Systematics and Biodiversity (2022), **20(1)**: 2039319

Taylor & Francis
Taylor & Francis Group

Research Article

The hidden diversity and inland radiation of Sri Lanka's ground-dwelling geckos of the genus *Cyrtodactylus* (Reptilia: Gekkonidae)

A. A. THASUN AMARASINGHE[1,2], SURANJAN KARUNARATHNA[3], PATRICK D. CAMPBELL[4], A. K. ANUSHA GAYAN[5], W. D. BHANUKA RANASINGHE[6], ANSLEM DE SILVA[7] & ZEESHAN A. MIRZA[8]

[1]Department of Biology, Faculty of Mathematics and Natural Sciences, Universitas Indonesia, Kampus UI, Depok 16424, Indonesia
[2]Association of Asian Herpetology (Asosiasi Herpetologi Asia), Jl. BSD Bintaro No. 88, Pondok Aren 15228, Tangerang Selatan, Indonesia
[3]Nature Explorations & Education Team, No: B-1/G-6, De Soysapura Flats, Moratuwa 10400, Sri Lanka
[4]Department of Life Sciences, Darwin Centre, Natural History Museum, Cromwell Road, South Kensington, London SW7 5BD, United Kingdom
[5]Institute of Biochemistry, Molecular Biology and Biotechnology, University of Colombo, Colombo, Sri Lanka
[6]Department of Building Studies, British College of Applied Studies, Kandy, Sri Lanka
[7]Amphibia and Reptile Research Organization of Sri Lanka (ARROS), 15/1, Dolosbage Road, Gampola, Sri Lanka
[8]National Centre for Biological Sciences, TIFR, GKVK campus, Bellary road, Bangalore, Karnataka 560065, India

(Received 15 September 2021; accepted 3 February 2022)

The genus *Cyrtodactylus* has recently been classified phylogenetically into several clades, subclades, groups, and some into Sri Lankan *Cyrtodactylus*. Certain complexes from the Indian subcontinent have been assigned to the "*C. triedrus* group". This group is comprised of medium-sized species (SVL 50.6–105.7 mm) and are composed of five major species complexes: *fraenatus*, *triedrus*, *deccanensis*, *jeyporensis*, and *collegalensis*. Among these complexes, the latter four are composed of ground and litter dwelling species, which were previously assigned to the genus *Geckoella*; and is currently being treated as a subgenus. *Cyrtodactylus triedrus*, an endemic species of Sri Lanka, has long been considered a widely distributed single species in this part of the world. Based on morphological and phylogenetic evidences, we demonstrate that *C.* (*G.*) *triedrus* is not a single species, but a species complex. We also describe a new species that is restricted to intermediate savanna-mixed dry lowland forested habitats. Furthermore, we resurrect *Geckoella punctata*, assign it to the genus *Cyrtodactylus* and designate a lectotype that we redescribe. The genetic divergence across species of the *C. triedrus* clade varies between 11–26% in the studied fragment of the mitochondrial NADH dehydrogenase subunit 2 gene. The molecular phylogeny of the ground dwelling radiation of the subgenus *Geckoella* indicates deep splits between the Indian species and Sri Lankan endemic *C.* (*G.*) *triedrus* sensu stricto, and between Indian dry and wet zone clades. *Cyrtodactylus* (*G.*). *triedrus* is restricted to the moist or submontane forests in the Central highlands of Sri Lanka and is redescribed herein based on its holotype.

http://zoobank.org/urn:lsid:zoobank:org:pub:3B37037C-EE9F-4011-BEC9-47E1F3BB6779

Key words: biogeography, cryptic species, *Geckoella*, island, new species, phylogeny, systematics

Introduction

Günther (1864) described a ground-dwelling gecko species, *Gymnodactylus triedrus*, based on a single specimen collected from Ceylon (Sri Lanka). Three years later, Gray (1867) described a closely related species to Günther's *Gymnodactylus triedrus*, *Geckoella punctata*, also from Ceylon, based on two specimens, an adult male and a female (*fide* Boulenger, 1885). Later, Boulenger (1885) synonymised Gray's species with *Gymnodactylus triedrus*. Boulenger (1885) referred to five specimens in the British Museum (now Natural History Museum London, NHMUK). Taylor (1953) in his review of the lizards of the island did not mention examining any specimens of this species. The species

Correspondence to: A.A. Thasun Amarasinghe. E-mail: thasun.amarasinghe@ui.ac.id; Suranjan Karunarathna. E-mail: suranjan.karu@gmail.com

ISSN 1477-2000 print / 1478-0933 online

https://dx.doi.org/10.1080/14772000.2022.2039319

Published online 29 Mar 2022

was assigned to the genus *Gymnodactylus* Spix, 1825 by most of the 19th century authors and later, it was attributed to the genus *Geckoella* Gray, 1867 in the 20th century. Although Underwood (1954) assigned the species to the genus *Cyrtodactylus* Gray, 1827, most of the subsequent authors disagreed with this until Wood et al. (2012) merged the genus *Geckoella* with the genus *Cyrtodactylus*. In a recent phylogenetic assessment, *Geckoella* was found to be embedded within the genus *Cyrtodactylus* (Grismer et al., 2021). The clade was well-supported in the Maximum likelihood (ML) analysis and was treated as the '*triedrus* group' with the subgeneric name *Geckoella* being available for the ground-dwelling members of the clade (Grismer et al., 2021).

Although Deraniyagala (1932) considered *C. triedrus* as a high altitude species, Das and de Silva (2005) stated that the distribution of this species was restricted below the elevation of 700 m above sea level. However, subsequent authors reported this species from several different habitats, including wet forest patches in the lowland dry zone (Somaweera & Somaweera, 2009), savanna forests in the eastern dry and intermediate lowlands (Karunarathna & Amarasinghe, 2011), south-western lowland rain forests (e.g. Karunarathna & Amarasinghe, 2010, 2012), the lofty elevations (975 m above sea level) of the Rakwana Hills (Janzen & Bopage, 2011) and the high elevations (2,200 m above sea level) of the Central Highlands (Manamendra-Arachchi, 1997) of the island. Such scattered distribution patterns of such a rare geckonid species (IUCN conservation status: Near threatened, NT) suggested either a lack sampling and/or that of a cryptic species occupying distinct ecological regimes.

Therefore, to ascertain the underlying cause, we reassessed the taxonomy and distribution of the *C. triedrus* species complex group, and then we applied an integrated taxonomic approach. We compared three different populations of *C. triedrus* sensu lato (Kandy–the Central Highlands, the Knuckles massif, and Yakunhela (Nilgala) in the eastern slopes of the dry zone) and revealed that these three populations represent three distinct species.

Materials and methods

For this study, we collected both morphological and genetic data for the *Cyrtodactylus triedrus* complex, which we compared to publicly available data. We collected all the necessary morphological data for species in the *C. triedrus* complex over the course of this study and compared our dataset to specimens and descriptions of all other congeners (see Appendix I). When diagnosing and describing the new species, we scored specimens for the same morphological and morphometric characters used in recent descriptions of the subgenus *Geckoella* in *C. triedrus* group (e.g. Agarwal, 2016; Agarwal et al., 2016). Molecular data for the mitochondrial NADH dehydrogenase subunit 2 (ND2) gene samples from GenBank (Supplemental Table S1).

Specimen collection

Our fieldwork in Sri Lanka took place between the years 2001–2021. We surveyed during the day and night. We collected the individuals (between 2018 and 2021, including the types designated herein) by hand, euthanized the specimens with sodium pentobarbital, and fixed the specimens in 10% buffered formalin solution prior to their storage in 70% ethanol. We preserved tissue samples for DNA analysis in 95% ethanol. Types and the vouchered specimens were deposited at the National Museums of Sri Lanka (NMSL), Colombo, Sri Lanka and we examined specimens from the Natural History Museum, London, UK (NHMUK). Museum acronyms are those of Uetz et al. (2019).

Molecular genetic data

Molecular data for the mitochondrial NADH dehydrogenase subunit 2 (ND2) gene was taken from previously published studies (Gamble et al., 2012; Grismer et al., 2021; Wood et al., 2012) and the selection of taxa for the analysis follows Grismer et al. (2021). Sequences were aligned with ClustalW (Thompson et al., 2003) in MegaX (Kumar et al., 2018) with default parameters. The aligned dataset was subjected to Maximum Likelihood phylogeny on the IQ-TREE (http://iqtree.cibiv.univie.ac.at/) online portal (Minh et al., 2020). The Sequence substitution model was selected using the auto parameter with provision for FreeRate heterogeneity (Supplemental Table S3) and the analysis was run with an ultrafast bootstrap option for 1000 iterations to assess clade support. The resultant tree was visualized and edited in FigTree v. 1.4.3. (Rambaut, 2012). The uncorrected *p*-distance (sequence divergence) was calculated in MegaX and a pairwise deletion approach was chosen to deal with gaps and or missing data.

Morphological character data

With a Mitutoyo digital caliper to the nearest 0.1 mm under a Leica Wild M3Z dissecting microscope on the left-hand side of the body, we measured snout–vent length (SVL, from tip of snout to anterior margin of vent), tail length (from the posterior margin of vent to the tip of tail), brachium length (on the dorsal surface from the axilla to the inflection of the flexed elbow),

forearm (antebrachium) length (on the dorsal surface from the posterior margin of the elbow while flexed to the inflection of the flexed wrist), thigh length (from the anterior margin of the hind limb at its insertion point on the body to the knee while flexed), tibia (crus) length (from the posterior surface of the knee while flexed to the base of the heel), axilla–groin (trunk) length (from the posterior margin of the forelimb at its insertion point on the body to the anterior margin of the hind limb at its insertion point on the body), body width (maximum width of the body), tail width (maximum width of the tail), head length (from posterior edge of mandible to tip of snout); head width (maximum width of head at the angle of the jaws), head depth (height) (maximum height of the head, from the occiput to the underside of the jaws), orbit (eye) diameter (the greatest horizontal diameter of the orbit); orbit–ear length (from posterior border of orbit to anterior border of tympanum), snout length (from anterior border of orbit to tip of snout), orbit–nostril length (from anterior border of orbit to middle of nostril), interorbital distance (shortest distance between the left and right supraciliary scale rows), ear length (greatest horizontal diameter of tympanum), internarial distance (shortest distance between dorsal margins of nostrils), orbit–mandible length (from posterior border of orbit to posterior tip of mandible), palm length [from wrist (carpus) to distal tip of longest finger], foot length (from heel to tip of longest toe), finger and toe lengths (from tip of claw to the nearest fork).

Most of the meristic data is self-explanatory; however, a few characters require further comment here. We counted supralabial and infralabial scales from below the middle of the orbit to the rostral and mental scales, respectively. We counted subdigital lamellae on finger/toe I and IV from the base of the first phalanx to the claw. We counted the number of longitudinal ventral scale rows (across belly) and number of dorsal tubercle rows at midbody. We evaluated the relative size and morphology of the subcaudal scales, the number of postcloacal tubercles (spur) on each side of the tail base and body colour pattern characteristics. The sex of the specimens was examined by observing hemipenal bulges and femoral pores in males. In order to examine the smaller characters such as keeling in the ventrals, we applied the reversible stain methylene blue in 70% ethanol, following Amarasinghe et al. (2015).

Results

Phylogenetic relationship

Molecular phylogenetics based on 1038bp of ND2 gene, recovered a clade consisting of three lineages corresponding to *Cyrtodactylus triedrus* sensu stricto, *C. punctatus* comb. nov. and an undescribed species. *Cyrtodactylus triedrus* sensu stricto and *C. punctatus* comb. nov. are sister taxa and the undescribed lineage is basal to these two species. The undescribed species is the population on the eastern slopes of the island, which is genetically highly divergent (Supplemental Tables S1 and S2). It is also morphologically highly distinct from the *C. triedrus* sensu stricto and *C. punctatus* comb. nov. The phylogenetic analysis suggests that the *C. triedrus* complex forms a monophyletic group, basal to the other members of the subgenus *Geckoella* (Fig. 1). The group includes *C. triedrus*, *C. punctatus*, and the new species described herein. In the *C. triedrus* subclade, *C. triedrus* from Peradeniya-Kandy (NMSL 0172, 0173) is most similar to the *C. punctatus* individual from the Knuckles massif (NMSL 0168, 0169) and the new species from Rathugala and Yakunhela (Nilgala), Bibile (NMSL 2021.07.01, 2021.07.02), thus these are grouped together.

Taxonomy

We present morphometric and meristic data taken for the type specimens (Table 1). Statistically informative tests could not be performed due to the small sample size of the new species and its congeners. Nonetheless, interspecific comparisons revealed a suite of characters that distinguish the new species from its congeners (Tables 2 and 3). These distinguishing features are summarised in the diagnosis and comparisons sections below.

Cyrtodactylus triedrus was described without a precise type locality; in order to achieve taxonomic stability, it is essential that we restrict the type locality for *C. triedrus*. Therefore, we compared the holotype of *C. triedrus*, to the specimens of *C. triedrus* sensu lato which were available to us from various populations, and it is revealed that the holotype is morphologically representive of the population around Kandy. Also, considering Annandale (1913) who first indicated a precise location "Peradeniya, Ceylon (ca. 1500 ft [alt. ∼460 m]" for this species, we here restrict the type locality to Peradeniya near Kandy – further clarification is explained below in the discussion. Because the original description of *C. triedrus* is vague, we redescribe this species based on the holotype.

The diagnostic characters distinguishing *C. triedrus* and its junior subjective synonym *Geckoella punctata*, reveal that the latter is a distinct species. Therefore, we resurrect *Geckoella punctata* from its synonymy and combine it with the genus *Cyrtodactylus*. As Gray (1867) did not provide precise type materials, *fide*

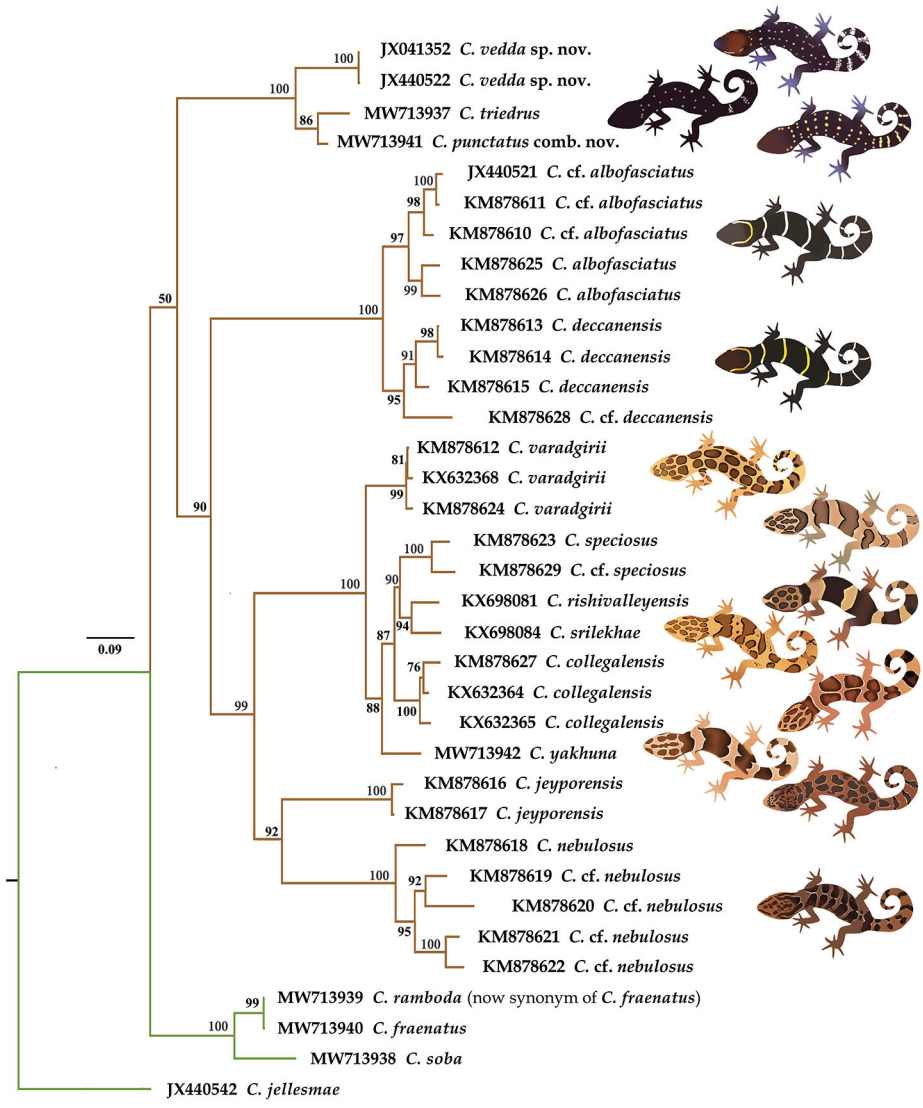

Fig. 1. Maximum likelihood (ML) phylogeny of ground-dwelling members of the genus *Cyrtodactylus* (subgenus *Geckoella*) based on 1038bp of the mitochondrial *ND2* gene. Numbers at nodes represent branch supports (bootstrap). Brown colour branches represent ground-dwelling members and arboreal members are in green.

Boulenger (1885) we propose the consideration that Gray's species was based on more than one single specimen, hence a type series, which makes this a syntype. There were three specimens catalogued as the "types" of *Geckoella punctata* at the Natural History Museum, London, and the population in the Knuckles massif is identical with two of the syntypes. Among the three syntypes catalogued, we identified the most closely matching specimen to Gray's original description and plate IX (see Fig. 2) of the original publication, this is NHMUK 1866.1.22.6. Therefore, in order to stabilize the nomen with a recognized name bearing type specimen, we designate this specimen (NHMUK 1866.1.22.6) as the lectotype for *Geckoella punctata*. We also redescribe it as a distinct species of the genus *Cyrtodactylus*. In the new generic combination of the species, the specific epithet "*punctata*" which is a Latin adjective in the feminine gender is converted to the masculine "*punctatus*", in order to be compatible with the generic epithet, *Cyrtodactylus* which is also masculine in gender. In addition, considering Ferguson (1877) who made the following statement "It is supposed to have been found about Mátalé" which is in the foothills of the Knuckles Massif (alt. ∼365 m above sea level), we restrict the distribution of *Cyrtodactylus punctatus* comb. nov. to the Knuckles massif – further clarification is explained below in the discussion.

We examined the lectotype of *Cyrtodactylus fraenatus* (Günther, 1864) which is restricted to the mid-

Table 1. Selected Morphometric (in mm), meristric, and morphological characters of the holotype of *Cyrtodactylus vedda* sp. nov., lectotype and paralectotype of *C. punctatus*, holotype of *C. triedrus* and other voucher specimens examined of each species; "—" = not evaluated.

	***C. vedda* sp. nov.**		***C. punctatus***			***C. triedrus***	
Character	**holotype NMSL 2021.07.01**	**paratype NMSL 2021.07.02**	**lectotype NHMUK 1866.1.22.6**	**paralectotype NHMUK 1866.1.22.7**	**Other ($n = 3$)**	**Holotype NHMUK 1855.2.12.7**	**Other ($n = 3$)**
snout–vent length	62.2	34.6	61.5	54.5	54.7–55.0	50.6	35.2–32.5
axilla–groin length	28.8	13.9	26.0	20.0	22.5–23.9	21.9	20.8–21.5
body width	15.6	5.2	14.4	12.0	9.5–9.8	9.3	7.3–8.2
tail length	51.6	26.3	broken	broken	46.4–48.5	broken	33.9–35.6
tail width	4.9	3.8	7.7	6.3	4.5–4.6	6.12	4.3–5.2
head length	20.1	12.3	18.9	17.3	16.7–17.9	15.2	16.4–17.1
head width	12.8	7.1	12.7	10.6	10.3–10.6	9.0	10.2–10.4
head depth	9.6	4.8	9.2	7.4	4.6–4.8	6.3	4.9–5.2
orbit diameter	4.4	2.8	4.6	3.2	4.6–4.7	3.3	3.4–3.7
snout length	8.2	4.8	7.8	6.3	6.7–6.9	5.9	6.6–6.9
orbit–nostril length	6.7	4.5	5.5	4.4	5.8–5.9	4.0	5.7–6.4
orbit–mandible length	3.6	—	8.4	7.7	—	6.9	—
orbit–ear length	5.8	3.6	5.3	4.8	3.8–3.9	4.4	3.9–4.1
ear length	1.4	1.2	1.1	1.0	1.2–1.3	0.4	1.2–1.4
interorbital distance	4.8	2.4	5.3	3.1	4.5–4.7	4.9	4.5–4.7
internarial distance	2.2	1.5	2.0	2.1	2.4–2.6	1.1	2.4–2.5
brachium length	9.6	6.1	7.7	7.7	6.5–6.6	6.4	6.4–7.0
forearm length	9.2	4.6	9.0	9.4	7.1–7.4	8.1	6.8–7.8
thigh length	11.6	6.7	10.4	9.4	7.9–8.1	9.0	7.6–8.7
tibia length	12.3	6.2	10.5	8.6	10.6–10.9	8.0	9.4–10.5
supralabials (mid orbit)	10	10	8	8	8, 9	8	9, 10
Infralabials	10	9	9	9	7, 8	9	8, 9
ventral rows across belly	25	23	29	27	27–29	22	19–21
lamellae on toe IV	15	15	15	16	16–18	16	17–19
precloacal pores	2	absent	4	absent	4	4	4
postcloacal spur pairs	3	0	2	2	2	2	2

Table 2. Selected diagnostic characters between *Cyrtodactylus vedda* sp. nov., *C. punctatus*, and *C. triedrus*.

Character	***C. vedda* sp. nov ($n = 2$)**	***C. triedrus* ($n = 4$)**	***C. punctatus* ($n = 5$)**
maximum adult SVL	62.2 mm	50.6 mm	61.5 mm
Body colouration	usually uniform black, sometimes few scattered white spots	irregularly scattered white spots	yellow spots arranged in regular 7–9 cross lines
Number of tubercles encompassed in each white spot	1	1	2–5
Number of dorsal granules encompassed in each white spot	1–3	0	10–20
Arrangement of dorsal granules	heterogeneous	homogeneous	homogeneous
Arrangement of dorsal tubercles	heterogeneous	heterogeneous	homogeneous
Number of dorsal granules between enlarged tubercles	1–3	3–5	1–3
Mid dorsal fold / furrow	indistinct	distinct	distinct
medial parasagittal row of tubercles	indistinct	distinct	distinct
Shape of the anterior dorsal tubercles (lateral view)	flat	bluntly pointed	bluntly pointed
Enlarged tubercles on flank	absent	absent	present
Body granules on flank	non-enlarged	non-enlarged	enlarged
Precloacal pores (in males)	2	4	4
Precloacal scales (in males)	bluntly pointed	bluntly pointed	rounded
Posterior thigh (in males)	granular	granular	granular with enlarged tubercles
Median subcaudal rows	1–3 rows enlarged	1–3 rows enlarged	6–7 rows enlarged
Subcaudals	wide	narrow	wide
Number of postcloacal spur pairs	3	2	2

Table 3. Selected diagnostic characters of the species of the *Cyrtodactylus triedrus* complex in Sri Lanka; "—" = not evaluated/not applicable; see Appendix for accession data

Character	*C. vedda* sp. nov. ($n = 2$)	*C. triedrus* ($n = 4$)	*C. punctatus* ($n = 5$)	*C. yakhuna* ($n = 4$)	*C. cracens* ($n = 5$)	*C. edwardtaylori* ($n = 3$)	*C. fraenatus* ($n = 15$)	*C. soba* ($n = 19$)
adult SVL (in mm)	62.2	50.6	61.5	35.7	104.6	95.5	99.1	105.7
mid-body tubercle rows arranged regular (0) or irregular (1)	1	1	1	0	0	0	0	0
mid-body tubercle rows	—	—	—	—	6–8	14–15	5–9	7–10
tubercles in each paravertebral row	—	—	—	—	21–27	38–45	17–22	25–31
dorsal tubercles flat (0) or pointed (1)	0	1	1	0	0	1	1	1
dorsal tubercles smooth (0), feebly keeled (1), strongly keeled (K)	1	1	1	0	0	2	0	2
abdominal scales rounded (0), bluntly pointed (1)	1	0	1	0	0	0	0	1
body colouration spotted (0), banded (1)	0	0	0	1	1	1	1	1
dorsal granules homogeneous (0) or heterogeneous (1)	1	0	0	0	1	1	1	1
precloacal pores	2	4	4	0	5, 6	6	4–6	5–8
ventral scale rows across belly	23–25	19–22	27–29	23–27	30–32	29–30	28–32	30–34
supralabials (mid-orbit position)	10	8–10	8, 9	8–9	7, 8	7	7, 8	8
lamellae on toe IV (basal + apical series)	15	16–19	15–18	15–17	20–24	18–23	21–27	20–24

Fig. 2. The original illustration depicted *Cyrtodactylus* (*Geckoella*) *punctatus* in the original description; reprinted from Gray (1867) [Proceedings of the Zoological Society of London, plate IX].

Central Highlands around Kandy (designated and restricted by Batuwita & Bahir, 2005). We also examined a closely related taxon, *C. ramboda* Batuwita & Bahir, 2005 which was described from the north-western slopes of the Central Highlands. We recognise that these two species are morphologically identical and that there are no diagnostic characters to separate them. This result is also supported by phylogenetic analyses using published mitochondrial gene data (Grismer et al., 2021 and this work), including *C. fraenatus* and *C. ramboda*, showing no significant genetic differences between the two. We therefore, in accordance with the principle of priority *sensu* Article 23 of the Code (ICZN 1999) synonymize *C. ramboda* with *C. fraenatus*. It is clear that both populations in the south-western and north-western slopes of the Central Highlands represent one species, *C. fraenatus*.

Finally, we examined the holotypes of *Cyrtodactylus cracens* Batuwita & Bahir, 2005 and *C. subsolanus* Batuwita & Bahir, 2005 which were described from the western and eastern sides of the Sinharaja World Heritage Site respectively, and observed the same scenario of *C. fraenatus* + *C. ramboda* respectively from the south-western and north-western Central Highlands. The two species, *C. cracens* and *C. subsolanus* are morphologically identical and there are no diagnostic characters to separate them, hence they are considered subjective synonyms. Therefore, one of the nomens

should be prioritised in accordance with the principle of priority *sensu* Article 23 of the Code (ICZN 1999). As names, *C. cracens* and *C. subsolanus* were published simultaneously; we give precedence to the nomen *C. cracens* in accordance with the principle of first reviser *sensu* Article 24 of the Code (ICZN 1999). Therefore, the two populations in the western and eastern sides of Sinharaja represent one species, which is *C. cracens*.

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

lsid:zoobank.org:act:3B37037C-EE9F-4011-BEC9-47E1F3BB6779

Geckoella triedra – Goonewardene et al., 2004, de Silva et al., 2004, Somaweera & Somaweera, 2009 [*partim*], Karunarathna et al., 2013

Geckoella triedrus (*sic*) – Karunarathna & Amarasinghe, 2011, Agarwal & Karanth, 2015

Cyrtodactylus (*Geckoella*) *triedra* (*sic*) – Wood et al., 2012

Holotype (Figs. 1, 3–7; Tables 1–5). Adult male, NMSL 2021.07.01, collected from Rathugala (7°17'42.08"N, 81°22'42.89"E, datum = WGS84; 300 m above sea level), Bibile, Monaragala District, Uva Province, Sri Lanka; collected by Suranjan Karunarathna collected on 25 June 2018.

Paratype. Subadult female, NMSL 2021.07.02, collected from Yakunhela (7°12'03.42"N, 81°19'47.03"E, datum = WGS84; 350 m above sea level), same collection data as the holotype.

Diagnosis. The following combination of characters distinguishes *Cyrtodactylus vedda* sp. nov. from all other congeners: adults reaching 62.2 mm SVL; absence of a precloacal groove; dorsal scalation of small heterogeneous carinate granules intermixed with flat, feebly carinate irregularly arranged tubercles; absence of enlarged femoral scales and femoral pores; two precloacal pores; dorsal furrow indistinct; two pairs of postmentals, secondary pair 1/2 of the primary pair in size; throat scales granular; no spine-like tubercles on nape; ventrals larger than dorsals, smooth, elongate, and bluntly pointed, with 23–25 rows across the belly at midbody; ten supralabials at mid-orbit position; scales on posterior thigh granular without enlarged tubercles; lamellae divided, eight subdigital lamellae below the first and 15 below the fourth toe; dorsal scales on tail enlarged, smooth, imbricate; subcaudal scales at base rounded and not-enlarged; medially with several enlarged and narrow rows of subcaudals; three pairs of postcloacal tubercle (spur); body usually uniform black on dorsum, sometimes with irregular tiny white spots. These differences are summarized for close congeners (Table 2), for all Sri Lankan members (Table 3), and for all members of the subgenus *Geckoella* in *C. triedrus* group (Table 4).

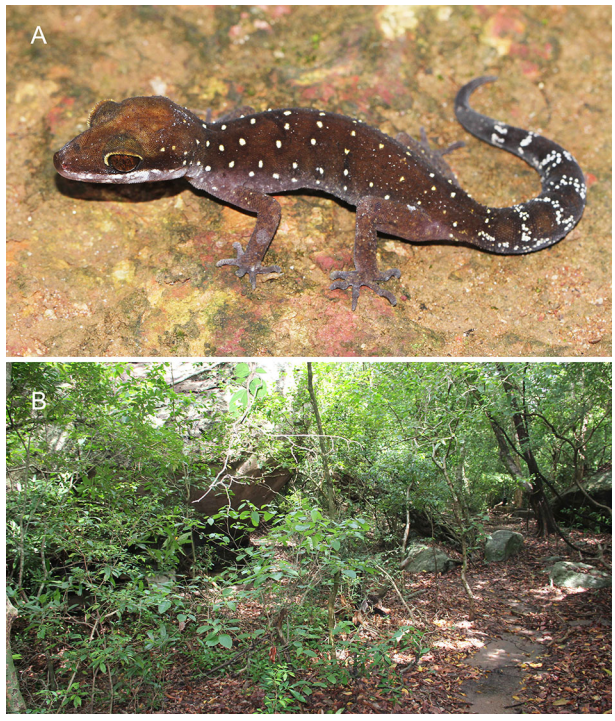

Fig. 3. (A) The holotype of *Cyrtodactylus* (*Geckoella*) *vedda* sp. nov. and (B) the intermediate forest habitat at Rathugala, Bibile, Sri Lanka. Photographs by S. Karunarathna.

Molecular diagnosis. The new species is a member of the *C. triedrus* group along with *C. triedrus* and *C. punctatus* comb. nov. The new species exhibits an uncorrected *p*-distance (sequence divergence) of 11% from *C. punctatus* comb. nov. and 12% from *C. triedrus* sensu stricto for the mitochondrial ND2 gene (Supplemental Table S2).

Comparison. *Cyrtodactylus vedda* sp. nov. is most similar to *C. triedrus* and *C. punctatus* comb. nov. (characters in parentheses), but it can be distinguished from these species by having heterogeneous and granular dorsal scalation at midbody (homogeneous in *C. triedrus* and *C. punctatus*); concave forehead in lateral view (convex in *C. triedrus*); indistinct mid dorsal furrow with unclear medial parasagittal row of tubercles (distinct with clear medial parasagittal row in *C.*

Table 4. Selected diagnostic characters of the species of the subgenus *Geckoella* in the *Cyrtodactylus triedrus* complex; "—" = not evaluated/unknown

Character	*C. vedda*	*C. albofasciatus*	*C. collegalensis*	*C. deccanensis*	*C. jeyporensis*	*C. nebulosus*	*C. punctatus*	*C. rishivalleyensis*	*C. speciosus*	*C. srilekhae*	*C. triedrus*	*C. varadgirii*	*C. yakhuna*
Maximum adult SVL (in mm)	62.2	67.0	54.0	63.0	53.0	52.0	61.5	50.0	47.0	50.0	50.6	56.0	35.7
Dorsal colouration with spots (1) stripes (2), blotches (3), cross bands (4): see Fig. 4.	1	2	3	2	3	3	1	4	4	3	1	3	4
Dorsal granules homogeneous (0), heterogeneous (1)	1	1	0	1	—	—	0	0	0	0	0	0	0
Precloacal pores absent (0), present (1)	1	0	0	0	0	0	1	0	0	0	1	0	0
Dorsal scales not intermixed with enlarged tubercles (0), intermixed with tubercles (1), have unique enlarged, hexagonal Scales (2)	1	1	0	1	2	1	1	0	0	0	1	0	0
Enlarged hexagonal scales on canthus rostralis absent (0), present (1)	0	—	0	—	—	—	0	0	0	0	0	1	0
Enlarged hexagonal scales beneath the angle of the lower jaw absent (0), present (1)	0	—	0	—	—	—	0	0	0	0	0	1	0
Ventral scale rows across belly	23–25	33	27–29	33	27	40	27–29	31–39	29–34	31–39	19–22	35–37	23–27
Lamellae on toe IV (basal + apical series)	15	—	15–19	—	—	—	15–18	15–19	7	15-18	16–19	16–21	15–17
Median subcaudals on original tail subequal (0), enlarged (1)	1	—	0	1	0	1	1	0	—	0	0	0	0

Fig. 4. a. Dorsal colouration of the known members of the sub genus *Geckoella* in the *Cyrtodactylus triedrus* Group. Illustration by A.A.T. Amarasinghe. **b (continued).** Dorsal colouration of the known members of the sub genus *Geckoella* in the *Cyrtodactylus triedrus* Group. Illustrations by A.A.T. Amarasinghe.

Fig. 4. Continued.

triedrus and *C. punctatus*); no enlarged tubercles on flank (present in *C. punctatus*) and body granules on flank not enlarged (enlarged in *C. punctatus*); subcaudals enlarged (not enlarged in *C. triedrus*); 1–3 dorsal granules between enlarged tubercles on dorsum (3–5 in *C. triedrus* and *C. punctatus*) – see Table 2 for further details.

The new species is also similar to other congeners of subgenus *Geckoella* in the *C. triedrus* group (*fide* Grismer et al., 2021) (Table 4), however it differs from them by having uniform blackish or brownish grey dorsum with a few tiny cream sports (yellow or white cross stripes in *C. albofasciatus* and *C. deccanensis*; white or black margined large brown blotches or wide cross bands on dorsum in *C. jeyporensis*, *C. nebulosus*, *C. yakhuna*, *C. varadgirii*, *C. collegalensis*, *C. speciosus*, *C. rishivalleyensis*, and *C. srilekhae*) – see Fig. 4, 2 precloacal pores (absent in *C. varadgirii*, *C. yakhuna*, *C. collegalensis*, *C. speciosus*, *C. rishivalleyensis*, *C. srilekhae*), heterogeneous dorsal scalation (homogeneous in *C. varadgirii*, *C. yakhuna*, *C. collegalensis*, *C. speciosus*, *C. rishivalleyensis*, *C. srilekhae*), dorsal granules intermixed with enlarged tubercles (absent in *C. varadgirii*, *C. yakhuna*, *C. collegalensis*, *C. speciosus*, *C. rishivalleyensis*, *C. srilekhae*, and unique enlarged, hexagonal scales in *C. jeyporensis*).

All the other congeners of the genus *Cyrtodactylus* (non *Geckoella*) from Sri Lanka (*C. cracens*, *C. edwardtaylori*, *C. fraenatus*, and *C. soba*) are larger bodied with SVL more than 98.0 mm in adults, but *Cyrtodactylus vedda* sp. nov. only grows to a maximum SVL of 62.2 mm. The new species further differs from them by having mid-body tubercle rows arranged irregularly (regular with 6–15 rows – see Table 3), dorsal

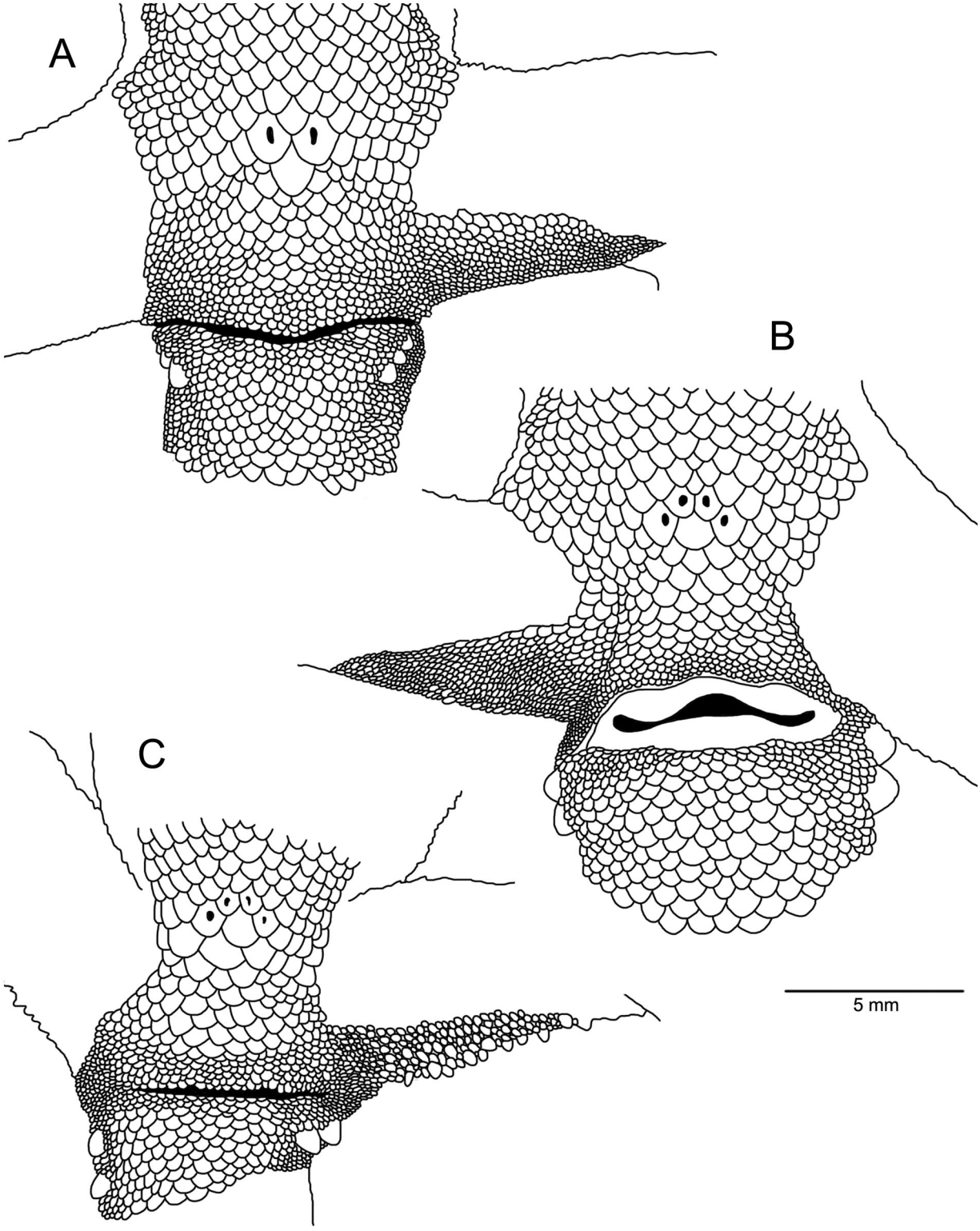

Fig. 5. Precloacal scales, posterior thigh, postcloacal spur, and the tail base of (A) *Cyrtodactylus vedda* sp. nov. holotype, (B) *C. triedrus* holotype, and (C) *C. punctatus* comb. nov. lectotype. Illustrations by A.A.T. Amarasinghe.

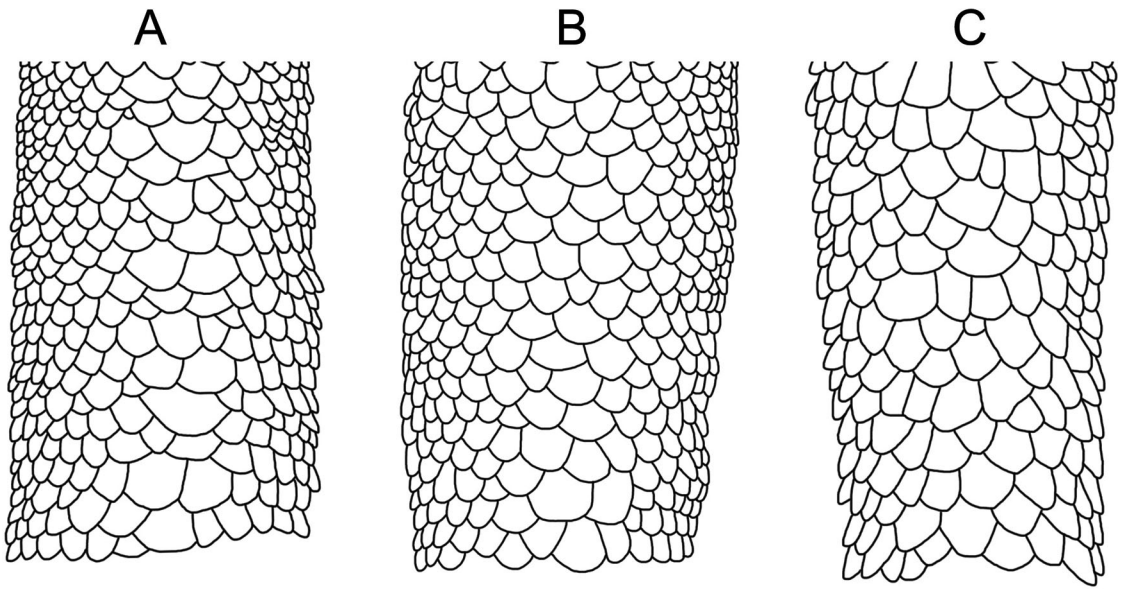

Fig. 6. Subcaudals of the original tail of (A) *Cyrtodactylus vedda* sp. nov. holotype, (B) *C. triedrus*, NMSL 0172, and (C) *C. punctatus* comb. nov., NMSL 0168 (not to scale). Illustrations by A.A.T. Amarasinghe.

tubercles flat (pointed in *C. edwardtaylori*, *C. fraenatus*, and *C. soba*), dorsal tubercles keeled (smooth in *C. cracens* and *C. fraenatus*), body colouration uniform (irregular banded), 23–25 scale rows across belly (28–34), and 15 lamellae beneath the fourth toe (18–27).

Description of holotype. The holotype is generally in good condition except that the tail tip was taken for molecular work.

An adult male, 62.2 mm SVL; head moderately large, elongate, its length 32.3% of SVL, narrow, head width 63.7% of head length and 20.6% of SVL, not strongly depressed, head depth 47.8% of head length, distinct from neck; snout elongate, its length 40.8% of head length and greater than orbit diameter, orbit diameter 53.6% of snout length; scales on snout, canthus rostralis, interorbital granular, bluntly pointed or flat, feebly carinate, twice larger than those on interorbital and occipital region; interorbital region relatively narrow; interorbital distance 23.9% of head length; occipital region has intermixed enlarged, dorsally rounded, flat, feebly carinate tubercles, which are 2–5 larger than adjacent granules; orbit large, its diameter 21.9% of head length, pupil vertically slit with crenulated margins; supraciliaries large, flat; diameter of orbit slightly greater than orbit–ear distance, orbit diameter 75.9% of orbit–ear distance; ear-opening small, shallow, oval. Rostral wider than deep, incompletely divided dorsally by weakly developed rostral groove, postero-ventrally in contact with first supralabial, contacted posteriorly by nostril, two supranasals, and an internasal; nostrils separated by two enlarged, subcircular supranasals; a single small, pentagonal internasal scale between supranasals; nostrils subcircular, dorsally orientated; four postnasals, lowest smaller, not in contact with first supralabial, separated by a small subnasal; loreal region slightly inflated and convex, canthus rostralis not prominent; three rows of scales separate orbit from supralabials at level of pupil; a single interrupted row of enlarged, elongate scales bordering supralabials; supralabials to the angle of jaw 15 on both sides, 10^{th} at mid-orbit position; infralabials to the angle of jaw 10 on both sides; enlarged tubercles on nape and temporal region bluntly pointed and rounded.

Mental subtriangular, shorten posteriorly to mid-level of second supralabial, wider than long, postero-laterally in contact with two postmental scales that contact posteriomedially for 60% of their length; primary postmentals bordered by two enlarged secondary postmentals (chin shields) and eight small gular scales, the enlarged chin shields arranged in one row grading posteriorly into smaller scales and extending posteriorly to the fifth infralabial; gular scales small and granular, grading posteriorly into slightly smaller, flatter; throat scales and scales on neck granular and smooth, smaller than on the ventral body.

Body slim, elongate, axilla–groin length 46.3% of SVL, no distinct ventrolateral fold; dorsal granules blunt and elliptical, heterogeneous, smooth or feebly carinate, intermixed with flat, feebly carinate, enlarged, heterogeneous tubercles; dorsal tubercles randomly arranged, flat middorsally and bluntly pointed laterally, and extending from occiput onto the tail, no tubercles on flanks; mid

dorsal furrow indistinct; each enlarged tubercle about 4 to 5 times as large as granules separating them, largest surrounded by 8 to 10 granules, 1–3 granules separate adjacent enlarged tubercles; dorsal granules at midbody smaller than ventral scales at same level; pectoral scales smaller in size with abdominal scales, pectoral and abdominal scales smooth, imbricate, bluntly pointed; scales smaller on femoral and largest on precloacal region; ventral scales in 25 rows across belly; ventro-lateral granules on trunk smooth, elliptical, and not enlarged, without enlarged tubercles; femoral scales smaller or granular and not bearing pores; precloacal scales enlarged and consisted of 15–20 enlarged scales, three of them distinctly enlarged and two bearing pores.

Arms moderately long; length of forearm 14.8% of SVL; length of brachium 15.4% of SVL; legs relatively longer; length of tibia 19.8% of SVL; thigh longer than tibia, its length 18.6% of SVL; brachium with flat, smooth granular scales which are larger than on dorsum, no tubercles intermixed; dorsal scales on forearm smaller than on brachium, bluntly pointed and feebly carinate, heterogeneous; scales on elbow are slightly enlarged, smooth and flat; ventral scales on brachium bluntly pointed and smooth, smaller than those on the ventral body; ventral scales on forearm enlarged; scales on the palm smooth, rounded or bluntly pointed; dorsal granules on leg bluntly pointed and feebly carinate, thigh with scales which are slightly larger than granules on dorsum, posterior edge of thigh granular; dorsal granules on tibia heterogeneous, predominantly bearing much smaller tubercles; scales on knee smooth, bluntly pointed; ventral scales on both thigh and tibia bluntly pointed and smooth, scales on tibia much more enlarged than those on the ventral side of the thigh, but smaller in size to the scales on precloacal area; scales on the foot smooth and bluntly pointed; digits moderately long, fourth finger 50% of forearm length, fourth toe 66.1% of tibia length, strongly clawed; all digits of manus and digits I–IV of pes not webbed; terminal phalanx of all digits curved; lamellae beneath each toe in straight transverse series, and entire: subdigital lamellae 9-9-11-12-8 in left manus, 8-10-12-13-10 in right manus, 8-11-13-15-14 in left pes, 7-12-13-15-14 in right pes; relative length of digits in mm: V, 3.5 > IV, 3.3 > III, 2.9 > II, 2.4 > I, 2.3 in left manus; IV, 4.8 > V, 5.1 > III, 4.7 > II, 4.5 > I, 4.2 in left pes.

Tail complete, length 51.6 mm, original, round, flat beneath, verticillate, with no median furrow; length of the tail shorter than snout-vent length, tail length 82.9% of SVL; dorsal scales on the tail imbricate, pointed, smooth, larger than granules on dorsum; tail not segmented with whorls of tubercles; three pairs of postcloacal spur present; ventral scales on tail base not enlarged, smooth, and rounded; four to five rows of the subcaudal scales enlarged, two to three rows among them two to four times larger than other subcaudals, smooth, bluntly pointed, wide, and imbricate.

Colouration. In life, the holotype of *Cyrtodactylus vedda* sp. nov. had a blackish gray ground colour with irregularly scattered white spots; dorsal head, snout dark blackish brown; labials purplish grey with white markings, posteriorly uniform white; temporal region dark brownish black; black postorbital band up to posterior edge of the head; superciliaries dark brown; few enlarged tubercles on neck and dorsum white including few surrounding granules; limbs darker; ventral side of the head, body, and limb purplish grey; chin and purplish grey; palms and feet grey; ventral tail dark grey, dorsally black with irregular white spots visible as broken cross bands, uniform grey distally.

In preservative, the black or dark grey ground colour faded to a uniform dark brown; dorsal head pale, snout light yellowish brown; labials dark grey with white margins, posteriorly uniform white; temporal region light brown; blackish brown postorbital band up to posterior edge of the head; superciliaries cream; a few enlarged tubercles on neck and dorsum white; limbs darker; ventral side of the head, body, and limb yellowish brown; chin and throat cream; palms and feet grey; ventral tail dark chestnut brown, dorsally dark brown with cream irregular cross markings, distally uniform brown.

Etymology. The specific epithet refers to the "veddas", a minority population of ancient aboriginal indigenous ethnic group of people living in the vicinity of the new species (e.g. Nilgala, Ratugala) in Sri Lanka is formed here as an invariable noun in apposition. Vedda clans are classified as a separate ethnic group. A clan of old descendants of the "rock veddas" or rock cave dwellers currently live in hamlets in Ratugala and Nilgala where probably the most established group of veddas in Sri Lanka still live (Osman Hill, 1932). However, some of them are now intermingled with the Sinhalese and Tamil ethnic groups. The original name for the vedda in Ratugala and Nilgala is "Danigala vedda" – they left the Danigala rock caves many years ago and settled in the Rathugla area. English name: Veddas ground-gecko, Sinhalese name: Vedi bim-hoona.

Distribution and natural history. This species is only distributed in savannah ecosystems in Rathugala, Yakunhela (near Nilgala), Karandugala, Nilgala and Maragalakanda (Monaragala) (Fig. 7) which are covered by large rock outcrops, it prefers shady habitats covered by monsoon forest type, large tall trees (above 10 m) e.g. *Terminalia belerica* (Combretaceae), *Ficus mollis*

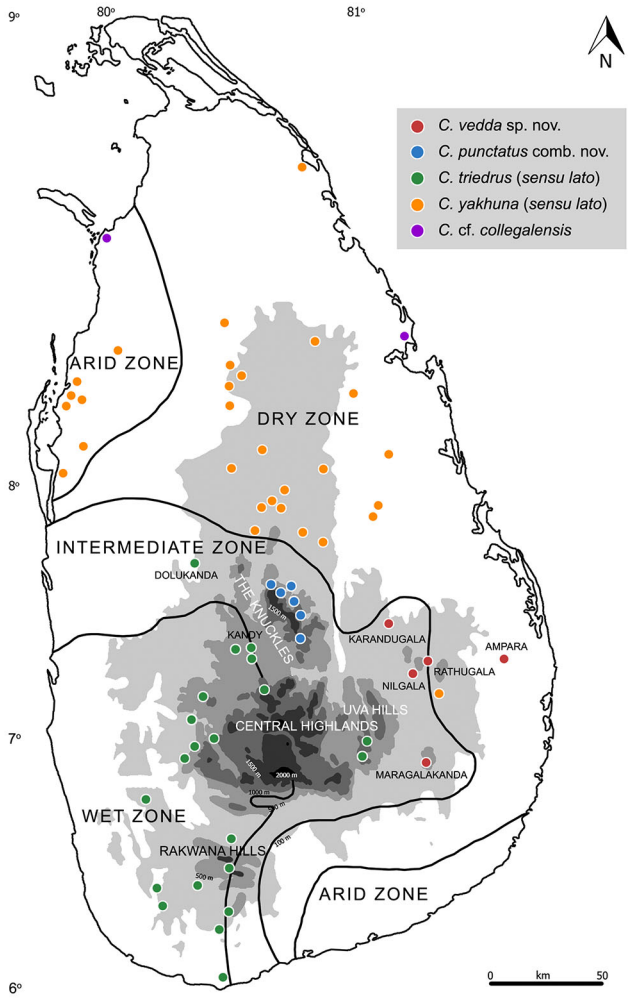

Fig. 7. Current distribution pattern of the terrestrial *Cyrtodactylus* (subgenus *Geckoella*) in Sri Lanka: *C. vedda* sp. nov. (red), *C. triedrus* (green), *C. punctatus* (blue), *C. yakhuna* (orange), and *C.* cf. *collegalensis* (purple).

(Moraceae), *Diospyros ebenum* and *D. malabarica* (Ebenaceae), *Terminalia bellirica* and *T. chebula* (Combretaceae), *Mangifera zeylanica* (Anacardiaceae), and *Madhuca longifolia* (Sapotaceae). They are always found on the forest floor covered thick leaf litter (above 10 cm thickness) close to streams, and are never found on rocks, trees or in caves. This species is always recorded from habitats away from seasonal or man-made forest fire, which is a common occurrence in the dry season (August–October). They are never found inside termite mounds similar to its congeners, *C. triedrus* and *C. punctatus*. This is a slow moving species which commonly hides under leaf litter, loose stones and fallen logs during the day. When disturbed, they run a short distance with considerable speed, then pausing for some time until the threat disappears. This is a nocturnal species mainly feeding on small insects. Juveniles are sometimes encountered in the open during the day (Somaweera & Somaweera, 2009), although we never found any juveniles during day time. The reports from Kokagala (Monaragala), Ampara (*fide* Somaweera & Somaweera, 2009) may refer to this new species. This species is sympatric with the diurnal *Cnemaspis kumarasinghei*, while *Cyrtodactylus* cf. *edwardtaylori* (taxonomic work in progress – Amarasinghe et al. in prep.), *Cyrtodactylus yakhuna*, *Hemidactylus hunae*, *H. parvimaculatus*, *H. triedrus*, *H. fraenatus*, *H. leschenaultii*, *H. depressus*, *Calodactylodes illingworthorum*, *Cnemaspis nilgala*, *Cnemaspis podihuna*, *Gehyra mutilata* are syntopic in the surrounding habitats.

Conservation status. The application of the IUCN Red List criteria (IUCN Standards & Petitions Subcommittee, 2019) shows that the new species is restricted to five localities (alt. 200–400 above sea level) with area of occupancy (AOO) of 15.5 km^2 where eight individuals (seven adults and a single juvenile) were recorded from these five localities in two main locations, Nilgala and Yakunhela with

extent of occurrence (EOO) of 192 km^2. Also given the isolated distribution, man-made forest fire, the rapid forest fragmentation due to chena cultivation, excessive application of agrochemicals, and the large-scale forest clearance for Maize, sugar cane, and rubber plantations within this range, *C. vedda* can be considered a Critically Endangered (CR) species. The current distributed localities lies within protected areas, Nilgala Forest Reserve, Galoya National Park and the Maragala Forest Reserve. However, the area within these protected ranges is highly threatened by man-made fire. New road constructions through primary forests are identified as a major and emerging threat to this terrestrial gecko species.

***Cyrtodactylus* (*Geckoella*) *punctatus* comb. nov.**

Knuckles ground-gecko (English), Dumbara bimhoona (Sinhalese)

Geckoella punctata Gray, 1867

Geckoella punctatus (*sic*) – Ferguson, 1877

Geckoella triedrus (*sic*) – Deraniyagala, 1953 [*partim*]

Geckoella triedra – Wickramasinghe & Somaweera, 2002 [*partim*], Somaweera & Somaweera, 2009 [*partim*]

Lectotype (Figs. 2, 4–8; Tables 1–5) designated herein. Adult male, NHMUK 1866.1.22.6, collected from Ceylon (Sri Lanka); probably collected from the environs of Matale (*fide* Ferguson, 1877; 7°28'02"N, 80°37'24"E, datum = WGS84; 365 m above sea level), Matale District, Central Province, Sri Lanka.

Paralectotype. Adult female, NHMUK 1866.1.22.7, same collection data as the lectotype.

Other specimens examined (*n* = 2). adult male, NMSL 0168, 0169, collected from Illukkumbura (7°31'50.94"N, 80°46'17.44"E, datum = WGS84; 700 m above sea level), Matale District, Central Province, Sri Lanka; collected by Suranjan Karunarathna on 12 August 2020.

Diagnosis. The following combination of characters distinguishes *Cyrtodactylus punctatus* comb. nov. from all other congeners: adults reaching 61.5 mm SVL; absence of a precloacal groove; dorsal scalation of small homogeneous, smooth, granules intermixed with bluntly pointed, feebly carinate irregularly arranged tubercles, except medial parasagittal row of tubercles arranged linearly; absence of enlarged femoral scales and no femoral pores; four pores on enlarged precloacal scales; dorsal furrow distinct; two pairs of postmentals, secondary pair 1/3 of the primary pair in size; throat scales granular; no spine-like tubercles on nape; ventrals larger than dorsals, smooth, elongate, and bluntly pointed, with 27–29 rows across belly; eight or nine supralabials at mid-orbit position; scales on posterior thigh granular with enlarged tubercles; lamellae divided, 8–10 subdigital lamellae below the first and 15–18 below the fourth toe; dorsal scales on tail not enlarged, smooth, imbricate; subcaudal scales at base bluntly pointed and enlarged; medially with three enlarged and wide rows of subcaudals; two distinct postcloacal tubercles (spur); body dorsum purplish black or dark brown with large yellow spots arranged in 7–9 cross lines with 4 or 5 spots in each line. These differences are summarized for close congeners (Table 2), for all Sri Lankan members (Table 3), and for all members of the subgenus *Geckoella* in *C. triedrus* group (Table 4).

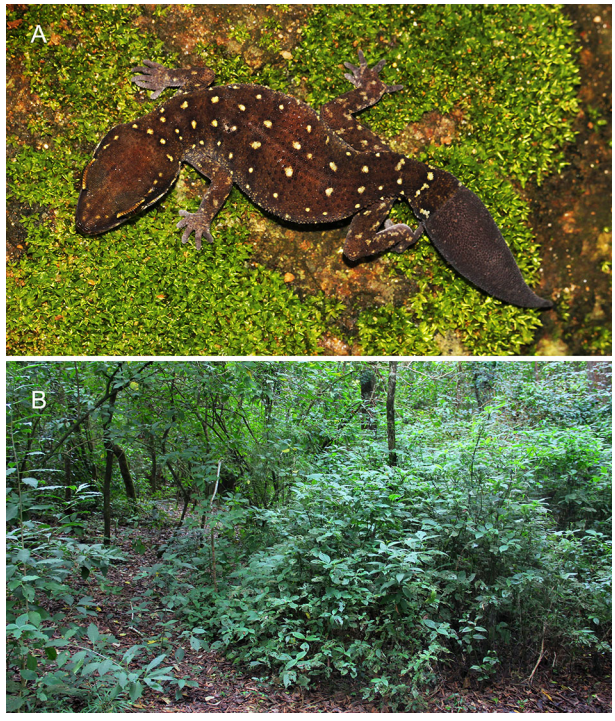

Fig. 8. (A) An adult male (not collected) of *Cyrtodactylus* (*Geckoella*) *punctatus* comb. nov. and (B) the submontane forest habitat at the Knuckles massif, Sri Lanka. Photographs by S. Karunarathna.

Description of lectotype. Based on NHMUK 1866.1.22.6. The lectotype is generally in good condition except the broken tail.

An adult male, 61.5 mm SVL; head moderately large, elongate, its length 30.7% of SVL, narrow, head width

67.2% of head length and 20.6% of SVL, not strongly depressed, head depth 48.7% of head length, distinct from neck; snout elongate, its length 41.3% of head length and greater than orbit diameter, orbit diameter 59.0% of snout length; scales on snout, canthus rostralis, interorbital granular, bluntly pointed, smooth, twice larger than those on interorbital and occipital region; interorbital region relatively narrow; interorbital distance 28.0% of head length; occipital region has intermixed enlarged, dorsally rounded, bluntly pointed, feebly carinate tubercles, which are 2–4 larger than adjacent granules; orbit large, its diameter 24.3% of head length, pupil vertically slit with crenulated margins; supraciliaries large, flat; diameter of orbit slightly shorter than orbit–ear distance, orbit diameter 86.8% of orbit–ear distance; ear-opening small, shallow, oval. Rostral wider than deep, incompletely divided dorsally by weakly developed rostral groove, postero-ventrally in contact with first supralabial, contacted posteriorly by nostril, two supranasals, and an internasal; nostrils separated by two enlarged, subcircular supranasals; a single small, circular internasal scale between supranasals; nostrils subcircular, dorsally orientated; six postnasals, lowest smaller, not in contact with first supralabial, separated by a small subnasal; loreal region slightly inflated and convex, canthus rostralis not prominent; four rows of scales separate orbit from supralabials at level of pupil; a single interrupted row of slightly enlarged, elongate scales bordering supralabials; supralabials to the angle of jaw 13 on left side and 12 on right side, 8^{th} at mid-orbit position; infralabials to the angle of jaw 9 on both sides; enlarged tubercles on nape and temporal region bluntly pointed and rounded.

Mental subtriangular, lengthen posteriorly to anterior margin of second supralabial, wider than long, postero-laterally in contact with two postmental scales that contact posteriomedially for 60% of their length; primary postmentals bordered by two enlarged secondary postmentals (chin shields) and six small gular scales, the enlarged chin shields arranged in one row grading posteriorly into smaller scales and extending posteriorly to the third infralabial; gular scales small and granular, grading posteriorly into slightly smaller, flatter; throat scales and scales on neck granular and smooth, smaller than on the ventral body.

Body slim, elongate, axilla–groin length 42.3% of SVL, no distinct ventrolateral fold; dorsal granules blunt and subcylindrical, homogeneous, smooth or feebly carinate, intermixed with bluntly pointed, feebly carinate, enlarged, homogeneous tubercles; dorsal tubercles bluntly pointed middorsally, randomly arranged except for the medial parasagittal rows of tubercles arranged linearly, and extending from occiput onto the tail; each enlarged tubercle about 4 to 5 times as large as granules separating them, largest surrounded by 8 to 10 granules, 1–3 granules separate adjacent enlarged tubercles; mid dorsal furrow distinct [folded in the lectotype, an artefact of preservation]; numerous enlarged tubercles on flanks; dorsal granules at midbody smaller than at flank and ventral scales at same level; pectoral scales smaller than abdominal scales, pectoral and abdominal scales smooth, imbricate, bluntly pointed, elongate; scales smaller on femoral and largest on precloacal region; ventral scales in 29 rows across belly; ventro-lateral granules on trunk smooth, round, and enlarged, intermixed with distinct enlarged tubercles; femoral scales smaller or granular and not bearing pores; precloacal scales enlarged and consists of 20–30 enlarged scales, four of them bearing pores.

Arms moderately long; length of forearm 14.6% of SVL; length of brachium 12.5% of SVL; legs relatively longer; length of tibia 17.1% of SVL; thigh slightly shorter than tibia, its length 16.9% of SVL; brachium with flat, smooth enlarged scales which are larger than on dorsum, no intermixed tubercles; dorsal scales on forearm smaller than on brachium, granular, bluntly pointed, smooth and intermixed with enlarged tubercles, homogeneous; scales on elbow are not enlarged, smooth and granular; ventral scales on brachium bluntly pointed and smooth, smaller than those on the ventral body; ventral scales on forearm enlarged; scales on the palm smooth, rounded or bluntly pointed; dorsal granules on leg bluntly pointed and feebly carinate, intermixed with numerous enlarged feebly carinate tubercles, thigh with scales which are larger than granules on dorsum, posterior edge of thigh granular intermixed with large tubercles posteriorly; dorsal granules on tibia homogeneous, predominantly bearing much smaller tubercles, intermixed with enlarged, pointed tubercles; scales on knee smooth, granular, and flat; ventral scales on both thigh and tibia bluntly pointed and smooth, scales on tibia much more enlarged than those on the ventral side of the thigh, but smaller in size to the scales on precloacal area; scales on the foot smooth and bluntly pointed; digits moderately long, strongly clawed; all digits of manus and digits I–IV of pes not webbed; terminal phalanx of all digits curved; lamellae beneath each toe in straight transverse series, and entire: subdigital lamellae 9-12-14-15-13 in left pes, 8-11-14-16-12 in right pes; relative length of digits: IV > V > III > II > I in manus; V > IV > III > II > I in pes.

Tail broken, length $45.4 + 4.2$ mm, original, round, flat beneath, verticillate, with a median furrow; length of the tail shorter than snout-vent length, tail length 80.6% of SVL; dorsal scales on the tail imbricate, pointed, smooth, larger than granules on dorsum; tail not segmented with whorls of tubercles; two prominent

postcloacal spurs; ventral scales on tail base enlarged, smooth, and bluntly pointed; three rows of the subcaudal scales enlarged, five to six times larger than on dorsal tail, and twice larger than subcaudals besides, smooth, pointed, wide, short, and imbricate.

Colouration. After more than 150 years in preservative, dorsum light brown ground colour; dorsal head paler, snout darker; labials cream with white markings; temporal region slightly darker with postorbital band up to posterior edge of the head; superciliaries cream; three white spots on nape and each spot includes an enlarged tubercle and surrounding 18–20 granular scales; similarly 7 rows of white spots across the dorsal body between nape and thigh, each row consists of 4 spots; the two spot lines on and along the vertebral line larger than the ones besides; each spot covers 1–5 enlarged tubercles plus 10–20 surrounding dorsal granules; each spot margined with dark brown ring; limbs same as body colour; ventral side of the head, body, and limb cream; chin whitish; palms and feet light brown; ventral tail darker, cream irregular cross markings dorsally, uniform brown distally.

In life, based on Figure 8A Dorsum purplish black or dark purplish brown ground colour; dorsal head paler, snout darker; labials purplish grey with white markings; temporal region black with postorbital band up to posterior edge of the head; superciliaries golden yellow; three golden or pale yellow spots on nape and each spot includes an enlarged tubercle and surrounding 18-20 granular scales; similarly 7-9 rows of yellow spots across the dorsal body between nape and thigh, each row consists of 4 or 5 spots; the two spot lines on the along the vertebral line larger than the ones besides; each spot covers 1-5 enlarged tubercles plus 10-20 surrounding dorsal granules; each spot margined with black or dark brown ring; limbs same as body colour; ventral side of the head, body, and limb purplish grey; chin purple; palms and feet purple; ventral tail darker, cream or pale yellow irregular cross markings dorsally, uniform dark brown or black distally.

Variation. The female paralectotype (NHMUK 1866.1.22.7) has the same colouration as the above described lectotype, but the body colour is paler and it has no precloacal pores. The male specimens (NHMUK 1866.1.22.6, NMSL 0168, 0169) has four precloacal pores.

Distribution and natural history. This species is only distributed in the submontane forests ecosystems in the mid elevations of the Knuckles massif around Illukumbura (700 m), Manigala (650 m), Meemure (480 m), and Dotalugala (1,000 m) (Fig. 7). The report from Gammaduwa (*fide* Deraniyagala, 1953) may also refer to this species. The preferred habitat of this species is composed of dense submontane forests covered with high canopy trees (above 10 m) e.g. *Creteava religiosa* (Capparaceae), *Phyllanthus indica* (Phyllanthaceae), *Sterculia foetida* (Malvaceae), *Bombax ceiba* (Malvaceae), *Dimocarpus longan* (Sapindaceae), *Palaquium hinmolpedda* (Sapotaceae) and *Vitex altissima* (Lamiaceae). They are always found on the forest floor covered with thick leaf litter (above 10 cm thickness), and never found on rocks, trees, or in caves. Commonly found inside termite mounds. A slow moving species mostly found hidden under leaf litter, loose soil and fallen logs during the day time. When disturbed run a short distance with considerable speed and pause for some time until the threat disappears. A nocturnal species mainly feeding on small insects.

Conservation status. The application of the IUCN Red List criteria (IUCN Standards & Petitions Subcommittee, 2019) shows that the new species is restricted to six localities (alt. 400–1,000 above sea level) with an area of occupancy (AOO) of 19.6 km^2 where 35 individuals (30 adults and five juveniles) were recorded from these six localities in four main locations with extent of occurrence (EOO) of 86.4 km^2. Also given the isolated distribution, man-made forest fire, the rapid forest fragmentation due to general cultivation activity, and the plans for large-scale forest clearance for hotel and other tourism constructions within this range, *C. punctatus* can be considered a Critically Endangered (CR) species. Most of the current distributed localities are placed outside protected areas except for two localities in Manigala and Dotalugala. Even though these localities occur within protected areas, this ground dwelling species is still highly threatened by cardamom cultivations which indiscriminately practice the use of pesticides. Illegal constructions at conservation areas at Knuckles in Illukumbura, where the healthiest population of this species is observed, are identified as a major threat for this terrestrial species. Massive hydropower projects and the expansion of cardamom cultivations with excessive use of agrochemicals are growing threats for the Knuckles forested area.

Cyrtodactylus (*Geckoella*) *triedrus* sensu stricto

Spotted ground-gecko (English), Pulli bimhoona (Sinhalese)

Gymnodactylus triedrus Günther, 1864

Gymnodactylus triedrus – Boulenger, 1885, 1890, Smith, 1935, Taylor, 1953, Wermuth 1965

Table 5. Current distribution patterns of the genus *Cyrtodactylus* in Sri Lanka in each biogeographic region; modified after Kanishka et al. (2020) and Amarasinghe et al. (2021); [1]Janzen & Bopage (2011);[2] Manamendra-Arachchi (1997).

	Cyrtodactylus	
Biogeographic region (alt. range a.s.l.)	**ground-dwelling**	**arboreal**
(1). Wet Zone		
Lowland and Rakwana hills (0–1,000 m)	*C.* cf. *triedrus*[1]	*C. cracens*
Central highland submontane (400–900 m)	*C. triedrus*	*C. fraenatus*
Central highland montane (above 900 m)	*C.* cf. *triedrus*[2]	*C. fraenatus*
(2). Intermediate Zone		
Lowland (0–400 m)	*C. vedda* sp. nov	*C.* cf. *edwardtaylori*
Uva hills (above 300 m)	*C. triedrus*	*C. edwardtaylori*
Central highland submontane (400–900 m)	*C. triedrus*	*C. fraenatus*
Knuckles sub/montane (above 400 m)	*C. punctatus*	*C. soba*
(3). Dry Zone		
Lowland (0–400 m)	*C.* cf. *punctatus*	*C.* cf. *fraenatus*

Cyrtodactylus triedrus – Underwood, 1954, Rösler, 2000

Geckoella triedrus (*sic*) – Deraniyagala, 1953 [*partim*], Kluge, 1993

Geckoella triedra – Wickramasinghe & Somaweera, 2002 [*partim*], Somaweera & Somaweera, 2009 [*partim*]

Holotype (Figs. 1, 4–7, and 9; Tables 1–5). Adult male, NHMUK 1855.2.12.7, collected from Ceylon (Sri Lanka); probably collected from the environs of Peradeniya (7°16'11"N, 80°35'37"E, datum = WGS84; 500 m above sea level), Kandy District, Central Province, Sri Lanka; collected by Hugh Cuming.

Other specimens examined ($n = 2$). Adult male (NMSL 0172, 0173) Dunumadalawa (7°16'51.45"N, 80°38'26.72"E, datum = WGS84; 650 m above sea level), near Kandy, Kandy District, Central Province, Sri Lanka, collected on 12 October 2018 by Suranjan Karunarathna.

Diagnosis. The following combination of characters distinguishes *C. triedrus* from all other congeners: adults reaching 50.6 mm SVL; absence of a precloacal groove; dorsal scalation of small homogeneous, smooth or feebly carinate granules intermixed with bluntly pointed, feebly carinate irregularly arranged tubercles, except medial parasagittal row of tubercles arranged linearly; absence of enlarged femoral scales and no femoral pores; 3 or 4 pores on enlarged precloacal scales; dorsal furrow distinct; two pairs of postmentals, secondary pair 1/3 of the primary pair in size; throat scales granular; no spine-like tubercles on nape; ventrals larger than dorsals, smooth, short, and rounded, with 19–22 rows across belly; 8–10 supralabials at mid-orbit position; scales on posterior thigh granular; lamellae divided, 9–11 subdigital lamellae below the first and 16–19 below the fourth toe; dorsal scales on tail not enlarged, smooth, imbricate; subcaudal scales at base bluntly pointed and enlarged; medially no enlarged subcaudals, subequal; two distinct postcloacal tubercles (spurs); body dorsum purplish black or dark brown with irregularly scattered, small white spots. These differences are summarized for close congeners (Table 2), for all Sri Lankan members (Table 3), and for all members of the subgenus *Geckoella* in *C. triedrus* group (Table 4).

Redescription of holotype. The holotype is generally in good condition except for the broken tail; there are several folds of skin on the head, neck, dorsum, and abdomen which are artifacts of preservation.

An adult male, 50.6 mm SVL; head moderately large, elongate, its length 30.0% of SVL, narrow, head width 59.2% of head length and 17.8% of SVL, not strongly depressed, head depth 41.4% of head length, distinct from neck; snout elongate, its length 38.8% of head length and greater than orbit diameter, orbit diameter 55.9% of snout length; scales on snout, canthus rostralis, interorbital granular, bluntly pointed, feebly carinate, twice larger than those on interorbital and occipital region; interorbital region relatively narrow; interorbital distance 2.2% of head length; occipital region has intermixed enlarged, dorsally rounded, bluntly pointed, feebly carinate tubercles, which are 2–3 larger than adjacent granules; orbit large, its diameter 21.7% of head length, pupil vertically slit with crenulated margins; supraciliaries large, flat; diameter of orbit shorter than orbit–ear distance, orbit diameter 75% of orbit–ear distance; ear-opening small, shallow, oval. Rostral wider than deep, incompletely divided dorsally by weakly developed rostral groove, postero-ventrally in contact with first supralabial, contacted posteriorly by nostril, two supranasals, and a large internasal; nostrils

Fig. 9. (A) An adult male (not collected) of *Cyrtodactylus* (*Geckoella*) *triedrus* and (B) the forest habitat in Kandy (type locality). Photographs by A.K.A. Gayan.

separated by two enlarged, subcircular supranasals; a single large, pentagonal internasal scale between supranasals; nostrils subcircular, dorsally orientated; six postnasals, lowest smaller, not in contact with first supralabial, separated by a small subnasal; loreal region strongly inflated and convex, canthus rostralis not prominent; three rows of scales separate orbit from supralabials at level of pupil; a single interrupted row of slightly enlarged, elongate scales bordering supralabials; supralabials to the angle of jaw 12 on left side and 11 on right side, 8th at mid-orbit position; infralabials to the angle of jaw 9 on both sides; enlarged tubercles on nape and temporal region bluntly pointed and rounded.

Mental subtriangular, lengthen posteriorly to anterior margin of second supralabial, wider than long, posterolaterally in contact with two postmental scales that contact posteriomedially for 70% of their length; primary postmentals bordered by two enlarged secondary postmentals (chin shields) and six small gular scales, the enlarged chin shields arranged in single row grading posteriorly into smaller scales and extending posteriorly to the third infralabial; gular scales small and granular, grading posteriorly into slightly smaller, flatter; scales on throat and neck granular and smooth, smaller than on the ventral body.

Body slim, elongate, axilla–groin length 43.3% of SVL, no distinct ventrolateral fold; dorsal granules blunt and subcylindrical, homogeneous, smooth or feebly carinate, intermixed with bluntly pointed, feebly carinate, enlarged, heterogeneous tubercles; dorsal tubercles bluntly pointed and round or oval in shape middorsally, randomly arranged and extending from occiput onto the tail; each enlarged tubercle about 5 to 8 times as large as granules separating them, largest surrounded by 8 to 12 granules, 3–5 granules separate adjacent enlarged tubercles; mid dorsal furrow indistinct; dorsal granules at midbody smaller than ventral scales at same level; pectoral scales similar in size with abdominal scales, smooth, imbricate, bluntly pointed, short; abdominal scales smooth, imbricate, rounded, short; scales smaller on femoral and largest on precloacal region; ventral scales in 22 rows across belly; ventro-lateral granules on trunk smooth, subcircular, and not enlarged, not intermixed with enlarged tubercles; femoral scales smaller and not bearing pores; precloacal scales enlarged and consisted of 15–20 enlarged scales, four of them bearing pores.

Arms moderately long; length of forearm 16.0% of SVL; length of brachium 12.6% of SVL; legs relatively longer; length of tibia 15.8% of SVL; thigh longer than tibia, its length 17.8% of SVL; brachium with bluntly pointed, smooth, granular scales which are similar in size to scales on dorsum, no tubercles intermixed; dorsal scales on forearm slightly larger than on brachium, granular, bluntly pointed, smooth and not intermixed with tubercles, homogeneous; scales on elbow are not enlarged, smooth and granular; ventral scales on brachium bluntly pointed and smooth, smaller than those on the ventral body; ventral scales on forearm enlarged; scales on the palm smooth, rounded or bluntly pointed; dorsal granules on thigh bluntly pointed and smooth, not intermixed with tubercles, thigh with scales which are larger than granules on dorsum, posterior edge of thigh granular; dorsal granules on tibia homogeneous, intermixed with enlarged, bluntly pointed tubercles; scales on knee smooth, granular, and flat; ventral scales on both thigh and tibia bluntly pointed and smooth, scales on tibia much more enlarged than those on the ventral side of the thigh, even larger in size to the scales on precloacal area; scales on the foot smooth and bluntly pointed; digits moderately long, strongly clawed; all digits of manus and digits I–IV of pes not webbed; terminal phalanx of all digits curved; lamellae beneath each toe in straight transverse series, and entire: subdigital lamellae 10-14-15-16-11 in left pes, 9-14-16-17-15 in right pes; relative length of digits in mm: IV > V > III > II > I in manus; V > IV > III > II > I in pes.

Tail broken, length 39.8 + 4.0 mm, original, round, flat beneath, verticillate, with a median furrow; length of the tail slightly shorter than snout-vent length, tail

length 86.6% of SVL; dorsal scales on the tail imbricate, pointed, smooth, larger than granules on dorsum; tail not segmented with whorls of tubercles; two prominent postcloacal spurs; ventral scales on tail base enlarged, smooth, and bluntly pointed; several rows of the subcaudal scales enlarged, six to eight times larger than on dorsal tail, and twice larger than subcaudals besides, smooth, pointed, wide, short, and imbricate.

Colouration. After more than 160 years in preservative, dorsum uniform light brown ground colour; dorsal head paler, snout darker; labials paler; temporal region slightly darker; limbs same as body colour; ventral side of the head, body, and limb cream; ventral tail darker, cream irregular cross markings dorsally, uniform brown distally.

In life, based on Figure 9A Dorsum purplish black or dark purplish brown ground colour; dorsal head paler, snout darker; labials purplish grey with white markings; temporal region black with postorbital band until posterior edge of the head; superciliaries cream; three cream or white spots on nape and each spot includes a single enlarged tubercle; similarly, few scattered spots on the dorsum; each spot covering only one enlarged tubercle; limbs same as body colour; ventral side of the head, body, and limb purplish grey; chin purple; palms and feet purple; ventral tail darker, cream or white irregular cross markings dorsally, uniform dark brown or black distally.

Distribution and natural history. *Cyrtodactylus triedrus* sensu lato is widely distributed in the wet and intermediate zones up to 1,000 m elevation (Fig. 5), and some isolated populations may represent distinct species. However, here we confirm that the populations distributed in rain and submontane forest ecosystems in the mid elevations of the Central Highlands around Hantana, Dunumadalawa, Gannoruwa, Peradeniya, and Udawattekale agree with the true *Cyrtodactylus triedrus*. The preferred habitat of this species is composed of dense rain forests covered with high canopy trees (above 20 m) e.g. *Artocarpus nobilis* (Moraceae), *Mangifera zeylanica* (Anacardiaceae), *Nothopegia beddomei* (Anacardiaceae), *Neolitsea cassia* (Lauraceae), *Pometia tomentosa* (Sapindaceae), *Diospyros racemosa* (Ebenaceae), *Hydnocarpus venenata* (Achariaceae), and *Myristica dactyloides* (Myristicaceae). They are always found on the forest floor covered with thick leaf litter (above 15 cm thickness), and never found on rocks, trees, or in caves. They are also commonly found inside termite mounds. This is a slow-moving species mostly hidden under leaf litter, loose soil and fallen logs during the daytime. When disturbed, they run a short distance with considerable speed and pause for some time until the threat disappears. It is a nocturnal species mainly feeding on small insects. Juveniles are sometimes encountered in the open during the daytime (Somaweera & Somaweera, 2009), but we found no juveniles during the daytime. During April to July, two eggs (12×10 mm) are laid at a time, either buried in loose soil beneath large stones or sometimes attached to the underside of a stone (Somaweera & Somaweera, 2009).

Conservation status. The application of the IUCN Red List criteria (IUCN Standards & Petitions Subcommittee, 2019) shows that *Cyrtodactylus triedrus* is restricted to the mid elevations of the central highlands, lowland rain forests, and some isolated localities in the Uva hills, and the Dolukanda hill in the intermediate zone with an area of occupancy (AOO) of 680 km^2 where recorded from 21 localities, with the extent of occurrence (EOO) of 3591 km^2. Given the patchy distribution, the rapid forest fragmentation and large-scale forest clearance for plantations and industries, the vulnerability of the remaining non-protected state forests in the wet zone (see Samarasinghe et al., 2020), and its habitat especiality for shady forest floors with thick leaf litter, *Cyrtodactylus triedrus* can be considered an Endangered (EN) species. Although, with several distributed localities placed within protected areas, some of the populations may be represented by different species from *Cyrtodactylus triedrus* sensu stricto. Hence, with an increase in fieldwork and knowledge leading to a better understanding of the taxonomic status in the future, the distribution range of this species may well prove to be narrower than currently known.

Discussion

Into India through trans-oceanic dispersal

Competition for resources could have possibly resulted in the two lineages of the genus *Cyrtodactylus* occupying distinct niches (ground-dwelling *vs* arboreal). Competition for niche between arboreal *Cyrtodactylus*, *Cnemaspis* and *Hemidactylus*, perhaps led to the most recent common ancestor of the subgenus *Geckoella* to take to the ground. The phylogeny of the ground dwelling radiation of the subgenus *Geckoella* shows a deep split between the Indian species and Sri Lankan endemic *C. triedrus*, and between Indian dry and wet zone clades, dating back to the late Oligocene (Agarwal & Karanth, 2015). The *C. triedrus* group likely evolved in Sri Lanka through a probable trans-oceanic dispersal through the Bay of Bengal into the island (Wood et al., 2012). A single dispersal event occurring probably over

a land bridge into India gave rise to the Indian members of this group. This dispersal could have been facilitated by low sea levels during the Oligocene as seen in bush frogs (Meegaskumbura et al., 2019). A back-dispersal event of a lineage of the dry zone clade (*C. collegalensis* clade) gave rise to *C. yakhuna*. The aforementioned biogeographic scenario must be tested with emphasis on the diversification on a temporal scale and after incorporation of *C. yakhuna* from throughout its range and from additional un-sampled taxa from the dry zones of Tamil Nadu. The basal lineage of *Geckoella* is *C. triedrus* sensu stricto, which is a wet zone species in Sri Lanka. However, It is unclear why *Geckoella* is absent from the highly biodiverse southern Western Ghats in India, and Agarwal and Karanth (2015) predicted that the restricted wet-zone distribution of the genus *Cnemaspis* may be an ancient element that competes with *Geckoella*. However, in the Sri Lankan wet zone, both *Cnemaspis* and *Geckoella* live sympatrically in most of the localities. The late Miocene burst in speciation in *Geckoella* may be linked to the expansion of rain forests during the mid-Miocene climatic optimum and subsequent fragmentation with increasing late Miocene aridification (Agarwal and Karanth, 2015). While *C. triedrus* and *C. punctatus* are wet zone and submontane species respectively distributed in the wet face of the mid highlands, the new species, *C. vedda* is a lowland species distributed in the dry face of the eastern slopes of Sri Lanka. This species complex, along with the other ground dwelling *Cyrtodactylus* in Sri Lanka are always syntopic with the arboreal *Cyrtodactylus* species in each biogeographic region (see Table 5).

C. triedrus sensu stricto

Günther (1864) described *Gymnodactylus triedrus* based on a 4-inched (~100 mm) single specimen collected from Ceylon (Sri Lanka), and he stated that the specimen was not in a good state of preservation and he did not observe any precloacal pores. The specimen was collected by Hugh Cuming (1791–1865), an English collector (*fide* Amarasinghe et al., 2009). Boulenger (1885) referred to five specimens (including the types of *Geckoella punctata*) in the collection of the British Museum (now Natural History Museum London, NHMUK), and also stated that the type specimen (holotype by monotypy) of *Gymnodactylus triedrus* was an adult male. Furthermore, Boulenger (1885 and 1890) stated that males of *Gymnodactylus triedrus* have three or four precloacal pores [*vs* pores absent, *fide* Günther, 1864]. Although Taylor (1953) has not examined any of the specimens of this species, he mistakenly mentioned this species has three to four femoral pores, in error. In the NHMUK there is a single specimen labelled as the "type" of *Gymnodactylus triedrus*, a male with four precloacal pores. This specimen agrees with Günther (1864) in every aspect, except for the presence of precloacal pores. Günther was probably not able to examine the specimen in detail because the "specimen was not in a good state of preservation" (*fide* Günther, 1864). Moreover, precloacal pores are often difficult to observe. However, because Boulenger (1885) also clearly observed precloacal pores in the same specimen, we accept that this specimen (NHMUK 1855.2.12.7) undoubtedly, has to be the correct holotype of *Cyrtodactylus* (*Geckoella*) *triedrus*. The specimen's collector, H. Cuming never visited Sri Lanka (Pethiyagoda, 2007). Cuming purchased most of his collections from Edgar Leopold Layard (1824–1900) and Robert Templeton (1802–1892) and their collections were comprised specimens from both the wet and dry zones of the island. Hence, it is possible that the specimen was collected (could be anywhere from the island) by them and subsequently sent to Cuming. Annandale (1913) examined two specimens of *Gymnodactylus triedrus*, and fixed one of them at least to a precise location "Peradeniya, Ceylon (ca. 1500 ft [alt. ~460 m]" the first precise location provided for this species.

Possible inland radiation

The lowland rainforest and lower Rakwana hill (0–900 m elevation) population may represent *C. triedrus*, as several research projects on different taxa have suggested morphological and phylogenetic similarity between the populations in the mid elevations of Central highlands and lowland rainforests (e.g. *Lankascincus gansi* in Kanishka et al., 2020, *Dendrelaphis wickrorum* in Danushka et al., 2020). On the other hand, this population may also represent a distinct species from *C. triedrus* sensu stricto, because for e.g. *Cyrtodactylus cracens* and *Ceratophora aspera* are distributed in the lowland rainforests; while *Cyrtodactylus fraenatus* and *Ceratophora ukuwelai* are distributed in the lower central highlands (see Batuwita & Bahir, 2005, Karunarathna et al., 2020). Therefore, for the moment, we leave the lowland rainforest and intermediate zone population as *Cyrtodactylus* cf. *triedrus* and acknowledge that research work on this population continues. The *C. triedrus* sensu lato reported from the high elevations (975 m above sea level) of the Rakwana Hills (*fide* Janzen & Bopage, 2011) may represent yet another distinct species. The morphological and genetic separation between lowland rainforest and upper Rakwana hills are evident for many taxa (e.g. *Lankascincus gansi* vs. *L. sameerai*, see Kanishka et al., 2020; *Calotes liolepis* vs. *C. desilvai*, see Amarasinghe et al., 2014;

Cnemaspis pulchra and *C. silvula* vs. *C. godagedarai*, see de Silva et al., 2019; *Ceratophora aspera* vs. *C. karu*, see Pethiyagoda & Manamendra-Arachchi, 1998). Similarly, if there is a population of *C. triedrus* sensu lato existing in high elevations (2,200 m above sea level) of the Central Highlands (*fide* Manamendra-Arachchi, 1997), that population may also represent a distinct population. Considering the higher genetic divergence between the *C. triedrus* sensu stricto and the new species, and given the biogeographical complexity of Sri Lanka with poorly known fragmented wet forests on the island's drier portion (see Amarasinghe et al., 2021, Karunarathna et al., 2019), more cryptic species of the *C. triedrus* complex may be found. Such isolated or cryptic populations have to be reinvestigated along with the support of phylogenetic studies (work in progress).

Central highlands and the Knuckles massif

Gray (1867) described a closely related species to Günther's, collected from Ceylon (Sri Lanka), but without any precise locality data and named it *Geckoella punctata*. Although in the original description Gray did not mention how many specimens he possessed, Boulenger (1885) stated that the type material represented two specimens, one adult male and one female. Currently there are three specimens labelled as "types" of *Geckoella punctata* (NHMUK 1866.1.22.6–8). Among these three specimens, NHMUK 1866.1.22.6 is an adult male, exactly matching Gray's (1867) original illustration of the plate IX (see Fig. 2) in the original publication. The other two specimens (NHMUK 1866.1.22.7–8) are adult female and male, respectively. Gray clearly stated that "The temple, occiput, and back with numerous small white spots; those on the back placed in four longitudinal rows…" and "The dorsal spots are formed of several white scales. There is a single spot in the centre of the hinder part of the occiput. The outer sides of the legs are obscurely spotted", but only NHMUK 1866.1.22.6 and 1866.1.22.7 agree with these colour descriptions, while NHMUK 1866.1.22.8 is uniform brown and has no markings. Therefore, following both Gray (1867) and Boulenger (1885) only one male (NHMUK 1866.1.22.6) and a female (NHMUK 1866.1.22.7) are acceptable as the correct syntypes of *Geckoella punctata*, hence NHMUK 1866.1.22.8 is rejected as a type herein. This specimen does not represent *Cyrtodactylus punctatus*, hence, we leave the identity of NHMUK 1866.1.22.8 as "*Cyrtodactylus* cf. *triedrus*" for the moment, as the studies on this cryptic species complex from other biogeographic regions are still in progress (Table 5). We believe this confusion appeared after the synonymy of *Geckoella punctata* with *Gymnodactylus triedrus* as Boulenger (1885) assigned all the specimens (including the type of *Geckoella punctata*) to *Gymnodactylus triedrus*. However, he clearly labelled one male as representing the holotype of *Gymnodactylus triedrus* (now NHMUK 1855.2.12.7), and a male and female together representing the syntypes of *Geckoella punctata* (NHMUK 1866.1.22.6–7), and another two voucher specimens representing a male and a female. Therefore NHMUK 1866.1.22.8 must be the male voucher specimen, but we were unable to trace the other female voucher specimen, probably misplaced.

Although Boulenger (1885) synonymised Gray's species with *Gymnodactylus triedrus*, here we resurrect the species and combine it with the genus *Cyrtodactylus* as it is morphologically and genetically a distinct species. Ferguson (1877) reported *Geckoella punctatus* (*sic*) from Sri Lanka for the first time, stating "This gecko was described by the late Dr. Gray from a single imperfect specimen. It is supposed to have been found about Mátalé" [a location in the Knuckles massif]. Although it seems Ferguson (1877) confused it with the type [because a single imperfect type specimen refers to *Geckoella triedra* (*fide* Günther, 1864, and also following our personal examination this appears to be true), and not of *Geckoella punctata*], but he correctly refers to the distribution of the species. The lectotype and the paralectotype of *Geckoella punctata* are perfect specimens, and identical with the other voucher specimens we collected from the Knuckles massif. Therefore, the type locality of *Geckoella punctata* can undoubtedly be assigned to Matale (altitude 365 m above sea level). However, currently this species is not recorded from as low an elevation as where Matale town is situated today and where the natural habitats have become very congested due to urbanisation. The lowest elevation we observed for this species was Meemure at 480 m elevation.

Acknowledgements

We thank the department of wildlife conservation and the department of forestry of Sri Lanka for providing collecting permits (Permit nos. WL/3/2/42/18–21 and R&E/RES/NFSRCM/2019-04) to SK, ADS, and K.D.B. Ukuwela (Rajarata University of Sri Lanka). N. Wickramasinghe (former director), S. Kasthuriarachchi (director), L. Somaratne, C. Kothalawala, C. Munasinghe, T. Gamage, R. Dasanayake, T. Dasanayake R. Wickramanayake, P. Gunasiri, and all the staff (employed since 2005) at NMSL are acknowledged for facilitating the in-house study of

specimens under their care. K.D.B. Ukuwela, N.H. Perera, S. Wickramarachchi, and N. Karunarathna are acknowledged for the assistance in the field, and Sanjaya Bandara for proof reading. ZAM thanks the Singinawa Conservation Foundation and National Centre for Biological Sciences for the support. Finally, we also thank R. Somaweera (Australia), J. Supriatna and the staff of the Research Center for Climate Change, University of Indonesia, for their support.

Disclosure statement

No potential conflict of interest was reported by the author(s).

Supplemental material

Supplemental material for this article can be accessed here: https://doi.org/10.1080/14772000.2022.2039319.

ORCID

A. A. Thasun Amarasinghe http://orcid.org/0000-0002-4151-1806
Suranjan Karunarathna http://orcid.org/0000-0003-0965-7781
Patrick D. Campbell http://orcid.org/0000-0001-7473-7740
A. K. Anusha Gayan http://orcid.org/0000-0003-3301-4081
W. D. Bhanuka Ranasinghe http://orcid.org/0000-0002-5081-039X
Anslem De Silva http://orcid.org/0000-0001-7899-5237
Zeeshan A. Mirza http://orcid.org/0000-0003-1685-9816

References

Agarwal, I. (2016). Two new species of ground-dwelling *Cyrtodactylus* (*Geckoella*) from the Mysore Plateau, South India. *Zootaxa*, *4193*, 228–244. https://doi.org/10.11646/zootaxa.4193.2.2

Agarwal, I. & K. P. Karanth. (2015). A phylogeny of the only ground-dwelling radiation of *Cyrtodactylus* (Squamata, Gekkonidae): Diversification of *Geckoella* across peninsular India and Sri Lanka. *Molecular Phylogenetics & Evolution*, *82*, 193–199.

Agarwal, I., Z. A. Mirza, S. Pal, S. T. Maddock, A. Mishra, & A. M. Bauer. (2016). A new species of the *Cyrtodactylus* (*Geckoella*) *collegalensis* (Beddome, 1870) complex (Squamata: Gekkonidae) from Western India. *Zootaxa*, *4170*, 339–354. https://doi.org/10.11646/zootaxa.4170.2.7

Amarasinghe, A. A. T., A. M. Bauer, I. Ineich, J. Rudge, M. M. Bahir, & D. E. Gabadage. (2009). The original descriptions and figures of Sri Lankan gekkonid lizards (Squamata: Gekkonidae) of the 18th, 19th and 20th centuries. *Taprobanica*, *1*, 83–106. https://doi.org/10.47605/tapro.v1i2.15

Amarasinghe, A. A. T., D. M. S. S. Karunarathna, & J. Fujinuma. (2014). A new *Calotes* species from Sri Lanka with a redescription of *Calotes liolepis* Boulenger, 1885. *Herpetologica*, *70*, 323–328. https://doi.org/10.1655/HERPETOLOGICA-D-13-00087

Amarasinghe, A. A. T., M. B. Harvey, A. Riyanto, & E. N. Smith. (2015). A new species of *Cnemaspis* (Reptilia: Gekkonidae) from Sumatra, Indonesia. *Herpetologica*, *71*, 160–167. https://doi.org/10.1655/HERPETOLOGICA-D-14-00034

Amarasinghe, A. A. T., & S. Karunarathna. (2020). A new diminutive day gecko species of the genus *Cnemaspis* Strauch, 1887 (Reptilia: Gekkonidae) from Pilikuttuwa, near the capital of Sri Lanka. *Taprobanica*, *9*, 71–82. https://doi.org/10.47605/tapro.v9i1.223

Amarasinghe, A. A. T., S. Karunarathna, P. D. Campbell, M. Madawala, & A. de Silva. (2021). A new species of *Hemidactylus* Goldfuss, 1820 (Reptilia: Gekkonidae) from Sri Lanka with redescription of *H. hunae* Deraniyagala, 1937. *Herpetologica*, *77*, 259–272. https://doi.org/10.1655/Herpetologica-D-21-00003.1

Annandale, N. (1913). Some new and interesting batrachian and lizards from India, Ceylon and Borneo. *Records of the Indian Museum Culcutta*, *14*, 301–307.

Batuwita, S., & Bahir, M. M. (2005). Description of five new species of *Cyrtodactylus* (Reptilia: Gekkonidae) from Sri Lanka. *Raffles Bulletin of Zoology*, Supplement No. 12, 351–380.

Boulenger, G. A. (1885). *Catalogue of the lizards in the British Museum (Natural History) I. Geckonidae, Eublepharidae, Uroplatidae, Pygopodidae, Agamidae*. Trustees of the British Museum (Natural History).

Boulenger, G. A. (1890). *The fauna of British India, including Ceylon and Burma. Reptilia and Batrachia*. Taylor & Francis.

Danushka, A. D., Kanishka, A. S., Amarasinghe, A. A. T., Vogel, G., & Seneviratne, S. S. (2020). A new species of *Dendrelaphis* Boulenger, 1890 (Reptilia: Colubridae) from the wet zone of Sri Lanka with a redescription of *Dendrelaphis bifrenalis* (Boulenger, 1890). *Taprobanica*, *9*, 83–102. https://doi.org/10.47605/tapro.v9i1.224

Das, I., & de Silva, A. (2005). *Photographic guide to snakes and other reptiles of Sri Lanka* (pp. 144). New Holland Publishers.

de Silva, A., A. M. Bauer, C. C. Austin, S. Goonawardena, Z. Hawke, V. Vanneck, A. Drion, P. de Silva, B. J. K. Perera, R. L. Jayaratne, & M. M. Goonasekera (2004). The diversity of Nilgala forest, Sri Lanka, with special reference to its herpetofauna. *Lyriocephalus*, *5*, 164–182.

de Silva A., Bauer, A. M., Botejue, M., & Karunarathna, S. (2019). A new species of endemic day gecko (Reptilia: Gekkonidae: *Cnemaspis*) from a wet zone forest in the second peneplain of Southern Sri Lanka. *Amphibian & Reptile Conservation*, *13*, 198–208.

Deraniyagala, P. E. P. (1932). The Gekkonoideae of Ceylon. *Spolia Zeylanica*, *16*, 291–310.

Deraniyagala, P. E. P. (1953). *A coloured atlas of some vertebrates from Ceylon: Vol. 2. Tetrapod Reptilia*. The Ceylon Government Press.

Ferguson, W. (1877). *Reptile fauna of Ceylon. Letter on a collection sent to the Colombo Museum*. William Henry Herbert, The Ceylon Government Press.

Gamble, T., Greenbaum, E., Jackman, T. R., Russell, A. P., & Bauer, A. M. (2012). Repeated origin and loss of adhesive toepads in geckos. *PLoS One*, *7*, e39429. https://doi.org/10.1371/journal.pone.0039429

Gray, J. E. (1827). A synopsis of the genera of Saurian Reptiles, in which some new Genera are indicated, and others reviewed by actual examination. *The Philosophical Magazine or Annals of Chemistry, Mathematics, Astronomy, Natural History, and General Science. Series 2*, *2*, 54–58.

Gray, J. E. (1867). On a new geckoid lizard from Ceylon. *Proc. zool. Soc. London*, *35*, 98–99. https://doi.org/10.1111/j.1469-7998.1867.tb00429.x

Grismer, L. L., Wood, Jr., P. L., Poyarkov, N. A., Le, M. D., Kraus, F., Agarwal, I., Oliver, P. M., Nguyen, S. N., Nguyen, T. Q., Karunarathna, S., Welton, L. J., Stuart, B. L., Luu, V. Q., Bauer, A. M., O'Connell, K. A., Quah, E. S. H., Chan, K. O., Ziegler, T., Ngo, H., Nazarov, R. A., Aowphol, A., Chomdej, S., Suwannapoom, C., Siler, C. D., Anuar, S., Tri, N. V., & Grismer, J. L. (2021). Phylogenetic partitioning of the third-largest vertebrate genus in the world, *Cyrtodactylus* Gray, 1827 (Reptilia; Squamata; Gekkonidae) and its relevance to taxonomy and conservation. *Vertebrate Zoology 71*,101–154. https://doi.org/10.3897/vertebrate-zoology.71.e59307

Goonewardene, S., Z. Hawke, V. Vanneck, A. Drion, A. de Silva, R. Jayaratne, & J. Perera. (2004). Diversity of Nilgala fire savannah, Sri Lanka: With special reference to its herpetofauna. (pp. 81). University of Edinburgh.

Günther, A. (1864). *The reptiles of British India*. Taylor & Francis.

IUCN Standards and Petitions Subcommittee. 2019. *Guidelines for using the IUCN red list categories and criteria.* Version 14. Prepared by the Standards and Petitions Subcommittee, IUCN.

Janzen, P., & Bopage, M. 2011. The herpetofauna of a small and unprotected patch of tropical rainforest in Morningside, Sri Lanka. *Amphibian & Reptile Conservation 5*, 1–13.

Kanishka, A. S., Danushka, A. D., & Amarasinghe, A. A. T. (2020). A new species of *Lankascincus* Greer, 1991 (Reptilia: Scincidae) with an overview of the *L. gansi* group. *Taprobanica*, *9*, 103–119. https://doi.org/10.47605/tapro.v9i1.225

Karunarathna, D. M. S. S., & Amarasinghe, A. A. T. (2010). Reptile diversity of a fragmented lowland rain forest patch in Kukulugala, Ratnapura District, Sri Lanka. *Taprobanica*, *2*, 86–94. https://doi.org/10.47605/tapro.v2i2.31

Karunarathna, D. M. S. S., & Amarasinghe, A. A. T. (2011). A preliminary survey of the reptile fauna in Nilgala forest and its vicinity, Monaragala District, Sri Lanka. *Taprobanica*, *3*, 69–76. https://doi.org/10.47605/tapro.v3i2.49

Karunarathna, D. M. S. S., Bauer, A. M., de Silva, A., Surasinghe, T., Somaratna, L., Madawala, M., Gabadage, D., Botejue, M., Henkanaththegedara, S., & Ukuwela, K. D. B. (2019). Description of a new species of the genus *Cnemaspis* Strauch, 1887 (Reptilia: Squamata: Gekkonidae) from the Nilgala Savannah forest, Uva Province of Sri Lanka. *Zootaxa*, *4545*, 389–407. https://doi.org/10.11646/zootaxa.4545.3.4

Karunarathna, S., N. A. Poyarkov, C. Amarasinghe, T. Surasinghe, A. V. Bushuev, M. Madawala, V. A. Gorin, & A. de Silva. (2020). A new species of the genus Ceratophora Gray, 1835 (Reptilia: Agamidae) from a lowland rainforest in Sri Lanka, with insights on rostral appendage evolution in Sri Lankan agamid lizards. *Amphibian & Reptile Conservation*, *14*, 103–126.

Karunarathna, D. M. S. S., & Amarasinghe, A. A. T. (2012). Reptile diversity in Beraliya Mukalana proposed forest reserve, Galle District, Sri Lanka. *Taprobanica*, *4*, 20–26. https://doi.org/10.47605/tapro.v4i1.61

Karunarathna, D. M. S. S., S. M. Henkanaththegedara, A. A. T. Amarasinghe, & A. de Silva (2013). Impact of vehicular traffic on herpetofaunal mortality in a savannah forest, Eastern Sri Lanka. *Taprobanica*, *5*, 111–119.

Kluge, A. G. (1993). *Gekkonoid lizard taxonomy*. (pp. 225). International Gecko Society, San Diego.

Kumar, S., Stecher, G., Li, M., Knyaz, C., & Tamura, K. (2018). MEGA X: molecular evolutionary genetics analysis across computing platforms. *Molecular Biology and Evolution*, *35*, 1547–1549. https://doi.org/10.1093/molbev/msy096

Manamendra-Arachchi, K. (1997). Gecko. *Sri Lanka Nature*, 1, 45–55.

Meegaskumbura, M., Senevirathne, G., Manamendra-Arachchi, K., Pethiyagoda, R., Hanken, J., & Schneider, C. J. (2019). Diversification of shrub frogs (Rhacophoridae, *Pseudophilautus*) in Sri Lanka—Timing and geographic context. *Molecular Phylogenetics and Evolution*, *132*, 14–24. https://doi.org/10.1016/j.ympev.2018.11.004

Minh, B., Schmidt, H., Chernomor, O., Schrempf, D., Woodhams, M., von Haeseler, A., Lanfear, R. (2020). IQ-TREE 2: New models and efficient methods for phylogenetic inference in the genomic era. *Molecular Biology and Evolution*, *37*, 1530–1534. https://doi.org/10.1093/molbev/msaa015

Osman Hill, W. C. (1932). Anthropology of Veddahs. *Nature*, *130*, 891–892. https://doi.org/10.1038/130891b0

Pethiyagoda, R. (2007). *Pearls, spices and green gold: An illustrated history of biodiversity in Sri Lanka*. WHT Publications (Pvt.) Ltd.

Pethiyagoda, R., & Manamendra-Arachchi, K. (1998). A revision of the endemic Sri Lankan agamid lizard genus *Ceratophora* Gray, 1835, with description of two new species. *Journal of South Asian natural History 3*, 1–50.

Rambaut, A. (2012). FigTree v1.4.3. Available at http://tree.bio.ed.ac.uk/software/figtree/

Samarasinghe, D. J. S., Wikramanayake, E. D., Jayakody, S., Fernando, S., Gunawardana, J., & Braczkowski, A. (2020). A biodiversity hotspot in turmoil: Doing away with circular5/2001 could have catastrophic consequences for Sri Lanka's forests. *Conservation Science & Practice*, *3*, e466.

Smith, M. A. (1935). *The fauna of British India including Ceylon and Burma, Reptilia and Amphibia, Vol II Sauria*. Taylor and Francis.

Somaweera, R., & Somaweera, N. (2009). *Lizards of Sri Lanka: A colour guide with field keys*. Chimaira.

Spix, J. B. (1825). *Animalia nova sive species novae lacertarum, quas in itinere per Brasiliam annis MDCCCXVII – MDCCCXX jussu et auspiciis Maximiliani Josephi I. Bavariae Regis suscepto collegit et descripsit*. F.S. Hübschmann.

Rösler, H. (2000). Die postanale Beschuppung bei *Cyrtodactylus* Gray 1827 und *Cyrtopodion* Fitzinger 1843 – funktionelle und taxonomische Aspekte (Sauria: Gekkonidae). *Gekkota*, *2*, 154–207.

Taylor, E. H. (1953). A review of the lizards of Ceylon. *The University of Kansas Science Bulletin*, *35*, 1525–1585. https://doi.org/10.5962/bhl.part.26732

Thompson, J. D., Gibson, T. J., & Higgins, D. G. (2003). Multiple sequence alignment using ClustalW and ClustalX. *Current Protocols in Bioinformatics*, *1*, 2–3. https://doi.org/10.1002/0471250953.bi0203s00

Uetz, P., Cherikh, S., Shea, G., Ineich, I., Campbell, P. D., Doronin, I. V., Rosado, J., Wynn, A., Tighe, K. A., McDiarmid, R., Lee, J. L., Köhler, G., Ellis, R., Doughty, P., Raxworthy, C. J., Scheinberg, L., Resetar, A., Sabaj, M., Schneider, G., Franzen, M., Glaw, F., Böhme, W., Schweiger, S., Gemel, R., Couper, P., Amey, A., Dondorp, E., Ofer, G., Meiri, S., & Wallach, V. (2019). A global catalog of primary reptile type specimens. *Zootaxa*, *4695*, 438–450. https://doi.org/10.11646/zootaxa.4695.5.2

Underwood, G. (1954). On the classifcation and evolution of geckos. *Proceedings of the Zoological Society of London*, *124*, 469–492.

Wickramasinghe, M. & R. Somaweera (2002). Distribution and current status of the endemic geckos of Sri Lanka. *Gekko*, *3*, 2–13.

Wood Jr, P.L., Heinicke, M. P., Jackman, T. R., & Bauer, A. M. (2012). Phylogeny of bent-toed geckos (*Cyrtodactylus*) reveals a west to east pattern of diversification. *Molecular Phylogenetics and Evolution*, *65*, 992–1003. https://doi.org/10.1016/j.ympev.2012.08.025

Associate Editor: Dr Susan Tsang