterolaterally in contact with two enlarged and shortened postmentals; postmentals medially separated by single postmental scale; postmentals bordered posteriorly by four smooth scales, including medial scale; scales on throat granular and smooth; five rows of small scales separate the orbit from the supralabials; 11 (right) and 13 (left) supralabials, 7th (right) and 8th (left) at mid-orbit position; 10 infralabials, decreasing in size towards angle of jaw.

Body slender, elongate; axilla–groin distance 40% of SVL; mid-dorsal granules bluntly pointed, homogeneous, smooth, intermixed with smooth, slightly enlarged tubercles; dorsal tubercles moderately prominent and randomly arranged; no tubercles on lower flanks; dorsal scales at midbody smaller than ventrals at the same level; paravertebral granules 127, rounded, smooth; abdominal scales subequal in size, smooth, bluntly pointed, juxtaposed; ventral scales 25 rows across midbody, ventrolateral scales on trunk bluntly pointed and smooth; no ventrolateral fold; five spine-like tubercles on upper flank, no tubercles on lower flank; 83 scale rows around midbody; 136 midventral scales.

Arms moderately short; length of forearm 19.8% of SVL; length of brachium 19.2% of SVL; legs relatively short; length of tibia 18.3% of SVL; dorsal scales on both arm and leg bluntly pointed and smooth; ventral scales on upper and lower arms smooth; scales on ventral surface of thigh bluntly pointed and smooth; four rows of enlarged thigh scales, including femoral scales row; 7 precloacal pores and 12 femoral pores, separated by 4 non-enlarged poreless scales; digits elongate, slender, all bearing slightly recurved claws; subdigital lamellae entire, on fingers: 9-14-16-17-14, on toes: 9-15-18-19-19; relative lengths of fingers and toes IV > III > V > II > I.

Tail complete, original; tail base swollen; single conical postcloacal spurs present on each side; dorsal scales on tail bluntly pointed and smooth; tail segmented with whorls of tubercles, each whorl consisting of conical, enlarged, smooth tubercles separated from one another by small scales; subcaudal scales at base bluntly pointed and smooth; distally, subcaudals slightly enlarged; subcaudals between whorls not enlarged; median series of subcaudals distinctly enlarged, semicircular.

Coloration. In life, the holotype had a dorsal pattern of black and yellow markings on a dark brown ground color; snout light brown, with a dark brown streak along the canthus; several radiated dark-brown streaks start from lower part of orbit, one towards nostril, four until upper labials, one towards tympanum; a prominent, black regular marking on the nape; a series (at least six) of black "W" shaped marking on the body starting between axilla until tail base; these markings turn in to scars on the tail, creating a series (at least eight) of obscure bands; bands on the tail not continuous ventrally; flanks, pectoral and abdominal area and ventral thigh and tail pale yellow; dorsal arms and legs uniform light brown, antebrachium, forearm, thigh, and tibia with obscure dark brown cross bands; ventral parts of forelimbs dark-grey; digits banded with dark brown.

In preservative, dorsal color changed into brownish-grey, black marking on the body faded; ventral body color turned into pale grey; limb color changed to grey.

Variation. The morphometric and meristic data variation among the type series is presented in Table 2. Paratype (ADBU 1114) is a female, so no precloacal or femoral pores. ADBU 1113 has 6 precloacal pores. Midventral scales vary from 130 to 138, and ventral scale rows across the belly vary from 21 to 25.

Comparison. *Cnemaspis brahmaputra* sp. nov. is most similar to *C. assamensis* sensu stricto, *C. molligodai*, and *C. manoae* (characters in parentheses), but it can be distinguished from these species by having three enlarged scale rows on thigh (absent in *C. molligodai*, and *C. manoae*), 12 femoral pores (10–12 in *C. assamensis*, eight or nine in *C. molligodai* and *C. manoae*) separated from precloacal pores by 4 nonenlarged scales (enlarged, seven or eight in *C. molligodai* and five or six in *C. manoae*), 130–138 midventral scales (125–129 in *C. assamensis* and 117–121 in *C. manoae*), 21–25 ventral scales rows across the belly (18–20 in *C. assamensis*, 15–19 in *C. molligodai* and *C. manoae*), 83–87 scale rows at midbody (92–94 in *C. assamensis*), 127–131 paravertebral granules (119–125 in *C. assamensis*, 76–83 in *C. molligodai*, and 119–126 in *C. manoae*), no spine-like tubercles on lower flanks (present in *C. assamensis*, *C. molligodai* and *C. manoae*), and 19 lamellae under fourth toe (15 or 16 in *C. manoae*).

The new species is further distinguished from the other two members of the *C. podihuna* group

Plate 10

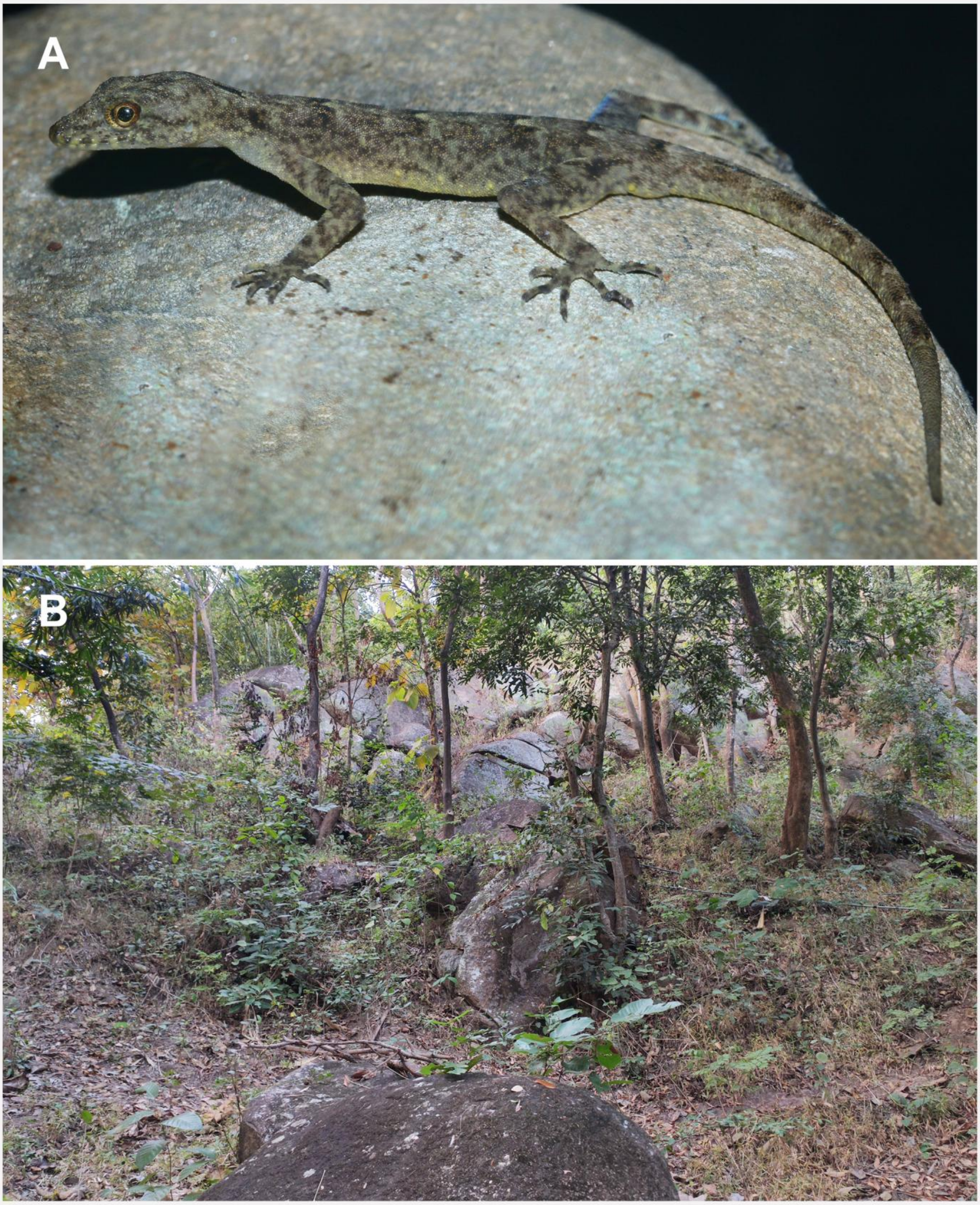

Figure 4. *Cnemaspis brahmaputra* sp. nov. **(A)** the holotype (ADBU1111; an adult male) and **(B)** the habitat near Dirgheswari Temple, North Guwahati, Assam, India. © Photo: A. Sayyed

by 130–138 midventral scales (111–118 in *C. podihuna*), 21–25 ventral scales rows across the belly (15–19 in *C. podihuna* and *C. kandambyi*), 83–87 scale rows at midbody (71–77 in *C. kandambyi*), males with 6–7 precloacal pores (3 or 4 pores in *C. podihuna* and *C. kandambyi*) and 12 femoral pores (3–6 pores in *C. podihuna* and *C. kandambyi*).

Other congeners from the *podihuna* clade—*C. scalpensis* group (*sensu* Amarasinghe & Karunarathna 2020): *C. scalpensis* (Ferguson, 1877); *C. gemunu* Bauer, de Silva, Greenbaum *et al*., 2007; *C. phillipsi* Manamendra-Arachchi, Batuwita, Pethiyagoda, 2007; *C. anslemi* Karunarathna & Ukuwela, 2019; *C. godagedarai* de Silva, Bauer, Botejue *et al*., 2019; and *C. alwisi* group (*sensu* Amarasinghe & Karunarathna 2020): *C. alwisi* Wickramasinghe & Munindradasa, 2007; *C. punctata* Manamendra-Arachchi, Batuwita, Pethiyagoda, 2007; *C. rammalensis* Vidanapathirana, Gehan-Rajeev, Wickramasinghe, 2014; *C. rajakarunai* Wickramasinghe, Vidanapathirana, Rathnayake, 2016; *C. hitihamii* Karunarathna, Poyarkov, de Silva *et al*., 2019a; *C. kohukumburai* Karunarathna, Poyarkov, de Silva, 2019a; *C. nilgala* Karunarathna, Bauer, de Silva, 2019b; *C. gunasekarai* Amarasinghe, Karunarathna, Madawal, 2021; *C. gunawardanai* Amarasinghe, Karunarathna, Madawal, 2021b; *C. jayaweerai* Karunarathna, Ukuwela, de Silva, 2023; *C.nanayakkarai* Karunarathna, Ukuwela, de Silva, 2023—have suites of characters that distinguish them from *C. brahmaputra* sp. nov. which have 6 or 7 precloacal pores (absent). Further differences are summarized for all the species in the *podihuna* group (Table 3) and *podihuna* clade (Sup. Table 4).

Table 2. Meristic and morphometric data of the type series of *Cnemaspis brahmaputra* sp. nov., measurements in mm; m = male, f = female, L = left, R = right

Character	Holotype	Paratypes		
	ADBU 1111 (m)	ADBU 1112 (m)	ADBU 1113 (m)	ADBU 1114 (f)
snout–vent length	30.8	33.2	30.9	35.7
axilla–groin length	12.4	13.6	14.1	14.1
head length	8.0	9.0	7.6	9.8
head width	5.3	5.6	5.1	5.8
head depth	2.9	3.3	2.9	2.6
orbit diameter	1.2	1.2	1.4	1.2
tympanum–eye length	2.4	2.6	2.6	2.6
snout length	3.8	3.8	3.6	4.0
eye–nostril length	3.2	3.3	2.9	3.1
interorbital width	2.9	3.2	2.7	3.2
tympanum diameter	0.6	0.6	0.6	0.6
internarial length	0.9	0.9	0.9	0.9
brachium length	5.9	6.2	6.1	6.8
forearm length	6.1	5.9	5.9	5.8
finger lengths I–V	1.7, 2.1, 2.5, 2.8, 2.4	1.6, 2.4, 2.9, 3.0, 2.6	1.4, 2.6, 2.7, 2.8, 2.4	2.0, 2.9, 3.1, 3.5, 2.5
thigh length	4.9	5.8	5.6	5.9
shank length	5.6	7.3	6.1	7.3
toe lengths I–V	1.6, 3.1, 3.2, 3.7, 3.1	1.6, 3.5, 3.6, 4.0, 3.4	1.3, 2.9, 3.0, 3.6, 3.1	1.9, 3.5, 3.9, 4.1, 3.5
tail length	35.5	40.4	broken	43.3
supralabials R/L (midorbit position)	11(7)/13(8)	11(7)/12(9)	13(8)/13(9)	13(8)/12(8)
infralabials R/L	10/10	8/9	12/10	11/11
paravertebral scales				
midbody scale rows	83	83	85	87
Midventral scales	136	130	138	136
ventral scale rows across the belly	25	24	21	24
Femoral pores	12	12	12	—
Precloacal pores	7	7	6	—
lamellae on fingers R	9–14–16–17–14	11–15–15–17–15	9–14–17–16–14	11–14–17–18–15
lamellae on toes R	9–15–18–19–19	11–16–19–19–19	10–16–19–19–19	11–16–17–19–19

Table 3. Main characters of the *Cnemaspis podihuna* group in Sri Lanka and *C. assamensis* group in India within the *podihuna* clade [modified after Amarasinghe & Karunarathna (2020)]. See text for explanations of the acronyms used in character: SVL = snout-vent length, En = enlarged, Ne = non-enlarged, p = present, a = absent, rs = robust & short, sl = slender & long

Character	*podihuna* (*n*=4)	*molligodai* (*n*=7)	*kandambyi* (*n*=2)	*manoae* (*n*=3)	*assamensis* (*n*=7)	*brahmaputra* sp. n. (*n*=4)
Maximum SVL	24.7	29	23.6	25.3	33.2	25.7
Midventrals	111–118	127–135	128–137	117–121	125–129	130–138
Midbody scale rows	79–83	73–82	71–77	79–83	92–94	83–87
Paravertebral granules	102–106	76–83	85–92	119–126	119–125	127–131
Precloacal pores	3, 4	4, 5	3, 4	5	6,7	6,7
Femoral pores	3–6	8, 9	5, 6	9	9–11	12–14
Poreless scales between pre-cloacal and femoral pores	En (3–6)	En (7–8)	En (7–8)	En (4–6)	Ne (4)	Ne (4)
Subdigital lamellae on toe IV	18, 19	19–23	19, 20	15, 16	18–20	19
Coloration of the vertebral column	bright yellow blotches	light gray with dark blotches	light gray with dark blotches	bright yellow stripe	light gray with pale blotches	light gray with pale blotches
Coloration of the ventral tail	white	pale yellow	white	bright yellow	pale yellow	pale yellow
Coloration of the dorsal tail	brownish gray	brown	brownish gray	pale yellow	brown	brownish gray
Black stripe on nape	a	p	a	p	p	p
Body shape	rs	sl	rs	sl	rs	sl

Etymology. The specific epithet is an invariable noun in apposition and refers to the antecedent river, 'Brahmaputra', which flows near the type locality. Brahmaputra (in the Sanskrit language) is a singular possessive noun with *Brahma* (=a name of the Hindu god, referred to as "the creator") and *putra* (=son, referred to here as offspring), thus the offspring of the creator. Brahmaputra River (3,969 km) flows through China, northeast India, and Bangladesh, and is one of the top ten largest rivers by discharge (Sarma 2004)—English name: Brahmaputra day gecko.

Distribution. Currently, the new species is only known from its type locality (on the north bank of the Brahmaputra River; Fig. 1) near the Dirgheswari Temple in north Guwahati, Assam, India.

Habitat and natural history. The humid and warm habitat of the type locality is characterized by a moist deciduous forest ecosystem, transitioning into semi-evergreen forest in some parts. The forest floor was covered with a thick layer of leaf litter, fallen branches, and other organic matter (Fig. 4). The habitat is also interspersed with granite gneiss and porphyritic granite rocky outcrops and scattered boulders (see Sengupta & Chakraborty 2017). Several streams and small water bodies are found within the habitat that connect to the main river. The other gekkonid species found in the same habitat was *Hemidactylus platyurus*. Other common reptiles encountered were *Amphiesma stolatum* and *Naja kaouthia*.

Discussion

South Asian *Cnemaspis* is believed to have originated in the rainforests of the Western Ghats during the Eocene-Paleocene Thermal Maxima (Agarwal *et al*. 2020), and the basal group of the *podihuna* clade is represented by *C. assamensis*. Probably the dispersal of these geckos was from northeastern India into Sri Lanka, which involved complex biogeographic processes. Although *C. assamensis* and the new species are nested within the *podihuna* clade along with Sri Lankan endemics, several distinct differences between these disjunct populations are adaptations to different microhabitats. For instance, the femoral pores of Sri Lankan species in the *C. podihuna* group are ventrally oriented, and in the Indian species of the *C. assamensis* group, they are posteriorly oriented on the thigh. That might be the reason the original authors of

C. assamensis (*i.e.*, Das & Sengupta) did not notice the femoral pores on their specimens. Actually, except for members of the *C. podihuna* group, the remaining members of the *podihuna* clade in Sri Lanka lack precloacal pores. Among the Sri Lankan members of the *podihuna* clade, there are no members that have more than 10 femoral pores, except for the members of the *C. scalpensis* group (11–16 femoral pores), *C. rammalensis* (14–16 femoral pores), and *C. jayaweerai* (9–12 femoral pores), but they lack precloacal scales, unlike the *C. assamensis* group. In addition, we have noticed that though the precloacal and femoral scales of the Sri Lankan members of the *podihuna* group are enlarged as one precloacofemoral scale series, there is a gap of a few 'enlarged' poreless scales between precloacal pore-scales and femoral pore-scales. On the other hand, in the Indian members of the *C. assamensis* group, these poreless scales are 'not enlarged'.

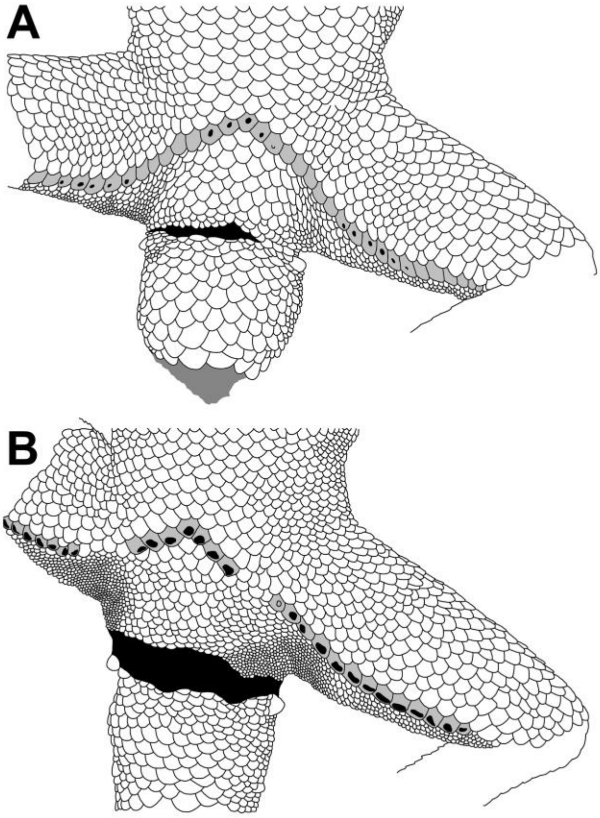

Figure 5. Precloacal and femoral area of **(A)** *C. podihuna* holotype (NHMUK 1946.8.1.20) and **(B)** *Cnemaspis brahmaputra* sp. nov. holotype (ADBU 1111); Note the continuous precloacofemoral scale series in *C. podihuna* and interrupted series in C. *Brahmaputra*—illustrations by AATA (not to scale).

Furthermore, there are multiple series of enlarged femoral pores in Indian members, which have never been observed in Sri Lankan members. We have noticed that having enlarged femoral scales or femoral pore-bearing scales is mostly associated with the saxicoline species; however, this hypothesis is yet to be verified. *Cnemaspis* that occur in Peninsular India in the dry zone outside the Western Ghats form independently derived clades that occur in significantly warmer and drier habitats than those in the Western Ghats (Agarwal *et al*. 2020). Agarwal *et al*. (2020) revealed that granite boulders act as deep-time climate refugia for the Miocene divergent clade of rupicolous *Cnemaspis* on the southern edge of the Mysore Plateau. Probably this is true for the rupicolous *podihuna* clade in northeastern India. With the wide distribution pattern now known of the *C. assamensis* group in India, it is likely many of them have gone unrecognized, due to their morphologically cryptic nature. The discovery of a genetically and morphologically distinct new *Cnemaspis* from the *podihuna* clade suggests additional unrecognized taxa await discovery and description in northeastern India.

Author contributions

All the authors contributed equally

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Research permits

State collection permit for Non-scheduled saurian fauna from non-protected areas of Assam. (No. WL/FG.31/Research Project/Dr. Madhurima Das).

Supplemental data

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Appendix: Other Specimens Examined

Cnemaspis alwisi.—Sri Lanka: NMSL 2004.09.01 (holotype), 2004.09.02–03 (paratypes), WHT 5918, 6518–9, 7336–8, 7343–6.

C. anslemi.—Sri Lanka: NMSL 2019.14.01 (holotype), 2019.14.02–03 (paratypes).

C. assamensis.—India: ZRC 2.4674 (holotype), ZRC 2.4675 (paratype), ZSI(WGRC) 3068–72.

C. gemunu.—Sri Lanka: AMB 7495 (holotype), 7507 (paratype), WHT 7221, 7347–8, NMSL 2006.11.01–04.

C. godagedarai.—Sri Lanka: NMSL 2019.09.01 (holotype), 2019.16.01–02 (paratypes).

C. hitihamii.—Sri Lanka: NMSL 2019.06.01 (holotype), 2019.06.02–03 (paratypes).

C. kandambyi.—Sri Lanka: WHT 9466 (holotype), 9467 (paratype).

C. kohukumburai.—Sri Lanka: NMSL 2019.05.01 (holotype), 2019.05.02–03 (paratypes).

C. manoae.—Sri Lanka: NMSL 2019.10.01 (holotype), 2019.10.02–03 (paratypes).

C. molligodai.—Sri Lanka: NMSL 2006.14.01 (holotype), 2006.14.02–05 (paratypes), NMSL uncat. (2 specimens).

C. nilgala.—Sri Lanka: NMSL 2018.07.01 (holotype), 2018.06.01–03 (paratypes).

C. phillipsi.—Sri Lanka: WHT 7248 (holotype), 7236–8 (paratypes).

C. podihuna.—Sri Lanka: NHMUK 1946.8.1.20 (holotype), NMSL 2006.10.02–04.

C. punctata.—Sri Lanka: WHT 7256 (holotype), 7223 (paratype), 7226 (paratype), 7243–4 (paratypes).

C. rajakarunai.—Sri Lanka: NMSL 2016.07.01 (holotype), DWC 2016.05.01–02 (paratypes).

C. rammalensis.—Sri Lanka: NMSL 2013.25.01 (holotype), DWC 2013.05.001.

C. scalpensis.—Sri Lanka: NMSL 2004.01.01 (neotype), 2004.02.01, 2004.03.01, 2004.04.01, WHT 7265, 7268–9, 7274–6, 7320.