



Two new species of South Asian *Cnemaspis* Strauch, 1887 (Squamata: Gekkonidae) from the Gingee Hills, Tamil Nadu, India

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<https://zoobank.org/28B74482-219B-4F3E-B3A0-086DA17CA02B>

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Academic editor Uwe Fritz

Received 3 August 2023

Accepted 20 September 2023

Published 2 October 2023

Citation: Khandekar A, Thackeray T, Kalaimani A, Agarwal I (2023) Two new species of South Asian *Cnemaspis* Strauch, 1887 (Squamata, Gekkonidae) from the Gingee Hills, Tamil Nadu, India. *Vertebrate Zoology* 73 887–913. <https://doi.org/10.3897/vz.73.e110512>

Abstract

We describe two new small-bodied, sympatric species of south Asian *Cnemaspis* belonging to the *mysoriensis* + *adii* clade from the Gingee Hills in Tamil Nadu, peninsular India. The two new species can be easily distinguished from the other eight described members of the *mysoriensis* + *adii* clade by their dorsal pholidosis, the configuration of femoral and preloacal pores in males, a number of meristic characters and subtle differences in colouration, beside 6.7–20.8 % uncorrected pairwise ND2 sequence divergence. The two species represent different ecomorphs, one a stouter, microhabitat generalist and the other a more slender, elongate rock specialist. The discovery of two new species from granite boulder habitats and Tropical Dry Evergreen Forests is indicative of the importance of these areas for biodiversity. It is likely that similar rocky habitats across southern peninsular India will harbour many more undescribed species.

Keywords

Endemic species, granite boulders, integrative taxonomy, micro-endemism, southern India

Introduction

South Asian *Cnemaspis* Strauch, 1887 (SAC) is an ancient, diverse radiation of gekkonid lizards with a Western Ghats origin, including >130 species distributed in peninsular India, northeast India, Sri Lanka, and in and around the Andaman Sea (Agarwal et al. 2020c, 2021a; Pal et al. 2021; Uetz et al. 2023). Mitochondrial phylogenies of the group reveal the presence of 13 broad clades: two in Sri Lanka (*kandiana* which includes the Andaman Sea subclade, and *podihuna*), *assamensis* in lowland northeast India, and ten in peninsular India (Agarwal et

al. 2020c, 2021a; Pal et al. 2021). The center of diversity in peninsular India is the cool Western Ghats region, where eight clades are represented (Agarwal et al. 2020c; Pal et al. 2021). Warmer, more arid habitats outside the Western Ghats include three clades of SAC: *bangara*, comprising four species distributed in and around the southern edge of the Mysore Plateau; *mysoriensis* + *adii*, including eight species distributed across the Mysore Plateau and hills off the southeastern edge of the Mysore Plateau (Fig. 1); and *gracilis* which includes 10 species

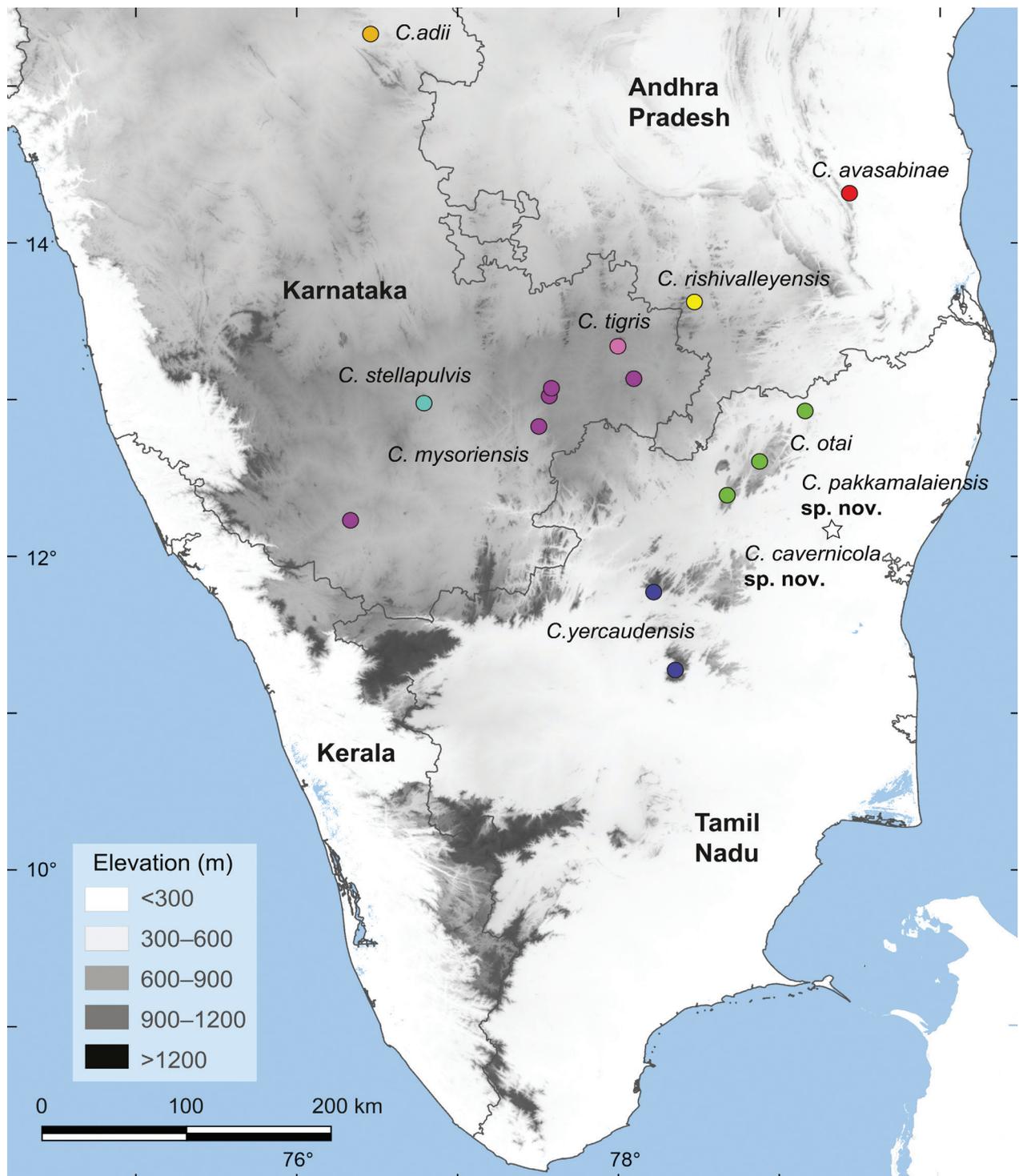


Figure 1. Elevational map of peninsular India showing our sampling of the *mysoriensis* + *adii* clade which includes typical or to-topotypical for all species.

outside the Western Ghats and three distributed in the Palghat Gap and the eastern slopes of the Western Ghats (Srinivasulu et al. 2015; Khandekar 2019; Khandekar et al. 2019, 2022; Agarwal et al. 2020c, 2022; Sayyed et al. 2023). The species *Cnemaspis umashaankeri* Narayanan & Aravind, 2022 from the Biligiri Rangan Hills, Karnataka is morphologically similar to members of the *gracilis* clade, with sexual dimorphism, but its relationships with other SAC clades are not well resolved (Narayanan and Aravind 2022).

Cnemaspis mysoriensis (Jerdon, 1853) was the only species known from peninsular India outside the Western Ghats till the turn of the century, when Das and Bauer (2000) described *C. otai* Das & Bauer, 2000 and *C. yercaudensis* Das & Bauer, 2000 from Tamil Nadu. An additional 16 species have been described from the region since, including five from the *mysoriensis* + *adii* clade (Srinivasulu et al. 2015; Khandekar 2019; Khandekar et al. 2020, 2022; Agarwal et al. 2022; Narayanan et al. 2023a). *Cnemaspis adii* Srinivasulu, Kumar & Srin-

vasulu, 2015 is the northernmost representative of the clade from Hampi, Karnataka; *C. avasabinae* Agarwal, Bauer & Khandekar, 2020 from the Velikonda Range of Andhra Pradesh the easternmost; *C. mysoriensis* is relatively widely distributed around Bangalore, Karnataka; *C. otai* is known from Vellore and the Jawadhu Hills; *C. rishivalleyensis* Agarwal, Thackeray & Khandekar, 2020 and *C. tigris* Khandekar, Thackeray & Agarwal, 2022 from the east of the Mysore Plateau and *C. stellapulvis* Khandekar, Thackeray & Agarwal, 2020 from the west of the Mysore Plateau; and *C. yercaudensis* is known from high elevations of Kollimalai and Yercaud (Das and Bauer 2000; Agarwal et al. 2020a, 2020b; Khandekar et al. 2020).

The *mysoriensis* + *adii* clade began diversifying in the late Oligocene to early Miocene, indicating a long history outside the Western Ghats (Agarwal et al. 2020c). All the species in the *mysoriensis* + *adii* clade are associated with granite boulders, and the Mysore Plateau or other upland areas, a combination of which has allowed them to persist in the warmest habitats occupied by any SAC (Agarwal et al. 2020c). As part of a larger project on the lizards of Tamil Nadu, we sampled Pakkamalai, Gingee Hills, Viluppuram District, during which time we collected two sympatric species of small-bodied *Cnemaspis*. One lineage is morphologically allied to *C. adii* and the other to *C. otai*. We describe these two lineages as new species based on morphology, with the mitochondrial ND2 gene confirming their distinctiveness.

Materials and methods

Taxon sampling

Specimens were hand-collected and euthanized using isoflurane and liver tissues or tail tips of 1–3 individuals and one or two entire juveniles of each new species were collected in molecular grade ethanol and subsequently stored at -20°C for genetic analysis. Specimens were fixed in 8% formaldehyde for ~12 hours, washed in water and transferred to 70% ethanol for long-term storage. Specimens are deposited in the Museum and Research Collection Facility at National Centre for Biological Sciences, Bengaluru (NRC-AA).

Molecular data and analyses

We extracted whole genomic DNA from a total of eight tissue samples of the two new species (Table 1) using the Qiagen DNeasy Blood & Tissue Kit. We generated sequences for the mitochondrial ND2 gene using the primers L4437 + H5540/ H5934 (Macey et al. 1997) with PCR and sequencing carried out by Barcode Biosciences, Bangalore. Bidirectional sequences were assembled in MEGA 5.2 (Tamura et al. 2011) and combined with 40 published sequences for the *mysoriensis* + *adii* clade and represen-

tatives of other South Asian *Cnemaspis* (after Khandekar et al. 2022; Table 1). Sequence alignment was carried out using default settings in ClustalW (Thompson et al. 1994) and uncorrected pairwise sequence divergence with the pairwise deletion option calculated in MEGA. A partitioned Maximum Likelihood analysis was carried out on the IQTREE webserver (Nguyen et al. 2015; Trifinopoulos et al. 2016), with partitioning scheme and substitution models selected in ModelFinder (Kalyaanamoorthy et al. 2017) that partitioned the data by codon position with the TVM+F+I+G4, TIM3+F+G4, and TIM+F+I+G4 models for positions 1–3). Analysis parameters were at default settings including edge-linked partitions and bootstrap support (BS) evaluated with 1000 ultrafast bootstraps (Hoang et al. 2018). We ran a partitioned Bayesian analysis in MrBayes 3.2 (Ronquist and Huelsenbeck 2003) using the best-fit models and partitions from ModelFinder (TIM and TVM were replaced with GTR). Analyses were run for 1,000,000 generations, sampling every 100 generations, with two parallel runs and four chains each (one cold and three hot). Convergence was determined based on the standard deviation of split frequencies ($<<0.01$) and ESS (>200), and a consensus tree built using the sumt command with the first 25% of trees discarded as burn-in.

We did not conduct any explicit species delimitation analyses but use the 3.7 % ND2 p-distance cutoff suggested by Agarwal et al. (2017) as well as the lowest divergence between described species of the *mysoriensis* + *adii* clade as indicative of species-level divergence.

Morphological and meristic data

Morphological data were collected from a total of 11 specimens of the two new species. We restricted comparisons to the *mysoriensis* + *adii* clade as molecular data placed the two lineages within this clade and no other *Cnemaspis* clades occur close to the Gingee Hills. Comparative morphological data of all other members of the *mysoriensis* + *adii* clade were obtained from the specimens listed in Appendix 1 as well as published literature (Srinivasulu et al. 2015; Agarwal et al. 2020a, 2020b; Khandekar et al. 2020, 2022). Counts and measurements were taken under a ZEISS Stemi 305 stereo dissecting microscope and on the left side of the body where possible. Colour pattern was recorded from photographs taken in life and measurements were taken with a Mitutoyo digital vernier calliper (to the nearest 0.1 mm). We follow Agarwal et al. (2020c) for body size categories for South Asian *Cnemaspis*; and Khandekar et al. (2022) for mensural, meristic and additional morphological character states which include the following measurements: snout vent length (SVL), tail length (TL), tail width (TW), forearm length (FL), crus length (CL), axilla to groin length (AGL), body height (BH), body width (BW), head length (HL), head width (HW), head depth (HD), eye diameter (ED), eye to ear distance (EE), eye to snout distance (ES), eye to nares distance (EN), internarial distance (IN), interorbital distance (IO), ear length (EL). Meristic data recorded for all specimens were number of supralabials (SL),

Table 1. List of *Cnemaspis* sequences used in this study (sequences generated in this study marked by *). Museum abbreviations are as follows: BNHS, Bombay Natural History Society; AK/AK-R, Akshay Khandekar field series; VG, Varad Giri field series; CES, Centre for Ecological Sciences, Bangalore; NRC-AA, National Centre for Biological Sciences; AA, Rohan Pethiyagoda field series; SB, Sayantan Biswas field series; USNM, United States National Museum; ZSI-R, Zoological Survey of India, Kolkata.

Species	Voucher	Locality	GenBank Accession number
<i>C. adii</i>	BNHS 2494	India, Karnataka, Ballari District, Hampi	MT188142
<i>C. agarwali</i>	AK 107	India, Tamil Nadu, Salem District, Sankari	MK792466
<i>C. amboliensis</i>	VG 394	India, Maharashtra, Sindhudurg District, Amboli	MK792481
<i>C. cf. assamensis</i>	BNHS 2808	India, Meghalaya, Ri Bhoi District, Saiden	MW3674
<i>C. avasabinae</i>	CES G416	India, Andhra Pradesh, Nellore District, Penchalakona	MT773207
<i>C. azhagu</i>	NRC-AA-1172 (AKR 671)	India, Tamil Nadu, Tirunelveli District, Thirukurungudi forest range	ON494554
<i>C. bangara</i>	BNHS 2584 (AK 292)	India, Karnataka, Kolar District, Paparajanahalli	MT188143
<i>C. cavernicola</i> sp. nov.	AK-R 134	India, Tamil Nadu, Viluppuram District, Pakkamalai RF	OR415867*
<i>C. cavernicola</i> sp. nov.	NRC-AA-1286 (AK-R 2339)	India, Tamil Nadu, Viluppuram District, Pakkamalai RF	OR415868*
<i>C. cavernicola</i> sp. nov.	NRC-AA-1287 (AK-R 135)	India, Tamil Nadu, Viluppuram District, Pakkamalai RF	OR415869*
<i>C. cavernicola</i> sp. nov.	NRC-AA-1289 (AK-R 2340)	India, Tamil Nadu, Viluppuram District, Pakkamalai RF	OR415870*
<i>C. cavernicola</i> sp. nov.	AK-R 2343	India, Tamil Nadu, Viluppuram District, Pakkamalai RF	OR415871*
<i>C. flaviventralis</i>	VG 354	India, Maharashtra, Sindhudurg District, Amboli	MK792495
<i>C. goaensis</i>	VG 385	India, Karnataka, Uttara Kannada District, Gund	MK792475
<i>C. gracilis</i>	CES G385	India, Kerala, Palakkad District, near Chittur River	MK792465
<i>C. graniticola</i>	BNHS 2589 (CES L839)	India, Andhra Pradesh, Chittoor District, Horsley hills	MT188145
<i>C. indica</i>	CES L291	India, Tamil Nadu, Nilgiris	MZ701810
<i>C. kallima</i>	AA 82	Sri Lanka, Matale District, Rattota, Gammaduwa	KY037970
<i>C. kolhapurensis</i>	unvouchered	India, Maharashtra, Kolhapur District, Dajipur	MK792501
<i>C. koynaensis</i>	CES G349	India, Maharashtra, Satara District, Humbarli	MK792490
<i>C. littoralis</i>	SB 151	India, Kerala, Thrissur District, Athirappilly Falls	KY038013
<i>C. magnifica</i>	unvouchered	India, Karnataka, Hassan District, Sakleshpur	MK792503
<i>C. mysoriensis</i>	unvouchered	India, Karnataka, Bangalore Urban District, IISc Campus	MK792474
<i>C. mysoriensis</i>	AK 570	India, Karnataka, Bangalore Urban District, NCBS Campus	MT773208
<i>C. mysoriensis</i>	AK 676	India, Karnataka, Mysore District, Hunsur	MT773209
<i>C. mysoriensis</i>	AK 851	India, Karnataka, Kolar District, Kolar	MT773210
<i>C. mysoriensis</i>	AK 852	India, Karnataka, Kolar District, Kolar	MT773211
<i>C. mysoriensis</i>	AK 979	India, Karnataka, Bangalore Rural District, near Thathaguni	MT773212
<i>C. otai</i>	AK 668	India, Tamil Nadu, Vellore District, Vellore Fort	MT188146
<i>C. otai</i>	AK 823	India, Tamil Nadu, Vellore District, Jawadhu Hills	MT773213
<i>C. otai</i>	AK 935	India, Tamil Nadu, Vellore District, Jawadhu Hills	MT773214
<i>C. pakkamalaiensis</i> sp. nov.	AK-R 121	India, Tamil Nadu, Viluppuram District, Pakkamalai RF	OR415864*
<i>C. pakkamalaiensis</i> sp. nov.	NRC-AA-1284 (AK-R 2344)	India, Tamil Nadu, Viluppuram District, Pakkamalai RF	OR415865*
<i>C. pakkamalaiensis</i> sp. nov.	NRC-AA-1285 (AK-R 122)	India, Tamil Nadu, Viluppuram District, Pakkamalai RF	OR415866*
<i>C. punctata</i>	AA 80	Sri Lanka, Matale District, Rattota, Gammaduwa	KY038007
<i>C. rishivalleyensis</i>	AK 659	India, Andhra Pradesh, Chittoor District, Rishi Valley School	MT773218
<i>C. rishivalleyensis</i>	AK 660	India, Andhra Pradesh, Chittoor District, Rishi Valley School	MT773219
<i>C. rubraoculus</i>	CES L114	India, Kerala, Idukki District, Upper Manalar	ON494559
<i>C. cf. schalleri</i>	SB 048	India, Karnataka, Kodagu District, Kumarahalli	KY037995
<i>C. stellapulvis</i>	AK 846	India, Karnataka, Mandya District, Yadiyur	MT773215
<i>C. stellapulvis</i>	AK 847	India, Karnataka, Mandya District, Yadiyur	MT773216
<i>C. thayawthadangyi</i>	USNM 595052	Myanmar, Tanintharyi Region, Myeik Archipelago, southeast side of Linn Lune Kyun	MN104950
<i>C. tigris</i>	NRC-AA-1160 (AK 884)	India, Karnataka, Chickballapur District, Kaiwara	OK424590
<i>C. tigris</i>	NRC-AA-1159 (AK 885)	India, Karnataka, Chickballapur District, Kaiwara	OK424591

Species	Voucher	Locality	GenBank Accession number
<i>C. umashaankeri</i>	BNHS 3127	India, Karnataka, Chamarajnagar District, BR Hills	OP358455
<i>C. umashaankeri</i>	ZSI-R-28301	India, Karnataka, Chamarajnagar District, BR Hills	OP358454
<i>C. vijayae</i>	BNHS 2815 (AK 599)	India, Karnataka, Kodagu District, Honey Valley Estate	OK424592
<i>C. yercaudensis</i>	CES G133	India, Tamil Nadu, Namakkal District, Kollimalai massif	MK792473
<i>C. yercaudensis</i>	AK 767	India, Tamil Nadu, Salem District, Yercaud massif	MT773217

infralabials (**IL**), supralabials at midorbital position (**SLM**), infralabials at midorbital position (**ILM**), paravertebral tubercles (**PVT**), dorsal tubercle rows including longitudinal rows of spine-like scales on lower flank (**DTR**), mid-body scale rows across the belly (**MVSR**), ventral scales (**VS**), transverse basal subdigital lamellae on finger 1 (**BLamF1**), finger 4 (**BLamF4**), toe 1 (**BLamT1**), toe 4 (**BLamT4**), and toe 5 (**BLamT5**); transverse distal subdigital lamellae on finger 1 (**DLamF1**), finger 4 (**DLamF4**), toe 1 (**DLamT1**), toe 4 (**DLamT4**), and toe 5 (**DLamT5**); preloacal pores (**PP**), femoral pores (**FP**), poreless scales between preloacal and femoral pores (**SBPP&FP**), and postloacal tubercles (**PCT**).

Morphological analyses were conducted in R 4.1.3 (R Core Team 2018) and used using the following mensural variables: AGL, CL, ES, HL, HW, SVL. We used Thorpe's (1975) size correction equation that standardizes variables by SVL as implemented in the R package GroupStruct (available at <https://github.com/chankinonn/GroupStruct>) (Chan and Grismer 2021, 2022). We pooled sexes and used a global mean SVL for the two new species. A principal components analysis (PCA) was then conducted using the `ez_pca` function to visualize the separation of the two species in multivariate morphospace using the size-corrected data (excluding SVL).

Results

Phylogenetic relationships

The final ND2 alignment was 1047 base pairs (bp; including a nine bp insertion in *C. tigris*, with newly added sequences ranging in length from 447–1047 bp and 1–3 complete ND2 sequences per species). We recovered the same broad relationships within SAC as previous authors, with successive basal splits separating the *wynadensis* clade, and then the *beddomei* clade from the remaining clades of the SAC (Fig. 2; Agarwal et al. 2020c; Pal et al. 2021). There is high support (BS \geq 90%; Posterior Probability, PP \geq 0.98) for all other clades and subclades except for relationships between the *gracilis* clade, *monticola* clade, *C. umashaankeri* and *C. adii*. The two new lineages from Pakkamalai are nested within a poorly supported *mysoriensis* + *adii* clade. *Cnemaspis adii* forms the sister taxon to a well-supported clade (BS = 100, PP = 1) within which the lineage allied to *C. adii* from Pakkamalai forms the sister taxon to the *C. mysoriensis* clade. The new species allied to *C. otai* is sister to a clade which includes *C.*

otai sister to *C. avasabinae* + *C. rishivalleyensis*, the four species collectively forming the sister taxon to a subclade including *C. stellapulvis*, *C. tigris* and *C. yercaudensis*. The lowest level of divergence between described species of the *mysoriensis* + *adii* clade is 5.6%, between *C. rishivalleyensis* and *C. avasabinae*. The lineage allied to *C. adii* is 15.6–20.8% divergent from members of the *mysoriensis* + *adii* clade and the lineage allied to *C. otai* 6.7–19.4% (Table 2).

Morphological analyses

Two factors with eigen values >1 were retained that cumulatively explained 89.2% of the variation in the dataset. Factor 1 explains 69.3% variance and loads strongly (factors not listed are < 0.40) for CL (0.52), ES (0.51), and HL (0.47). Factor 2 explains 19.8% variance and loads strongly for AGL (−0.76) and HW (−0.55). The two divergent lineages are completely separated across these two PCA factors, with the lineage allied to *C. adii* showing up as having longer limbs, a longer and narrower head, longer snout and shorter trunk (Fig. 2). We describe the two genetically and morphologically divergent lineages as new species below.

Systematics

Cnemaspis pakkamalaiensis sp. nov.

<https://zoobank.org/DE8A33FA-D466-46B9-9472-9F24FA78B486>

Figures 3–7, Tables 3–5

Chresonymy. *Cnemaspis otai* Ganesh et al. (2018); Karthik et al. (2018)

Holotype. NRC-AA-1280 (AK-R 124), adult male (SVL = 29.0 mm), from Pakkamalai Reserve Forest (12.17224°N, 79.31907°E; elevation ca. 400 m asl.), Gingee Hills, Viluppuram district, Tamil Nadu state, India, collected by Akshay Khandekar, Swapnil Pawar and team, on 3rd April 2021.

Paratypes (n = 5). NRC-AA-1281 (AK-R 123) and NRC-AA-1282 (AK-R 126), adult males, same collection data as holotype; NRC-AA-1283 (AK-R 131) and NRC-

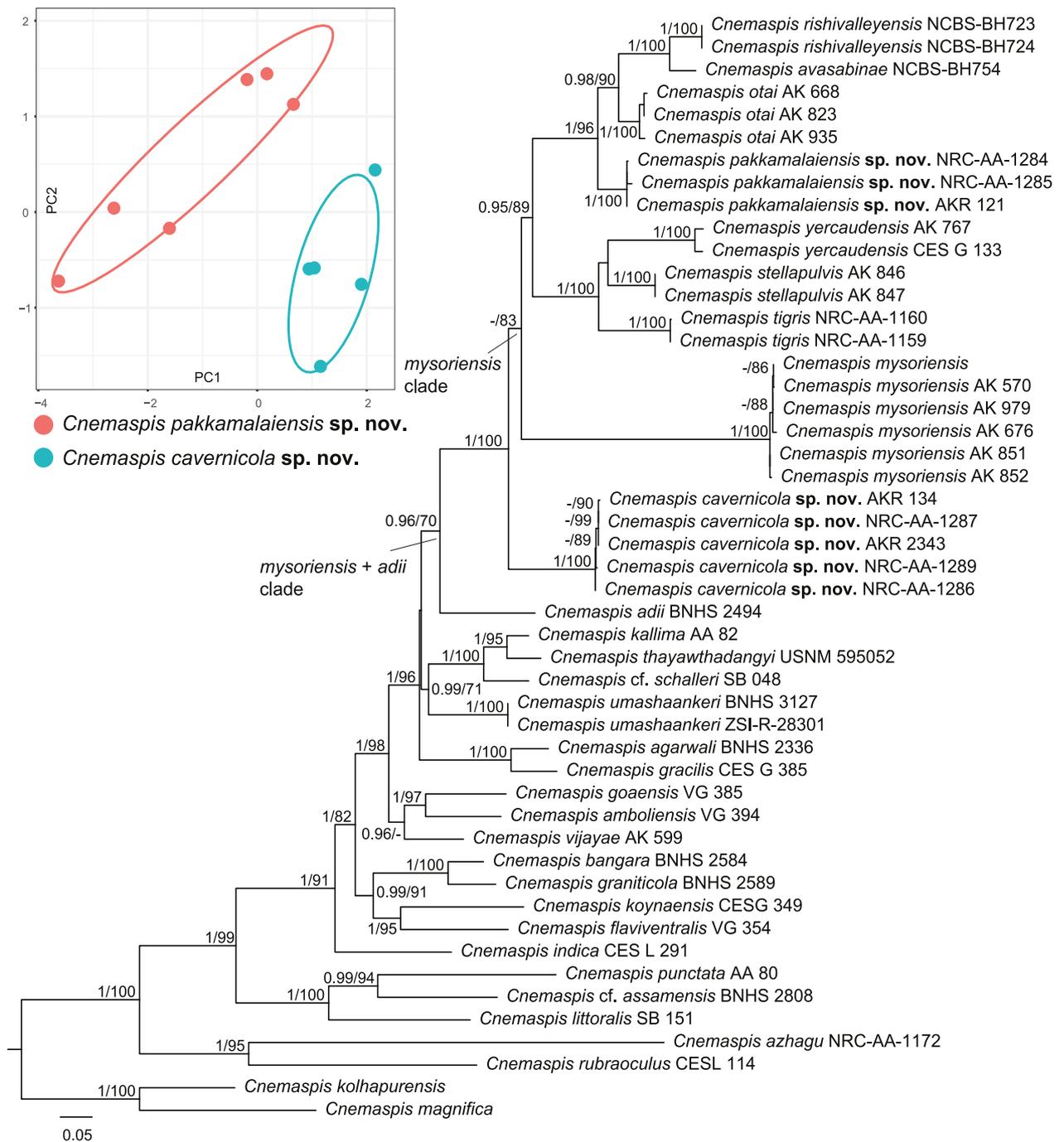


Figure 2. Maximum likelihood phylogeny of South Asian *Cnemaspis* based on the mitochondrial ND2 gene. Posterior probability (≥ 0.95) and bootstrap support (≥ 70) shown at nodes. Inset, plot of the first two principal components for mensural data of the two new species.

AA-1284 (AK-R 2344), adult males, and NRC-AA-1285 (AK-R 122), adult female, from another side of Pakkamalai Reserve Forest (12.16936°N, 79.30614°E; elevation ca. 400 m asl.), Gingee Hills, Viluppuram district, Tamil Nadu state, India, collected by Akshay Khandekar, Ishan Agarwal, Swapnil Pawar and team, on 19th September 2022.

Referred specimens (n = 1). AK-R 121, juvenile specimen, from Pakkamalai Reserve Forest (12.17343°N, 79.31772°E; elevation ca. 400 m asl.), same collection data as holotype.

Etymology. The specific epithet is a toponym for Pakkamalai, Gingee Hills in Viluppuram district of Tamil Nadu state, the type and only known locality for this species.

Suggested Common Name. Pakkamalai dwarf gecko.

Diagnosis. A small-sized *Cnemaspis*, snout to vent length less than 29 mm (n = 6). Dorsal pholidosis heterogeneous; weakly keeled, granular scales intermixed with a few scattered enlarged keeled tubercles on vertebral and paravertebral region and about three irregularly arranged rows of large, weakly keeled, tubercles on each side of

Table 2. Pairwise uncorrected ND2 sequence divergence within the *mysoriensis* + *adii* clade, numbers in bold along diagonal represent intraspecific genetic diversity (– indicates only a single sequence available).

	Species	1	2	3	4	5	6	7	8	9	10
1	<i>C. cavernicola</i> sp. nov.	0.0									
2	<i>C. pakkamalaiensis</i> sp. nov.	16.0	0.0								
3	<i>C. adii</i>	18.9	17.2	–							
4	<i>C. avasabinae</i>	16.0	8.7	18.5	–						
5	<i>C. mysoriensis</i>	20.8	19.4	22.6	20.2	1.0					
6	<i>C. otai</i>	17.3	6.7	18.5	8.3	20.0	1.0				
7	<i>C. rishivalleyensis</i>	17.6	9.0	19.2	5.6	21.6	8.3	0.0			
8	<i>C. stellapulvis</i>	15.6	15.3	18.9	15.9	21.4	15.2	15.8	0.0		
9	<i>C. tigris</i>	16.9	16.2	20.4	15.6	23.4	16.5	17.2	12.1	0.0	
10	<i>C. yercaudensis</i>	18.5	18.3	20.2	17.9	22.6	18.3	18.4	13.4	14.5	2.0

flank, tubercles in lowest row largest, spine-like; six rows of dorsal tubercles; ventral scales smooth, subcircular, subimbricate, 25–27 scales across belly, 100–112 longitudinal scales from mental to cloaca; subdigital scancers smooth, entire, unnotched; 8–11 total lamellae under digit I of manus and pes, 14–16 lamellae under digit IV of manus and 17–21 lamellae under digit IV of pes; males ($n = 5$) with two femoral pores on each thigh separated on either side by 8–11 poreless scales from two continuous precloacal pores; tail with enlarged, strongly keeled, distinctly pointed, conical tubercles forming whorls; a median row of subcaudals smooth, slightly enlarged. Dorsal colouration straw brown with a broad, light mid-dorsal streak formed by five or six fused elongate chain-links from occiput to tail base, single medial dark spot on nape, dark paired spots on either side of mid-dorsal streak, four pairs between forelimb insertions and tail base, tail with nine alternating light and dark markings.

Comparison with members of *C. mysoriensis* + *adii* clade. *Cnemaspis pakkamalaiensis* sp. nov. can be distinguished from all eight members of the *mysoriensis* + *adii* clade on the basis of the following differing or non-overlapping characters: males with two femoral pores on each thigh separated on either side by 8–11 poreless scales from two continuous precloacal pores (*versus* femoral pores absent, continuous series of 2–5 precloacal pores in *C. avasabinae*; three femoral pores on each thigh separated on either side by nine or 10 poreless scales from continuous series of four precloacal pores in *C. otai*; a single femoral pore on each thigh, separated on either side by 10 poreless scales from continuous series of three precloacal pores in *C. rishivalleyensis*; three femoral pores on each thigh, separated by five or six poreless scales from two continuous precloacal pores in *C. yercaudensis*); six rows of dorsal tubercles at mid-body (*versus* dorsal pholidosis homogeneous in *C. adii*, dorsal tubercles irregularly arranged at mid-body in *C. avasabinae*, 7–10 rows of dorsal tubercles at mid-body in *C. stellapulvis*); 25–27 ventral scales across belly at mid-body (*versus* 17–20 ventral scales across belly at mid-body in *C. avasabinae*, 18 ventral scales across belly at mid-body in *C. otai*, 20 or 21 ventral scales across belly at mid-body in *C. mysoriensis*, 20–22 ventral scales across belly at mid-body

in *stellapulvis*, 18–20 ventral scales across belly at mid-body in *C. yercaudensis*); spine-like tubercles present on flank (*versus* spine-like tubercles absent on flank in *C. adii*, and *C. avasabinae*); a single distinct black dorsal ocellus on mid-dorsal streak just anterior to forelimb insertions (*versus* distinct black dorsal ocellus just anterior to forelimb insertions absent in *C. mysoriensis* and *C. yercaudensis*); a light mid-dorsal streak formed by five or six fused, elongate chain-links that run from occiput to tail base (*versus* mid-dorsal streak absent in *C. adii*, a continuous light mid-dorsal streak runs from occiput onto tail base in *C. mysoriensis*, *C. stellapulvis*, *C. tigris*, and *C. yercaudensis*). *Cnemaspis pakkamalaiensis* sp. nov. is diagnosed against the second new species as part of its description below.

Description of the holotype. Adult male in good state of preservation except for tail tip slightly bent towards the right, partially everted hemipenis on the left, tail marginally detached just posterior to tail base on the left (Fig. 3A–E). SVL 29.0 mm, head short (HL/SVL 0.26), wide (HW/HL 0.70), not strongly depressed (HD/HL 0.42), distinct from neck. Loreal region slightly inflated, canthus rostralis not prominent. Snout marginally less than half the head length (ES/HL 0.48), more than twice eye diameter (ES/ED 2.31); scales on snout and canthus rostralis large, subcircular, smooth to weakly keeled; much larger than those on forehead and interorbital region; occipital and temporal region with much smaller, weakly keeled granules (Fig. 4A). Eye small (ED/HL 0.20); with round pupil; orbit with extra-brillar fringe scales that are largest anteriorly; supraciliaries not elongate; six interorbital scale rows across narrowest point of frontal; 25 or 26 scale rows between left and right supraciliaries at mid-orbit (Fig. 4A, C). Ear-opening deep, oval, small (EL/HL 0.05); eye to ear distance greater than diameter of eye (EE/ED 1.60; Fig. 4C). Rostral twice as wide (1.3 mm) than long (0.6 mm), incompletely divided dorsally by a strongly developed rostral groove for more than half its length; a single enlarged supranasal on each side, marginally larger than postnasals, separated from each other by a single enlarged internasal; rostral in contact with nostril, supralabial I, supranasal and internasal; nostrils oval, each surrounded by postnasals, supranasal, rostral and su-

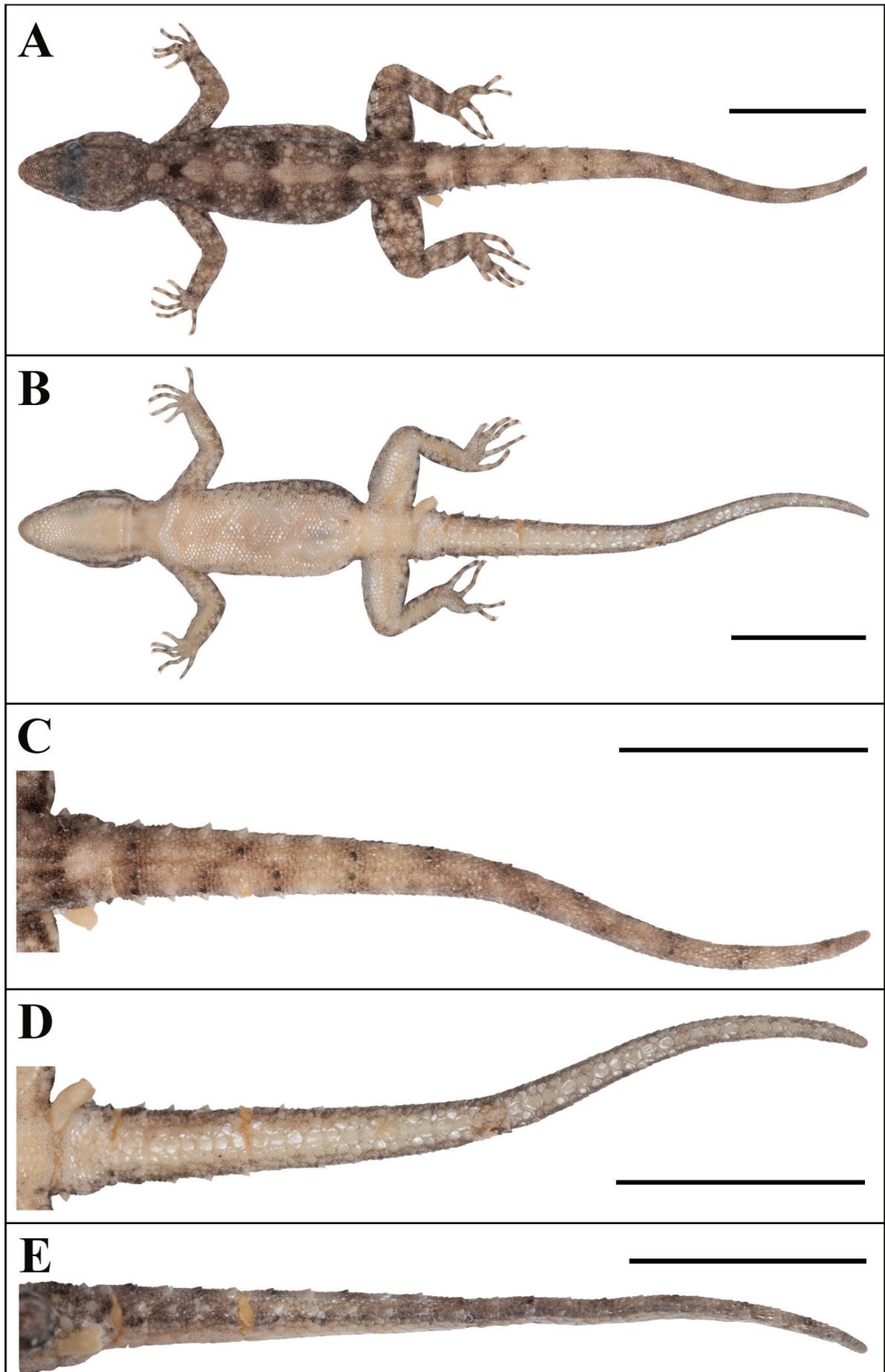


Figure 3. *Cnemaspis pakkamalaiensis* sp. nov. (holotype, NRC-AA-1280): **A** dorsal view of body, **B** ventral view of body, **C** dorsal view of tail, **D** ventral view of tail, **E** lateral view of tail. Scale bars 10 mm; photos by Akshay Khandekar.

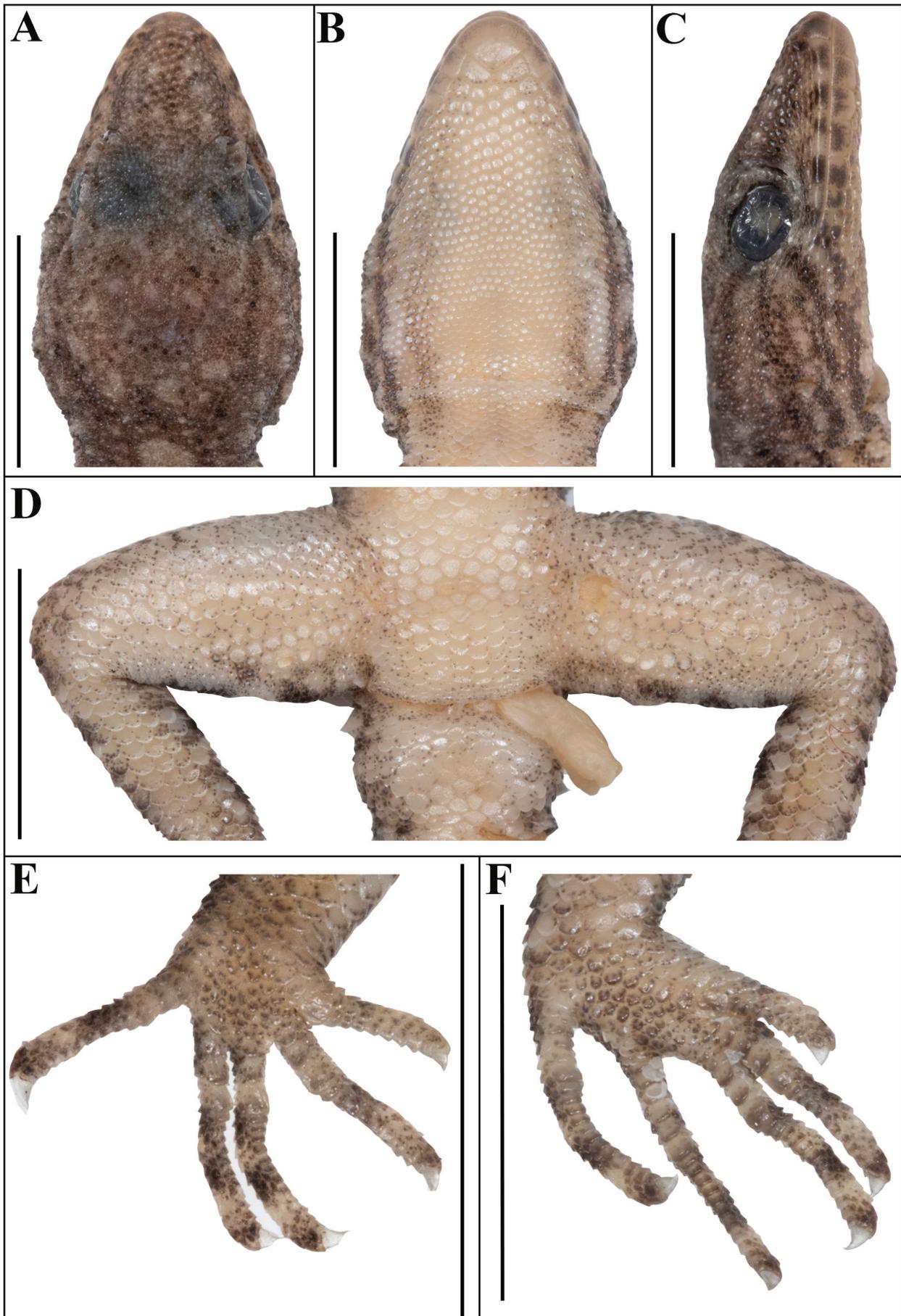


Figure 4. *Cnemaspis pakkamalaiensis* sp. nov. (holotype, NRC-AA-1280): **A** dorsal view of head, **B** ventral view of head, **C** lateral view of head on right, **D** view of cloacal region showing femoral and precloacal pores, **E** ventral view of left manus, **F** ventral view of left pes. Scale bars 5 mm; photos by Akshay Khandekar.

pralabial I; two rows of scales separate the orbit from the supralabials (Fig. 4A, C). Mental enlarged, subtriangular, marginally wider (1.6 mm) than long (1.2 mm); two pairs of postmentals, inner pair slightly larger than outer pair, roughly rectangular, in median contact with each other below mental; inner pair bordered by mental, infralabial I, outer postmental and three enlarged chin shields on either side; outer postmentals roughly square, bordered by inner postmentals, infralabial I and II, and three enlarged chin shields on either side; three enlarged gular scales prevent contact of left and right outer postmentals; chin shields bordering postmentals flat, smooth, smaller than outermost postmentals, rest flattened, smooth, even smaller (Fig. 4B). Infralabials bordered below by a row or two of slightly enlarged scales, decreasing in size posteriorly. Seven supralabials up to angle of jaw on either side, and six at midorbital position on each side; supralabial I largest, decreasing in size posteriorly; seven infralabials up to angle of jaw, five at midorbital position on left and six on right side; infralabial I largest, infralabials decreasing in size posteriorly (Fig. 4C).

Body relatively slender (BW/AGL 0.52), trunk less than half of SVL (AGL/SVL 0.42) without ventrolateral folds; three spine-like scales on left flank and two on right flank. Dorsal pholidosis heterogeneous; weakly keeled, granular scales intermixed with a few scattered enlarged keeled tubercles on vertebral and paravertebral region and about three irregularly arranged rows of large, weakly keeled, tubercles on each side of flank (Fig. 5A–C). Scales on occiput and nape slightly smaller than those on paravertebral rows and weakly keeled; scales on flank slightly larger than those on dorsum, weakly keeled, conical or spine-like. Ventral scales much larger than granular scales on dorsum, those on belly smooth, subcircular-subimbricate, equal from chest to vent except for those on precloacal region which slightly larger; mid-body scale rows across belly 25; 112 scales from mental to anterior border of cloaca (Fig. 5B). Scales on throat slightly smaller than those on belly, imbricate; gular region with much smaller, flattened scales with those on chin bordering postmentals, enlarged, juxtaposed and flattened (Fig. 4B). Two femoral pores on each thigh separated by 11 poreless scales on left and nine on right (count incomplete due to injury) from two continuous precloacal pores (Fig. 4D).

Scales on dorsal aspect of manus heterogenous, upper arm scales much larger than dorsal granules, strongly keeled, imbricate; those near forelimb insertion much smaller than scales on upper arm; dorsal aspect of lower arm and elbow with scales much smaller than those on upper arm, weakly keeled, flat, roughly rounded; dorsal aspect of hand predominantly bearing large, flattened, weakly keeled, imbricate scales. Ventral aspect of upper arm with smooth, roughly rounded, subimbricate scales; scales on lower arm and wrist large, smooth, imbricate; scales on palm and sole smooth, flat and subcircular. Scales on anteriodorsal aspect of thigh much larger than enlarged scales on body dorsum, strongly keeled, and imbricate except those near hindlimb insertion which are granular, much smaller than dorsal granules and conical;

scales on posteriodorsal aspect smaller, weakly keeled, granular. Scales on dorsal aspect of knee and shank smaller than those on dorsum of thigh, subimbricate, weakly keeled; dorsal aspect of foot predominantly bearing small, flattened, strongly keeled, imbricate scales; scales on ventral aspect of thigh and shank larger than those on mid-body ventrals, smooth, subimbricate on thigh and imbricate on shank (Fig. 3A, B).

Fore-limbs and hind-limbs long, slender (LAL/SVL 0.14); (CL/SVL 0.17); digits long, with a strong, recurved claw, distinctly inflected, distal portions laterally compressed conspicuously. Series of unpaired lamellae on basal portion of digits, separated from unpaired, narrower distal lamellae by a single large scale at the inflection; basal lamellae series: 1-3-3-4-4 (right manus), 3-4-4-7-4 (right pes), 1-3-3-4-4 (left manus; Fig. 4E), 3-4-4-6-4 (left pes; Fig. 4F); distal lamellae series: 8-9-12-11-9 (right manus), 8-10-12-12-12 (right pes), 8-9-12-11-9 (left manus; Fig. 4E), 8-10-12-11-12 (left pes; Fig. 4F). Relative length of digits (measurements in mm in parentheses): IV (2.5) > III (2.4) > II (2.2) > V (2.1) > I (1.6) (left manus); IV (3.2) > V (3.1) > III (2.9) > II (2.7) > I (1.6) (left pes).

Tail entire and original except for extreme tip which is regenerated, subcylindrical, relatively slender, flattened beneath, slightly longer than snout-vent length (TL/SVL 1.18) (Fig. 3C–E). Dorsal scales at tail base granular, similar in size and shape to those on midbody dorsals, gradually becoming larger, flatter, subimbricate posteriorly, intermixed with much enlarged, strongly keeled, distinctly pointed, conical tubercles forming whorls; six tubercles on first nine whorls. Scales on ventral aspect of original tail much larger than those on dorsal aspect, subimbricate, smooth, with a series of three enlarged subcaudal scales of which the median series is slightly larger than adjunct two rows, roughly pentagonal; those on tail base much smaller, imbricate and smooth, a single enlarged, smooth precloacal spur on each side (Fig. 3D).

Colouration in life (Fig. 6A). Dorsal ground colour of head, body, limbs and tail straw-brown; head mottled with fine dark speckles and larger dark blotches. Fine dark brown preorbital streak runs from snout to orbit, two fine dark brown postorbital streaks extend till neck; labials light grey/cream with lighter and darker bars. A straw-coloured mid-dorsal streak that is formed by five fused elongate chain-links runs from occiput to tail base; a dark ocellus fringed by a few orange scales anterior to forelimb insertions forms the posterior boundary of the first chain-link, flanked on either side by a wishbone shaped marking opening on neck and near forelimb insertions; followed by four pairs of dark brown blotches, one pair at the posterior boundary of each chain link with a spot on either side. Flank with smaller dark spots and light-yellow markings. Tail with nine incomplete bands and no black tip. Dorsum of forelimbs and femur with few light and dark blotches, tibia with brown bands, two strong dark streaks on the posterior of femur, digits with alternating dark and light bands. Ventral surfaces dull white, limbs finely speckled with brown especially

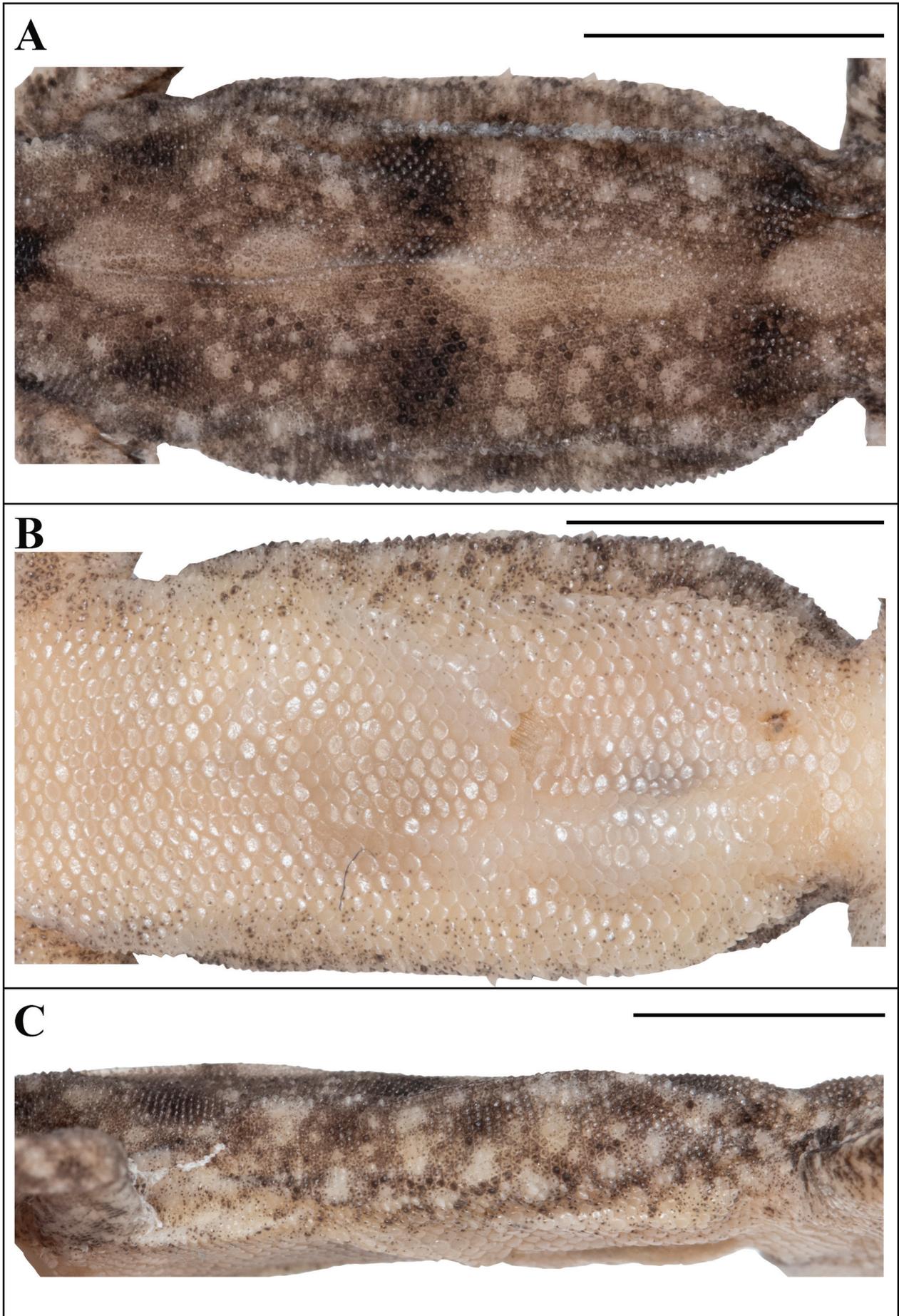


Figure 5. *Cnemaspis pakkamalaiensis* sp. nov. (holotype, NRC-1280): **A** dorsal view of mid-body, **B** ventral view of mid-body, **C** lateral view of mid-body. Scale bars 5 mm; photos by Akshay Khandekar.



Figure 6. *Cnemaspis pakkamalaiensis* sp. nov., in life: **A** adult male (holotype, NRC-AA-1280), **B** adult female (paratype, NRC-AA-1285). Photos by Akshay Khandekar.

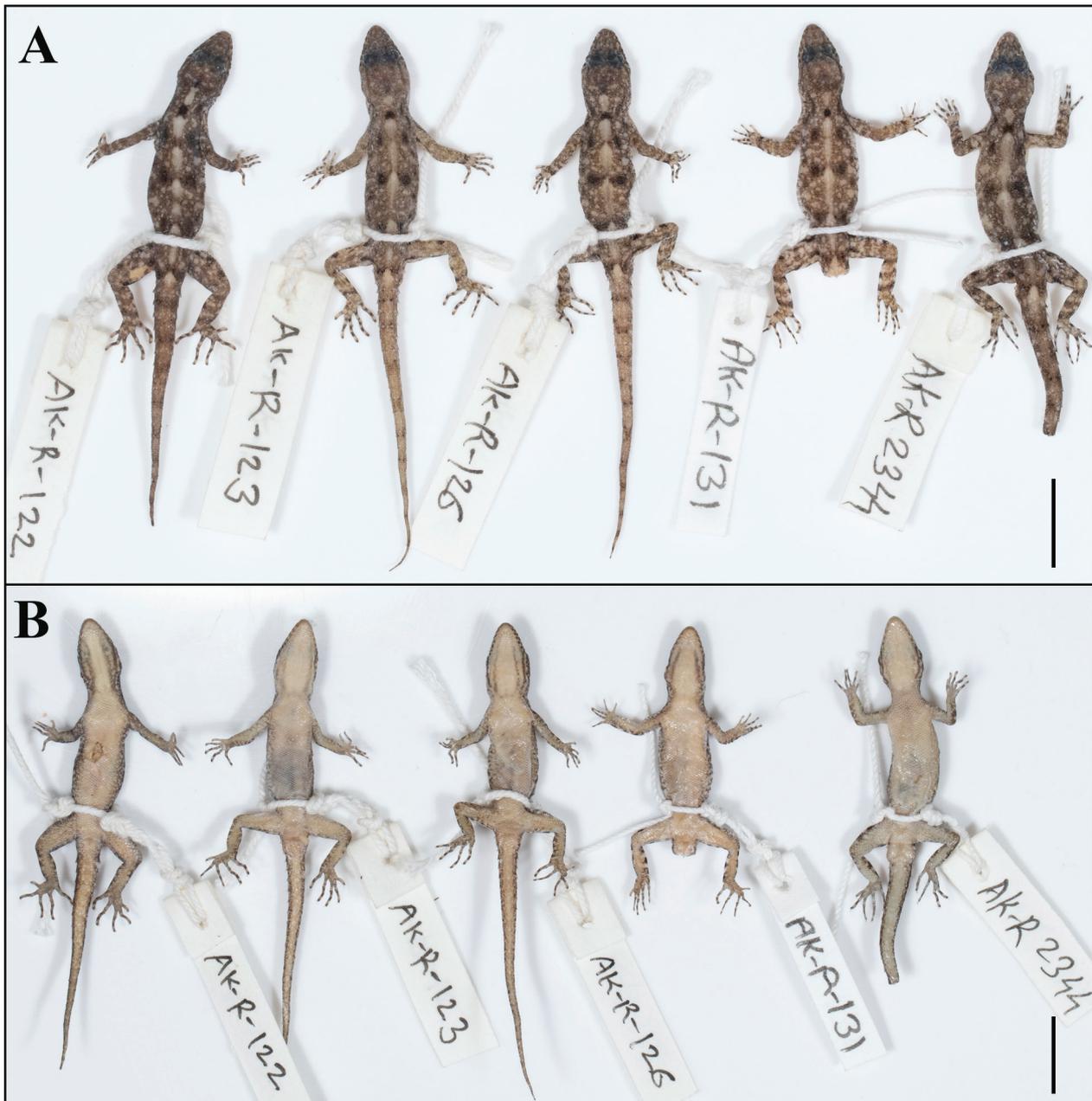


Figure 7. Paratype series of *Cnemaspis pakkamalaiensis* sp. nov., from left to right, NRC-AA-1285, NRC-AA-1281–1284: **A** dorsal view, **B** ventral view. Scale bar 10 mm; photos by Akshay Khandekar.

prominent under forelimbs, throat with a pair of broken up light grey longitudinal stripes on each side, no dark markings on belly, underside of tail lined by a fine dark border. Pupil black, iris silver with an orange streak toward the antero-posterior of the pupil.

Variation and additional information from paratype series. Mensural, meristic and additional character state data for the paratype series is given in Tables 3–5 respectively. There are four males and a single female ranging in size from 26.9–28.9 mm (Fig. 7A, B). All paratypes resemble the holotype except as follows: inner postmental separated from each other below mental by an enlarged chin scale in NRC-AA-1285; outer postmental separated from each other by two enlarged chin scales in NRC-AA-1281, outer postmental bordered by four chin scales

on left and three on right side in NRC-AA-1283. Three paratypes—NRC-AA-1285, NRC-AA-1281, and NRC-AA-1282 with original and complete tail, marginally or slightly longer than body (TL/SVL 1.04, 1.23, and 1.21 respectively); NRC-AA-1283 without tail; and NRC-AA-1284 with half of the tail missing (Fig. 7A, B). All paratypes agree with the holotype in overall colouration except dorsal tail colouration of female paratype (NRC-AA-1285) is overall duller than rest of the male types (Fig. 6B).

Distribution and natural history. *Cnemaspis pakkamalaiensis* sp. nov. is known only from its type locality (Pakkamalai Reserve Forest, Gingee Hills in Viluppuram district, Tamil Nadu), at elevations of ca. 200–400 m asl., though all specimens were collected at ~ 400 m asl.

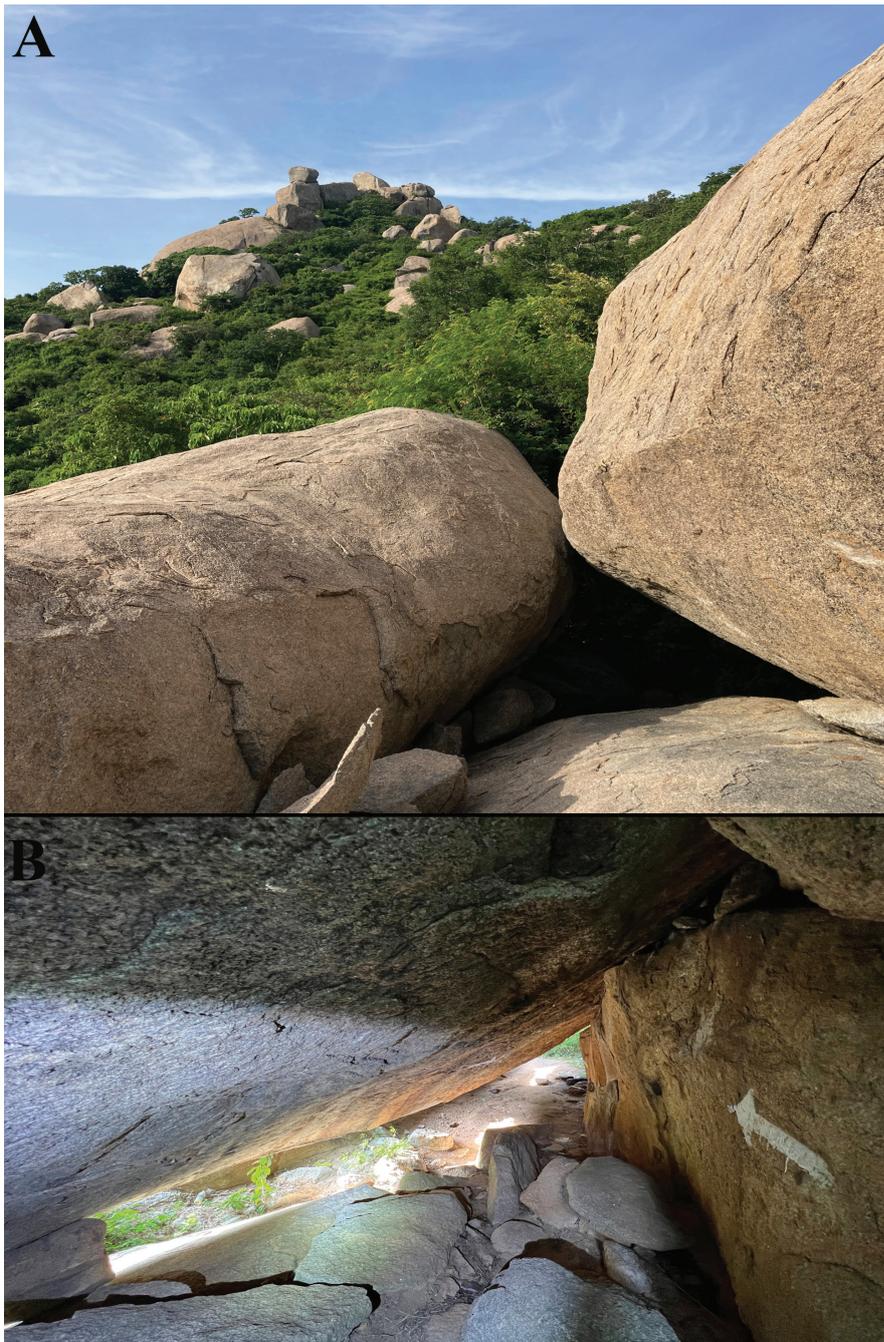


Figure 8. Habitat of *Cnemaspis pakkamalaiensis* **sp. nov.**, and *C. cavernicola* **sp. nov.** at the type locality: **A** general view showing granite boulders surrounded by tropical dry evergreen forests, **B** granite boulder cave from where individuals of the new species were collected. Photos by Akshay Khandekar

(Fig. 1). *Cnemaspis pakkamalaiensis* **sp. nov.** was encountered during a single day of fieldwork each on two different fieldtrips in Pakkamalai. Individuals were observed active in large numbers (>50 in 2 hrs) in the morning (0730–0930 hrs) and late evening (1700–1930 hrs), in shaded and relatively cooler areas among large granite boulders (< 2m high) in tropical dry evergreen forest (Fig. 8A, B). A few individuals (<10) were also observed moving in the leaf litter on the ground just after dark. Sympatric lizards recorded by us at the type locality include *Calodactylodes aureus* (Beddome, 1870), *Hemidactylus frenatus* Duméril and Bibron, 1836; *H. pakkamalaiensis* Narayanan et al., 2023, *H. whitakeri* Mirza et al., 2018, *Eutropis carinata* (Schneider, 1801), *Psammophilus dorsalis* (Gray, 1831), and a second new species of *Cnemaspis*, described below.

Cnemaspis cavernicola **sp. nov.**

<https://zoobank.org/AEFA6F98-35EF-4F2E-AED8-2FABFD139924>

Figures 9–13, Tables 3–5

Holotype. NRC-AA-1286 (AK-R 2339), adult male (SVL 32.2 mm), from Pakkamalai Reserve Forest (12.17224°N, 79.31907°E; elevation ca. 400 m asl.), Gingee Hills, Villuppuram district, Tamil Nadu state, India, collected by Akshay Khandekar, Ishan Agarwal, Swapnil Pawar and team, on 19th September 2022.

Paratypes (n = 4). NRC-AA-1287 (AK-R 135) and NRC-AA-1288 (AK-R 2341), adult males, same collection data

Table 3. Mensural (mm) data for the type series of the new species. Abbreviations are listed in Materials and Methods; * = tail incomplete.

Species	<i>Cnemaspis pakkamalaiensis</i> sp. nov.						<i>Cnemaspis cavernicola</i> sp. nov.				
	Holotype	Paratypes					Holotype	Paratypes			
Specimen number	NRC-AA-1280	NRC-AA-1281	NRC-AA-1282	NRC-AA-1283	NRC-AA-1284	NRC-AA-1285	NRC-AA-1286	NRC-AA-1287	NRC-AA-1288	NRC-AA-1289	NRC-AA-1290
Sex	Male	Male	Male	Male	Male	Female	Male	Male	Male	Female	Female
SVL	29.0	27.9	27.5	26.9	28.9	28.1	32.2	32.1	28.2	34.0	30.6
TL	34.3	34.5	33.4	1.9*	18.1*	29.5	31.2	35.5	11.0*	23.7	37.1
TW	3.1	3.0	2.6	2.9	2.9	2.9	2.8	3.1	2.4	2.9	2.4
LAL	4.1	4.3	4.2	3.8	4.1	4.5	4.8	5.1	4.1	4.7	4.2
CL	5.2	5.3	5.3	4.5	5.1	5.4	5.6	6.1	5.4	5.8	5.7
AGL	12.3	11.5	11.7	11.8	13.3	12.1	14.2	13.3	12.7	14.6	14.6
BH	3.5	2.9	3.2	2.7	3.6	2.3	2.6	2.6	2.8	2.8	2.9
BW	6.5	5.0	5.1	6.0	5.7	5.2	5.9	5.7	5.1	6.3	5.5
HL	7.7	7.7	7.6	6.9	7.8	7.5	8.3	8.0	7.1	8.4	7.6
HW	5.4	4.6	4.5	4.8	5.1	4.6	5.1	4.7	4.4	5.0	4.5
HD	3.3	2.6	2.7	2.9	3.1	2.6	2.8	3.1	2.5	2.8	2.8
ED	1.6	1.5	1.6	1.5	1.5	1.5	1.6	1.6	1.5	1.7	1.4
EE	2.6	2.5	2.4	2.1	2.4	2.6	2.6	2.3	2.2	2.4	2.3
ES	3.7	3.6	3.5	2.6	3.7	3.6	3.8	4.0	3.2	3.9	3.6
EN	3.0	2.8	2.7	2.7	3.0	2.8	2.9	3.1	2.6	3.3	2.8
IN	1.0	0.8	0.9	0.9	0.9	0.9	0.9	1.0	0.8	0.8	0.8
IO	1.6	1.6	1.7	1.5	2.2	1.7	2.5	1.9	1.8	2.3	2.0
EL	0.4	0.4	0.7	0.3	0.5	0.6	0.4	0.6	0.4	0.6	0.3

as holotype except for NRC-AA-1287 which was collected by Akshay Khandekar, Swapnil Pawar and team on 3rd April 2021; NRC-AA-1289 (AK-R 2340) and NRC-AA-1290 (AK-R 2342), adult females, from near Sri Vanadurgai Amman Temple, Pakkamalai Reserve Forest (12.16991°N, 79.30865°E; elevation ca. 480 m asl.), Gingee Hills, Viluppuram district, Tamil Nadu state, India, same collection data as holotype.

Referred specimens (n = 2). AK-R 134, AK-R 2343, juveniles, from Pakkamalai Reserve Forest (12.16825°N, 79.31971°E; elevation ca. 400 m asl.), same collection data as holotype.

Etymology. The specific epithet is an adjective formed from the Latin “caverna” for cave and “cola” meaning inhabitant or dweller, as the species is only known to occur in caves and crevices below large granite boulders.

Suggested Common Name. Cave-dwelling dwarf gecko.

Diagnosis. A small-sized *Cnemaspis*, snout to vent length less than 34 mm (n = 5). Dorsal pholidosis heterogeneous; weakly keeled, granular scales in vertebral and paravertebral region, intermixed with about two or three regularly arranged rows of large, weakly keeled tubercles on each side of flank, tubercles in lowest row largest and spine-like; 4–6 rows of dorsal tubercles; ventral scales smooth, subcircular, subimbricate, 28–32 scales across belly, 116–125 longitudinal scales from mental to cloaca; subdigital scans smooth, entire, unnotched; 10–12 total lamellae under digit I of manus and pes, 15–19 lamellae under dig-

it IV of manus and 18–21 lamellae under digit IV of pes; males (n = 3) with one or two femoral pores on each thigh separated on either side by 8–10 poreless scales from a continuous series of three precloacal pores; tail with enlarged, strongly keeled, distinctly pointed, conical tubercles forming whorls; a median row of subcaudals smooth, distinctly enlarged. Dorsal colouration grey-brown with a single medial dark spot on nape followed by four light blotches from forelimb insertions to tail base, tail with 12–14 alternating light and dark bars.

Comparison with members of *C. mysoriensis* + *adii* clade. *Cnemaspis cavernicola* sp. nov. can be distinguished from all eight members of the *mysoriensis* + *adii* clade on the basis of the following differing or non-overlapping characters: 28–32 scales across belly at mid-body (versus 22–26 ventral scales across belly at mid-body in *C. adii*, 17–20 ventral scales across belly at mid-body in *C. avasabinae*, 20 or 21 ventral scales across belly at mid-body in *C. mysoriensis*, 18 ventral scales across belly at mid-body in *C. otai*, 25–27 ventral scales across belly at mid-body in *C. pakkamalaiensis* sp. nov., 23–25 ventral scales across belly at mid-body in *C. rishivalleyensis*, 20–22 ventral scales across belly at mid-body in *C. stellapulvis*, 23–25 scales across belly in *C. tigris*, and 18–20 ventral scales across belly at mid-body in *C. yercaudensis*); 116–125 longitudinal scales from mental to cloaca (versus 102–114 longitudinal scales from mental to cloaca in *C. avasabinae*, 93–98 longitudinal scales from mental to cloaca in *C. otai*, 100–112 longitudinal scales from mental to cloaca in *C. pakkamalaiensis* sp. nov., 102–112 longitudinal scales from mental to cloaca in *C. rishivall-*

Table 4. Meristic data for the type series of the new species. Abbreviations are listed in Materials and Methods except for: L&R = Left & Right; irr = irregularly arranged; abs. = absent; * = damaged.

Species	<i>Cnemaspis pakkamalaiensis</i> sp. nov.						<i>Cnemaspis cavernicola</i> sp. nov.				
	Holotype	Paratypes					Holotype	Paratypes			
Specimen number	NRC-AA-1280	NRC-AA-1281	NRC-AA-1282	NRC-AA-1283	NRC-AA-1284	NRC-AA-1285	NRC-AA-1286	NRC-AA-1287	NRC-AA-1288	NRC-AA-1289	NRC-AA-1290
Sex	Male	Male	Male	Male	Male	Female	Male	Male	Male	Female	Female
SL L&R	7&7	7&7	8&7	7&7	7&7	8&7	7&8	8&8	8&8	8&7	8&8
IL L&R	7&7	7&7	7&7	6&6	6&7	7&7	7&7	8&8	7&7	7&7	7&8
SL M L&R	6&6	6&6	7&6	7&6	7&7	6&6	6&6	7&7	7&6	7&6	6&6
IL M L&R	5&6	5&6	6&5	5&5	5&6	5&5	6&5	6&6	5&5	6&6	5&5
PVT	irr	irr	irr	irr	irr	irr	abs.	abs.	abs.	abs.	abs.
DTR	6	6	6	6	6	6	6	4	6	6	4
MVSR	25	25	27	27	25	27	29	32	29	29	28
VS	112	111	105	107	100	105	123	125	116	118	125
DLam1F L&R	8&8	8&8	8&8	8&7	7&7	9&9	9&9	10&10	9&10	8&9	10&10
BLam1F L&R	1&1	1&1	1&1	1&1	1&1	1&2	2&2	2&2	2&2	2&2	2&2
DLam4F L&R	11&11	12&12	11&12	11&12	10&10	11&11	13&12	12&12	12&12	11&12	12*&13
BLam4F L&R	4&4	4&4	4&4	4&4	4&4	4&4	5&5	4&4	5&4	4&4	4&6
DLam1T L&R	8&8	8&9	8&8	8&7	7&7	8&8	9&9	9&9	9&9	8&8	9&10
BLam1T L&R	3&3	2&2	1&1	2&2	2&1	2&2	2&2	2&2	2&2	2&2	2&2
DLam4T L&R	11&12	12&12	13&13	13&13	11&11	12&12	14&14	13&13	13&12	12&*	14&14
BLAM4T L&R	6&7	8&8	8&8	7&7	7&6	7&7	6&6	7&7	7&6	8&5*	7&7
DLAM5T L&R	12&12	12&11	12&13	11&12	11&11	12&12	13&13	12&13	13&13	12&*	13&13
BLam5T L&R	4&4	5&5	6&6	6&6	4&3	6&6	5&6	6&6	3&4	3&3	4&5
PP L&R	2	2	2	2	2	abs.	4	3	3	abs.	abs.
FP L&R	2&2	2&2	2&2	2&2	2&2	abs.	1&2	2&2	2&1	abs.	abs.
SB PP&FP L&R	11&9*	9&9	9&8	11&11	9&10	abs.	8&10	10&9	9&10	abs.	abs.
PCT L&R	1&1	1&1	1&1	1&1	1&1	1&1	1&1	1&1	1&1	1&1	1&1

eyensis, 90–107 longitudinal scales from mental to cloaca in *C. stellapulvis*, 91–107 longitudinal scales from mental to cloaca in *C. tigris*, and 90–105 longitudinal scales from mental to cloaca in *C. yercaudensis*); a median row of subcaudals distinctly enlarged (versus a median row of subcaudals slightly enlarged in *C. avasabinae*, *C. mysoriensis*, *C. otai*, *C. pakkamalaiensis* sp. nov., *C. rishivalleyensis*, *C. stellapulvis*, *C. tigris*, and *C. yercaudensis*); enlarged tubercles in vertebral and paravertebral region absent, about two or three regularly arranged rows of large, weakly keeled tubercles on each side of flank (versus dorsal pholidosis homogeneous in *C. adii*, granular scales in the vertebral and paravertebral region with a few scattered enlarged keeled tubercles in *C. mysoriensis*, *C. otai*, *C. pakkamalaiensis* sp. nov., *C. stellapulvis*, *C. tigris*, and *C. yercaudensis*); a mid-dorsal streak absent (versus a continuous light mid-dorsal streak runs from

occiput onto tail base in *C. mysoriensis*, *C. stellapulvis*, *C. tigris*, and *C. yercaudensis*); a light mid-dorsal streak formed by seven fused, elongate chain-links that runs from occiput to tail base in *C. avasabinae*, *C. otai*, *C. pakkamalaiensis* sp. nov., and *C. rishivalleyensis*).

Description of the holotype. Adult male in good state of preservation except extreme tail tip missing, partially everted hemipenis on left side, and a 4.0 mm long incision in sternal region for tissue collection (Fig. 9A–E). SVL 32.2 mm, head short (HL/SVL 0.25), wide (HW/HL 0.61), not strongly depressed (HD/HL 0.33), distinct from neck. Loreal region slightly inflated, canthus rostralis not prominent. Snout marginally less than half the head length (ES/HL 0.45), more than twice eye diameter (ES/ED 2.37); scales on snout and canthus rostralis large, subcircular, smooth; much larger than those on forehead

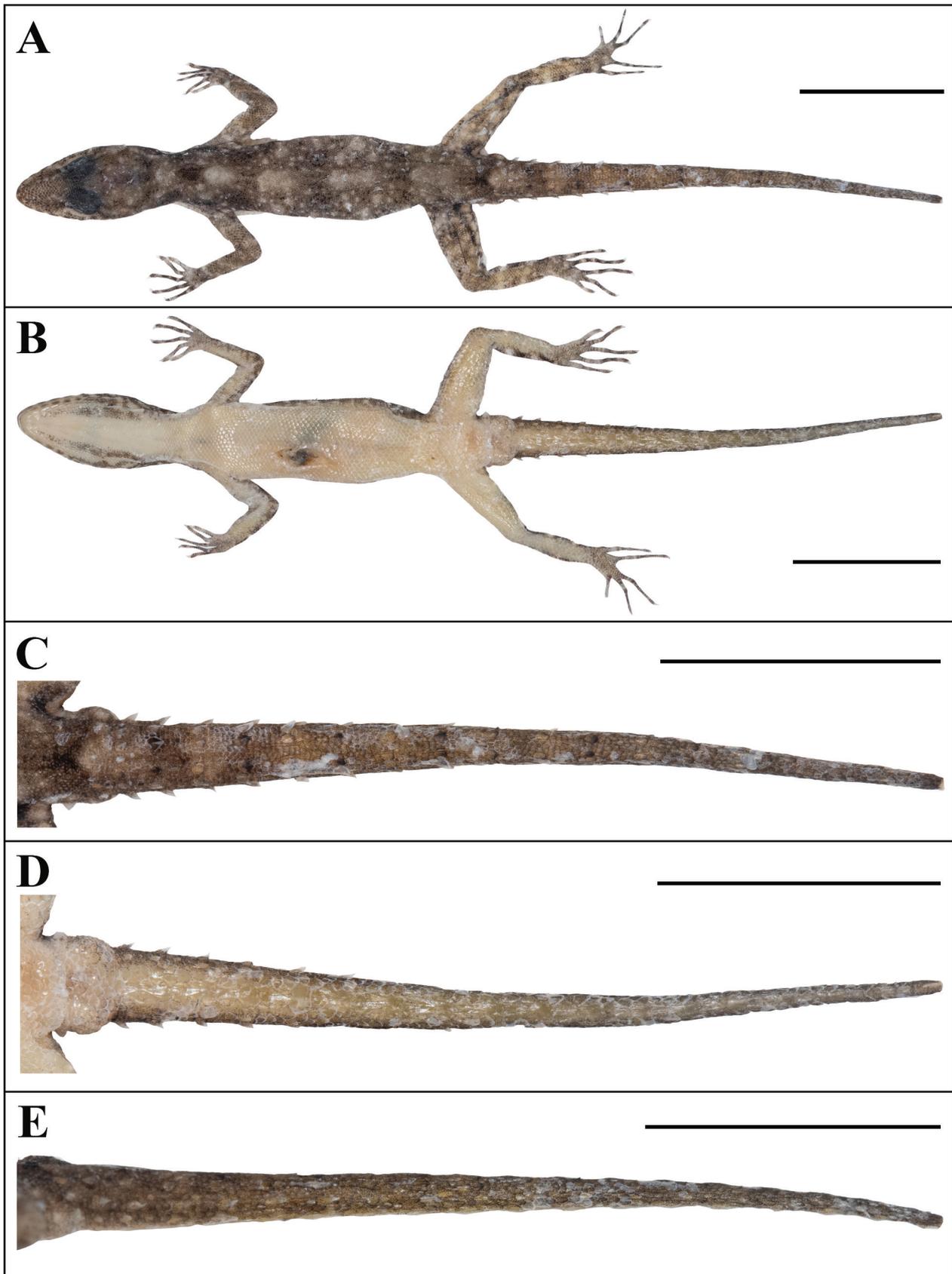


Figure 9. *Cnemaspis cavernicola* sp. nov. (holotype, NRC-AA-1286): **A** dorsal view of body, **B** ventral view of body, **C** dorsal view of tail, **D** ventral view of tail, **E** lateral view of tail. Scale bars 10 mm; photos by Ishan Agarwal (A), and Akshay Khandekar (B).

and interorbital region; occipital and temporal region with much smaller, weakly keeled granules (Fig. 10A, C). Eye small (ED/HL 0.19); with round pupil; orbit with

extra-brillar fringe scales that are largest anteriorly; supraciliaries not elongate; interorbital scale rows across narrowest point of frontal nine; 28 or 29 scale rows be-

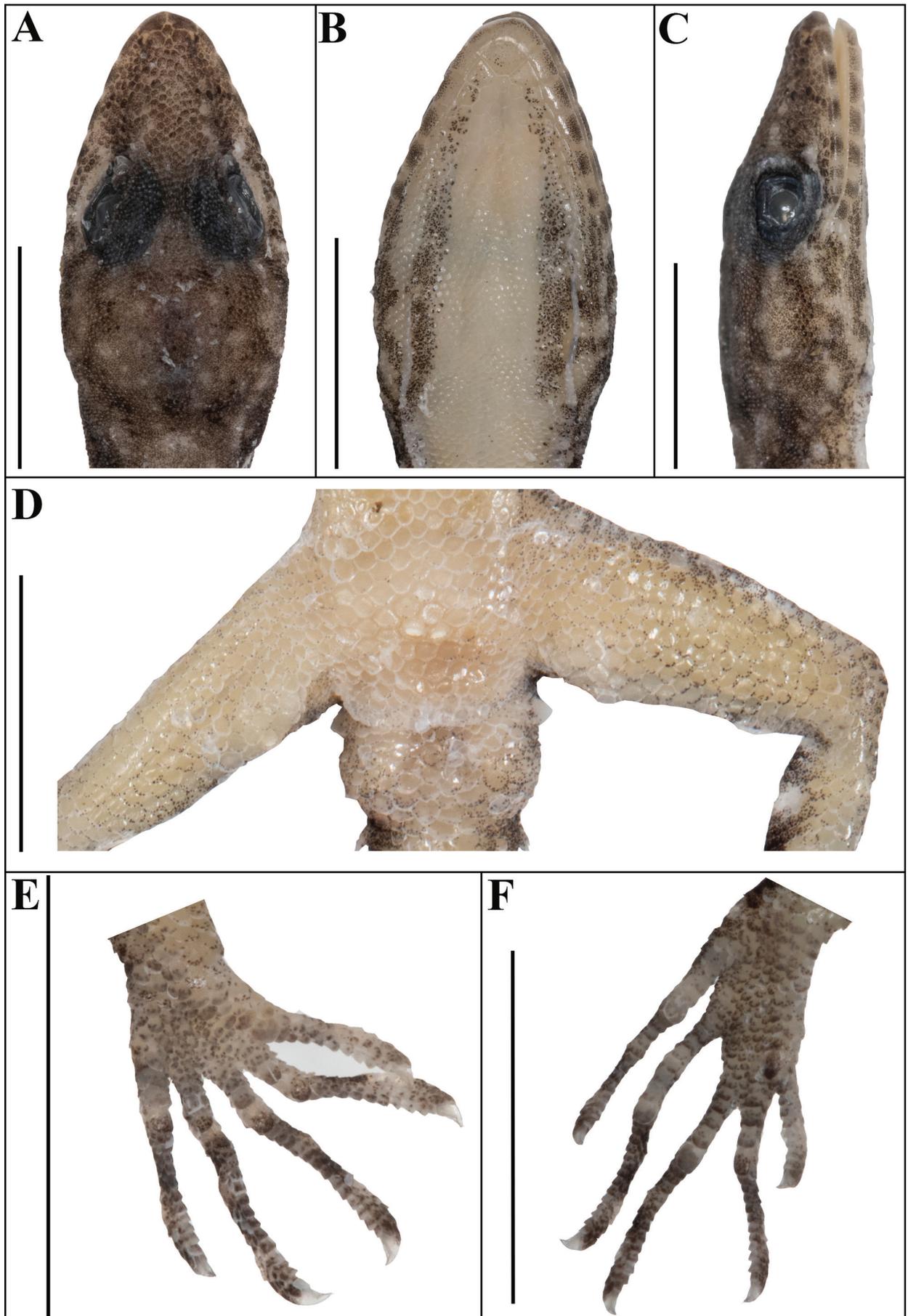


Figure 10. *Cnemaspis cavernicola* sp. nov. (holotype, NRC-AA-1286): **A** dorsal view of head, **B** ventral view of head, **C** right side lateral view of head, **D** view of cloacal region showing femoral and precloacal pores, **E** ventral view of left manus, **F** ventral view of left pes. Scale bars 5 mm; photos by Akshay Khandekar.

Table 5. Additional morphological characters for the type series of the new species. abs. = absent; / = data unavailable.

Species	<i>Cnemaspis pakkamalaiensis</i> sp. nov.						<i>Cnemaspis cavernicola</i> sp. nov.				
	Holo-type	Paratypes					Holo-type	Paratypes			
Specimen number	NRC-AA-1280	NRC-AA-1281	NRC-AA-1282	NRC-AA-1283	NRC-AA-1284	NRC-AA-1285	NRC-AA-1286	NRC-AA-1287	NRC-AA-1288	NRC-AA-1289	NRC-AA-1290
Sex	Male	Male	Male	Male	Male	Female	Male	Male	Male	Female	Female
Anterior extra-brillar fringe scales enlarged (1) or not enlarged (0)	1	1	1	1	1	1	1	1	1	1	1
Ventral scales keeled (1) or smooth (0)	0	0	0	0	0	0	0	0	0	0	0
Gular scales keeled (1) or smooth (0)	0	0	0	0	0	0	0	0	0	0	0
Pectoral scales keeled (1) or smooth (0)	0	0	0	0	0	0	0	0	0	0	0
Precloacal pores continuous (1) or separated (0)	1	1	1	1	1	abs.	1	1	1	abs.	abs.
Precloacal pores elongate (1) or round (0)	1	1	1	1	1	abs.	1	1	1	abs.	abs.
Femoral pores elongate (1) or round (0)	1	1	1	1	1	abs.	1	1	1	abs.	abs.
Dorsal pholidosis homogeneous (1) or heterogeneous (0)	0	0	0	0	0	0	0	0	0	0	0
Dorsal tubercles keeled (1) or not keeled (0)	1	1	1	1	1	1	1	1	1	1	1
Tubercles linearly arranged (1) or more random (0)	0	0	0	0	0	0	1	1	1	1	1
Spine-like tubercles on flank present (1) or absent (0)	1	1	1	1	1	1	1	1	1	1	1
Lateral caudal furrows present (1) or absent (0)	0	0	0	/	0	0	0	0	0	/	0
Subcaudals keeled (1) or smooth (0)	0	0	0	/	0	0	0	0	0	0	0
Single median row of keeled subcaudals (1) or smooth (0)	0	0	0	/	0	0	0	0	0	0	0
Caudal tubercles encircle tail (1) or not (0)	1	1	1	/	1	1	1	1	1	/	1
Median subcaudal scale row enlarged (1) or slightly enlarged (0)	0	0	0	/	0	0	1	1	1	1	1
Enlarged femoral scales present (1) or absent (0)	1	1	1	1	0	1	0	1	0	0	0
Subtibial scales keeled (1) or smooth (0)	0	0	0	0	0	0	0	0	0	0	0

tween left and right supraciliaries at mid-orbit (Fig. 10C). Ear-opening deep, oval, small (EL/HL 0.04); eye to ear distance greater than diameter of eye (EE/ED 1.62; Fig. 10C). Rostral twice wider (1.3 mm) than long (0.6 mm),

incompletely divided dorsally by a strongly developed rostral groove for more than half of its length; a single enlarged supranasal on each side, marginally larger than postnasals, separated from each other by a single

enlarged internasal and a smaller scale on snout; rostral in contact with nostril, supralabial I, supranasal and internasal; nostrils oval, each surrounded by postnasals, supranasal, rostral and supralabial I; two rows of scales separate the orbit from the supralabials (Fig. 10C). Mental enlarged, subtriangular, marginally wider (1.5 mm) than long (1.2 mm); two pairs of postmentals, inner pair slightly larger than outer pair, roughly square, separated from each other below mental by an enlarged chin scale; inner pair bordered by mental, infralabial I and II, outer postmental and three enlarged chin shields on either side; outer postmentals roughly square, bordered by inner postmentals, infralabial II, and four enlarged chin shields on either side; three enlarged gular scales prevent contact of left and right outer postmentals; chin shields bordering postmentals flat, smooth, smaller than outermost postmentals, rest flattened, smooth, even smaller (Fig. 10B). Infralabials bordered below by a row or two of slightly enlarged scales, decreasing in size posteriorly. Seven supralabials up to angle of jaw on left and eight on right, six at midorbital position; supralabial I largest, decreasing in size posteriorly; seven infralabials up to angle of jaw, six at midorbital position on left and five on right; infralabial I largest, infralabials decreasing in size posteriorly (Fig. 10C).

Body relatively slender (BW/AGL 0.52), trunk less than half of SVL (AGL/SVL 0.41) without ventrolateral folds; three spine-like scales on either side of flank. Dorsal pholidosis heterogeneous; weakly keeled, granular scales on the vertebral and paravertebral region, intermixed with about three irregularly arranged rows of large, weakly keeled, tubercles on each side of flank (Fig. 11A–C). Scales on occiput and nape much smaller and weakly keeled than those on paravertebral rows; scales on flank slightly larger than those on dorsum, weakly keeled, conical or spine-like. Ventral scales much larger than granular scales on dorsum, those on belly smooth, subcircular subimbricate, equal from chest to vent except for those on precloacal region which slightly larger; mid-body scale rows across belly 29; 123 scales from mental to anterior border of cloaca (Fig. 11B). Scales on throat slightly smaller than those on belly, imbricate; gular region with much smaller, flattened scales with those on chin bordering postmentals, enlarged, juxtaposed and flattened (Fig. 10B). A single femoral pore on left thigh and two on right separated by eight poreless scales on left and 10 on right from a continuous series of three precloacal pores (Fig. 10D).

Scales on dorsal aspect of manus heterogeneous, upper arm with scales much larger than dorsal granules, weakly keeled, imbricate; those near forelimb insertion much smaller than scales on upper arm; dorsal aspect of lower arm and elbow with scales much smaller than those on upper arm, weakly keeled, flat, roughly rounded; dorsal aspect of hand predominantly bearing large, flattened, smooth to weakly keeled, imbricate scales. Ventral aspect of upper arm with smooth, roughly rounded, subimbricate scales; scales on lower arm and wrist large, smooth, imbricate; scales on palm and sole smooth, flat and subcircular. Scales on anterodorsal aspect of thigh much larger

than those on dorsal granules, weakly keeled, imbricate except those near hindlimb insertion which are granular, much smaller than dorsal granules, conical; scales on posterodorsal aspect smaller, smooth to weakly keeled, granular. Scales on dorsal aspect of knee and shank fairly smaller than those on dorsum of thigh, subimbricate, weakly keeled; dorsal aspect of foot predominantly bearing small, flattened, smooth to weakly keeled, imbricate scales; scales on ventral aspect of thigh and shank more or less equal to those on mid-body ventrals, smooth, subcircular, subimbricate on thigh and imbricate on shank (Fig. 9A, B).

Fore-limbs and hind-limbs moderately long, slender (LAL/SVL 0.14); (CL/SVL 0.17); digits long, with a strong, recurved claw, distinctly inflected, distal portions laterally compressed conspicuously. Series of unpaired lamellae on basal portion of digits, separated from unpaired, narrower distal lamellae by a single large scale at the inflection; basal lamellae series: 2-3-3-5-4 (right manus), 2-4-6-6-6 (right pes), 2-3-4-5-4 (left manus; Fig. 10E), 2-5-6-6-5 (left pes; Fig. 10F); distal lamellae series: 9-10-13-12-11 (right manus), 9-11-13-14-13 (right pes), 9-10-13-12-11 (left manus; Fig. 10E), 9-11-13-14-13 (left pes; Fig. 10F). Relative length of digits (measurements in mm in parentheses): IV (2.7) > III (2.5) > II (2.3) = V (2.3) > I (1.7) (left manus); IV (3.7) > III (3.6) > V (3.2) > II (2.8) > I (1.8) (left pes).

Tail entire except for extreme tip which is missing, original, subcylindrical, relatively slender, flattened beneath, marginally shorter than snout-vent length (TL/SVL 0.96) (Fig. 9C–E). Dorsal scales at tail base granular, similar in size and shape to those on midbody dorsals, gradually becoming larger, flatter, subimbricate posteriorly, intermixed with much enlarged, strongly keeled, distinctly pointed, conical tubercles forming whorls; six tubercles on first eight whorls. Scales on ventral aspect of original tail much larger than those on dorsal aspect, subimbricate, smooth, with a series of three enlarged subcaudal scales of which the median series is distinctly larger than adjunct two rows, covering almost entire portion of the tail; those on tail base much smaller, imbricate and smooth, a single enlarged, smooth postcloacal spur on each side (Fig. 9D).

Colouration in life (Fig. 12A). Dorsal ground colour of head, body, limbs and tail grey-brown; head mottled, with a few dark blotches; anterior of brille yellow. Fine dark brown preorbital streak runs from nasal to orbit, two fine dark brown postorbital streaks extend till neck; labials yellow with darker bars. Dorsal markings consist of a dark ocellus outlined by brown just anterior to forelimb insertions followed by four off-white blotches from forelimb insertions to tail base; rest of dorsum strongly mottled with light grey blotches and fine black spots. Flank with smaller dark spots and light grey markings. Tail more grey than body, with 14 alternating light and dark bands, tail tip black. Dorsum of limbs with scattered light grey, brown and black markings; two strong dark streaks on the posterior of femur, digits with alternating dark and light bands. Ventral surfaces dull white, fine speckling

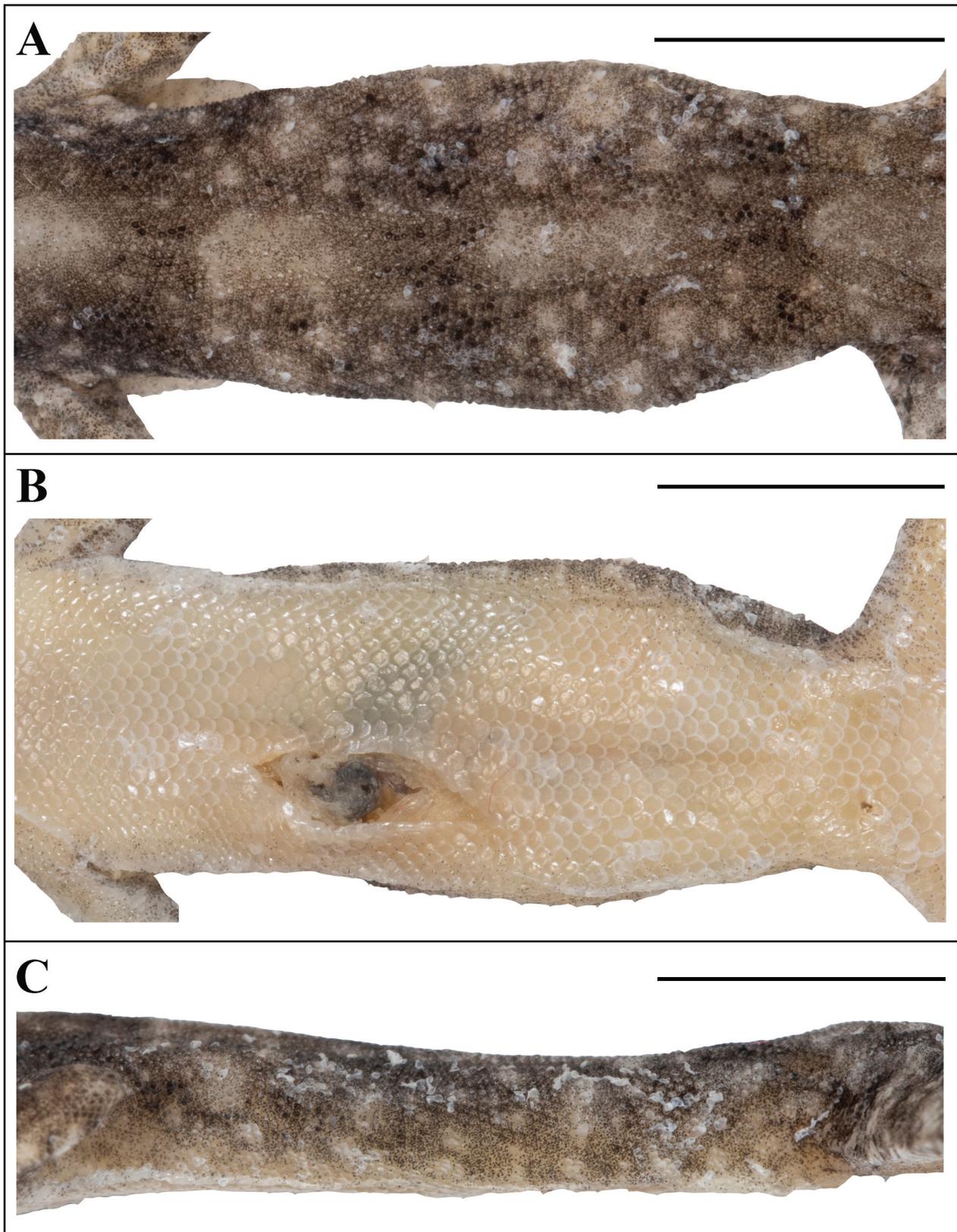


Figure 11. *Cnemaspis cavernicola* sp. nov. (holotype, NRC-AA-1286): **A** dorsal view of mid-body, **B** ventral view of mid-body, **C** lateral view of mid-body. Scale bars 5 mm; photos by Akshay Khandekar.

under forelimbs, throat with a grey longitudinal stripe on each side with some dark markings below eye and angle of jaw, no dark markings on belly, underside of tail lined by a fine dark border. Pupil black, iris silver with an orange streak toward the posterior of the pupil.

Variation and additional information from paratype series. Mensural, meristic and additional character states evaluation data for the paratype series is given in Tables 3–5 respectively. There are two males and two females ranging in size from 28.2–34.0 mm (Fig. 13A, B). All

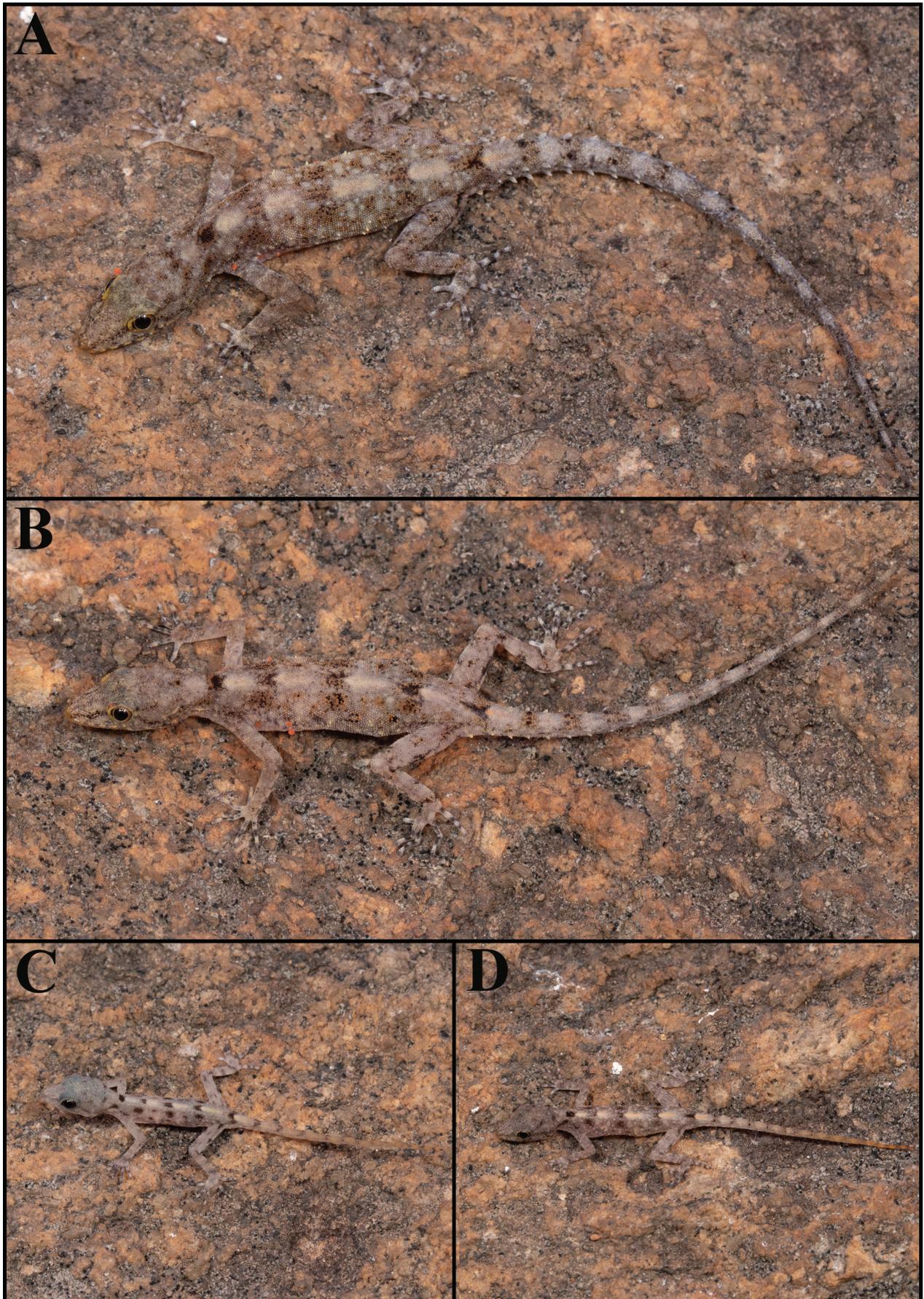


Figure 12. *Cnemaspis cavernicola* sp. nov. in life: **A** adult male (holotype, NRC-AA-1286), **B** adult female (paratype, NRC-AA-1290), **C** juvenile (AK-R 134), **D** juvenile (AK-R 2343). Photos by Akshay Khandekar.



Figure 13. Paratype series of *Cnemaspis cavernicola* sp. nov., from left to right, NRC-AA-1287, NRC-AA-1289, NRC-AA-1288, and NRC-AA-1290: **A** dorsal view, **B** ventral view. Scale bar 10 mm; photos by Akshay Khandekar.

paratypes resemble the holotype except as follows: two internasals separating the supranasals behind rostral in NRC-AA-1288. Inner postmental bordered by infralabial I on either side in NRC-AA-1287, NRC-AA-1289, NRC-AA-1288; inner postmentals bordered by infralabi-

al I and II on left and infralabial I on right side in NRC-AA-1290. Outer postmentals bordered by infralabial I & II in NRC-AA-1287, NRC-AA-1289, NRC-AA-1288; outer postmentals bordered by infralabial II on left and infralabials I & II on right side in NRC-AA-1290; outer

postmental bordered by four gular scales on left and three on right side in NRC-AA-1289; and by five gular scales on left and three on right side in NRC-AA-1290. Two paratypes—NRC-AA-1287 and NRC-AA-1290 with original and complete tail, marginally and slightly longer than body (TL/SVL 1.10 and 1.21 respectively); NRC-AA-1289 with half original half regenerated tail; NRC-AA-1288 with half of the tail missing (Fig. 13A, B). All paratypes agree with the holotype in overall colouration except for unvouchered hatchling and a juvenile which are overall duller than adults and have orange tail tips. (Fig. 12B–D).

Distribution and natural history. *Cnemaspis cavernicola* **sp. nov.** is known only from its type locality (Pakkamalai Reserve Forest, Gingee Hills in Viluppuram district, Tamil Nadu), at elevations of ca. 400–480 m asl. (Fig. 1). *Cnemaspis cavernicola* **sp. nov.** was encountered during a single day of fieldwork each on two different fieldtrips in Pakkamalai. Individuals were observed in small numbers (>10 in 2 hrs) and only in the higher reaches of Pakkamalai in shaded and relatively cooler areas among very large granite boulders. A few individuals were seen moving around in the morning (0930–1130 hrs) on granite rocks ≥ 2 m above the ground and NRC-AA-1287 and a juvenile specimen were seen inactive in a small rock crevice located inside a granite cave in the evening (Fig. 8A, B). Sympatric lizards recorded by us at the type locality include *Cnemaspis pakkamalaiensis* **sp. nov.**, *Calodactylodes aureus*, *Hemidactylus frenatus*, *H. pakkamalaiensis*, *H. whitakeri*, *Eutropis carinata*, and *Psammophilus dorsalis*.

Discussion

The high rate of discovery of South Asian *Cnemaspis* in peninsular India, especially from regions outside the Western Ghats, shows no signs of abating. The discovery of these two species takes the number of peninsular Indian *Cnemaspis* known from outside the Western Ghats to 24, all but one of which have been described since the turn of the century (Jerdon 1853; Das and Bauer 2000; Khandekar 2019; Khandekar et al. 2019, 2020, 2022, Agarwal et al. 2020a, 2020b, 2020c; 2021b, 2022; Narayanan et al. 2022, 2023b). Tamil Nadu is turning out to be particularly diverse, with 13 endemic species of *Cnemaspis* outside the Western Ghats (Das and Bauer 2000; Khandekar 2019; Khandekar et al. 2019, Agarwal et al. 2020c, 2021b, 2022; Sayyed et al. 2023).

The discovery of two more lineages of SAC from peninsular India outside the Western Ghats, including the relict *Cnemaspis cavernicola* **sp. nov.** that has no close extant relatives, is indicative of the long-term persistence of *Cnemaspis* in refugia provided by boulder habitats (Srinivasulu et al. 2015; Agarwal et al. 2020c). This emphasizes the fact that at least for lizards, the true biogeographic unit is peninsular India (and Sri Lanka), though

past climate change has wiped out many cool adapted species from regions outside the Western Ghats, except in refugia linked with boulder habitats, high elevations and or forest (Agarwal et al. 2019, 2020c). Granite boulders in particular have been shown to allow the persistence of *Cnemaspis* outside the Western Ghats, and it is likely that there is high biodiversity across other taxa linked to these refugia (Agarwal et al. 2020c). Rocky, granite habitats are not recognised by the general public or forest department as important habitats with endemic biodiversity and are under immense anthropogenic pressure from quarrying.

Tropical Dry Evergreen Forests (TDEFs) are an important habitat type along the southeast coast of India (Champion and Seth 1968; Meher-Homji 2007). Tropical dry evergreen habitats have been lost across most of their original extent and are restricted to small patches around temples (sacred groves) and a few larger reserve forest areas (Parthasarathy et al. 2008). Previous studies have focused on the floristic diversity of TDEFs, but recent discoveries show the presence of endemic species of lizards including *Cnemaspis avasabinae*, *Cyrtodactylus irulaorum* Agarwal, Thackeray & Khandekar, 2023 and *Cy. relictus* Agarwal, Thackeray & Khandekar, 2023, and *Hemidactylus pakkamalaiensis* (Agarwal et al. 2020a, 2023; Narayanan et al. 2023b). Pakkamalai and the associated Gingee Hills are unique for their extremely rocky formations and the presence of TDEFs, with a unique floristic assemblage including a number of Western Ghats species (Balachandran and Rajendiran 2018). These hills also have numerous endemic species including two species of trees (Ramachandran et al. 2015; Balachandran and Rajendiran 2016) and the recently described *Hemidactylus pakkamalaiensis* (Narayanan et al. 2023b), in addition to the two new species described herein.

Though both new species are sympatric at the type locality, *Cnemaspis pakkamalaiensis* **sp. nov.** is morphologically typical of *mysoriensis* clade species — with a relatively short and broad head, short snout and limbs, and longer trunk; and is distributed between 200–400 m asl. and found < 2 m from ground level on rocks and on the ground. On the other hand, *Cnemaspis cavernicola* **sp. nov.** has the typical morphology of a rock specialist, with a longer and narrower head, elongate snout and limbs and short trunk (Grismer et al. 2015); and has only been recorded from 400–480 m asl. and found >2 m from ground level on rocks. A detailed morphological comparison is needed, but members of the *bangara* clade, *C. adii* and *C. cavernicola* **sp. nov.** are all rock specialists and share a similar morphology, with a relatively elongate head and limbs, and short trunk — adaptations seen in other cave and karst adapted geckos (e.g., Grismer et al. 2015). *Cnemaspis* species from divergent clades are sympatric at many localities in the Central and Southern Western Ghats; while in regions of peninsular India outside the Western Ghats, rock-dwelling (*C. adii*, *bangara* clade species, *C. cavernicola* **sp. nov.**) and generalist ecomorphs (*mysoriensis* clade) are sympatric wherever the former occur, including multiple localities on the Mysore Plateau and Pakkamalai (e.g. Agarwal et al. 2017, 2020c, 2021b, 2022). Much sampling remains to be carried out to first

understand patterns of diversity and distribution within this hyper-diverse genus, and to then try and unravel ecology and behaviour of individual species and communities.

Acknowledgements

We are thankful to the Tamil Nadu Forest Department for permits (permit no. 53/2018), and Teja Bhargava (TN FD) for all his help with coordination. Fieldwork wouldn't have been possible without the help of Satpal Gangalmale, Swapnil Pawar, Vaibhav Patil and Vivek Waghe. Satpal and Vivek helped with morphological data collection. We thank Uma Ramakrishnan for lab support and Yeshwant HM, Vivek Ramachandran and Tarun Karmakar (NCBS field station and museum facility, Bengaluru) for specimen registrations. Suranjan Karunarathna and two anonymous reviewers provided valuable inputs on the manuscript.

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Appendix 1

Specimens examined.

Museum abbreviations are as follows: Bombay Natural History Society, Mumbai (**BNHS**), National Centre for Biological Sciences (**NCBS/NRC-AA**, including Akshay Khandekar field series [**AK**]) and Centre for Ecological Sciences, Bangalore (**CES G**).

Cnemaspis adii: BNHS 2464, and BNHS 2465 from near Hampi, Ballary District, Karnataka, India.

Cnemaspis avasabinae: holotype, NCBS-BH754 (adult male); paratypes, NCBS-BH755, NCBS-BH756, (adult males) from Penchalakona, Nellore District, Andhra Pradesh, India.

Cnemaspis mysoriensis: AK569, AK570, AK 571 from National Centre for Biological Sciences (NCBS) campus, Bengaluru, Bengaluru District; AK 676 from Hunsur, Mysore District; AK 851, AK 852 from Kolar, Kolar District; BNHS 1701–1705 and BNHS 1831–1835, AK 979 from near Thathaguni, Bangalore Rural District, Karnataka, India.

Cnemaspis otai: BNHS 2511, BNHS 2512 and AK 668 from Vellore Fort; AK 823, AK 935 from Jawadhu Hills, Vellore District, Tamil Nadu, India.

Cnemaspis rishivalleyensis: holotype, NCBS-BH723 (adult male); paratypes NCBS-BH724, NCBS-BH725, NCBS-BH726, NCBS-BH727 (adult females), from Cave Rock Hill, near Rishi Valley School, Chittoor District, Andhra Pradesh, India.

Cnemaspis stellapulvis: holotype, NCBS-BH757 (adult male); paratypes, NCBS-BH759, NCBS-BH664 (adult males), NCBS-BH758, NCBSBH760, NCBS-BH761, NCBS-BH762 (adult females), from near Haddina Kallu Anjaneya Temple, at the base of granite rocky hillock near Yadiyur, Mandya District, Karnataka, India.

Cnemaspis tigris: holotype, NRC-AA-1159 (adult male); paratypes, NRC-AA-1160, BNHS 2809, and BNHS 2810 (adult males), BNHS 2811 (adult female), from near Kaiwara, Chickballapur District, Karnataka, India.

Cnemaspis yercaudensis: NCBS-BH678 (adult male), and NCBS-BH677 (adult female), AK 767, from near Grange resort, Yercaud town, in the Shevaroys, Salem District; NCBS-BH679, BNHS 2533 (adult males), NCBS-BH680, BNHS 2532, BNHS 2534 (adult females), from near Nallathambi resort, Kollimalai, Namakkal District, Tamil Nadu, India.