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Two new spotted species of the *Cyrtodactylus* (*Geckoella*) *collegalensis* (Beddome, 1870) complex from the south-eastern coast of India (Reptilia: Squamata)

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Abstract

We describe two new spotted species of ground-dwelling gecko of the genus *Cyrtodactylus* (*Geckoella*) from southeastern India in an integrative taxonomic framework. The new species are recovered as sister taxa within the *C. collegalensis* species complex, with 13.0–16.7% uncorrected mitochondrial sequence divergence from the other eight members of the *C. collegalensis* complex and 10.4% from one another. The new species are morphologically diagnosed by a spotted dorsal pattern of four pairs of spots (occasionally fused into figure 8-shaped markings) from the banded species *C. aravindi*, *C. speciosus*, *C. rishivalleyensis* and *C. yakhuna*; and from the spotted species with three or fewer pairs of spots in *C. collegalensis* and *C. srilekhae*; and from *C. chengodumalaensis* by the absence of any enlarged dorsal scales and from *C. varadgirii* by the absence of a patch of enlarged roughly hexagonal scales on the canthus rostralis and beneath the angle of the lower jaw. The two new species can only be differentiated from each other based on slight differences in body size, relative body width and other statistically significant, size-corrected morphometric characters. These are among the first endemic lizards from Tropical Dry Evergreen habitats along the southeast coast of India.

Keywords

Cryptic species, endemic species, integrative taxonomy, mitochondrial DNA, southern India, taxonomy

Introduction

Peninsular India is an incredibly biodiverse landscape, encompassing part of the Western Ghats-Sri Lanka Biodiversity Hotspot. Besides the unique geological history of the Indian plate (Chatterjee et al. 2013), the varied topography, presence of east and west coasts and two distinct monsoon seasons in certain regions, combined with longitudinal and latitudinal gradients in temperature and rainfall are some major contributing factors to the high species diversity and endemism (Karanth 2015). The dry or semi-arid zone is the most conspicuous feature, with >75% of tropical peninsular India receiving <1,400 mm annual rainfall (Ficks and Hijman 2017). The dry zone comprises mainly warm and open habitats including vast agricultural and otherwise human modified landscapes, with forests and relatively cool habitats patchily distributed across hilly and coastal areas. Some of the gekkonid

genera typical of cool habitats in peninsular India include *Calodactylodes* Strand, 1928, *Cnemaspis* Strauch, 1887, *Cyrtodactylus* Gray, 1827 and *Hemiphyllodactylus* Bleeker, 1860 (Smith 1935; Srinivasulu et al. 2014; Agarwal et al. 2019).

The genus *Cyrtodactylus* is the most diverse gekkonid and third most diverse vertebrate genus, including over 340 species distributed from the Western Himalayas through South and Southeast Asia to the Western Pacific (Wood et al. 2012; Grismer et al. 2021; Uetz et al. 2023). The vast majority of species in the genus are scansorial, with one major terrestrial radiation, the subgenus *Geckoella* Gray, 1867 (Agarwal and Karanth 2015) that corresponds to the *triedrus* clade within the *triedrus* group (Grismer et al. 2021). *Cyrtodactylus* (*Geckoella*) includes 10 species that are endemic to peninsular India and four to Sri Lanka (Smith 1935; Agarwal 2016; Agarwal et al. 2016; Amarasinghe et al. 2022; Narayanan et al. 2022; Agarwal et al. 2023).

Phylogenetic relationships within *Geckoella* are well understood, the Sri Lankan *C. triedrus* (Günther, 1864) complex forming the sister taxon to the remaining species; which are split into a wet zone subclade that includes the *C. albofasciatus* (Boulenger, 1885) and *C. deccanensis* (Günther, 1864) complexes; and a dry zone subclade which includes *C. jeyporensis* (Beddome, 1878) as the sister taxon to the *C. nebulosus* (Beddome, 1870) complex; and the *C. collegalensis* (Beddome, 1870) complex with seven species in India and one in Sri Lanka (Smith 1935; Somaweera and Somaweera 2009; Agarwal and Karanth 2015; Agarwal 2016; Agarwal et al. 2016; Narayanan et al. 2022; Agarwal et al. 2023).

Beddome (1870) described two species of *Geckoella* from southern India, *Cyrtodactylus* (*Geckoella*) *collegalensis* from the BR Hills, Karnataka and *C. speciosus* (Beddome, 1870) from near Erode, Tamil Nadu. The latter species was treated as a synonym of *C. collegalensis* soon after (Boulenger 1885) though numerous colour forms of *Cyrtodactylus* (*Geckoella*) *collegalensis* were known from across southern India and Sri Lanka (Smith 1935). The only treatment of any of these colour morphs was by Deraniyagala (1945), who described *C. yakhuna* (Deraniyagala, 1945) from Sri Lanka. The *C. collegalensis* complex has long been suspected to include multiple taxa in India (Mirza and Pal 2010) and besides the recognition of *C. speciosus* as a distinct form (Agarwal and Karanth 2015), five species have been described since 2016 (Agarwal 2016; Agarwal et al. 2016; Narayanan et al. 2022; Agarwal et al. 2023). These include *C. varadgirii* Agarwal et al., 2016 from central and western India, *C. rishivalleyensis* Agarwal, 2016 and *C. srilekhae* Agarwal, 2016 from the southern edge of the Mysore Plateau, *C. aravindi* Narayan et al., 2022 from southern Tamil Nadu and *C. chengodumalaensis* Agarwal et al., 2023 from coastal Kerala (Fig. 1). Examination of spotted morphs from the southeast coast of Andhra Pradesh and Tamil Nadu that were collected between 2012–2014 reveal the presence of two more unnamed species. We use mitochondrial sequence data and morphological data to describe these below.

Materials and Methods

Taxon sampling

Specimens were collected by hand and photographed with a Nikon D300 SLR camera with a 60 mm macro lens and external flashes, followed by euthanasia with an overdose of halothane/ isoflurane. Liver or tail samples were collected in molecular grade ethanol and subsequently stored at –20 °C. Specimens were fixed in 4% formaldehyde for ~24 hours to a few weeks, subsequently rinsed in water and transferred to 70% ethanol for long-term storage. Specimens are deposited in the museum and research collection facility at the National Centre for Biological Sciences, Bengaluru (**NCBS/NRC**).

Molecular Data

We extracted genomic DNA from liver/tail-tips using the Qiagen DNeasy kit and amplified and sequenced the mitochondrial gene ND2 (1038 base pairs, bp) using the primers MetF1 (L4437) and H5540 (Macey et al. 1997). PCR volume was 25 µl and reactions were executed on an Eppendorf thermocycler, with an initial denaturation for 2 minutes at 95°C, followed by 95°C for 35 s, annealing at 50°C for 35 s, and extension at 72°C for 150 s for 32 cycles. Purification and sequencing of PCR products was outsourced to Amnion Biotech Pvt. Ltd. (Bangalore, India). Complementary strands were sequenced in most cases and manually assembled to ensure sequence accuracy. The new sequences were combined with published sequences for all members of the *triedrus* group (Grismer et al. 2021), with members of the *Cyrtodactylus fraenatus* group as the outgroup (Table 1). Sequence alignment was carried out using CLUSTAL W (Thompson et al. 1994) in MEGA 5.2 (Tamura et al. 2011), with translation to amino acids to verify (the protein-coding) sequences.

Uncorrected p-distance between members of the *C. collegalensis* complex was calculated in MEGA 5.2 using the pairwise deletion option (Table 2). A Maximum Likelihood (ML) analysis was carried out using the IQ-TREE webserver (Nguyen et al. 2015; Trifinopoulos et al. 2016), with selection of partitioning scheme and substitution models in ModelFinder (Kalyaanamoorthy et al. 2017), which selected two partitions — codon position (1+2) and codon position (3), applying the TIM+F+G4 and TIM2+F+I+G4 models, respectively. Settings for the analysis included edge-linked partitions, 1000 ultrafast bootstraps and other parameters at default settings. PartitionFinder 2.1.1 (Lanfear et al. 2012) was used to pick the best-fitting partitioning scheme and models of sequence evolution for ML analyses in RaXML HPC 8.2.12 (Stamatakis 2014) and Bayesian Inference (BI) in MrBayes 3.2.7 (Ronquist and Huelsenbeck 2003). The best partitioning scheme was by codon position, with the HKY+G, GTR+G, GTR+I+G models selected for codon positions 1–3. A ML phylogeny was reconstructed using the ND2 data partitioned by codon position in RAxML as imple-

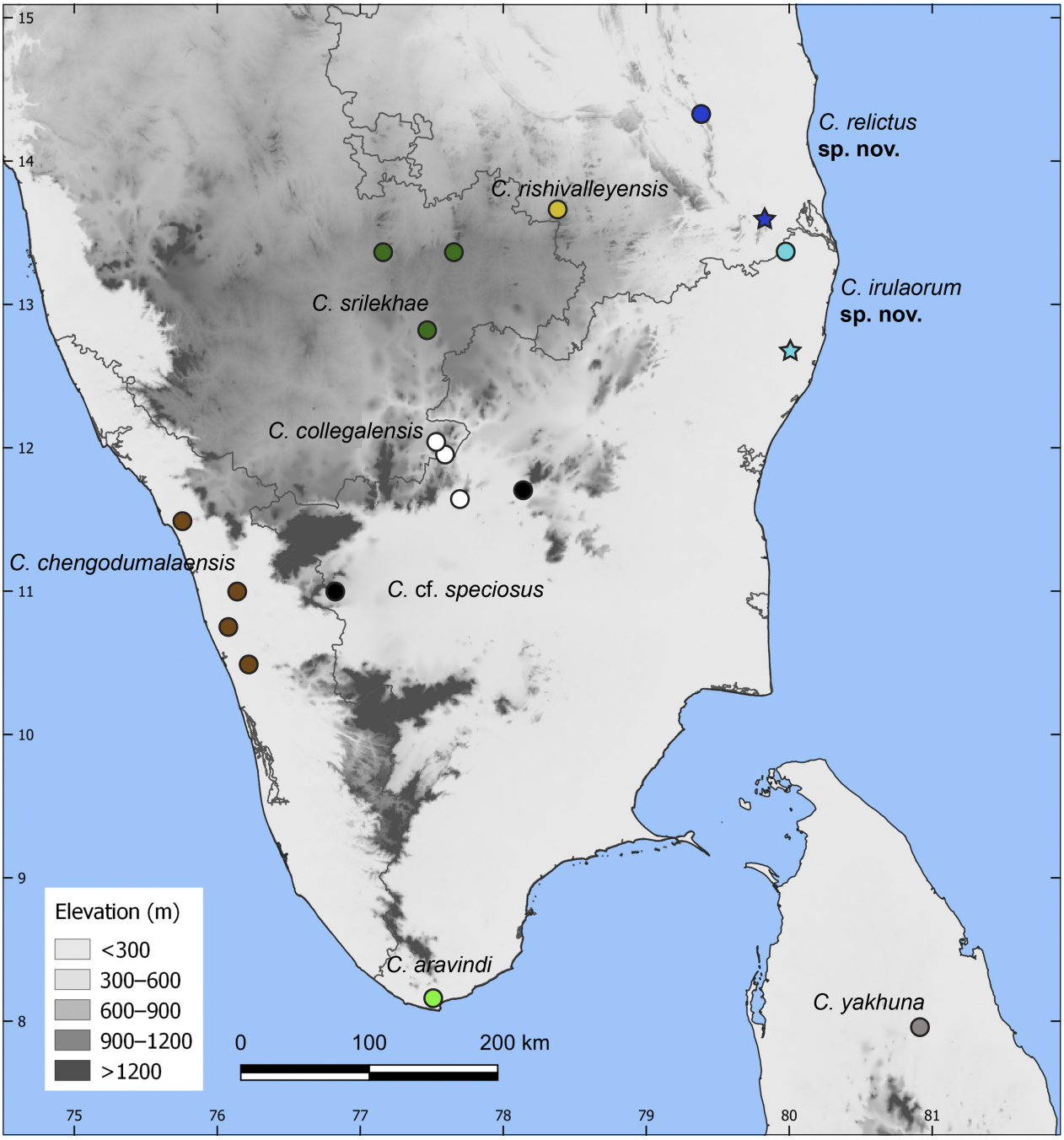

Figure 1. Map showing localities sampled for phylogenetic analyses of members of the *Cyrtodactylus* (*Geckoella*) *collegalensis* complex in southern India and Sri Lanka (*C. varadgirii* is not shown), stars represent the type localities of the two new species. Light blue, *C. irulaorum* **sp. nov.**; dark blue, *C. relictus* **sp. nov.**; light green, *C. aravindi*; brown, *C. chengodumalaensis*; white fill, *C. collegalensis*; black, *C. speciosus*; dark green, *C. srilekhae*; yellow, *C. rishivalleyensis*; grey fill, *C. yakhuna*.

mented in the raxmlGUI 2.0.10 (Edler et al. 2020), applying the GTR+G model, 1000 thorough bootstraps and 10 independent starting trees.

We conducted partitioned BI in MrBayes using the best-fit models and parameters estimated in PartitionFinder 2. The analysis had two parallel runs and four chains each (one cold and three hot) and was run for 2,000,000 generations sampling every 200 generations. Convergence was determined based on the standard deviation of split frequencies (<<0.01) and the first 25% of trees were discarded as burn-in. A Maximum Clade Credibility tree was generated using TreeAnnotator 1.10.4 (Drummond et al. 2012).

Species Delimitation

Our phylogeny and dataset overlap almost entirely with a recently published phylogeny that used a distance-based and two tree-based methods for species delimitation (Agarwal et al. 2023). They found congruence between their distance-based method and one tree-based analysis, with relative over-splitting applying the second tree-based method (Agarwal et al. 2023). We therefore chose to use the more simplistic distance-based method which relies on the lowest pairwise distance between species of the *Cyrtodactylus* (*Geckoella*) *collegalensis* complex that

Table 1. List of sequences used in this study with museum number, locality and GenBank accession number. Museum and voucher abbreviations: ADS = Anselm de Silva field series; BNHS = Bombay Natural History Society, Mumbai; CES/ESV = Centre for Ecological Sciences, Bangalore; DMSSK = D.M.S. Suranjan Karunarathna field series; IAG = Ishan Agarwal field series; JB = John Boone private collection; NCBS/ NRC = National Centre for Biological Sciences, Bangalore; ZSI = Zoological Survey of India, Kolkata.

Species	Museum No.	Locality	GenBank Accession Numbers	
C. aravindi	ZSI-R 28275	India: Tamil Nadu, Kanyakumari district, Nagercoil	OP131039	*collegalensis* complex
C. chengodumalaensis	NRC-AA-1163 (CES09/1410)	India: Kerala, Thrissur District, Mannuthy	OP271668	
C. chengodumalaensis	NRC-AA-1166 (CES09/1411)	India: Kerala, Thrissur District, Mannuthy	OP271669	
C. chengodumalaensis	BNHS 2812 (CES09/1412)	India: Kerala, Calicut District, Narayamkulam	OP271670	
C. chengodumalaensis	NRC-AA-1161 (CES09/1449)	India: Kerala, Malappuram District, Kumaragiri Estate	OP271671	
C. chengodumalaensis	BNHS 2817 (AK665)	India: Kerala, Palakkad District, Cheeni Paara	OP271672	
C. collegalensis	CES09/1403	India: Tamil Nadu, Salem District, Mettur Taluk	KX632365	
C. collegalensis	CES09/1442	India: Karnataka, Chamarajanagar District, Male Mahadeshwar Hills	KX632362	
C. collegalensis	CES09/1443	India: Karnataka, Chamarajanagar District, Kollegal Taluk	KX632363	
C. collegalensis	CES09/1444	India: Karnataka, Chamarajanagar District, MM Hills	KM878627	
C. collegalensis	CES09/1463	India: Karnataka, Chamarajanagar District, MM Hills	KX632364	
C. irulaorum **sp. nov.**	CES09/1363	India: Tamil Nadu, Villupuram District, near Vallam RF	OQ674252	
C. irulaorum **sp. nov.**	CES09/1365	India: Tamil Nadu, Villupuram District, near Vallam RF	OQ674252	
C. irulaorum **sp. nov.**	NRC-AA-1266 (CES09/1438)	India: Tamil Nadu, Villupuram District, near Vallam RF	OQ674252	
C. irulaorum **sp. nov.**	NRC-AA-1270 (CES09/1441)	India: Tamil Nadu, Villupuram District, near Vallam RF	OQ674253	
C. irulaorum **sp. nov.**	NRC-AA-1271 (IAG 193)	India: Tamil Nadu, Tiruvallur District, near Thervoy Kandigai	OQ674254	
C. relictus **sp. nov.**	NRC-AA-1275 (CES09/1470)	India: Andhra Pradesh, Chittoor District, Kambakkam Durg	OQ674255	
C. relictus **sp. nov.**	NRC-AA-1276 (CES09/1471)	India: Andhra Pradesh, Nellore District, near Penchalakona	OQ674256	
C. relictus **sp. nov.**	NRC-AA-1274 (CES09/1472)	India: Andhra Pradesh, Nellore District, near Penchalakona	OQ674257	
C. rishivalleyensis	ESV 104 (CES09/1245)	India: Andhra Pradesh, Chittoor District	KX698080	
C. rishivalleyensis	ESV 103 (CES09/1452)	India: Andhra Pradesh, Chittoor District	KX698081	
C. cf. *speciosus*	CES09/1405	India: Tamil Nadu, Coimbatore District, Coimbatore North Taluk	KM878623	
C. cf. *speciosus*	CES09/1249	India: Tamil Nadu, Salem District, below Yercaud	KM878629	
C. srilekhae	ESV 101 (CES09/1432)	India: Karnataka, Bengaluru Rural District	KX698082	
C. srilekhae	ESV 102 (CES09/1461)	India: Karnataka, Bengaluru Rural District	KX698083	
C. srilekhae	CES09/1536	India: Karnataka, Tumkur District, Devarayandurga	KX698084	
C. varadgirii	BNHS 1848	India: Maharashtra, Mumbai	KX632366	
C. varadgirii	BNHS 1849	India: Maharashtra, Mumbai	KX632367	
C. varadgirii	BNHS 2099	India: Gujarat, Navsari District, Vansda	KX632368	
C. varadgirii	CES09/1381	India: Gujarat, Navsari District, Chikhli	KM878612	
C. varadgirii	CES09/1433	India: Gujarat, Navsari District, Kangvai	KX632369	
C. yakhuna	DMSSK 159	Sri Lanka: Polonnaruwa District, Giritale Forest	MW713942	
C. albofasciatus	CES09/1109	India: Karnataka, Chikmagalur District, Kudremukh	KM878626	*Geckoella*
C. albofasciatus	CES09/1117	India: Karnataka, Shimoga District, Nagavalli	KM878625	
C. cf. *albofasciatus*	CES09/1391	India: Maharashtra, Kolhapur District, Patgaon	KM878610	
C. cf. *albofasciatus*	CES09/1418	India: Goa, North Goa District, Chorla Ghat	KM878611	
C. cf. *albofasciatus*	JB7	India: captive (from Indian stock)	JX440521	
C. deccanensis	CES09/1112	India: Maharashtra, Satara District, Bhairavgad	KM878615	
C. deccanensis	CES09/1243	India: Maharashtra, Thane District, Malshej Ghat	KM878614	
C. deccanensis	CES09/1380	India: Maharashtra, Nashik District, Amboli	KM878613	
C. cf. *deccanensis*	CES09/1396	India: Maharashtra, Kolhapur District, Panhala	KM878628	
C. jeyporensis	CES09/1206	India: Orissa, Koraput District, Deomali	KM878617	
C. jeyporensis	CES09/1356	India: Andhra Pradesh, Visakhapatnam District, Araku Valley	KM878616	
C. nebulosus	CES09/1351	India: Andhra Pradesh, Visakhapatnam District, Narsipatnam	KM878618	
C. cf. *nebulosus*	CES09/1118	India: Orissa, Mayurbhanj District, Baripada	KM878620	
C. cf. *nebulosus*	CES09/1119	India: Orissa, Mayurbhanj District, Tikarpada	KM878619	
C. cf. *nebulosus*	CES09/1205	India: Orissa, Koraput District, Gupteswar	KM878621	
C. cf. *nebulosus*	CES09/1374	India: Madhya Pradesh, Anuppur District, Amarkantak	KM878622	
C. punctatus	DMSSK 180	Sri Lanka: Matale District, Knuckles	MW713941	
C. triedrus	DMSSK 011	Sri Lanka: Kandy District, Dunumadalawa Forest	MW713937	
C. vedda	ADS35	Sri Lanka: Yakkunehela	JX440522	

Species	Museum No.	Locality	GenBank Accession Numbers	
Cyrtodactylus fraenatus	DMSSK 046	Sri Lanka: Kandy District, Gannoruwa	MW713940	*fraenatus* group
Cyrtodactylus soba	DMSSK 124	Sri Lanka: Matale District, Knuckles	MW713938	

Table 2. Uncorrected pairwise genetic distance (mitochondrial ND2 gene, 1038 nt) between species of the *Cyrtodactylus* (*Geckoella*) *collegalensis* complex. Along diagonal, range of variation within species with multiple samples.

	Species	1	2	3	4	5	6	7	8	9
1	*C. irulaorum* **sp. nov.**	0.0–0.6								
2	*C. relictus* **sp. nov.**	10.4	0.7–1.6							
3	*C. aravindi*	13.2	13.7	-						
4	*C. chengodumalaensis*	14.2	14.8	10.5	0.1–1.3					
5	*C. collegalensis*	16.7	16.6	14.7	14.5	0.0–4.7				
6	*C. rishivalleyensis*	15.6	14.6	12.0	11.7	13.4	0.6			
7	*C.* cf. *speciosus*	15.2	14.7	12.8	13.0	14.4	12.0	6.4		
8	*C. srilekhae*	16.0	15.4	12.1	12.3	14.1	8.7	11.3	0.8–1.0	
9	*C. varadgirii*	13.0	13.7	11.8	13.6	14.3	11.0	13.8	12.4	0.1–1.6
10	*C. yakhuna*	13.7	15.0	10.5	10.0	13.8	11.9	12.8	11.8	11.4

can be distinguished based on morphology (Table 2; test analyses using the same tree-based methods as Agarwal et al. 2023 yielded identical results).

Morphological and meristic data

A total of eight and three specimens of each new species were used for morphological data and comparisons were made with all species of the *Cyrtodactylus collegalensis* complex based on material in the collections of the Natural History Museum, London (**BMNH**), Bombay Natural History Society, Mumbai (**BNHS**), Centre for Ecological Sciences, Bangalore (**CES**), National Centre for Biological Sciences, Bangalore (**NRC**) (Appendix 1) as well as the original published description of *C. yakhuna* (Deraniyagala 1945). We follow Agarwal et al. (2023) for morphological data. We recorded colour pattern from live photographs or specimens and took counts and measurements under a ZEISS Stemi 305 stereo dissecting microscope, with bilateral scale counts taken on the left and right of specimens. When summarizing measurements, mean is presented ± standard deviation. We took the following measurements on the right side of the body, where possible, with a Mitutoyo digital vernier caliper (to the nearest 0.1 mm): snout vent length (**SVL**, from tip of snout to cloacal opening); tail length (**TL**, from cloaca to tip of tail); tail width (**TW**, measured at tail base); lower arm length (**LAL**, from elbow to distal end of wrist); crus length (**CL**, from knee to heel); axilla to groin length (**AGL**, from posterior margin of forelimb insertion to anterior margin of hindlimb insertion); body height (**BH**, maximum body height); body width (**BW**, maximum body width); head length (**HL**, distance between retroarticular process of lower jaw and tip of snout); head width (**HW**, maximum width of head); head depth (**HD**, maximum head depth at occiput); eye diameter (**ED**, greatest horizontal diameter of eye); eye to ear distance (**EE**, distance from anterior edge of ear opening to posterior margin of eye); eye to snout distance (**ES**, distance between anterior margin of eye and tip of snout); eye to nares distance (**EN**, distance between anterior margin of eye and posterior edge of nostril); internarial distance (**IN**, distance between nares); interorbital distance (**IO**, shortest interorbital distance across frontal between the orbits); ear length (**EL**, maximum length of ear opening). Following meristic data were recorded for all specimens: number of supralabials and infralabials (**SL** and **IL**, from rostral and mental, respectively, to posterior-most enlarged scale at angle of the jaw); supralabials and infralabials at midorbital position (**SL M** and **IL M**, from rostral and mental, respectively, to below the middle of the eye); subdigital lamellae (**TLam**) were counted in two series, basal lamellae series (**BLam**, includes scales at least twice the diameter of palmar scales to and including large scale at digital inflection), and distal lamellae series (**DLam**, with lamellae distal to digital inflection including ventral claw sheath), counted on manus: digit 1 (**F1**), digit 4 (**F4**), on pes: digit 1 (**T1**), and digit 4 (**T4**); post cloacal tubercles (**PCT**, number of enlarged tubercles counted on either side of the tail base).

Colour pattern

We recorded colour pattern elements following Agarwal (2016). Head marking elements based on position include a prefrontal spot; two interorbital spots; interparietal

streak/spots flanked by two parietal spots; a post-occipital collar that may be entire or broken into spots; and a preocular and postocular streak (s). Body pattern includes the following characters: dorsum with dark bands/paired spots/mid-vertebrally fused blotches; width of bands/spots relative to lighter interspaces; relative width/size of dorsal bands/spots; number of dark bands/paired spots posterior to post-occipital collar and up to hindlimb insertion; number of dark bands on original tail; presence/absence of stippling between bands/spots; presence/absence of lateral spots; presence/absence of streaks/spots on forelimb/hindlimb; presence/absence and extent of gular streaks.

Morphological analyses

As preliminary data demonstrated the two new species described herein were easily diagnosable in colour pattern from all known species of the *collegalensis* complex, but not from each other (see results), we conducted detailed morphological analyses for only the two new species. Analyses were conducted in R 4.1.3 (R Core Team 2018) using the following mensural variables: AGL, BW, CL, ES, HL, HW, LAL, SVL (tail measurements were not included because of missing data and smaller head measurements were excluded). The low sample sizes for each sex and species, and that *Cyrtodactylus* and *Cyrtodactylus* (*Geckoella*) species are not known to be strongly sexually dimorphic (e.g., Agarwal et al. 2016; Grismer et al. 2018, 2020) meant that we pooled both sexes to maximize sample size (test analyses that are not shown which used only females, for which the sample size was >2 for both species, yielded similar results to the pooled data). We also chose to include all 11 individuals of both species in the analysis as the minimum SVL was >70% of maximum SVL (i.e., no juveniles that could skew results; Chan and Grismer 2022). We used three different data treatment techniques to distinguish between the two species: raw data (log transformed), ratios (trait/ SVL) and allometric size correction (Chan and Grismer 2021, 2022). Raw data does not capture how shape might scale with size, while ratios are easy to interpret and can be useful in keys and diagnoses, though allometric size correction is considered superior to these methods (Chan and Grismer 2022). The allometric size correction used Thorpe's (1975) equation which standardizes variables by SVL for each species relative to the global mean SVL, as implemented in the R package GroupStruct (available at https://github.com/chankinonn/GroupStruct) (Chan and Grismer 2021, 2022). A principal components analysis (PCA) was conducted to verify the two new species occupied different positions in multivariate morphospace using the size-corrected data (excluding SVL) as well as the ratio and raw data. Individual traits from all three datasets were compared using t-tests as p-values of Levene's tests on each trait were >0.05.

Results

Phylogenetic relationships

Our dataset overlaps closely with recently published phylogenies for the group (Narayanan et al. 2022; Agarwal et al. 2023) and we recover the same broad relationships within a well-supported, monophyletic *Geckoella* (entire tree not shown). A basal split separates the *Cyrtodactylus* (*Geckoella*) *triedrus* complex from a clade grouping a wet zone clade (*C. albofasciatus* + *C. deccanensis* complexes) and a dry zone clade (not shown). Within the latter clade, the *C. collegalensis* complex is the sister taxon to *C. jeyporensis* + the *C. nebulosus* complex (not shown). The two putative new species are sister taxa within the *C. collegalensis* complex, and together form the sister taxon to the remaining species (Fig. 2). The new species are 13.0–16.7% divergent from members of the *C. collegalensis* complex and 10.4% (10.0–11.5%) divergent from each other (Table 2).

Species Delimitation

The lowest genetic divergence between described members of the *collegalensis* complex is at 8.7% between *Cyrtodactylus* (*Geckoella*) *srilekhae* and *C. rishivalleyensis*. Employing this cut-off recovered 11 species — *C. aravindi*, *C. collegalensis*, *C. chengodumalaensis*, *C. rishivalleyensis*, *C.* cf. *speciosus* (two lineages), *C. srilekhae*, *C. varadgirii*, *C. yakhuna* and one unnamed lineage each from southeast coastal regions of Andhra Pradesh and Tamil Nadu.

Morphological analyses

The PCAs using raw data and size corrected data were qualitatively very similar and showed the two putative species separated across PC1 (Fig. 2), while the ratio data did not show much separation. PC1 accounted for >90% of variation in all analyses, though all traits contributed to some extent and it was not possible to determine which were the most discriminatory variables. There were significant differences ($p < 0.05$) between the two lineages in all the dependent variables in the size corrected dataset, all except AGL and LAL in the raw data, but the only significantly different character in the ratio data was BW/ SVL.

The two lineages from the southeast coast are genetically divergent from one another and reciprocally monophyletic, besides being separated in multivariate morphological space with significantly different values for traits using different analytical methods. Below, we formally describe *Cyrtodactylus* (*Geckoella*) *irulaorum* **sp. nov.** and *C. relictus* **sp. nov.** based on morphological data.

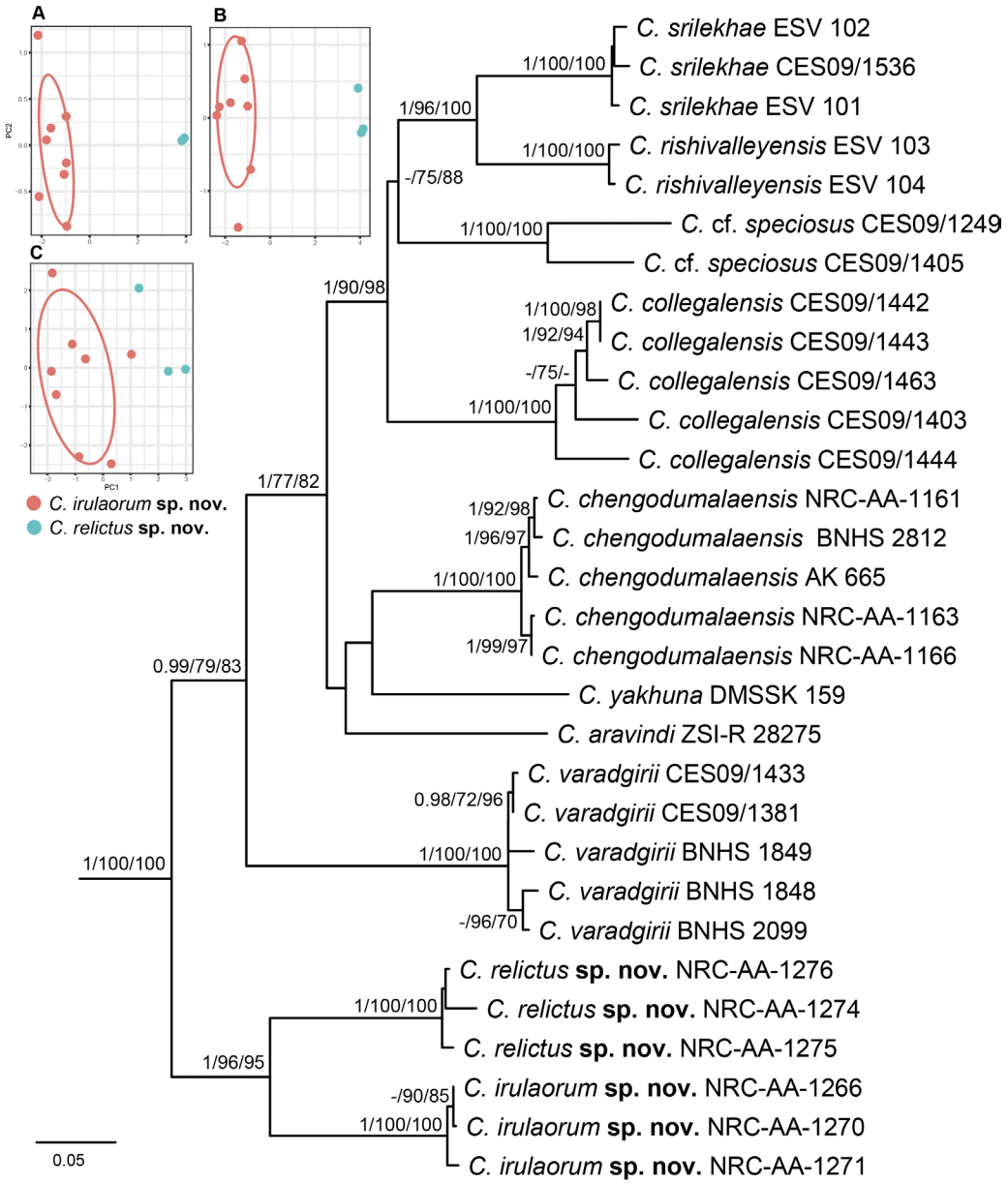

Figure 2. Maximum likelihood phylogeny of the *Cyrtodactylus* (*Geckoella*) *collegalensis* complex with inset showing PCA plots for the three data treatments: **A** allometric, **B** raw and **C** ratios. Other members of the *triedrus* group are not shown. Posterior probability (≥0.98)/ ML bootstrap support (≥70) for RaXML/ IQTree shown at nodes. Note that sequences for CES09/1363 and CES09/1365 are identical to NRC-AA-1266 and are not shown in the tree (Table 1).

Systematics

Cyrtodactylus (*Geckoella*) *irulaorum* sp. nov.

https://zoobank.org/972542B9-EF36-4D70-922B-499C49370E18

Figs 3–8; Table 3

Holotype. NRC-AA-1266 (CES09/1438), adult male, from a farm near Vallam Reserve Forest (12.6920°N, 80.0263°E; ca. 55 m asl.), Kancheepuram District, Tamil Nadu, India, collected by Ishan Agarwal on 10th April 2013.

Paratypes. NRC-AA-1267 (CES09/1437), NRC-AA-1268 (CES09/1439), NRC-AA-1269 (CES09/1440), NRC-AA-1270 (CES09/1441), adult males, same collection data as holotype; NRC-AA-1272 (AK 105), NRC-AA-1273 (AK 106), adult females, same collection data as holotype except collected by Ishan Agarwal, Akshay Khandekar, R. Chaitanya and Caleb Daniel on 11th November 2017; NRC-AA-1271 (IAG 193), adult female, from Thervoy Kandigai (13.3713°N, 79.9791°E; ca. 30 m asl.), Tiruvallur District, Tamil Nadu, India, collected by R. Chaitanya on date 14th December 2015.

Etymology. The specific epithet is a patronym in honour of the Irula tribe, an indigenous Dravidian group who are expert snake trackers and catchers. Romulus Whitaker,

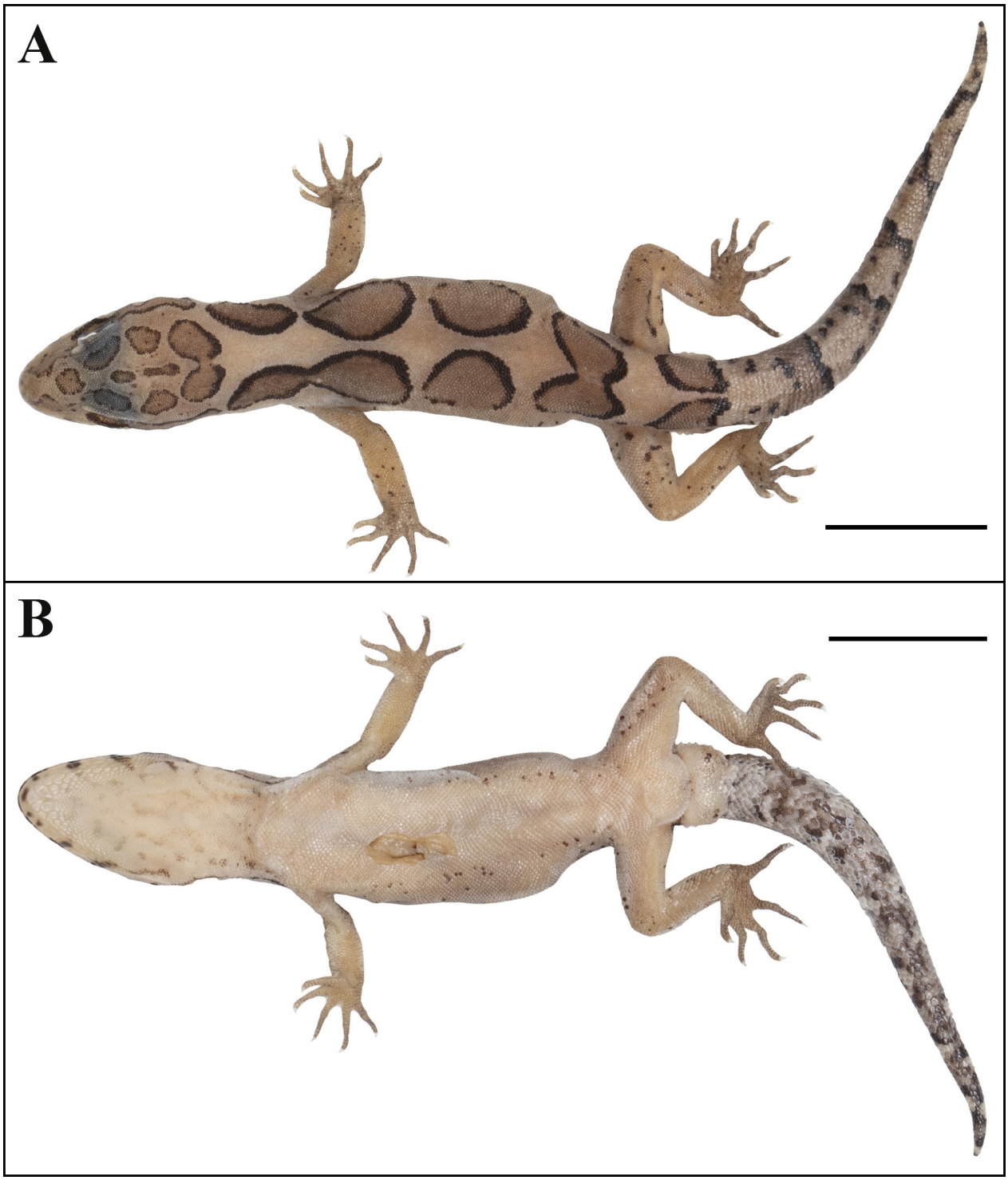

Figure 3. *Cyrtodactylus* (*Geckoella*) *irulaorum* **sp. nov.** (holotype, NRC-AA-1266): **A** dorsal view of body, **B** ventral view of body. Scale bars 10 mm; photos by Akshay Khandekar.

whose farm the type series was collected at, has worked closely with the Irulas for decades and helped them set up a venom extraction cooperative in 1978. The Irula Snake Catchers' Industrial Cooperative Society is the largest contributor to antivenom production in India.

Suggested common name. Irula *Geckoella*.

Diagnosis. A small-sized *Cyrtodactylus* (*Geckoella*), snout to vent length up to 51 mm (n = 8); tail shorter than SVL. Dorsal pholidosis on trunk homogeneous; covered with smooth, subcircular, weakly conical granular scales; scales on occiput and nape slightly smaller and more rounded than those on body dorsum, scales on flank slightly larger than those on dorsum; ventral scales much larger than dorsal scales, smooth, somewhat elongate, subimbricate, subequal from chest to vent; femoral and precloacal pores absent; enlarged precloacal or femoral scales absent, no precloacal groove; four pairs of dark rounded spots from behind occiput to hindlimb inser-

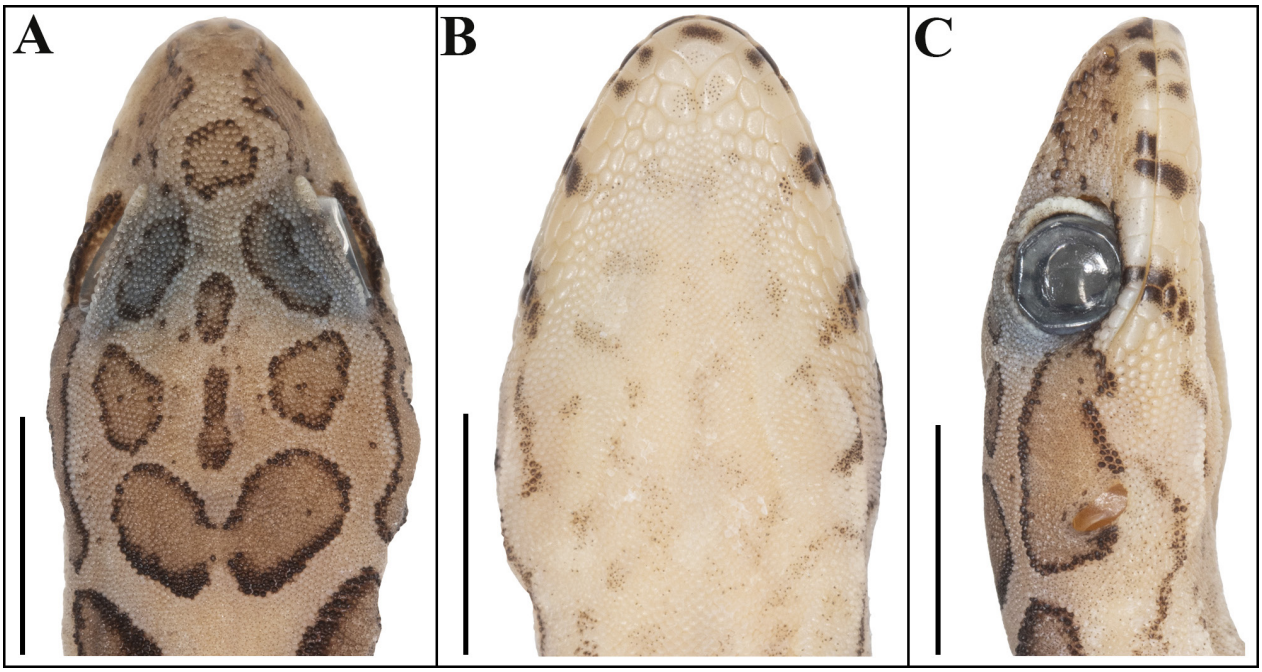

Figure 4. *Cyrtodactylus* (*Geckoella*) *irulaorum* **sp. nov.** (holotype, NRC-AA-1266): **A** dorsal view of head, **B** ventral view of head, **C** right side lateral view of head. Scale bars 5 mm; photos by Akshay Khandekar.

tions, spots occasionally fused along mid-vertebral line forming horizontal figure 8-shaped marking; post-occipital collar broken into a pair of spots.

Comparison with members of the *collegalensis* complex. The diagnostic characters listed above for *Cyrtodactylus* (*Geckoella*) *irulaorum* **sp. nov.** easily differentiate the new species from all other *Cyrtodactylus* and *Cyrtodactylus* (*Geckoella*) apart from members of the *collegalensis* complex. *Cyrtodactylus* (*Geckoella*) *irulaorum* **sp. nov.** can be differentiated from the other members of the complex by its dorsal colour pattern of four pairs of dark spots from behind occiput to hindlimb insertions (spots may be fused centrally forming horizontal figure 8-shaped markings) from *C. aravindi* (a single dark broad band and one or two single dark spots on dorsum), *C. collegalensis* (three pairs of dark spots that may be fused forming horizontal figure 8-shaped markings), *C. rishivalleyensis* (two broad dark bands on dorsum), *C. srilekhae* (three rows of irregular dark blotches), *C. speciosus* (two broad dark bands on dorsum) and the Sri Lankan species *C. yakhuna* (one or two broad dark bands or spots on dorsum in both subspecies). The new species is most similar in colour pattern to *C. chengodumalaensis* and *C. varadgirii* (4–6 pairs of dark spots on dorsum) but can be distinguished by the absence of a few, enlarged dorsal tubercles on the dorsum (versus the presence of these tubercles in *C. chengodumalaensis*) and by the absence of a patch of enlarged roughly hexagonal scales on the canthus rostralis and beneath the angle of the lower jaw (versus the presence of these enlarged scales in *C. varadgirii*). *Cyrtodactylus* (*Geckoella*) *irulaorum* **sp. nov.** is closely allied to *Cyrtodactylus* (*Geckoella*) *relictus* **sp. nov.** and is diagnosed as part of the species description below.

Description of holotype. Adult male in good state of preservation except head slightly bent towards left and tail significantly bent towards right side, and a 5.7 mm vertical incision in the sternal region for liver tissue collection (Fig. 3A, B). SVL 41.5 mm, head short (HL/SVL 0.24), wide (HW/HL 0.70), not strongly depressed (HD/HL 0.46), almost as broad as body (HW/BW ratio 0.96), and distinct from neck (Fig. 4A–C). Loreal region slightly inflated, canthus rostralis not prominent. Snout marginally less than half the head length (ES/HL 0.44), slightly longer than eye diameter (ED/ES 0.61); scales on snout, canthus rostralis, and loreal region large, subcircular, smooth and, flattened; much larger than granular scales on forehead and interorbital region; occipital and temporal region with much smaller, smooth granules (Fig. 4A, C). Eye small (ED/HL 0.27); pupil, dilated, vertical with crenate margins; supraciliaries short, larger anteriorly, not elongate; 12 interorbital scale rows across narrowest point of frontal; 37 scale rows between left and right supraciliaries at mid-orbit (Fig. 4A, C). Ear-opening oval, small (EL/HL 0.12); eye to ear distance almost same as eye diameter (EE/ED 1.07). Rostral twice wider (2.1 mm) than deep (1.1 mm), incompletely divided dorsally by weakly developed rostral groove for half of its height; a single enlarged supranasal on each side, more than twice the size of the postnasals, separated from each other by a single enlarged internasal on the snout; three subequal postnasals, much smaller than supranasals; rostral in contact with nostril, supralabial I, supranasals, and internasals on either side; nostrils rounded, directed outwards, covering most of the nasal scale; surrounded on either side by supralabial I, rostral, supranasals, and postnasals; a single row of smaller scales separate the orbit from the supralabials (Fig. 4A, C). Mental enlarged, triangular, wider (1.6 mm) than long (1.2 mm); two pairs

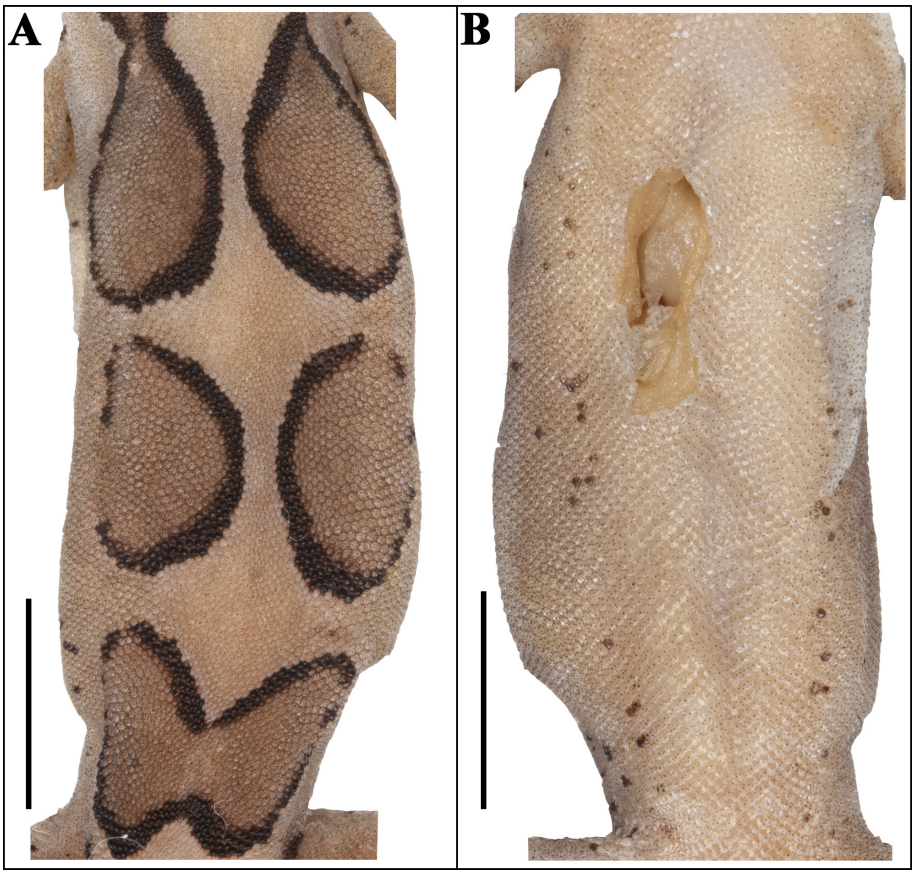

Figure 5. *Cyrtodactylus* (*Geckoella*) *irulaorum* **sp. nov.** (holotype, NRC-AA-1266): **A** dorsal view of midbody, **B** ventral view of midbody. Scale bars 5 mm; photos by Akshay Khandekar.

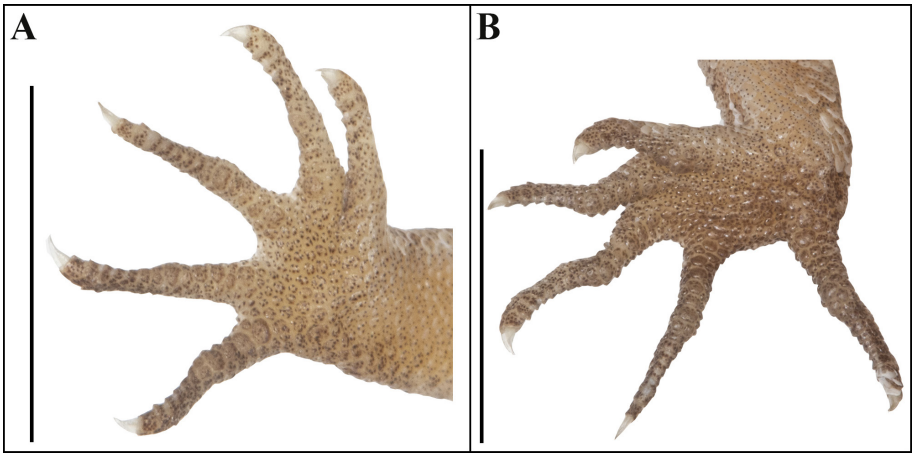

Figure 6. *Cyrtodactylus* (*Geckoella*) *irulaorum* **sp. nov.** (holotype, NRC-AA-1266): **A** ventral view of right manus, **B** ventral view of right pes. Scale bars 5 mm; photos by Akshay Khandekar.

of postmentals; inner pair in strong contact with each other, roughly pentangular and same length (1.2 mm) as mental; bordered by mental, infralabial I, outer postmental and two enlarged chin shields on left and a single on right side; outer postmentals separated from each other by left inner postmental and an enlarged chin scale, roughly rectangular and half the size (0.6 mm) of inner pair; bordered by inner postmentals and five enlarged chin shields on either side; chin shields bordering postmentals and infralabials flat, smooth, smaller than outermost postmentals, rest flattened, small, smooth; two or three rows of enlarged elongated scales separating gular scales from infralabials (Fig. 4B). Twelve supralabials up to angle of jaw on left and 10 on right side, and eight at midorbital position on left and seven on right side; nine infralabials up to angle of jaw on either side, and six infralabials at midorbital position on both sides (Fig. 4C).

Body relatively slender (BW/AGL 0.41), trunk less than half of SVL (AGL/SVL 0.43) without ventrolateral folds. Dorsal pholidosis on trunk homogeneous; covered with smooth, subcircular, weakly conical granular scales; 20 dorsal midbody scale rows across trunk contained within one eye diameter (Fig. 5A). Granular scales on occiput and nape slightly smaller and rounded than those on body dorsum; granular scales on flank slightly larger than those on dorsum. Ventral scales much larger than granular scales on dorsum, smooth, somewhat elongate, subimbricate, subequal from chest to vent; 15 ventral midbody scale rows across belly contained within one eye diameter (Fig. 5B). Scales on throat slightly smaller than those

Figure 7. *Cyrtodactylus* (*Geckoella*) *irulaorum* **sp. nov.** in life: **A** holotype, NRC-AA-1266, **B** paratype, NRC-AA-1268, **C** paratype, NRC-AA-1269, **D** paratype, NRC-AA-1270. Photos by Ishan Agarwal.

on belly; gular region with much smaller, granular scales with those on chin bordering postmentals, enlarged, juxtaposed and flattened (Fig. 4B). No enlarged precloacal or femoral scales, no precloacal or femoral pores; no precloacal groove (Fig. 3B).

Scales on palm and soles granular, smooth, rounded; scales on dorsal aspects of limbs heterogeneous in shape and size; mixture of small, granules similar to dorsum and many smooth flattened and imbricate scales which are much larger than granules on the body dorsum, largest on anterior aspect of the hands and feet; lateral and ventral aspects of limbs with small granular scales (Fig. 3A, B). Fore-limbs and hind-limbs long, slender (LAL/SVL 0.13; CL/SVL 0.16); digits short, slender, with a strong, recurved claw, moderately inflected, distal portions laterally compressed. Series of unpaired lamellae on basal portion of digits except one or two which on some digits which are paired, separated from narrower distal lamellae by a single large lamella at the inflection, unpaired except one or two which are divided; basal lamellae series: (5-6-5-6-7 right manus, Fig. 6A; 3-6-6-8-6 right pes, Fig. 6B), (5-5-6-6-7 left manus; 3-5-6-7-6 left pes); distal lamellae series: (7-6-8-7-7 right manus, Fig. 6A; 7-7-9-9-9 right pes, Fig. 6B), (7-6-8-7-7 left manus; 8-7-9-8-9 left pes). Relative length of digits (measurements in mm in parentheses): IV (3.1) > III (2.9) > II (2.6) > V (2.3) > I (1.8) (right manus); IV (3.9) > III (3.4) > V (3.3) > II (3.0) > I (1.8) (right pes).

Tail original, circular in cross section with indistinct median dorsal furrow, relatively thick, tapering gradually to tip, unsegmented, slightly shorter than snout-vent length (TL/SVL ratio 0.78). Scales on dorsal aspect of tail base similar to body dorsum; scales on dorsal aspect of tail large flat, subcircular, smooth, and imbricate, becoming slightly larger towards the lateral aspect, largest on ventral side, but not forming median row of transversely enlarged subcaudal scales. Three small, smooth, subequal, conical postcloacal spurs on left side and two on right side of tail base; prominent hemipenal swelling, flap of skin covering cloacal aperture. Tail slightly constricted at the base (Fig. 3B).

Colouration in Life (Fig. 7A). Dorsal ground colour light tan, four pairs of dark brown spots from behind occiput to hindlimb insertions and a smaller darker pair above tail base. Spots on the left side of the body in the first and second pair fused, other pairs except the fourth separated mid-vertebrally, second pair of spots slightly larger than the rest and first smallest. Spots edged by black on the outer 1–5 rows of scales, finest along flanks and absent in fused portion of fourth set of spots. Flank with only a few scattered fine black spots. Tail dorsum similar in ground colour to body dorsum except slightly suffused with yellow; a dark small pair of spots on tail base and six indistinct darker crossbars reducing in size toward tail-tip, anteriorly forming black edged brown

Figure 8. Paratypes of *Cyrtodactylus* (*Geckoella*) *irulaorum* **sp. nov.** from left to right, NRC-AA-1267–NRC-AA-1273: **A** dorsal view, **B** ventral view. Scale bars 10 mm; photos by Akshay Khandekar.

bands. Dorsum of limbs similar in colour to trunk with a few scattered black spots, digits with indistinct mottling. Post-occipital collar formed of two fused brown spots edged with black and a finer light border forming a horizontally 8-shaped marking. Central spots on post-occipital collar roughly subequal to smallest dorsal blotches. Crown of the same shade as trunk with a few small scattered black spots, and seven dark brown markings that have a darker border flanked by a finer light border; a pre-frontal spot that is shorter than two interorbital spots which are similar in length to the longer part of the (broken) interparietal streak and two parietal spots. Brille similar in colour to light scales on crown. Postocular streak runs from posterior edge of eye to just beyond tympanum, separated from dorsolateral markings of collar and first pair of dorsal spots on neck or just meeting above tympanum (L/R); preocular streak extends till nostril. All head markings separated from each other. Labials with dark streaks, a few unmarked scales finely spotted with black. A fine dark streak from below anterior edge of ear opening extends onto start of the forearm. Ventral aspects dirty white with few spots on the lateral edge of the belly and numerous thick streaks and spots on infralabials and gular region; ventral aspect of tail many-coloured with dark with few scattered light streaks.

Variation and additional information from paratypes (Figs 7B–D; 8A, B). Mensural and meristic data for the type series is given in Table 3. There are five adult males and three adult female specimens, SVL ranging from 39.8–50.5 mm. All specimens resemble the holotype male (NRC-AA-1266) except for the following variations: two internasals between supranasals behind rostral in NRC-AA-1267. Inner postmental separated from each other below mental by single smaller chin shield in NRC-AA-1268; inner postmental bordered by mental, infralabial I, outer postmental in all paratypes; bordered

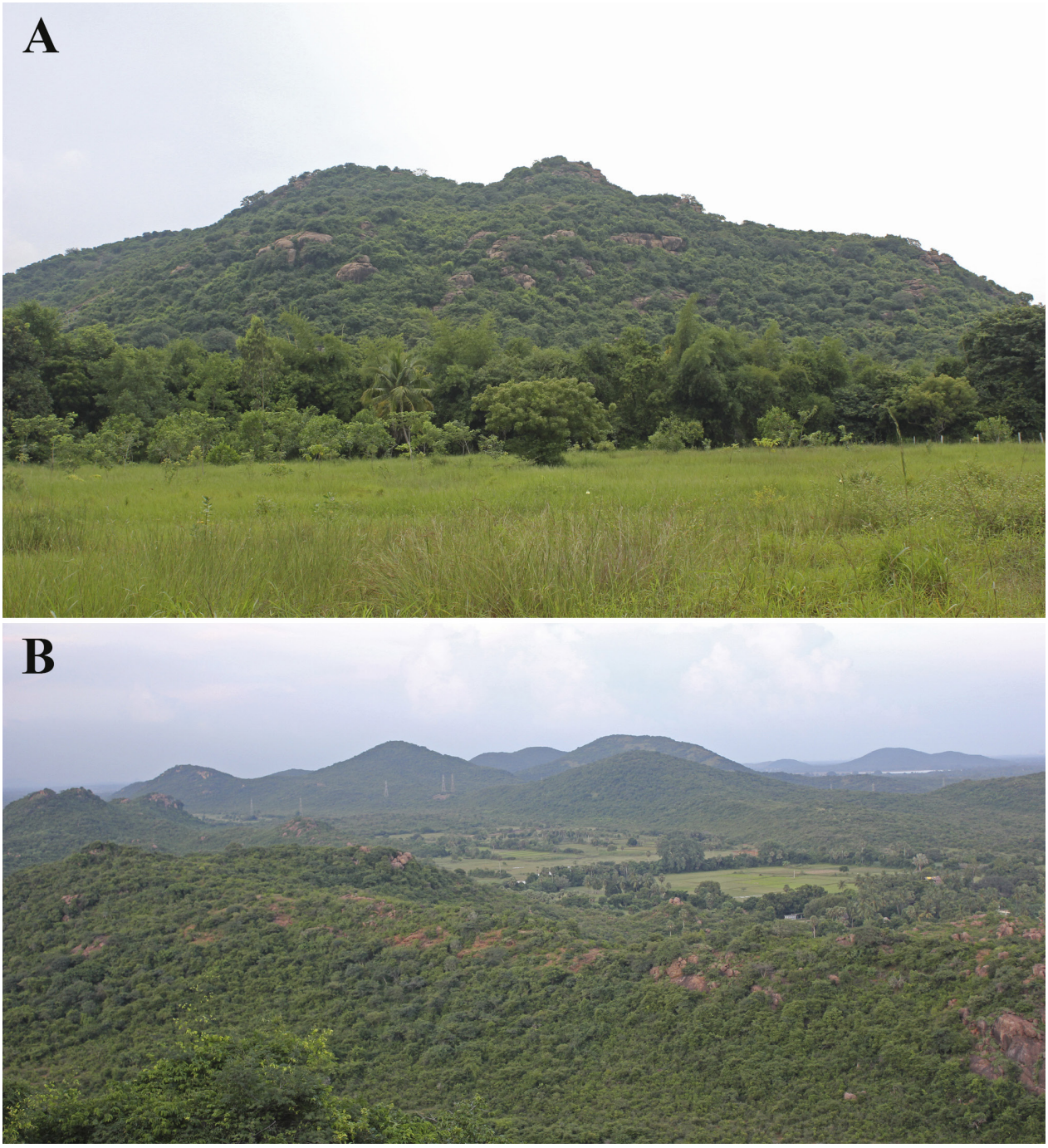

Figure 9. Habitat photos at type locality of *Cyrtodactylus* (*Geckoella*) *irulaorum* **sp. nov.**: **A** farm at base of the hill, from where the holotype and a few paratypes were collected; **B** a general view from the hill located behind farm, showing the tropical dry evergreen forests. Photos by Akshay Khandekar.

by four enlarged chin scales in NRC-AA-1267, NRC-AA-1269, NRC-AA-1272, NRC-AA-1273, by three enlarged chin scales in NRC-AA-1270, by five enlarged chin scales in NRC-AA-1271, by six enlarged chin scales in NRC-AA-1268. Outer postmental bordered by inner pair, infralabial I and II and three enlarged chin scales in NRC-AA-1267, NRC-AA-1268; outer postmental bordered by inner pair, infralabial I and II and two enlarged chin scales in NRC-AA-1271; outer postmental bordered by inner pair, infralabial I and II on either side and by two enlarged chin scales on left and, three on right side in NRC-AA-1272; outer postmental bordered by inner pair, infralabial I and II on either side and four enlarged chin scales on left and two on right side in NRC-AA-1269; outer postmental bordered by inner postmental, infralabial I and II, and four enlarged chin scales on right and by inner postmental, and five enlarged chin scales on left side in NRC-AA-1270; outer postmental bordered by inner postmental, infralabial I and II, and four enlarged chin scales on right and by inner postmental, and six enlarged chin scales on left side in NRC-AA-1273. Three paratypes (NRC-AA-1270, NRC-AA-1272, and NRC-AA-1271) have an original and complete tail, slightly shorter than body (TL/SVL 0.77, 0. 72, and 0.81 respectively); NRC-

Figure 10. *Cyrtodactylus* (*Geckoella*) *relictus* **sp. nov.** (holotype, NRC-AA-1274): **A** dorsal view of body, **B** ventral view of body. Scale bars 10 mm; photos by Akshay Khandekar.

AA-1273 with partially regenerated tail, NRC-AA-1268 and NRC-AA-1269 with fully regenerated tails, NRC-AA-1267 with original but incomplete tail, all having shorter tails than body. Ground colour varies from light khaki to brown; dorsal pairs of spots may be fused along mid-vertebral line and the first two pairs of spots may be fused on one or both sides; pair of spots on collar separated or just in contact; post-orbital streak sometimes fused with first pair of spots; head pattern variable; regenerated tail greyish brown or grey with or without a few scattered spots, original tail with 6–8 indistinct bands.

Distribution and Natural History. *Cyrtodactylus* (*Geckoella*) *irulaorum* **sp. nov.** is known from only two localities 75 km apart at elevations below ~60 m (Fig. 1). The type locality is a small farm adjacent to low hills with largely tropical dry evergreen scrub (Fig. 9A, B), while the other locality was a patch of deciduous forest. Individuals were spotted at night (from about 45 minutes to two hours after sunset) mainly by eye-shine and were found in leaf litter and on the ground. Four individuals were spotted in about half an hour by IA on 10th April 2013 and a few individuals have been spotted on multiple occasions.

Cyrtodactylus (*Geckoella*) *relictus* sp. nov.

https://zoobank.org/32D66610-81DF-42A4-B05F-4B90344A25C4

Figs 10–15; Table 3

Holotype. NRC-AA-1274 (CES09/1472), adult male, from near Ubbalamadagu waterfalls, Kambakkam Durg (13.6100°N, 79.8431°E; ca. 120 m asl.), Tirupati District, Andhra Pradesh, India, collected by Ishan Agarwal and team on 18th March 2014.

Paratypes. NRC-AA-1275 (CES09/1470), NRC-AA-1276 (CES09/1471), adult females, from near Penchalakona (14.3266°N, 79.4219°E; ca. 170 m asl.), Nellore District, Andhra Pradesh, India, collected by Ishan Agarwal and team on 17th March 2014.

Etymology. The specific epithet is from the Latin relictus; which refers to an organism or species that has survived from an earlier period with different environmental conditions. Peninsular India was covered by wet forests and has gradually become more arid since at least the Miocene (Morley 2007; Patnaik et al. 2012; Pound et al.

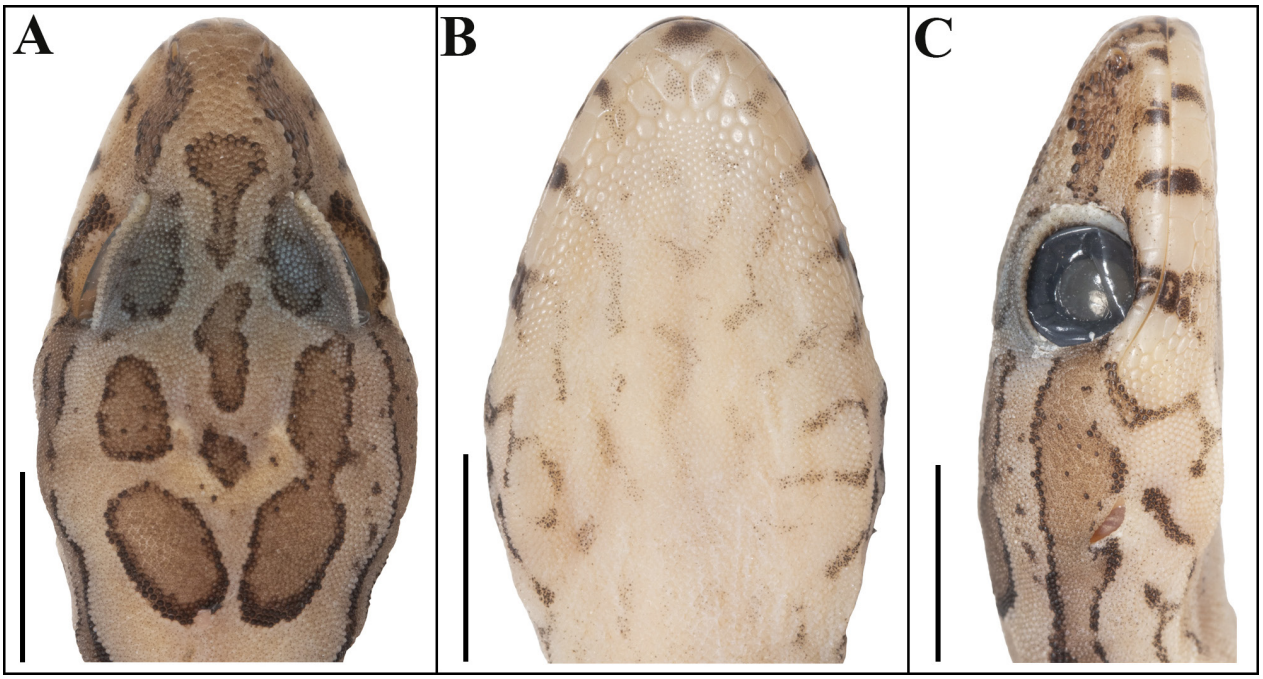

Figure 11. *Cyrtodactylus* (*Geckoella*) *relictus* **sp. nov.** (holotype, NRC-AA-1274): **A** dorsal view of head, **B** ventral view of head, **C** right side lateral view of head. Scale bars 5 mm; photos by Akshay Khandekar.

2012). This is apt for the new species as it is known only from small areas of relatively cool, closed canopy habitats in a matrix of otherwise warm and open habitats.

Suggested common name. Relict *Geckoella*.

Diagnosis. A small-sized *Cyrtodactylus* (*Geckoella*), snout to vent length up to 53 mm (n = 3); tail shorter than SVL. Dorsal pholidosis on trunk homogeneous; covered with smooth, subcircular, weakly conical granular scales; scales on occiput and nape slightly smaller and rounded than those on body dorsum, scales on flank slightly larger than those on dorsum; ventral scales much larger than scales on dorsum, smooth, subcircular, subimbricate, subequal from chest to vent; absence of femoral and precloacal pores; absence of enlarged precloacal or femoral scales, no precloacal groove; four pairs of dark rounded spots from occiput to hindlimb insertions, spots rarely just in contact along mid-vertebral line; post-occipital collar broken into a pair of spots (1/3) or forming a U-shaped band (2/3).

Comparison with members of the *collegalensis* complex. The diagnostic characters listed above for *Cyrtodactylus* (*Geckoella*) *relictus* **sp. nov.** easily differentiate the new species from all other *Cyrtodactylus* and *Cyrtodactylus* (*Geckoella*) apart from members of the *collegalensis* complex. *Cyrtodactylus* (*Geckoella*) *relictus* **sp. nov.** can be differentiated from the other members of the *collegalensis* complex by its dorsal colour pattern of four pairs of dark spots from behind occiput to hindlimb insertions (first pair fused with postocular streak on either side, spots may be just in contact centrally) from *C. aravindi* (a single dark broad band and one or two single dark spots on dorsum), *C. collegalensis* (three pairs of dark spots that may be fused forming horizontal figure 8-shaped markings), *C. rishivalleyensis* (two broad dark bands on dorsum), *C. srilekhae* (three rows of irregular dark blotches), *C. speciosus* (two broad dark bands on dorsum) and the Sri Lankan species *C. yakhuna* (one or two broad dark bands or spots on dorsum in both subspecies). The new species is most similar in colour pattern to *C. chengodumalaensis*, *Cyrtodactylus* (*Geckoella*) *irulaorum* **sp. nov.** and *C. varadgirii* (which all have 4–6 pairs of dark spots on dorsum); but can be distinguished by the absence of a few, enlarged dorsal tubercles on the dorsum (versus the presence of these tubercles in *C. chengodumalaensis*), its SVL up to 52.7 mm (versus SVL up to 47.6 mm in *C. chengodumalaensis*) and by the absence of a patch of enlarged roughly hexagonal scales on the canthus rostralis and beneath the angle of the lower jaw (versus the presence of these enlarged scales in *C. varadgirii*).

Cyrtodactylus (*Geckoella*) *relictus* **sp. nov.** overlaps in colour pattern with *C. irulaorum* **sp. nov.** almost completely, except that the first pair of spots is fused with the postocular streak in *C. relictus* **sp. nov.** (versus postocular streak usually separated from first pair of spots in *C. irulaorum* **sp. nov.**). The two species occupy distinct positions in multivariate morphospace (Fig. 2) and differ significantly across a number of size-corrected morphometric variables. Additionally, *Cyrtodactylus* (*Geckoella*) *relictus* **sp. nov.** is slightly larger (maximum SVL 52.7 mm, mean 51.5 versus maximum SVL 50.5 mm, mean 43.4 mm in *C. irulaorum* **sp. nov.**) and has a significantly ($p < 0.05$) wider body (BW/SVL mean 0.215, range 0.201–0.230 versus BW/SVL mean 0.167, range 0.141–0.188 in *C. irulaorum* **sp. nov.**) and wider head (HW/SVL mean 0.182, range 0.180–0.186 versus mean 0.175, range 0.163–0.182 in *C. irulaorum* **sp. nov.**).

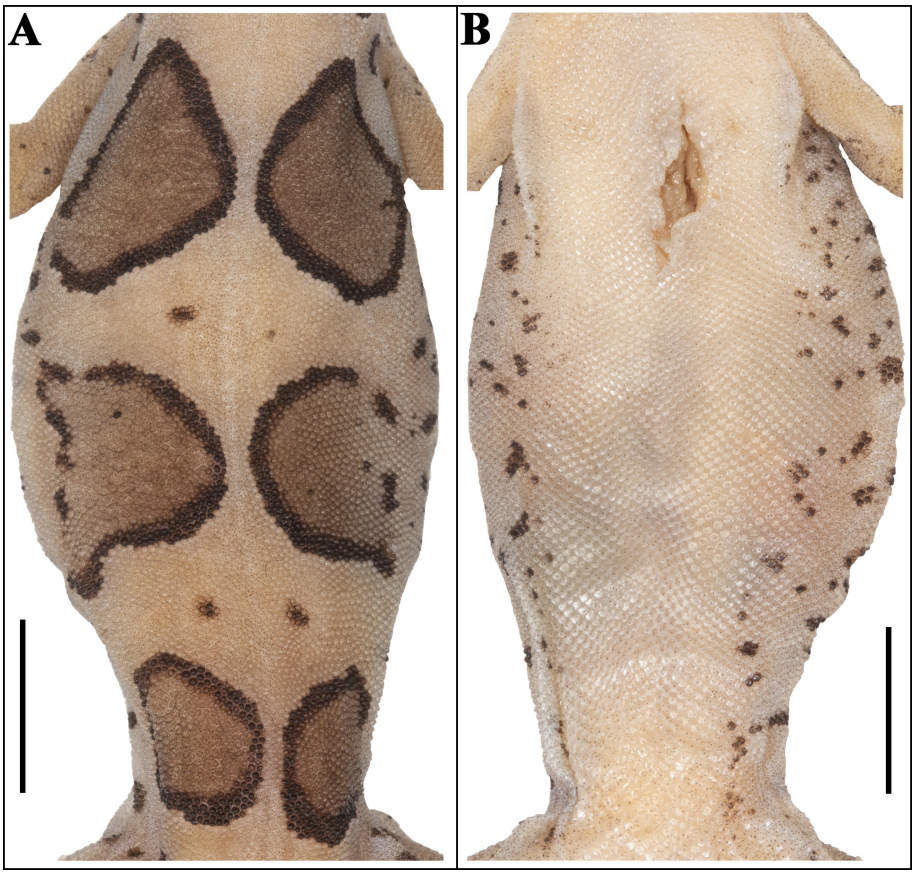

Figure 12. *Cyrtodactylus* (*Geckoella*) *relictus* **sp. nov.** (holotype, NRC-AA-1274): **A** dorsal view of midbody, **B** ventral view of midbody. Scale bars 5 mm; photos by Akshay Khandekar.

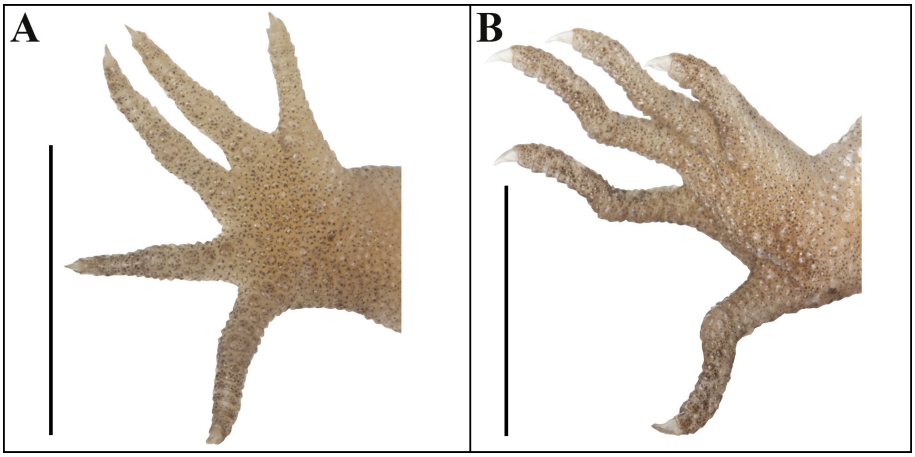

Figure 13. *Cyrtodactylus* (*Geckoella*) *relictus* **sp. nov.** (holotype, NRC-AA-1274): **A** ventral view of right manus, **B** ventral view of right pes. Scale bars 5 mm; photos by Akshay Khandekar.

Description of holotype. Adult male in good state of preservation except a 4.7 mm vertical incision in the sternal region for liver tissue collection (Fig. 10A, B). SVL 49.1 mm, head short (HL/SVL 0.25), wide (HW/HL 0.71), not strongly depressed (HD/HL 0.45), slightly narrower than body (HW/BW ratio 0.78), and distinct from neck (Fig. 11A–C). Loreal region slightly inflated, canthus rostralis not prominent. Snout marginally less than half the head length (ES/HL 0.45), slightly longer than eye diameter (ED/ES 0.52); scales on snout, canthus rostralis, and loreal region large, subcircular, smooth and, flattened; much larger than granular scales on forehead and interorbital region; occipital and temporal region with much smaller, smooth granules (Fig. 11A, C). Eye small (ED/HL 0.24); pupil vertical, dilated with indistinct crenate margins; supraciliaries short, larger anteriorly, not elongate; interorbital scale rows across narrowest point of frontal 15; 42 scale rows between left and right supraciliaries at mid-orbit (Fig. 11A, C). Ear-opening oval, small (EL/HL 0.08); eye to ear distance slightly more than eye diameter (EE/ED 1.26). Rostral almost twice wider (2.5 mm) than deep (1.4 mm), incompletely divided dorsally by weakly developed rostral groove for half of its height; a single enlarged supranasal on each side, much larger than postnasals, separated from each other by two enlarged internasals on the snout; three subequal postnasals, much smaller than supranasals; rostral in contact with nostril, supralabial I, supranasals, and internasals on either side; nostrils oval, directed outwards, covering most of the nasal scale; surrounded on either side by su-

Table 3. Measurements (mm) and meristic data for the type series of the two new species described herein. Abbreviations are listed in Materials and Methods except for * = tail incomplete or regenerated; L and R = left and right; M = male; F = female.

Species	***Cyrtodactylus* (*Geckoella*) *irulaorum* sp. nov.**								***Cyrtodactylus* (*Geckoella*) *relictus* sp. nov.**		
Type	**Holotype**	**Paratypes**							**Holotype**	**Paratypes**	
Museum number	NRC-AA-1266	NRC-AA-1267	NRC-AA-1268	NRC-AA-1269	NRC-AA-1270	NRC-AA-1271	NRC-AA-1272	NRC-AA-1273	NRC-AA-1274	NRC-AA-1275	NRC-AA-1276
Sex	M	M	M	M	M	F	F	F	M	F	F
SVL	41.5	41.7	43.4	41.5	39.8	40.8	48.2	50.5	49.1	52.7	52.7
TL	32.7	18.5*	12.8*	22.0*	30.7	33.4	35.1	29.3*	35.1	22.3*	22.0*
TW	4.4	4.3	4.6	4.4	4.2	3.1	3.5	3.5	5.2	4.8	4.3
LAL	5.6	5.8	6.1	5.9	5.9	5.1	7.2	7.3	6.6	7.2	7.2
CL	6.9	6.8	7.2	7.0	6.9	7.0	8.0	8.5	8.1	8.5	8.5
AGL	18.1	18.1	18.2	18.0	16.8	16.7	21.8	22.9	20.1	22.8	23.5
BH	3.3	4.8	4.3	3.7	3.5	3.4	4.1	4.7	3.6	4.7	7.2
BW	7.6	7.0	7.6	7.8	6.9	6.7	6.9	7.1	11.3	11.3	10.6
HL	10.3	10.5	11.5	10.5	10.1	10.1	12.5	13.0	12.5	14.3	13.7
HW	7.3	6..8	7.9	7.4	6.9	7.3	8.4	8.6	8.9	9.5	9.8
HD	4.8	4.3	4.9	4.7	4.5	4.5	5.8	5.5	5.7	6.6	6.6
ED	2.8	2.7	3.0	2.7	2.5	2.6	3.0	3.0	3.0	3.6	3.4
EE	3.0	3.0	3.6	3.4	3.4	3.2	3.9	4.1	3.8	4.2	4.1
EL	1.3	1.0	1.4	1.0	0.9	1.0	1.5	1.2	1.1	1.1	0.9
ES	4.6	4.5	5.3	4.8	4.6	4.6	5.9	5.5	5.7	6.1	6.0
EN	3.5	3.4	3.9	3.4	3.4	3.3	4.5	4.2	4.1	4.4	4.3
IN	1.6	1.6	1.8	1.7	1.6	1.5	1.9	1.9	1.9	1.9	2.1
IO	2.0	1.9	2.0	2.0	2.0	1.9	2.3	2.3	2.3	2.6	2.7
SL L&R	12&10	9&10	9&10	10&10	10&10	9&10	10&10	9&10	10&10	8&10	11&9
IL L&R	9&9	8&9	9&8	9&8	8&8	9&9	8&8	8&8	8&8	8&8	8&8
SL M L&R	8&7	6&7	7&7	7&7	7&7	7&7	7&7	6&7	7&7	6&6	7&7
IL M L&R	6&6	6&6	6&5	6&5	5&5	6&6	6&6	6&6	6&6	5&5	5&6
DLamF1 L&R	7&7	7&7	7&7	6&7	7&7	6&7	7&7	6&7	8&8	6&6	7&7
BLamF1 L&R	5&5	2&3	4&5	3&3	3&3	3&2	3&3	5&3	5&4	3&4	3&2
DLamF4 L&R	7&7	7&7	7&6	8&7	7&6	8&7	7&7	7&7	6&6	6&6	9&7
BLamF4 L&R	6&6	6&6	5&6	5&5	5&5	6&6	6&5	5&5	6&6	5&5	3&5
DLamT1 L&R	8&7	7&7	6&7	8&7	8&7	8&8	8&7	8&7	8&8	8&8	8&7
BLamT1 L&R	3&3	4&3	3&5	3&3	3&2	3&3	2&2	2&3	4&4	3&2	3&3
DLamT4 L&R	8&9	9&8	8&8	9&9	7&7	9&9	9&9	8&9	8&9	7&7	8&8
BLamT4 L&R	7&8	7&7	8&7	8&8	7&7	8&8	9&8	9&8	10&9	7&8	8&6
PCT L&R	3&2	3&3	2&2	3&2	3&3	2&2	2&2	3&3	3&3	2&1	3&3

pralabial I, rostral, supranasals, and postnasals; a single row of smaller scales separate the orbit from the supralabials (Fig. 11C). Mental enlarged, triangular, wider (2.0 mm) than long (1.3 mm); two pairs of postmentals; inner pair in strong contact with each other, roughly pentangular and slightly longer than mental (1.2 mm) as mental; bordered by mental, infralabial I, outer postmental and two enlarged chin shields on either side; outer postmentals separated from each other by inner pair, roughly rectangular and half the size (0.8 mm) of inner pair; bordered by inner postmentals, infralabial I and II on either side and three enlarged chin shields on left and four on right side; chin shields bordering postmentals and infralabials flat, smooth, smaller than outermost postmentals, rest flattened, small, smooth; two or three rows of enlarged elongated scales separating gular scales from infralabials (Fig. 11B). Ten supralabials up to angle of jaw and seven at midorbital position on each side; eight infralabials up to angle of jaw, and six infralabials at midorbital position on both sides (Fig. 11C).

Body somewhat slender (BW/AGL 0.56), trunk less than half of SVL (AGL/SVL 0.40) without ventrolateral folds. Dorsal pholidosis on trunk homogeneous; covered with smooth, subcircular, weakly conical granular scales;

Table 4. Selected morphometric, meristic and colour pattern characters of the two new species. Mean (range) presented for morphometric characters and ratios; median (range) presented for meristic characters (* indicates all unique values) from the right side of specimens.

Character	*Cyrtodactylus* (*Geckoella*) *irulaorum* sp. nov.	*Cyrtodactylus* (*Geckoella*) *relictus* sp. nov.
SVL	43.4 (39.8–50.5)	51.5 (49.1–52.7)
LAL	6.1 (5.1–7.3)	7.0 (6.6–7.2)
CL	7.3 (6.8–8.5)	8.4 (8.1–8.5)
AGL	18.8 (16.7–22.9)	22.1 (20.1–23.5)
BW	7.2 (6.7–7.8)	11.1 (10.6–11.3)
BW/ SVL	0.167 (0.141–0.188)	0.215 (0.201–0.230)
HL	11.1 (10.1–13.0)	13.5 (12.5–14.3)
HW	7.6 (6.8–8.6)	9.4 (8.9–9.8)
HW/ SVL	0.175 (0.163–0.182)	0.182 (0.180–0.186)
ES	5.0 (4.5–5.9)	5.9 (5.7–6.1)
SL	10 (10)	10 (9–10)
IL	8 (8–9)	8 (8)
SL M	7 (7)	7 (6–7)
IL M	6 (5–6)	6 (5–6)
TLam F1*	10 (9–12)	*(9–12)
TLam F4	12 (11–13)	12 (11-12)
TLam T1	10 (9–12)	10 (10–12)
TLam T4*	17 (14–17)	*(14–18)
Dorsum banded/spotted (B/S)	S	S
Pairs of dark markings on dorsum	4 (often fused on midline)	4 (separate or just in contact on midline)
First pair spots and postocular streak	Separate or fused	Fused
Spots on flank present	Dots	Dots (1/ 3 specimens)
Collar	Pair of spots just in contact	Pair of spots/ fused (2/3 specimens)

17 dorsal midbody scale rows across trunk contained within one eye diameter (Fig. 12A). Granular scales on occiput and nape slightly smaller than those on body dorsum; granular scales on flank slightly larger than those on dorsum. Ventral scales much larger than granular scales on dorsum, smooth, subcircular, subimbricate, subequal from chest to vent; 15 ventral midbody scale rows across belly contained within one eye diameter (Fig. 12B). Scales on throat slightly smaller than those on belly; gular region with much smaller granular scales, those on chin bordering postmentals, enlarged, juxtaposed and flattened (Fig. 11B). No enlarged precloacal or femoral scales, no precloacal or femoral pores; no precloacal groove (Fig. 10B). Scales on palm and soles granular, smooth, rounded to oval; scales on dorsal aspects of limbs heterogeneous in shape and size; mixture of small, granules similar to dorsum and many smooth flattened and subimbricate scales which are much larger than granules on the body dorsum, largest on anterior aspect of the hands and feet; lateral and ventral aspects of limbs with small granular scales (Fig. 10A, B).

Fore-limbs and hind-limbs slightly long, slender (LAL/SVL 0.13; CL/SVL 0.16); digits short, slender, with a strong, recurved claw, moderately inflected, distal portions laterally compressed. Series of unpaired lamellae on basal portion of digits except one or two which on some digits are paired, separated from narrower distal lamellae by a single large lamella at the inflection, unpaired except one or two which are divided; basal lamellae series: (4-5-6-6-6 right manus, Fig. 13A; 4-6-7-9-7 right pes, Fig. 13B), (5-5-6-6-6 left manus; 4-6-7-10-7 left pes); distal lamellae series: (8-7-8-6-7 right manus, Fig. 13A; 8-8-9-9-9 right pes, Fig. 13B), (8-7-8-6-7 left manus; 8-8-9-8-10 left pes).Relative length of digits (measurements in mm in parentheses): III (3.5) > IV (3.2) > II (3.0) > V (2.7) > I (2.2) (right manus); III (4.4) > IV (3.9) > V (3.7) = II (3.7) > I (2.2) (right pes).

Tail original, circular in cross section with indistinct median dorsal furrow, relatively thick, tapering gradually to tip, unsegmented, slightly shorter than snout-vent length (TL/SVL ratio 0.71). Scales on dorsal aspect of tail base similar to body dorsum except marginally larger; scales on dorsal aspect of tail large flat, subcircular, smooth, and imbricate, becoming slightly larger towards lateral aspect, largest on ventral side, but not forming median row of transversely enlarged subcaudal scales. Three small, smooth, subequal, conical postcloacal spurs on each side of tail base; prominent hemipenal swelling, flap of skin covering cloacal aperture. Tail slightly constricted at the base (Fig. 10A, B).

Colouration in Life (Fig. 14A). Dorsal ground colour faded light tan, four pairs of dark brown spots from behind occiput to hindlimb insertions. All spots separated except those forming first pair fused with postocular streak on either side; edged by black on the outer 1–5 rows of scales, finest along flanks; anterior two pairs of spots largest. Flank with scattered fine black spots. Tail dorsum similar in ground colour to body dorsum except slightly suffused with yellow; a dark small pair of spots on tail base and

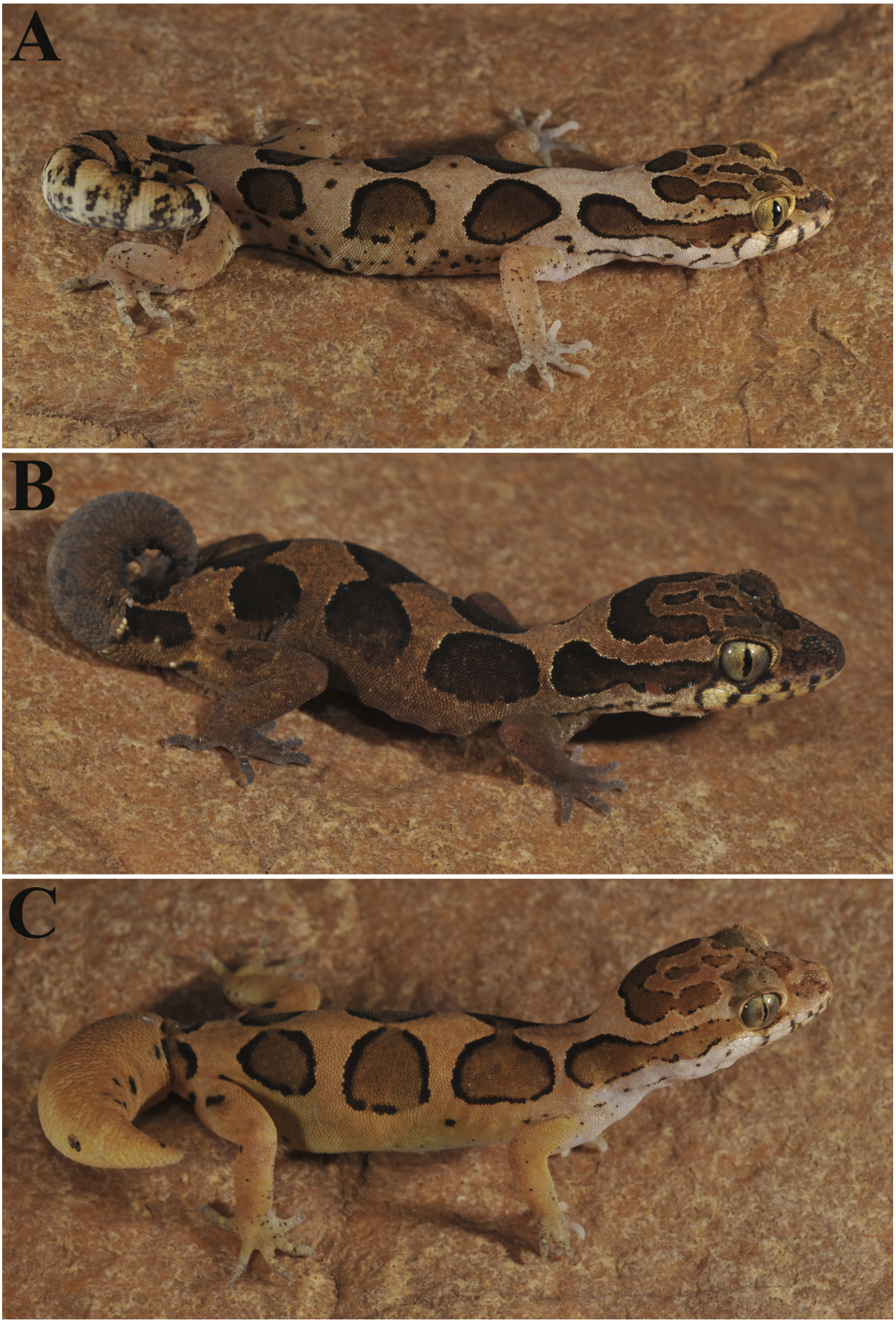

Figure 14. *Cyrtodactylus* (*Geckoella*) *relictus* **sp. nov.** in life: **A** holotype, NRC-AA-1274, **B** paratype, NRC-AA-1275, **C** paratype, NRC-AA-1276. Photos by Ishan Agarwal.

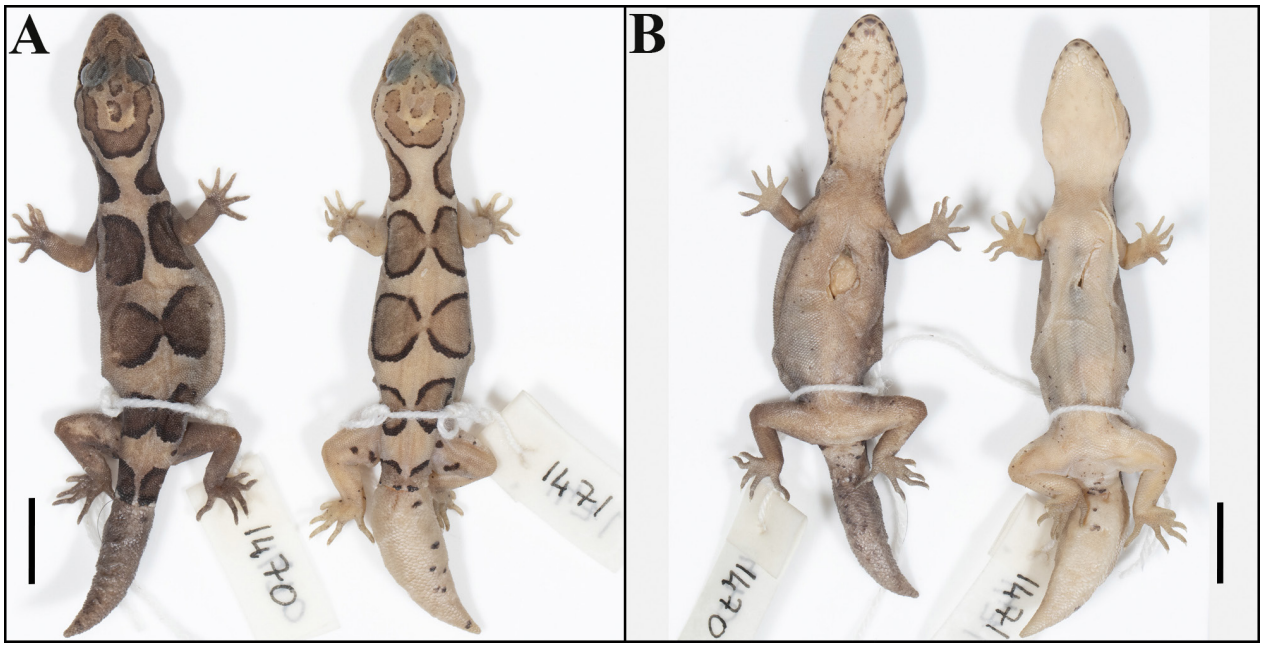

Figure 15. Paratypes of *Cyrtodactylus* (*Geckoella*) *relictus* **sp. nov.** from left to right, NRC-AA-1275 and NRC-AA-1276: **A** Dorsal view, **B** ventral view. Scale bars 10 mm; photos by Akshay Khandekar.

eight indistinct black edged brown crossbars reducing in size toward tail-tip. Dorsum of limbs and digits similar in colour to trunk with scattered black spots. Post-occipital collar formed of two brown spots edged with black and a finer light border. Spots on post-occipital collar smaller than the smallest dorsal blotches. Crown slightly darker than trunk with a few small scattered black spots, and seven dark brown markings that have a darker border flanked by a finer light border; a pre-frontal spot that is longer than two interorbital spots and similar in length to the longer part of the (broken) interparietal streak and two parietal spots. Brille similar in colour to light scales on crown. Postocular streak extends from posterior edge of eye through tympanum and fuses with first pair of spots on the neck, separated from dorsolateral markings of collar; preocular streak extends till nostril. All head markings separated from each other except post-occipital and parietal spots fused on right. Labials with dark streaks, a few unmarked scales finely spotted with black. A fine dark streak extends from angle of jaw onto start of forearm, discontinuous until below anterior edge of ear opening. Ventral aspects dirty white with scattered spots on the lateral edge of the belly and numerous grey streaks and spots on infralabials and gular region; ventral aspect of tail many-coloured with indistinct dark reticulations.

Variation and additional information from paratypes (Figs 14B, C 15A, B). Mensural and meristic data for the type series is given in Table 3. There are two adult female specimens, both having same SVL (52.7 mm). All specimens resemble the holotype male (NRC-AA-1274) except for the following variations: single internasal between supranasals behind rostral in both the female paratypes. Inner postmental bordered by mental, infralabial I, outer postmental on either side and bordered by two enlarged chin scales on left and four on right side in NRC-AA-1276. Outer postmental bordered by inner pair, infralabial I and II and three enlarged chin scales on either side in NRC-AA-1275; outer postmental bordered by inner pair, infralabial I and II and two enlarged chin scales on either side in NRC-AA-1276. Both female paratypes with complete but fully regenerated tail, slightly shorter than body (TL/SVL 0.42 in both). Ground colour varies from light khaki to yellowish and brown, dorsal pairs of spots may be fused mid-vertebrally but individual spots from adjacent pairs do not fuse; collar fused in paratypes, post-orbital streak fused with first pair of spots; few dark spots on the flanks; regenerated tail similar to ground colouration with a few spots.

Distribution and Natural History. *Cyrtodactylus* (*Geckoella*) *relictus* **sp. nov.** is known from only two localities about 90 km apart and at elevations of 120 m and 170 m (Fig. 1). The type locality is at the base of Kambakkam, an isolated massif that reaches a maximum elevation of just over 820 m from a base elevation of 30 m to the east (Fig. 16). The paratypes were collected from the eastern slopes at the base of the Velikonda Range that reaches a maximum elevation of over 1100 m from a base elevation of ~150 m in the east. Both collection localities are along streams with riparian gallery forest which cuts through open, arid and scrubby habitats at the type locality and dry evergreen forest at the paratype locality. The holotype was collected in about an hour of search in leaf litter along the stream while the paratypes were collected in about an hour and a half of search with one found in riparian habitat and the other in a patch of dry evergreen forest. The new species is sympatric with the endemic *Cnemaspis avasabinae* Agarwal, Bauer & Khandekar, 2020 at the paratype locality and an undescribed species of *Cnemaspis* at the type locality (Agarwal et al. 2020; Agarwal unpublished data).

Figure 16. Habitat photos at type locality of *Cyrtodactylus* (*Geckoella*) *relictus* **sp. nov.**: **A** general habitat, **B** tropical dry evergreen riparian forests around where the new species was collected. Photos by Karanth Lab (A. Datta-Roy, A. Lajmi, V. Deepak).

Discussion

Cyrtodactylus (*Geckoella*) *irulaorum* **sp. nov.** and *Cyrtodactylus relictus* **sp. nov.** are the 9th and 10th species of the *Cyrtodactylus* (*Geckoella*) *collegalensis* complex to be described from peninsular India. Apart from *C. varadgirii*, the known species of the complex are associated with hilly landscapes in southern India. The two new species extend the range of the *Cyrtodactylus* (*Geckoella*) *collegalensis* complex north and east into the Velikonda range. These are the first records of the group from south-eastern India and it remains to be seen how much further north the *C. collegalensis* complex is distributed. We surveyed Andhra Pradesh in 2014, but these were the only members of the *Cyrtodactylus* (*Geckoella*) *collega-*

lensis complex we collected, besides *C. rishivalleyensis*; with the most southern confirmed records of *C. nebulosus* Beddome about 275 km N-NE of the Velikonda range (Agarwal unpubl. data).

Interestingly, though both new species are both distributed at low elevations (<180 m), they occur within just 30 km of one another and are 10.0–11.5% divergent in mitochondrial sequence data; while each species occurs at two localities 75–90 km apart with ≤ 1.2% divergence. There are no obvious geographic barriers between the known range of the two new species, and *Cyrtodactylus* (*Geckoella*) *relictus* **sp. nov.** is found associated with riparian and tropical dry evergreen forests at the base of larger mountains while *C. irulaorum* **sp. nov.** is found in areas of little relief with tropical dry evergreen scrubland and forest. *Cyrtodactylus* (*Geckoella*) *rishivalleyensis* also occurs within ~50 and ~75 km of the new species, though the former is only known from elevations above 1,000 m (Agarwal 2016). At the coarse scale of 1 km^2, the two new species occupy a similar range of annual temperatures and precipitation (not shown), but the fact that *Cyrtodactylus* (*Geckoella*) *relictus* **sp. nov.** is associated with mountains while *C. irulaorum* **sp. nov.** is found in areas of little relief, suggests there are likely to be fine scale environmental differences between the niches of both species. Expanded geographic sampling and nuclear data are needed to understand the distributional range of each species as well as potential speciation mechanisms.

Tropical dry evergreen forests (TDFs) are a unique ecoregion restricted to lowland pockets along the east coast in India and covering much of the Sri Lankan lowlands (Champion and Seth 1968). Though there is some debate on if this represents a climax community (Daniels et al. 2007), this ecoregion includes a distinctive assemblage of species and is largely dependent on the northeast monsoon, which is received between about October to December, driven mainly by cyclonic depressions in the Bay of Bengal (Meher-Homji 2007; Parthasarathy et al. 2008). Including the subcategory of Tropical Dry Evergreen Scrub (Champion and Seth 1968), this ecoregion has lost practically its entire natural cover and TDFs are restricted to small patches around temples (sacred groves, protected for religious purposes), apart from a few larger reserve forest areas (Parthasarathy et al. 2008). Several endemic plant species are known from TDFs (Balachandran et al. 2018), but few studies have been carried out on the fauna of these habitats. These are the first endemic vertebrates to be described from TDFs after *Cnemaspis avasabinae*, and further surveys are vital to evaluate the biodiversity of these unique habitats.

The *Cyrtodactylus* (*Geckoella*) *collegalensis* complex has seen the most new species discovery within Indian *Geckoella*, with seven of the nine Indian species described since 2016 (Agarwal 2016; Agarwal et al. 2016; Narayanan et al. 2022; Agarwal et al. 2023). Though the newly described species are distinct in colouration and mitochondrial sequence data, members of the *collegalensis* complex (and other species complexes within *Geckoella*) lack numerous characters that are frequently used in gekkonid taxonomy such as precloacal or femoral pores and the presence of dorsal tubercles; besides having limited variation or overlapping ranges in meristic characters. Even multivariate analyses of morphology do not separate all species (e. g. Agarwal et al. 2016). Multi-locus nuclear data are required to understand species boundaries and patterns of gene flow within *Geckoella*.

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Appendix 1

Material examined

Museum and institutional abbreviations given in the Materials and methods except for: Akshay Khandekar field series (AK-R).

Cyrtodactylus (*Geckoella*) *aravindi*: AK-R 682, AK-R 683, AK-R 1007– AK-R 1011, adult males and females, from Thirukurungudi, Tirunelveli District, Tamil Nadu, India.

Cyrtodactylus (*Geckoella*) *chengodumalaensis*: holotype, NRC-AA-1161, adult male, from Kumaragiri Estate, Malappuram District, Kerala, India; paratypes; BNHS 2812, BNHS 2816, BNHS 2817, adult males, NRC-AA-1162, NRC-AA-1163, NRC AA-1166, adult females, BNHS 2813, subadult female, all from Kerala, India.

Cyrtodactylus (*Geckoella*) *collegalensis*: holotype, BMNH 1946.8.25.28, adult male, from near BR Hills, CES09/1444, subadult male and CES09/1463, adult female, from near MM Hills; all from Chamarajanagar District, Karnataka, India.

Cyrtodactylus (*Geckoella*) *speciosus*: AK-R 2689–2693, adult males and females, from near Erode, Erode District, Tamil Nadu, India.

Cyrtodactylus cf. *speciosus*: CES09/1405–1408, from near Coimbatore, Coimbatore District, Tamil Nadu, India.

Cyrtodactylus (*Geckoella*) *srilekhae*: holotype, NCBS AQ740, adult male, near Thathaguni, Bangalore Urban District; paratypes, ESV 101, adult male, BNHS 2325, NCBS AQ427, adult females, same data as holotype; ESV 102, adult male, from Nandi Hills, Chikkaballapur District; NCBS AQ510, juvenile, Savandurga, Ramanagara District, Karnataka, India.

Cyrtodactylus (*Geckoella*) *rishivalleyensis*: holotype, NCBS AQ742, adult female, Horsley Hills, Chittoor District, Andhra Pradesh; paratypes; NCBS AQ744, NCBS AQ743, adult males, ESV 103, BNHS 2326, adult females, ESV 104 juvenile, same locality as holotype.

Cyrtodactylus (*Geckoella*) *varadgirii*: holotype, NCBS AQ475, adult male, from Ulhasnagar, Thane District, Maharashtra, India; paratypes, NCBS AQ191, adult male, same locality as holotype; CES09/1381, adult male, from Chikhli, Navsari District, Gujarat; CES/09/1368, adult male, Chandrapur District, Maharashtra; CES09/1536, adult male and CES09/1537, adult female, from Amravati District, Maharashtra; BNHS 1427, adult male from Sanjay Gandhi National Park, Mumbai, Thane and Mumbai Suburban Districts, Maharashtra, BNHS 1434, subadult male, from Junagadh District, Gujarat; NCBS AQ192, adult male, BNHS 1848, adult male, and BNHS 1849, adult female, BNHS 1929, subadult female, from Aarey Milk Colony, Mumbai, Mumbai Suburban District, Maharashtra; BNHS 2099; adult female, from Vansda National Park, Navsari District, Gujarat, India.