

CALOTES DESILVAI, A NEW SPECIES OF AGAMID LIZARD FROM MORNINGSIDE FOREST, SRI LANKA

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ABSTRACT. –The genus *Calotes* Cuvier has been considered to be represented in Sri Lanka by six species. A seventh species, *C. desilvai*, evidently restricted to a single site, Morningside Forest ($\sim 10 \text{ km}^2$) on the eastern side of the Sinharaja World Heritage Site, is described. Among the Sri Lankan *Calotes*, the new species seems most closely related to *C. liolepis* Boulenger, which is widely distributed in the island's lowland rain forest and a few isolated moist forests in the dry zone. *Calotes desilvai* is distinguished from *C. liolepis* by having the fifth toe 42.6–47.0% of head length in males, 41.9–45.9% in females (vs. 31.0–39.5% and 33.0–40.5% respectively, in *C. liolepis*); bands on gular area distinct, black (vs. bands on gular area faint, brown); shoulder pit black (vs. shoulder pit cream white to brown); and scales on ventral surface of thigh smooth (vs. scales on the ventral surface of thigh carinate). Males of *C. desilvai* may also be distinguished from males of *C. liolepis* by their longer upper arm and femur (49.6–50.0 and 70.3–75.0% of head length, respectively) vs. shorter upper arm and femur (40.3–49.3 and 57.1–69.5%, respectively) and a comparatively short posterior supratympanic spine (1.7–2.7% of head length), longer in *C. liolepis* (3.1–12.9%).

KEYWORDS. – Agamidae, *Calotes*, new species, distribution, Sri Lanka.

INTRODUCTION

Agamid lizards of the genus *Calotes* Cuvier, 1817 are at present represented in Sri Lanka by six species, at least four of which appear to form an endemic radiation (Macey et al., 2000): *C. nigrilabris* Peters, 1860; *C. liocephalus* Günther, 1872; *C. ceylonensis* (Müller, 1887); and *C. liolepis* Boulenger, 1885. *Calotes calotes* (Linnaeus, 1758) is recorded also from India, while *C. versicolor* (Daudin, 1802) is widely distributed through tropical Asia, from Iran to China and southwards, having been introduced also to several oceanic islands in this region (Smith, 1935; Deraniyagala, 1953; Taylor, 1953; Moody, 1980; I. Das, pers. comm.). Thus far, *C. liolepis* has been considered to be a species with a distribution restricted to Sri Lanka's south-western "wet zone" quarter (rainfall $> 2,000 \text{ mm yr}^{-1}$) (Deraniyagala, 1953; Smith, 1935; Taylor, 1953; Erdelen, 1984; Manamendra-Arachchi & Liyanage, 1994).

Here we describe a new species of *Calotes* from Morningside Forest Reserve on the eastern border of the Sinharaja

World Heritage Site. Though not previously treated in the literature, the new species has hitherto been confused by field workers with *C. liolepis*. A wide sampling of *C. liolepis* from 22 locations across its range in Sri Lanka shows the new species to be consistently diagnosable from this and all other Sri Lankan *Calotes*. Despite being a small, relatively disturbed low-elevation cloud forest, recent exploration of Morningside has yielded a wealth of new species (Fernando & Siriwardana, 1996; Ng & Tay, 2001; Manamendra-Arachchi & Pethiyagoda, 2001, 2005; Batuwita & Bahir, 2005; Bahir & Ng, 2005; Meegaskumbura & Manamendra-Arachchi, 2005) including two other agamid lizards of the endemic Sri Lankan genus *Ceratophora* (Pethiyagoda & Manamendra-Arachchi, 1998). In this paper we describe the new species as *Calotes desilvai* so as to make a name available in order that this obviously threatened lizard could be included in the conservation planning process for Morningside Forest (for a conservation assessment of this and other Sri Lankan agamid species, see Bahir & Surasinghe, 2005).

MATERIALS AND METHODS

This study is a result of a survey (1998–2004) of saurian diversity in Sri Lanka with the goal of assessing diversity, distribution and endemism so as to facilitate conservation activity. The material referred to in this paper is deposited in the following institutions: Wildlife Heritage Trust of Sri Lanka (WHT); National Museum of Sri Lanka, Colombo (NMSL); The Natural History Museum, London (BMNH). In material examined, “others” refers to specimens identified for purposes of distribution but not measured for purposes of analysis.

Counts and measurements. – Scale counts and observations of external anatomy were made on the left side (unless otherwise stated) of specimens using a Motic K400 dissecting microscope. Sex was determined by the presence of hemipenial bulges and gular sacs. Coloration is based on freshly-preserved materials. Photographs were taken with a Cannon EOS-10D digital camera (Figs. 2, 4); and a Nikon D70 digital camera (Figs. 1, 3, 5). Photographs are of preserved specimens unless otherwise stated. Altitudes are given in metres above mean sea level (alt.); geographic co-ordinates are derived from the inch-to-the-mile topographical map series of the Sri Lanka Survey Department.

Measurements were made to the nearest 0.1 mm using KWB dial vernier callipers, abbreviated as follows: AG, distance between axilla and groin; DHW, dorsal head width (width of head at mid-orbit); ED, horizontal diameter of orbit; FEL, femur length (distance between groin and knee); FL, finger length (distance between tip of claw and nearest fork); HD, head depth at mid-orbital position; HL, head length (distance between posterior edge of mandible to tip of snout); HW, head width (maximum head width at angle of gape); LAL, lower arm length (distance from elbow to wrist, with both upper arm and palms flexed); LS, length of longest spine on nuchal crest; MHW, maximum head width; NE, distance between anterior-most point of orbit and mid-point of nostril; S1, length of longest anterior supratympanic spine; S2, length of longest posterior supratympanic spine; SA, snout to axilla distance (distance between tip of snout and axilla); SN, distance between middle of nostril and tip of snout; SL, snout length (distance between anterior-most point of orbit and tip of rostral scale); SVL, snout-vent length (distance from tip of snout to anterior margin of cloaca); TAL, tail length (distance from tip of tail to anterior margin of cloaca); TBL, tibia length (distance between knee and heel with both tibia and tarsus flexed); TL, toe length (distance between tip of claw and the nearer fork); UAL, upper arm length (distance between axilla and elbow).

Scale counts were made as follows. Canthus rostralis: from rostral scale along scale row passing over nostril to posterior end of superciliary ridge. Supralabials: from anterior-most scale to that at angle of gape, not including median scale (when present). Infralabials: from first scale posterior to mental, to angle of gape. Mid-ventrals: from first scale posterior to mental to last scale anterior to cloaca. Scales around mid-body: from mid-dorsal scale row (between axilla and groin), forwards and downwards to mid-venter and upwards and

backwards mid-dorsal. Supraorbital scale rows: from canthus rostralis to row of enlarged, keeled scales bordering inner edge of mid-orbit. Scales on ventral surface of digits: from nearest fork to base of claw. Mid-dorsal head scales: from scale behind rostral to scale immediately in front of anterior-most nuchal spine.

Principal components analysis was done using SAS/STAT® Version 6.12 (SAS Institute, Inc., USA) and hierarchical cluster analysis was done using Minitab® Version 11 (Minitab Inc., USA). Only male specimens were used in this analysis, using the following nine measurements normalised to head length: upper arm length, lengths of fingers 2–4, femur length, and lengths of toes 2–5. We chose these techniques primarily because we wished to investigate the degree and levels of relationships between the species, to which multivariate and hierarchical cluster analyses are well suited.

TAXONOMY

Calotes desilvai, new species

(Figs. 1, 2; Table 1)

Material examined. – Holotype - male (76.0 mm SVL) (WHT 1832), Morningside Forest, Eastern Sinharaja, Sri Lanka, 06°24'N, 80°36'E, alt. 1080 m.

Paratypes - 1 male (73.6 mm SVL) (WHT 503), 2 females (59.9 mm, 75.5 mm SVL, NMSL uncat., formerly WHT 1412 and WHT 5998 respectively); all from type locality.

Diagnosis. – Of the Sri Lankan species of *Calotes*, *C. desilvai* new species most closely resembles *C. liolepis* Boulenger, 1885, from which it is distinguished as follows (proportions are given as a percentage of HL): fifth toe longer, 42.6–47.0% in males, 41.9–45.9% in females (vs. 31–39.5% in males, 33–40.5% in females in *C. liolepis*); temporal region without large carinate scales (Fig. 1C) (vs. temporal region with 3–5 and 3–4 large carinate scales in males and females, respectively (Figs. 4D, 5C)); gular area with distinct transverse black bands (Fig. 1D) (vs. gular area without black bands (Figs. 4C, 5D)); shoulder pit black (Figs. 1C, 2) (vs. shoulder pit cream white to brown (Figs. 4D, 5C)); scales on ventral surface of thigh smooth (Fig. 1F) (vs. scales on ventral surface of thigh carinate (Fig. 5E)). Additionally males of *Calotes desilvai* are diagnosable from those of *C. liolepis* by having upper arm and femur longer: 49.6–50.0% and 70.3–75.0%, respectively (vs. upper arm and femur shorter: 40.3–49.3% and 57.1–69.5%, respectively); having second, third and fourth fingers longer: 29.3–30.3%, 40.6–42.2% and 42.2–44%, respectively (vs. second, third and fourth fingers shorter: 19.9–27.1%, 28.4–38.6% and 29.4–38.8%, respectively); having second, third and fourth toes longer: 30.9–31.5%, 51.2–54.3% and 63.8–64.1% respectively (vs. second, third and fourth toes shorter: 21.9–26.8%, 38–48.3% and 43.2–55.4% respectively); and possessing a shorter posterior supratympanic spine: 1.7–2.7% (vs. comparatively longer: 3.1–12.9%). Females of *C. desilvai* differ from those of *C. liolepis* by possessing 72–77 ventral scales (vs. 81–106 in *C. liolepis*).

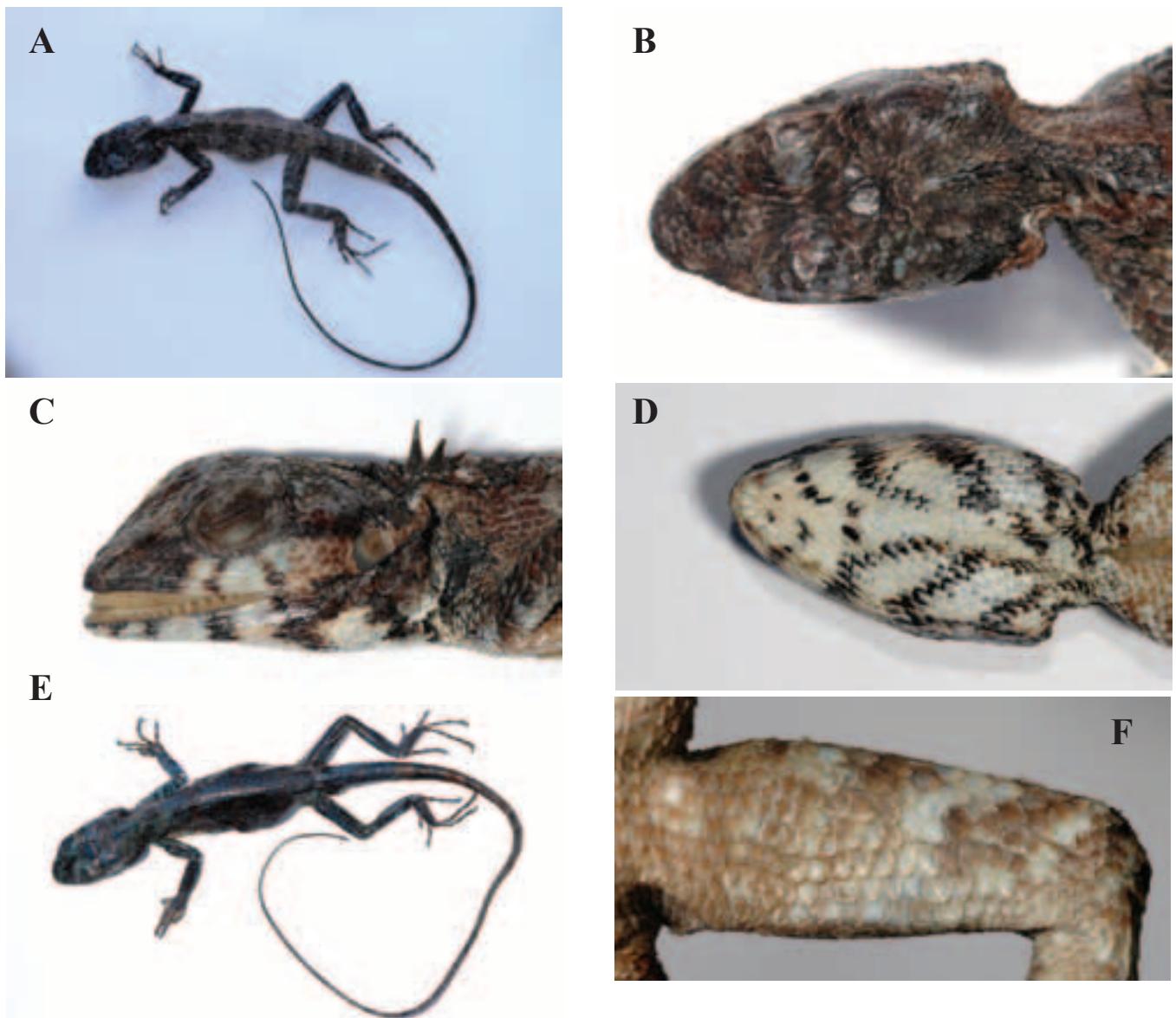


Fig. 1. *Calotes desilvai*, A–D, F, holotype male, 76.0 mm SVL, WHT 1832 and E, paratype female, 75.5 mm, WHT 5998. A, dorsal aspect; B, dorsal aspect of head; C, lateral aspect of head; D, ventral aspect of head; E, dorsal aspect; F, ventral aspect of thigh.

Description.—(see table 1 for morphometric data; scalation based on holotype male, 76.0 mm SVL, WHT 1832; variations in paratypes are given in square brackets). Head longer than broad, HL 176.6% of HW [182.5% in male, 175.7–183.1% in females]; head subtriangular in dorsal and ventral aspects (Fig. 1A, B, D) in males [oval in dorsal and ventral aspects in females (Fig. 1E)]; interorbital area concave; area between snout tip and interorbital flat. Orbital rim prominent. Supraorbital ridge with a row of large, carinate scales. Temporal region without enlarged scales (Fig. 1B, C). Area between upper temporal fossae slightly concave. Rostral scale surrounded by first supralabials and four other small scales [rostral scale surrounded by first supralabials and 3 other small scales in male; by first supralabials and 3 or 4 other small scales in females]. Cephalic scales (except for supraorbitals) irregular, smaller than dorsal scales except for mid-occipital scale, smooth or feebly carinate. Canthus rostralis with 11 [10] strongly carinate scales; two scales between nasal and rostral [2 in male, 1 or 2 in females], nasal scale undivided. Nostril oval,

laterally orientated. Nasal scales large, horizontally oval, above second and third supralabials, separated from second and third supralabials by a single row of scales and from each other by 8 scales [7 in male, 6 in females] including two scales of canthus rostralis; 7 [6 or 7 in females] scales between nostril and anterior margin of orbit; 5 [3 in male, 3 or 4 in females] scale rows between inferior medial orbit and supralabials. Superciliary scales conical, granular. Supralabials 11 [10 in male, 9 in females]; infralabials, 11 [9]. Some cephalic scales, some supralabials, some infralabials, rostral scale, dorsals and ventrals each with 1–9 [1–18 in male, 1–8 in females] pores, some pores with a sensory seta; rostral scale with 5 [7 in male, 6–12 in females] pores. Tympanum rounded. Dorsinuchal crest with 12 [13 in males, 9 in females] spines up to level of axilla, posterior to which spines reduce gradually in size to strongly keeled scales at base of tail. Supratympanic spines in two distinct clusters, each with a larger medial spine; length of anterior supratympanic spine (S1) 4.7%, length of posterior spine (S2) 2.7% of head length [S1 = 6.5%,

Table 1. Measurements (as a percentage of head length; head length itself is given as a percentage of SVL), of holotype male, paratype male and two paratype females of *Calotes desilvai*, and 18 males and 12 females of *Calotes liolepis* (see measured material for specimen data).

	males						females					
	<i>Calotes liolepis</i>			<i>Calotes desilvai</i>			<i>Calotes liolepis</i>			<i>Calotes desilvai</i>		
	range	mean	s.d.									
Snout-vent length	272.1 – 308.3	291.1	10.5	296.9 – 317.2	307.0	14.4	321.6 – 347.5	327.3	9.3	298.4 – 323.8	311.1	17.9
Head length (% SVL)	32.4 – 36.8	34.4	1.2	28.8 – 31.9	30.6	0.9	31.5 – 33.7	32.6	1.5	30.9 – 33.5	32.2	1.9
Head width	49.8 – 61.1	55.2	3.4	56.6 – 54.7	55.7	1.3	52.9 – 62.2	55.9	2.9	54.6 – 56.9	55.7	1.6
Dorsal head width	42.3 – 48.7	46.1	2.1	48.7 – 48.8	48.7	0.1	44.7 – 50.0	48.1	1.7	47.4 – 49.2	48.3	1.2
Nostril-eye length	18.2 – 22.4	20.8	1.0	21.6 – 21.9	21.7	0.2	20.5 – 26.5	23.0	1.5	22.5 – 23.8	23.1	0.9
Snout length	8.1 – 12.5	10.5	1.5	10.2 – 11.6	10.9	1.0	7.7 – 14.1	12.1	1.8	13.0 – 14.6	13.8	1.1
Eye diameter	25.6 – 30.7	28.1	1.5	28.4 – 29.7	29.1	0.9	28.8 – 34.8	31.3	2.0	28.9 – 30.8	29.8	1.4
Tympanum width	11.6 – 15.4	13.4	1.1	13.4 – 14.5	13.9	0.8	11.6 – 14.9	12.7	0.1	12.3 – 14.1	13.1	1.3
Longest nuchal spine	11.6 – 24.5	18.1	3.7	19.5 – 19.8	19.7	0.2	8.1 – 12.2	10.5	1.5	9.7 – 13.4	11.6	2.6
Upper-arm length	40.3 – 49.3	43.9	3.1	49.6 – 50	49.8	0.3	42.7 – 53.6	48.6	3.8	48.2 – 49.2	48.7	0.7
Lower-arm length	47.3 – 59.5	53.3	3.5	52.3 – 54.3	53.3	1.4	51.4 – 66.5	57.3	4.7	54.1 – 54.9	54.5	0.6
Finger 1 length	13.5 – 18.6	15.4	1.5	18.1 – 19.5	18.8	1.0	15.1 – 19.8	17.4	1.4	19.0 – 22.7	20.8	2.6
Finger 2 length	19.9 – 27.1	23.4	2.2	29.3 – 30.3	29.7	0.6	23.9 – 31.0	26.4	2.4	25.5 – 36.2	30.8	7.6
Finger 3 length	28.4 – 38.6	32.2	2.6	40.6 – 42.2	41.4	1.1	31.0 – 40.5	35.9	3.8	36.4 – 43.2	39.8	4.9
Finger 4 length	29.4 – 38.8	33.1	2.8	42.2 – 44.0	43.1	1.2	32.4 – 41.9	36.9	2.5	36.8 – 45.4	41.1	6.1
Finger 5 length	17.9 – 27.5	21.9	2.1	27.2 – 29.7	28.4	1.8	21.0 – 27.0	23.9	2.0	23.7 – 27.0	25.3	2.2
Femur length	57.1 – 69.5	63.7	4.3	70.3 – 75.0	72.6	3.3	53.8 – 72.1	64.5	5.1	63.2 – 73.0	68.1	6.9
Tibia length	62.0 – 75.0	67.2	3.7	71.5 – 75.9	73.6	3.1	69.3 – 77.9	71.5	3.3	69.2 – 75.1	72.1	4.2
Toe 1 length	13.2 – 19.5	15.5	1.6	18.4 – 18.5	18.4	0.1	15.5 – 18.7	16.9	1.1	17.8 – 18.2	18.0	0.2
Toe 2 length	21.9 – 26.8	23.9	1.6	30.9 – 31.5	31.1	0.4	22.8 – 31.5	26.9	3.1	29.2 – 34.0	31.6	3.4
Toe 3 length	38.0 – 48.3	42.3	2.9	51.2 – 54.3	52.2	2.2	44.6 – 52.0	46.5	2.8	49.4 – 54.6	52.0	3.7
Toe 4 length	43.2 – 55.4	48.4	3.6	63.8 – 64.1	63.9	0.2	49.0 – 56.1	50.9	2.7	55.7 – 62.2	58.9	4.5
Toe 5 length	31.0 – 39.5	34.76	2.8	42.6 – 47.0	44.8	3.1	33.0 – 40.5	36.4	2.1	41.9 – 45.9	43.9	2.9
Axilla–groin distance	144.2 – 171.3	159.1	8.8	168.1 – 193.4	180.7	17.8	177.9 – 201	185.3	9.1	174.7 – 183.8	179.2	6.4
Snout–axilla length	119.7 – 143.4	129.3	6.6	137.1 – 186.2	161.5	34.7	129.2 – 146.7	140.9	12.0	129.2 – 134.4	131.8	3.7
Tail length	640.7 – 789.3	710.7	44.3	750.0 – 750.0	750.0	0.0	708.1 – 862.9	780.4	63.3	806.3 – 854.1	830.2	33.7
Anterior supratympanic spine length	5.7 – 17.4	11.0	5.2	4.7 – 6.5	5.6	1.2	2.0 – 6.7	4.3	1.8	1.2 – 3.2	2.2	1.5
Posterior supratympanic spine length	3.1 – 12.9	7.12	3.0	1.7 – 2.7	2.2	0.7	2.0 – 4.6	3.1	0.9	1.6 – 2.0	1.8	0.2
Maximum head width	46.8 – 71.0	62.7	6.0	56.6 – 58.8	57.6	1.4	55.0 – 61.1	58.6	3.0	59.5 – 58.1	58.8	1.0
Head depth	37.7 – 55.3	49.0	3.6	48.8 – 51.7	50.3	2.0	46.4 – 55.2	51.5	2.4	47.4 – 53.0	50.2	3.9

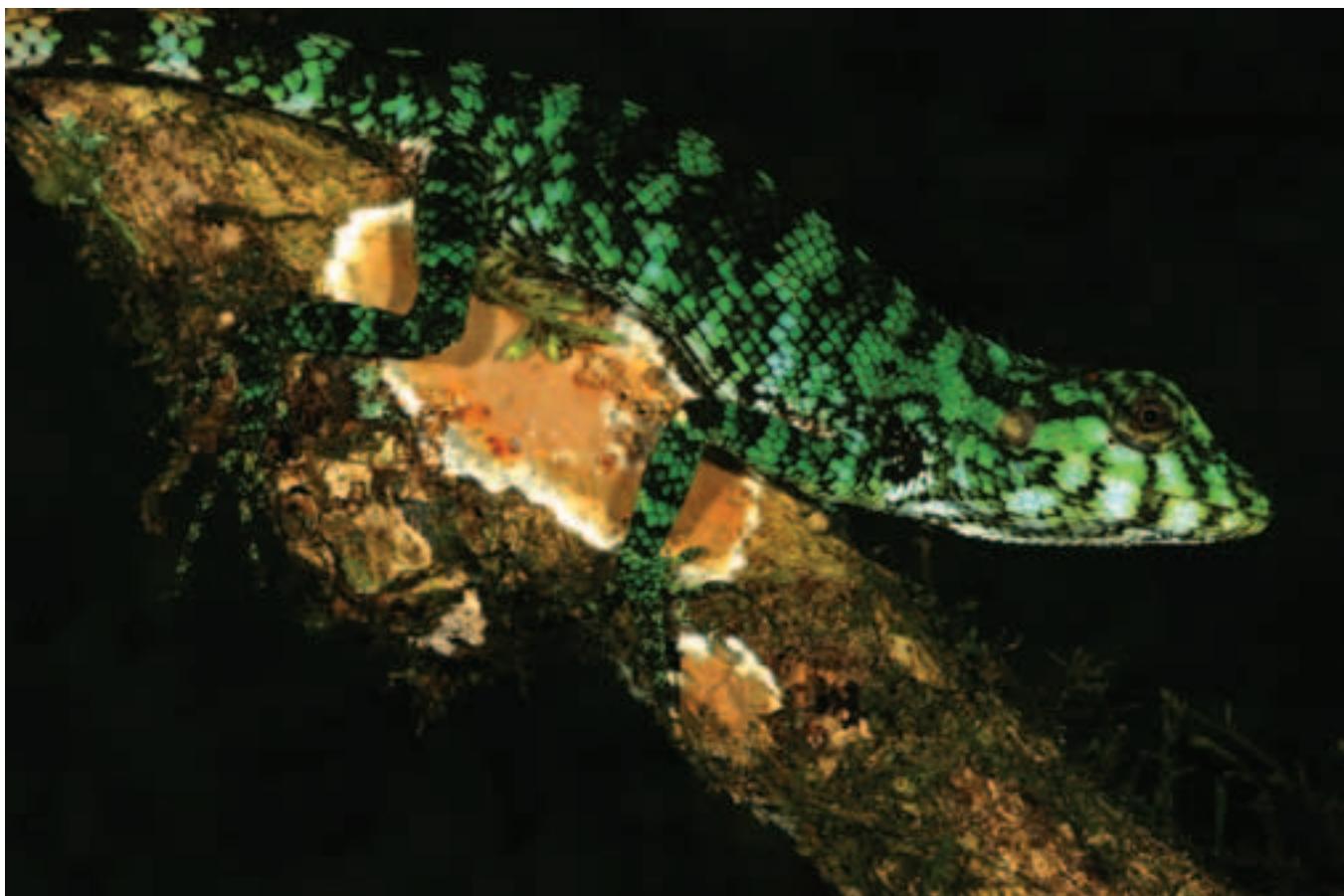


Fig. 2. *Calotes desilvai*, paratype female, 75.5 mm SVL, WHT 5998: dorsolateral view, in life.

$S2=1.7\%$ in male, $S1=3.1-3.2$, $S2=1.6-2.0\%$ in females]. $S1$ surrounded by 5 and $S2$ by 6 [$S1$ by 4, $S2$ by 6 in male, $S1$ by 2–4, $S2$ by 5 or 6 in females] small acute scales. Mental scale seven-sided [hexagonal in male, hexagonal or seven-sided in females], longer than wide, longer than length of rostral scale. A single pair of post-mentals, smaller than mental, in contact with first and second infralabials [in contact with first infralabial]. Gular sac reduced [absent in females]. Gular scales carinate (Fig. 1D), subequal to ventrals, rhombic, set in regular series in males, smaller than lateral body scales. A black shoulder pit present (Figs. 1C, 2).

Body subtriangular in section in males [subtriangular or suboval in females]. Body scales (except mid-dorsal series) slightly larger than ventrals, smooth (Fig. 1A; see also Fig. 2). Scales of the 5 scale rows bordering mid-dorsal row point backwards [4 rows in male, 5 and 2 in females]; other lateral body scales point backwards and downwards; ventral scales uniform, strongly carinate.

Caudals strongly carinate. Base of tail markedly swollen in males [not swollen in females]. Scales on tail base enlarged, those of upper median row largest, more distinctly keeled, forming a distinct ridge in males (Fig. 1A) [scales on tail base not enlarged, similar in size to body scales in females]. Subcaudals strongly carinate. Tail rounded in cross-section. Scales on forelimbs (both upper and lower arm) feebly carinate, smaller than lateral body scales. Subdigitals

bicarinate; distal end of keels on those of palm and foot elevated, acuminate. Digits covered dorsally and laterally with elongate, carinate scales. Subdigital squamation as follows: first finger with 10 [9–12 in females], second finger with 16 [14–16 in females], third finger with 24 [22 in male, 22–23 in females], fourth finger with 25 [23 in male, 22–23 in females] and fifth finger with 17 [14 in male, 13–14 in females] scales. Scales on dorsal surface of hind limbs (thigh and tibia) feebly carinate dorsally, subequal to lateral body scales; those on ventral thigh smooth (Fig. 1F), on ventral tibia carinate, smaller. Subdigitals of pes bicarinate; subdigital squamation as follows: first toe with 10 [11 in male, 10–11 in females], second toe with 16 [15 in male, 13–15 in females], third toe with 24 [23 in male, 24 in females],



Fig. 3. Type locality of *Calotes desilvai*, Morningside Forest, eastern border of Sinharaja World Heritage Site.

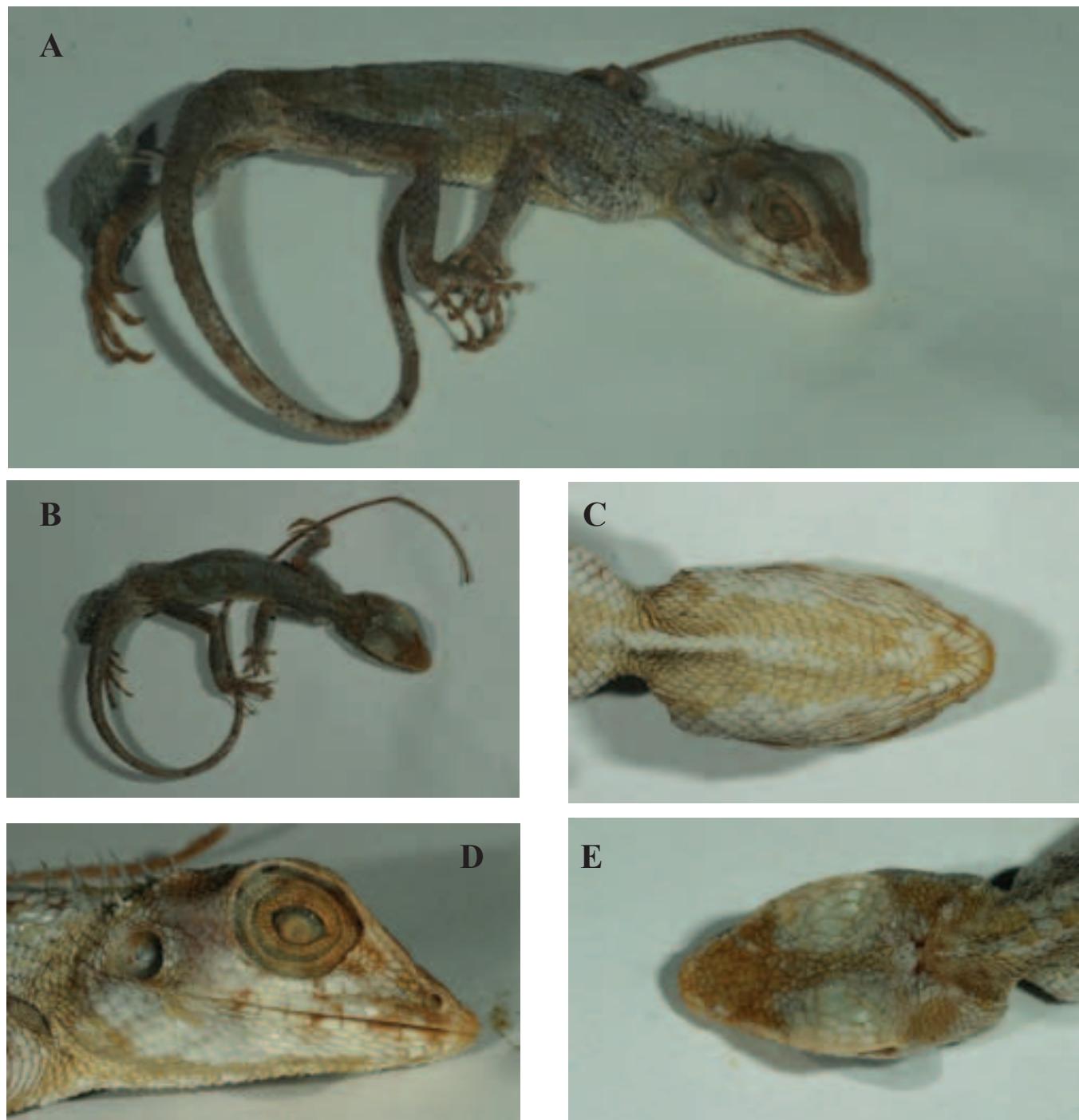


Fig. 4. *Calotes liolepis*, syntype female, mm BMNH 69.7.24.2 : A, dorsolateral aspect; B, dorsal aspect; C–E, dorsal, ventral and lateral aspects, respectively, of head.

fourth toe with 28 [29 in male, 27–29 in females], fifth toe with 19 [18 in male, 16–18 in females] scales. Some dorsal, lateral, caudal, subcaudal and limb scales with sensory pores, some pores with sensory setae. Each ventral scale with a sensory pore at posterior end, some pores with a sensory seta. Digits and claws laterally compressed, claws gently curved, pointed, each claw between two scales, one above and one below. Scales between mental and cloaca 85 [71 in male, 72–77 in females]. Scale rows at mid-body 54 [48 in male, 42–51 in females].

Digital formula: relative finger lengths, F1<F2<F5<F3<F4 [F1<F5<F2<F3<F4]. Relative toe lengths, T1<T2<T5<T3<T4.

Measurements of holotype, adult male WHT 1832, in millimetres: AG, 49.5 ; DHW, 12.5; ED, 7.6; FL1, 5.0; FL2, 7.5; FL3, 10.4; FL4, 10.8; FL5, 7.6; FEL, 18.0; HD, 12.5; HL, 25.6; HW, 14.5; LAL, 13.4; LS, 5.0; MHW, 14.5; NE, 5.6; S1, 1.6; S2, 0.7; SVL, 76.0; SN, 2.6; TL1, 4.7; TL2, 7.9; TL3, 13.1; TL4, 16.4; TL5, 10.9; TAL, 192.0; TBL, 18.3; UAL, 12.8 (Fig. 1A).

Colour in life. – (based on paratype female, 75.5 mm SVL, WHT 5998). Base colour bright “luminous” green. Some lateral scales ashy blue. Body with four black, irregular, broad bars, partially interrupted with green blotches. Two narrower black bands on neck. Two black bands between tympanum and posterior orbit, reaching first band on neck. Three lighter

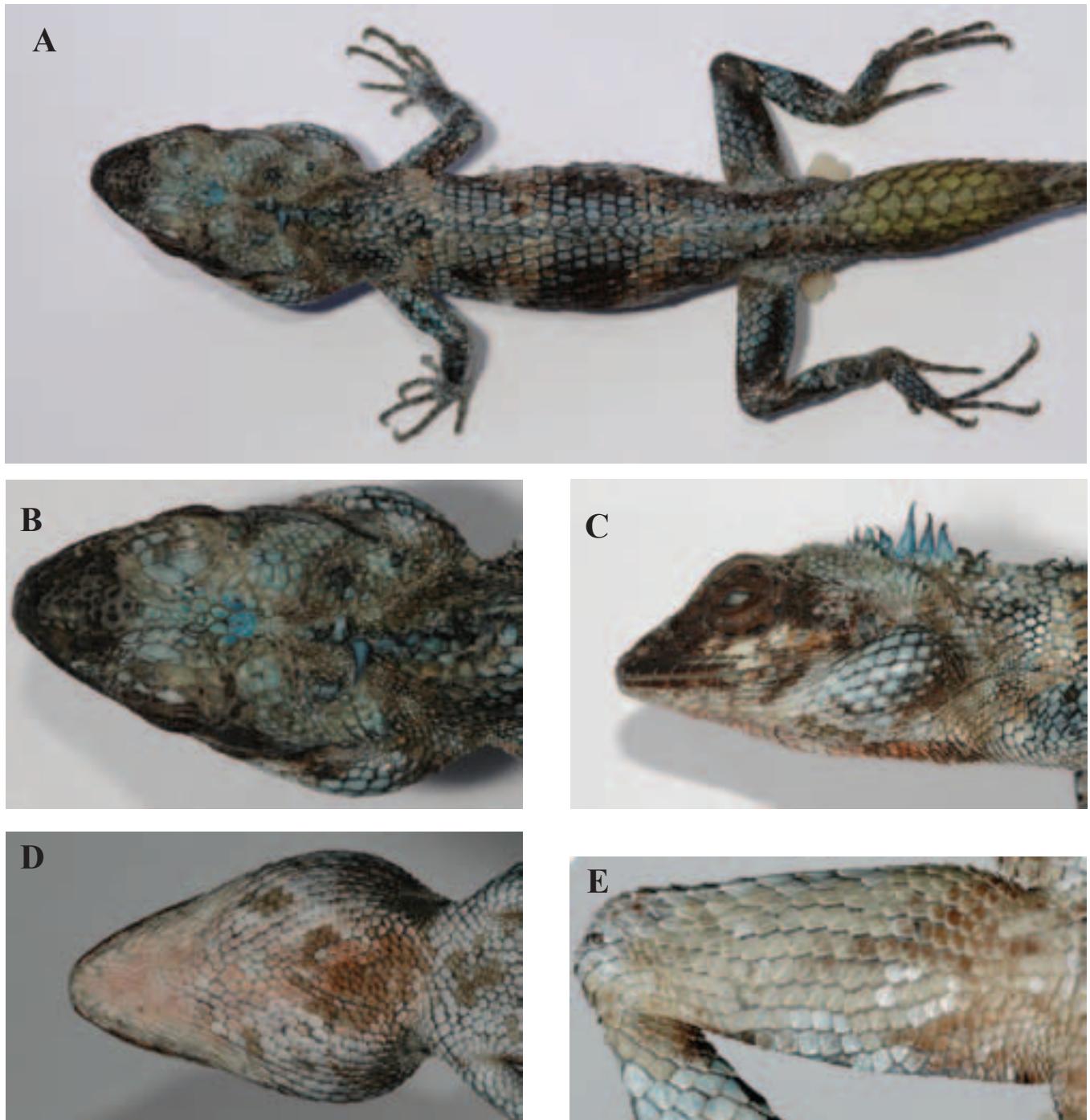


Fig. 5. *Calotes liolepis*, male 91.6 mm SVL, WHT 6229: A, dorsal aspect; B–D, dorsal, lateral and ventral aspects, respectively, of head; E, ventral aspect of thigh.

blotches under eye (bluish nearer eye), outlined in black. A black band extends from eye, below canthus rostralis, to first supralabial. Gular area lighter, with 10 transverse black bands. Eyelids brown. Tympanum brown with yellowish centre. Shoulder pit black. Fore and hind limbs each with seven or eight black cross-bars. Fingers and toes with black cross-bars. Tail with about 18 transverse black bands (see Fig. 2).

Colour in alcohol. – (based on holotype male about 7 years after preservation, 76.0 mm SVL, WHT 1832). Base colour olive brown. Some lateral scales bluish, marked by four broader black bands on body and two less distinct narrow bands on neck. A black band extends from post-orbital area to above tympanum; a

broader, chocolate-brown band extends from level of axilla to under eye. Area below eye lighter, with three vertical black bands. Snout, cheek and dorsal head darker, interspersed with lighter scales. Gular area lighter, with 10 diagonal black lines. Eyelids dark brown. Tympanum bluish brown with brown centre. Shoulder pit black. Fore and hind limbs each with about 7 black cross-bars. Fingers and toes with black cross-bars. A few ashy-blue scales scattered on lighter areas of hind limbs. Tail with about 15 dark transverse bands (see Fig. 1A–D).

Colour of female (based on paratype female, about nine months after preservation, 75.5 mm SVL, WHT 5998). Base colour “luminous” green. Some lateral scales on body ashy

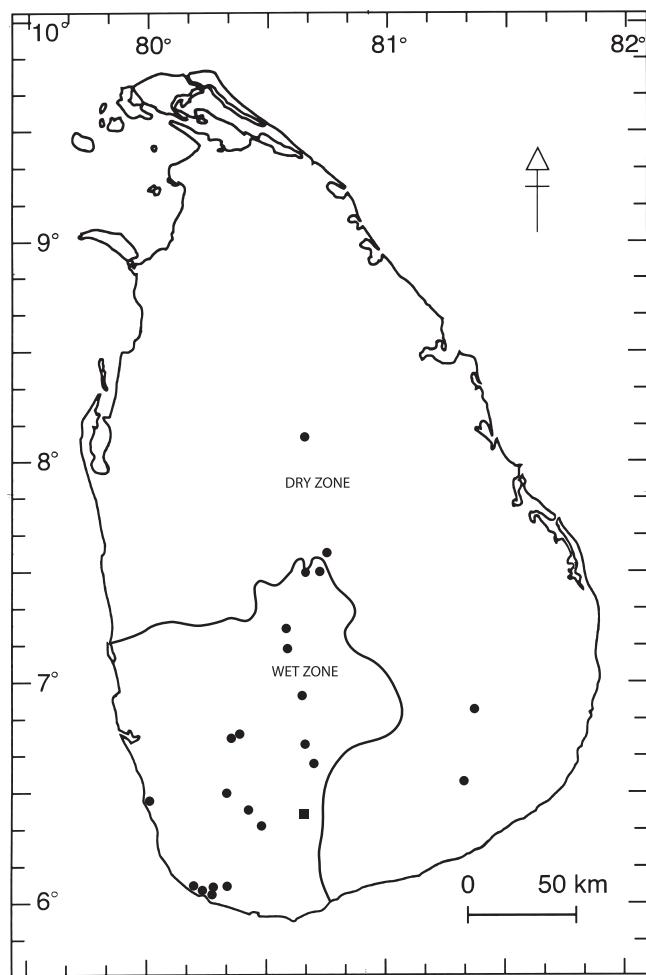


Fig. 6. Map of Sri Lanka illustrating the distribution of *Calotes liolepis* (solid circles) and *Calotes desilvai* (solid square), based on material examined in this study.

blue. Body marked by 4 broad, irregular black bars centred with greenish patches in mid-dorsal area. Two narrow transverse bands dorsally on neck. Two black stripes from posterior orbit across tympanum to first band on neck. Three light blotches under eye, somewhat bluish nearer to eye. A black bar extends from eye below canthus rostralis to first supralabial. Gular area lighter, with 10 transverse black bands. Eyelids brown. Tympanum brown with yellowish centre. Shoulder pit black. Fore and hind limbs each with seven or eight black cross-bars. Fingers and toes with black cross-bars. Tail with about 18 transverse black bands (Fig. 1E).

Etymology. – The species epithet is an eponym Latinized in the genitive singular, honouring Anslem de Silva, founder of the Amphibia and Reptile Research Organisation (ARROS) and patron of herpetology in Sri Lanka for more than the past three decades.

Distribution. – *Calotes desilvai* is known only from the type locality, Morningside Forest Reserve (1,080 m alt.) and adjacent forest, over a range of ~10 km² at the eastern border of Sinharaja World Heritage Site (Fig. 3).

Natural history notes. – We observed egg-bearing females at the type locality in February, 2004. Female paratype WHT

5998, 75.5 mm SVL, had two creamy-white eggs measuring 16.2×8.9 mm and 16.5×8.5 mm. This lizard was observed only on tree trunks 2–5 m above ground between 9 and 15 h. It is restricted to areas of dense, undisturbed forest, being absent from secondary forest and scrub habitats.

Calotes desilvai is sympatric in its type locality with the agamids *Otocryptis wiegmanni* Wagler, 1830, *Cerataphora erdleni* and *C. karu* Pethiyagoda & Manamendra-Arachchi, 1998, all of which are endemic to Sri Lanka. We recorded *C. desilvai* only from undisturbed, closed-canopy forest at Morningside. *Calotes liolepis* however, inhabits all forest types, including home gardens and rubber plantations; we even observed this species on shade trees in tea plantations.

The conservation status of *C. desilvai* is discussed in a separate paper (Bahir & Surasingha, 2005: this volume).

DISCUSSION

Sri Lankan *Calotes* have received significant attention in the literature (Boulenger, 1890, 1891; Deraniyagala, 1931, 1953; Günther, 1864, 1872; Taylor, 1953; Erdelen, 1984, 1986; Manamendra-Arachchi & Liyanage, 1994; Smith, 1935). The last species to be described from the island however, was *C. ceylonensis* (Müller, 1887). No previous treatments have involved a sample representative of all or almost all of the key habitats and vegetation types found in the island. While some previous workers (e.g. Taylor, 1953) noted important differences between individuals of some species, the sample size available was too small to establish whether these were intraspecific variations occurring randomly across the species, or whether they represented characters consistent across distinct, reproductively isolated populations.

Calotes desilvai is diagnosable from other Sri Lankan *Calotes* by several consistent characters, as follows (see also Table 2). It is distinguished from *C. calotes* and *C. versicolor* by having the lateral body scales pointing downwards and backwards (vs. lateral body scales pointing upwards and backwards). It differs from *C. ceylonensis* by having a distinct nuchal crest and lateral body scales directed backwards and downwards (vs. nuchal crest poorly defined and lateral body scales directed entirely backwards). It may also be distinguished from *C. nigrilabris* and *C. liocephalus* by having two distinct clusters of supratympanic spines (vs. a single continuous row of spines above and behind tympanum, and supratympanic spines absent, respectively). While *C. desilvai* is distinguished from its closest congener, *C. liolepis* by its longer limbs and digits, and its distinctly shorter posterior supratympanic spine (see Diagnosis), the two species are unambiguously separated also by principal component and hierarchical cluster analyses using a normalised set of nine measurements (see Figs. 7, 8; Tables 3–5). Cluster analysis shows a similarity of 33.07 % (Fig. 7; Table 3).

Smith (1935) recognized four species groups in *Calotes* (viz., the *C. cristatellus* group; the *C. microlepis* group; the *C.*

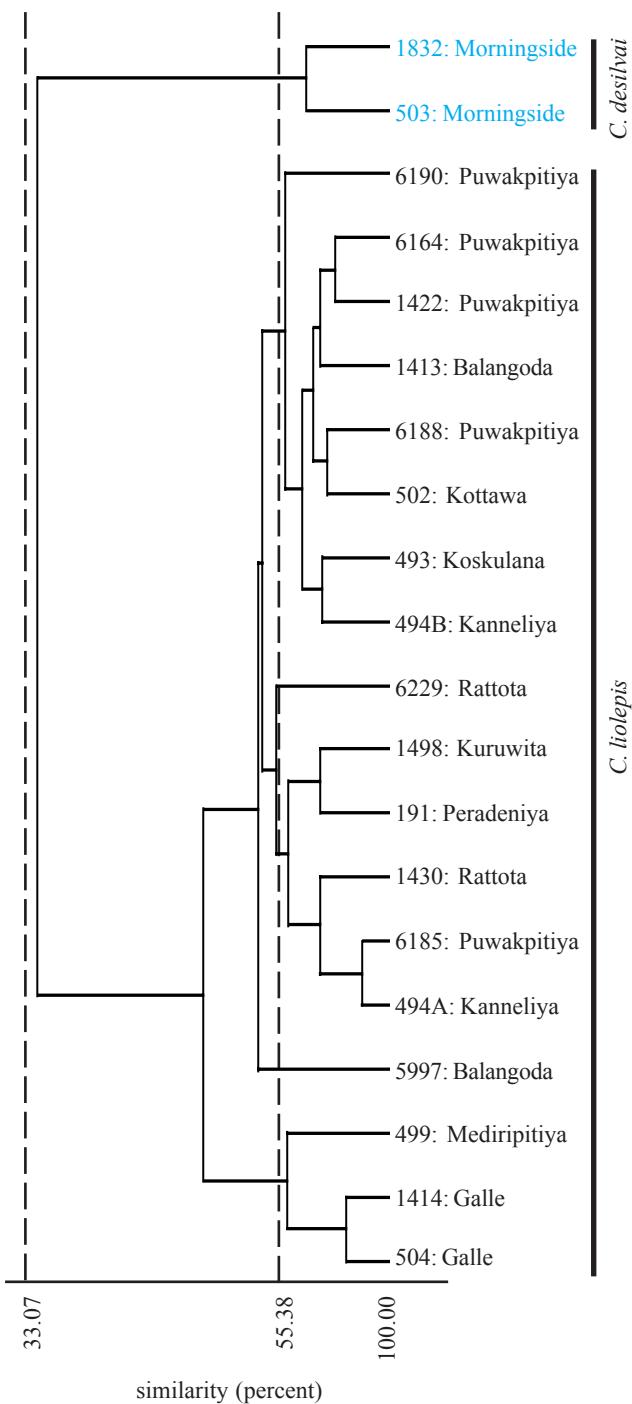


Fig. 7. Hierarchical cluster analysis using 9 measurements (see Table 1) of 2 male *Calotes desilvai* and 18 male *C. liolepis* shows a similarity of 33.07% between them. See Table 3 for numerical values.

versicolor group; and the *C. liocephalus* group). He included all the endemic Sri Lankan species, i.e., *C. nigrilabris*, *C. liocephalus*, *C. ceylonensis* and *C. liolepis* in his *C. liocephalus* group, together with *C. andamanensis* Boulenger, 1891, a species restricted to the Western Ghats mountains of southern India (Ishwar & Das, 1998; Das, 1999). All these species share a common set of characters: "Scales on the sides of the body pointing backwards or backwards and downwards. The head is comparatively short and the cheeks of the adult are always swollen. There is a triangular pit or curved fold in front of the shoulder. The tail in the fully-

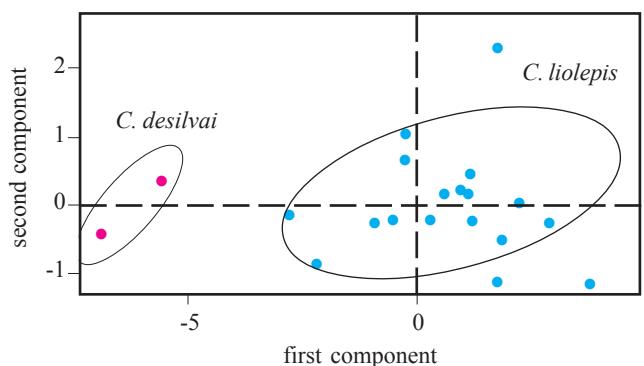


Fig. 8. Principal component analysis based on 9 metric variables normalised to head length, of 2 male *Calotes desilvai* and 18 male *Calotes liolepis* (ellipses indicate 95-percent confidence boundary).

grown male is strongly swollen at the base, the scales on that part of it being thickened, those of the upper median row forming a ridge" (Smith, 1935: 182–183). Macey et al.'s (2000) molecular phylogenetic analysis (in which *C. andamanensis* was, however, not included) supports Smith's (1935) grouping. *Calotes desilvai* exhibits all the characters of Smith's *C. liocephalus* group except that the cheeks in this species are not as markedly swollen as in the others.

In observations made in the course of ~ 15 visits to Morningside (the only locality from which it has been recorded) in the period 1997–2004, we noted that *Calotes desilvai* is exceedingly rare. Because of its rarity and obvious endangerment, we restricted our collections to four specimens, two of each sex, as we felt this to be the minimum sample necessary for a reliable description of the species. Extensive searches showed *C. desilvai* to be absent in the lowland forests that surround the Morningside plateau, in which it is replaced by *C. liolepis*. Sampling of agamid lizards across Sri Lanka (see Manamendra-Arachchi & Liyanage, 1994; Pethiyagoda & Manamendra-Arachchi, 1998; Bahir & Surasinghe, 2005) has shown *C. desilvai* to be present only at Morningside, material from which is poorly represented in older collections, e.g. at NMSL and BMNH: we think it unlikely therefore that material of *C. desilvai* could be present in such collections.

Calotes desilvai is the third recently-discovered agamid lizard that is more or less restricted to Morningside Forest. *Calotes liolepis* occurs in the surrounding areas, at elevations lower than about 850 m. The highly restricted range and habitat of *C. desilvai* underlines yet again the need for urgent conservation measures to be taken to secure this important low-elevation cloud forest. While the adjacent Sinharaja World Heritage Site has been relatively well explored, the value of this small forest area on its eastern border has only recently begun to be appreciated. Fresh exploration of this unique habitat in the past decade has led to the discovery of seven new species of frogs (Fernando & Siriwardana, 1996; Manamendra-Arachchi & Pethiyagoda, 2001, 2005; Meegaskumbura & Manamendra-Arachchi, 2005), two agamid lizards (Pethiyagoda & Manamendra-Arachchi, 1998), a gecko (Batuwita & Bahir, 2005) and three freshwater crabs (Ng &

Table 2. External morphological character variation in Sri Lankan *Calotes* based on (for specimen details see Measured Material and Comparative Material).

character	<i>C. calotes</i>	<i>C. versicolor</i>	<i>C. ceylonensis</i>	<i>C. liolepis</i>	<i>C. desilvai</i>	<i>C. liocephalus</i>	<i>C. nigrilabris</i>
lateral body-scale orientations	upwards and backwards	upwards and backwards	backwards	downwards and backwards	downwards and backwards	downwards and backwards	downwards and backwards
shoulder pit	present	absent	present	present	present	present	present
supratympanic spines	single continuous row	two clusters	two clusters	two clusters	two clusters	absent	single continuous row
size of ventral scales relative to dorsals	similar	smaller	smaller	smaller	smaller	smaller	similar
Scales on ventral thigh	keeled	keeled	smooth	keeled	smooth	smooth	keeled

Table 3. Euclidean distance, average linkage and amalgamation steps in hierarchical cluster analysis of nine metric characters (see Materials and Methods) normalised to head length, in males of *Calotes leolepis* and *C. desilvai* (see also Fig. 7).

step	number of clusters	similarity level	distance level	clusters joined	new cluster	number of observations in new cluster
15	5	77.23	0.101	2 15	2	6
16	4	74.65	0.112	1 2	1	14
17	3	73.89	0.115	1 11	1	15
18	2	63.49	0.161	1 4	1	18
19	1	33.07	0.296	1 19	1	20

Table 4. Within-cluster sum of squares and distance from centroid in the final partition of clusters using nine metric characters (see Materials and Methods) normalised to head length, in males of *Calotes leolepis* and *C. desilvai* (see also Fig. 7).

	number of observations	within-cluster sum of squares	average distance from centroid	maximum distance from centroid
Cluster 1	15	0.076	0.068	0.121
Cluster 2	5	0.046	0.091	0.132

Tay, 2001; Bahir & Ng, 2005), all restricted to this forest and its environs. More species are expected to be added to this list, including species of angiosperms (Gunatilleke et al., 2005).

For its area, Morningside appears to possess a remarkably rich and endemic fauna and flora within an area already celebrated on both counts (Gunatilleke et al., 2005). The primary threat to this forest is that it is surrounded by lands to which title is not clear, making them susceptible to encroachment and land-use change. In 2004, the Land Reform Commission leased out for tea cultivation a large extent of forest land adjoining the reserve, which action was cancelled only after this activity was publicized by the Wildlife Heritage Trust. Even as we write, however, expanses of neighbouring

Table 5. Eigenvectors and eigenvalues of the correlation matrix for the principal components analysis in Fig. 8, using 9 metric variables normalised to head length, of 2 male *Calotes desilvai* and 18 male *C. liolepis*.

variable	eigenvectors	
	PC 1	PC 2
Upper-arm length	0.062000	0.982532
Finger length 1	0.360638	-0.037521
Finger length 2	0.369424	0.013353
Finger length 3	0.375251	0.004579
Femur length	0.321491	0.083772
Toe length 2	0.314662	0.011647
Toe length 3	0.360088	-0.074651
Toe length 5	0.335682	-0.011452
Toe length 4	0.379598	-0.142012

	eigenvalue	difference	proportion	cumulative
PC 1	6.45854	5.45415	0.717616	0.71762
PC 2	1.00440	0.52067	0.111600	0.82922
PC 3	0.48373	0.10724	0.053748	0.88296

privately-owned forest are being cleared for tea and cardamom cultivation.

Morningside provides a landscape and biota with obvious potential for nature-based tourism. It is important however, that such inevitable development be carefully planned in advance so as to minimize its impact and assure genuine sustainability, noting that cloud-forest habitats are extremely sensitive to even relatively minor disturbances, as evidenced by the serious recent decline in habitat quality at Horton Plains National Park in Sri Lanka's central highlands (Werner, 2001; pers. obs.). Given the low human presence in the Morningside area, this site represents a unique opportunity set against formidable threats, presenting a stimulating challenge to conservation planners and managers.

COMPARATIVE MATERIAL

Calotes liolepis Boulenger, 1885. Measured material – male (91.6 mm SVL) (WHT 6229), Midlands Estate near Rattota, 07°31'N, 80°44'E, alt. 915 m; male (89.2 mm SVL) (WHT 1430), Halgolla

near Rattota, 07°31'N, 80°40'E, alt. 610 m; male (80.8 mm SVL) (WHT 502), female (64.8 mm SVL) (WHT 491B), female (66.8 mm) (WHT 495), female (65.9 mm SVL) (WHT 491A) Kottawa, 06°06'N, 80°20'E, alt. 60 m; male and female (79.8 mm SVL and 69.8 mm SVL) (WHT 499A-B respectively), Mederipitiya, 06°21'N, 80°29'E, alt. 365 m; female (76.6 mm SVL) (WHT 192), Batadomabalena near Kuruwita, 06°47'N, 80°23'E, alt. 460 m; male (74.6 mm SVL) (WHT 1414) female (63.1 mm SVL) (WHT 1415), Richmond Hill near Galle, 06°04'N, 80°13'E, alt. 15 m; female (68.8 mm SVL) (WHT 489), Hapugala near Galle, 06°05'N, 80°12'E, alt. 15 m; female (59.5 mm SVL) (WHT 176), Dimbula near Kotagala, 06°57'N, 80°38'E, alt. 1220 m; two males (72.1 mm SVL and 71.2 mm SVL) (WHT 494A, 494B), Kanneliya, 06°15'N, 80°20'E, alt. 150 m; male (81.3 mm SVL) (WHT 191), Peradeniya, 07°15'N, 80°35'E, alt. 457 m; male (87.0 mm SVL) (WHT 5997), Bogawantalawa-Balangoda road near Udugama, 06°44'N, 80°41'E, alt. 810 m; male (84.3 mm SVL) (WHT 1413), Balangoda, 06°39'N, 80°42'E, alt. 450 m; male (81.6 mm SVL) (WHT 1498), Warnagalla near Kuruwita, 06°46'N, 80°22'E, alt. 25 m; male (72.6 mm SVL) (WHT 504), Navinna near Galle, 06°04'N, 80°16'E, alt. 15 m; male (78.0 mm SVL) (WHT 493), Koskulana near Panapola, 06°26'N, 80°27'E, alt. 460 m; five males (86.8 mm SVL, 79.2 mm SVL, 65.3 mm SVL, 90.5 mm SVL and 87.4 mm SVL (WHT 1422, WHT 6164, WHT 6190, WHT 6185 and WHT 6188 respectively) Puwakpitiya, Knuckles, 07°34'N, 80°45'E, alt. 450 m; female (79.9 mm SVL) (WHT 6177), Ritigala, 08°07'N, 80°40'E, alt. 400 m; female (73.4 mm SVL) (WHT 6162), Kumaradola Group, Moneragala, 06°53'N, 81°22'E, alt. 400 m; three females 79.1 mm SVL, 77.4 mm SVL and 75.6 mm SVL (WHT 6177, WHT 6186 and 6184 respectively). Others – female (57.6 mm SVL) (WHT 6230), Beruwala, 06°28'N, 79°58'E, alt. 5 m; female (56.5 mm SVL) (WHT 508), Ambuluwawa near Gampola, 07°10'N, 80°33'E, alt. 915 m; female (61.1 mm SVL) (WHT 479), Karapitiya near Galle, 06°04'N, 80°14'E, alt. 10 m.

Calotes calotes (Linnaeus, 1758). Male (85.0 mm SVL) (WHT 108), Laggala, Knuckles, 07°33'N, 80°44'E, alt. 1220 m; female (110.5 mm SVL) (WHT 107), Induruwa, Ratnapura, 06°45'N, 80°26'E, alt. 150 m; male (123.0 mm SVL) (WHT 616), Koskulana near Panapola, 06°25'N, 80°27'E, alt. 460 m.

Calotes versicolor (Daudin, 1802). Male (95.0 mm SVL) (WHT 165), Mousakanda, Knuckles, 07°34'N, 80°42'E, alt. 915 m; male (81.5 mm SVL) (WHT 105), Pallegama, Knuckles, 07°32'N, 80°50'E, alt. 183 m; male (80.5 mm SVL) (WHT 384), Peradeniya, 07°15'N, 80°35'E, alt. 457 m; male (86.0 mm SVL) (WHT 382), Warnagalla near Kuruwita, 06°50'N, 80°27'E, alt. 760 m; female (76.2 mm SVL) (WHT 6172), Puwakpitiya, Knuckles, 07°34'N, 80°45'E, alt. 450 m; female (81.5 mm SVL) (WHT 193), Attidiya, Colombo, 06°50'N, 79°53'E, alt. 8 m.

Calotes nigrilabris Peters, 1860. Female (78.5 mm SVL) (WHT 379), Kuda-oya near Labugolla, 07°01'N, 80°44'E, alt. 1670 m; Male (100.5 mm SVL) (WHT 173A); female (79.0 mm SVL) (WHT 1773B-D), Nagrak Division, Nonpareil Estate, 06°46'N, 80°47'E, alt. 100 m.

Calotes liocephalus Günther, 1872. Male (89.0 mm SVL) (WHT 6241), Corbett's Gap, 07°22'N, 80°50'E, alt. alt. 1,000 m; (07°22'N, 80°50'E); female (90.5 mm SVL) (WHT 1667), Moray Estate, Rajamally, alt. 1,370 m (06°48'N, 80°53'E), alt. 1370 m; female (83.0 mm SVL) (WHT 106A), Mousakanda-Gammaduwa, Knuckles alt. 915 m (07°34'N, 80°42'E), alt. 915 m.

Calotes ceylonensis (Müller, 1887). Male (79.5 mm SVL) (WHT 1428), Rathugala near Bulupitiya, 07°17'N, 81°24'E, alt. 100 m; male (75.0 mm SVL) (WHT 515), Pallegama, Knuckles, 07°32'N, 80°49'E, alt. 185 m; female (78.5 mm SVL) (WHT 1427) Pallegama, near Wasgamuwa, 07°40'N, 80°59'E, alt. 50 m.

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LITERATURE CITED

- Bahir, M. M. & P. K. L. Ng, 2005. Description of ten new species of freshwater crabs (Crustacea: Decapoda: Parathelphusidae: *Ceylonthelphusa*, *Mahatha*, *Perbrinckia*) from Sri Lanka. In: Yeo, D. C. J., P. K. L. Ng & R. Pethiyagoda (eds.), Contributions to biodiversity exploration and research in Sri Lanka. *The Raffles Bulletin of Zoology*, Supplement No. 12: 47–75.
- Bahir, M. M. & T. Surasingha, 2005. A conservation assessment of the agamid lizards of Sri Lanka. In: Yeo, D. C. J., P. K. L. Ng & R. Pethiyagoda (eds.), Contributions to biodiversity exploration and research in Sri Lanka. *The Raffles Bulletin of Zoology*, Supplement No. 12: 407–412.
- Batuwita, S. & M. M. Bahir, 2005. Description of five new species of *Cyrtodactylus* (Reptilia: Gekkonidae) from Sri Lanka. In: Yeo, D. C. J., P. K. L. Ng & R. Pethiyagoda (eds.), Contributions to biodiversity exploration and research in Sri Lanka. *The Raffles Bulletin of Zoology*, Supplement No. 12: 351–380.
- Boulenger, G. A., 1885. *Catalogue of lizards in the British museum* (Natural History). Second edition. Vol. 1. Geckonidae, Eublepharidae, Uroplatidae, Pygopodidae, Agamidae. British Museum (Natural History), London. xii + 436 pp + Pl. I–XXXII.
- Boulenger, G. A., 1890. *The Fauna of British India, including Ceylon and Burma: Reptilia and Batrachia*. Taylor and Francis, London. xviii + 541 pp.
- Boulenger, G. A., 1891. On new or little known Indian and Malayan reptiles and batrachians. *Annals and Magazine of Natural History*, (6) 8: 288–292.
- Cuvier, G. L. C. F. D., 1817. *Le règne animal distribué d'après son organisation, pour servir de base à l'histoire naturelle des animaux et d'introduction à l'anatomie comparée*, Vol. 2. Deterville, Paris. i–xviii + 1–532 pp.
- Das, I., 1999. Biogeography of the amphibians and reptiles of the Andaman and Nicobar Islands. In: Ota, H. (ed.), *Tropical island herpetofauna: origin, current diversity and conservation*. Elsevier

- Science B.V., Amsterdam. Pp. 43–77.
- Daudin, F.-M., 1802. *Histoire Naturelle, générale et particulière des reptiles, ouvrage faisant suite, à l'histoire naturelle, générale et particulière composée par Leclerc de Buffon, et redigée par C. S. Sonnini*. Vol. 3. Dufart, Paris. 443 pp.
- Deraniyagala, P. E. P., 1931. Some Ceylon lizards. *Ceylon Journal of Science, section B*, **16**: 139–180.
- Deraniyagala, P. E. P., 1953. *A Colored Atlas of Some Vertebrates from Ceylon*. Tetrapod Reptilia, Vol. 2. Ceylon National Museums, Colombo. i–vii+1–101 pp., i–xi+1–35pls.
- Erdelen, W., 1984. The genus *Calotes* (Sauria Agamidae) in Sri Lanka: distribution patterns. *Journal of Biogeography*, **11**: 515–525.
- Erdelen, W., 1986. The genus *Calotes* (Sauria: Agamidae) in Sri Lanka: Clutch sizes and reproductive seasonality of *Calotes versicolor*—preliminary results. *Spixiana*, **9**: 111–115.
- Fernando, P & M. Siriwardhana, 1996. *Microhyla karunaratnei* (Anura: Microhylidae), a new species of frog endemic to Sri Lanka. *Journal of South Asian Natural History*, **2**: 135–142.
- Gunatilleke, I. A. U. N., Gunatilleke, C. V. S. & Dilhan, M. A. A. B. 2005. Ecological plant geography and conservation of the southwestern hill forests of Sri Lanka. In: Yeo, D. C. J., P. K. L. Ng & R. Pethiyagoda (eds.), Contributions to biodiversity exploration and research in Sri Lanka. *The Raffles Bulletin of Zoology*, Supplement No. **12**: 9–22.
- Günther, A. L. C. G., 1864. *The reptiles of British India*. Ray Society, London. xxvii + 452 pp., xxvi pl.
- Günther, A. L. C. G., 1872. Descriptions of some Ceylonese reptiles and batrachians. *Annals and Magazine of Natural History*, **4**: 85–88.
- Ishwar, N. M. & I. Das, 1998. Rediscovery of *Calotes andamanensis* Boulenger, 1891, and a reassessment of the type locality. *Journal of the Bombay Natural History Society*, **95**: 513–514.
- Linnaeus, C., 1758. *Systema naturae*. 12th Edition. Laurentii Salvii, Stockholm. 824 pp.
- Macey, J. R., Schulte, J. A. Larson, A. Ananjeva, N. B. Wang, Y. Rastegar-Pouyani, N. Pethiyagoda, R. & T. J. Papenfuss, 2000. Evaluating trans-Tethys migration: An example using acrodont lizard phylogenetics. *Systematic Biology*, **49**: 233–256.
- Manamendra-Arachchi, K. & S. Liyanage, 1994. Conservation and distribution of the Agamid lizards of Sri Lanka, with illustrations of the extant species. *Journal of South Asian Natural History*, **1**: 77–96.
- Manamendra-Arachchi, K. & R. Pethiyagoda, 2001. *Polepedates fastigo*, a new tree frog (Ranidae: Rhacophoridae) from Sri Lanka. *Journal of South Asian Natural History*, **5**: 191–199.
- Manamendra-Arachchi, K. & R. Pethiyagoda, 2005. The Sri Lankan shrub-frogs of the genus *Philautus* Gistel, 1848 (Ranidae: Rhacophorinae), with description of 27 new species. In: Yeo, D. C. J., P. K. L. Ng & R. Pethiyagoda (eds.), Contributions to biodiversity exploration and research in Sri Lanka. *The Raffles Bulletin of Zoology*, Supplement No. **12**: 163–303.
- Meegaskumbura, M. & K. Manamendra-Arachchi, 2005. Montane isolates and cryptic diversity: description of eight new species of shrub frogs (Ranidae: Rhacophorinae: *Philautus*) from Sri Lanka. In: Yeo, D. C. J., P. K. L. Ng & R. Pethiyagoda (eds.), Contributions to biodiversity exploration and research in Sri Lanka. *The Raffles Bulletin of Zoology*, Supplement No. **12**: 305–338.
- Moody, S. M., 1980. *Phylogenetic and historical biogeographical relationships of the genera in the family Agamidae (Reptilia: Lacertilia)*. PhD dissertation, University of Michigan, Ann Arbor. 373 pp.
- Müller, F., 1887. Funfter nachtrag zum Katalog der herpetologischen sammlung des Basler Museums. *Verhandlungen der Naturforschenden Gesellschaft in Basel*, **8**: 249–266.
- Ng, P. K. L. & W. M. Tay, 2001. The freshwater Crabs of Sri Lanka (Decapoda: Brachyura: Parathelphusidae). *Zeylanica*, **6**: 113–199.
- Peters, W., 1860. Über einiger interessante Amphibien, welche von dem durch seine zoologischen Schriften rühmlichst bekannten österreichischen Naturforscher Professor Schmarda während seiner auf mehre Welttheile ausgedehnten, besonders auf wirbellose Thiere gerichteten, naturwissenschaftlichen Reise, mit deren Veröffentlichung Hr. Schmarda genenwärtig in Berlin beschäftigt ist, auf der Insel Ceylon gesammelt wurden. *Monatsberichte der Preussischen Akademie der Wissenschaften zu Berlin*, **1860**: 182–186.
- Pethiyagoda, R. & K. Manamendra-Arachchi, 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.
- Smith, M. A., 1935. *The fauna of British India, including Ceylon and Burma. Reptilia and Amphibia*. Vol. II, Sauria. Taylor & Francis, London. xiii + 440 pp., 1 pl., 2 maps.
- Taylor, E. H., 1953. A review of the lizards of Ceylon. *University Kansas Science Bulletin*, **35**: 1525–1585.
- Wagler, J., 1830. *Natürliches System der Amphibien, mit vorangehender Classification der Säugethiere und Vögel*. JG Cotta'sche Buchhandlung, München. vii+354 pp., 9 pls.
- Werner, W., 2001. *Sri Lanka's magnificent cloud forests*. WHT Publications, Colombo. 96 pp.