

A NEW *CALOTES* SPECIES FROM SRI LANKA WITH A REDESCRIPTION OF *CALOTES LIOLEPIS* BOULENGER, 1885

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ABSTRACT: Based on morphological evidence, we describe a new species of agamid lizard of the genus *Calotes* that is restricted to a single site on the northern face of the Knuckles massif (~1000 m above sea level) of Sri Lanka. The genus *Calotes* consists of eight species in Sri Lanka, six of which appear to form an endemic radiation. The new species, *Calotes manamendrai*, most closely resembles *Calotes liolepis* Boulenger, 1885, which is widely distributed in mid-elevations in the central highlands, lowland rain forests, and a few isolated moist forests in the dry zone of Sri Lanka. Females of *Calotes manamendrai* sp. nov. differ from the females of *Calotes liolepis* in having nonenlarged pectoral scales; keeled dorsal scales on the body; smaller midgular scales than the rest of the throat scales; brown color, seven distinct stripes each side on gular area; black color shoulder pit; and upper arm with carinate ventral scales. Finally, we provide a complete redescription for *Calotes liolepis* based on the adult female syntypes.

Key words: Agamidae; Biogeography; *Calotes manamendrai* sp. nov.; Conservation; Knuckles massif; Systematics

THE AGAMID genus *Calotes* Cuvier, 1817, currently consists of 25 species (Hartmann et al., 2013; Amarasinghe et al., 2014). Eight of these species are represented in Sri Lanka, of which six appear to form an endemic radiation (Macey et al., 2000; Somaweera and Somaweera, 2009; Wickramasinghe, 2012): *Calotes nigrilabris* Peters, 1860; *Calotes liocephalus* Günther, 1872; *Calotes liolepis* Boulenger, 1885; *Calotes ceylonensis* Müller, 1887; *Calotes desilvai* Bahir and Maduwage, 2005; and *Calotes pethiyagodai* Amarasinghe, Karunaratna, and Hallermann in Amarasinghe et al. (2014). Of the remaining species occurring in Sri Lanka, *Calotes calotes* (Linnaeus, 1758) is also distributed in India, whereas *Calotes versicolor* (Daudin, 1802) is widely spread through tropical Asia (Smith, 1935; Deraniyagala, 1953; Taylor, 1953; Manthey, 2008; Das, 2010; Venugopal, 2010). Thus far, *Calotes liolepis* has been considered to be a widely distributed species in lowland rain forests and a few isolated moist forests in the dry zone of Sri Lanka (Bahir and Maduwage, 2005; Asela et al., 2012).

After examining material in the National Museum of Sri Lanka (NMSL), the first two authors discovered two specimens (NMSL5976

and NMSL5977) assigned to the *Calotes liolepis* complex that were collected from Riverstone–Knuckles. When these two specimens were compared with the type and other voucher specimens of *Calotes liolepis* and *Calotes desilvai*, and also with all other species of *Calotes*; these two specimens presented several differences in morphological and morphometric characters. Based on this material, we describe the new species, evidently restricted to the Riverstone area (~1000 m above sea level [a.s.l.]) on the northern side of the Knuckles massif.

Among the Sri Lankan *Calotes*, the new species is phenotypically closest to *Calotes liolepis* Boulenger, 1885 (having a wide distribution in mid-elevations in the central highlands, lowland rain forests and a few isolated moist forests in the dry zone), and to *Calotes desilvai* Bahir and Maduwage, 2005 (known only from Morningside in the Rakwana highlands; >700 m a.s.l.). Boulenger (1885) used a female syntype and a juvenile syntype to describe *Calotes liolepis* (BMNH 69.7.24.2) without a precise location. On the basis of the available specimens and lack of male specimens among the syntypes of *Calotes liolepis*, we use female specimens to diagnose this new species.

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MATERIALS AND METHODS

Museum acronyms follow Sabaj Pérez (2013). Specimens were examined in the holdings of British Museum of Natural History, UK (BMNH); Museum National d'Histoire Naturelle, France (MNHN); Naturhistorisches Museum, Switzerland (NMB); National Museum of Sri Lanka, Sri Lanka (NMSL); Naturhistorisches Museum Wien, Austria (NMW); Swedish Museum of Natural History, Sweden (NRM); and Wildlife Heritage Trust, Sri Lanka (WHT). Morphometric and meristic data for species comparisons were obtained from examined specimens (see Appendix). We examined the external morphology of specimens with a Wild M3Z stereomicroscope (Leitz Microsystems, Germany) and photographed them with an EOS 7D SLR digital camera (Canon Inc., Japan). Conservation status of the new species was evaluated based on the Red List categories and criteria in International Union for Conservation of Nature (IUCN, 2013) to assess their risk of extinction. Sex was determined by the absence of hemipenes or hemipenal bulges.

The following characters were measured with a digital calipers (± 0.1 mm) on the left side of the body for symmetrical characters: axilla–groin length (AG), distance between axilla and groin; eye diameter (ED), horizontal diameter of orbit; eye–nostril length (EN), distance between anteriormost point of orbit and middle of nostril; femur length (FEL), distance between groin and knee; head length (HL), distance between posterior edge of mandible and tip of snout; head width (HW), maximum width of head; head depth (HD), distance between occiput and throat; interorbital width (IO), least distance between upper margins of orbits; lower arm length (LAL), distance from elbow to wrist with both upper arm and palm flexed; snout–vent length (SVL), measured from tip of snout to anterior margin of vent; tail length (TAL), measured from anterior margin of vent to tail tip; tibia length (TBL), distance between knee and heel, with both tibia and tarsus flexed; toe length (TL), distance between tip of claw and nearest fork; upper arm length (UAL), distance between axilla and angle of elbow; tympanum–eye length (TYE), distance be-

tween anterior most margin of tympanum and posterior most margin of the orbit; and tympanum diameter (TYD), longest diameter of the tympanum. Meristic characters were taken as follows: supralabials (SUP) and infralabials (INF), first labial scale to last labial scale toward gape, which is distinctly larger than the granular scales at gape; canthus rostralis (CR), counted from first scale posterior to supranasal, to end of supraciliary ridge; midbody scales (MBS), counted from center of middorsal row forward and downward across ventrals; dorsinuchal crest spines (DS), counted from first spine of nuchal crest to the level of axilla; midventral scales (MVS), counted from first scale posterior to mental, to last scale anterior to vent; and subdigital lamellae on Toe IV (SDL), from first proximal enlarged scansor wider than twice the width of the largest palm scale, to distal most lamella at tip of digit. All morphological, morphometric, and meristic data were recorded by the first author. All the measurements were normalised to the percentage of HL (HL itself is given as a percentage of SVL) consistent with Bahir and Maduwage (2005).

We conducted a principal component analysis (PCA) to project the less-dimensional representation of morphometric variation and to determine the relative position of the new species within the *Calotes liolepis* complex. A series of components, exceeding 80% of eigenvalues as a whole, were taken into account when inspecting the ordination. Only female specimens were included in this analysis, using the following 12 measurements normalized to the percentage of HL: SVL, HL (percentage of SVL), HW, AG, ED, EN, TYE, FEL, TBL, TL5, UAL, and LAL. Before the ordination, these measurements were standardized by scaling them to a SD of 1.0 and a mean of 0.0. All analyses were performed in the statistical software environment R, version 2.15.0 (R Development Core Team, 2011).

RESULTS

Standard morphometric and meristic statistics are presented in Table 1. Statistically informative tests could not be performed on separate sexes because of the absence of male specimens among the type materials of

TABLE 1.—Morphometric and meristic characters (as a percentage of head length [HL]; HL itself is given as a percentage of snout-vent length [SVL]), of holotype and the paratype of *Calotes manamendrai* sp. nov., two paratypes of *Calotes desilvai*, and nine specimens (including syntype) of *Calotes liolepis*. All specimens are female (see Appendix for accession data).

Character ^a	Females					
	<i>Calotes manamendrai</i> sp. nov. (n = 2)		<i>Calotes desilvai</i> (n = 2)		<i>Calotes liolepis</i> (n = 9)	
	Range	Mean ± SD	Range	Mean ± SD	Range	Mean ± SD
SVL	296.0–321.1	308.5 ± 17.7	298.4–323.8	311.1 ± 18.0	307.5–350.7	326.8 ± 14.7
AG	141.6–157.1	149.3 ± 11.0	174.7–183.8	179.2 ± 6.4	151.8–175.6	161.6 ± 6.9
HL (% SVL)	31.1–33.8	32.4 ± 1.9	30.9–33.5	32.2 ± 1.8	28.5–32.5	30.6 ± 1.4
HW	59.4–60.4	59.9 ± 0.7	58.1–59.5	58.8 ± 1.0	55.0–58.8	56.7 ± 1.5
HD	52.1–55.9	54 ± 2.7	47.4–53.0	50.2 ± 3.9	46.4–58.7	51.5 ± 2.4
TYD	12.0–13.4	12.7 ± 1.0	12.3–14.1	13.2 ± 1.3	11.6–15.1	12.7 ± 0.1
ED	30.2–30.9	30.5 ± 0.5	28.9–30.8	29.8 ± 1.3	32.0–38.6	34.9 ± 2.1
EN	19.8–20.3	20.0 ± 0.3	22.5–23.8	23.1 ± 0.9	18.4–24.0	21.4 ± 1.8
IO	39.2–46.5	42.8 ± 5.2	47.4–49.2	48.3 ± 1.3	33.3–50.0	48.1 ± 1.7
FEL	63.9–74.6	69.2 ± 7.6	63.2–73.0	68.1 ± 6.9	63.8–84.6	72.7 ± 8.4
TBL	76.9–79.2	78.0 ± 1.6	69.2–75.1	72.1 ± 4.2	69.1–90.5	77.7 ± 8.1
TL5	31.3–38.6	34.9 ± 5.2	41.9–45.9	43.9 ± 2.8	31.1–48.2	38.6 ± 5.3
UAL	54.4–55.4	54.9 ± 0.7	48.2–49.2	48.7 ± 0.7	49.1–67.0	57.2 ± 7.0
LAL	61.4–64.5	62.9 ± 2.2	54.1–54.9	54.5 ± 0.6	51.8–61.0	56.8 ± 2.7
TAL	745.2–785.1	765.1 ± 28.2	806.3–854.1	830.2 ± 33.8	708.1–862.9	780.4 ± 63.3
SUP	10–11		9		10–11	
INF	10		9		9–11	
CR	7–8		10		7–9	
MBS	41–45		42–51		36–43	
DS	11–12		9		13–15	
MVS	90–94		72–77		81–106	
SDL	27		27–29		26–30	

^a SVL, measured from tip of snout to anterior margin of vent; AG = axilla-groin length, distance between axilla and groin; HL, distance between posterior edge of mandible and tip of snout; HW = head width, maximum width of head; HD = head depth, distance between occiput and throat; TYD = tympanum diameter, longest diameter of the tympanum; ED = eye diameter, horizontal diameter of orbit; EN = eye-nostril length, distance between anteriormost point of orbit and middle of nostril; IO = interorbital width, least distance between upper margins of orbits; FEL = femur length, distance between groin and knee; TBL = tibia length, distance between knee and heel, with both tibia and tarsus flexed; TL = toe length, distance between tip of claw and nearest fork; UAL = upper arm length, distance between axilla and angle of elbow; LAL = lower arm length, distance from elbow to wrist with both upper arm and palm flexed; TAL = tail length, measured from anterior margin of vent to tail tip; SUP = supralabials; INF = infralabials, first labial scale to last labial scale toward gape, which is distinctly larger than the granular scales at gape; CR = canthus rostralis, counted from first scale posterior to supranasal, to end of supraclavicular ridge; MBS = midbody scales, counted from center of middorsal row forward and downward across ventrals; DS = dorsinuchal crest spines, counted from first spine of nuchal crest to the level of axilla; MVS = midventral scales, counted from first scale posterior to mental, to last scale anterior to vent; SDL = subdigital lamellae on Toe IV, from first proximal enlarged scensor wider than twice the width of the largest palm scale, to distal most lamella at tip of digit.

Calotes liolepis and the new species and the lack of a precise provenance of the *Calotes liolepis* specimens to identify the exact matching population among its widely distributed populations in mid-elevations in the central highlands, lowland rain forests, and a few isolated moist forests in the dry zone.

We retained the first four components for the inspection of the PCA result (Fig. 1), because it entailed the first four principal components (PCs) covering more than 80% of the whole eigenvalues. The eigenvalues were allocated 35%, 25%, 14%, and 9% on Component 1, 2, 3, and 4, respectively (Table 2). The first axis was moderately correlated with several measurements, where ED/HL (loading value, -0.42), SVL/HL (-0.38), TYE/HL (0.37), and HW/HL (0.37) are the four

most correlated measurements among the 12 measurements. The second axis was characterized mostly by EN/HL (0.51), AG/HL (0.44), and LAL/HL (-0.43). The third axis was dominated by TL5/HL (-0.66) exclusively. For the fourth axis, AG/HL (-0.49), FEL/HL (-0.40), and TYE/HL (-0.37) were the most influential measurements. Two specimens of the new species are distinctively distributed along the first, second, and third axis from nine *Calotes liolepis* specimens and two *Calotes desilvai* specimens. The fourth axis did not reveal any remarkable pattern among groups. According to PCA spatial distribution, the new species is characterized by relatively smaller ED and SVL and by large TYE and HW compared with *Calotes liolepis*. Moreover, the new species tended to have

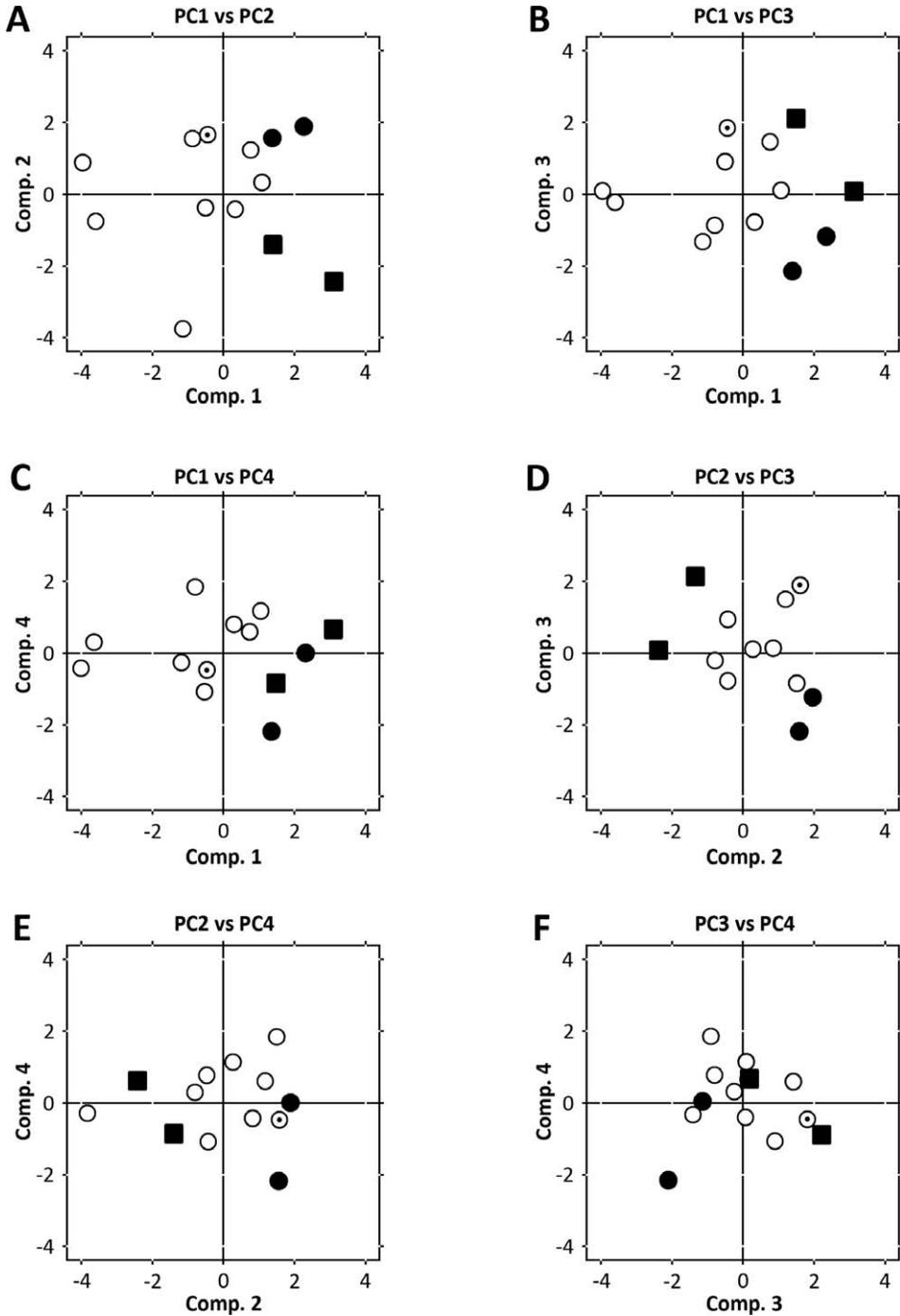


FIG. 1.—Morphometric analysis of *Calotes liolepis* (open circles), *Calotes desilvai* (filled circles), and *Calotes manamendrai* sp. nov. (filled squares). (A) Principle component (PC) 1 vs. PC2. (B) PC1 vs. PC3. (C) PC1 vs. PC4. (D) PC2 vs. PC3. (E) PC2 vs. PC4. (F) PC3 vs. PC4. The open circle with dot in the middle represents the examined syntype of *Calotes liolepis*.

TABLE 2.—Loadings for the first four principal components (PCs) of morphometric characters in *Calotes liolepis*, *Calotes desilvai*, and *Calotes manamendrai* sp. nov.

Character ^a	PC1	PC2	PC3	PC4
SVL	-0.37611	0.18588	0.28270	-0.25220
AG	-0.09697	0.43703	-0.22357	-0.48685
HL	0.33781	-0.20321	-0.37023	-0.01511
HW	0.36543	-0.06627	0.26987	-0.31470
ED	-0.41753	-0.02994	0.20893	0.05974
EN	-0.02924	0.50937	-0.04906	-0.19979
TYE	0.37304	-0.10057	0.09003	-0.36595
FEL	-0.31955	-0.28843	-0.07390	-0.39894
TBL	-0.31387	-0.32097	-0.10638	-0.24833
TL5	-0.08299	-0.17187	-0.65899	-0.20985
UAL	-0.27435	-0.24146	-0.09622	0.25090
LAL	0.06606	-0.42923	0.38173	-0.30804
Eigenvalue	3.92696	2.78574	1.54795	1.01235
Proportion of variance	0.35452	0.25149	0.13974	0.09139
Cumulative proportion	0.35452	0.60601	0.74575	0.83714

^a SVL = snout-vent length, measured from tip of snout to anterior margin of vent; AG = axilla-groin length, distance between axilla and groin; HL = head length, distance between posterior edge of mandible and tip of snout; HW = head width, maximum width of head; ED = eye diameter, horizontal diameter of orbit; EN = eye-nostril length, distance between anteriormost point of orbit and middle of nostril; TYE = tympanum-eye length, distance between anteriormost margin of tympanum and posteriormost margin of the orbit; FEL = femur length, distance between groin and knee; TBL tibia length, distance between knee and heel, with both tibia and tarsus flexed; TL = toe length, distance between tip of claw and nearest fork; UAL = UAL = upper arm length, distance between axilla and angle of elbow; LAL = LAL = lower arm length, distance from elbow to wrist with both upper arm and palm flexed.

smaller EN, AG, and TL5 and larger LAL than *Calotes desilvai*.

SYSTEMATICS

Calotes manamendrai Amarasinghe & Karunarathna sp. nov.
(Tables 1, 3; Figs. 2–4)

Holotype.—NMSL5976, adult female, SVL 69.7 mm, collected at Riverstone, Knuckles, Sri Lanka; 1000 m a.s.l. (collector and the date unknown).

Paratype.—NMSL5977, adult female, SVL 59.8 mm; other details are the same as the holotype.

Diagnosis.—Females of *Calotes manamendrai* sp. nov. are different from the females of *Calotes liolepis* by having nonenlarged pectoral scales (vs. enlarged); dorsal scales on the body, carinate (vs. smooth); midgular scales smaller than rest of the throat scales (vs. midgular scales same size with throat scales); seven stripes each side on gular area distinct, brown (vs. bands on gular area faint, brown); shoulder pit, black (vs. cream white to brown); and upper arm with carinate ventral scales (vs. smooth). Females of *Calotes manamendrai* sp. nov. differ from females of *Calotes desilvai* by having scales on the ventral surface of thigh,

carinate (vs. smooth); midgular scales smaller than rest of the throat scales (vs. midgular scales same size with throat scales); seven stripes each side on gular area distinct, brown (vs. bands on gular area, black); shorter AG (141.6%–157.1% of HL) vs. longer AG (174.7%–183.8% of HL); longer upper arm (54.4%–55.4% of HL) vs. shorter upper arm (48.2%–49.2% of HL); Toe V 31.3%–38.6% of HL (vs. 41.9%–45.9% of HL); temporal region with large carinate scales (vs. without large carinate scales); 90–94 ventrals (vs. 72–77); dorsal scales on the body carinate (vs. smooth). *Calotes manamendrai* sp. nov. further differs from congeners by the following opposing characters: *Calotes nigrilabris*: ventral scales larger than dorsal; *Calotes ceylonensis*: lateral scales pointing straight backward; *Calotes liocephalus* and *Calotes pethiyagodai*: spines above the tympanum absent; *Calotes calotes* and *Calotes versicolor*: lateral scales pointing backward and upward.

Description of Holotype.—An adult female, 69.7 mm SVL; head moderately large (HL 31.1% of SVL), elongate (HW 60.4% of HL), narrow (HW 18.8% of SVL), distinct from neck; snout elongate (ES 65.7% of HW); snout length greater than ED (77.4% of ES); interorbital distance broad (IO 39.3% of HL); eye large (ED 30.8% of HL); pupil rounded; ear opening shallow and with smooth scales,

TABLE 3.—External morphological character variation in Sri Lankan *Calotes* species based on examined specimens (see Appendix).

Character	<i>C. calotes</i>	<i>C. versicolor</i>	<i>C. ceylanensis</i>	<i>C. krolepis</i>	<i>C. desilvai</i>	<i>C. manamendurai</i> sp. nov.	<i>C. itoecephalus</i>	<i>C. pathiyagodai</i>	<i>C. nigritlabris</i>
Lateral body-scale orientation (backward)	Upward	Upward	Straight	Downward	Downward	Downward	Downward	Downward	Downward
Shoulder pit	Present	Absent	Present	Present	Present	Present	Present	Present	Present
Supratympanic spines	Single continuous row	Two clusters	Two clusters	Two clusters	Two clusters	Two clusters	Absent	Absent	Single continuous row
Size of ventral scales relative to dorsals	Similar	Smaller	Smaller	Smaller	Smaller	Smaller	Smaller	Larger	Larger
Scales on ventral thigh	Keeled	Keeled	Smooth	Keeled	Smooth	Keeled	Keeled	Keeled	Keeled

its greatest diameter dorsoventrally, tympanum smaller than orbit (TYD 39.5% of ED); supratympanic spines in two distinct clusters, each with a larger medial spine; anterior spine and posterior spine separated from the tympanum by seven and four smaller scale rows, respectively; diameter of eyes greater than eye-to-ear distance (ED 156.0% TYE); forehead concave; scales on snout smooth, more or less similar in size than those of occipital region; scales on interorbital and supercillium area smooth; no nuchal crest; dorsal crest rudimentary, consisting of 12 spines up to the level of axilla; rostral scale much wider than high, ventroposteriorly in contact with first supralabial, contacted posteriorly by four equal-sized postrostral scales; around nostrils on each side one supranasal, two postnasals, two prenasals, and a subnasal, which separate nasal from supralabials; nostrils oval located dorsally in an undivided nasal plate; canthus rostralis and supraciliary edges sharp; eight canthus rostralis; parietal plate larger than adjacent plates, 12 scales around the parietal plate; mental subtriangular, length about as long as wide, posteriolaterally in contact with two enlarged postmentals separated by a smaller scale not allowing contact between them; each postmental pair bordered posteriorly by four (left side) and three (right side) smooth scales, including the medial scale, but exclusive of infralabial. Gular pouch present; throat scales and midgular scales carinate and overlapped; four scale rows separate orbit from supralabials; supralabials 10 (eighth in midorbit position); infralabials 10, decreasing in size toward gape; ventral scales on the neck carinate.

Body slender (AG 48.9% of SVL); dorsal scales equal, slightly keeled and overlapped; scales on dorsum at midbody larger in size than those of venter at same level; lateral body scales strongly keeled, pointed, smaller than dorsals; directed backward and downward; 45 scales around the midbody; pectoral scales and abdominal scales carinate, not enlarged, overlapped and keels forming regular and parallel continuous ventral ridges; abdominal scales larger than pectoral scales; ventrals, 94; no preanal or femoral pores.

Forelimbs moderately short (LAL 20.1% of SVL, UAL 17.0% of SVL); hind limbs

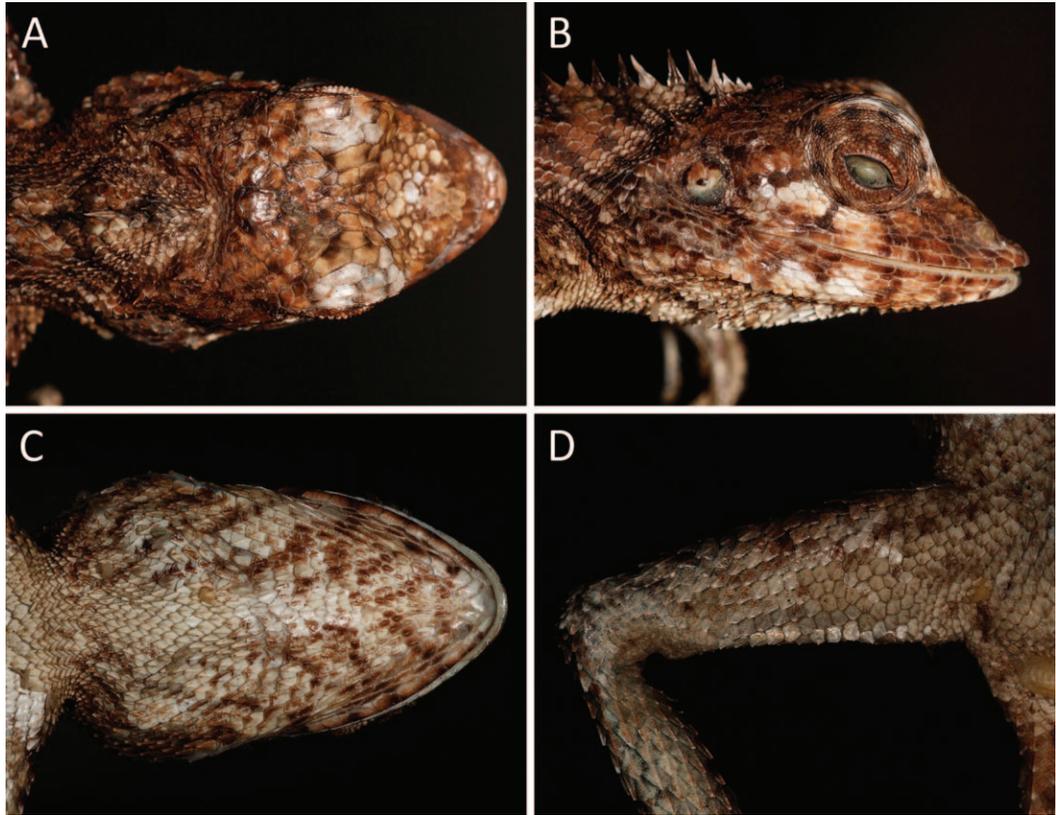


FIG. 2.—Holotype female (snout–vent length [SVL] = 69.7 mm) of *Calotes manamendrai* sp. nov., NMSL5976. (A) Dorsal head. (B) Lateral head. (C) Ventral head; (D) Ventral thigh and tail base (photos by M. De Silva). (A color version of this figure is available online.)

relatively long (TBL 23.9% of SVL, FEL 23.2% of SVL); tibia comparatively long (FEL 97.1% of TBL). Dorsal scales on fore- and hind limbs keeled, overlapped and mucronate; ventral scales on upper arm smooth and lower arm keeled, overlapped, and not pointed; scales on ventral surface of thigh keeled, overlapped and not pointed; keels on tibia forming a series of continuous parallel ridges. Digits elongate, slender, all bearing slightly recurved claws; claws are sharp and elongate; subdigital lamellae entire and regular, subdigital lamellae on Toe IV, 27; interdigital webbing absent; relative length of digits (fingers) $4 > 3 > 2 > 5 > 1$; (toes) $4 > 3 > 5 > 2 > 1$.

Tail complete (216.1 mm); ventral scales on tail base carinate and overlapped; dorsal scales on tail enlarged, pointed, elongate, overlapped, directed backward, keels forming

continuous parallel ridges; tail with subcaudals on median row not enlarged, keeled, mucronate, overlapped.

Measurements (mm) of Holotype.—HL, 21.7; HW, 13.1; HD, 11.3; EN, 4.4; ES, 8.6; TYD, 2.6; IN, 4.5; IO, 8.5; TBW, 5.4; SVL, 69.7; AG, 34.1; TAL, 161.7; ED, 6.7; TYE, 4.3; UAL, 11.8; LAL, 14.0; FEL, 16.2; TBL, 16.7; FOL, 20.7; T1, 3.1; T2, 5.6; T3, 9.6; T4, 10.7; T5, 6.8.

Color in Preservative.—Dorsum gray; four V-shaped brown markings on the body; spines white and black; each limb with seven black crossbars; tail with gray and brown markings; three brown lines from orbit to supralabials, another line from orbit to tympanum; seven brown stripes on each side of gular pouch; venter light gray.

Variation in Paratype.—The paratype has dorsal crest consisting of 11 spines up to the

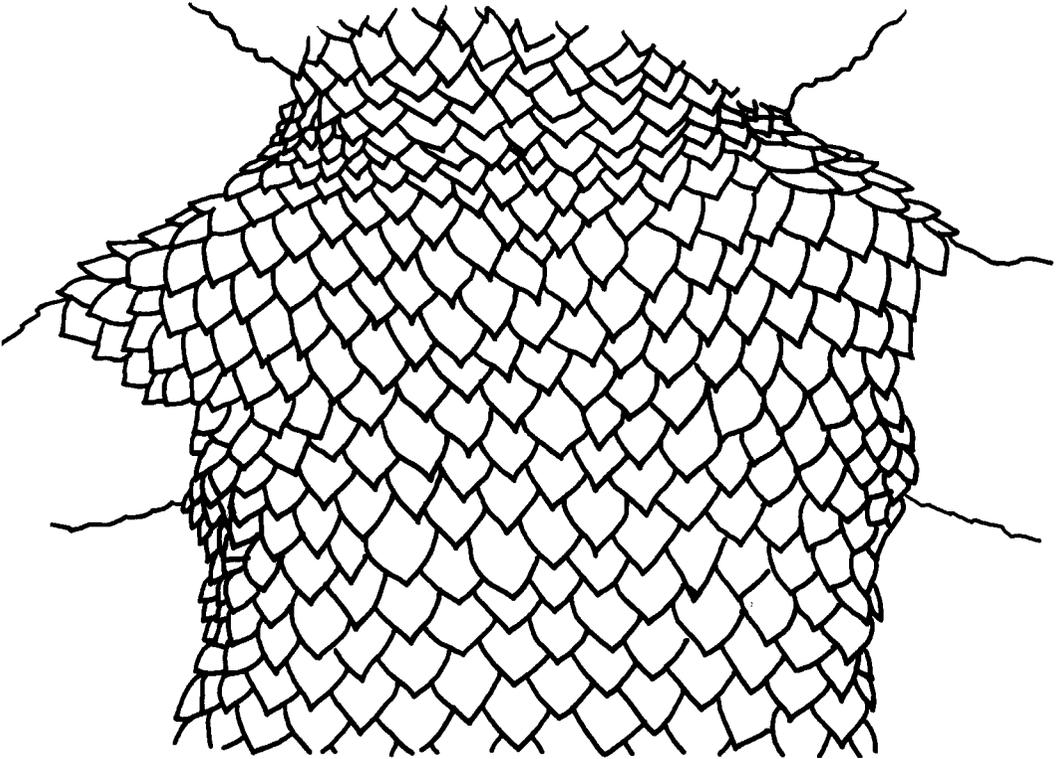


FIG. 3.—Pectoral scales of holotype female (snout–vent length [SVL] = 69.7 mm) of *Calotes manamendrai* sp. nov., NMSL5976. Note the nonenlarged pectoral scales.

level of axilla; seven canthus rostralis; eight scales around the parietal plate; each postmental pair bordered posteriorly by three (left side) and three (right side) smooth scales including the medial scale, but exclusive of infralabial; supralabials 11; 41 scales around the midbody; ventrals, 90; In preservative, five V-shaped brown markings on the body.

Color in Life.—Dorsum pale white; five V-shaped brown markings on the body; spines white and black; each limb with seven black crossbars; tail with gray and brown markings; three brown lines from orbit to supralabials, another line from orbit to tympanum; seven brown stripes on each side of gular pouch; venter pale white.

Etymology.—The species epithet is an eponym Latinized in the genitive singular, honoring Kelum Nalinda Manamendra-Arachchi for his generous teaching and guidance in taxonomic studies for the first two authors as well as his remarkable contributions to herpetology, zooarchaeology, and

biodiversity conservation in Sri Lanka. Suggested English name: Manamendra-Arachchi's Whistling Lizard; Sinhala (local) name: Manamendra-Arachchigē Uruwan Katussa.

Distribution and Habitat.—De Silva et al. (2005) observed *Calotes liolepis* from several locations of the Knuckles massif and the following locations might be referable to *Calotes manamendrai* sp. nov.: Dumbanagala (1132 m a.s.l.), Corbet's Gap (1223 m a.s.l.), Dawatagala (1344 m a.s.l.), Dotalugala (1227 m a.s.l.), Kalupahana (1002 m a.s.l.), Kobonilagala (1191 m a.s.l.), Loolwatte (1191 m a.s.l.), and Kobonilla (1025 m a.s.l.). We observed one live female (Fig. 4) at the type locality; we have also observed two adult males from Riverstone of the Knuckles.

Natural History.—The habitats where *Calotes manamendrai* sp. nov. occurs harbor many medium-canopy trees (~8 m above ground level) such as *Creteava religiosa*, *Phyllanthus indika*, *Sterculia foetida*, *Bombax ceiba*, *Dimocarpus longan*, *Palaquium himmolpedda*,



FIG. 4.—*Calotes manamendrai* sp. nov., a live female (not collected) at the type locality (Riverstone, Knuckles massif, Sri Lanka). (A color version of this figure is available online.)

and *Vitex altissima*. The subcanopy level (~5 m above ground level) consists of *Breynia vitisidea*, *Miliusa indica*, *Pavetta indica*, and *Streblus asper* trees. Shrub cover (~2 m above ground level) consists of *Begonia hirtella*, *Carex filicina*, *Carex jakiana*, *Curculio orchioides*, and *Procris crenata*. The Knuckles forest range is extremely wet throughout the year, with an average annual rainfall >4000 mm, although the lower eastern slopes are much drier. Most of the habitats had 50%–65% ($\bar{X} \pm 1$ SD = 57.7% \pm 7.5%) canopy cover and the undergrowth consisted of shrubs and herbs. The range of temperature and range of relative humidity were 25.5°C–26.8°C (\bar{X} = 26.2°C \pm 0.7°C) and 65%–74% (\bar{X} = 69.0% \pm 4.6%), respectively. The evergreen submontane forests represent the major natural vegetation type in Riverstone area. The ovipositional behavior of *Calotes liolepis* described by Karunarathna

et al. (2009) in Knuckles (Manigala) is probably also referable to *Calotes manamendrai* sp. nov., as the Manigala population (~900 m a.s.l.) is isolated from the Knuckles population of *Calotes liolepis* (e.g., Puwakpitiya, ~400 m a.s.l.). The males are similar to females in body color pattern but with larger gular sacs. When distressed, males made a low-frequency short whistle sound; we observed this behavior among *Calotes liolepis* males as well.

Calotes liolepis Boulenger, 1885
(Tables 1, 3; Figs. 5, 6)

Syntype.—BMNH 69.7.24.2, adult female, SVL 75.4 mm, collected from Sri Lanka by R.H. Barnes; date unknown (the other juvenile syntype was not examined).

Redescription of Syntype.—An adult female, 75.4 mm SVL; head moderately large



FIG. 5.—Syntype female (snout–vent length [SVL] = 75.4 mm) of *Calotes liolepis*, BMNH 69.7.24.2 (photo by C. McCarthy). (A color version of this figure is available online.)

(HL 29.8% of SVL), elongate (HW 57.8% of HL), narrow (HW 17.2% of SVL), distinct from neck; snout elongate (ES 66.9% of HW); snout length greater than ED (93.1% of ES); interorbital distance broad (IO 33.3% of HL); eye large (ED 36.0% of HL); pupil rounded; ear opening shallow with smooth scales, its greatest diameter dorsolaterally, tympanum smaller than orbit (TYD 42.0% of ED); supratympanic spines in two distinct clusters, each with a larger medial spine; anterior spine and posterior spine separated from the tympanum by seven and six smaller scale rows, respectively; diameter of eyes greater than eye-to-ear distance (ED 188.4% TYE); forehead concave; scales on snout smooth, smaller in size than those of occipital region; scales on interorbital and supercillium area smooth; no nuchal crest; dorsal crest rudimentary, consisting of 14 spines up to the level of axilla; rostral scale much wider than

high, ventroposteriorly in contact with first supralabial, contacted posteriorly by four equal-sized postrostral scales; around nostrils on each side two supranasals, two postnasals, two prenasals, and two subnasals, which separate nasal from supralabials; nostrils round located posteriorly in an undivided nasal plate; canthus rostralis and supraciliary edges sharp; nine canthus rostralis; parietal plate larger than adjacent plates, 10 scales around the parietal plate; mental subtriangular, length about as long as wide, posteriorly laterally in contact with two enlarged postmentals separated by a smaller scale not allowing contact between them; each postmental pair bordered posteriorly by three (left side) and four (right side) smooth scales including the medial scale, but exclusive of infralabial. Gular pouch present; throat scales and midgular scales carinate and overlapped; two scale rows separate orbit from supra-

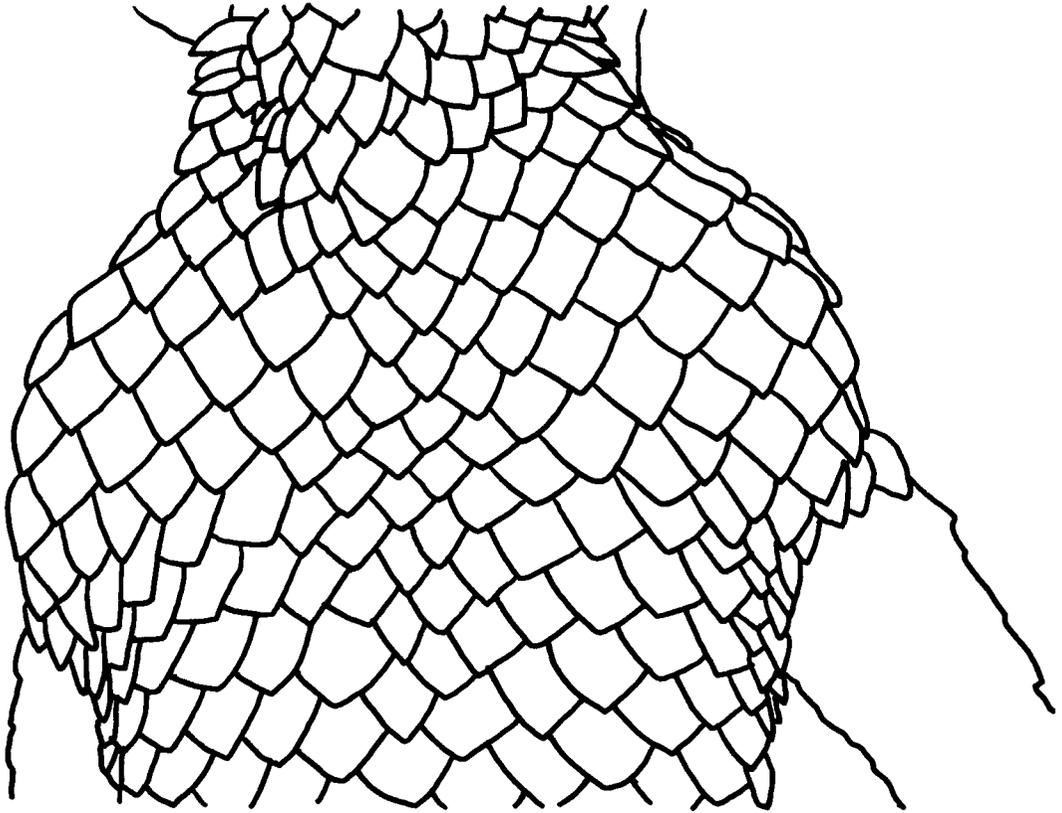


FIG. 6.—Pectoral scales of syntype female (75.4 mm snout–vent length [SVL]) of *Calotes liolepis*, BMNH 69.7.24.2. Note the enlarged pectoral scales.

labials; supralabials 10 (seventh in midorbit position); infralabials 9, decreasing in size toward gape; ventral scales on the neck carinate.

Body slender (AG 49.6% of SVL); dorsal scales equal, smooth and overlapped; scales on dorsum at midbody about three times larger in size than those of venter at same level; lateral body scales keeled, pointed, similar size in dorsals; directed backward and downward; 43 scales around the midbody; pectoral scales and abdominal scales carinate, overlapped and keels forming regular and parallel continuous ventral ridges; pectoral scales enlarged; ventrals, 88; no preanal or femoral pores.

Forelimbs moderately short (LAL 17.5% of SVL, UAL 15.4% of SVL); hind limbs relatively long (TBL 22.0% of SVL, FEL 21.1% of SVL); tibia comparatively long (FEL 95.8% of TBL). Dorsal scales on fore- and

hind limbs keeled, overlapped and mucronate; ventral scales on upper arm smooth and lower arm keeled, overlapped, and pointed; scales on ventral surface of thigh keeled, overlapped and pointed; keels on tibia forming a series of continuous parallel ridges. Digits elongate, slender, all bearing slightly recurved claws; claws are sharp and elongate; subdigital lamellae entire and regular, subdigital lamellae on Toe IV, 29; interdigital webbing absent; relative length of digits (fingers) $4 > 3 > 2 > 5 > 1$; (toes) $4 > 3 > 5 > 2 > 1$.

Tail complete (216.1 mm); ventral scales on tail base carinate and overlapped; dorsal scales on tail enlarged, pointed, elongate, overlapped, directed backward, keels forming continuous parallel ridges; tail with subcaudals on median row not enlarged, keeled, mucronate, overlapped.

Measurements (mm) of Syntype.—HL, 22.5; HW, 13.0; HD, 11.6; EN, 5.4; ES, 8.7; TYD,

3.4; IN, 5.5; IO, 7.5; TBW, 7.4; SVL, 75.4; AG, 37.4; TAL, 276.4; ED, 8.1; TYE, 4.3; UAL, 11.6; LAL, 13.2; FEL, 15.9; TBL, 16.6; FOL, 20.5; T1, 3.6; T2, 5.1; T3, 9.6; T4, 10.5; T5, 7.0.

Color in Preservative.—Dorsum gray; light brown markings on the body; spines gray in color; limbs darker in color; tail with light brown markings; three brown lines from orbit to supralabials, another line from orbit to tympanum; gular pouch pale cream and light brown; venter pale white.

DISCUSSION

Since the description of *Calotes liolepis* Boulenger, 1885, the *Calotes liolepis* complex was considered a single species until Bahir and Maduwage (2005) described *Calotes desilvai* from the Morningside forest of Rakwana highlands. Boulenger (1885) described the species based on two specimens (two syntypes of a female and one of a juvenile), without a precise location within Sri Lanka. Therefore, many isolated populations in high elevations (e.g., Knuckles massif, Peak wilderness, Balangoda Mountains), lowland rain forests (e.g., Rakwana, Galle), and moist forests in the dry zone (e.g., Ritigala, Nilgala, Monaragala) have not been compared thoroughly. Small sample sizes from these populations have added to the difficulty of establishing the extent of intraspecific variation occurring across the range of the species, or of determining whether certain characters are consistently distinct between reproductively isolated populations. Bahir and Maduwage (2005) treated *Calotes liolepis*, including some populations restricted to a few isolated moist forests in the dry zone, as one species, while separating *Calotes desilvai* as a distinct species. The *Calotes liolepis* population distributed in Ritigala (an isolated moist forest in the dry zone), however, seems to be a distinct species; it is morphologically similar to the new species described here. Helgen and Groves (2005:199) argued that “there may sometimes be stronger faunal differentiation between wet, dry, and cloud forest zones within Sri Lanka than between that island’s dry zone and the dry country of South India.” The lowlands (~500 m a.s.l.) of the Mahaweli River appear to have served as a barrier

separating the central highlands from the Knuckles massif (Manamendra–Arachchi et al., 2006; Amarasinghe et al., 2014) and other mountain ranges (Fernando et al., 2007; see Asela et al., 2012, for further discussions on the distribution of the *Calotes liolepis* complex). Two specimens of *Calotes manamendrai* sp. nov. did not show separation from other *Calotes liolepis* complex (Fig. 1C, E, F), possibly because the characters related with PC 4, such as AG, FEL, or TYE, were not species specific; instead, they might represent traits that vary among individuals which were discernible globally across the genus. As demonstrated by Bahir and Maduwage (2005), *Calotes desilvai* separated clearly from most of *Calotes liolepis* specimens on PCA space except along the fourth axis (Fig. 1).

The two specimens deposited at NMSL (now the holotype and the paratype of *Calotes manamendrai* sp. nov.) could be a part of WHT collection made after Bahir and Maduwage (2005). Based on observations made in the course of ~25 visits to the Knuckles massif from 2005 to 2010, we note that *Calotes manamendrai* sp. nov. is extremely rare (only three records in addition to the type materials). Because of this rarity and conservation concern, we described the species based on the two specimens at the NMSL. More field explorations are needed to find male specimens to make a complete description of this species. The results of the application of the IUCN (2013) Red List criteria show that *Calotes manamendrai* sp. nov. is Critically Endangered (CR): it is restricted to an area of occupancy < 2 km² (three spotting sites) and extent of occurrence < 10 km² in Riverstone (Knuckles massif; Fig. 7). Applicable criteria from the IUCN are B2 a, b (iii), with the same site.

We failed to locate any specimens of *Calotes manamendrai* sp. nov. from the collections at BMNH, MNHN, NMB, and NMW. Most *Calotes liolepis* specimens deposited in these collections are from the central highlands of Sri Lanka and were collected during the late 19th century. The syntype of *Calotes liolepis* was likely also collected from the mid-elevations of the central highlands (perhaps around Kandy). Our searches for *Calotes manamendrai* sp. nov. indicate its absence

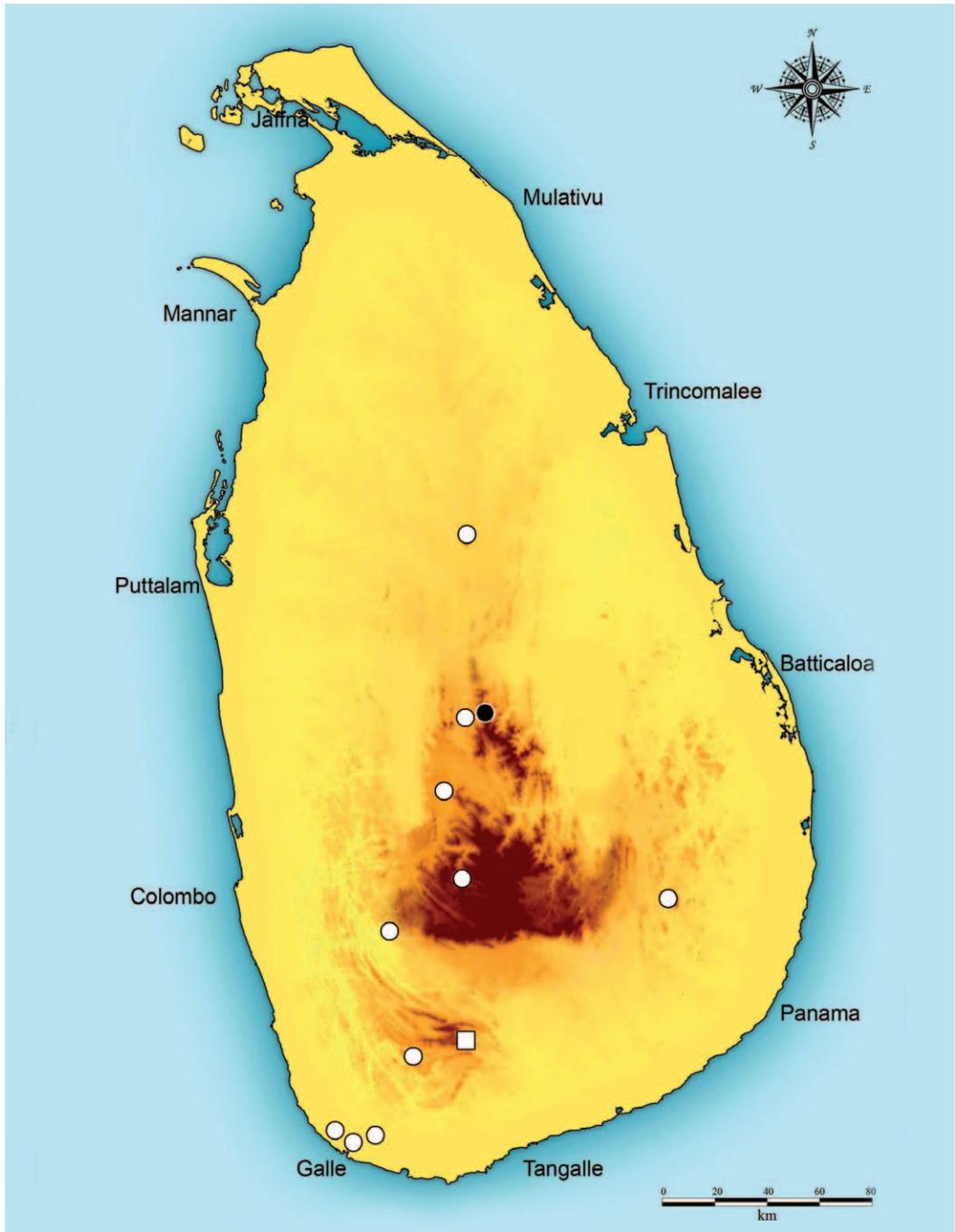


FIG. 7.—Distribution map of *Calotes liolepis* (open circles), *Calotes desilvai* (open squares), and *Calotes manamendrai* sp. nov. (filled circles) based on examined specimens. (A color version of this figure is available online.)

from the lowland forests surrounding the Knuckles massif, where it is replaced by *Calotes liolepis*, a similar scenario to *Calotes desilvai* in Morningside (see Bahir and Maduwage, 2005).

Chena (shifting) cultivations, illegal harvesting of in- and above-ground resources, human-caused fires, soil erosion, and other forms of habitat destruction are all contributing to the loss and fragmentation of habitat in the Knuckles range (Amarasinghe and Karunarathna, 2010). These threats to *Calotes manamendrai* sp. nov. could be exacerbated by the surrounding cardamom (Zingiberales: Zingiberaceae) cultivations that indiscriminately use pesticides (Bahir and Surasinghe, 2005). Roadkills might be an additional threat to *Calotes manamendrai* sp. nov., because we have observed many road-killed specimens of the sympatric *Calotes pethiyagodai* during the past decade in the Riverstone area. Specimens of *Calotes pethiyagodai* have also been found dead for unknown reasons (Amarasinghe et al., 2009, 2014). *Calotes manamendrai* sp. nov. might also face the same unidentified threat, possibly linked to climatic change.

According to our observations, the endemic agamid lizards in Sri Lanka show a unique distribution pattern along the three major mountain ranges. In Rakwana highlands, *Calotes desilvai* (see Bahir and Maduwage, 2005), *Ceratophora erdeleni*, *Ceratophora karu* (see Pethiyagoda and Manamendra-Arachchi, 1998), and *Cophotis* sp. (D. Gabadage, personal communication) occur in areas > 700 m a.s.l., whereas *Calotes liolepis*, *Otocryptis wiegmanni*, *Ceratophora aspera*, and *Lyricephalus scutatus* (see Karunarathna and Amarasinghe, 2013) replace them in areas < 700 m a.s.l. In the Central highlands, *Calotes* cf. *liolepis*, *Calotes liocephalus* (see Amarasinghe et al., 2014), *Calotes nigrilabris* (see Amarasinghe et al., 2012), *Ceratophora stoddartii* (see Pethiyagoda and Manamendra-Arachchi, 1998), and *Cophotis ceylanica* (see Manamendra-Arachchi et al., 2006) are distributed in areas > 1000 m a.s.l., whereas *Calotes liolepis*, *O. wiegmanni*, and *L. scutatus* (see Karunarathna and Amarasinghe, 2013) replace them in areas < 1000 m a.s.l. Similar to these distribution patterns, in the Knuckles massif, areas > 800 m a.s.l. are occupied by

Calotes manamendrai sp. nov., *Calotes pethiyagodai* (see Amarasinghe et al., 2014), *Ceratophora tennentii* (see Pethiyagoda and Manamendra-Arachchi, 1998), and *Cophotis dumbara* (see Manamendra-Arachchi et al., 2006), whereas habitats < 800 m a.s.l. contain *Calotes liolepis*, *O. wiegmanni* (in wet slopes), *Otocryptis nigristigma* (in dry slopes), and *L. scutatus* (see Karunarathna and Amarasinghe, 2013).

Finally, we highlight the unexpectedly high diversity of the *Calotes liolepis* complex. Phylogenetic research should be conducted to further understand the biogeography of the genus *Calotes*. Such studies are particularly needed for the *Calotes liolepis* and *Calotes liocephalus* complexes for which data are insufficient to support exact maps of their distributions since Erdelen (1984).

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APPENDIX

Specimens Examined

Calotes calotes (Linnaeus, 1758).—Sri Lanka: NRM 106; Laggala–Knuckles: WHT 108A–B; Puttalam: WHT 182; Yatapatha, Lihinigala: WHT 187–88; Warnagalla (near Erathne): WHT 381A; Koskulana near Panapola: WHT 616; Induruwa, Ratnapura: WHT 107. *Calotes ceylonensis* (Müller, 1887).—Kumbukkan Oya: NMB 3340–41; Wasgamuwa: WHT 1427A–B, 1624A, 1625A–B, 7397; Giritale: WHT 7514; Tatugala–Bulupitiya: WHT 1428; Pallegama: WHT 0515, 1427; Konketiya–Buttala: WHT 0511, 0522; Yala: WHT 0519–20. *Calotes desilvai* Bahir and Maduwage, 2005: Morningside Forest, Eastern Sinharaja: WHT 503, 1412, 1832, 5998. *Calotes liocephalus* Günther, 1872.—Sri Lanka: BMNH 1946.8.11.33, NHMW 21097; Talawakelle–Dickoya: NMB 3353–54; Pundaluoya: BMNH 95.7.24; Agrapatanas: WHT 6503, WHT 6504; Moray Estate, Rajamally: WHT 1667. *Calotes liolepis* Boulenger, 1885.—Sri Lanka: BMNH 69.7.24.2; Peradeniya: NMB 3345; Kottawa: WHT 491B; Mederipitiya: WHT 499B; Batadomabalena near Kuruwita: WHT 192; Richmond Hill near Galle: WHT 1415; Hapugala near Galle: WHT 489; Karapitiya near Galle: WHT 479; Ritigala: WHT 6177. *Calotes nigrilabris* Peters, 1860.—Nuwara Eliya: NMW 23355; Horton Plains: WHT 380C; Hakgala: WHT 1555, 2262; Kudaoya near Labugolla: WHT 379; Nagrak Division, Nonpareil Estate: WHT 1773A–D. *Calotes pethiyagodai* Amarasinghe, Karunarathna, and Hallermann, 2014.—Knuckles: WHT6211, 6154A–B, 6241, 106A, 1435. *Calotes versicolor* (Daudin, 1802).—Mousakanda–Knuckles: WHT 165; Pallegama–Knuckles: WHT 105; Peradeniya: WHT 384; Warnagalla near Kuruwita: WHT 382; Laggala–Knuckles: WHT 104; Mahapellasa near Kirinda: WHT 164A; Nagamuwa–Puttalam: WHT 181; Bundala–Hambantota: WHT 204; Siribopura–Hambantota: WHT 205; Pannipitiya–Maharagama: WHT 199; Puwakpitiya, Knuckles: WHT 6172; Attidiya, Colombo: WHT 193.