



# A phylogenetic and taxonomic assessment of the *Cnemaspis alwisi* group (Reptilia: Gekkonidae) in Sri Lanka with a description of two new species from isolated misty-mountains

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## Abstract

Sri Lanka is a local hotspot for *Cnemaspis* day geckos with 40 currently known species with 100% endemism. In this paper, we evaluate the phylogenetic relationships of *Cnemaspis* species belonging to the *alwisi* group of the *podihuna* clade and describe two additional new species of *Cnemaspis* from Sri Lanka; one from Galgiriya mountain, Kurunegala District, and another from Ethagala mountain, Ampara District. These new species were recorded from granite caves within forested areas in isolated mountains in the dry bioclimatic zone (point-endemics). Both new species are microhabitat specialists with narrow niches limited to humid, cool, canopy-shaded granite caves and old buildings associated with granite caves, where they are camouflaged by their cryptic morphology and body colouration. Furthermore, both species prefer narrow (~ 6–12 mm), long (~ 120–450 mm) and deep (~ 80–260 mm) crevices as refugia. The regions in which these habitats are located receive relatively low annual rainfall (1,000–1,500 mm). These new species are medium in size (28.5–36.8 mm SVL) and can be differentiated from all other Sri Lankan *Cnemaspis* by the presence of clearly enlarged, subhexagonal subcaudal scales and the absence of preloacal pores in males. Both species described here are categorised herein as Critically Endangered (CR) under the IUCN Red List criteria. The major threats for these new species are habitat loss due to expansion of commercial-scale agriculture, illicit forest encroachments, and forest fires. Therefore, we recommend that relevant authorities take immediate conservation action to ensure the protection of these forest areas with their buffer zones in the near future.

## Keywords

Biodiversity hotspots, dry zone forest, genetic distance, granite caves, mtDNA, natural history, species delimitation, systematics

## Introduction

Sri Lanka, along with the Western Ghats of India, is ranked as one of the world's smallest biodiversity hotspots (Mee-gaskumbura et al. 2002). Of the 242 species of reptiles described, ~66% are endemic to the country, and thus Sri Lanka is also considered a reptile diversity hotspot (Roll et al. 2017; Karunaratna et al. 2020). Within this rich reptile assemblage, the diversity of geckos (Family Gekkonidae) is remarkable; 63 species (from eight genera) have been described so far, accounting for ~26% of the overall reptilian species-richness (de Silva et al. 2019; Amarasinghe and Karunaratna 2020; Amarasinghe et al. 2021b). Of these, 53 species (~84%) are endemic and 48 species (~76%) are threatened and vulnerable to extinction due to ongoing climate change effects, irresponsible development, loss of good quality habitats, and forest fragmentation (Amarasinghe and Karunaratna 2020; Dayananda et al. 2021).

Despite the recent resurrection of the genus *Ancylo-dactylus* Müller, 1907 to accommodate African species formerly assigned to *Cnemaspis* Strauch, 1887 (Malonza and Bauer 2022), more than 200 species of *Cnemaspis* are currently recognized, making it the second most speciose gekkonid genus in the world after *Cyrtodactylus* Gray, 1827 (Grismer et al. 2021; Uetz et al. 2022). The genus *Cnemaspis* comprises 40 species in Sri Lanka, all of which are endemic (Manamendra-Arachchi et al. 2007; Wickramasinghe et al. 2016; Batuwita et al. 2019; Karunaratna et al. 2021). Sri Lankan *Cnemaspis* represent about ~20% of global *Cnemaspis* richness despite occupying a small fraction of the global distribution area of the genus. Recent progress in studying the herpetofauna of the island has resulted in the discovery of many new species of *Cnemaspis* (de Silva et al. 2019; Karunaratna et al. 2019a, 2019b, 2019c) of which 50% have been described in the last decade. Most (~73%) of the *Cnemaspis* species in Sri Lanka occur within the wet bioclimatic zone (annual rainfall  $\geq$  2500 mm). However, the most recent species to be described from Sri Lanka (~27%) were recorded from small isolated forest areas or hillocks in the dry bioclimatic zone (annual rainfall between 1000–2000 mm) (Batuwita et al. 2019; Karunaratna and Ukuwela 2019; Vidanapathirana et al. 2014).

Sri Lankan *Cnemaspis* species represent two distinct evolutionary lineages, the *kandiana* and *podihuna* clades (Agarwal et al. 2017; Karunaratna et al. 2021; Pal et al. 2021). The species of the *kandiana* clade are morphologically characterized by small and irregularly shaped subcaudal scales, and the species of the *podihuna* clade are characterized by clearly enlarged, hexagonal or subhexagonal subcaudal scales (Karunaratna et al. 2019c). The high *Cnemaspis* species richness in Sri Lanka may be ac-

counted for by possible multiple colonizations from the Indian mainland with isolated *in-situ* speciation and radiation (Agarwal et al. 2017, 2020; Pal et al. 2021). Most of the Sri Lankan *Cnemaspis* are point-endemics with distribution ranges limited to very small land areas. It is very likely that future studies on the taxonomy and biogeography of *Cnemaspis* in Sri Lanka will highlight the importance of these isolated habitats in generating and maintaining the diversity of these unique groups of geckos in the island (Deraniyagala 1944; Bauer et al. 2007; Wickramasinghe and Munindradasa 2007; Batuwita and Udugampola 2017). During recent fieldwork in lowland dry plains of northwestern and northeastern Sri Lanka, we discovered two unidentified populations of day geckos, which closely resemble species of the *alwisi* (comprising *C. alwisi* Wickramasinghe & Munindradasa, 2007; *C. gunasekarai* Amarasinghe et al., 2021a; *C. hitihamii* Karunaratna et al., 2019c; *C. kohukumburai* Karunaratna et al., 2019c; *C. nilgala* Karunaratna et al., 2019a; *C. punctata* Manamendra-Arachchi et al., 2007) and *rammalensis* (comprising *C. gunawardanai* Amarasinghe et al., 2021a; *C. rajakarunai* Wickramasinghe et al., 2016; *C. rammalensis* Vidanapathirana et al., 2014) groups (Amarasinghe et al. 2021a) in the *podihuna* clade, yet had apparent morphological differences from all currently known species. Thus, on the basis of an integrative taxonomic approach, we describe them below as two new species.

## Material and methods

### Field sampling and specimens

We conducted field surveys in 173 different locations distributed across several bioclimatic regions (e.g. Semi-arid zone, dry zone, intermediate zone and wet zone) in Sri Lanka as a part of an on-going island-wide survey of lizards under permit number WL/3/2/42/18 (a–d), issued by the Department of Wildlife Conservation (DWC) and permit number R&E/RES/NFSRCM/2019-04, issued by the Forest Department of Sri Lanka to KDBU, ADS and SK. At each location, we surveyed and documented gecko species recorded with special attention to the focal genus *Cnemaspis*. On average, per location, we spent 12 man-hours per survey. Museum acronyms follow Uetz et al. (2019) and Sabaj (2020). The type materials reported in this paper is deposited in the National Museum of Sri Lanka (NMSL), Colombo. Specimens were caught by hand and photographed in life. They were subsequently

ethanised using halothane and fixed in 10% formaldehyde for two days, washed in water and transferred to 70% ethanol for long-term storage. Tail tips were collected as tissue samples before fixation and were stored in 95% ethanol. For comparison, we examined 479 *Cnemaspis* specimens (catalogued and uncatalogued) representing all recognised Sri Lankan species, including all type specimens housed at the National Museum of Sri Lanka (NMSL), The Natural History Museum, London (BMNH), Museum of the Department of Wildlife Conservation, Giritale, Sri Lanka (DWC) and specimens collected by Ansem de Silva (bearing the field codes ADS), Aaron Bauer (bearing the field codes AMB) and Suranjan Karunarathna (bearing the field codes SSK and DMSSK), which have been deposited in the NMSL (see Appendix 1). Specimens that formerly belonged to the Wildlife Heritage Trust (WHT) collection, which bear WHT numbers, are currently deposited at the NMSL, and were catalogued under their original numbers. Additional information on the morphology and natural history of Sri Lankan *Cnemaspis* species was obtained from the relevant literature (Bauer et al. 2007; Manamendra-Arachchi et al. 2007; Wickramasinghe and Munindradasa 2007; Vidanapathirana et al. 2014; Wickramasinghe et al. 2016; Agarwal et al. 2017; Batuwita and Udugampala 2017; Batuwita et al. 2019; de Silva et al. 2019; Karunarathna et al. 2019a, 2019b, 2019c; Karunarathna and Ukuwela 2019; Amarasinghe and Karunarathna 2020; Karunarathna et al. 2021; Amarasinghe et al. 2021a). Assignment of unidentified specimens to the new species was based on their morphometric and meristic characters, colour patterns and the level of geographic isolation, and the species limits were tested independently by molecular phylogenetic methods. These new species have not been included in previously published phylogenies (see Agarwal et al. 2017; Karunarathna et al. 2019c, 2021).

## Morphometric characters

Forty morphometric measurements were taken from the two new populations of *Cnemaspis* from Ethagala mountain and Galgiriya mountain and representative individuals of the members of the *alwisi* and *rajarunai* groups using a Mitutoyo digital Vernier calliper (to the nearest 0.1 mm). Detailed observations of scales and other structures were made through Leica Wild M3Z and Leica EZ4 dissecting microscopes. The following symmetrical meristic characters were taken on the left side of the body: eye diameter (ED, horizontal diameter of eye ball); orbital diameter (OD, the greatest diameter of orbit); eye to nostril length (EN, the distance between the anteriormost point of the orbit and the posterior border of nostril); snout length (ES, the distance between the anteriormost point of the orbit and the tip of snout); snout to nostril length (SN, the distance between the tip of snout and the anteriormost point of nostril); nostril width (NW, the maximum horizontal width of nostril); eye to ear distance (EE, the distance between the posterior border of eye and the anteriormost point of ear opening); snout to

axilla distance (SA, the distance between axilla and the tip of snout); ear length (EL, the maximum length of ear opening); interorbital width (IO, the shortest distance between the left and right supraciliary scale rows); inter-ear distance (IE, the distance across the head between the two ear openings); head length (HL, the distance between the posterior edge of mandible and the tip of snout); head width (HW, the maximum width of head in-between the ears and the orbits); head depth (HD, the maximum height of head at the eye level); jaw length (JL, the distance between the tip of snout and the corner of mouth); internarial distance (IN, the smallest distance between the inner margins of nostrils); snout to ear distance (SED, the distance between the tip of snout and the anteriormost point of ear); upper-arm length (UAL, the distance between axilla and the angle of elbow); lower-arm length (LAL, the distance from elbow to wrist with palm flexed); palm length (PAL, the distance between wrist (carpus) and the tip of longest finger excluding the claw); lengths of digits I–V of manus (DLM, the distance between the juncture of the basal phalanx with the adjacent digit and the tip of the digit, excluding the claw); snout-vent length (SVL, the distance between the tip of snout and the anterior margin of vent); trunk length (TRL, the distance between axilla and groin); trunk width (TW, the maximum width of body); trunk depth (TD, the maximum depth of body); femur length (FEL, the distance between groin and knee); tibia length (TBL, the distance from knee to heel with ankle dorsiflexed); heel length (HEL, the distance between ankle (tarsus) and the tip of longest toe [excluding the claw] with both foot and tibia flexed); lengths of pedal digits I–V (DLP, the distance between the juncture of the basal phalanx with the adjacent digit and the digit tip, excluding the claw); tail length (TAL, the distance between the anterior margin of vent and the tail tip); tail base depth (TBD, the maximum height of the tail base); tail base width (TBW, the widest point of the tail base).

## Meristic characters

Thirty discrete characters were observed and recorded using Leica Wild M3Z and Leica EZ4 dissecting microscopes on both the left (L) and the right (R) side of the body (reported in the L/R order): number of supralabials (SUP) and infralabials (INF) between the first labial scale and the corner of the mouth; number of interorbital scales (INOS) between the left and right supraciliary scale rows; number of postmentals (PM) bordered by chin scales, 1<sup>st</sup> infralabial on the left and right and the mental; number of chin scales (CHS) touching medial edge of infralabials and mental between juncture of 1<sup>st</sup> and 2<sup>nd</sup> infralabials on the left and right; number of supranasal (SUN) scales between nostrils; presence of the postnasal (PON) scales posterior to the naris; presence of the internasal (INT) scale between supranasals; number of supraciliary scales (SUS) above the eye; number of scales between the eye and tympanum (BET) from posterior-most point of the orbit to anterior-most point of the tympanum; number of canthal scales (CAS), number of scales from posteri-

or-most point of naris to anteriormost point of the orbit; total lamellae on manus I–V (TLM) counted from first proximal enlarged scensor, greater than twice the width of the largest palm scale, to distalmost lamella at tip of digits; number of dorsal paravertebral granules (PG) between pelvic and pectoral limb insertion points along a straight line immediately left of the vertebral column; number of mid-body scales (MBS) from the centre of mid-dorsal row diagonally towards the ventral scales; number of mid-ventral scales (MVS) from the first scale posterior to the mental to last scale anterior to the vent; number of belly scales (BLS) across the ventre between the lowest rows of granular dorsal scales; total lamellae on pes I–V (TLP), counted from first proximal enlarged scensor greater than twice the width of the largest heel scale, to distalmost lamella at tip of digits; number of femoral pores (FP) present on the femur; number of non-pored interfemoral scales (IFS), counted between pore-bearing femoral rows; numbers of non-pored distal femoral scales (DFS) counted from distal ends of femoral pore rows to knee. In addition, we also evaluated the texture [keeled (KD) or smooth (SM)] of the ventral scales, the texture [heterogeneous (HET) or homogeneous (HOM)] of the dorsal scales, the number of spinous scales on the flanks (FLSP) and characteristics, such as appearance of the caudal scales (except in specimens with regenerated tails). Colouration was determined from digital images of living specimens and also from direct observations in the field.

## Distribution and natural history

During the surveys, behavioural and other aspects (e.g. habitat, microhabitat) of natural history of the focal species were observed through opportunistic and non-systematic means. Our surveys covered a wide variety of habitats, including open woodlands, primary and secondary forests, pine plantations, home gardens, and various agricultural lands (coconut, rubber, tea, cardamom, cinnamon, oil palm plantations, and paddy fields). Observations of geckos were made by the naked eye at a distance of 2 to 3 m without making any disturbance.

The ambient temperature and the substrate temperature were measured using a standard thermometer and a N19 Q1370 infrared thermometer (Dick Smith Electronics, Shanghai, China), respectively. The relative humidity and light intensity were measured with a QM 1594 multifunction environment meter (Digitek Instruments Co., Ltd., Hong Kong, China). To record elevation and georeference species locations, an eTrex 10 GPS (Garmin) was used (map datum WGS1984). Sex was determined by the presence of hemipenial bulges and femoral pores in males (M) or absence of the above in females (F).

## DNA Based Species Delimitation

To determine genetic distinctiveness of the two new species from the already known *Cnemaspis* species, we examined the mitochondrial NADH dehydrogenase subunit

2 gene (ND2) including the adjacent tRNA regions. ND2 gene is commonly used as a genetic marker for geckos and other reptiles and a majority of DNA sequences available in GenBank for *Cnemaspis* species are of this gene. Genetic distinctiveness was determined by examining the haplotype clusters through phylogenetic analysis (Wiens and Penkrot 2002), estimation of the uncorrected pairwise genetic distances among taxa, and species delimitation analysis.

## DNA isolation, PCR amplification and sequencing

Total genomic DNA was extracted from ethanol-preserved tail tissue samples using standard phenol-chloroform-proteinase K extraction procedures with consequent isopropanol precipitation (protocols followed Hillis et al. 1996, and Sambrook and Russell 2001). The isolated total genomic DNA was visualized in 1% agarose gel electrophoresis in the presence of ethidium bromide. The concentrations of total DNA in the extracts were determined using a NanoDrop 2000 Nano-spectrophotometer (Thermo Scientific, USA), and consequently adjusted to ca. 100 ng DNA/ $\mu$ L.

PCR amplification was performed in 20  $\mu$ L reactions using ca. 50 ng genomic DNA, 0.4  $\mu$ L of each primer (10 nmol), 0.4  $\mu$ L of dNTPs (15 nmol), 0.4  $\mu$ L of additional  $MgCl_2$  (50 nmol), 5  $\mu$ L of Taq PCR buffer (10 mM Tris-HCl, pH 8.3, 50 mM KCl, 1.1 mM  $MgCl_2$  and 0.01% gelatine), 0.2  $\mu$ L of Taq DNA polymerase (1 U) and water to reach a volume of 20  $\mu$ L. Primers used in PCR and sequencing followed Agarwal et al. (2017) and included two forward primers: Metf1, used for amplification ((5'-AAGCTTTCGGGCCCATACC-3'; Macey et al. (1997)), and ND2f17, used for sequencing ((5'-TG-ACAAAAATTGCNCC-3'; Macey et al. (2000)), and two reverse primers: CO1R1, used for amplification ((5'-AGRGTGCCAATGTCTTTGTGRTT-3'; Macey et al. (1997)); and ND2r102, used for sequencing ((5'-CAG-CCTAGGTGGGCGATTG-3'; Greenbaum et al. (2007)). The PCR conditions followed Agarwal et al. (2017).

PCR products were visualized through ethidium bromide stained 1% agarose gel electrophoresis and purified using 2  $\mu$ L of a 1:4 dilution of ExoSapIt (Amersham, UK) per 5  $\mu$ L of PCR product prior to cycle sequencing. Successful targeted PCR products were outsourced to Gene-tech Sri Lanka Pvt. Ltd. Colombo for purification and bidirectional sequencing. Consensus sequences from forward and reverse reads were assembled in GENEIOUS PRO 5.6 software (Drummond et al. 2009). The obtained sequences were deposited in GenBank under the accession numbers OL657119–OL657164 and OL741433 (Table S1).

## Phylogenetic analyses

We downloaded most of the available ND2 sequences for *Cnemaspis* species of the South Asian radiation (Table S1) from GenBank. However, we did not include *Cnemaspis* sensu stricto from Southeast Asia as they are known to form a separate clade, unrelated from the South

Asian *Cnemaspis* species except for *C. modiglianii* Das, 2005, *C. tanintharyi* Lee et al., 2019, and *C. thayawthadangi* Lee et al., 2019 which are known to be nested within the South Asian radiation (Agarwal et al. 2017; Lee et al. 2019). Additionally, we included three *Cnemaspis* (*C. alwisi* [n = 8], *C. molligodai* [n = 3] and *C. kandambyi* [n = 1]) species generated in this study that have not been included in previous phylogenies. We used *Calodactylodes illingworthorum* Deraniyagala, 1953 as an outgroup to root the tree as it has been shown that *Calodactylodes* Strand, 1928 is the sister lineage to the South Asian *Cnemaspis* lineage (Agarwal et al. 2017). In total, we analysed 142 sequences of the fragment of mitochondrial ND2 gene and flanking tRNA genes.

Nucleotide sequences were initially aligned in GENEIOUS PRO 5.6 software (Drummond et al. 2009) with default parameters, and subsequently checked by eye and slightly adjusted. The final alignment contained 1328 bp. Partitioning schemes and optimal substitutional models for the alignment were estimated using the BIC criterion implemented in PartitionFinder (Lanfear et al. 2012). BIC indicated four partitions; each codon position of the ND2 gene and the adjacent tRNA region. GTR+I+G substitution model was selected for each of the codon positions of the ND2 gene while GTR was selected for adjacent tRNA region.

We inferred the matrilineal genealogy using Bayesian Inference (BI) and Maximum Likelihood (ML) approaches. Partitioned Bayesian analysis was performed in MrBayes 3.2.6 (Ronquist and Huelsenbeck 2003) with unlinked model parameters using default priors for 80 million generations with two independent runs and four chains (one hot and three cold chains), sampling every 10000 generations. Convergence of the independent runs was assessed by examining split frequencies (<0.01) of clades across runs, effective sample sizes (ESS values) and likelihood plots in Tracer v1.4.1 (Rambaut et al. 2018). An all compatible consensus tree was built after first 25% of sampled trees were discarded as burn-in. We assessed confidence in tree topology by the frequency of nodal resolution (posterior probability; BI PP) (Huelsenbeck and Ronquist 2001). A partitioned ML analysis was implemented in RAxML 7.2.6. (Stamatakis et al. 2008) with 200 independent ML searches using the rapid hill climbing algorithm. Analysis involved same partitioning schemes and with GTR+G as the substitution model for each partition. Branch support was estimated using 1000 bootstrap (BS) pseudoreplicates. In both analyses, we regarded tree nodes with BI PP over 0.95 and BS values over 70 to be sufficiently resolved. Bayesian inference PP values between 0.95 and 0.90 were regarded as tendencies. Lower values were considered to indicate unresolved nodes (Huelsenbeck and Hillis 1993; Minh et al. 2013). Mean uncorrected genetic distances (*p*-distances) between sequences of mitochondrial ND2 gene (excluding the flanking tRNA) were calculated in MEGA X with an average site cut-off of 95% (Kumar et al. 2018).

Species delimitation analysis using Poisson Tree Process (PTP) (Zhang et al. 2013) was conducted using the rooted BI tree with 142 taxa as an input tree. The cal-

culations were performed on the PTP web server (<http://species.h-its.org/ptp>), with 500,000 MCMC generations, thinning set to 100 and burn-in set at 25%. The outgroup (*C. illingworthorum*) was removed from the tree, prior to the analysis to improve its performance. The probability of each node representing a species was calculated with both Maximum Likelihood (PTP) and Bayesian (bPTP) models.

## Statistical analyses

All statistical analyses were conducted using R Core Team (2018). The 40 morphometric, 26 meristic, and six categorical color pattern characters used in statistical analyses are listed in (Table S2). To remove the effects of allometry in the morphometric characters (sec. Chan and Grismer 2022), size was normalized using the following equation:  $X_{adj} = \log(X) - \beta[\log(SVL) - \log(SVL_{mean})]$ , where  $X_{adj}$  = adjusted value;  $X$  = measured value;  $\beta$  = unstandardized regression coefficient for each population; and  $SVL_{mean}$  = overall average SVL of all populations (Thorpe 1975, 1983; Turan 1999; Leonart et al. 2000, accessible in the R package *GroupStruct* (available at <https://github.com/chankinonn/GroupStruct>). The morphometrics of each species were normalized separately and then concatenated so as not to conflate potential intra- with interspecific variation (Reist 1986; McCoy et al. 2006). Precloacal and femoral pores were omitted from the multivariate analyses due to their absence in females.

Based on Levene's test for the normalized morphometric and meristic characters, equal variances were recovered for all species. Characters were then analyzed using an analysis of variance (ANOVA) and TukeyHSD post hoc test to search for statistically significant mean differences between all combinations of species pairs (Table S3). A principal coordinate analysis (PCoA) using a Gower (dis)similarity index was employed on a concatenated meristic and normalized morphometric data set. The dissimilarity matrix, not the original variables themselves, is used as the input to the analysis. Therefore, information concerning the original variables cannot be recovered. Because this unsupervised multivariate analysis is based on a (dis)similarity index, it is appropriate for data sets containing discrete characters (scale counts) because it does not require the data to fulfill the assumptions of linearity or unimodality (Marhold 2011; Paliy and Shankar 2016), thus allowing more flexible handling of mixed data sets. Average values were used for meristic data containing right and left counts.

Discriminant analysis of principal components (DAPC) from the ADEGENET package in R (Jombart 2021) was performed on the concatenated data set. The DAPC is a supervised analysis that places individuals from each predefined population into separate clusters (i.e., plots of points) bearing the smallest within-group variance that produce linear combinations of centroids having the greatest between-group variance (i.e., linear distance; Jombart et al. 2010). DAPC relies on scaled data from an internal PCA as a prior step to ensure that

variables analyzed are not correlated and number fewer than the sample size. Dimension reduction of the DAPC prior to plotting is accomplished by retaining the first set of PCs that account for approximately 90% of the variation in the data set (Jombart and Collins 2015) as determined from a scree plot generated as part of the analysis. Retaining too many PCs forces false structure to appear in the data, while retaining too few runs the risk of missing true structure.

Morphospacial clustering and positioning among the species/populations were finally also analyzed using multiple factor analysis (MFA) on a concatenated data set comprised of 40 morphometric, 26 meristic, and six categorical color pattern characters (Table S3). The MFA was implemented using the *mfa()* command in the R package *FactoMineR* (Husson et al. 2017) and visualized using the *Factoextra* package (Kassambara and Mundt 2017). MFA is a global, unsupervised, multivariate analysis that incorporates qualitative and quantitative data (Pagès 2015), making it possible to analyze different data types simultaneously in a nearly total evidence environment. In an MFA, each individual is described by a different set of variables (i.e. characters), which are structured into different data groups in a global data frame—in this case, quantitative data (i.e. meristics and adjusted morphometrics) and categorical data (i.e. scale, tubercle, and caudal morphology). In the first phase of the analysis, separate multivariate analyses are carried out for each set of variables—principal component analyses (PCA) for the quantitative data sets and a multiple correspondence analysis (MCA) for categorical data. The data sets are then normalized separately by dividing all their elements by the square root of their first eigenvalues. For the second phase of the analysis, the normalized data sets are concatenated into a single matrix for a global PCA of the data. Standardizing the data in this manner prevents one data type from overleveraging another. In other words, the normalization of the data in the first phase prevents data types with the most number of characters or the greatest amount of variation from outweighing other data types in the second phase. This way, the contribution of each data type to the overall variation in the data set is scaled to define the morphospacial distance between individuals as well as calculating each data type's contribution to the overall variation in the analysis (Pagès 2015; Kassambara and Mundt 2017).

Non-parametric permutation multivariate analyses of variance (PERMANOVA) from the *vegan* package 2.5–3 in R (Oksanen et al. 2020) were used to determine if the centroid locations and group clustering of each species/population in the multivariate analyses were statistically different from one another (Skalaski et al. 2018). Each analysis was based on the calculation of a Euclidean (dis) similarity matrix using 50,000 permutations of the input data, not on the output data of the multivariate analyses. A pairwise *post hoc* test calculates the differences between all combinations of population pairs, generating a Bonferroni-adjusted *p* value and a pseudo-*F* ratio (*F* statistic). A *p* < 0.05 is considered significant and larger *F* statistics indicate more pronounced group separation. A rejection of the null hypothesis (i.e., centroid positions and/or the

spread of the data points (i.e., clusters) are no different from random) signifies a statistically significant difference between species/populations.

## Assessment of the conservation status

The conservation status of the newly described species of the *alwisi* group were assessed through the application of the IUCN Red List criteria, Extent of Occurrence (EOO) and Area of Occupancy (AOO). Extent of Occurrence and Area of Occupancy of each species was determined following the guidelines of the IUCN Red List Categories and Criteria (IUCN Standards and Petitions Committee 2022).

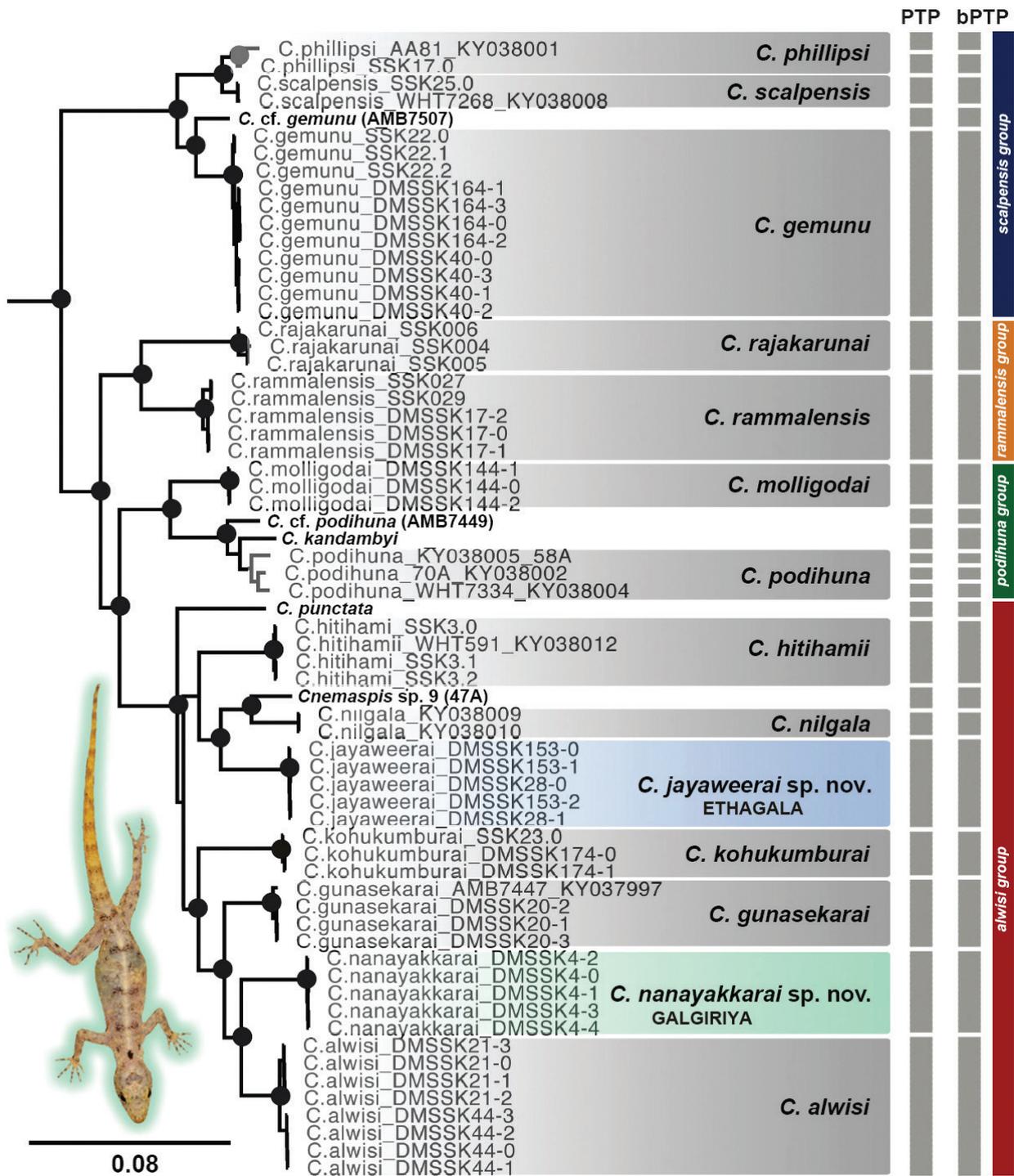
## Results

### ND2 gene genealogy

Reconstructions using BI and ML methods resulted in highly similar topologies and branch lengths and hence only the Bayesian tree is shown (Fig. S1). Topology was identical in both ML and BI analyses for the *podihuna* clade. However, there were slight differences in the topology in the *kandiana* clade but none of these differences were not strongly supported (Fig. S1). Our data confirm the results of both Agarwal et al. (2017) and Karunarathna et al. (2021) in the monophyly of *podihuna* (1.0/97; hereafter node support values are given for BI PP/BS respectively) and *kandiana* clades (1.0/99) (Fig. 1). The two novel species reported here were recovered with the *Cnemaspis podihuna* clade and hence only the *C. podihuna* clade is shown in Fig. 1 for clarity. Both new species were recovered in a strongly supported (1.0/100) monophyletic group comprising *C. alwisi*, *C. gunasekari*, *C. hitihamii*, *C. kohukumburai*, *C. nilgala*, and *C. punctata* within the *C. podihuna* clade. The new species collected from Ethagala mountain, Ampara was monophyletic (1.0/100) and was recovered in a strongly supported clade (1.0/99) comprising *C. nilgala* and the undescribed species *Cnemaspis* sp. 9 (Fig. 1). The new species collected from Galgiriya mountain, Kurunegala was also monophyletic (1.0/100) and was recovered as the sister species (1.0/80) to *C. alwisi*, for which genetic data are presented here for the first time (Fig. 1). The newly included *C. molligodai* was monophyletic (1.0/100) and was recovered as sister to a clade (1.0/100) comprising *C. podihuna* and *C. kandambyi*. *Cnemaspis kandambyi* however, was recovered as nested inside *C. podihuna* (Fig. 1).

### Sequence divergence

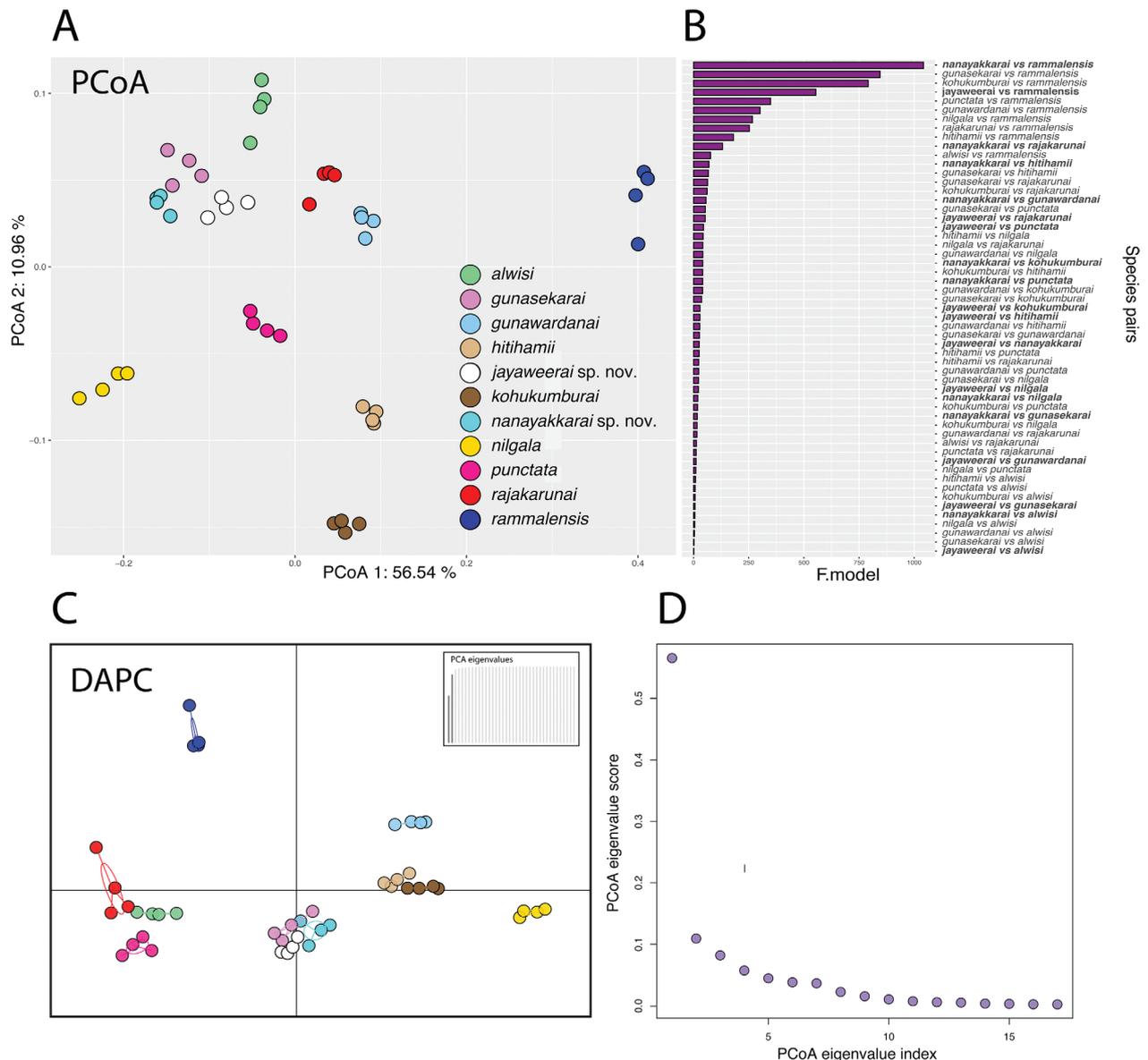
The average uncorrected pairwise genetic *p*-distance between new species from Ethagala mountain, Ampara and other taxa in the *C. podihuna* clade was 16.3%



**Figure 1.** Bayesian inference tree of the *podihuna* clade derived from the analysis of 1347 bp of the *ND2* gene sequences representing 142 taxa (see Fig. S1 for the complete tree). Inset: *Cnemaspis nanayakkarai* sp. nov. from Galgiriya mountain. The black circles at nodes correspond to BI PP and ML BS support values greater than 0.95 and 70 respectively. For voucher specimen information and GenBank accession numbers see Table S1. The grey vertical bars indicate results of molecular species delimitation analyses (bPTP and PTP).

(range 11.7–20.6%) (Table 1) while it was 27.7% (range 20.8–32.1%) between the former and Indian *Cnemaspis* species (Table S6) exclusive of the members of the *C. kandiana* clade. The *p*-distance between new species from Ethagala Mountain, Ampara and other taxa in the *C. kandiana* clade was 28.3% (range 26.9–29.8%) (Fig. S1). The undescribed *Cnemaspis* sp. 9 has the lowest *p*-distance (11.7%) to the new species from Ethagala

mountain, Ampara. The *p*-distance between the new species from Galgiriya mountain, Kurunegala and other taxa in the *C. podihuna* clade was 15.7% (range 8.9–19.5%) (Table 1) while it was 27.7% (range 20.1–32.1%) between the former and Indian *Cnemaspis* species, exclusive of the members of the *C. kandiana* clade. The *p*-distance between the new species from Galgiriya mountain, Kurunegala and other taxa in the *C. kandiana* clade was



**Figure 2.** **A** Principal coordinate analysis (PCoA) of the meristic and normalized morphometric characters showing the morphospacial relationships of *Cnemaspis jayaweerae* sp. nov. and *C. nanayakkarai* sp. nov. to the other species in an unsupervised analysis. **B** Distribution of the F.model values between all possible pairs of species analyzed. The higher the F.model value the more significantly different are the species of each species pair. **C** Discriminant analysis of principal components (DAPC) of the meristic and normalized morphometric characters showing the morphospacial relationships of *Cnemaspis jayaweerae* sp. nov. and *C. nanayakkarai* sp. nov. to the other species in a supervised analysis. **D** Color coding matches that of Eigenvalue scree plot of the PCoA showing the contribution of each axis to the variation in the data set.

29.5% (range 28.4–31.2%) (Fig. S1). *Cnemaspis alwisi* has the lowest  $p$ -distance (8.9%) to new species from Galgiriya mountain, Kurunegala. Species delimitation analyses was congruent among PTP and bPTP models, and confirmed all presently recognized species presented in the dataset, as well as the two newly described species (see the systematics section below).

### Statistical ordination

The ANOVA and TukeyHSD *post hoc* tests recovered significant differences ( $p < 0.05$ ) between the new populations from Ethagala mountain and Galgiriya mountain

forests and among them and all other species of *Cnemaspis* in the analyses across all meristic and normalized morphometric characters (Tables S2–S4). These analyses were corroborated by all three multivariate analyses that recovered notable morphospacial separation among several species. In the PCoA, the new population from Ethagala mountain was separated from all species except *C. alwisi*, *C. gunasekarai*, and *C. punctata* along PCoA axis 1 which accounted for 56.54% of the variation in the data set (Fig. 2A–D). It was separated from all species except *C. gunasekarai*, *C. rajakarunai*, *C. gunawardanai*, and *C. rammalensis* along PCoA axis 2 which accounts for an additional 10.96% of the data set. The new population from Galgiriya mountain was separated from

**Table 1.** Uncorrected pairwise genetic distances in the ND2 gene between *Cnemaspis jayaveerai* sp. nov. and *Cnemaspis nanayakkarai* sp. nov. and the members of the *podihuna* clade in which these two new species belong.

Species	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18
1 <i>C. atwisi</i>	–																	
2 <i>C. cf. gemunu</i>	17.28	–																
3 <i>C. gemunu</i>	18.97	6.44	–															
4 <i>C. gunasekarai</i>	9.52	16.60	17.76	–														
5 <i>C. hitihamii</i>	11.53	15.68	17.92	11.53	–													
6 <i>C. jayaveerai</i> sp. nov. from Ethagala mountain	13.95	18.64	20.64	14.83	13.50	–												
7 <i>C. kohukumburai</i>	12.70	17.23	18.38	12.22	13.48	16.33	–											
8 <i>C. molligodai</i>	16.26	17.41	19.55	16.33	15.00	15.92	17.32	–										
9 <i>C. nanayakkarai</i> sp. nov. from Galgiriya mountain	8.98	17.55	18.32	10.20	12.89	15.37	13.65	17.55	–									
10 <i>C. nilgala</i>	13.67	17.01	19.48	13.88	12.55	13.20	14.92	17.01	15.37	–								
11 <i>C. philipsi</i>	18.27	9.18	10.64	17.55	18.23	18.71	18.73	19.05	18.64	17.41	–							
12 <i>C. podihuna</i>	16.72	17.55	19.16	17.11	15.92	17.28	17.60	12.18	17.93	16.73	17.69	–						
13 <i>C. punctata</i>	12.79	17.96	19.67	13.88	13.74	15.51	14.83	16.46	14.56	14.29	18.44	18.03	–					
14 <i>C. rajakarunai</i>	18.13	16.74	18.80	17.58	17.02	17.70	18.43	16.42	19.35	18.52	20.43	17.34	19.12	–				
15 <i>C. rammalensis</i>	14.63	17.53	19.96	15.91	14.77	17.01	17.34	15.44	16.59	16.12	18.77	16.45	16.76	12.94	–			
16 <i>C. scalpensis</i>	18.95	10.23	10.74	18.46	18.24	19.46	19.83	19.23	19.52	18.24	4.34	18.12	19.60	20.49	19.83	–		
17 <i>Cnemaspis</i> sp.9	12.99	17.55	18.73	12.93	11.26	11.70	13.97	16.33	13.61	7.76	17.55	16.09	13.47	18.02	15.97	18.24	–	
18 <i>C. kandambyi</i>	16.19	17.69	19.26	16.46	14.86	16.60	16.64	12.24	17.14	16.19	16.94	6.26	17.69	17.93	15.74	18.10	16.05	–

all species except *C. gunasekarai* along axis 1, and the new population from Ethagala mountain, *C. rajakarunai*, *C. gunawardanai*, and *C. rammalensis* along axis 2. The PERMANOVA analysis of the PCoA data recovered statistically significant differences ( $p < 0.05$ ) among the centroid positions of the new taxa and all other species with a wide range of F.model values (Fig. 2B). These results were mirrored and corroborated in the DAPC, with the retention of the first two PCs accounting for 89.5% of the variation in the data set (Fig 2C).

The global MFA analysis recovered the greatest amount of separation among the species (Fig. 3A–C) with the first five dimensions accounting for 77.5% of the variation (Fig. 3C). Dimension 1 accounted for 41.6% of the variation and loaded most heavily for meristic data (Fig. 3B,C) followed by color pattern data for dimensions 2–4 and morphometric data for dimension 5 (Fig. 3C). The PERMANOVA analysis of the loadings of the first five dimension of the MFA data recovered statistically significant differences ( $p < 0.05$ ) in the position of nearly all species' centroids with a wide range of F.model values. However, the centroid position of the new population from Ethagala mountain was not significantly different from that of *C. gunasekarai* given their overlap along dimension 1.

## Systematics

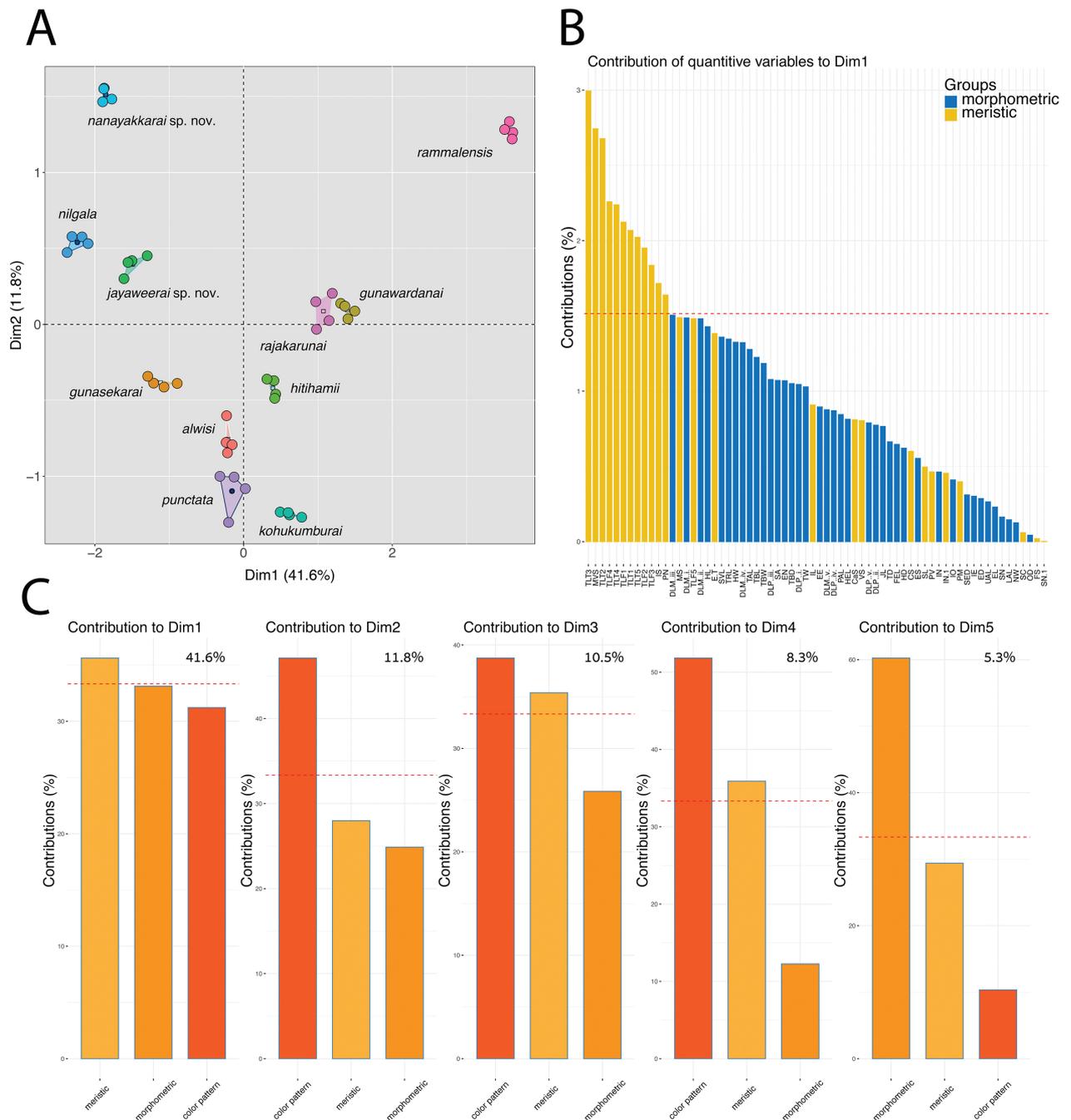
### *Cnemaspis jayaveerai* sp. nov.

<https://zoobank.org/F5F6B187-FC1F-4756-A738-DB2869214187>

Figs 4, 5, S1; Tables 1–4 and Tables S1–S5

**Holotype.** NMSL.2019.23.01, adult male, 36.8 mm SVL, collected inside a granite cave, Ethagala mountain, Ampara District, Eastern Province, Sri Lanka (7.5092N, 81.5198 E, WGS1984; elevation 220 m a.s.l., around 10.00 hrs) on 20 July 2019 by Suranjan Karunarathna.

**Paratypes (n = 2).** NMSL.2019.23.02, adult female, 34.8 mm SVL and NMSL.2019.23.03, adult female, 28.5 mm SVL, collected from a granite cave close to a stream in Ethagala mountain, Ampara District, Eastern Province, Sri Lanka (7.4978 N, 81.5084 E, WGS1984; elevation



**Figure 3.** A Global multiple factor analysis (MFA) of the color pattern, meristic, and normalized morphometric characters showing the complete separation in the morphospacial relationships of *Cnemaspis jayaweera* sp. nov. and *C. nanayakkarai* sp. nov. and all other species in an unsupervised analysis. B Bar graph showing the percent contribution of each meristic and normalized morphometric character to the variation in the data set. C The percent contribution of each data type to the first five dimensions of the MFA.

238 m a.s.l., around 12.00 hrs) collected on 20 July 2019 Suranjan Karunaratna.

**Diagnosis.** *Cnemaspis jayaweera* sp. nov., is readily distinguished from its Sri Lankan congeners by a combination of the following morphological and meristic characteristics and also color pattern: maximum SVL 36.8 mm; dorsum with homogeneous, smooth granular scales; 2/2 supranasals, 1 internasal and 1/1 postnasal present; 3 enlarged postmentals; postmentals bounded by 5 or 6 chin scales (Fig. 4); smooth chin and gular scales, granular, juxtaposed; pectoral and abdominal

scales smooth; 6 or 7 poorly developed tubercles on posterior flank; 121–126 paravertebral granules linearly arranged; 22 or 23 belly scales across the venter; preloacal pores absent in males, 9–12 femoral pores on each side in males, separated by 15–17 unpaired inter-femoral scales, 5–7 unpaired posterior femoral scales; 121–129 ventral scales; 70–77 midbody scales; subcaudals smooth, subhexagonal, enlarged, subequal, forming a regular median row; 7–9 supralabials; 7 or 8 infralabials; 15 or 16 total lamellae on digit IV of manus, and 17 or 18 total lamellae on digit IV of pes. It is also differentiated by its significantly different morphospa-



**Figure 4.** *Cnemaspis jayaweerae* sp. nov. male holotype (NMSL.2019.23.01): **A** dorsal aspect of head, **B** lateral aspect of head, **C** ventral aspect of head, **D** homogeneous scales on dorsal surface of trunk, **E** lateral surface of trunk, **F** smooth ventral scales, **G** cloacal characters with only femoral pores, **H** subdigital lamellae of manus, **I** subdigital lamellae of pes, **J** dorsal side of tail, **K** lateral side of tail, **L** large subhexagonal subcaudals. Scale bar: 2 mm. Photos: Suranjan Karunarathna.

tial placement in the PCoA and the MFA except for *C. gunasekarai* in the latter.

**Comparisons with other Sri Lankan species.** Among species of the *podihuna* clade, *Cnemaspis jayaweerae* sp. nov. can be readily differentiated from *C. kandambyi* Ba-

tuwita & Udugampala, 2017, *C. manaoe* Amarasinghe & Karunarathna, 2020, *C. molligodai* Wickramasinghe & Munindradasa, 2007 and *C. podihuna* Deraniyagala, 1944 by the absence (vs presence) of precloacal pores, and subhexagonal (vs hexagonal) subcaudals; from *C. anslemi* Karunarathna & Ukuwela, 2019 by the presence of fewer

midbody scales (70–77 vs 87–91), more non-pored interfemoral scales (15–17 vs 9 or 10), greater number of flank spines (6 or 7 vs 3 or 4), fewer femoral pores (10 or 11 vs 14 or 15), and fewer lamellae under the 4<sup>th</sup> toe (17 or 18 vs 20 or 21); from *C. gemunu* Bauer et al., 2007 by the presence of greater number of belly scales (22 or 23 vs 13–16), greater number of paravertebral granules (121–126 vs 79–93), more non-pored interfemoral scales (15–17 vs 10–12), and greater number of ventral scales (121–129 vs 112–118); from *C. godagedarai* De Silva et al., 2019 by the presence of fewer ventral scales (121–129 vs 133–137), fewer midbody scales (70–77 vs 98–102), greater number of paravertebral granules (121–126 vs 101–106), more non-pored interfemoral scales (15–17 vs 7–9), and fewer lamellae under 4<sup>th</sup> toe (17 or 18 vs 20 or 21); from *C. phillipsi* Manamendra-Arachchi et al., 2007 by the presence of a greater number of paravertebral granules (121–126 vs 86–93), more non-pored interfemoral scales (15–17 vs 11–14), fewer femoral pores (10 or 11 vs 15 or 16), and throat color (bright yellow vs white); from *C. scalpensis* (Ferguson, 1877) by the presence of greater number of belly scales (22–23 vs 17–19), greater number of paravertebral granules (121–126 vs 102–112), more non-pored interfemoral scales (15–17 vs 8–12), fewer flank spines (6 or 7 vs 9–11), and fewer femoral pores (10 or 11 vs 13–15); from *C. alwisi* Wickramasinghe & Munindradasa, 2007 by the presence of fewer ventral scales (121–129 vs 145–153), fewer belly scales (22 or 23 vs 27–31), greater number of paravertebral granules (121–126 vs 89–97), and throat color (bright yellow vs dirty white); from *C. gunasekarai* Amarasinghe et al., 2021a by the presence of fewer midbody scales (70–77 vs 89–95), more femoral pores (10 or 11 vs 7 or 8), and ventral head color (bright yellow vs dirty white); from *C. gunawardanai* Amarasinghe et al., 2021a by the presence of fewer ventral scales (121–129 vs 159–162), fewer midbody scales (70–77 vs 96–98), fewer paravertebral granules (121–126 vs 148–155), fewer non-pored interfemoral scales (15–17 vs 21–23), more femoral pores (10 or 11 vs 6 or 7), fewer lamellae under 4<sup>th</sup> finger (15 or 16 vs 19–21), and fewer lamellae under 4<sup>th</sup> toe (17 or 18 vs 21–23); from *C. hitihami* Karunarathna et al., 2019c by the presence of fewer midbody scales (70–77 vs 96–99), fewer paravertebral granules (121–126 vs 143–149), fewer non-pored interfemoral scales (15–17 vs 24–26), fewer lamellae under 4<sup>th</sup> toe (17 or 18 vs 21 or 22), and lower SVL (36.8 mm vs 41.7 mm); from *C. kohukumburai* Karunarathna et al., 2019c by the presence of fewer paravertebral granules (121–126 vs 150–159), fewer non-pored interfemoral scales (15–17 vs 22–26), fewer lamellae under 4<sup>th</sup> finger (15 or 16 vs 21 or 22), and fewer lamellae under 4<sup>th</sup> toe (17 or 18 vs 23–25); from *C. nilgala* Karunarathna et al., 2019a by the presence of a greater number of belly scales (22 or 23 vs 17–19), fewer paravertebral granules (121–126 vs 179–187), greater flank spines (6 or 7 vs 3 or 4), and greater femoral pores (10 or 11 vs 7–9); from *C. punctata* Manamendra-Arachchi et al., 2007 by the presence of greater number of paravertebral granules (121–126 vs 83–91), fewer non-pored interfemoral scales (15–17 vs 25–27), fewer flank spines (6 or 7 vs 11–13), and more

femoral pores (10 or 11 vs 5–7); from *C. rajakarunai* Wickramasinghe et al., 2016 by the presence of fewer ventral scales (121–129 vs 146–186), fewer belly scales (22 or 23 vs 26–29), greater number of paravertebral granules (121–126 vs 81–85), fewer non-pored interfemoral scales (15–17 vs 20–22), and more femoral pores (10 or 11 vs 7 or 8); from *C. rammalensis* Vidanapathirana et al., 2014 by the presence of fewer ventral scales (121–129 vs 186–207), fewer midbody scales (70–77 vs 119–131), greater number of paravertebral granules (121–126 vs 94–96), fewer femoral pores (10 or 11 vs 14–16), fewer lamellae under 4<sup>th</sup> finger (15 or 16 vs 22 or 23), and fewer lamellae under 4<sup>th</sup> toe (17 or 18 vs 22 or 23) respectively.

Among species of the *kandiana* clade, *Cnemaspis jayaweeraei* **sp. nov.** differs by the presence (vs absence) of clearly enlarged, subhexagonal subcaudal scales and absence (vs presence) of precloacal pores from the following species: *C. amith* Manamendra-Arachchi et al., 2007; *C. butewai* Karunarathna et al., 2019c; *C. dissanayakai* Karunarathna et al., 2019b; *C. gotaimbarai* Karunarathna et al., 2019c; *C. ingerorum* Batuwita et al., 2019; *C. kalima* Manamendra-Arachchi et al., 2007; *C. kandiana* (Kelaart, 1852); *C. kawminiae* Karunarathna et al., 2019b; *C. kivulegedarai* Karunarathna et al., 2019c; *C. kotagamai* Karunarathna et al., 2019b; *C. kumarasinghei* Wickramasinghe & Munindradasa, 2007; *C. latha* Manamendra-Arachchi et al., 2007; *C. lokugei* Karunarathna et al., 2021; *C. menikay* Manamendra-Arachchi et al., 2007; *C. nandimithrai* Karunarathna et al., 2019c; *C. pava* Manamendra-Arachchi et al., 2007; *C. pulchra* Manamendra-Arachchi et al., 2007; *C. retigalensis* Wickramasinghe & Munindradasa, 2007; *C. samanlensis* Wickramasinghe & Munindradasa, 2007; *C. silvula* Manamendra-Arachchi et al., 2007; *C. tropidogaster* (Boulenger, 1885), and *C. upendrai* Manamendra-Arachchi et al., 2007.

**Description of holotype.** An adult male, 36.8 mm SVL, and 41.1 mm TAL. Body slender, relatively long (TRL/SVL ratio 41.3%). Head relatively small (HL/SVL ratio 27.8% and HL/TRL ratio 67.4%), very narrow (HW/SVL ratio 16.8% and HW/HL ratio 60.4%), less depressed (HD/SVL ratio 10.3% and HD/HL ratio 36.9%) and distinct from neck. Snout relatively short (ES/HW ratio 80.6% and ES/HL ratio 48.7%), more than thrice the eye diameter (ED/ES ratio 37.6%), more than half the length of jaw (ES/JL ratio 88.5%), snout slightly concave in lateral view; eye relatively small (ED/HL ratio 18.3%), twice larger than the ear (EL/ED ratio 50.3%), pupil rounded; orbit length equal to eye to ear distance (OD/EE ratio 100.0%) and shorter than digit IV of the manus (OD/DLM IV ratio 92.4%); supraocular ridges not prominent; ear opening very small (EL/HL ratio 9.2%), deep, taller than wide, larger than nostrils; single row of scales separate orbit from supralabials; interorbital distance is narrow (IO/ES ratio 76.7%), shorter than head length (IO/HL ratio 37.3%); eye to nostril distance shorter than the eye to ear distance (EN/EE ratio 83.9%).

Dorsal surface of the trunk with small, smooth, homogeneous granules, 126 paravertebral granules; 129 smooth midventral scales; 74 midbody scales across belly; 6/7

**Table 2.** Comparison of morphological and morphometric characters of *C. jayaweeraei* sp. nov. (from Ethagala mountain) and *C. nanayakkarai* sp. nov. (from Galgiriya mountain) with the other congeners of the *podithuna* clade in Sri Lanka that can be used to diagnose two new species from the *C. alwisi* group and *C. rammalensis* group (Abbreviations: HOMG – homogenous, SMOO – smooth, SUBX – subhexagonal, mm – millimetres).

Characters	<i>C. alwisi</i>	<i>C. gunasekari</i>	<i>C. gunawardana</i>	<i>C. hitthani</i>	<i>C. jayaweeraei</i> sp. nov.	<i>C. kohkumburai</i>	<i>C. nanayakkarai</i> sp. nov.	<i>C. nigala</i>	<i>C. punctata</i>	<i>C. rajakarni</i>	<i>C. rammalensis</i>
Maximum SVL (mm)	40.4	34.6	40.5	41.7	36.8	34.5	32.6	32.9	39.9	40.2	53.8
Maximum head length (mm)	10.2	9.9	10.5	11.4	8.5	11.2	10.2	9.4	9.4	10.5	14.6
Maximum snout to axilla distance (mm)	16.1	15.9	16.4	18.8	14.9	17.1	15.9	16.7	16.3	20.2	27.5
Maximum trunk length (mm)	17.2	14.6	17.6	17.8	12.7	14.1	15.2	15.4	17.1	17.9	24.1
Dorsal scales type	HOMG	HOMG	HOMG	HOMG	HOMG	HOMG	HOMG	HOMG	HOMG	HOMG	HOMG
Gular scales type	SMOO	SMOO	SMOO	SMOO	SMOO	SMOO	SMOO	SMOO	SMOO	SMOO	SMOO
Pectoral scales type	SMOO	SMOO	SMOO	SMOO	SMOO	SMOO	SMOO	SMOO	SMOO	SMOO	SMOO
Abdomen scales type	SMOO	SMOO	SMOO	SMOO	SMOO	SMOO	SMOO	SMOO	SMOO	SMOO	SMOO
Subcaudals scales type	SUBX	SUBX	SUBX	SUBX	SUBX	SUBX	SUBX	SUBX	SUBX	SUBX	SUBX
Supralabials	8–10	9–11	8–9	8–9	7–9	8–9	7–9	7–8	7–10	8–9	8–10
Infralabials	7–9	8–9	8–9	7–9	7–8	7–8	7–8	6–7	7–9	9–11	8–9
Ventrals	145–153	119–127	159–162	132–135	121–129	131–134	116–122	122–129	129–137	146–186	186–207
Belly scales	27–31	20–22	25–27	21–23	22–23	23–25	25–27	17–19	20–29	26–29	25–28
Midbody scales	71–78	89–95	96–98	96–99	70–77	81–88	86–99	71–78	71–78	69–74	119–131
Paravertebrals	89–97	117–126	148–155	143–149	121–126	150–159	122–131	179–187	83–91	81–85	94–96
Inter femoral scales	18–19	15–17	21–23	24–26	15–17	22–26	20–22	14–15	25–27	20–22	19–24
Flank spines	4–5	4–5	3–4	4–5	6–7	7–8	5–6	3–4	11–13	5–6	4–5
Femoral pores	7–9	9–10	6–7	5–10	10–11	6–9	7–8	7–9	5–7	7–8	14–16
Lamellae on 4 <sup>th</sup> finger	15–17	16–17	19–21	18–19	15–16	21–22	16–17	17–18	17–18	16–20	22–23
Lamellae on 4 <sup>th</sup> toe	17–21	19–21	21–23	21–22	17–18	23–25	17–18	17–18	17–23	19–22	22–23

**Table 3.** Morphometric measurements (mm) of holotypes and paratypes of *Cnemaspis jayaweerai* sp. nov. (Ethagala mountain) and *Cnemaspis nanayakkarai* sp. nov. (Galgiriya mountain) from the dry bioclimatic zone in Sri Lanka (Abbreviations: Ho – holotype; Pa – paratype; M – male; F – female).

Measurements	<i>C. jayaweerai</i> sp. nov.			<i>C. nanayakkarai</i> sp. nov.		
	Ho (M)	Pa (F)	Pa (F)	Ho (M)	Pa (M)	Pa (F)
Snout-vent length	36.8	34.8	28.5	32.6	31.2	30.6
Snout to axilla distance	15.9	14.9	14.7	14.9	14.5	14.2
Head length	10.2	9.7	9.6	8.5	8.3	8.2
Head width	6.2	5.9	5.8	4.8	4.7	4.6
Head depth	3.8	3.6	3.5	3.1	2.9	2.8
Trunk length	15.2	14.1	13.6	12.7	12.3	12.1
Trunk width	5.5	5.3	5.2	5.5	5.4	5.6
Trunk depth	3.4	3.2	3.2	3.6	3.5	3.5
Jaw length	5.6	5.2	5.2	5.7	5.6	5.6
Tail length	41.1	39.2	38.3	35.7	33.8	33.3
Tail base width	3.6	3.1	2.9	3.1	3.1	2.9
Tail base depth	2.9	2.8	2.7	2.8	2.7	2.5
Snout length	5.0	4.6	4.3	3.6	3.7	3.6
Snout to nostril	1.6	1.6	1.6	1.3	1.4	1.3
Eye diameter	1.9	1.8	1.9	1.9	1.8	1.9
Orbital diameter	3.4	3.2	3.1	3.2	3.1	3.2
Eye to nostril length	2.9	2.8	2.7	3.2	3.1	2.9
Snout to ear distance	10.5	9.9	9.8	7.6	7.7	7.5
Eye to ear distance	3.4	3.2	3.1	2.6	2.5	2.5
Ear length	0.9	0.8	0.7	0.9	0.9	0.8
Interorbital width	3.8	3.7	3.7	3.6	3.6	3.5
Internarial distance	3.8	3.7	3.6	3.8	3.7	3.9
Internarial distance	1.6	1.5	1.4	1.6	1.5	1.6
Nostril width	0.3	0.3	0.3	0.2	0.2	0.2
Upper-arm length	4.1	3.7	3.8	4.7	4.6	4.6
Lower-arm length	4.7	4.3	4.1	4.3	4.2	4.3
Palm length	3.7	3.4	3.5	3.8	3.6	3.3
Digit length of manus (I)	2.2	1.9	1.8	1.6	1.5	1.5
Digit length of manus (II)	2.7	2.5	2.5	1.9	1.8	1.9
Digit length of manus (III)	2.9	2.7	2.7	2.6	2.5	2.5
Digit length of manus (IV)	3.7	3.3	2.9	3.1	3.2	3.1
Digit length of manus (V)	2.4	2.2	2.2	2.2	2.1	2.2
Femur length	7.9	7.2	7.1	7.3	7.1	6.9
Tibia length	6.9	5.9	5.3	6.2	6.1	5.9
Heel length	6.3	5.9	5.5	5.1	5.2	4.9
Digit length of pes (I)	2.1	1.8	1.8	1.9	1.8	1.7
Digit length of pes (II)	3.9	3.7	3.8	2.8	2.8	2.9
Digit length of pes (III)	4.3	4.2	4.1	3.7	3.6	3.7
Digit length of pes (IV)	5.3	4.9	4.8	4.3	4.1	4.2
Digit length of pes (V)	4.3	4.1	4.1	3.4	3.3	3.3

weakly developed tubercles on the flanks; ventrolateral scales small; granules on snout smooth and flat, larger than those on interorbital and occipital regions; canthus rostralis less pronounced, 12/13 smooth oval scales from eye to nostril; scales of the interorbital region oval and smooth; ear opening vertically oval, slanting from anterodorsal to posteroventral, 23/22 scales between anterior margin of the ear opening and the posterior margin of the eye. Supralabials 8/9 and infralabials 7/8, becoming smaller towards the gape. Rostral scale wider than long, partially divided (70%) by a median groove, in contact with first supralabial. Nostrils separated by 2/2 enlarged

supranasals with 1 internasal and 1/1 postnasal; no enlarged scales behind the supranasals. Nostrils oval, dorso-laterally orientated, not in contact with first supralabials.

Mental subtriangular, as wide as long, posteriorly in contact with 3 enlarged postmentals (smaller than mental, and larger than chin scales); postmentals contact and bordered posteriorly by 6 smooth chin scales (larger than nostrils), contact with the 1<sup>st</sup> infralabials; ventral scales larger than chin scales, and larger than nostrils. Smooth, rounded, juxtaposed granular scales on chin and gular region; pectoral and abdominal scales smooth, subimbricate towards precloacal region, abdominal scales larger

**Table 4.** Meristic data of holotypes and paratypes of *Cnemaspis jayaweerae* sp. nov. (Ethagala mountain) and *Cnemaspis nanayakkarai* sp. nov. (Galgiriya mountain) from the dry bioclimatic zone in Sri Lanka (Abbreviations: Ho – holotype; Pa – paratype; M – male; F – female).

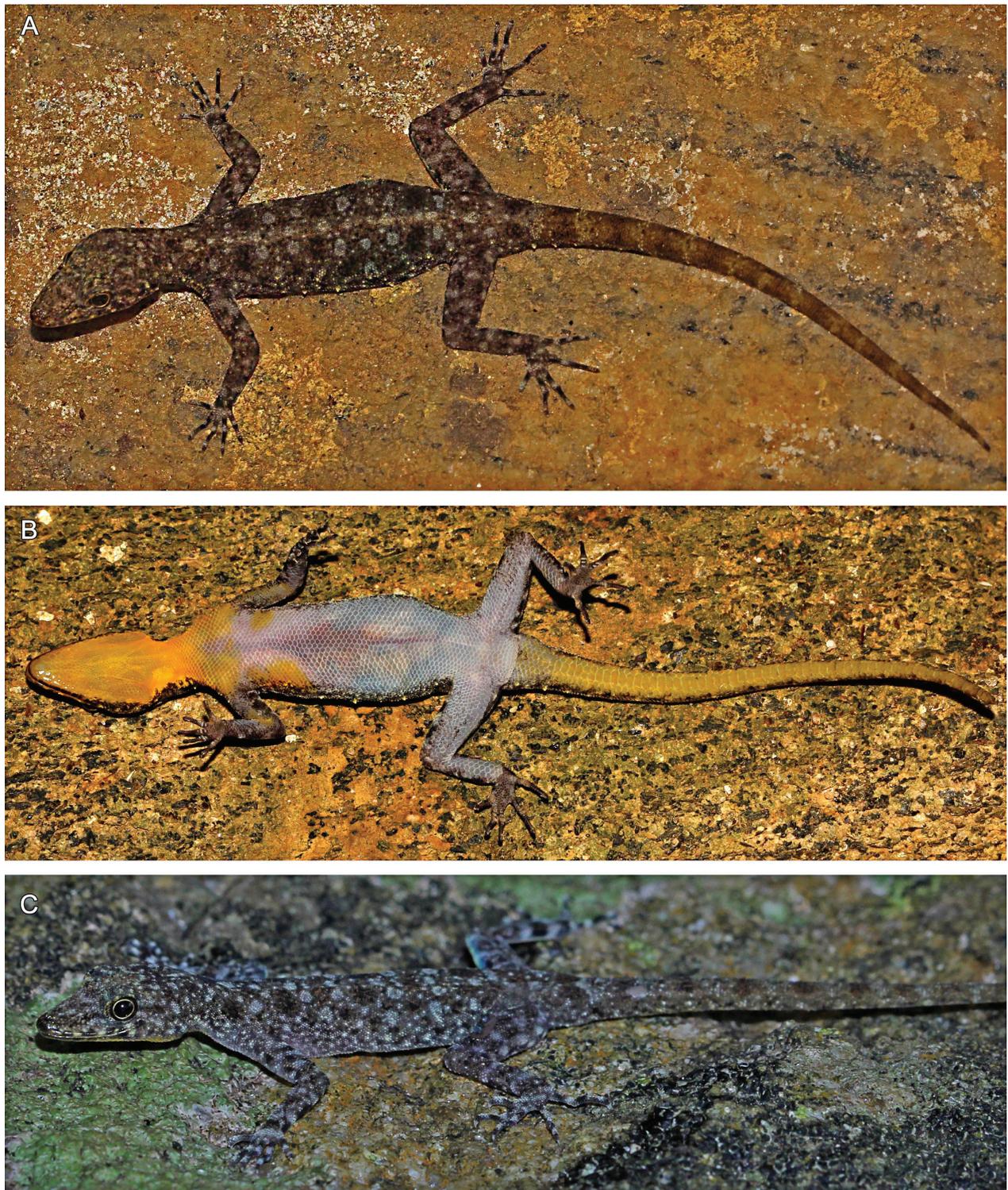
Characters	<i>C. jayaweerae</i> sp. nov.			<i>C. nanayakkarai</i> sp. nov.		
	Ho (M)	Pa (F)	Pa (F)	Ho (M)	Pa (M)	Pa (F)
Supralabials (L, R)	9, 8	8, 8	7, 8	8, 9	8, 8	7, 8
Infralabials (L, R)	8, 7	8, 8	8, 7	7, 7	7, 8	7, 7
Flank spines (L, R)	6, 7	6, 6	7, 6	6, 6	6, 5	5, 5
Interorbital scale	28	26	26	33	26	28
Postmentals	3	3	3	4	4	4
Chin scales	6	5	6	6	6	6
Supranasal (L, R)	2, 2	2, 2	2, 2	2, 2	2, 2	2, 2
Postnasal (L, R)	1, 1	1, 1	1, 1	1, 1	1, 1	1, 1
Internasal	1	1	1	3	3	3
Supraciliaries (L, R)	14, 15	14, 14	14, 14	16, 15	15, 16	16, 16
Eye to tympanum scales (L, R)	23, 22	22, 21	23, 23	23-21	22, 20	21, 22
Canthal scales (L, R)	12, 13	12, 12	13, 12	13, 14	12, 13	12, 13
Total lamellae on manus – I (L, R)	11, 11	10, 11	11, 10	12, 11	11, 11	11, 12
Total lamellae on manus – II (L, R)	15, 14	15, 15	14, 14	14, 15	14, 14	14, 14
Total lamellae on manus – III (L, R)	15, 15	14, 15	14, 15	17, 16	16, 17	16, 16
Total lamellae on manus – IV (L, R)	16, 16	15, 16	16, 16	17, 17	16, 16	16, 17
Total lamellae on manus – V (L, R)	16, 15	15, 16	16, 16	14, 13	14, 14	13, 13
Paravertebrals	126	124	121	131	126	122
Midbody scales	74	70	77	88	86	99
Midventral scales	129	125	121	122	116	120
Belly scales	23	22	23	25	26	27
Total lamellae on pes – I (L, R)	10, 10	9, 10	10, 9	11, 12	11, 12	11, 11
Total lamellae on pes – II (L, R)	14, 13	13, 14	14, 14	15, 14	15, 15	15, 15
Total lamellae on pes – III (L, R)	16, 16	16, 15	16, 15	17, 16	16, 17	16, 17
Total lamellae on pes – IV (L, R)	18, 18	17, 18	18, 18	18, 18	17, 18	17, 17
Total lamellae on pes – V (L, R)	16, 15	15, 16	16, 16	18, 17	17, 17	18, 18
Femoral pores (L, R)	10, 11	–	–	8, 7	7, 7	–
Post femoral scales (L, R)	7, 6	–	–	6, 6	7, 6	–
Inter femoral scales	16	–	–	22	20	–

than dorsals; 23 belly scales across venter; smooth, subimbricate scales around vent and base of tail; 10/11 femoral pores; 16 unpored interfemoral scales; 7/6 small posterior femoral scales. Original tail of holotype longer than snout-vent length (TAL/SVL ratio 111.8%); hemipenial bulge greatly swollen (TBW 3.6 mm), homogeneous scales on the dorsal aspect of the tail directed backwards, spine-like tubercles absent at base of tail, latter very smooth; tail with 3 or 4 enlarged flattened obtuse scales forming whorls; a very small, round post-cloacal spur on each side; smooth subcaudals are arranged into a median series of clearly enlarged, subhexagonal scales.

Forelimbs moderately short, slender (LAL/SVL ratio 12.7% and UAL/SVL ratio 11.3%) lower arm longer than upper arm; hind limbs moderately long, tibia little shorter than the femur (TBL/SVL ratio 18.8% and FEL/SVL ratio 21.5%). Dorsal, anterior, ventral and posterior surfaces of upper arm and lower arms with smooth scales, those on anterior surface twice as large as those on other faces of limb; scales on dorsal, anterior, ventral and posterior surfaces of the femur and tibia smooth and flat granular, scales on the ventral surface is twice the size of those of the other parts. Dorsal and ventral scales on the manus

and the pes smooth, granular; dorsal surfaces of digits with granular scales. Digits elongate and slender with inflected distal phalanges, all bearing slightly recurved claws. Subdigital lamellae entire (except divided at first interphalangeal joint), unnotched; total lamellae on manus (left/right): digit I (11/11), digit II (15/14), digit III (15/15), digit IV (16/16), digit V (16/15); total lamellae on pes (left/right): digit I (10/10), digit II (14/13), digit III (16/16), digit IV (18/18), digit V (16/15); interdigital webbing absent; length order of digits of left manus: I (2.2 mm), V (2.4 mm), II (2.7 mm), III (2.9 mm), IV (3.7 mm); length order of digits of left pes: I (2.1 mm), II (3.9 mm), III (4.3 mm), V (4.3 mm), IV (5.3 mm).

**Variation of the type series.** The SVL of adult specimens in the type series of *Cnemaspis jayaweerae* sp. nov. (n = 3) ranges from 28.5 to 36.8 mm; number of supralabials 7–9, and infralabials 7 or 8; spines on flank 6 or 7; interorbital scales 26–28; supraciliaries 14 or 15; canthal scales 12 or 13; scales from eye to tympanum 21–23; total lamellae under digits of the manus: digit I (10 or 11), digit II (14 or 15), digit III (14 or 15), digit IV (15 or 16), digit V (15 or 16); total lamellae under digits of the pes: digit I (9 or

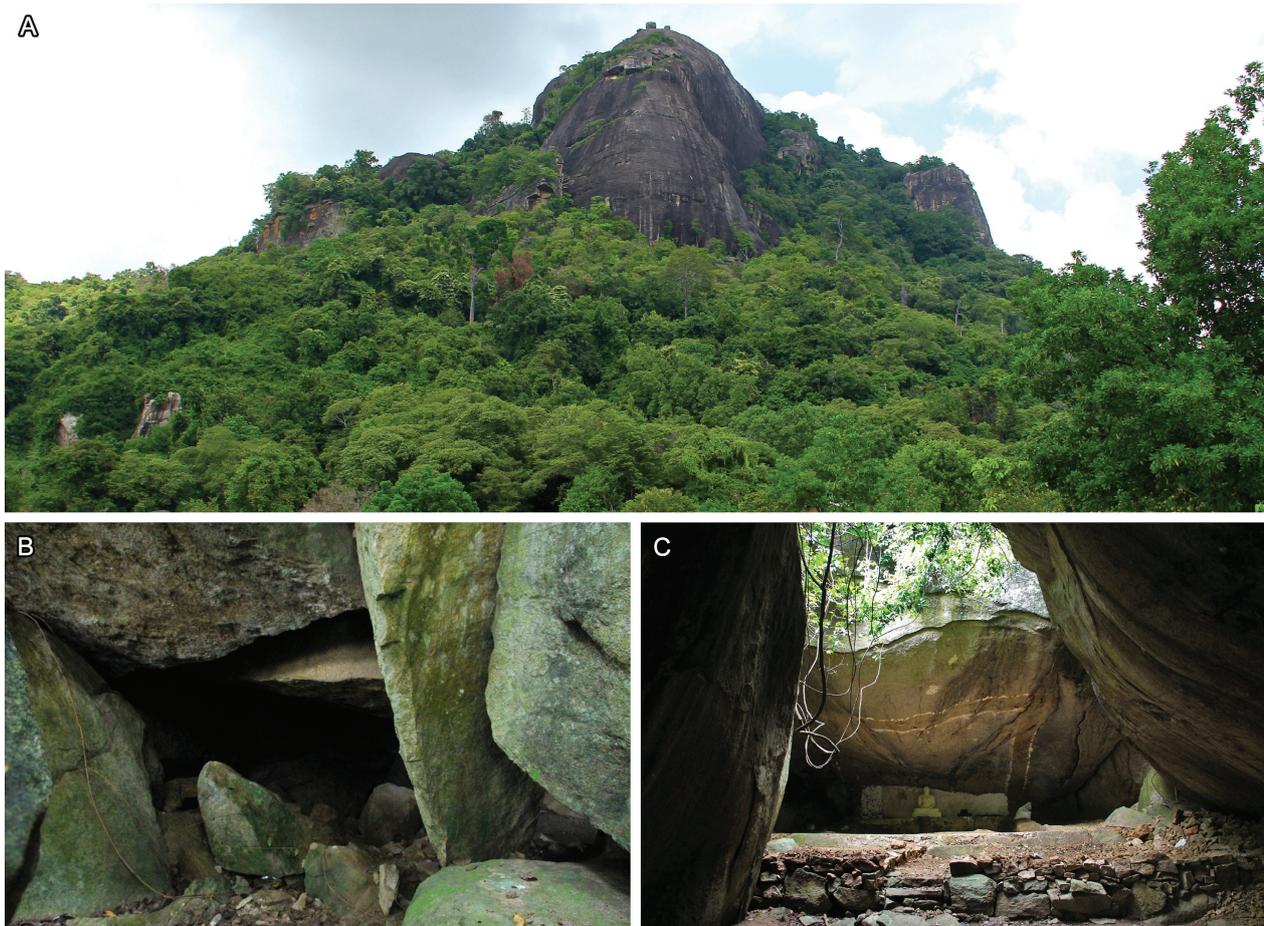


**Figure 5.** *Cnemaspis jayaweerae* sp. nov. female paratype (NMSL.2019.23.02): **A** dorsal view in life in-situ, **B** ventral aspect showing gular, ventral, and tail coloration, **C** lateral aspect of male holotype (NMSL.2019.23.01) in life in-situ. Photos: Suranjan Karunaratna.

10), digit II (13 or 14), digit III (15 or 16), digit IV (17 or 18), digit V (15 or 16); ventral scales 121–129, midbody scales 70–77; paravertebral granules 121–126; chin scales 5 or 6; belly scales 20–23; femoral pores in males 9–12; unpored interfemoral scales in males 15–17, and unpored posterior femoral scales in males 5–7 (Tables 2–4).

**Color of living specimens.** The dorsal color of the head, body and limbs generally from black-brown to ash with

four or five paired black blotches; in between black blotches on the dorsum are small grey-white paravertebral blotches; tail is light-brown with 11–14 faded grey cross bands along the tail dorsum (Fig. 5); a small black spot is present in the occipital area; dorsal pattern on head reticulated; pupil circular and black with the surrounding scales yellowish white; limbs with black and grey band like dorsal patches; manus and pes with irregular, wide, black and white crossbands on the dorsum;



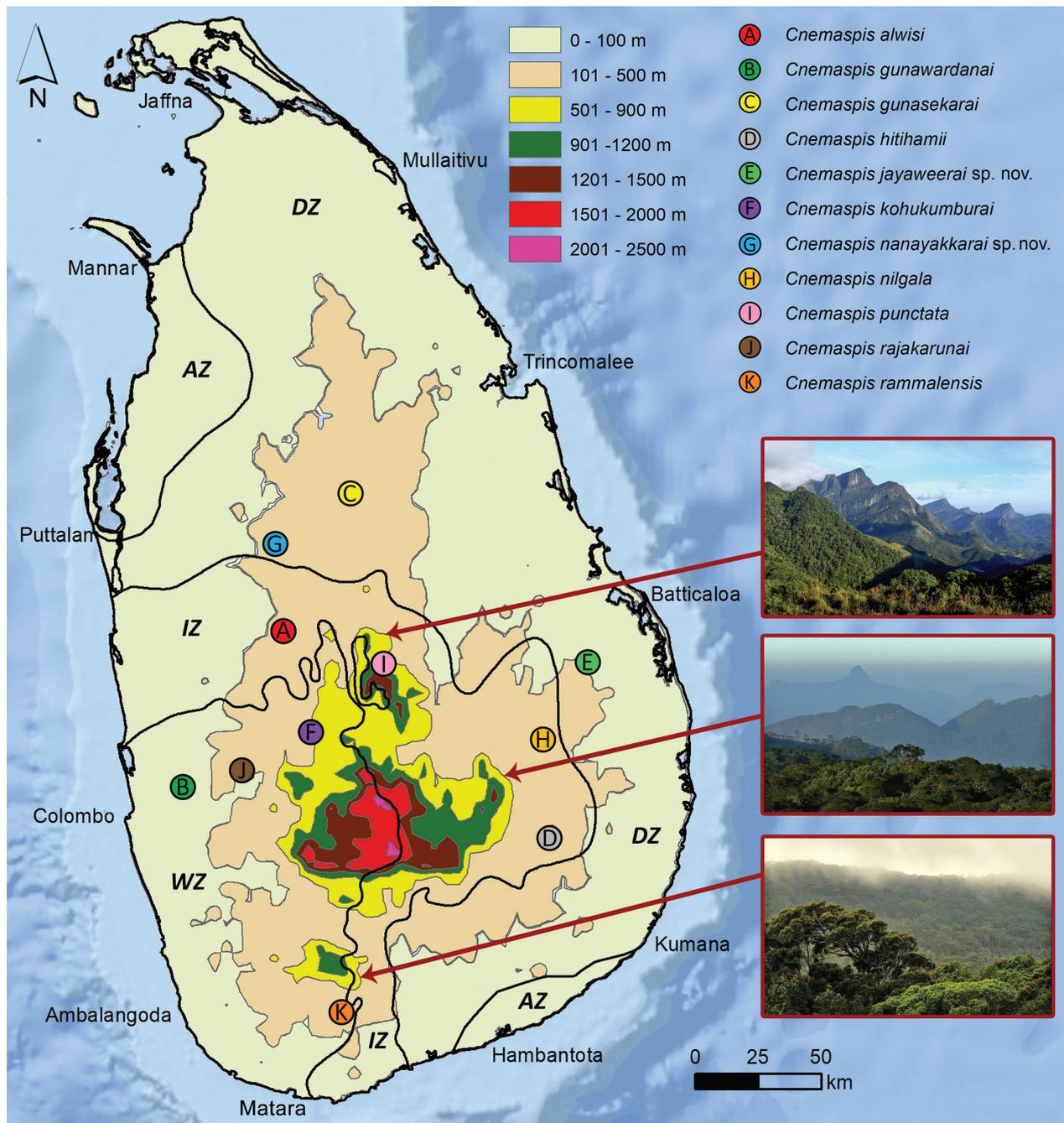
**Figure 6.** General habitat of *Cnemaspis jayaweerai* sp. nov. in Ethagala, Ampara District of Sri Lanka: **A** an isolated granite mountain with dense forest and canopy cover, **B** a granite cave habitat with lots of cracks and crevices, **C** historic granite caves with ancient inscriptions in a Buddhist monastery in Ethagala. Photos: Suranjan Karunarathna.

supralabials and infralabials are dirty white and dusted with black; lateral body has a combination of 8–10 black and grey spots; chin, gular, and throat scales are bright yellow without dark spots in males; whole ventral side with dirty white without dark spots in females; pectoral region, arms, abdomen and cloacal scales dirty white; post-cloacal spur and subcaudal scales pale yellow, without spots.

**Color of preserved specimens.** Both males and females dorsally light brown, mixed with dirty white and dark paravertebral blotches; dark and grey cross bands on the dorsum of the tail; limbs with brown and dirty white band like dorsal patches; ventral surface dirty white without markings; subcaudals with dark brown margins; ventrolateral side of the trunk dusted with black.

**Etymology.** The specific epithet (*jayaweerai*) is a Latinized eponym in the masculine genitive singular, honouring Mr. Shanthasiri Jayaweera (a senior member and former president of the Young Zoologists' Association (YZA) of Sri Lanka; founder of the Junior YZA; senior instructor of the Fish study group of the YZA; renowned wildlife artist; a great educator; wildlife conservationist) for his friendship and valuable contribution to environmental conservation in Sri Lanka.

**Distribution and natural history.** The type locality, Ethagala forest (7.487114 to 7.514992N and 81.489325 to 81.525203E) is an isolated mountain with large pointed granite rock outcrops supporting a forest dominated by tall shade-bearing trees and bushes (e.g. *Vatica obscura*). The dominant vegetation type is dry mixed semi-evergreen forests (Gunatileke and Gunatileke 1990), and the mean annual rainfall varies between 1000 and 1500 mm, received mainly during the northeast monsoon (November–February) (Somasekaram et al. 1988). The land area is approximately 450 ha and situated in the Ampara District, Eastern Province (dry bioclimatic zone) of Sri Lanka. The mean annual temperature of the area is 29.8–31.2°C, and its elevational range is 100–450 m a.s.l. Based on our preliminary investigations *Cnemaspis jayaweerai* sp. nov. appeared to be uncommon in Ethagala. Our survey of 20 ha revealed 16 ( $\pm 0.3$ ) geckos for 35 man-hours (field work done on 20 July 2019, 13–14 September 2019, and 18–19 March 2020). This species was restricted to granite caves (mainly those modified by natives 1,000 years ago) in closed canopy forest, and abandoned buildings associated with granite caves inside the forest (Fig. 6). Further, it prefers narrow (~6–10 mm), long (~120–390 mm) and deep (~80–260 mm) crevices as hiding sites. These microhabitats were poorly illuminated (light intensity: 0–621 Lux), relatively moist (relative hu-



**Figure 7.** Currently known distribution of the members of the *alwisi* and *rammalensis* groups with new species – *Cnemaspis jayaweerai* sp. nov. and *Cnemaspis nanayakkarai* sp. nov. with the three major mountain habitats and seven elevational ranges in Sri Lanka (abbreviations: AZ Semi-arid zone, DZ dry zone, IZ intermediate zone, and WZ wet zone; Inset top to bottom: Knuckles mountain massif, Central highlands, and Rakwana mountain massif). Photos: Vimukthi Weeratunga and Ashan Geganage. Map: Buddhika Madurapperuma.

midity: 68–81% and canopy cover: 75–90%) and relatively cool (ambient temperature: 31.4–32.9°C and substrate temperature: 28.2–29.1°C). The new species was sympatric with several other gecko species: *Calodactylodes illingworthorum*, *Cnemaspis podihuna*, *Gehyra mutilata* (Wiegmann, 1834); *Hemidactylus depressus* Gray, 1842; *H. frenatus* Duméril & Bibron, 1836; *H. hunae* Deraniyagala, 1937; *H. leschenaultii* Duméril & Bibron, 1836; *H. parvimaculatus* Deraniyagala, 1953, and *H. triedrus* Daudin, 1802. During the study periods, eggs, hatchlings, juveniles and gravid females were not observed.

**Conservation status.** Application of the IUCN Red List criteria indicates that *Cnemaspis jayaweerai* sp. nov. is Critically Endangered (CR) due to having an area of occupancy (AOO) <10 km<sup>2</sup> (five locations – single forest block, 0.16 km<sup>2</sup> in total assuming a 100 m radius around each georeferenced location) and an extent of occurrence (EOO) <100 km<sup>2</sup> (3.19 km<sup>2</sup>) in Eastern Province of Sri Lanka [Applicable criteria B2-b (iii)] (Fig. 7).

***Cnemaspis nanayakkarai* sp. nov.**

<https://zoobank.org/E489F4E7-4827-4830-A046-30C1F05589E2>

Figs 8, 9, S1; Tables 1–4 and Tables S1–S5

**Holotype.** NMSL.2021.06.01, adult male, 32.6 mm SVL, collected from a large granite cave covered with dense canopy close to a freshwater tank in Galgiriya mountain range, Kurunegala District, North Western Province, Sri Lanka (7.915631N, 80.379361E, WGS1984; elevation 218 m a.s.l., around 11.00 hrs) on 22 December 2019 by Suranjan Karunarathna.

**Paratypes (n = 2).** NMSL.2021.06.02, adult male, 31.2 mm SVL and NMSL.2021.06.03, adult female, 30.6 mm SVL, collected from a large granite cave covered with dense canopy cover close to a freshwater tank, Galgiriya mountain range, Kurunegala District, North Western Province, Sri Lanka (7.911525N, 80.382047E, WGS1984; elevation 225 m a.s.l., around 14.00 hrs) on 22 December 2019 by Suranjan Karunarathna.

**Diagnosis.** *Cnemaspis nanayakkarai* sp. nov., can be readily distinguished from its Sri Lankan congeners by a combination of the following morphological and meristic characteristics and also color pattern: maximum SVL 32.6 mm; dorsum with homogeneous, smooth granular scales; 2/2 supranasals, 3 internasals and 1/1 postnasal; 4 enlarged postmentals; postmentals bounded by 6 chin scales; smooth chin and gular scales, granular, juxtaposed (Fig. 8); pectoral and abdominal scales smooth and sub-imbriate; 5 or 6 poorly developed tubercles on posterior flank; 122–131 paravertebral granules linearly arranged; 25–27 belly scales across the venter; precloacal pores absent in males, 7 or 8 femoral pores in males, on each side separated by 20–22 unpored interfemoral scales, 6 or 7 unpored posterior femoral scales; 116–122 ventral scales; 86–99 midbody scales; subcaudals smooth, subhexagonal, enlarged, subequal, forming a regular median row; 7–9 supralabials; 7 or 8 infralabials; 16 or 17 total lamellae on digit IV of manus, and 17 or 18 total lamellae on digit IV of pes. It is also differentiated by its significantly different morphospacial placement in the multivariate analyses.

**Comparisons with other Sri Lankan species.** Among species of the *podihuna* clade, *Cnemaspis nanayakkarai* sp. nov. readily differs from *C. kandambyi*, *C. manaoe*, *C. molligodai* and *C. podihuna* by the absence (vs presence) of precloacal pores, and subhexagonal (vs hexagonal) subcaudals; from *C. anslemi* by the presence of more belly scales (25–27 vs 19–21), more non-pored interfemoral scales (20–22 vs 9 or 10), fewer femoral pores (7 or 8 vs 14 or 15), and fewer lamellae under 4<sup>th</sup> toe (17 or 18 vs 20 or 21); from *C. gemunu* by the presence of a greater number of belly scales (25–27 vs 13–16), greater number of paravertebral granules (122–131 vs 79–93), more non-pored interfemoral scales (20–22 vs 10–12), and fewer

femoral pores (7 or 8 vs 11–14); from *C. godagedarai* by the presence of fewer ventral scales (116–122 vs 133–137), more paravertebral granules (122–131 vs 101–106), more non-pored interfemoral scales (20–22 vs 7–9), fewer femoral pores (7 or 8 vs 12 or 13), and fewer lamellae under 4<sup>th</sup> toe (17 or 18 vs 20 or 21); from *C. jayaweerai* sp. nov. by the presence of a greater number of midbody scales (86–99 vs 70–77), more non-pored interfemoral scales (20–22 vs 15–17), and fewer femoral pores (7 or 8 vs 10 or 11); from *C. phillipsi* by the presence of fewer ventral scales (116–122 vs 128–143), more paravertebral granules (122–131 vs 86–93), more non-pored interfemoral scales (20–22 vs 11–14), and fewer femoral pores (7 or 8 vs 15 or 16); from *C. scalpensis* by the presence of a greater number of belly scales (25–27 vs 17–19), more paravertebral granules (122–131 vs 102–112), more non-pored interfemoral scales (20–22 vs 8–12), fewer flank spines (5 or 6 vs 9–11), and fewer femoral pores (7 or 8 vs 13–15); from *C. alwisi* by the presence of fewer ventral scales (116–122 vs 145–153), more midbody scales (86–99 vs 71–78), more paravertebral granules (122–131 vs 89–97), and a smaller SVL (32.6 mm vs 40.4 mm); from *C. gunasekarai* by the presence of a greater number of belly scales (25–27 vs 20–22), more non-pored interfemoral scales (20–22 vs 15–17), and fewer femoral pores (7 or 8 vs 9 or 10); from *C. gunawardanai* by the presence of fewer ventral scales (116–122 vs 159–162), fewer paravertebral granules (122–131 vs 148–155), fewer lamellae on 4<sup>th</sup> finger (16 or 17 vs 19–21), and fewer lamellae on 4<sup>th</sup> toe (17 or 18 vs 21–23); from *C. hitihamii* by the presence of fewer ventral scales (116–122 vs 132–135), fewer paravertebral granules (122–131 vs 143–149), fewer non-pored interfemoral scales (20–22 vs 24–26), and fewer lamellae on 4<sup>th</sup> toe (17 or 18 vs 21 or 22); from *C. kohukumburai* by the presence of fewer ventral scales (116–122 vs 131–134), fewer paravertebral granules (122–131 vs 150–159), fewer lamellae under 4<sup>th</sup> finger (16 or 17 vs 21 or 22), and fewer lamellae under 4<sup>th</sup> toe (17 or 18 vs 23–25); from *C. nilgala* by the presence of a greater number of belly scales (25–27 vs 17–19), more midbody scales (86–99 vs 71–78), fewer paravertebral granules (122–131 vs 179–187), and greater non-pored interfemoral scales (20–22 vs 14 or 15); from *C. punctata* by the presence of fewer ventral scales (116–122 vs 129–137), more midbody scales (86–99 vs 71–78), more paravertebral granules (122–131 vs 83–91), fewer non-pored interfemoral scales (20–22 vs 25–27), and fewer flank spines (5 or 6 vs 11–13); from *C. rajakarunai* by the presence of fewer infralabials (7 or 8 vs 9–11), fewer ventral scales (116–122 vs 146–186), more midbody scales (86–99 vs 69–74), and more paravertebral granules (122–131 vs 81–85), from *C. rammalensis* by the presence of fewer ventral scales (116–122 vs 186–207), fewer midbody scales (86–99 vs 119–131), more paravertebral granules (122–131 vs 94–96), fewer femoral pores (7 or 8 vs 14–16), fewer lamellae under 4<sup>th</sup> finger (16 or 17 vs 22 or 23), fewer lamellae under 4<sup>th</sup> toe (17 or 18 vs 22 or 23), and a smaller SVL (32.6 mm vs 53.8 mm) respectively.

Among species of the *kandiana* clade, *Cnemaspis nanayakkarai* sp. nov. differs by the presence (vs absence)



**Figure 8.** *Cnemaspis nanayakkarai* sp. nov. male holotype (NMSL.2021.06.01): **A** dorsal aspect of head, **B** lateral aspect of head, **C** ventral aspect of head, **D** homogeneous scales on dorsal surface of trunk, **E** lateral surface of trunk, **F** smooth ventral scales, **G** cloacal characters with only femoral pores, **H** subdigital lamellae of manus, **I** subdigital lamellae of pes, **J** dorsal side of tail, **K** lateral side of tail, **L** large subhexagonal subcaudals. Scale bar: 2 mm. Photos: Suranjan Karunaratna.

of clearly enlarged, subhexagonal subcaudal scales and absence (vs presence) of precloacal pores from the following species: *C. amith*, *C. butewai*, *C. dissanayakai*, *C. gotaimbarai*, *C. ingerorum*, *C. kallima*, *C. kandiana*, *C. kawminiae*, *C. kivulegedarai*, *C. kotagamai*, *C. kumarasinghei*, *C. latha*, *C. lokugei*, *C. menikay*, *C. nandimithrai*,

*C. pava*, *C. pulchra*, *C. retigalensis*, *C. samanalisensis*, *C. silvula*, *C. tropidogaster*, and *C. upendrai*.

**Description of holotype.** An adult male, 32.6 mm SVL, and 35.7 mm TAL. Body somewhat stout, relatively short (TRL/SVL ratio 39.0%). Head relatively small (HL/

SVL ratio 26.1% and HL/TRL ratio 66.9%), very narrow (HW/SVL ratio 14.8% and HW/HL ratio 56.7%), less depressed (HD/SVL ratio 9.5% and HD/HL ratio 36.6%) and distinct from neck. Snout relatively very long (ES/HW ratio 74.0% and ES/HL ratio 41.9%), more than twice the eye diameter (ED/ES ratio 52.8%), more than half length of jaw (ES/JL ratio 62.2%), snout slightly concave in lateral view; eye relatively large (ED/HL ratio 22.1%), less than twice larger than the ear (EL/ED ratio 47.3%), pupil rounded; orbit length greater than eye to ear distance (OD/EE ratio 122.9%) and little longer than digit IV of the manus (OD/DLM IV ratio 103.2%); supraocular ridges not prominent; ear opening relatively large (EL/HL ratio 10.5%), deep, taller than wide, larger than nostrils; 2 rows of scales separate orbit from supralabials; interorbital distance is relatively broad (IO/ES ratio 99.7%), shorter than head length (IO/HL ratio 41.8%); eye to nostril distance greater than the eye to ear distance (EN/EE ratio 122.9%).

Dorsal surface of the trunk with small, smooth, homogeneous granules, 131 paravertebral granules; 122 smooth midventral scales; 88 midbody scales across belly; 6/6 weakly developed, large tubercles on the flanks; ventrolateral scales not enlarged; granules on snout smooth and flat, larger than those on interorbital and occipital regions; canthus rostralis not pronounced, 13/14 smooth oval scales from eye to nostril; scales of the interorbital region round and smooth; ear opening vertically oval, slanting from anterodorsal to posteroventral, 23/21 scales between anterior margin of the ear opening and the posterior margin of the eye. Supralabials 8/9 and infralabials 7/7, becoming smaller towards the gape. Rostral scale longer than wide, partially divided (90%) by a median groove, in contact with first supralabial. Nostrils separated by 2/2 enlarged supranasals with 3 internasal and 1/1 postnasal; no enlarged scales behind the supranasals. Nostrils oval, dorsolaterally orientated, not in contact with first supralabials.

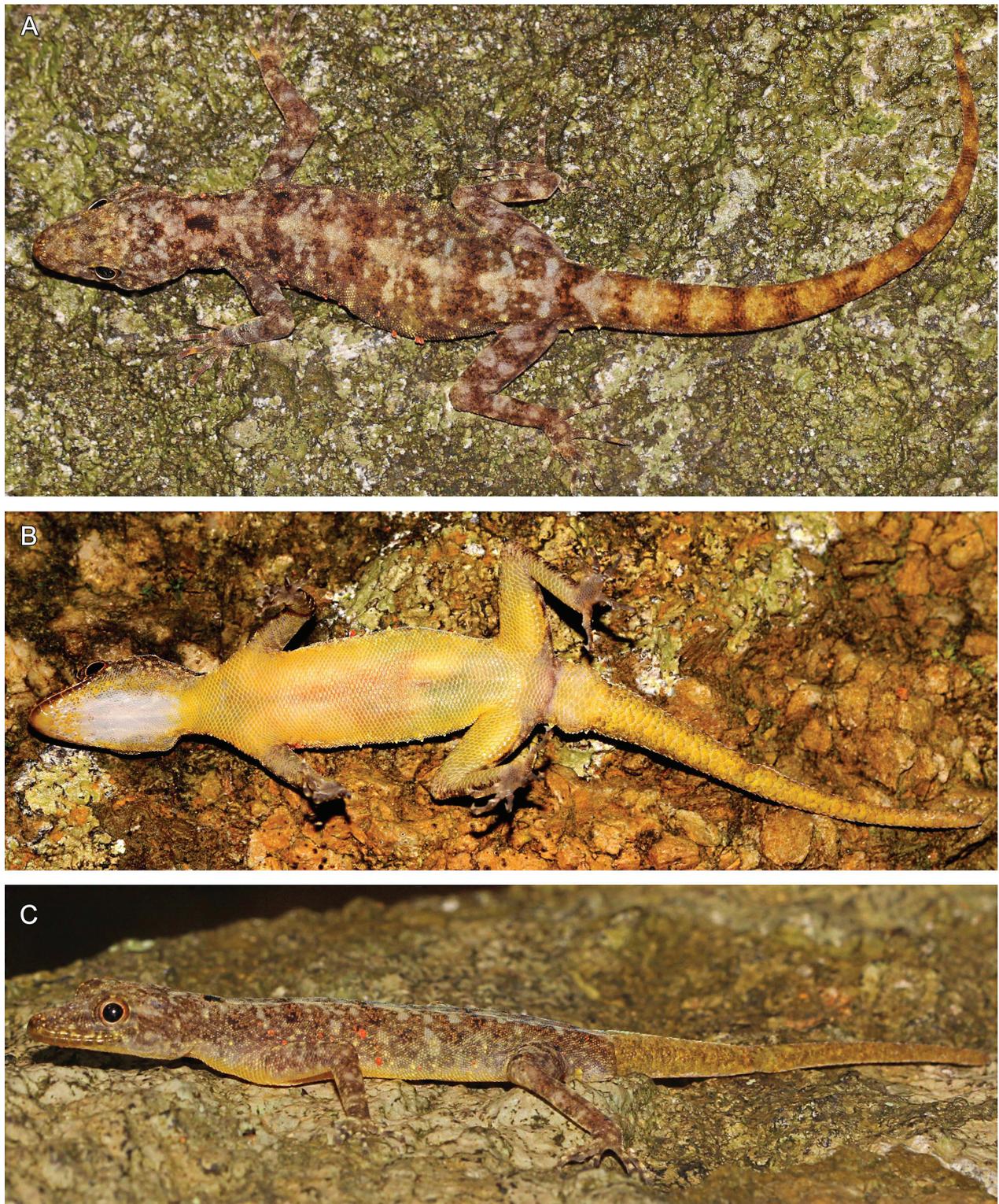
Mental quadriangular, longer than wide, posteriorly in contact with 4 enlarged postmentals (smaller than mental, and larger than chin scales); postmentals contact and bordered posteriorly by 6 smooth chin scales (larger than nostrils), contact with the 1<sup>st</sup> infralabials; ventral scales larger than chin scales, and larger than nostrils. Smooth, rounded, juxtaposed granular scales on chin and gular region; pectoral and abdominal scales smooth, subimbricate towards precloacal region, abdominal scales larger than dorsals; 25 belly scales across venter; smooth, subimbricate scales around base of the tail; 8/7 femoral pores; 22 unpored interfemoral scales; 6/6 large posterior femoral scales. Original tail of holotype longer than snout-vent length (TAL/SVL ratio 109.6%), less spine-like tubercles along tail side, homogeneous scales on the dorsal aspect of the tail directed backwards, tail with 2 or 3 enlarged flattened obtuse scales forming whorls; hemipenial bulge greatly swollen (TBW 3.1 mm), a very small, round post-cloacal spur on each side; smooth subcaudals are arranged into a median series of clearly enlarged, subhexagonal scales.

Forelimbs moderately short, slender, upper arm little longer than lower arm (LAL/SVL ratio 13.3% and

UAL/SVL ratio 14.5%); hind limbs relatively long, tibia shorter than the femur (TBL/SVL ratio 19.1% and FEL/SVL ratio 22.5%). Anterior, dorsal and posterior surfaces of upper arm and lower arms with somewhat keeled scales, ventral surface smooth, those on ventral surface little large than those on other faces of limb. Scales on anterior and posterior surfaces of the femur and tibia somewhat keeled, scales on the dorsal surface granular, ventral surface smooth, anterior surface is twice the size of those of the other parts. Dorsal and ventral scales on the manus and the pes smooth, granular; dorsal surfaces of digits with granular scales. Digits elongate and slender with inflected distal phalanges, all bearing slightly recurved claws. Subdigital lamellae entire (except divided at first interphalangeal joint), unnotched; total lamellae on manus (left/right): digit I (12/11), digit II (14/15), digit III (17/16), digit IV (17/17), digit V (14/13); total lamellae on pes (left/right): digit I (11/12), digit II (15/14), digit III (17/16), digit IV (18/18), digit V (18/17); interdigital webbing absent; length order of digits of left manus: I (1.6 mm), II (1.9 mm), V (2.2 mm), III (2.6 mm), IV (3.1 mm); length order of digits of left pes: I (1.9 mm), II (2.8 mm), V (3.4 mm), III (3.7 mm), IV (4.3 mm).

**Variation of the type series.** The SVL of adult specimens in the type series of *Cnemaspis nanayakkarai* sp. nov. (n = 3) ranges from 30.6 to 32.6 mm; number of supralabials 7–9, and infralabials 7 or 8 (Tables 2–4); spines on flank 5 or 6; interorbital scales 26–33; supraciliaries 15 or 16; canthal scales 12–14; scales from eye to tympanum 20–23; ventral scales 116–122, midbody scales 86–99; paravertebral granules 122–131; belly scales 25–27. Precloacal pores absent in males, femoral pores in males 7 or 8; unpored interfemoral scales in males 20–22, and unpored posterior femoral scales in males 6 or 7. Total lamellae under digits of the manus: digit I (11 or 12), digit II (14 or 15), digit III (16 or 17), digit IV (16 or 17), digit V (12–14); total lamellae under digits of the pes: digit I (11 or 12), digit II (14 or 15), digit III (16 or 17), digit IV (17 or 18), digit V (17 or 18).

**Color of living specimens.** The dorsal color of the head, body and limbs generally grey to brown, with 5–7 paired small black and white paravertebral blotches and 4–6 white crown-like markings along vertebra in both sexes; tail is cinnamon-brown on the dorsum with 12–14 faded cream-white and dark crossbands along its length (Fig. 9); a large blackish nuchal dash present on the head, reticulated pattern on the occipital area, snout yellowish; the pupil circular and black with the surrounding scales reddish brown in both sexes; supraciliaries grey; supralabials and infralabials yellowish and dusted with black; a straight, thin and dark postorbital stripe on either side running towards ear; chin and gular region pure white; throat, pectoral, abdomen, cloacal and subcaudal scales are bright-yellow without dark spots; limbs, pale-yellow ventrally, with white dorsal spots and dark irregular bands dorsally in both sexes; manus and pes with irregular black and white crossbands on dorsum.



**Figure 9.** Body coloration of *Cnemaspis nanayakkarai* sp. nov.: **A** dorsal view in life in-situ of female paratype (NMSL.2021.06.03), **B** ventral aspect of male holotype (NMSL.2021.06.01) showing gular, ventral, and tail coloration, and **C** lateral aspect of male holotype in life in-situ with parasites. Photos: Suranjan Karunaratna.

**Color of preserved specimens.** Dorsum faded brown intermixed with pale crown-like markings; paravertebral blotches distinct light-brown and dirty white spots intermixed; reticulated pattern on the occipital clearly distinct in both sexes; limbs with dark and light dorsal spots; dorsal tail is pale-brown with dark cross bands; chin, gular, pectoral, cloacal and subcaudals dirty white with some

scales on thigh, tail base and arms with irregular dark-brown margins in both sexes.

**Etymology.** The specific epithet (*nanayakkarai*) is a Latinized eponym in the masculine genitive singular, honouring Mr. Ananda Lal Nanayakkara (a senior member and a senior instructor of the reptile study



**Figure 10.** General habitat of *Cnemaspis nanayakkarai* sp. nov. in Galgiriya, Kurunegala District of Sri Lanka: **A** an isolated granite mountain ridge with a dense forest, **B** historic granite cave complex with lots of cracks and holes in a Buddhist monastery, **C** dense canopy cover with humid conditions inside the forest. Photos: Suranjan Karunaratna.

group of the Young Zoologists' Association (YZA) of Sri Lanka; reputed lawyer; policy maker, researcher) for his friendship and valuable contribution to reptile conservation in Sri Lanka.

**Distribution and natural history.** The type locality, Galgiriya (8.0910 to 8.1514N and 80.6246 to 80.6896E), is an isolated mountain range with granite rock outcrop forests dominated by tall shade-bearing trees (e.g. *Hopea brevipedicularis*), belonging to the dry mixed semi-evergreen forest type (Gunatilleke and Gunatilleke 1990). The land area is approximately 1000 ha and situated in the Kurunegala District, North Western Province (dry bioclimatic zone) of Sri Lanka. The mean annual rainfall varies between 1,000 and 1,500 mm, which is received mainly during the northeast monsoon (November–February), but a lesser amount during the southwest monsoon (May–September). The mean annual temperature of the area is 29.2–30.5°C, and its elevational range is 120–550 m a.s.l. Based on our preliminary investigations (22 December 2019, 10 February 2020, and 16 August 2020), *Cnemaspis nanayakkarai* sp. nov. appeared to be common in Galgiriya forest. Our survey of 12 ha revealed 32 ( $\pm 0.2$ ) geckos for 24 man-hours. This species was restricted to granite caves (mainly prehistoric granite caves modified 1,000 years ago by natives) in closed canopy forest, and old buildings associated with

granite caves within the forest (Fig. 10). Furthermore, this species prefers narrow (~7–12 mm), long (~180–450 mm) and deep (~130–210 mm) crevices as hiding places. These microhabitats were poorly illuminated (light intensity: 246–692 Lux), relatively moist (relative humidity: 65–80% and canopy cover: 70–95%) and moderately cool (ambient temperature: 29.5–31.2°C and substrate temperature: 28.2–29.4°C). The new species was sympatric with several other gecko species: *Gehyra mutilata*, *Hemidactylus depressus*, *H. frenatus*, *H. parvimaclulatus*, and *H. triedrus*. Eggs, hatchlings and juveniles were not observed in the habitat, but gravid females were observed in year 2019 and 2020.

**Conservation status.** Application of the IUCN Red List criteria indicates that *Cnemaspis nanayakkarai* sp. nov. is Critically Endangered (CR) due to having an area of occupancy (AOO) <10 km<sup>2</sup> (six locations – single forest block, 0.27 km<sup>2</sup> in total assuming a 100 m radius around each georeferenced location) and an extent of occurrence (EOO) <100 km<sup>2</sup> (1.45 km<sup>2</sup>) in the North Western Province [Applicable criteria B2-b (iii)] (Fig. 7) of Sri Lanka.

## Discussion

Sri Lanka's terrestrial habitats are home to unique assemblages of floral and faunal communities with high endemism (Pethiyagoda and Sudasinghe 2021). It is also one of the smallest biodiversity hotspots in the world (IUCN-SL and MOE-SL 2012). With 244 known reptile species inhabiting the island, reptiles represent a major contributor to Sri Lankan vertebrate diversity. Nonetheless, they are also threatened, mainly due to loss of habitat, climate change, and pollution across all reptile distribution zones (MOMDE 2019; Dayananda et al. 2021). Amongst the diverse reptile fauna of the island, the diversity of geckos (Family Gekkonidae) is remarkable; reaching now 65 species, which accounts for ~27% of the overall reptilian richness. With the inclusion of these two new species described herein, the species richness of *Cnemaspis* rises to 42 (of which 20 species have been described from 1852–2007, and 22 species described from 2008–2023), making it the most species-rich reptile genus of Sri Lanka. The two new species described in this paper have not been included in any previous phylogenies of the genus (Agarwal et al. 2017; Karunaratna et al. 2021).

Taxonomy of the genus *Cnemaspis* recently started to receive special attention with several revisionary attempts providing a more of less detailed subgeneric system for the genus (Bauer et al. 2007; Manamendra-Arachchi et al. 2007; Wickramasinghe and Munindradasa 2007; Vidanapathirana et al. 2014; Wickramasinghe et al. 2016; Agarwal et al. 2017; Batuwita and Udugampala 2017; Batuwita et al. 2019; de Silva et al. 2019; Karunaratna et al. 2019a, 2019b, 2019c, 2021; Karunaratna and Ukuwela 2019; Amarasinghe and Karunaratna 2020; Amarasinghe et al. 2021a; Pal et al. 2021). Molecular phylogenies, based on mitochondrial genes (ND2, Cyt *b*) and nuclear genes have showed that Sri Lankan *Cnemaspis* belong to two unrelated lineages, namely the *kandiana* clade and the *podihuna* clade (Agarwal et al. 2017). The results of phylogenetic analyses comprising only mitochondrial ND2 gene in the current paper and previous studies (Karunaratna et al. 2019c) generally supported results of Agarwal et al. (2017) and Karunaratna et al. (2021). Other notable results of our phylogenetic analyses include phylogenetic placement of *C. molligodai* as sister species to *C. podihuna* (Fig. 1), and of *C. gunasekarai* as sister to *C. alwisi* and the new species from Galgiriya mountain, *C. nanayakkarai* **sp. nov.** Also our results suggest the placement of the new species from Ethagala mountain, *C. jayaweerae* **sp. nov.** as a sister species to a lineage comprising *C. nilgala* and the undescribed species *Cnemaspis* sp. 9 (Fig. 1).

Three species (*C. gunasekarai*, *C. kandambyi* and *C. molligodai*) were described on the sole basis of morphological data, while “*Cnemaspis alwisi*”, which appeared in previous works (Agarwal et al. 2017; Karunaratna et al. 2019c, 2021) under the voucher number AMB7447 has recently been described as *C. gunasekarai* (Amarasinghe et al. 2021a). Our sequences of the specimens from the type locality of *C. alwisi* are notably distinct from AMB7447, so in the present paper

we provide the molecular data for this species for the first time and, on the basis of their genetic distinctiveness, we thus confirm the species-level status of *C. alwisi* (*p*-distances > 8.98%), *C. gunasekarai* (*p*-distances > 9.52%) and *C. molligodai* (*p*-distances > 13.61%). Interestingly, our analysis recovered *C. kandambyi* to be nested within *C. podihuna* (Fig. 1) and this clade was strongly supported (1.0/100). Species delimitation analyses, however indicated that *C. podihuna* comprises four distinct ‘species’ and further validated the species level distinction of *C. kandambyi*. The genetic distinctiveness of these populations was shown to be greater than the proposed species-level divergence threshold of 3.7% for ND2 (Agarwal et al. 2017), and, as we show below, both taxa demonstrated significant morphological differences from all other congeners (Figs 2, 3).

Since the revisions of Agarwal et al. (2017) and Karunaratna et al. (2019c), the number of known Sri Lankan *Cnemaspis* has increased rapidly. The number of described species of the *podihuna* clade for which their phylogenetic placement was confirmed by molecular data arose from six to 14 (Agarwal et al. 2017; Karunaratna et al. 2019c, 2021; present paper). With several lineages with unclear status, the number of species in this clade is likely to increase from 20 in the coming years. Lineages and groupings for Sri Lankan *Cnemaspis* seem to be stable (Agarwal et al. 2017; Karunaratna et al. 2019c) and the current study further emphasises this fact. Currently being the most complete, our reconstruction of phylogenetic relationships between species of the *podihuna* clade is also quite strongly supported. These findings suggest that the mitochondrial ND2 gene to be extremely effective in species recognition and resolving interspecific relationships for this genus.

According to the morphological data and the molecular phylogeny, here we identify four groups (generally shown in phylogenetic tree, see Fig. 1) within the *podihuna* clade: (i) the *alwisi* group consisting of eight species (*C. alwisi*, *C. gunasekarai*, *C. hitihamii*, *C. kohukumburai*, *C. nilgala*, *C. punctata*, *C. jayaweerae* **sp. nov.** and *C. nanayakkarai* **sp. nov.**), (ii) *rammalensis* group consisting of three species (*C. gunawardanai*, *C. rajakarunai*, *C. rammalensis*), (iii) the *podihuna* group consisting of four species (*C. kandambyi*, *C. manoeae*, *C. molligodai* and *C. podihuna*), and (iv) the *scalpensis* group consisting of five species (*C. anslemi*, *C. gemunu*, *C. godagedarai*, *C. phillipsi* and *C. scalpensis*). *Cnemaspis molligodai*, *C. alwisi* and *C. gunasekarai* which were included in the phylogenetic analyses for the first time in the present study were recovered within the *podihuna* clade. This was expected because of their morphological similarity to other members of the *podihuna* clade characterised by the presence of enlarged hexagonal/subhexagonal subcaudal scales, and homogeneous dorsal scales. It is interesting to note the recovery of *C. kandambyi* within *C. podihuna* which rendered the latter paraphyletic. The confirmation from the species delimitation analyses of the presence of four genetically distinct species within *C. podihuna* including *C. kandambyi* may indicate the presence of cryptic species. However, additional samples are necessary to

examine the validity of these putative taxa, given that *C. podihuna* is a widespread species that may comprise several genetically distinct lineages.

The two new species were recovered within the *alwisi* group of the *podihuna* clade (Fig. 1) indicating speciation in the isolated mountains within the dry and intermediate bioclimatic zone of Sri Lanka. Most members of *alwisi* group have a cryptic morphology and coloration, both of which serve as camouflage. Our findings suggest that these geckos prefer narrow (~6–12 mm), long (~120–450 mm), and deep (~80–260 mm) crevices as microhabitats and refugia. Interestingly, the ventral and dorsal coloration of their tails is unique to each species and may serve as intraspecific communication. These crepuscular geckos are mostly rupicolous, found in granite caves, and are occasionally found in old buildings (cement walls or clay bricks walls) associated with granite caves. The members of the *alwisi* group are widely distributed in the dry and intermediate bioclimatic zones (~200–500 m, a.s.l.) with the exception of *C. kohukumburai*, which is recorded from the wet bioclimatic zone which is quite unusual. Remarkably, both the *rammalensis* and *scalpensis* groups are restricted to the wet zone, and the *podihuna* group is found in both the dry and intermediate zones. It is possible and our unpublished data also suggest that the rupicolous species (*alwisi* group) in the *podihuna* clade may have higher speciation rates compared to the arboreal species (*podihuna* group) of this clade, probably due to the isolation in the clustered rocky habitats scattered in the intermediate and dry zones, as well as in the wet bioclimatic zone.

According to the estimations by Agarwal et al. (2021), the *podihuna* clade diverged from other South Asian *Cnemaspis* in the mid-Eocene (~40–50 mya). The clade then went through two independent dispersal events into Sri Lanka and two recent independent dispersals to SE Asia (Agarwal et al. 2020; Pal et al. 2021). The time of divergence in the *alwisi* group was estimated at ~12 mya in mid-Miocene (Agarwal et al. 2017, 2020), and the *in-situ* speciation was probably triggered by the loss of rainforest belt between India and Sri Lanka at that time (Morley 2018; Pethiyagoda and Sudasinghe 2021). Our research shows the distribution and divergence of the *alwisi* group has taken place along the 500 meter contour in Sri Lanka, and further emphasize the importance of isolated misty-mountains (Fig. 7). Recent studies (Agarwal et al. 2020; Pal et al. 2021) indicate that South Asian species of *Cnemaspis* originated in the rainforests of Western Ghats during the Eocene–Paleocene (~50–60 mya), and diversification is believed to have happened in the late Paleocene (~30–40 mya) and Miocene (23–25 mya) during a period of global warming. At that time, lowland rainforests of Malaysia, Philippines, India, Seychelles, Africa, Indonesia, and Sri Lanka were dominated by tree species of the family Dipterocarpaceae (Ashton and Gunatilleke 1987; Rust et al. 2010).

A few species of Dipterocarpaceae (e.g. *Hopea* sp. and *Vatica* sp.) that usually dominate the rainforest flora of Sri Lanka are found in several small isolated mountains (~400 m asl.) in the dry and intermediate bioclimat-

ic zones of Sri Lanka. Soil erosion and weathering are believed to have contributed greatly to the isolation of these dry and intermediate zone mountains from central highlands and shaping these forest types with their unique biodiversity (Karunaratna et al. 2021; Pethiyagoda and Sudasinghe 2021) in this bioclimatic region. These isolated mountains are usually covered with mist after 1700 hrs to early morning (ca. 0800 hrs) most of the year, and therefore, the forests in these mountains maintain wet microclimates which are well suited for moisture dependant herpetofauna as well as other faunal groups (Amarasinghe et al. 2021a; Karunaratna et al. 2019c). However, these moist microclimates are not found on isolated mountains that do not reach 300 m in elevation in the dry and intermediate bioclimatic zones, and most of them have dry conditions with low faunal diversity.

Almost all species of the *alwisi* group are found within relatively cool, moist habitats (substrate temperature: 25–29°C; relative humidity: 70–90%), which are well shaded (canopy cover: 60–90%; light intensity: 380–850 Lux) and have high-profile mature trees. The species in the *alwisi* group are point-endemic microhabitat specialists where distribution ranges are limited to <20 km<sup>2</sup>. Our studies suggest the possibility of speciation of *alwisi* group (currently comprising eight species) found in geographically isolated mountains with granite caves, rock outcrops and favourable environmental conditions; we therefore predict that the number of species will likely increase to more than 16 species in total. The high species richness of *Cnemaspis* in Sri Lanka may be accounted by the possibility of multiple, independent colonization events from the Indian mainland with subsequent, geographically-isolated *in-situ* speciation (Agarwal et al. 2020; Pal et al. 2021; Pethiyagoda and Sudasinghe 2021). It is also interesting to note that species like *C. alwisi* have genetically distinct populations on either sides of the mountains on which they occur (Fig. 1). Such findings need further investigation and may suggest the low dispersability of these small geckos, which prefer specific microhabitats.

Ethagala and Galgiriya are isolated misty-mountains and rock outcrops embedded within forest habitats having granite caves incorporated with historical Buddhist monasteries. These forest habitats with Buddhist monasteries serve as refugia for reptiles and other faunal groups, and it is imperative to conserve these habitats. Consequently, out of the 42 *Cnemaspis* species occurring in Sri Lanka, 35 (~84%) species are found inside Buddhist monasteries with granite caves (Manamendra-Arachchi et al. 2007; Wickramasinghe et al. 2016; Karunaratna et al. 2019c, Amarasinghe et al. 2021a). It is very likely that future studies on the biogeography of *alwisi* group in Sri Lanka will highlight the importance of these isolated habitats in generating and maintaining the diversity of these unique groups of geckos on the island. At the same time, it is important to note that the point-endemic and range-restricted species described herein, which are highly sensitive to changes in the habitat, would be severely affected by habitat degradation. Hence, past and present studies have emphasized the importance of conserving such iso-

lated habitats throughout the country (Amarasinghe et al. 2021b). All these isolated habitats are susceptible to human-induced habitat degradation, including clear cutting and timber felling, forest fragmentation, granite mining, rubber cultivation, irresponsible vegetable farming, invasive species, human settlements, road and other infrastructure development, and waste disposal. It is evident that conservation of isolated misty mountains is crucial in conservation of the unique fauna and flora of the island. It is also imperative to inform the general public, educators, natural resource and land managers, and private entrepreneurs about environmental legislation through printed and electronic media and outreach activities (Karunaratna et al. 2017a, 2017b).

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## Appendix 1

### Comparative material examined from Sri Lankan species

- Cnemaspis alwisi*: NMSL 2004.09.01 (holotype), NMSL 2004.09.02 (paratype), NMSL 2004.09.03 (paratype), WHT 5918, WHT 6518, WHT 6519, WHT 7336, WHT 7337, WHT 7338, WHT 7343, WHT 7344, WHT 7345, WHT 7346, including 12 uncatalogued specimens.
- C. anslemi*: NMSL 2019.14.01 (holotype), NMSL 2019.14.02 (paratype), NMSL 2019.14.03 (paratype), including 3 uncatalogued specimens.
- C. amith*: BMNH 63.3.19.1066A (holotype), BMNH 63.3.19.1066B (paratype), BMNH 63.3.19.1066C (paratype).
- C. butewai*: NMSL 2019.07.01 (holotype), NMSL 2019.07.02 (paratype), NMSL 2019.07.03 (paratype), including 5 uncatalogued specimens.
- C. dissanayakai*: NMSL 2019.20.01 (holotype), NMSL 2019.20.02 (paratype), NMSL 2019.20.03 (paratype), including 2 uncatalogued specimens.
- C. gemunu*: AMB 7495 (holotype), AMB 7507 (paratype??), WHT 7221, WHT 7347, WHT 7348, NMSL 2006.11.01, NMSL 2006.11.02, NMSL 2006.11.03, NMSL 2006.11.04, including 7 uncatalogued specimens.
- C. godagedarai*: NMSL 2019.09.01 (holotype), NMSL 2019.16.01 (paratype), NMSL 2019.16.02 (paratype), including 2 uncatalogued specimens.
- C. gotaimbarai*: NMSL 2019.04.01 (holotype), NMSL 2019.04.02 (paratype), NMSL 2019.04.03 (paratype), including 4 uncatalogued specimens.
- C. gunasekarai*: NMSL 2019.17.01 (holotype), NMSL 2019.17.02 (paratype), NMSL 2019.17.03 (paratype), including 3 uncatalogued specimens.
- C. gunawardanai*: NMSL 2021.05.01 (holotype), NMSL 2021.05.02 (paratype), including 2 uncatalogued specimens.
- C. hitihamii*: NMSL 2019.06.01 (holotype), NMSL 2019.06.02 (paratype), NMSL 2019.06.03 (paratype), including 9 uncatalogued specimens.
- C. ingerorum*: WHT 7332 (holotype), WHT 7330 (paratype) WHT 7331 (paratype), including 4 uncatalogued specimens.
- C. kallima*: WHT 7245 (holotype), WHT 7222 (paratype), WHT 7227 (paratype), WHT 7228 (paratype), WHT 7229 (paratype), WHT 7230 (paratype), WHT 7239 (paratype), WHT 7249 (paratype), WHT 7251 (paratype), WHT 7252 (paratype), WHT 7253 (paratype), WHT 7254 (paratype), WHT 7255 (paratype), including 5 uncatalogued specimens.
- C. kandambyi*: WHT 9466 (holotype), WHT 9467 (paratype), including 7 uncatalogued specimens.
- C. kandiana*: BMNH 53.4.1.1 (lectotype), BMNH 80.2.2.119A (paralectotype), BMNH 80.2.2.119B (paralectotype), BMNH 80.2.2.119C (paralectotype), WHT 7212, WHT 7213, WHT 7267, WHT 7305, WHT 7307, WHT 7308, WHT 7310, WHT 7313, WHT 7319, WHT 7322, including 15 uncatalogued specimens.
- C. kawminiae*: NMSL 2019.18.01 (holotype), NMSL 2019.18.02 (paratype), NMSL 2019.18.03 (paratype), including 6 uncatalogued specimens.
- C. kivulegedarai*: NMSL 2019.08.01 (holotype), NMSL 2019.08.02 (paratype), NMSL 2019.08.03 (paratype), including 7 uncatalogued specimens.
- C. kohukumburai*: NMSL 2019.05.01 (holotype), NMSL 2019.05.02 (paratype), NMSL 2019.05.03 (paratype), including 4 uncatalogued specimens.
- C. kotagamai*: NMSL 2019.15.01 (holotype), NMSL 2019.15.02 (paratype), NMSL 2019.15.03 (paratype), including 7 uncatalogued specimens.
- C. kumarasinghei*: NMSL 2006.13.01 (holotype), NMSL 2006.13.02 (paratype), including 10 uncatalogued specimens.
- C. latha*: WHT 7214 (holotype), including 5 uncatalogued specimens.
- C. lokugei*: NMSL 2021.01.01 (holotype), NMSL 2021.01.02 (paratype), NMSL 2021.01.03 (paratype), including 5 uncatalogued specimens.

- C. manoa*: NMSL 2019.10.01 (holotype), NMSL 2006.10.02 (paratype), NMSL 2006.10.03 (paratype), including 9 uncatalogued specimens.
- C. menikay*: WHT 7219 (holotype), WHT 7218 (paratype), WHT 7349 (paratype), including 14 uncatalogued specimens.
- C. molligodai*: NMSL 2006.14.01 (holotype), NMSL 2006.14.02 (paratype), NMSL 2006.14.03 (paratype), NMSL 2006.14.04 (paratype), NMSL 2006.14.05 (paratype), including 7 uncatalogued specimens.
- C. nandimithrai*: NMSL 2019.03.01 (holotype), NMSL 2019.03.02 (paratype), NMSL 2019.03.03 (paratype), including 4 uncatalogued specimens.
- C. nilgala*: NMSL 2018.07.01 (holotype), NMSL 2018.06.01 (paratype), NMSL 2018.06.02 (paratype), NMSL 2018.06.03 (paratype), including 18 uncatalogued specimens.
- C. pava*: WHT 7286 (holotype), WHT 7281 (paratype), WHT 7282 (paratype), WHT 7283 (paratype), WHT 7285 (paratype), WHT 7288 (paratype), WHT 7289 (paratype), WHT 7290 (paratype), WHT 7291 (paratype), WHT 7292 (paratype), WHT 7293 (paratype), WHT 7294 (paratype), WHT 7295 (paratype), WHT 7296 (paratype), WHT 7297 (paratype), WHT 7298 (paratype), WHT 7299 (paratype), WHT 7300 (paratype), WHT 7301 (paratype), WHT 7302 (paratype), including 5 uncatalogued specimens.
- C. phillipsi*: WHT 7248 (holotype), WHT 7236 (paratype); WHT 7237 (paratype); WHT 7238 (paratype), including 8 uncatalogued specimens.
- C. podihuna*: BMNH 1946.8.1.20 (holotype), NMSL 2006.10.02, NMSL 2006.10.03, NMSL 2006.10.04, including 15 uncatalogued specimens.
- C. pulchra*: WHT 7023 (holotype), WHT 1573a (paratype), WHT 7011 (paratype), WHT 7021 (paratype), WHT 7022 (paratype), including 9 uncatalogued specimens.
- C. punctata*: WHT 7256 (holotype), WHT 7223 (paratype), WHT 7226 (paratype), WHT 7243 (paratype), WHT 7244 (paratype), including 11 uncatalogued specimens.
- C. rajakarunai*: NMSL 2016.07.01 (holotype), DWC 2016.05.01 (paratype), DWC 2016.05.02 (paratype), including 8 uncatalogued specimens.
- C. rammalensis*: NMSL 2013.25.01 (holotype), DWC 2013.05.001, including 4 uncatalogued specimens.
- C. retigalensis*: NMSL 2006.12.01 (holotype), NMSL 2006.12.02 (paratype), NMSL 2006.12.03 (paratype), NMSL 2006.12.04 (paratype), including 5 uncatalogued specimens.
- C. samanalis*: NMSL 2006.15.01 (holotype), NMSL 2006.15.02 (paratype), NMSL 2006.15.03 (paratype), NMSL 2006.15.04 (paratype), NMSL 2006.15.05 (paratype), including 12 uncatalogued specimens.
- C. scalpens*: NMSL 2004.01.01 (neotype), NMSL 2004.02.01, NMSL 2004.03.01, NMSL 2004.04.01, WHT 7265, WHT 7268, WHT 7269, WHT 7274, WHT 7275, WHT 7276, WHT 7320, including 3 uncatalogued specimens.
- C. silvula*: WHT 7208 (holotype), WHT 7206 (paratype), WHT 7207 (paratype), WHT 7209 (paratype), WHT 7210 (paratype), WHT 7216 (paratype), WHT 7217 (paratype), WHT 7018, WHT 7027, WHT 7202, WHT 7203, WHT 7220, WHT 7354, WHT 7333, including 2 uncatalogued specimens.
- C. tropidogaster*: BMNH 71.12.14.49 (lectotype), NMSL 5152, NMSL 5151, NMSL 5159, NMSL 5157, NMSL 5970, NMSL 5974, including 3 uncatalogued specimens.
- C. upendrai*: WHT 7189 (holotype), WHT 7184 (paratype), WHT 7187 (paratype), WHT 7188 (paratype), WHT 7181 (paratype), WHT 7182 (paratype), WHT 7183 (paratype), WHT 7185 (paratype), WHT 7190 (paratype), WHT 7191 (paratype), WHT 7192 (paratype), WHT 7193 (paratype), WHT 7194 (paratype), WHT 7195 (paratype), WHT 7196 (paratype), WHT 7197 (paratype), WHT 7260 (paratype), including 2 uncatalogued specimens.

## Supplementary material 1

### Figure S1

**Authors:** Karunarathna S, Ukuwela KDB, De Silva A, Bauer AM, Madawala M, Poyarkov NA, Botejue M, Gabadage D, Grismer LL, Gorin VA (2023)

**Data type:** .pdf

**Explanation notes:** Bayesian inference tree of south Asian *Cnemaspis* lineage with BI PP and ML BS values. The black circles at nodes correspond to BI PP and ML BS support values greater than 0.95 and 70 respectively. Colours of the branches indicates the geographical origin of the taxa where green, blue and brown indicate Sri Lankan, Indian and Southeast Asian taxa respectively.

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**Link:** <https://doi.org/10.3897/vz.73.e90979.suppl1>

## Supplementary material 2

### Table S1

**Authors:** Karunarathna S, Ukuwela KDB, De Silva A, Bauer AM, Madawala M, Poyarkov NA, Botejue M, Gabadage D, Grismer LL, Gorin VA (2023)

**Data type:** .xlsx

**Explanation notes:** Specimens, voucher numbers and GenBank accession numbers of the taxa used for phylogenetic analyses and the DNA-based species delimitation in this study (AA – Rohan Pethiyagoda field series, ADS – An-slem de Silva field series, AMB – Aaron M. Bauer field series, SSK and DMSSK – Suranjan Karunarathna field series, NMSL – National Museum Sri Lanka, and WHT – Wildlife Heritage Trust).

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**Link:** <https://doi.org/10.3897/vz.73.e90979.suppl2>

## Supplementary material 3

### Table S2

**Authors:** Karunarathna S, Ukuwela KDB, De Silva A, Bauer AM, Madawala M, Poyarkov NA, Botejue M, Gabadage D, Grismer LL, Gorin VA (2023)

**Data type:** .xls

**Explanation notes:** Summary statistics from the ANOVA and TukeyHSD post hoc analyses of the normalized morphometric data.

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**Link:** <https://doi.org/10.3897/vz.73.e90979.suppl3>

## Supplementary material 4

### Table S3

**Authors:** Karunarathna S, Ukuwela KDB, De Silva A, Bauer AM, Madawala M, Poyarkov NA, Botejue M, Gabadage D, Grismer LL, Gorin VA (2023)

**Data type:** .xlsx

**Explanation notes:** Summary statistics from the ANOVA and TukeyHSD post hoc analyses of the meristic data.

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**Link:** <https://doi.org/10.3897/vz.73.e90979.suppl4>

## Supplementary material 5

### Table S4

**Authors:** Karunaratna S, Ukuwela KDB, De Silva A, Bauer AM, Madawala M, Poyarkov NA, Botejue M, Gabadage D, Grismer LL, Gorin VA (2023)

**Data type:** .xlsx

**Explanation notes:** Pairwise matrices of species bearing characters with significantly different mean values of those of *Cnemaspis jayaweerae* **sp. nov.** and *C. nanayakkarai* **sp. nov.**

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**Link:** <https://doi.org/10.3897/vz.73.e90979.suppl5>

## Supplementary material 6

### Table S5

**Authors:** Karunaratna S, Ukuwela KDB, De Silva A, Bauer AM, Madawala M, Poyarkov NA, Botejue M, Gabadage D, Grismer LL, Gorin VA (2023)

**Data type:** .xlsx

**Explanation notes:** Average uncorrected pairwise genetic distance between Sri Lankan and Indian *Cnemaspis* species.

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**Link:** <https://doi.org/10.3897/vz.73.e90979.suppl6>