



A systematic revision of *Calotes* Cuvier, 1817 (Squamata: Agamidae) from the Western Ghats adds two genera and reveals two new species

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Abstract

Lizards of the genus *Calotes* are geographically restricted to South Asia, Indo-China and parts of Southeast Asia. The greatest diversity of the genus is from the biodiversity hotspots in South Asia: Western Ghats (Peninsular India), Sri Lanka and Indo-Burma. Here, we present a systematic revision of members of the genus *Calotes* from Peninsular India using a combination of molecular phylogeny, geographical distribution and morphological characters. We show that *Calotes* from the Western Ghats is paraphyletic and consists of three major clades, one of which is widely distributed in South and Southeast (SE) Asia, while the others are restricted to Peninsular India. The Peninsular Indian clade is composed of two sister clades: *Psammophilus*, with a wider distribution and a second clade, composed of two extant species, *Calotes rouxii* and *Calotes ellioti* and two new species, all restricted to the Western Ghats region. Based on morphological differences, we retain the generic status of *Psammophilus* and assign its sister clade to a new genus *Monilesaurus* **gen. nov.** and transfer the following species, *C. rouxii* and *C. ellioti*, to this new genus. We also provide diagnoses and descriptions for two new species recognized within *Monilesaurus* **gen. nov.** In addition, *Calotes aurantolabium* from the Western Ghats was observed to be deeply divergent and to share a sister-relationship with the clade composed of *Calotes*, *Monilesaurus* **gen.**

nov., and *Psammophilus*. Based on its phylogenetic position and morphological attributes, we assign this species to a new genus *Microauris* **gen. nov.** These new discoveries highlight the evolutionary significance of the Western Ghats in housing novel lizard diversity.

Key words: Agamidae, *Calotes*, new genus, *Microauris*, *Monilesaurus*, *Psammophilus*, Western Ghats

Introduction

Lizards of the family Agamidae include around 480 species found over much of the Old World, including continental Africa, Australia and Southern Asia with some extending into the warmer regions of Europe (Uetz and Hošek 2016). Most agamid lizards occurring in the tropical forests of south and SE Asia belong to the clade Draconinae (Pyron *et al.* 2013). This clade comprises 27 genera and 214 species and thus represents about 50% of all agamid lizards (Grismer JL *et al.* 2016, Uetz and Hošek 2016). Lizards of the genus *Calotes* Cuvier, 1817, belonging to this clade include 26 species, of which six have been described in the past 10 years (Zug and Vindum 2006; Zug *et al.* 2006; Hartmann *et al.* 2013; Amarasinghe *et al.* 2014a,b; Krishnan 2008). Peninsular India, Northeast India, SE Asia and Sri Lanka represent much of the geographical range of this genus. Within these regions, the diversity of *Calotes* is concentrated in the biodiversity hotspots: Western Ghats, Sri Lanka and Indo-Burma.

Other than the description of *Calotes aurantolabium* Krishnan, 2008 and resolution of the systematic relationship of *Calotes minor* (Hardwicke & Gray, 1827; Deepak *et al.* 2015), there has been little substantial work towards resolving the taxonomy and systematics of the Western Ghats members of this genus since their original description. All the other species belonging to this genus from the Western Ghats were described before 1875 and information on most of the type specimens and appropriate type localities is lacking. Although there have been a few molecular genetic studies in recent times on agamid lizards and squamates as a whole, none of these included endemic Peninsular Indian agamids such as members of the genus *Psammophilus* Fitzinger, 1843 and endemic *Calotes* species from the Western Ghats (Honda *et al.* 2000; Macey *et al.* 2000; Pyron *et al.* 2013; Deepak *et al.* 2015; Grismer JL *et al.* 2016). In addition, studies on the widely distributed *Calotes versicolor* (Daudin, 1802) have shown that it is a species complex composed of several lineages (Zug *et al.* 2006; Huang *et al.* 2013).

The Western Ghats, a global biodiversity hotspot, is a highly heterogeneous landscape that supports large evolutionary radiations (Van Bocxlaer *et al.* 2012; Vijayakumar *et al.* 2016). In the past few years, there has been a tremendous increase in the number of species described from this region especially among amphibians and reptiles, made possible by the use of modern molecular techniques and improved sampling (e.g. Biju *et al.* 2014a,b; Vijayakumar *et al.* 2014; Deepak *et al.* 2016; Dahanukar *et al.* 2016). These studies suggest that the actual diversity of herpetofauna in Peninsular India, especially in the Western Ghats, has long been underestimated. In this paper, using extensive spatial and taxon sampling, we test for the presence of new lineages and reassess the systematic status of *Calotes* species in the Western Ghats. We aimed to locate populations of extant species and to validate their taxonomic and systematic status. The field sampling was designed to incorporate the heterogeneity in the topography and ecology of the Western Ghats as this is known to influence speciation.

Here, we present the results of a multi-criteria approach that uses molecular phylogeny, genetic distance, morphology and geographical distribution for species delimitation. Combining pre-existing data with the results of our taxon sampling, we show that *Calotes* from the Western Ghats is paraphyletic and resolve this by creating two new genera. We also re-describe all the extant species from the Western Ghats and describe two new species.

Methods

Field Sampling and specimen collection. Studies aiming to resolve the systematics of highly diverse taxa and address taxonomic problems must use multiple lines of evidence including molecular tools, morphological data as well as geography (e.g. Vijayakumar *et al.* 2014; Deepak *et al.* 2016). An emphasis in our approach is to increase taxon sampling and address the lack of knowledge of geographical distribution. We identified major hill ranges in the Western Ghats and also stratified the elevational gradient such that sampling sites could be selected in low, medium, high, and montane habitats in each hill range. We carried out extensive visual encounter surveys in each of these selected sites with multiple observers across all seasons over a period of four years. Different vegetation

types were searched both during the day and at night using existing trails. Geographical coordinates were recorded for each individual observed during sampling, which was later used for mapping distributions. We also made targeted attempts to sample individuals of extant species from their type localities.

Two to three individuals were captured from a population, but this number varied based on the encounter rate of a species. Specimens were hand captured or using a noose, especially for inaccessible individuals, like when perched high on a tree branch. One or more individuals from each population were photographed in controlled conditions to obtain details of coloration and morphological characters. Collected specimens were euthanized and fixed in 4% formaldehyde for about 24 hours. Tissues (liver/muscle) were extracted before fixing and stored in 95% ethanol. The fixed specimens were later stored in 70% ethanol and are maintained in the herpetological collection at the Centre for Ecological Sciences (CES), Indian Institute of Science (IISc). The type specimens are deposited in the collection of the Bombay Natural History Society (BNHS), Mumbai.

DNA Extraction and sequencing. We selected representative individuals that matched the descriptions of extant species from their respective type localities. To this, we added additional individuals from populations of different species from different geographical locations. In total, we selected 42 individuals for our phylogenetic analysis, which included members of the genus *Calotes* as well as representatives of other agamid genera from the Western Ghats. DNA was extracted from liver and muscle tissues for all 42 samples using the phenol-chloroform-isoamyl alcohol method (Sambrook *et al.* 1989), dissolved in 50 μ l of 0.1% TE buffer (pH 7.6–8.0, 10mM TrisHCl, 0.1mM EDTA) and stored at 4°C. The DNA was checked using a 1% Agarose gel and electrophoresed at 70V. Using the purified DNA, we generated sequences for three mitochondrial genes: 16S gene was amplified for sequencing using both the forward and reverse strands using the primers 16Sar: (5'-CGCCTGTTTATCAAAAACAT-3' and 16Sbr: 5'-CTCCGGTTTGAAGTCAGATCA-3') (Simon *et al.* 1991) respectively. ND1—(NDH-L: 5'-AAACTATTTAYYAAAGARCC-3', NDH-T: 5'-GGGTATGANGCTCGNACCCA-3', ND H-W: 5'-GGGTATGANGCTCGNATTCA-3') and ND2 (H5540: 5'-TTTAGGGCTTTGAAGGC-3', L4437b: 5'-AAGCAGTTGGGCCCATACC-3') were sequenced for a subset of the individuals. We also generated data for one nuclear gene R35 (R35F: 5'-GACTGTGGAYGAYCTGATCAGTGTGGTGCC-3', R35R: 5'-GCCAAAATGAGSGAGAARCGCTTCTGAGC-3'). We used published sequences for many extant species belonging to different genera of Draconinae and Agaminae (Appendix 1).

The PCR was carried out in 25 μ l reaction volume containing 2.5 μ l of 1X Taq buffer, 2.5 μ l of 2.5mM dNTP, 2.5 μ l of 2.5 mM of MgCl₂, 0.25 μ l each for the forward and reverse primer, 0.66 μ l of 2 units of Taq DNA polymerase, 1 μ l of extracted DNA of the sample and the volume was made up using ultrapure Milli Q water. The PCR conditions were as follows: Initial denaturation at 94°C for 3 minutes, denaturation for 35 cycles at 94°C for 50 seconds, annealing at 45°C for 1 minute, and extension at 72°C for 40 seconds. The final extension was at 72°C for 5 minutes. The amplified PCR products were checked using a 2% Agarose Gel and viewed under the AlphaDigiDoc RT2 System. The PCR samples were purified using QIAquick® PCR Purification Kit. Four genes were amplified and sequenced using a 3130xl Genetic Analyzer.

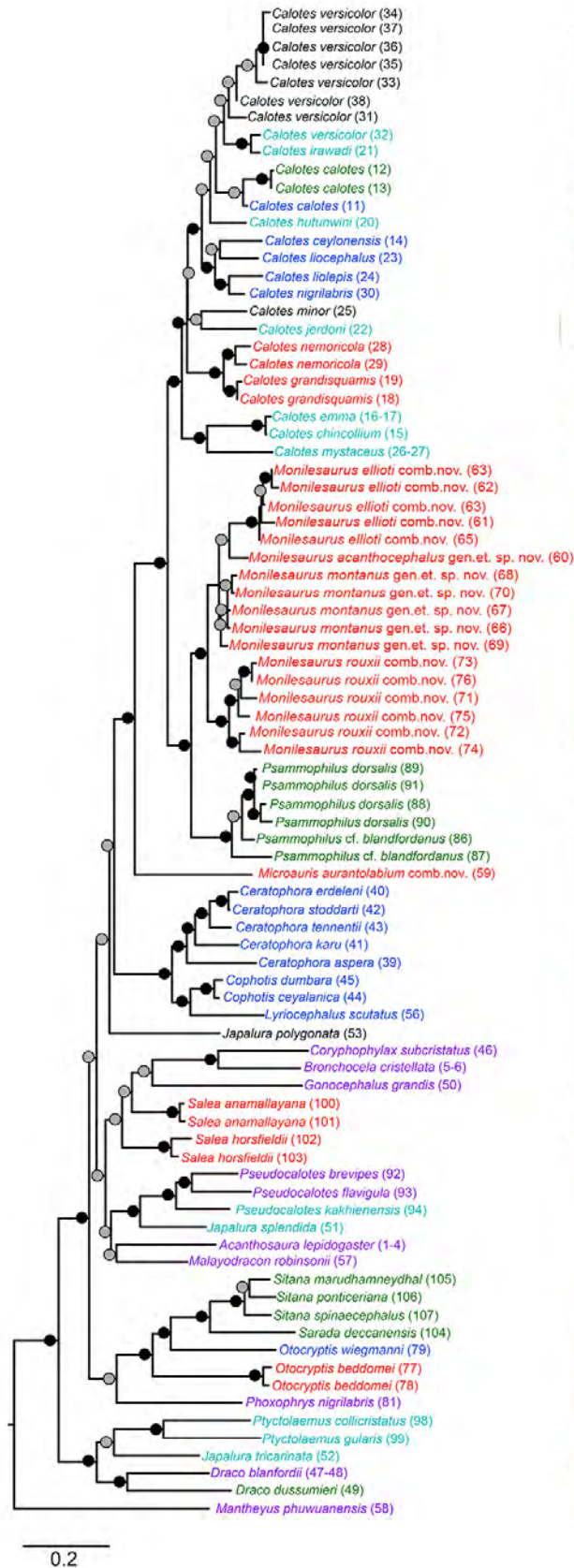
Phylogenetic analysis. We generated phylogenetic trees using both maximum likelihood (ML) and Bayesian approaches (BI). We sequenced 16S and ND1 mitochondrial DNA for most of our samples and supplemented it with some ND2 mitochondrial and R35 nuclear genes. Gene sequences were aligned using ClustalW in MEGA 5 (Tamura *et al.* 2011). The final dataset with three mitochondrial (ND1+ND2+16S) and one nuclear (R35) gene consisted of 2771bp from 96 individuals of agamid lizards including from our collection and published sequences. A partitioned, concatenated mtDNA and nuDNA (ND2+R35+16S+ND1) Maximum Likelihood (ML) tree was generated using the GUI version of RaXML (Silvestro & Michalak, 2012; Stamatakis *et al.* 2005) with bootstrap 1000 replicates in ML + rapid bootstrap settings. RaxML provides only one model of sequence evolution; therefore, we used GTR+G for all six partitions for the mtDNA and nuDNA datasets (Table 1). The program MrBayes 3.2 (Ronquist *et al.* 2012) was used to generate the Bayesian tree with default prior settings and all six partitions were assigned their optimum model as determined by PartitionFinder. Markov chains were sampled every 100 generations from a total of 1,000,000 generations. We assessed convergence by confirming that the average standard deviation of split frequencies was < 0.01 and that all the parameters had reached stationarity and had attained sufficient effective sample sizes (>200) using TRACER v1.6 (Rambaut *et al.* 2014). The first 25% (1250) of the trees were discarded as “burn-in”. Pairwise uncorrected genetic distance was determined between individuals within and among each haplotype cluster for 16S mtDNA using MEGA 5 (Tamura *et al.* 2011).

TABLE 1. Partitions and models of sequence evolution used in the Maximum Likelihood (ML) and Bayesian Analysis (BI).

Partitions	Sites	ML	BI
P1	ND2 1 st	GTR+G	GTR+I+G
P2	ND2 2 nd	GTR+G	HKY+G
P3	ND2 3 rd	GTR+G	HKY+I+G
P4	R35 1 st , 2 nd	GTR+G	K80+G
P5	R35 3 rd	GTR+G	K80+G
P6	16S, ND1 tRNAs	GTR+G	GTR+I+G

Morphology. A total of 76 individuals of agamid lizards were examined for morphological analysis. The following characters were measured with a Mitutoyo digital caliper to the nearest 0.1 mm and on the left side of the body for symmetrical characters: SVL (snout to vent length), TaL (tail length), TaW (maximum tail width, taken posterior to the vent), TaD (maximum tail height, taken posterior to the vent), HL (head length from posterior point of tympanum to the tip of the snout), JawL (from posterior point of jaw to snout tip) HW (head width at its widest point), HD (maximum head depth taken at the rear axis of the jaw), IN (internarial distance), IO (distance between anterior-most border of orbits), OrbD (maximum diameter of the orbit), NO (from posterior point of nostril to anterior point of orbit), SO (snout tip to anterior point orbit), OTym (posterior point of orbit to anterior point of tympanum), TymD (maximum diameter of the tympanum), TrL (trunk length from axilla to groin), TrW (trunk width at its widest point), PectW (pectoral width taken between left and right axilla when forelimbs are held at a right angle to the body), PelvW (pelvis width taken between left and right groin when hind limbs are held at a right angle to the body), UpArmL (upper arm length), LowArmL (lower arm length), HandL (hand length, from the wrist to the tip of the 4th finger, excluding the claw), F (length of finger taken from base of finger to the tip of the finger, excluding the claw), UpLegL (upper leg length), CrusL (crus length, from the knee to the heel), FootL (length of the foot from the heel to the tip of the 4th toe, excluding the claw), T (length of toe, taken from base of toe to the tip of the toe, excluding the claw), LongN (length of the longest nuchal spine). The following meristic data was also recorded: SL Lt/Rt (number of supralabials on the left (Lt) and right (Rt)), LongN (longest nuchal spine), IL Lt/Rt (number of infralabials on the left (Lt) and right (Rt)), MD (middorsal scales, counted from the first erect nuchal crest scale to the level above the vent), MB (circummarginal scale rows at mid body length), FLam (finger lamellae from the base of the finger to the tip) and TLam (toe lamellae from the base of the toe to the tip), Neck fold P/A (fold present (P) on neck or absent (A)), Canthal (number of canthals), Ventrals (number of ventral scales from postmental till vent), Ventrals till the fold (number of ventral scales from fold of skin on throat till vent), Hd scales (Scales of head, Keeled (Kl) or Unkeeled (UnKl)), Sn scales (Scales of snout keeled (Kl) or unkeeled (UnKl)), MB scales (Mid-body scales) keeled (Kl) or unkeeled (UnKl)), Nuchals spines (number of nuchal spines), Tmp Spines (tympanic spines in clusters, rows or isolated spines) 1stPostM (1st pair of post mental (Joined/ Separated)), Ventrals (Ventral scales keeled (Kl), partially keeled (Pkl), strongly keeled (Stkl) or unkeeled (UnKl)), Thigh scales (scales on the thigh keeled (Kl), partially keeled (Pkl), strongly keeled (Stkl) or unkeeled (UnKl)). The recorded morphometric data, range and mean of meristic characters and ratio of morphometric data for all studied specimens is provided in Appendix 2, 3 & 6. Mean and range of ratios for morphometric data is provided in Table 2. Additionally, we checked published literature and type descriptions of the known *Calotes* spp. for morphological comparisons Hardwicke & Gray, 1827; Duméril and Bibron, 1837; Gray, 1845; Jerdon, 1854; Günther, 1864; Günther, 1870; Günther, 1872; Günther, 1875; Boulenger, 1885; Biswas, 1975; Zhao & Li, 1984; Hallerman, 2000; Vindum *et al.* 2003; Bahir & Maduwage, 2005; Zug *et al.* 2006; Manthey, 2008; Krishnan, 2008; Hartmann *et al.* 2013; Amarasinghe *et al.* 2014a,b; Deepak *et al.* 2015).

Abbreviations. AKM—Ashok Kumar Mallik; BNHS—Bombay Natural History Society; CESL—Centre for Ecological Sciences Lizards; KPD—K.P. Dinesh; MNHN—National Museum of Natural History (France); NHM—Natural History Museum, London; MVP—Mrungank V. Prabhu; OTU—Operational Taxonomic Unit; SPP—Saunak P. Pal; SPV—S.P. Vijayakumar; SRC—S.R. Chandramouli; VRT—Varun R. Torsekar.



Monilesaurus rouxii comb.nov.



Microauris aurantolabium comb. nov.



Psammophilus dorsalis



Salea horsfieldii



FIGURE 1. Pruned ML phylogeny of Draconinae showing the relationship of *Calotes* and its sister clades *Monilesaurus*, *Psammophilus* and *Microauris*. Western Ghats endemics are marked in red, Sri Lankan endemics in dark blue, Indo-Burmese species in light blue and species endemic to India excluding North-east and North West are marked in green, and other wide spread species are marked black. Dark circles indicate bootstrap support >75 and light circles indicate bootstrap support <75. Insert photo: representative species of the four genera endemic to Peninsular India.

TABLE 2 A. Mean & range of ratios for female specimens.

RATIOS	<i>C. grandisquamis</i>			<i>C. cf. versicolor</i>			<i>M. montanus</i>			<i>M. ellioti</i>					
	N=1			N=3			N=4			N=3					
	MEAN	RANGE		MEAN	RANGE		MEAN	RANGE		MEAN	RANGE				
HL/SVL	0.28	0.28		0.24	0.23-0.26		0.25	0.23-0.29		0.28	0.27-0.29		0.29	0.29-0.30	
JawL/SVL	0.31	0.31		0.28	0.26-0.30		0.28	0.23-0.30		0.30	0.29-0.30		0.31	0.29-0.31	
HW/SVL	0.17	0.17		0.16	0.15-0.17		0.17	0.15-0.18		0.18	0.17-0.18		0.18	0.17-0.18	
HD/SVL	0.15	0.15		0.15	0.14-0.15		0.16	0.14-0.17		0.16	0.15-0.17		0.16	0.16-0.17	
TrL/SVL	0.50	0.50		0.52	0.49-0.55		0.46	0.45-0.49		0.50	0.49-0.52		0.49	0.46-0.51	
TaW/SVL	0.08	0.08		0.10	0.09-0.10		0.10	0.09-0.11		0.08	0.08-0.09		0.09	0.09	
TaD/SVL	0.08	0.08		0.10	0.09-0.11		0.11	0.09-0.12		0.08	0.07-0.10		0.07	0.07-0.08	
TrW/SVL	0.26	0.26		0.18	0.15-0.22		0.20	0.19-0.22		0.21	0.17-0.23		0.22	0.19-0.26	
IN/SVL	0.07	0.07		0.06	0.06-0.07		0.07	0.07		0.07	0.06-0.08		0.07	0.07	
IO/SVL	0.15	0.15		0.12	0.11-0.13		0.11	0.11		0.13	0.12-0.14		0.13	0.12-0.13	
NO/SVL	0.09	0.09		0.05	0.04-0.06		0.07	0.06-0.12		0.09	0.08-0.09		0.09	0.08-0.09	
SO/SVL	0.13	0.13		0.10	0.10-0.11		0.11	0.10-0.13		0.13	0.12-0.14		0.13	0.12-0.13	
Otyrn/SVL	0.07	0.07		0.06	0.06		0.06	0.06-0.07		0.08	0.07-0.09		0.07	0.07	
TaL/SVL	2.29	2.29		3.51	3.16-3.86		2.22	1.81-2.49		1.91	1.70-2.13		2.52	2.40-2.76	
OrbD/SVL	0.06	0.06		0.09	0.08-0.10		0.08	0.08-0.09		0.09	0.08-0.09		0.09	0.08-0.09	
TymD/SVL	0.04	0.04		0.04	0.03-0.04		0.04	0.03-0.04		0.04	0.03-0.04		0.04	0.04	
LongN/SVL	0.04	0.04		0.05	0.04-0.07		0.05	0.03-0.06		0.03	0.03		0.04	0.03-0.05	
PectW/SVL	0.16	0.16		0.14	0.13-0.14		0.15	0.12-0.17		0.14	0.13-0.16		0.14	0.13-0.14	
PelvW/SVL	0.13	0.13		0.13	0.13-0.14		0.13	0.07-0.15		0.12	0.11-0.13		0.11	0.11-0.12	
UpArmL/SVL	0.19	0.19		0.18	0.15-0.20		0.17	0.16-0.19		0.14	0.14-0.15		0.15	0.14-0.16	
LowArmL/SVL	0.16	0.16		0.19	0.15-0.21		0.17	0.15-0.19		0.16	0.15-0.17		0.17	0.16-0.18	
HandL/SVL	0.16	0.16		0.18	0.16-0.19		0.16	0.14-0.18		0.17	0.16-0.19		0.18	0.18-0.20	
(UpArmL+LowArmL+HandL)/SVL	0.51	0.51		0.55	0.49-0.58		0.51	0.48-0.55		0.48	0.46-0.49		0.50	0.47-0.53	
UpLegL/SVL	0.22	0.22		0.29	0.26-0.30		0.24	0.22-0.26		0.23	0.21-0.25		0.25	0.22-0.27	
CrusL/SVL	0.20	0.20		0.29	0.28-0.32		0.23	0.20-0.26		0.20	0.19-0.22		0.23	0.20-0.25	
FootL/SVL	0.28	0.28		0.39	0.37-0.40		0.31	0.27-0.36		0.29	0.26-0.30		0.31	0.30-0.33	
HW/HL	0.62	0.62		0.67	0.60-0.73		0.69	0.60-0.74		0.62	0.60-0.67		0.61	0.58-0.64	
(UpLegL+CrusL+FootL)/SVL	0.69	0.69		0.97	0.95-1.01		0.78	0.72-0.88		0.72	0.67-0.77		0.79	0.73-0.85	
HW/HD	1.16	1.16		1.11	1.00-1.17		1.11	1.05-1.14		1.12	1.10-1.17		1.10	1.09-1.11	
OrbD/ SO	0.46	0.46		0.86	0.86-0.87		0.74	0.68-0.78		0.66	0.58-0.71		0.66	0.63-0.70	
TymD/OrbD	0.58	0.58		0.42	0.34-0.49		0.45	0.39-0.52		0.46	0.41-0.52		0.51	0.48-0.52	
HW/JawL	0.56	0.56		0.57	0.54-0.63		0.63	0.57-0.73		0.59	0.57-0.62		0.59	0.55-0.62	
LongN/ OrbD	0.61	0.61		0.63	0.38-0.84		0.57	0.35-0.76		0.37	0.35-0.41		0.48	0.35-0.60	

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TABLE 2A. (Continued)

	<i>M. rouxii</i>			<i>M. aurantolabium</i>			<i>P. dorsalis</i>			<i>S. horsfieldii</i>		
	N=3			N=2			N=4			N=3		
	MEAN	RANGE		MEAN	RANGE		MEAN	RANGE		MEAN	RANGE	
HL/SVL	0.30	0.25-0.36		0.22	0.19-0.26		0.26	0.25-0.27		0.25	0.23-0.26	
JawL/SVL	0.28	0.27-0.29		0.24	0.18-0.30		0.34	0.32-0.35		0.30	0.29-0.31	
HW/SVL	0.19	0.17-0.22		0.14	0.12-0.17		0.23	0.22-0.24		0.17	0.15-0.18	
HD/SVL	0.15	0.14-0.16		0.15	0.15-0.16		0.14	0.13-0.15		0.16	0.15-0.17	
ThI/SVL	0.54	0.49-0.61		0.53	0.51-0.54		0.44	0.36-0.50		0.48	0.43-0.50	
TaW/SVL	0.10	0.09-0.11		0.08	0.08		0.13	0.12-0.14		0.10	0.09-0.11	
TaD/SVL	0.08	0.07-0.08		0.07	0.07		0.10	0.09-0.11		0.10	0.10	
TrW/SVL	0.19	0.16-0.22		0.22	0.20-0.25		0.25	0.22-0.31		0.21	0.17-0.28	
IN/SVL	0.07	0.06-0.08		0.06	0.06-0.07		0.07	0.06-0.08		0.06	0.04-0.07	
IO/SVL	0.14	0.12-0.17		0.13	0.13		0.12	0.12		0.12	0.12-0.13	
NO/SVL	0.07	0.05-0.08		0.08	0.07-0.10		0.07	0.07-0.08		0.07	0.07	
SO/SVL	0.12	0.10-0.15		0.12	0.10-0.14		0.11	0.10-0.12		0.12	0.11-0.12	
Otym/SVL	0.06	0.06-0.07		0.08	0.07-0.09		0.09	0.07-0.12		0.07	0.07	
TaL/SVL	2.00	1.89-2.11		1.65	1.59-1.71		1.56	1.25-1.93		1.80	1.48-2.11	
OrbD/SVL	0.10	0.08-0.12		0.08	0.07-0.09		0.09	0.08-0.09		0.06	0.06-0.07	
TymD/SVL	0.05	0.04-0.06		0.01	0.01		0.05	0.04-0.05		0.03	0.03-0.04	
LongN/SVL	0.03	0.01-0.05		—	—		—	—		0.06	0.02-0.12	
PectW/SVL	0.15	0.14-0.17		0.15	0.15-0.16		0.22	0.21-0.25		0.14	0.14-0.15	
PelW/SVL	0.11	0.10-0.13		0.11	0.11-0.12		0.17	0.15-0.19		0.14	0.13-0.14	
UpArmL/SVL	0.17	0.15-0.19		0.17	0.17-0.18		0.17	0.15-0.21		0.14	0.13-0.15	
LowArmL/SVL	0.17	0.16-0.18		0.19	0.18-0.20		0.18	0.18-0.19		0.15	0.14-0.17	
HandL/SVL	0.18	0.18-0.19		0.14	0.12-0.16		0.17	0.16-0.18		0.16	0.15-0.17	
(UpArmL+LowArmL+HandL)/SVL	0.52	0.50-0.53		0.50	0.49-0.50		0.52	0.50-0.55		0.45	0.43-0.48	
UpLegL/SVL	0.27	0.24-0.33		0.22	0.20-0.23		0.26	0.25-0.28		0.18	0.17-0.19	
CrusL/SVL	0.23	0.21-0.27		0.20	0.19-0.22		0.27	0.25-0.29		0.16	0.15-0.17	
FootL/SVL	0.33	0.29-0.40		0.23	0.19-0.26		0.30	0.28-0.31		0.25	0.24-0.25	
HW/HL	0.64	0.61-0.67		0.64	0.63-0.65		0.89	0.87-0.93		0.68	0.62-0.74	
(UpLegL+CrusL+FootL)/SVL	0.84	0.76-1.00		0.65	0.64-0.65		0.84	0.83-0.86		0.59	0.57-0.60	
HW/HD	1.24	1.18-1.43		0.94	0.80-1.08		1.58	1.43-1.81		1.05	0.92-1.26	
OrbD/ SO	0.80	0.75-0.82		0.71	0.47-0.96		0.78	0.73-0.85		0.53	0.51-0.55	
TymD/OrbD	0.50	0.45-0.57		0.17	0.14-0.19		0.52	0.49-0.54		0.56	0.53-0.59	
HW/JawL	0.69	0.61-0.83		0.60	0.56-0.64		0.68	0.64-0.75		0.56	0.52-0.62	
LongN/ OrbD	0.29	0.16-0.38								1.02	0.37-1.93	

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TABLE 2 B. Mean & range of ratios for male specimens.

	<i>C. grandisquamis</i>			<i>C. cf. versicolor</i>			<i>C. nemoricola</i>			<i>M. acanthocephalus</i>		
	N=2			N=4			N=5			N=3		
	MEAN	RANGE		MEAN	RANGE		MEAN	RANGE		MEAN	RANGE	
HL/SVL	0.29	0.28-0.30		0.24	0.22-0.28		0.27	0.25-0.28		0.29	0.25-0.28	0.29
JawL/SVL	0.32	0.31-0.34		0.30	0.28-0.33		0.30	0.28-0.33		0.32	0.22-0.33	0.31-0.32
HW/SVL	0.17	0.16-0.19		0.20	0.16-0.26		0.17	0.15-0.26		0.19	0.15-0.19	0.18-0.19
HD/SVL	0.17	0.16-0.17		0.16	0.14-0.19		0.16	0.14-0.19		0.17	0.14-0.17	0.16-0.18
TrL/SVL	0.50	0.5		0.45	0.45-0.47		0.47	0.44-0.50		0.46	0.44-0.50	0.45-0.48
TaW/SVL	0.10	0.09-0.12		0.11	0.10-0.12		0.10	0.07-0.12		0.10	0.07-0.12	0.09-0.11
TaD/SVL	0.11	0.10-0.11		0.13	0.11-0.15		0.10	0.09-0.11		0.14	0.09-0.11	0.13-0.14
TrW/SVL	0.17	0.12-0.22		0.17	0.13-0.21		0.20	0.16-0.24		0.19	0.16-0.24	0.17-0.21
IN/SVL	0.06	0.06-0.07		0.06	0.05-0.07		0.07	0.06-0.07		0.07	0.06-0.07	0.07-0.08
IO/SVL	0.14	0.12-0.15		0.11	0.10-0.11		0.12	0.11-0.14		0.14	0.11-0.14	0.13-0.16
NO/SVL	0.07	0.07		0.05	0.05		0.07	0.06-0.08		0.10	0.06-0.08	0.09-0.11
SO/SVL	0.12	0.11-0.12		0.09	0.08-0.10		0.11	0.06-0.13		0.14	0.06-0.13	0.12-0.14
Otyrn/SVL	0.08	0.07-0.08		0.06	0.06-0.08		0.06	0.06-0.07		0.08	0.06-0.07	0.08-0.09
TaL/SVL	2.05	1.96-2.15		1.57	0.91-2.23		2.15	1.78-2.36		2.99	1.78-2.36	2.96-3.03
OrbD/SVL	0.08	0.08		0.08	0.07-0.10		0.08	0.07-0.09		0.08	0.07-0.09	0.08
TymD/SVL	0.04	0.03-0.05		0.04	0.03-0.04		0.04	0.03-0.04		0.04	0.03-0.04	0.04
LongN/SVL	0.09	0.08-0.09		0.06	0.04-0.07		0.06	0.06-0.07		0.08	0.06-0.07	0.08-0.09
PectW/SVL	0.14	0.13-0.15		0.16	0.15-0.16		0.15	0.15-0.16		0.15	0.15-0.16	0.14-0.17
PelvW/SVL	0.12	0.11-0.12		0.14	0.14-0.15		0.13	0.11-0.14		0.12	0.11-0.14	0.12-0.13
UpArmL/SVL	0.18	0.16-0.19		0.16	0.14-0.17		0.16	0.14-0.19		0.15	0.14-0.19	0.14-0.15
LowArmL/SVL	0.18	0.16-0.21		0.18	0.16-0.19		0.15	0.13-0.17		0.16	0.13-0.17	0.16-0.17
HandL/SVL	0.15	0.14-0.16		0.17	0.14-0.18		0.15	0.13-0.18		0.20	0.13-0.18	0.18-0.20
(UpArmL+LowArmL+HandL)/SVL	0.51	0.49-0.53		0.50	0.48-0.53		0.47	0.44-0.48		0.50	0.44-0.48	0.50-0.51
UpLegL/SVL	0.24	0.22-0.25		0.23	0.22-0.24		0.20	0.17-0.22		0.25	0.17-0.22	0.24-0.26
CrusL/SVL	0.23	0.22-0.24		0.24	0.23-0.26		0.20	0.19-0.22		0.22	0.19-0.22	0.22-0.23
FootL/SVL	0.23	0.23-0.24		0.31	0.30-0.33		0.25	0.19-0.28		0.34	0.19-0.28	0.34-0.35
HW/HL	0.60	0.57-0.63		0.84	0.71-0.95		0.65	0.54-0.75		0.66	0.54-0.75	0.64-0.66
(UpLegL+CrusL+FootL)/SVL	0.70	0.7		0.79	0.75-0.81		0.66	0.60-0.71		0.82	0.60-0.71	0.79-0.84
HW/HD	1.05	1.01-1.10		1.22	1.12-1.32		1.11	0.95-1.16		1.11	0.95-1.16	1.05-1.15
OrbD/ SO	0.68	0.65-0.71		0.89	0.66-1.24		0.83	0.66-1.32		0.59	0.66-1.32	0.53-0.68
TymD/OrbD	0.50	0.40-0.60		0.45	0.43-0.54		0.45	0.40-0.51		0.49	0.40-0.51	0.49-0.50
HW/JawL	0.54	0.52-0.56		0.67	0.57-0.78		0.58	0.47-0.70		0.60	0.47-0.70	0.59-0.60
LongN/ OrbD	1.08	1.06-1.10		0.74	0.48-1.10		0.72	0.66-0.78		0.99	0.66-0.78	0.95-1.05

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TABLE 2 B. Mean & range of ratios for male specimens.

	<i>C. grandisquamis</i>			<i>C. cf. versicolor</i>			<i>C. nemoricola</i>			<i>M. acanthocephalus</i>		
	N=2			N=4			N=5			N=3		
	MEAN	RANGE		MEAN	RANGE		MEAN	RANGE		MEAN	RANGE	
HL/SVL	0.29	0.28-0.30		0.24	0.22-0.28		0.27	0.25-0.28		0.29	0.29	0.29
JawL/SVL	0.32	0.31-0.34		0.30	0.28-0.33		0.30	0.28-0.33		0.32	0.31-0.32	0.32
HW/SVL	0.17	0.16-0.19		0.20	0.16-0.26		0.17	0.15-0.19		0.19	0.18-0.19	0.19
HD/SVL	0.17	0.16-0.17		0.16	0.14-0.19		0.16	0.14-0.19		0.17	0.16-0.18	0.17
Trl/SVL	0.50	0.5		0.45	0.45-0.47		0.47	0.44-0.50		0.46	0.45-0.48	0.46
TaW/SVL	0.10	0.09-0.12		0.11	0.10-0.12		0.10	0.07-0.12		0.10	0.09-0.11	0.10
TaD/SVL	0.11	0.10-0.11		0.13	0.11-0.15		0.10	0.09-0.11		0.14	0.13-0.14	0.14
TrW/SVL	0.17	0.12-0.22		0.17	0.13-0.21		0.20	0.16-0.24		0.19	0.17-0.21	0.19
IN/SVL	0.06	0.06-0.07		0.06	0.05-0.07		0.07	0.06-0.07		0.07	0.07-0.08	0.07
IO/SVL	0.14	0.12-0.15		0.11	0.10-0.11		0.12	0.11-0.14		0.14	0.13-0.16	0.14
NO/SVL	0.07	0.07		0.05	0.05		0.07	0.06-0.08		0.10	0.09-0.11	0.10
SO/SVL	0.12	0.11-0.12		0.09	0.08-0.10		0.11	0.06-0.13		0.14	0.12-0.14	0.14
OtyM/SVL	0.08	0.07-0.08		0.06	0.06-0.08		0.06	0.06-0.07		0.08	0.08-0.09	0.08
TaL/SVL	2.05	1.96-2.15		1.57	0.91-2.23		2.15	1.78-2.36		2.99	2.96-3.03	2.99
OrbD/SVL	0.08	0.08		0.08	0.07-0.10		0.08	0.07-0.09		0.08	0.08	0.08
TymD/SVL	0.04	0.03-0.05		0.04	0.03-0.04		0.04	0.03-0.04		0.04	0.04	0.04
LongN/SVL	0.09	0.08-0.09		0.06	0.04-0.07		0.06	0.06-0.07		0.08	0.08-0.09	0.08
PectW/SVL	0.14	0.13-0.15		0.16	0.15-0.16		0.15	0.15-0.16		0.15	0.14-0.17	0.15
PelW/SVL	0.12	0.11-0.12		0.14	0.14-0.15		0.13	0.11-0.14		0.12	0.12-0.13	0.12
UpArmL/SVL	0.18	0.16-0.19		0.16	0.14-0.17		0.16	0.14-0.19		0.15	0.14-0.15	0.15
LowArmL/SVL	0.18	0.16-0.21		0.18	0.16-0.19		0.15	0.13-0.17		0.16	0.16-0.17	0.16
HandL/SVL	0.15	0.14-0.16		0.17	0.14-0.18		0.15	0.13-0.18		0.20	0.18-0.20	0.20
(UpArmL+LowArmL+HandL)/SVL	0.51	0.49-0.53		0.50	0.48-0.53		0.47	0.44-0.48		0.50	0.50-0.51	0.50
UpLegL/SVL	0.24	0.22-0.25		0.23	0.22-0.24		0.20	0.17-0.22		0.25	0.24-0.26	0.25
CrusL/SVL	0.23	0.22-0.24		0.24	0.23-0.26		0.20	0.19-0.22		0.22	0.22-0.23	0.22
FootL/SVL	0.23	0.23-0.24		0.31	0.30-0.33		0.25	0.19-0.28		0.34	0.34-0.35	0.34
HW/HL	0.60	0.57-0.63		0.84	0.71-0.95		0.65	0.54-0.75		0.66	0.64-0.66	0.66
(UpLegL+CrusL+FootL)/SVL	0.70	0.7		0.79	0.75-0.81		0.66	0.60-0.71		0.82	0.79-0.84	0.82
HW/HD	1.05	1.01-1.10		1.22	1.12-1.32		1.11	0.95-1.16		1.11	1.05-1.15	1.11
OrbD/ SO	0.68	0.65-0.71		0.89	0.66-1.24		0.83	0.66-1.32		0.59	0.53-0.68	0.59
TymD/OrbD	0.50	0.40-0.60		0.45	0.43-0.54		0.45	0.40-0.51		0.49	0.49-0.50	0.49
HW/lawL	0.54	0.52-0.56		0.67	0.57-0.78		0.58	0.47-0.70		0.60	0.59-0.60	0.60
LongN/ OrbD	1.08	1.06-1.10		0.74	0.48-1.10		0.72	0.66-0.78		0.99	0.95-1.05	0.99

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TABLE 2B. (Continued)

	<i>M. montanus</i>			<i>M. ellioti</i>			<i>M. rouxii</i>			<i>P. dorsalis</i>		
	N=4			N=6			N=6			N=3		
	MEAN	RANGE		MEAN	RANGE		MEAN	RANGE		MEAN	RANGE	
HL/SVL	0.29	0.28-0.31		0.29	0.28-0.31		0.29	0.29-0.30		0.25	0.24-0.26	
JawL/SVL	0.30	0.29-0.31		0.31	0.29-0.33		0.31	0.30-0.33		0.35	0.34-0.36	
HW/SVL	0.19	0.17-0.20		0.18	0.18-0.20		0.20	0.19-0.23		0.25	0.24-0.28	
HD/SVL	0.17	0.16-0.17		0.17	0.16-0.17		0.17	0.16-0.19		0.16	0.15-0.17	
Th/SVL	0.49	0.47-0.50		0.47	0.45-0.50		0.45	0.43-0.46		0.44	0.43-0.44	
TaW/SVL	0.10	0.09-0.10		0.10	0.09-0.11		0.11	0.10-0.12		0.13	0.12-0.14	
TaD/SVL	0.11	0.10-0.12		0.11	0.09-0.11		0.12	0.10-0.14		0.13	0.12-0.14	
TrW/SVL	0.17	0.16-0.18		0.17	0.15-0.21		0.17	0.15-0.21		0.26	0.25-0.26	
IN/SVL	0.07	0.07		0.07	0.06-0.08		0.07	0.06-0.07		0.06	0.05-0.07	
IO/SVL	0.13	0.12-0.14		0.13	0.13-0.14		0.13	0.12-0.14		0.12	0.12	
NO/SVL	0.09	0.09-0.10		0.09	0.08-0.10		0.08	0.07-0.08		0.07	0.06-0.08	
SO/SVL	0.13	0.12-0.14		0.13	0.12-0.14		0.11	0.11-0.12		0.11	0.11-0.12	
OtyM/SVL	0.08	0.07-0.08		0.07	0.07-0.08		0.08	0.07-0.08		0.07	0.07-0.08	
TaL/SVL	2.11	1.47-2.43		2.45	1.93-2.85		2.07	1.58-2.60		1.38	1.15-1.63	
OrbD/SVL	0.08	0.08-0.09		0.09	0.08-0.10		0.09	0.09		0.08	0.07-0.08	
TymD/SVL	0.04	0.03-0.04		0.04	0.04-0.05		0.05	0.05		0.04	0.03-0.05	
LongN/SVL	0.04	0.03-0.05		0.06	0.06		0.03	0.03-0.04		—	—	
PectW/SVL	0.13	0.13-0.15		0.14	0.13-0.15		0.15	0.14-0.16		0.22	0.21-0.23	
PelvW/SVL	0.11	0.10-0.12		0.11	0.11-0.12		0.12	0.12-0.13		0.17	0.16-0.18	
UpArmL/SVL	0.15	0.13-0.16		0.16	0.15-0.17		0.17	0.16-0.18		0.15	0.14-0.16	
LowArmL/SVL	0.17	0.16-0.18		0.19	0.17-0.20		0.19	0.18-0.21		0.17	0.16-0.18	
HandL/SVL	0.18	0.17-0.19		0.20	0.18-0.21		0.20	0.20-0.21		0.17	0.15-0.18	
(UpArmL+LowArmL+HandL)/SVL	0.50	0.48-0.53		0.55	0.52-0.58		0.56	0.54-0.59		0.49	0.44-0.52	
UpLegL/SVL	0.23	0.22-0.25		0.28	0.27-0.30		0.28	0.26-0.31		0.25	0.23-0.27	
CrusL/SVL	0.21	0.19-0.23		0.26	0.23-0.27		0.25	0.24-0.26		0.27	0.23-0.30	
FootL/SVL	0.30	0.29-0.32		0.35	0.31-0.36		0.34	0.32-0.37		0.29	0.24-0.32	
HW/HL	0.64	0.60-0.67		0.63	0.61-0.64		0.70	0.65-0.75		1.01	0.93-1.10	
(UpLegL+CrusL+FootL)/SVL	0.74	0.71-0.79		0.89	0.82-0.96		0.88	0.82-0.94		0.81	0.71-0.88	
HW/HD	1.11	1.05-1.16		1.11	1.06-1.15		1.20	1.15-1.30		1.63	1.57-1.66	
OrbD/ SO	0.64	0.56-0.72		0.71	0.66-0.74		0.78	0.75-0.82		0.66	0.66-0.67	
TymD/OrbD	0.45	0.39-0.52		0.48	0.38-0.56		0.56	0.52-0.61		0.55	0.40-0.63	
HW/JawL	0.62	0.57-0.66		0.59	0.58-0.61		0.65	0.61-0.69		0.72	0.69-0.78	
ongN/ OrbD	0.53	0.39-0.67		0.66	0.60-0.72		0.36	0.30-0.41		—	—	

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TABLE 2B. (Continued)

	<i>P. sp.</i>			<i>S. horsfieldii</i>			<i>S. anamallayana</i>			<i>D. dussumierii</i>			<i>O. beddomii</i>		
	N=1			N=2			N=3			N=1			N=3		
	MEAN	RANGE		MEAN	RANGE		MEAN	RANGE		MEAN	RANGE		MEAN	RANGE	
HL/SVL	0.25	0.25		0.28	0.26-0.30		0.27	0.25-0.27		0.20	0.20		0.23	0.22-0.24	
JawL/SVL	0.36	0.36		0.34	0.33-0.34		0.33	0.31-0.34		0.21	0.21		0.33	0.32-0.34	
HW/SVL	0.27	0.27		0.19	0.18-0.20		0.18	0.18-0.19		0.14	0.14		0.20	0.19-0.22	
HD/SVL	0.15	0.15		0.17	0.15-0.19		0.16	0.15-0.16		0.10	0.10		0.18	0.18-0.20	
TrI/SVL	0.41	0.41		0.46	0.46		0.46	0.43-0.48		0.53	0.53		0.40	0.37-0.42	
TaW/SVL	0.13	0.13		0.10	0.10-0.11		0.08	0.08		0.08	0.08		0.13	0.12-0.14	
TaD/SVL	0.13	0.13		0.12	0.11-0.13		0.11	0.10-0.12		0.06	0.06		0.15	0.14-0.15	
TrW/SVL	0.21	0.21		0.16	0.15-0.17		0.13	0.11-0.14		0.19	0.19		0.18	0.17-0.20	
IN/SVL	0.06	0.06		0.07	0.07		0.06	0.06		0.04	0.04		0.08	0.08-0.09	
IO/SVL	0.11	0.11		0.12	0.12		0.11	0.10-0.11		0.09	0.09		0.14	0.13-0.15	
NO/SVL	0.06	0.06		0.07	0.07		0.08	0.08		0.05	0.05		0.09	0.09-0.10	
SO/SVL	0.10	0.10		0.12	0.12		0.12	0.11-0.13		0.06	0.06		0.14	0.13-0.15	
Otyrn/SVL	0.08	0.08		0.08	0.08-0.09		0.08	0.07-0.08		0.05	0.05		0.09	0.09-0.10	
TaL/SVL	1.75	1.75		2.46	2.22-2.70		1.65	1.22-1.93		1.56	1.56		1.26	0.75-1.65	
OrbD/SVL	0.07	0.07		0.07	0.07		0.08	0.08-0.09		0.06	0.06		0.10	0.10	
TymD/SVL	0.04	0.04		0.04	0.04		0.04	0.04-0.05		0.03	0.03		0.10	0.10	
LongN/SVL	—	—		0.12	0.09-1.14		0.09	0.08-0.11		—	—		—	—	
PectW/SVL	0.22	0.22		0.15	0.15		0.13	0.12-0.14		0.18	0.18		0.15	0.14-0.16	
PelvW/SVL	0.17	0.17		0.16	0.13-0.20		0.11	0.10-0.11		0.09	0.09		0.13	0.12-0.14	
UpArmL/SVL	0.14	0.14		0.16	0.15-0.16		0.14	0.13-0.15		0.13	0.13		0.17	0.16-0.19	
LowArmL/SVL	0.17	0.17		0.16	0.15-0.16		0.16	0.15-0.17		0.14	0.14		0.19	0.18-0.20	
HandL/SVL	0.15	0.15		0.18	0.17-0.19		0.15	0.14-0.16		0.14	0.14		0.17	0.16-0.18	
(UpArmL+LowArmL+HandL)/SVL	0.46	0.46		0.49	0.49		0.45	0.45-0.46		0.42	0.42		0.53	0.50-0.56	
UpLegL/SVL	0.23	0.23		0.20	0.20		0.20	0.19-0.20		0.17	0.17		0.36	0.35-0.36	
CrusL/SVL	0.25	0.25		0.19	0.18-0.19		0.18	0.18		0.17	0.17		0.34	0.34-0.35	
FootL/SVL	0.25	0.25		0.30	0.29-0.31		0.26	0.26-0.27		0.19	0.19		0.43	0.42-0.43	
HW/HL	1.07	1.07		0.68	0.66-0.70		0.69	0.65-0.71		0.72	0.72		0.88	0.79-0.92	
(UpLegL+CrusL+FootL)/SVL	0.74	0.74		0.69	0.67-0.71		0.64	0.64-0.65		0.53	0.53		1.12	1.12-1.13	
HW/HD	1.72	1.72		1.12	1.08-1.16		1.18	1.10-1.25		1.37	1.37		1.10	1.07-1.13	
OrbD/ SO	0.73	0.73		0.56	0.54-0.58		0.71	0.63-0.76		0.91	0.91		0.73	0.70-0.77	
TymD/OrbD	0.60	0.60		0.53	0.51-0.56		0.49	0.43-0.54		0.47	0.47		0.62	0.57-0.66	
HW/JawL	0.74	0.74		0.56	0.54-0.59		0.55	0.53-0.57		0.68	0.68		0.62	0.57-0.66	
LongN/ OrbD	—	—		1.67	1.33-2.02		1.10	0.95-1.30		—	—		—	—	

Results

This study shows that members of the genus *Calotes* from the Western Ghats are paraphyletic in nature. We identified three well supported clades within the Western Ghats, a *Calotes* clade, a clade composed of members of genus *Psammophilus* and a third clade of endemic small to medium sized agamid lizards including *Calotes ellioti*, *Calotes rouxii* Duméril & Bibron, 1837 and two new lineages (Fig. 1). Based on their phylogenetic position and morphology, we assign members of this third clade to a new genus *Monilesaurus* **gen. nov.** (Fig. 1). This new genus is sister to the other Peninsular Indian endemic genus *Psammophilus* and together they are sister to the widespread *Calotes* clade distributed in South and SE Asia (Fig. 1). *Calotes aurantolabium* was recovered as sister to the clade composed of *Calotes*, *Psammophilus* and *Monilesaurus* **gen. nov.** (Fig. 1). Based on its phylogenetic position, we designate *Calotes aurantolabium* as a new genus *Microauris* **gen. nov.** Both ML (Fig. 1) and Bayesian (BI) trees (Appendix. 4) show high node support for the relationships of these genera. The larger clade including these four genera (*Calotes*, *Psammophilus*, *Monilesaurus* **gen. nov.** and *Microauris* **gen. nov.**) is sister to the Sri Lankan clade composed of the genera *Ceratophora* Gray, 1834, *Cophotis* Peters, 1861, and *Lyriocephalus* Merrem, 1820 (Fig. 2).

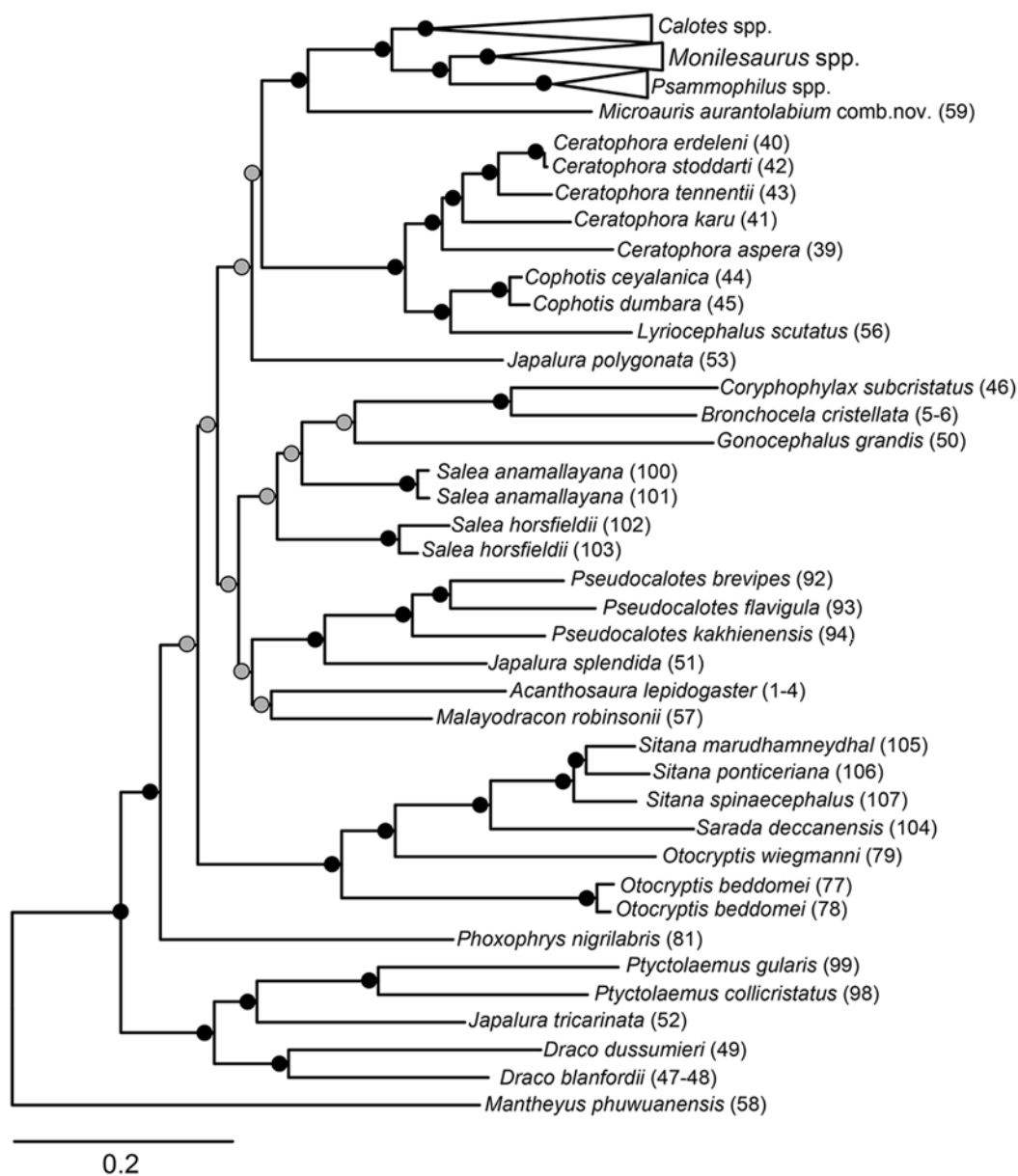


FIGURE 2. ML phylogeny for Draconinae showing the relationship of most of the Indian genera with other draconine genera distributed in Sri Lanka, South-east Asia, Indo-China and Indo-Burma. Dark circles indicate bootstrap support >75 and light circles indicate bootstrap support <75.

Our analysis also revealed new lineages belonging to *Monilesaurus* **gen. nov.** that could be differentiated along multiple axes including genetic distance, morphology, phylogenetic position and geography. Here, we choose to describe two of these lineages that can be easily separated using the above criteria. Extant members of the genus *Monilesaurus* **gen. nov.**, *M. ellioti* and *M. rouxii*, are widespread across the Western Ghats (Fig. 3). We found *M. ellioti* to be distributed across the central and southern Western Ghats (13–8 N) and *M. rouxii* from the northern to the southern Western Ghats (19–10 N). Along with the gradient in distribution, there are also distinct haplotype clusters within the species and significant genetic variance among members of these species (Fig. 1 and Appendix 5).

Between genera, genetic differences calculated (*p*-distance) using the 16S mitochondrial gene shows that *Microauris* differs from *Calotes* by 11–15%, from *Monilesaurus* by 11–14%, and from *Psammophilus* by 13–15%. *Calotes* differs from *Monilesaurus* by 5–11%, and from *Psammophilus* by 7–12%; *Monilesaurus* differs from *Psammophilus* by 4–7% (Appendix 5). Within species, genetic differences calculated (*p*-distance) using the 16S gene show variation of 0–5% for *Calotes versicolor* Daudin, 1802, 0–1% for *Calotes calotes*, Linnaeus, 1758, 0% for *Calotes grandisquamis* Günther, 1875, 2% for *Calotes nemoricola*, Jerdon, 1853, 0–2% for *Monilesaurus ellioti*, 0–1% for *Monilesaurus montanus* **sp. nov.**, 1–3% for *Monilesaurus rouxii*, 0–1% for *Psammophilus dorsalis*, 0% for *Salea anamallayana* (Beddome, 1878) and 1% for *Otocryptis* Wagler, 1830 (Appendix 5).

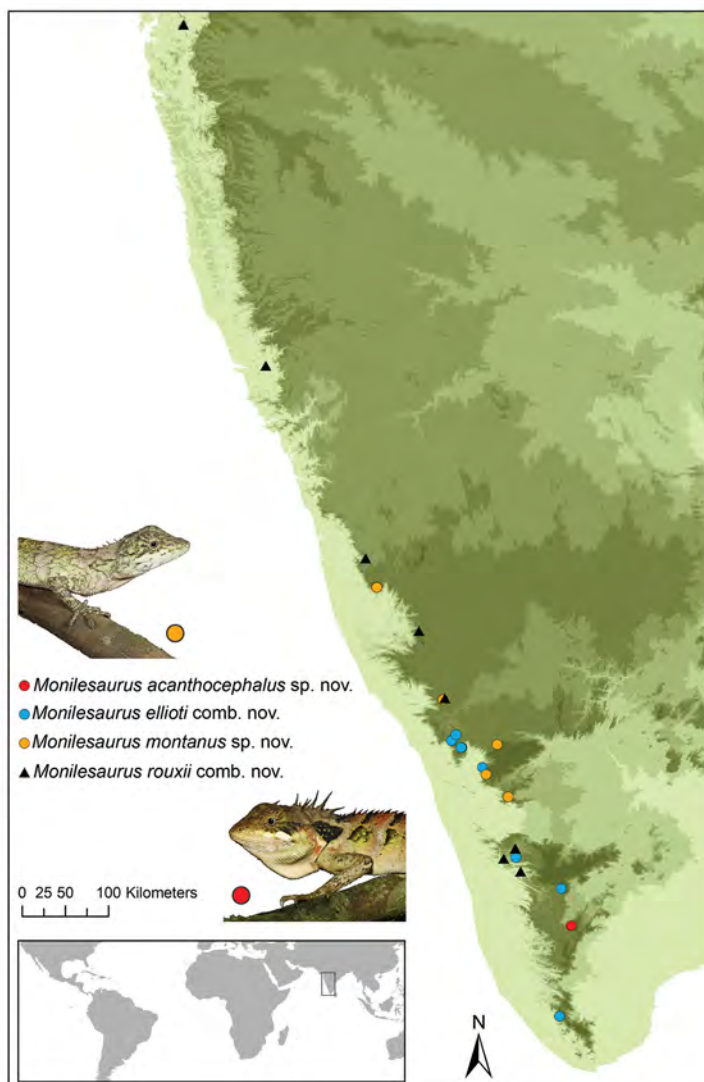


FIGURE 3. Map showing distribution of members of *Monilesaurus* gen. nov. across the Western Ghats, India. Coloured symbols indicate selected sampling localities.

The southern Western Ghats has higher richness (12 species, 4 endemics) of agamid species than the rest of the Western Ghats; with the two new species described here, the Western Ghats has a total of sixteen species.

Genus description

Calotes Cuvier, 1817

The genus *Calotes* Cuvier, 1817 with the type species *Lacerta calotes* Linnaeus, 1758 belongs to the subfamily Draconinae of the family Agamidae, containing 26 species. The geographical distribution of this genus is largely restricted to South Asia and Indo-china, except for one isolated species *Calotes nigriplicatus* Hallermann, 2000 found in Ambon Island in Indonesia. The greatest diversity of the genus is in the Western Ghats and Sri Lanka. Four species of *Calotes* (*C. grandisquamis*, *C. nemoricola*, *Calotes* cf. *versicolor*, *Calotes calotes*) are known from the Western Ghats of which two are endemic to this region.



FIGURE 4. Lateral photograph showing live coloration of A. adult female *C. calotes* and B. adult male *C. cf. versicolor*.

Diagnosis. Medium to large sized agamids with a relatively broader head; dorsal and lateral scales uniform, arranged in rows of backwardly pointed scales; dorsal and nuchal crest more or less developed; groups or rows of spines from eye to above tympanum; often an antehumeral skin fold or pit present covered with small scales; gular sac usually present; tympanum naked; tail long and slender, usually swollen and rounded at the base in males; no preanal or femoral pores.



FIGURE 5. Lateral photograph showing live coloration of A. adult male *C. grandisquamis* and B. adult male *C. nemoricola*.

Distribution. Lizards belonging to the Genus *Calotes* are widely distributed across Iran, Afghanistan, Bhutan, Bangladesh, Maldives, Nepal, India, Pakistan and Sri Lanka as well as southern China; parts of Myanmar, Thailand, Laos, Cambodia, Vietnam, Peninsular Malaysia and parts of Indonesia. Moreover, *Calotes versicolor* has been introduced into Kenya, Borneo, Sulawesi, Seychelles, Mauritius, Oman and Florida (USA) (Das *et al.* 2008; Manthey, 2008; Uetz and Hošek, 2016).



FIGURE 6. Lateral photograph showing live coloration of A. adult male *Monilesaurus rouxii* **comb. nov.** and B. adult male *Monilesaurus ellioti* **comb. nov.**

Taxonomic groups. Smith (1935) separated members of the genus *Calotes* into four distinct groups, I. *C. cristatella* group, II. *C. microlepis* group, III. *C. versicolor* group, and IV. *C. liocephalus* group, each composed of multiple species and another group composed of two dwarf species based on their morphological similarities. Later, Moody (1980) separated the genus into four different genera, namely *Bronchocela* Kaup, 1827 (group I of Smith), *Dendragama* Doria, 1888, *Pseudocalotes* Fitzinger, 1843 (group II of Smith) and *Calotes* (group III, IV and the two dwarf species of Smith). Most of the *Calotes* species occurring in the Western Ghats belong to the *Calotes versicolor* group of Smith (1935) except *Calotes rouxii* and *Calotes ellioti*, which belong to the dwarf group. Here, we transfer these two species to the new genus *Monilesaurus* **gen. nov.** In the present study, we follow Smith's species groups for taxonomic accounts and morphological comparisons. Since Smith, there have been various new additions to the genus *Calotes* and to the *Calotes versicolor* group. In this study, we compare each individual species only with members of their own group.

***Calotes versicolor* group.** Members of the *C. versicolor* group are characterized by a medium to large adult body size; body more or less compressed, dorsal and lateral scales large, uniform, smooth or feebly keeled and oriented postero-dorsally; antehumeral fold absent; dorsal scales larger than the ventrals except in *C. calotes* where it is equal to or slightly smaller than the ventrals; nuchal and dorsal crest well developed, continuous, at least till behind the shoulders; postorbital spine absent except in *C. emma* Gray, 1845; supratympanic spines in form of paired patches or as a single longitudinal series of spines (Fig. 4 & 5). For taxonomic comparisons, we add the recently designated *C. minor* to Smith's *C. versicolor* group (See Deepak *et al.* 2015).



FIGURE 7. Lateral photograph showing live coloration of A. adult male *Monilesaurus acanthocephalus* **gen. et sp. nov.** and B. adult male *Monilesaurus montanus* **sp. nov.**

Content. *Calotes bachae* Hartmann, Geissler, Poyarkov, Ihlow, Galoyan, Rödder & Böhme, 2013; *C. bhutanensis* Biswas, 1975; *C. calotes*; *C. ceylonensis* Müller, 1887; *C. chincollium* Vindum, 2003; *C. desilvai* Bahir & Maduwage, 2005; *C. emma*; *C. grandisquamis*, *C. hutunwini* Zug & Vindum, 2006; *C. irawadi* Zug, Grown, Schulte & Vindum, 2006; *C. jerdoni* Günther, 1870; *C. liocephalus* Günther, 1872; *C. liolepis* Boulenger, 1885; *C. versicolor*, *C. manamendrai* Amarasinghe & Karunarathna, 2014; *C. maria* Gray, 1845; *C. medgoensis* Zhao & Li, 1984; *C. minor*; *C. mystaceus* Duméril & Bibron, 1837; *C. nemoricola*, *C. nigrilabris* Peters, 1860; *C.*

nigriplicatus Hallermann, 2000 and *C. pethiyagodai* Amarasinghe, Karunarathna, Hallermann, Fujinuma, Grillitsch & Campbell, 2014.

Diagnosis. All the species belonging to this group can be differentiated from the other groups of *Calotes* based on the combination of the following characters: From members of the genus *Monilesaurus* **gen.nov.**, they can be easily distinguished morphologically based on a larger adult size (vs. smaller); dorsal and lateral scales rows directed posterodorsally, much larger in size (vs. posteroventrally, smaller in size); dorsal and lateral scales larger than ventrals, except in *C. calotes* (vs. not larger than ventrals) (Fig. 4–5 vs 6–7) and absence of antehumeral fold (vs. presence of a well developed antehumeral fold) (Fig. 10). From members of the genus *Psammophilus*, group they can be distinguished by the presence of compressed body shape (vs. depressed) (Fig. 4–5 vs 8a); absence of an antehumeral fold (vs. antehumeral fold present) (Fig. 10f vs 10g); lateral scales much larger (vs. smaller); presence of well developed nuchal crest (vs. reduced) and lesser number of midbody scale rows, less than 60 (vs. scale rows higher in number, more than 80). From *Microauris* **gen. nov.** by having a relatively large tympanum (Fig. 9a vs 9b); scales on head large uniform shield like (vs. small, sub-triangular) (Fig. 10b vs 10d).



FIGURE 8. Lateral photograph showing live coloration of A. adult male *Psammophilus dorsalis* and B. adult female *Microauris aurantolabium comb. nov.*

Calotes calotes (Linnaeus, 1758)

Lacerta calotes—Linnaeus, 1758. Syst. Nat. 10th ed. 1758: 207.

Iguana calotes—Laurenti 1768. Syn. Rept. 1768: 49.

Agama calotes—Daudin 1802. Hist. Nat. Rept. iii.1802: 361.

Calotes calotes—Lönnerberg 1896. Bih. Svensk. Vet. Akad. Stockholm, xxii. 1896:15.

Original description. Linnaeus, C. 1758. Systema naturae per regna tria naturae, secundum classes, ordines, genera, species, cum characteribus, differentiis, synonymis, locis. Tomus I. Editio decima, reformata. Laurentii Salvii, Holmiae. 10th Edition, 1758: 207.

Taxonomic comments. *Calotes calotes* was described based on specimens collected from ‘Zeylona’ (Sri Lanka). This species is currently known to commonly occur in the wet zones of Sri Lanka and dry zones of southern India. Smith (1935) reported this species from the Nicobar Islands but this was not included in later works (Harikrishnan *et al.* 2010). The original description by Linnaeus was a two-line description, which was translated by Amarasinghe *et al.* (2009). Our analysis shows 1% genetic variance (in the 16S gene) between the Sri Lankan and the Peninsular Indian population of *Calotes calotes*. This suggests that these species moved between the dry zones in Peninsular India and Sri Lanka.

Material examined. CESL 037 adult female collected from Peppara Wildlife Sanctuary, Kerala; CESL 374 adult male collected from Marayoor, Kerala and BNHS 378 adult male collected Chatikulam, Sri Lanka. Details of collection locality, specimen voucher and GenBank accession number in Appendix 1.

Diagnosis and comparison. A medium to large sized *Calotes* characterized by the posterodorsal orientation of lateral scales; antehumeral pit indistinct; 30–35 midbody scale rows; nuchal and dorsal crest continuous, nuchal crest composed of long lanceolate spines; dorsal spines smaller, gradually diminishing in size, extending beyond the midbody; a row of 8–9 compressed supratympanic spines, divided into two groups; dorsal and lateral scales large, smooth or feebly keeled, ventral scales strongly keeled, mucronate, equal to or slightly larger than laterals; paired postmentals, first pair separated by 1 to 2 median scales; 21–24 subdigital lamellae under fourth finger, 27–29 subdigital lamellae under fourth toe; 10–12 supralabials and 9–11 infralabials; uniform, bright green above, with 5–6 thin white transverse stripes, often continuing on the tail as indistinct bands; a bright red horizontal stripe across the orbit; posterior part of the tail dull brown; ventrally pale green; juveniles bright green, white transverse stripes indistinct.

From other members of Smith’s *C. versicolor* group (*C. versicolor*, *C. nemoricola*, *C. grandisquamis*, *C. minor*, *C. maria*, *C. jerdoni*, *C. emma* and *C. mystaceus*) *C. calotes* can be distinguished by a combination of the following characters: smaller body size: adult SVL 73.6–96.8 mm, n=3 (vs. *C. nemoricola*, adult SVL 112–134.8 mm, n=7; and *C. grandisquamis*, adult SVL 110.0–136.5 mm, n=5); 30–35 midbody scale rows (vs. 38–45 in *C. versicolor*, n=9, 36–43 in *C. nemoricola*; 58–63 in *C. maria*; 45–57 in *C. jerdoni*; 49–65 in *C. emma*; 48–58 in *C. mystaceus* and 48–60 in *C. minor*); ventral scales equal to or slightly larger than laterals (vs. ventral scales smaller than laterals in *C. nemoricola*, *C. grandisquamis*, *C. versicolor*, *C. minor*, *C. maria*, *C. jerdoni*, *C. emma* and *C. mystaceus*); crescent-shaped patch of granular scales in front of the shoulder absent (vs. present in *C. nemoricola*, *C. grandisquamis*, *C. jerdoni*, *C. emma* and *C. mystaceus*); and a row of 8–9 compressed supratympanic spines (vs. row of 3–4 compressed supratympanic spines in *C. nemoricola* and *C. grandisquamis*; two well separated supratympanic spines in *C. versicolor*; two parallel rows of compressed supratympanic scales in *C. maria* and *C. jerdoni*; single well developed postorbital spine in *C. emma*).

Description. Based on specimen CESL 374. A large sized adult male (SVL-84.7 mm) collected from a shrub along the road near Marayoor, Kerala. Morphometric and meristic data are summarised in Appendix 2 & 3. General habitus moderately compressed. Head moderate (HL/SVL ratio 0.23), elongate (HW/HL ratio 0.73), maximum height slightly less than maximum width; snout pointed; rostral broader than high; nostrils in single nasal shield which is separated from rostral by three scales; mental shield broader than rostral; two postmentals, first pair separated from each other by two small scales; genials smooth; gular sac small, indistinct, composed of strongly keeled scales, slightly smaller than genials; scales on top of snout smooth; scales on top of head heterogenous in size and shape, smooth; canthus-rostralis and supraciliary edge sharp; a row of 8 compressed, spines divided into two groups above the tympanum, the one closer to the nuchal crest longer; orbit diameter 86% of distance between anterior border of orbit and snout tip; tympanum exposed, its greatest diameter 49% of horizontal diameter of orbit; partially keeled, scales between tympanum and orbit smooth, some enlarged, a few with partially keeled edges; posterior region of jaws swollen; supralabials 10/11; infralabials 10/10.

Nuchal crest well developed, dorsal crest slightly reduced, continuous; nuchal crest composed of 12 long, conical spines, the first being the smallest; dorsal crest composed of much smaller spines reaching slightly behind midbody; 30 longitudinal scale rows around midbody; dorsal and lateral scales sub-triangular, smooth, ones on the lower back feebly keeled, oriented postero-dorsally; ventrals strongly keeled, mucronate, almost equal to the dorsal and lateral scales.

Limbs slender and covered with keeled scales forming parallel longitudinal rows; scales under thighs weakly keeled; length of hindlimb ca. 101 % SVL; relative length of fingers 4>3>5>2>1, second and fifth finger almost equal; relative lengths of toes 4>3>5>2>1; fourth toe much longer than fifth finger; 21 subdigital lamellae under fourth finger; 27 subdigital lamellae under fourth toe; subdigital lamellae with sharp keels, bicarinate; slender, swollen at the base; dorsal and ventral tail scales keeled, ventral tail scales mucronate, strongly keeled; tail length 268 mm.

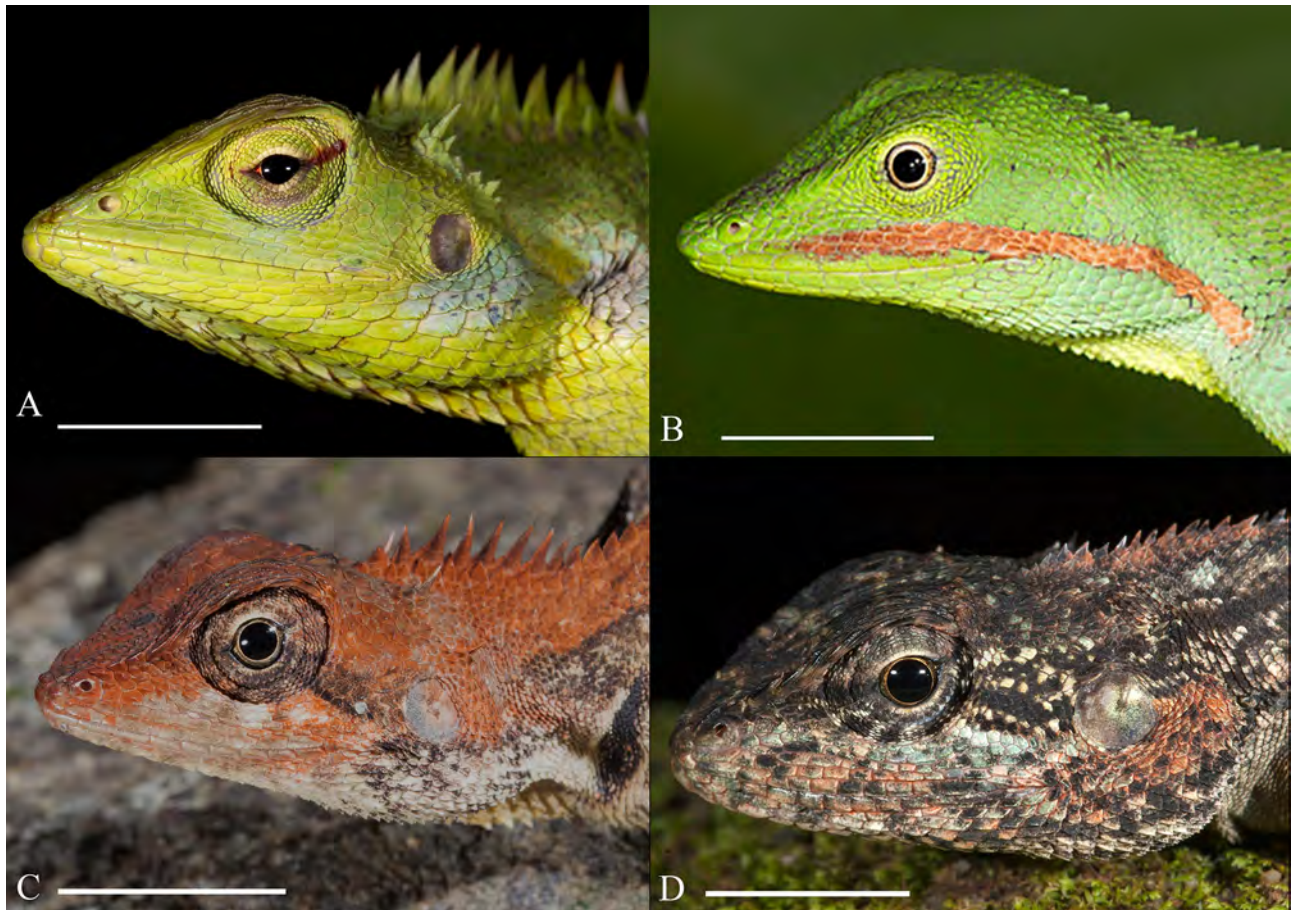


FIGURE 9. Lateral close-up of head characteristics of the four sister clades A. *Calotes*, B. *Microauris*, C. *Monilesaurus* and D. *Psammophilus*. Scale bar: 10 mm.

Colouration. In life: dorsum and head uniform, bright green with 5 thin, white transverse stripes, continuing on the tail as indistinct bands; head bright green laterally, lighter towards the cheeks; nuchal spines brownish, a brick red horizontal stripe from posterior corner of the eye till end of orbit, darker behind the eye; few blackish scales below the eye; gular scales lighter, yellowish green; posterior half of the tail dull greyish brown with alternating white bands; tympanum pale grey with greenish edge, ventrally lighter, uniform pale green. Representative image showing live colouration (Fig. 4a). In preservative: colouration mostly similar to that in life, except overall paler.

Variation and secondary sexual characteristics. Meristic and morphometric data of two adult males and one adult female are given in Appendix 2 & 3. The examined specimens agree with each other in general morphology and scalation. The examined female specimen (CESL 037) is slightly larger in size and has much smaller nuchal spines, compared to the males, almost equal to the dorsal spines.

Distribution. *Calotes calotes* is distributed in the low and medium elevation dry forests (up to 1000 m asl) of

the southern Western Ghats, Eastern Ghats and across Sri Lanka. In the present study, *C. calotes* was recorded from various sites in the low to mid elevation dry and deciduous forests of the southern Western Ghats (See Appendix 1 for details). This species is common in and around open scrub, secondary and degraded forest patches.

Ecology and natural history. *Calotes calotes* is a diurnal lizard, semi-arboreal to arboreal in habit, and so far, has been recorded mostly in scrub, secondary deciduous forests and plantations. Individuals were mostly seen perching on shrubs, bushes and on trees near edges of forests. In some instances, it has also been observed near villages and within plantations. During this study, it was never recorded from primary evergreen forests. In some sites, they might occur syntopically in the same habitat as *C. versicolor*.

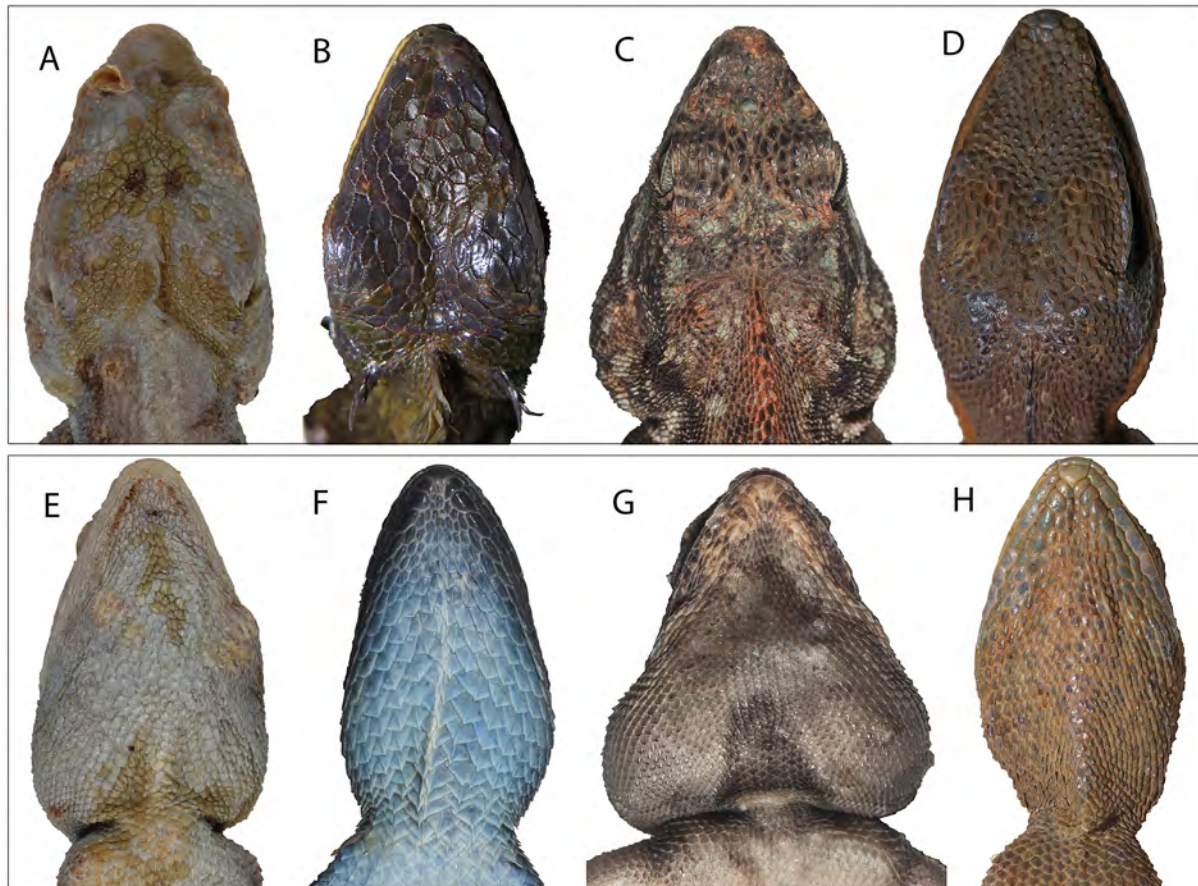


FIGURE 10. Dorsal and ventral close-ups of head characteristics of the four sister clades A., E. *Monilesaurus*; B., F. *Calotes*; C., G. *Psammophilus*; and D., H. *Microauris*.

Calotes versicolor (Daudin, 1802)

Original description. Daudin, 1802. Hist. Nat., Rept. iii, 1802: 395, xlv.

Taxonomic comments. *Calotes versicolor* was described in 1802 by Daudin, based on specimens at MNHN. There is no mention of a precise locality or even a type specimen. Later Smith (Smith 1935) and other workers designated the type-locality to populations from Pondicherry on the east coast of India, Chennai (Madras), and Kolkata (Calcutta) (Zug *et al.* 2006). The specimen MNHN 2548, collected from Pondicherry by Leschenault, cannot be a syntype of *C. versicolor* Daudin 1802, because Leschenault visited Pondicherry only after 1816 (Amarasinghe *et al.* 2009). Amarasinghe *et al.* (2009) clarified that MNHN 2548 collected from Pondicherry by Leschenault is the syntype of *Agama tiedemanni* Kuhl, 1820. Gowande *et al.* (2016) synonymized *Calotes tiedemanni* and designated a neotype from Pondicherry without any comparison with the syntype of *Calotes tiedemanni*. This neotype designation was recently invalidated (Chaitanya *et al.* 2017).

Currently, *Calotes versicolor* is the most widely distributed species of the genus *Calotes*. Many researchers

have mentioned the high level of morphological variation in this species across different populations and some have even considered it to be a species complex (Zug *et al.* 2006). Recently two new species were described from dry zone populations of *C. versicolor* from Myanmar based on DNA sequence and morphological analysis (Zug *et al.* 2006). In our phylogenetic analyses, the southern Western Ghats population forms a distant cluster within the *C. versicolor* clade (Fig. 1). The studied specimens also show 0–5% genetic divergence across their distribution. This shows that the Indian population might also be a species complex (see Gowande, 2016). A phylogeographic study with thorough sampling across its range and a rigorous comparison of the available type materials for the existing species and subspecies is necessary to resolve the complexity in this species. Since we did not study any historical type materials of *Calotes versicolor* or the synonyms, we consider the populations in this study as *Calotes cf. versicolor*. The diagnosis is based on specimens collected from the Southern Western Ghats only and used to separate *Calotes cf. versicolor* from other distinct species.

Diagnosis and comparison. A medium to large sized *Calotes* (SVL up to 99.4 mm) characterized by the posterodorsal orientation of lateral scales; antehumeral fold absent; 38–44 midbody scale rows; nuchal and dorsal crest well developed, continuous, extending till the start of tail in males; two well separated supratympanic spines; dorsal and lateral scales large, more or less distinctly keeled, ventral scales strongly keeled, mucronate; paired postmentals, first pair separated by 1–2 median scales; 15–22 subdigital lamellae under fourth finger, 21–25 subdigital lamellae under fourth toe; 10–12 supralabials and 9–11 infralabials; uniform, light brown or greyish above, juveniles and females with darker cross bars or blotches on lateral side, often with paired lighter dorso-lateral stripes, gular pouch brick red and overall body reddish in breeding males.

From other members of Smith's *C. versicolor* group (*C. nemoricola*, *C. grandisquamis*, *C. calotes*, *C. minor*, *C. maria*, *C. jerdoni*, *C. emma* and *C. mystaceus*) *C. cf. versicolor* can be distinguished by a combination of the following characters: smaller body size: adult SVL 73.8–99.4 mm, n=9 (vs. *C. nemoricola*, adult SVL 112–134.8 mm, n=7, n=5; and *C. grandisquamis*, adult SVL 110.0–136.5 mm, n=5); 38–44 midbody scale rows (vs. 27–35 in *C. grandisquamis*; 30–35 in *C. calotes*, n=3; 36–43 in *C. nemoricola*; 58–63 in *C. maria*; 45–57 in *C. jerdoni*; 49–65 in *C. emma*; 48–58 in *C. mystaceus* and 48–60 in *C. minor*); crescent-shaped patch of granular scales in front of the shoulder absent (vs. present in *C. nemoricola*, *C. grandisquamis*, *C. emma*, *C. mystaceus* and *C. jerdoni*); nuchal and dorsal crest well developed, composed of almost equal spines (vs. nuchal spines much longer, dorsal crest reduced in *C. nemoricola* and *C. maria*; nuchal spines much longer than dorsal spines in *C. grandisquamis*, *C. calotes* and *C. emma*); two well separated supratympanic spines (vs. row of 3–4 compressed supratympanic spines in *C. nemoricola* and *C. grandisquamis*; 8–9 compressed spines in *C. calotes*; two parallel rows of compressed supratympanic scales in *C. maria* and *C. jerdoni*; single well developed postorbital spine in *C. emma*). *Calotes cf. versicolor* can be distinguished from its other Sri Lankan congeners based on posterodorsal orientation of lateral scales and absence of oblique fold or pit in front of the shoulder.

Description. Based on specimen CESL 182. A large sized adult male (SVL 99.4 mm), morphometric and meristic data are summarised in Appendix 2 & 3. General habitus moderately compressed. Head moderate (HL/SVL ratio 0.22), slightly elongate (HW/HL ratio 0.95), maximum height slightly less than maximum width; snout pointed; rostral broader than high; nostrils in single nasal shield which is separated from rostral by two scales; mental shield narrower than rostral; two postmentals, first pair separated from each other by two small scales; genials keeled; gular sac small, composed of strongly keeled scales, slightly smaller than genials; scales on top of snout smooth except median row, which is keeled; scales on top of head heterogenous in size and shape, keeled; supraorbital scales keeled; canthus-rostralis and supraciliary edge sharp; two separated spines on posterior end of head, the anterior much longer, closer to the nuchal crest, posterior above tympanum; orbit diameter 87% of distance between anterior border of orbit and snout tip; tympanum exposed, its greatest diameter 42% of horizontal diameter of orbit; slightly keeled, scales between tympanum and orbit smooth, slightly enlarged; posterior region of jaws swollen; supralabials 11/10; infralabials 10/10.

Nuchal and dorsal crest well developed, continuous; nuchal crest composed of 11 long, conical spines, the first being the smallest; dorsal crest composed of 33 curved spines till above the vent, slightly smaller than the nuchal spines; 36 longitudinal scale rows around midbody; dorsal and lateral scales sub-triangular, keeled, oriented postero-dorsally; ventrals strongly keeled, mucronate, smaller than dorsal and lateral scales.

Limbs slender and covered with strongly keeled scales, similar to laterals, forming parallel longitudinal rows; scales under thighs weakly keeled; length of hindlimb ca. 75 % SVL; relative length of fingers 4>3>2>5>1, third and fourth finger almost equal; relative lengths of toes 4>3>5>2>1; fourth toe much longer than fifth finger; 21

subdigital lamellae under fourth finger; 25 subdigital lamellae under fourth toe; subdigital lamellae with sharp keels, bicarinate; slender, swollen at the base; dorsal and ventral tail scales mucronate, strongly keeled; tail broken, incomplete; tail length 90 mm.

Colouration. In life: dorsum and head uniform, greyish-brown with irregular darker patches towards the flank; each lateral scale with a darker blackish spot towards the base, followed by lighter grey edges; head laterally paler, whitish towards the cheeks; a small, thin darker stripe from posterior corner of the eye till end of orbit; legs with irregular dark crossbars; a black coloured patch above the shoulder, near throat; tympanum pale grey with many small black spots, ventral uniformly lighter, pale grey; tail with alternating dark and light bands. Representative image showing live colouration (Fig. 4b). In preservative: colouration mostly similar to that in life, except overall paler.

Variation and secondary sexual characteristics. Meristic and morphometric data of four adult male and four adult female specimens are given in Appendix 2 & 3. The examined specimens agree with each other in general morphology and scalation. All the examined female specimens (CESL 048, CESL 163, CESL 306 and BNHM 374) have much smaller nuchal and dorsal spines compared to the males and lack a gular sac.

Distribution. *Calotes cf. versicolor* is common in the Western Ghats at elevations between 70 m to 1250 m M.S.L. (See Appendix 1 for details).

Ecology and natural history. *Calotes cf. versicolor* is a diurnal lizard, semi-arboreal to arboreal in habit, and so far, has been recorded mostly in scrub, deciduous forests and plantations. Individuals were mostly seen perching on shrubs, hedges, gardens and along compound walls of houses in villages along forests. *C. cf. versicolor* has often been found within plantations and prefers open patches to forested areas. During this study, it was never recorded from primary evergreen forests. In some sites, they might occur syntopically in the same habitat as *M. rouxii* **comb. nov.** but tend to be restricted to forest edges.

***Calotes grandisquamis* Günther, 1875**

Calotes grandisquamis—Günther, 1875. Proc. Zool. Soc. 1875: 226.

Original description. Günther, 1875. Proceedings of the Zoological Society, 1875: 226, Plate xxx.

Taxonomic comments. *Calotes grandisquamis* was described based on specimens collected from ‘foot of Canoot Ghat, near Manantoddy, Bramagherry hills’. This large bodied, green *Calotes* is a well-defined species and can be distinguished from the closely related *C. nemoricola*.

Syntypes. BMNH 1946.8.11.44 to 47, collected from ‘foot of the Canoot Ghat, near Manantoddy, Bramagherry hills’ (presently near Mananthawadi in the Brahmagiri hills, Kerala).

Material examined. CESL 035 adult female collected from near Chemunji, Peppara Wildlife Sanctuary, Kerala; CESL 120 adult male collected from Upper Manalar, Periyar tiger reserve, Kerala and CESL 191 adult male collected from near Pulmeedu, Periyar tiger reserve, Kerala; BMNH 1946.8.11.44 female, BMNH 1946.8.11.45 juvenile, BMNH 1946.8.11.46 juvenile, BMNH 1946.8.11.47 male all deposited by R.H. Beddome collected from the foothills of “Coonoor Ghat. Details of collection locality, specimen voucher and GenBank accession number in Appendix 1.

Diagnosis and comparison. A large sized *Calotes* (SVL up to 136.5 mm) characterized by the posterodorsal orientation of lateral scales; antehumeral fold absent; 27–35 midbody scale rows; nuchal and dorsal crest well developed, continuous, nuchal crest composed of long, curved spines, dorsal spines smaller, gradually reducing in length and reaches till above the tail base; row of 3–4 compressed supratympanic spines; postorbital spine absent; a crescent-shaped patch of granular scales in front of the shoulder present; dorsal and lateral scales large, smooth, subtriangular, ventral scales keeled, mucronate; paired postmentals, first pair separated by a single median scale; 22–25 subdigital lamellae under fourth finger, 27–30 subdigital lamellae under fourth toe; 10 supralabials and 9–10 infralabials; green above, often with 2–3 broad black transverse bars on the lateral side, lateral side of head darker, blackish, ventral pale green.

Calotes grandisquamis can be distinguished from members of Smith’s *C. versicolor* group by a combination of the following characters: larger body size: adult SVL 110.0–136.5 mm, n=5 (vs. *C. versicolor*, adult SVL 73.8–99.4 mm, n=9 and *C. calotes*, adult SVL 73.6–96.8 mm, n=3); 27–35 midbody scale rows (30–35 in *C. calotes*, n=3;

38–44 in *C. versicolor*; 58–63 in *C. maria*; 45–57 in *C. jerdoni*; 49–65 in *C. emma*; 48–58 in *C. mystaceus* and 48–60 in *C. minor*); nuchal crest well developed with much longer spines than dorsal spines (vs. nuchal and dorsal crest well developed, composed of almost equal spines in *C. versicolor* and *C. mystaceus*; nuchal spines long, dorsal crest reduced in *C. maria*); row of 3–4 compressed supratympanic spines (vs. two well separated supratympanic spines in *C. versicolor* and 8–9 compressed spines in *C. calotes*, two parallel rows of compressed supratympanic scales in *C. maria* and *C. jerdoni*; single well developed postorbital spine in *C. emma*); presence of a crescent-shaped patch of granular scales in front of the shoulder (vs. absent in *C. versicolor*, *C. calotes* and *C. maria*) and lateral scales much larger than ventrals (vs. almost equal to the ventrals in *C. calotes*). For distinguishing from *C. nemoricola*, see comparison section of *C. nemoricola*.

Description. Based on specimen CESL 191. A large sized adult male (SVL-136.5 mm), morphometric and meristic data are summarised in Appendix 2 & 3. General habitus compressed. Head moderately large (HL/SVL ratio 0.28), elongate (HW/HL ratio 0.60), maximum height slightly less than maximum width; snout pointed; rostral broader than high; nostrils in single nasal shield which is separated from rostral by two scales; mental shield narrower than rostral; two postmentals, first pair separated from each other by a single scale; genials smooth; gular sac well developed, composed of mostly smooth scales, weakly keeled only at the medial row, slightly smaller than genials; scales on top of snout smooth except median row, which is keeled; scales on top of head heterogenous in shape and size, keeled towards the edges; supraorbital scales weakly keeled; canthus-rostralis and supraciliary edge sharp; 3 supratympanic spines in a row, compressed; orbit diameter 71% of distance between anterior border of orbit and snout tip; tympanum exposed, its greatest diameter 41% of horizontal diameter of orbit; partially keeled, scales between tympanum and orbit smooth, enlarged, slightly smaller than the tympanum; posterior region of jaws distinctly swollen with large scales, equal to or slightly larger than tympanum; supralabials 10/10; infralabials 10/9.

Nuchal and dorsal crest well developed, continuous; composed of 28 long, conical spines, the first being the smallest; dorsal crest reaching above the tail base gradually decreasing in length, continues till the end of tail as a serrated ridge; longest nuchal spine 107% of the orbit; 30 longitudinal scale rows around midbody; dorsal and lateral scales sub-triangular, smooth, oriented postero-dorsally; ventrals strongly keeled, mucronate, smaller than dorsal and lateral scales; a crescent-shaped patch of small, granular scales present in front of the shoulder.

Limbs moderate and covered with smooth scales, weakly keeled scales towards the end; scales under thighs weakly keeled; length of hindlimb ca. 70 % SVL; relative length of fingers 4>3>2>5>1, third and fourth finger almost equal; relative lengths of toes 4>3>5>2>1; fourth toe much longer than fifth finger; 22 subdigital lamellae under fourth finger; 29 subdigital lamellae under fourth toe; subdigital lamellae with sharp keels, bicarinate; slender, swollen at the base; dorsal tail scales keeled, median row forming a serrated ridge, ventral tail scales mucronate, strongly keeled; tail length 267 mm (tail incomplete, broken at the tip).

Colouration. In life: dorsum and head uniform, green above with slightly yellowish lateral scales; three broad black bands on the lateral side; dorsal and scales around the orbit greenish yellow with thick black edges forming an indistinct black band from behind the nostril till above the tympanum; head laterally yellow, bluish below the cheeks; pupil black surrounded by a brick red iris; a thin black stripe across the horizontally orbit; lip scales yellow; gular pouch yellow with few slightly orange scales; legs uniform lighter shade of green; tympanum pale bluish green; ventral pale green; tail banded with thick dark and light bands, dark bands almost black near the end. Representative image showing live colouration (Fig. 5a). In Preservative: colouration mostly similar to that in life, except overall paler.

Variation and secondary sexual characteristics. Meristic and morphometric data of the examined specimens are given in Appendix 2 & 3. The examined specimens agree with each other in general morphology and scalation. The female specimen (CESL 035) has a reduced nuchal crest composed of shorter spines, dorsal crest almost indistinct and ending at mid body; gular pouch absent.

Distribution. *Calotes grandisquamis* is endemic to the Western Ghats and is distributed across the high elevation evergreen (above 1000 m msl) forests of the southern part of central Western Ghats (south of Brahmgiiri hills) and the southern Western Ghats. During the present study, this species was recorded from various sites in the hills of the southern Western Ghats (See Appendix 1 for details). The only record of *C. grandisquamis* in Central Western Ghats is from Agumbe (Ganesh *et al.* 2013).

Ecology and natural history. *Calotes grandisquamis* is a diurnal lizard, mostly arboreal in habit, and so far, has been recorded from primary evergreen forests and montane shola forests. Individuals were mostly seen perched on branches, high in the canopy and actively moving on tree trunks inside forests. In a few instances, it was found

sleeping on lower branches at night. This species has mostly been recorded from higher elevations (above 1000 m msl) in the southern Western Ghats although there are some reports of it from lower elevations.

***Calotes nemoricola* Jerdon, 1853**

Calotes nemoricola—Jerdon, 1853. J. Asiat. Soc. Beng. xxii, 1853: 471.

Original description. Jerdon, 1853. Journal of the Asiatic Society of Bengal, xxii, 1853: 471.

Taxonomic comments. *Calotes nemoricola* was described based on specimens collected from ‘Foot of “Coonor Ghat, Nilgherries’ (“Coonor”, Nilgiri hills, Tamil Nadu, India). The type collected by Jerdon is a much mutilated male specimen (Smith 1935) and is housed in the collection of ZSIK (Das *et al.* 1998). Another male topotype is housed in the collection of BNHS (BNHS 373) (Smith 1935).

Holotype: ZSI 6560. The specimen is in poor condition; the posterior part of the body along with the hindlimbs and tail is broken.

Material examined. CESL 038 adult male collected from Bonaccord, Peppara Wildlife Sanctuary, Kerala; CESL 406 adult male collected from Kanyakumari Wildlife Sanctuary, Tamil Nadu; CESL 545 adult male collected from Makuta, Brahmagiri Wildlife Sanctuary, Karnataka; CESL 555 adult male collected from Bidahalli, Pushpagiri Wildlife Sanctuary, Karnataka; BNHS 1778 adult male collected from Kudremukh National Park, Karnataka; BNHS 373 adult male collected from “Coonor” Ghat, Nilgiri hills, Tamil Nadu; BMNH 74.4.29.224 male, 74.4.29.225 female both collected from Malabar and ZSI 6560 male collected from the foothills of “Coonor Ghat. Details of collection locality, specimen voucher and GenBank accession number in Appendix 1.

Diagnosis and comparison. A large sized *Calotes* (SVL up to 134.8 mm) characterized by the posterodorsal orientation of lateral scales; antehumeral fold absent; 36–43 midbody scale rows; nuchal crest well developed composed of long spines, dorsal crest reduced, almost indistinct behind the midbody; row of 3–4 compressed supratympanic spines; postorbital spine absent; a crescent-shaped patch of granular scales in front of the shoulder present; dorsal and lateral scales large, mostly smooth, weakly keeled towards the flanks, ventral scales strongly keeled, mucronate; paired postmentals, first pair separated by 1–2 median scales; 21–23 subdigital lamellae under fourth finger, 25–31 subdigital lamellae under fourth toe; 10–12 supralabials and 10–11 infralabials; green to brownish above, uniform, often with a dark streak from eye to above tympanum, ventral white to pale grey.

C. nemoricola can be distinguished from members of Smith’s *C. versicolor* group by a combination of the following characters: larger body size: mean adult SVL 125.8 mm, n=7 (vs. *C. versicolor*, adult SVL 73.8–99.4 mm, n=9 and *C. calotes*, adult SVL 73.6–96.8 mm, n=3); 36–43 midbody scale rows (30–35 in *C. calotes*, n=3, 38–44 in *C. versicolor*; 58–63 in *C. maria*; 45–57 in *C. jerdoni*; 49–65 in *C. emma*; 48–58 in *C. mystaceus* and 48–60 in *C. minor*); nuchal crest well developed with longer spines, dorsal crest reduced (vs. nuchal and dorsal crest well developed, composed of almost equal spines in *C. versicolor* and *C. mystaceus*); row of 3–4 compressed supratympanic spines (vs. two well separated supratympanic spines in *C. versicolor*, 8–9 compressed spines in *C. calotes*, two parallel rows of compressed supratympanic scales in *C. maria* and *C. jerdoni*; single well developed postorbital spine in *C. emma*); presence of a crescent-shaped patch of granular scales in front of the shoulder (vs. absent in *C. versicolor*, *C. calotes* and *C. maria*) and lateral scales much larger than ventrals (vs. almost equal to the ventrals in *C. calotes*).

Morphologically, it is mostly similar to the closely related *C. grandisquamis* but can be distinguished based on higher number of midbody scale rows (36–43 vs. 27–35); smaller scales between eye and tympanum, much smaller than tympanum (vs. much larger scales, almost equal to the tympanum); scales on the cheek smaller, weakly keeled (vs. larger, smooth); gular scales keeled, smaller than mental (vs. gular scales smooth, equal to or slightly larger than the mental) and dorsal crest reduced, not extending beyond mid body (dorsal crest well developed, till above the base of tail). Even though these two large bodied species show the above-mentioned morphological differences, there has been some confusion in their correct identification in the recent past. To clarify this, a detailed comparison to distinguish these two species was provided by Ganesh & Chandramouli (2013).

Description. Based on specimen CESL 555. A large sized adult male (SVL-120.4 mm), morphometric and meristic data are summarised in Appendix 2 & 3. General habitus compressed. Head moderate (HL/SVL ratio

0.25), elongate (HW/HL ratio 0.75), maximum height slightly less than maximum width; snout pointed; rostral broader than high; nostrils in single nasal shield which is separated from rostral by two scales; mental shield narrower than rostral; two postmentals, first pair separated from each other by two small scales; genials keeled; gular sac small, composed of keeled scales, strongly keeled towards the medial row, slightly smaller than genials; scales on top of snout smooth except median row, which is keeled; scales on top of head heterogenous in shape and size, keeled towards the edges; supraorbital scales keeled; canthus-rostralis and supraciliary edge sharp; 4 supratympanic spines in a row, compressed; orbit diameter 69% of distance between anterior border of orbit and snout tip; tympanum exposed, its greatest diameter 46% of horizontal diameter of orbit; partially keeled, scales between tympanum and orbit smooth, not enlarged; posterior region of jaws distinctly swollen; supralabials 11/11; infralabials 11/11.

Nuchal crest well developed, continuous with the much reduced dorsal crest; dorsal crest reaching slightly behind midbody; nuchal crest composed of 16 long, conical spines, the first being the smallest and fourth the longest; longest nuchal spine 65% of the orbit; dorsal spines less than half the nuchal spines in length; 41 longitudinal scale rows around midbody; dorsal and lateral scales sub-triangular, smooth, oriented postero-dorsally; a crescent-shaped patch of small, granular scales present in front of the shoulder.

Limbs moderate and covered with weakly keeled scales, stronger towards the end forming parallel longitudinal rows; scales under thighs weakly keeled; length of hindlimb ca. 71 % SVL; relative length of fingers 4>3>2>5>1, third and fourth finger almost equal; relative lengths of toes 4>3>5>2>1; fourth toe much longer than fifth finger; 21 subdigital lamellae under fourth finger; 27 subdigital lamellae under fourth toe; subdigital lamellae keeled, bicarinate; slender, swollen at the base; scales on dorsal and ventral surface of tail keeled, ventral tail scales mucronate; tail length 268 mm.

Colouration. In life: dorsum and head uniform, light green above with slightly brownish lateral scales; a thick milky white band from behind the head till end of nuchal crest extending across the neck; head laterally brighter green, whitish below the cheeks; pupil black surrounded by a brick red iris; lip scales green; legs uniform darker shade of green; tympanum pale bluish green; ventral uniformly white; tail greenish at the start turning dull brownish towards the end. This individual changed colour at the slightest disturbance and turned dark brown overall with a dark olive head and a prominent white band behind the head. Representative image showing live colouration (Fig. 5b). In preservative: colouration mostly similar to that in life, except overall paler.

Variation and secondary sexual characteristics. Meristic and morphometric data of the examined specimens are given in Appendix 2 & 3. The examined specimens agree with each other in general morphology and scalation. The only female specimen we examined (BMNH 74.4.29.255) had no cheek pouches or a swollen tail base.

Distribution. *Calotes nemoricola* is endemic to the Western Ghats and is distributed in the low to mid elevation evergreen forests of the southern part of central Western Ghats (Agumbe and south) and the southern Western Ghats (Inger *et al.* 1984; Naniwadekar & Deepak 2008). During the present study, this species was recorded from various sites in the hills of central and southern Western Ghats (See Appendix 1 for details).

Ecology and natural history. *Calotes nemoricola* is a diurnal lizard, mostly arboreal in habit, and so far, has been recorded mostly from primary evergreen forests. Individuals were mostly seen perched on high branches and actively moving on tree trunks inside forests. In a few instances, it was also found sleeping on lower branches at night. This species has mostly been recorded from low elevations (up to 600 m msl) in the southern Western Ghats but has sometimes been recorded from high elevation evergreen forests in the central Western Ghats (around 1000 m msl). It might overlap in distribution with the other large green agamid *C. grandisquamis* at its higher elevation range extremes given their preference of similar microhabitat. During this study, they were not recorded to be syntopic at any site.

***Monilesaurus* gen. nov.**

Type species. *Calotes rouxii* (Duméril & Bibron, 1837)

Content. *Monilesaurus ellioti* **comb. nov.**, *Monilesaurus montanus* **gen. et sp. nov.**, *Monilesaurus rouxii* **comb. nov.** and *Monilesaurus acanthocephalus* **gen. et sp. nov.**

Etymology. The genus epithet is derived by adding the word ‘Monile’ meaning necklace in Latin referring to the distinct neck fold in this genus and the Greek word *sauros* meaning lizard which is latinized here as *saurus*.

Diagnosis. *Monilesaurus* **gen. nov.** can be easily diagnosed from all members of draconinae lizards from the Indian subcontinent except *Psammophilus* in having an antehumeral fold, which mostly extends below the dewlap forming a fused fold on the shoulder and the neck. It differs from *Psammophilus* in having a dorso-laterally compressed body and lower number of scales on the mid-body. Supratympanic spines are present, in the form of two separated spines vs clusters in *Calotes* and *Psammophilus*. From *Microauris* **gen. nov.** by having a relatively large tympanum (Fig. 9c vs. 9b). Scales on head large uniform shield like (vs small, sub-triangular) (Fig. 10a vs 10d).

Monilesaurus **gen. nov.** can be easily diagnosed from the genera *Otocryptis*, *Sarada* Deepak, Karanth & Giri, 2016 and *Sitana* Cuvier, 1829 by the presence of a well-developed fifth toe (Smith, 1935; Deepak *et al.* 2016). *Monilesaurus* **gen. nov.** differs from *Mantheyus phuwuanensis* by the absence of femoral pores (Manthey & Nabhitabhata, 1991; Ananjeva & Stuart 2001); from the members of the genus *Bronchocela* by the presence of postorbital and supratympanic spines (Hallermann & Böhme 2000); from *Cophotis*, *Ceratophora*, *Lyriocephalus*, *Ptyctolaemus* Peters, 1864, *Phoxophrys* Hubrecht, 1881 by the presence of external tympanum (Boulenger, 1885; Smith, 1935; Inger, 1960; Pethiyagoda & Manamendra-Arachchi 1998; Schulte II *et al.* 2004; Bahir & Silva 2005; Manamendra-Arachchi *et al.* 2006; Samarawickrama *et al.* 2006). *Monilesaurus* **gen. nov.** can be diagnosed from *Japalura*, Gray 1853 by the absence of heterogenous dorsal scales and short and thick nuchal scales; from *Salea* Gray, 1845 (*S. anamallayana* and *S. horsfieldii*) by the presence of small regular lateral scales and the absence of enlarged plate like scales between the eye and tympanum (Smith, 1935); from *Complictus nigrigularis* (Ota & Hikida, 1991), *Hypsiccalotes kinabaulensis* (de Grijs, 1937), *Malayadracon robinsonii* (Boulenger, 1908), *Oriocalotes* (Günther, 1864) *Pseudocophotis* (Manthey & Grossmann, 1997) and *Pseudocalotes* by the absence of enlarged row of suborbital scales (Smith, 1935; Taylor 1963; Ota & Hikida, 1991; Manthey & Denzer 1992; Inger & Steubing 1994; Ota & Hikida, 1996; Hallermann & Böhme 2000; Manthey & Denzer, 2000; Hallermann & McGuire 2001; Leong 2001; Manamendra-Arachchi *et al.* 2006; Samarawickrama *et al.* 2006; Ananjeva *et al.* 2007; Hallermann & Böhme 2007; Das & Lakim 2008; Hallermann *et al.* 2010; Mahony 2010; Harvey *et al.* 2014; Denzer *et al.* 2015; Grismer LL *et al.* 2016; Harvey *et al.* 2017).

Taxonomic comments. *Monilesaurus rouxii* **comb. nov.** was described as *Calotes rouxii* (Duméril & Bibron, 1837). The name bearing type is a male specimen housed at MNHN. The type locality of this species is named as “Indes orientales”. Günther (1864) described another similar looking species from southern India, *Calotes ellioti*. Based on their size similarity Smith (1935) called them dwarf species. Here, we formally transfer these two extant species to this new genus. We also describe two new species belonging to this genus based on similar morphological characters and their phylogenetic position.

***Monilesaurus rouxii* (Duméril & Bibron, 1837) comb.nov.**

Calotes rouxii—Duméril & Bibron, 1837. Erp. Gen, iv, 1837: 407.

Calotes ellioti—(not of Günther) Stoliczka, 1872. J. Asiat. Soc. Beng. (2) xli, 1872: 113.

Calotes rouxii—Smith, 1935. Fauna of British India, ii, 1935: 206.

Syntypes. MNHN—MNHN-RA-0.6894 & MNHN-RA-1994.1857 collected from “Indes Orientales” and deposited in the National Museum of Natural History (France).

Original description. Duméril, A. M. C. and G. Bibron. 1837. Erpétologie Générale ou Histoire Naturelle Complete des Reptiles. Vol. 4. Libr. Encyclopédique Roret, Paris, 570 pp.

Taxonomic comments. The exact type locality of *M. rouxii* **comb.nov.** is unknown, as the localities for the syntypes in MNHN and in the original publication are given as “Indes Orientales” or India. The only precise locality of a specimen in the catalogue of British Museum is given as “Matheran, Bombay Presidency” (Boulenger 1885, 1890); Smith (1935) gives the range of *M. rouxii* **comb. nov.** as “Bombay Presidency (Matheran, Khandala, Kanara, Jog); Travancore”. Of these, other than “Travancore” all the other localities are from the northern and central Western Ghats.

Material examined. CESL 129, adult male collected from Matheran, Maharashtra; CESL 523, adult male collected from Brahmagiri Wildlife Sanctuary, Karnataka; CESL 554, adult male collected from Pushpagiri Wildlife Sanctuary, Karnataka; CESL 669, adult female collected from Bondla Wildlife Sanctuary, Goa; CESL 834, adult female collected from Narsimparvata, Kudremukh National Park, Karnataka, CESL 678, adult male

collected from Madhei wildlife sanctuary, Goa; CESL 875, juvenile collected from Radhanagri, Maharashtra; CESL 095, juvenile, collected from Agumbe, Karnataka; 072, adult male collected from Wayanad wildlife sanctuary, Kerala; CESL 123 and CESL 153 adult males collected from Vazhachal, Kerala; CESL 215, adult male collected from near Parambikulam wildlife sanctuary, Kerala and CESL 581, adult male collected from near Pooyamkutty, Kerala. MNHN-RA-0.6894 (photographs only). Details of collection locality, specimen voucher and GenBank accession number in Appendix 1.

Diagnosis and comparisons. A small sized *Monilesaurus* (SVL up to 74.8 mm) characterized by the posteroventral orientation of lateral scales; antehumeral fold small, triangular spines; two separated small supratympanic spines; dorsal and lateral scales keeled, ventral scales strongly keeled; paired postmentals, first pair in contact or separated by a single scale; 18–21 subdigital lamellae under fourth finger, 24–29 subdigital lamellae under fourth toe; 9–10 supralabials and 8–9 infralabials; olive-brown to above, antehumeral fold black, top of head often darker than dorsum, body often speckled with dark and light blotches, prominent in juveniles and sub-adults.

Morphologically, *M. rouxii* comb.nov. is superficially similar to *M. montanus* **gen. et sp. nov.**, *M. ellioti* **comb. nov.**; and *M. acanthocephalus* **gen. et sp. nov.**, but can be distinguished by a combination of the following characters: 52–56 midbody scale rows (vs. 46–52 in *M. montanus* **gen. et sp. nov.**, 62–64 in *M. acanthocephalus* **gen. et sp. nov.**, and 52–58 in *M. ellioti* **comb. nov.**) spine in the posterior corner of orbit absent (vs. very small, indistinct tubercle like in *M. montanus* **gen. et sp. nov.**, long, distinct in *M. ellioti* comb.nov. and much longer in *M. acanthocephalus* **gen. et sp. nov.**); 7–8 small nuchal spines (vs. 3–6 small nuchal spines in *M. montanus* **gen. et sp. nov.**, 6 much longer nuchal spines in *C. acanthocephalus* **gen. et sp. nov.**, 3–4 long nuchal spines in *M. ellioti* comb.nov.); small isolated spines on the back of head and above tympanum (vs. longer, prominent spines in *M. ellioti* **comb. nov.** and *M. acanthocephalus* **gen. et sp. nov.**) white spot below the eye absent (vs. present in *M. ellioti* comb.nov. and *M. acanthocephalus* **gen. et sp. nov.**; in the form of a band in *M. montanus* **gen. et sp. nov.**) and smaller body size: adult SVL 51.4–74.8 mm, n=9 (vs. *C. montanus* **gen. et sp. nov.**, adult SVL 61–83.4 mm, n=8; and *M. acanthocephalus* **gen. et sp. nov.** adult SVL 68.9–72.6 mm, n=3).

Description. Based on CESL 129. A medium sized adult male (SVL-74.79 mm). Morphometric and meristic data are summarised in Appendix 2 & 3. General habitus moderately compressed. Head moderately large (HL/SVL ratio 0.29), elongate (HW/HL ratio 0.73), maximum height less than maximum width; snout pointed; rostral broader than high; nostrils in single nasal shield, which is separated from rostral by a single scale; mental shield narrower than rostral; two postmentals; first pair in contact with each other; genials keeled; gular scales strongly keeled, slightly smaller than genials; scales on top of snout smooth except median row, which is keeled; scales on top of head heterogenous in size and shape, keeled; supraorbital scales keeled; canthus-rostralis and supraciliary edge sharp; two separated spines on posterior end of head, the anterior slightly longer, midway between nuchal crest and tympanum, posterior above tympanum; orbit diameter 75% of distance between anterior border of orbit and snout tip; tympanum exposed, its greatest diameter 58% horizontal diameter of orbit; enlarged keeled scale between tympanum and orbit; posterior region of jaws swollen; supralabials 10/10; infralabials 9/9.

Nuchal crest well developed, composed of eight primary, broadly conical spines, the first and last smaller than the rest; the remaining vertebral scales slightly enlarged relative to adjacent rows and possessing a more pronounced median keel forming a serrated ridge like the dorsal crest which continues till the tail base; 56 longitudinal scale rows around midbody; scales on dorsum keeled, oriented postero-dorsally, while lateral ones oriented postero-ventrally; lateral scales smaller than dorsal, keeled; ventrals strongly keeled, irregular, slightly smaller than dorsals but of similar size as laterals, genials and gular scales; a strong, oblique antehumeral fold, nearly extending across the throat.

Limbs slender and covered with strongly keeled scales, larger than laterals, forming parallel longitudinal rows; scales under thighs weakly keeled; length of hindlimb ca. 82% SVL; relative length of fingers 4>3>2>5>1; relative lengths of toes 4>3>5>2>1; fourth toe longer than fifth finger; 20 subdigital lamellae under fourth finger; 24 subdigital lamellae under fourth toe; subdigital lamellae with sharp keels, bicarinate; tail slender, swollen at the base; scales on dorsal and ventral surface of tail with sharp keels, mucronate, slightly larger than laterals; tail length 118 mm (tail incomplete, broken at the tip).

Colouration. In life: dorsum uniform blackish-brown; head bright reddish-orange, from snout tip to slightly behind mid vertebral; laterally a blackish-brown stripe from above nostril to anterior margin of orbit extending till the tympanum from the posterior margin of orbit in the form of black band; a bright reddish-orange stripe from snout covering labials till the anterior margin of tympanum, continuing backwards from posterior margin and

ending abruptly in the antehumeral fold; tympanum pale grey; ventral uniformly black; gular pouch with a small orange stripe in the median row. Representative image showing live colouration (Fig. 6a). In preservative: colouration pattern mostly similar to that in life, except overall paler; bands on the head dull greyish brown.

Variation and secondary sexual characteristics. The other specimens examined agree with CESL 129 in general morphology and scalation except for some differences that are summarised in Appendix 2 & 3. Both the examined female specimens (CESL 669 and CESL 834) have much smaller nuchal spines and lack a dorsal crest and gular sac; overall colouration olive-brown, lighter head and vertebral region, a dark band along the side of the head to the neck and the presence of a black antehumeral fold.

Genetic distance. *M. rouxii* **comb. nov.** shows 1% intraspecific genetic divergence in the 16S gene; 4–7% interspecific genetic divergence from *M. ellioti* **comb. nov.**; 6% genetic divergence from *M. acanthocephalus* **gen. et sp. nov.** and 7–8% interspecific genetic divergence from *M. montanus* **gen. et sp. nov.** (Appendix. 5).

Distribution. *Monilesaurus rouxii* **comb. nov.** is distributed across the low and medium elevation forests (up to 1000 m asl) of the Western Ghats and has also been reported from parts of the southern Eastern Ghats (Daniels & Ishwar 1994). This is one of the most common forest dwelling agamid lizards in the northern and central Western Ghats. During this study, *M. rouxii* **comb. nov.** was recorded in various sites across the Western Ghats (See Fig. 3 & Appendix 1 for details).

Ecology and natural history. *Monilesaurus rouxii* is a diurnal lizard, semi-arboreal to arboreal in habit, and has so far been recorded mostly in deciduous, secondary and semi-evergreen forests. Individuals were mostly seen perching on branches and actively moving on tree trunks. In some instances, it has also been observed in forest fragments and plantations. In some sites, they occur syntopically in the same habitat as *C. versicolor*, but tend to prefer higher and thicker perches than *C. versicolor*, and were found to be more abundant than *C. versicolor* inside forests. In many instances, gravid females were recorded during pre and mid monsoon (June–August), which suggests that monsoon might be a breeding season for this species.

***Monilesaurus ellioti* (Günther, 1864) comb. nov.**

Calotes rouxii—(not of Dum. & Bibr., 1837), Jerdon, 1853. J. Asiat. Soc. Beng. (2) xxii, 1853: 471

Calotes ellioti—Günther, 1864. Rept. Brit. Ind. 1864: 142.

Bronchocela indica—Theobald, 1876. Cat. Rept. Brit. Ind. 1876: 105.

Calotes ellioti—Smith, 1935. Fauna of British India, ii, 1935: 207.

Original description. Günther, A. 1864. The Reptiles of British India. London (Taylor & Francis), xxvii, 452 pp.

Taxonomic comments. *Monilesaurus ellioti* was described, based on Jerdon's observation of *C. rouxii* like animals from "Malabar" in his list of Reptiles of Southern India, 1853 and a collection of drawings of this species in the possession of W. Elliot. Historically, southern Karnataka and northern Kerala have been referred to as Malabar. Boulenger (1885) gave a short description of this species based on the collections made by Col. R.H. Beddome from Anamalai hills, Sivagiri Ghat, Tirunelveli and Malabar. As there are no type specimens associated with this species, we hereby designate a neotype for this species. The selection of the neotype is roughly congruent with the original type locality of this species "Malabar" as mentioned by Jerdon (1853). Murthy (1978) described a subspecies *Calotes ellioti amarambalamensis* the type locality of which is Amarambalam, Nilambur. The holotype of this species is now at ZSI Madras (ZSI Madras 159) (Das *et al.* 1998). We were unable to trace the specimen in ZSI collections despite repeated attempts. For now, the specimen may be considered as lost. Hence, we compare another specimen collected from the same locality (BNHS 1033), a female individual whose characters match well with other *M. ellioti* and the description provided by Murthy. Also, the locality is within the distribution range of *M. ellioti* and contiguous with the type locality. Therefore, we consider *Calotes ellioti amarambalamensis* as a junior synonym of *M. ellioti* (Günther, 1864). ZSI Madras 159 is wrongly mentioned as a type specimen of *Calotes ellioti* (Uetz & Hošek, 2016).

Neotype. CESL 045, adult male collected from Chembra reserve forest, Kerala by SPP, MVP and SPV on 10th June 2010.

Other material examined. ZSI 4325 gravid female & ZSI 4328 male collected from Southern India; CESL 042 adult male collected from Manikunjmalai, Wayanad reserve forest, Kerala; CESL 045 adult male collected from Chembra reserve forest, Kerala; CESL 047 adult female collected from Vaithiri, Wayanad reserve forest,

Kerala; CESL 057, CESL 059 and CESL 061 adult females and CESL 058 and CESL 060 adult males collected from Vallerimala, Wayanad reserve forest, Kerala; CESL 077, adult female collected from Arlam Wildlife Sanctuary, Kerala; CESL 033 adult male collected from Bonacord, Peppara Wildlife Sanctuary, Kerala; CESL 162, adult male collected from Sholyar, Vazhachal reserve forest, Kerala; CESL 204, adult female collected from Pamba, Periyar tiger reserve, Kerala and CESL 369 adult male collected from Peppara, Cardemom hills, Kerala and BNHS 1033, adult female collected from Nilambur reserve forest, Kerala. Details of collection locality, specimen voucher and GenBank accession number in Appendix 1.

Diagnosis and comparison. A small sized *Monilesaurus* (SVL up to 73.8 mm) characterized by the posteroventral orientation of lateral scales; antehumeral fold well developed, extending across the throat; 52–58 midbody scale rows; nuchal crest composed of 3–4 long, well developed spines; two separated supratympanic spines; a long, distinct isolated postorbital spine; dorsal and lateral scales keeled, ventral scales strongly keeled; paired postmentals, first pair separated by a single scale; 24–28 subdigital lamellae under fourth finger, 26–34 subdigital lamellae under fourth toe; 9–10 supralabials and 8–9 infralabials; olive brown above with angular darker cross bars on dorsum, a white spot below the eye.

Morphologically *M. ellioti* is superficially similar to *M. montanus* **gen. et sp. nov.**, *M. rouxii* **comb. nov.**; and *M. acanthocephalus* **gen. et sp. nov.**, but can be distinguished by a combination of the following characters: 52–58 midbody scale rows (vs. 46–52 in *M. montanus* **gen. et sp. nov.**, 62–64 in *M. acanthocephalus* **gen. et sp. nov.**, and 52–56 in *M. rouxii*) presence of a long, distinct isolated spine in the posterior corner of orbit (vs. absent in *M. rouxii*; very small, indistinct tubercle like in *M. montanus* **gen. et sp. nov.**, and much longer in *M. acanthocephalus* **gen. et sp. nov.**); 3–4 long nuchal spines (vs. 3–6 small nuchal spines in *M. montanus* **gen. et sp. nov.**, 6 much longer nuchal spines in *M. acanthocephalus* **gen. et sp. nov.**, 7–8 smaller nuchal spines in *C. rouxii*); longer, prominent isolated spine on the back of head and above tympanum (vs. much smaller in *M. montanus* **gen. et sp. nov.**, and *M. rouxii*) and presence of a white spot below the eye (vs. absent in *M. rouxii*; in the form of a band in *M. montanus* **gen. et sp. nov.**) and smaller body size: adult SVL 59.4–73.8 mm, n=9 (vs. *C. montanus* **gen. et sp. nov.**, adult SVL 61–83.4 mm, n=8; and *M. acanthocephalus* **gen. et sp. nov.** adult SVL 68.9–72.6 mm, n=3).

Description. Based on CESL 045. A medium sized adult male (SVL-63.7 mm), Morphometric and meristic data are summarised in Appendix 2 & 3. General habitus moderately compressed. Head moderately large (HL/SVL ratio 0.29), elongate (HW/HL ratio 0.63), maximum height less than maximum width; snout pointed; rostral broader than high; nostrils in single nasal shield, which is separated from rostral by a single scale; mental shield narrower than rostral; two postmentals, first pair in contact with each other; genials keeled; gular scales strongly keeled, slightly smaller than genials; scales on top of snout smooth except median row, which is keeled; scales on top of head heterogenous in size and shape, keeled; supraorbital scales keeled; canthus-rostralis and supraciliary edge sharp; a spine at the posterior corner of the orbit; two separated long spines on posterior end of head, the anterior slightly longer, midway between nuchal crest and tympanum, posterior above tympanum; orbit diameter 70% of distance between anterior border of orbit and snout tip; tympanum exposed, its greatest diameter 54% horizontal diameter of orbit; enlarged keeled scale between tympanum and orbit; posterior region of jaws swollen; supralabials 10/10; infralabials 9/9.

Nuchal crest well developed, composed of four primary, long conical spines, the first being the smallest and the third longest; the remaining vertebral scales slightly enlarged relative to adjacent rows and possess a more pronounced median keel forming a serrated ridge like the dorsal crest which continues till the tail base; 54 longitudinal scale rows around midbody; scales on dorsum keeled, oriented postero-dorsally, while lateral ones oriented postero-ventrally; lateral scales smaller than dorsal, keeled; ventrals strongly keeled, irregular, slightly smaller than dorsals but of similar size as laterals, genials and gular scales; a strong, oblique antehumeral fold, nearly extending across the throat.

Limbs slender and covered with strongly keeled scales, larger than laterals, forming parallel longitudinal rows; scales under thighs weakly keeled; length of hindlimb ca. 87% SVL; relative length of fingers 4>3>2>5>1; relative lengths of toes 4>3>5>2>1; fourth toe longer than fifth finger; 23 subdigital lamellae under fourth finger; 27 subdigital lamellae under fourth toe; subdigital lamellae with sharp keels, bicarinate; tail slender, swollen at the base; scales on dorsal and ventral surface of tail with sharp keels, larger than laterals; tail length 172 mm.

Colouration. In life: dorsum and head blackish-brown with irregular lighter patches on the back; a light brown band from above the shoulder till the dorsal crest forming a 'v' shape; head laterally dark blackish with a white spot below the posterior end of eye; stripe from above nostril to anterior margin of orbit extending till the tympanum

from the posterior margin of orbit in the form of a black band; tympanum pale grey, lip scales white; a blackish triangular patch behind the tympanum continuing to the antehumeral fold; ventral uniformly lighter, pale grey; gular pouch with a reddish stripe extending beyond the throat; tail with alternating dark and light blotches forming irregular bands towards the end. Representative image showing live colouration (Fig. 6b). In preservative: colouration pattern mostly similar to that in life, except overall paler; bands on the head dull greyish brown.

Variation and secondary sexual characteristics. The other specimens examined agree with the CESL 045 in general morphology and scalation except for some differences that are summarised in Appendix 2 & 3. All the examined female specimens (CESL 047, CESL 058 and CESL 061) have much smaller nuchal spines compared to the males, reduced postero-orbital spine; lack a dorsal crest and gular sac; overall colouration olive-brown, lighter head and vertebral region, a dark band along the side of the head to the neck and presence of a black antehumeral fold.

Genetic distance. *M. ellioti* **comb. nov.** shows 1–2% intraspecific genetic divergence in the 16S gene; 4–7% interspecific genetic divergence from *M. rouxii* **comb. nov.**; 5–7% interspecific genetic divergence from *M. acanthocephalus* **gen. et sp. nov.** and 4–8% interspecific genetic divergence from *M. montanus* **gen. et sp. nov.** (Appendix 5).

Distribution. *Monilesaurus ellioti* **comb. nov.** is endemic to the Western Ghats and is distributed across the low and medium elevation forests (up to 1000 m asl) of southern parts of central Western Ghats (Coorg plateau and south) and the southern Western Ghats. This is one of the most common evergreen forest dwelling agamid lizards in this region. During this study, *M. ellioti* **comb. nov.** was recorded in various sites in the central and southern Western Ghats (See Fig. 3 & Appendix 1 for details).

Ecology and natural history. *Monilesaurus ellioti* is a diurnal lizard, semi-arboreal to arboreal in habit, and so far, has been recorded mostly in semi-evergreen and evergreen forests. Individuals were mostly seen perching on shrubs, branches and actively moving on tree trunks. In some instances, it has also been observed in coffee plantations surrounded by evergreen forests. In some sites like Parambikulam, Vazhachal reserve forest and Brahmagiri hills, it was observed to occur syntopically in the same habitat as *M. rouxii* **comb. nov.**, but more abundant within dense forests, while *M. rouxii* **comb. nov.** is generally restricted to forest edges. In some instances, gravid females were recorded during pre-and mid monsoon (June–August), which hints that monsoon might be a breeding season for this species.

Monilesaurus acanthocephalus **gen. et sp. nov.**

(Fig. 7a)

Etymology. The species epithet is derived by combining the Greek word ‘acanthos’, meaning spine or thorn, and ‘kephale’ latinized as ‘cephalus’ meaning head; referring to the long posterorbital and supratympanic spines.

Holotype. BNHS 2409, an adult male (Fig. 11) collected from a disturbed habitat, adjoining evergreen forest—tea garden edge in Upper Manalar (Fig. 12), Periyar tiger reserve, Megamalai (93°35. 81"N, 77°20'11. 43"E; 1562 m a.s.l) by SPV on 8th April 2009.

Paratypes. CESL 001 adult male and CESL 112 juvenile male collected by SPV on 8th April 2009; BNHS 2410 adult male collected by SPP on 4th September 2011 from Upper Manalar, Periyar tiger reserve, Megamalai (9°34'18. 25"N, 77°20'5. 02"E, 1547 m).

Diagnosis and comparison. A medium sized agamid (SVL = 72.6 mm) characterized by backward and downward orientation of lateral body scales; antehumeral fold present, throat fold present; 62–64 midbody scale rows; nuchal crest composed of 6 long, well developed spines; dorsal crest developed, in the form of a serrated ridge; two long, separated supratympanic spines; a long, well developed postorbital spine; dorsal and lateral scales keeled, ventral scales strongly keeled; paired postmentals, first pair separated by a 1 or 2 scales; 22–24 subdigital lamellae under fourth finger, 27–31 subdigital lamellae under fourth toe; 9 supralabials and 8 infralabials; reddish brown above with alternating dark and light crossbars on the dorsum, two white spots below the eye.

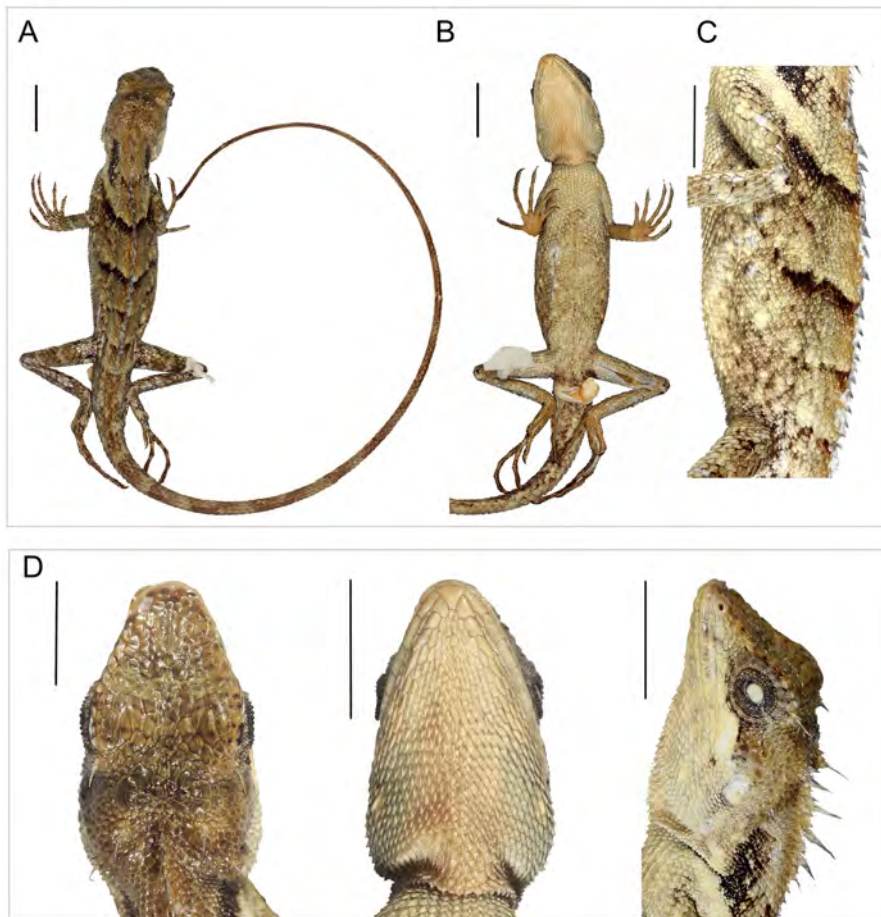


FIGURE 11. Holotype of *Monilesaurus acanthocephalus* **gen. et sp. nov.** (BNHS 2409). (A) full body dorsal (B) ventral (C) flank region (D) dorsal, ventral and lateral views of head. Scale bar: 10 mm.

Monilesaurus acanthocephalus **gen. et sp. nov.** can be distinguished from its congeners by a combination of the following characters: 62–64 midbody scale rows (vs. 46–52 in *M. montanus* **gen. et sp. nov.**, 52–58 in *M. ellioti* and 52–56 in *M. rouxii*); presence of much longer, distinct isolated spine in the posterior corner of orbit (vs. absent in *M. rouxii*; very small, indistinct tubercle like in *M. montanus* **gen. et sp. nov.**, and smaller in *M. ellioti*); 6 very long nuchal spines (vs. 3–6 small nuchal spines in *M. montanus* **gen. et sp. nov.**, 3–4 long nuchal spines in *M. ellioti*, 7–8 smaller nuchal spines in *C. rouxii*); longer, prominent isolated spine on the back of head and above tympanum (vs. much smaller in *M. montanus* **gen. et sp. nov.**, and *M. rouxii*) and presence of a white spot below the eye (vs. absent in *M. rouxii*; in the form of a band in *M. montanus* **gen. et sp. nov.**).

Description of holotype. BNHS 2409, a medium sized adult male (SVL: 72.6 mm), morphometric and meristic data are summarised in Appendix 2 & 3. General habitus moderately compressed. Head moderately large (HL/SVL ratio: 0.29), broad (HW/HL ratio: 0.65), maximum height less than maximum width; snout pointed; rostral broader than high; nostrils in single nasal shield, which is separated from rostral by a single scale; mental shield narrower than rostral; two postmentals; first pair in contact with each other; genials keeled; gular scales strongly keeled, slightly smaller than genials; scales on top of snout smooth except median row, which is keeled; scales on top of head heterogenous in size and shape, keeled; supraorbital scales keeled; canthus-rostralis and supraciliary edge sharp; a long, well developed, thick spine at the posterior corner of the orbit, ca. 54% the orbit in length; two separated spines on posterior end of head, the anterior much longer, between the nuchal crest and tympanum, posterior above tympanum; orbit diameter 56% of distance between anterior border of orbit and snout tip; tympanum exposed, its greatest diameter 49% horizontal diameter of orbit; enlarged keeled scale between tympanum and orbit; posterior region of jaws swollen; supralabials 9/8; infralabials 8/8.

Nuchal crest well developed, composed of six primary, long conical spines, the first being the smallest and the fourth longest; the remaining vertebral scales subtriangular, pointed, much larger than adjacent rows of scales, and

possessing a strong, median keel forming an elevated, serrated ridge like the dorsal crest which continues till the tail base; 62 longitudinal scale rows around midbody; scales on dorsum keeled, oriented postero-dorsally, while lateral ones oriented postero-ventrally; lateral scales smaller than dorsal, keeled; ventrals strongly keeled, irregular, slightly smaller than dorsals but of similar size as laterals, genials and gular scales; a strong, oblique antehumeral fold, extending across the throat.

Limbs long, slender and covered with strongly keeled scales, larger than laterals, forming parallel longitudinal rows; scales under thighs keeled; length of hindlimb ca. 79 % SVL; relative length of fingers 4>3>5>2>1; relative lengths of toes 4>3>5>2>1; fourth toe longer than fifth finger; 22 subdigital lamellae under fourth finger; 27 subdigital lamellae under fourth toe; subdigital lamellae with sharp keels, bicarinate; tail slender, swollen at the base; scales on dorsal and ventral surface of tail with sharply keeled, mucronate, larger than laterals; tail length 215 mm.



FIGURE 12. Habitat of *Monilesaurus acanthocephalus* **gen. et sp. nov.** at the type locality in Upper Manalar, Megamalai showing disturbed habitat comprising evergreen forests adjoining tea estates.

Colouration. In life: dorsum olive red with a light brown head, irregular alternating red and black blotches on the mid dorsum, the black blotches extend to the lateral side in the form of alternate ‘v’ shaped bands; 4–5 light green blotches on the lateral side followed by thin whitish stripes from behind shoulder till start of tail; two light broken dorsolateral stripes present; head laterally light olive with three dark black bands from posterior part of eye till tympanum and two white spots below the eye; tympanum off-white with light green edge, lip scales light grey; a large blackish triangular patch behind the tympanum continuing to the antehumeral fold; ventral uniformly white; gular pouch light reddish; tail with alternating spaced dark blotches forming irregular bands towards the end. In preservative: dorsum and head uniform light brown, back banded with five ‘U’ shaped black bands from neck to start of tail; the black bands extend midway laterally forming an alternating pale brown and black pattern; tail banded with alternating thick brown and grey blotches; head laterally pale brown with yellowish white lip scales, tympanum pale grey; ventrally uniform pale whitish yellow with darker blotches below the limbs.

Variation and secondary sexual characteristics. Morphometric and meristic data for the type specimens is presented in Appendix 2 & 3. The adult paratypes are all males and range from 68.9–72 mm in SVL. The paratypes agree with the holotype (CESL 002) in general morphology and scalation except for the following characters: 62–64 longitudinal scale rows around midbody; 22–24 subdigital lamellae under fourth finger, 27–31 subdigital lamellae under fourth toe; infralabials 9 on the left in CESL 001 and 9 on the right in CESL 410; 1st pair separated by a single scale in CESL 410. Dorsal and nuchal crest, spines above the orbit and tympanum not developed in the juvenile paratype CESL 112.

Genetic distance. *M. acanthocephalus* **gen. et sp. nov.** shows 4–6% interspecific genetic divergence in the 16S gene from *M. rouxii* **comb. nov.**; 5–6% interspecific genetic divergence from *M. ellioti* **comb. nov.** and 2–3% interspecific genetic divergence from *M. montanus* **gen. et sp. nov.** (Appendix 5).

Distribution. *Monilesaurus acanthocephalus* **gen. et sp. nov.** is currently known only from high elevations (above 1500 m asl) of Megamalai hills of southern Western Ghats (See Fig. 3 & Appendix 1 for details).

Ecology and natural history. *Monilesaurus acanthocephalus* **gen. et sp. nov.** is a diurnal lizard, semi-arboreal to arboreal in habit, and has, so far, been recorded from high elevation evergreen forests and along forest-tea garden edges (Fig. 12). Individuals were seen perching on shrubs, branches and on tree trunks. One of the type specimens (CESL 410) was found sleeping on a tree branch in a forest patch.

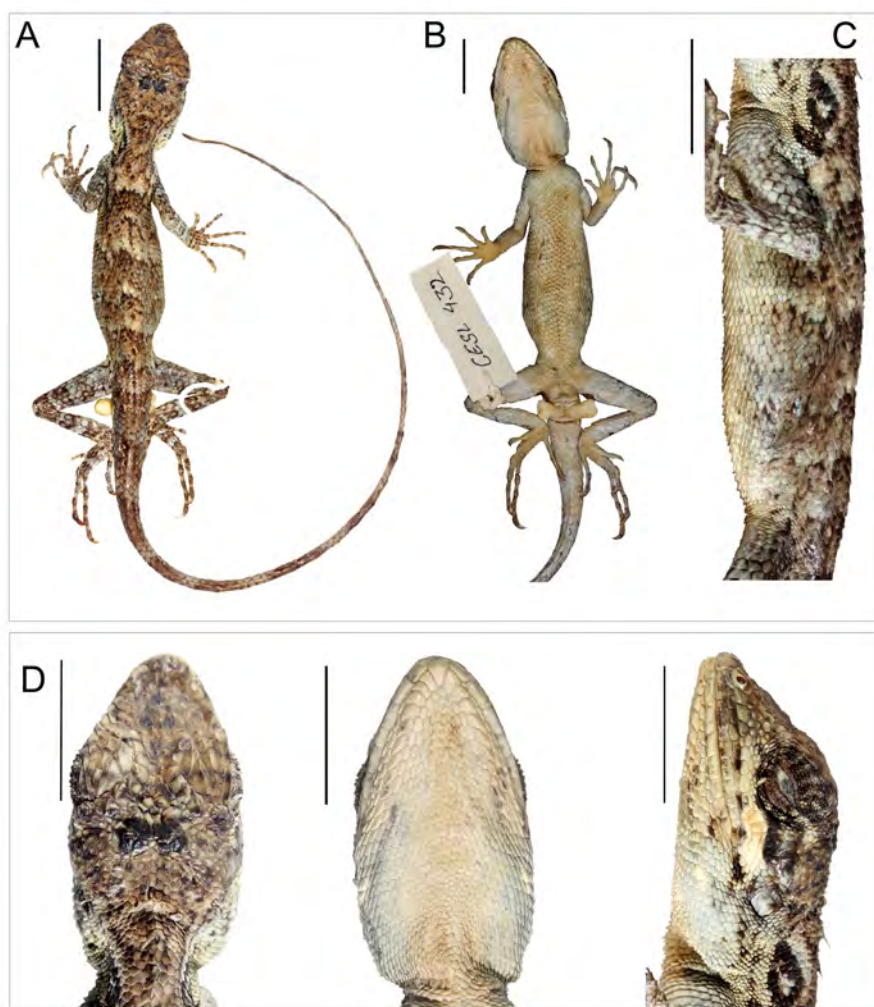


FIGURE 13. Holotype of *Monilesaurus montanus* **sp. nov.** (BNHS 2411). (A) full body dorsal (B) ventral (C) flank region (D) dorsal, ventral and lateral views of head. Scale bar: 10 mm.

***Monilesaurus montanus* gen. et. sp. nov.**

(Fig. 7b)

Etymology. The species epithet is derived from the word 'montane' referring to the restricted distribution of this species to high elevation forests (> 1500 m a.s.l.).

Holotype. BNHS 2411, adult male (Fig. 13), collected at Kudremukh National Park (Fig. 14), Karnataka (1307'54" N, 07516'39" E; 1534.9 m a.s.l.); by SPP, SPV and KPD on 28th September 2011.

Paratypes: BNHS 2412, adult male and BNHS 2413, adult female collected from Kudremukh National Park, Karnataka by SPV and ADR on 21st August 2009; CESL 131, adult female collected from Siruvani reserve forest, Kerala by SPP and MPV on 06th July 2010; CESL 133, adult female collected from Walakkad, Silent Valley National Park, Kerala by SPP and MPV on 23rd November 2010; CESL 330 adult female and CESL 331 an adult male collected from Naduvattam, Tamil Nadu by SPP on 23rd June 2011 and CESL 529 adult male collected from Narimala, Brahmagiri Wildlife Sanctuary, Karnataka by SPP and SRC on 09th March 2012.

Diagnosis and comparison. A medium sized *Monilesaurus* with a maximum SVL of 83.4 mm, arboreal species characterized by the backward and downward orientation of lateral body scales; presence of antehumeral fold, throat fold not prominent as the antehumeral fold; 46–52 midbody scale rows; nuchal crest composed of 3–6 small spines; two small separated supratympanic spines; a very small tubercle like postorbital spine barely distinguishable from the surrounding head scales; dorsal and lateral scales feebly keeled, stronger towards ventrals, ventral scales strongly keeled; scales on ventral thigh region feebly keeled; paired postmentals, first pair separated by a single scale; 21–24 subdigital lamellae under fourth finger, 25–30 subdigital lamellae under fourth toe; 9–10 supralabials and 8–9 infralabials; greenish brown above with darker dorsum, a white band below the eye extending till end of jaw.

Monilesaurus montanus gen. et sp. nov. can be distinguished from its sister species based on the combination of following characters: larger body size: adult SVL 61–83.4 mm, n=8 (vs. *M. ellioti* comb. nov. adult SVL 59.4–73.8 mm, n=9; *M. rouxii* comb. nov. adult SVL 51.4–74.8 mm, n=9); lower number of midbody scale rows 46–52 (vs. 62–64 in *Monilesaurus acanthocephalus* gen. et sp. nov., 52–58 in *M. ellioti* comb. nov., 52–56 in *M. rouxii* comb. nov.), presence of a very small, indistinct tubercle like, isolated spine in the posterior corner of orbit (vs. absent in *M. rouxii* comb. nov., long, distinct isolated spine in *M. ellioti* comb. nov. and *M. acanthocephalus* gen. et sp. nov.), 3–6 small nuchal spines (vs. 7–8 small nuchal spines in *M. rouxii* comb. nov., 6 much longer nuchal spines in *C. acanthocephalus* gen. et sp. nov., 3–4 long nuchal spines in *M. ellioti* comb. nov.); small isolated spine on the back of head and above tympanum (vs. longer, prominent spines in *M. ellioti* comb. nov. and *M. acanthocephalus* gen. et sp. nov.) presence of white band below the eye (vs. none in *M. rouxii* comb. nov.; in the form of a spot in *M. ellioti* comb. nov. and *M. acanthocephalus* gen. et sp. nov.).

Description of holotype. BNHS 2411, a medium sized agamid, adult male (SVL-78.2 mm). Morphometric and meristic data are summarised in Appendix 2 & 3. General habitus moderately compressed. Head moderately large (HL/SVL ratio 0.31), broad (HW/HL ratio 0.64), maximum height less than maximum width; snout pointed; rostral broader than high; nostrils in single nasal shield, which is separated from rostral by a single scale; mental shield narrower than rostral; two postmentals; first pair separated from each other by a single, small scale; genials keeled; gular sac small, composed of strongly keeled scales, slightly smaller than genials; scales on top of snout smooth except median row, which is keeled; scales on top of head heterogenous in size and shape, keeled; supraorbital scales keeled; canthus-rostralis and supraciliary edge sharp; a very small tubercle like spine at the posterior corner of the orbit; two separated small spines on posterior end of head, the anterior slightly longer, midway between nuchal crest and tympanum, posterior above tympanum; orbit diameter 59% of distance between anterior border of orbit and snout tip; tympanum exposed, its greatest diameter 48% of horizontal diameter of orbit; slightly keeled, enlarged scales between tympanum and orbit; posterior region of jaws swollen; supralabials 9/9; infralabials 8/8.

Nuchal crest well developed, composed of three primary, conical spines, the first being the shortest, the third longest; the remaining vertebral scales slightly enlarged relative to adjacent rows and possess a median keel forming a slightly elevated ridge like dorsal crest which continues till the tail base; 50 longitudinal scale rows around midbody; 40 scales on the mid dorsum; scales on dorsum feebly keeled, oriented backwards, lateral scales smaller than dorsal, keeled, oriented backwards and downwards; ventrals strongly keeled, irregular, slightly smaller than dorsals but of similar size as laterals, genials and gular scales; an oblique antehumeral fold present, weakly developed, feebly extending into a throat fold which is not prominent.

Limbs slender and covered with strongly keeled scales, larger than laterals, forming parallel longitudinal rows; scales under thighs weakly keeled; length of hindlimb ca. 71% SVL; relative length of fingers 4>3>2>5>1; relative lengths of toes 4>3>5>2>1; fourth toe much longer than fifth finger; 23 subdigital lamellae under fourth finger; 28 subdigital lamellae under fourth toe; subdigital lamellae with sharp keels, bicarinate; slender, swollen at the base; scales on dorsal and ventral surface of tail with sharp keels, mucronate; tail length 190 mm.

Colouration. In life: dorsum and head yellowish-green with irregular, alternating light and dark brown patches on the back; a dark brownish band from above the shoulder till the dorsal crest forming a ‘v’ shape; head laterally greenish with a whitish band below the posterior end of eye to end of jaw; broken dark striations from above nostril to anterior margin of orbit extending till the tympanum from the posterior margin of orbit in the form of black band; tympanum pale green, lip scales white; thick blackish triangular patch behind the tympanum continuing to the antehumeral fold; an indistinct thin stripe above the labials from the nostril, ending into a black spot anterior to the tympanum; ventral uniformly lighter, pale grey; gular pouch white, irregular dark striations on the sides; tail with alternating dark and light blotches forming irregular bands towards the end.

In preservative: dorsum and head buff to light brown with irregular, alternating grey and darker brown patches on the back; tail banded with alternating thick brown and grey blotches; laterally paler with darker brown blotches extending down from the dorsum; head laterally speckled with grey and brown with a whitish yellow below the posterior end of eye to end of jaw; tympanum pale white, lip scales whitish yellow; ventrally uniform pale grey, lighter below the limbs.



FIGURE 14. Habitat of *Monilesaurus montanus* gen. et sp. nov. at the type locality in Kudremukh hills, showing montane forests.

Variation and secondary sexual characteristics. Morphometric and meristic data for the type specimens is presented in Appendix 2 & 3. Adult male paratypes range from 61–78.8mm in SVL, whereas adult female paratypes range from 68.4–83.4mm in SVL. The paratypes agree with the holotype (BNHS 2411) in general morphology and scalation except for the following characters: 46–52 longitudinal scale rows around midbody; 21–24 subdigital lamellae under fourth finger, 25–30 subdigital lamellae under fourth toe. Supralabials 8 on the right in CESL 124; infralabials 8 on the right in CESL 133 and 8 on the left in CESL 529. All the examined female

paratypes (CESL 126, CESL 131, CESL 133 and CESL 331) have slightly smaller nuchal spines compared to the males; lack a dorsal crest and gular sac.

Genetic distance. *M. montanus* **gen. et sp. nov.** shows 0–1% intraspecific genetic divergence in the 16S gene; 7–8% interspecific genetic divergence from *M. rouxii* **comb. nov.**; 4–8% interspecific genetic divergence from *M. ellioti* **comb. nov.** and 2–3% interspecific genetic divergence from *M. acanthocephalus* **gen. et sp. nov.** (Appendix 5).

Distribution. *Monilesaurus montanus* **gen. et sp. nov.**, is endemic to the Western Ghats and distributed across the high elevation evergreen forests (above 1250 m asl) of central Western Ghats. During this study, *M. montanus* **gen. et sp. nov.** was recorded from montane forests of the following hill ranges: Kudremukh, Brahmagiri, Nilgiri and Elivalmalai (See Fig. 3 & Appendix 1 for details).

Ecology and natural history. *Monilesaurus montanus* **gen. et sp. nov.**, is a diurnal lizard, semi-arboreal to arboreal in habit and so far, has been recorded from montane shola forests (Fig. 14). Individuals were mostly found at night, sleeping on branches of stunted trees within sholas or actively moving on tree trunks. Only in one instance, a female specimen (CESL 133) was found in evergreen forest at a slightly lower elevation (ca. 1250 m asl). In some sites, the lower elevational limits of their distributional range might overlap with the range of *M. ellioti* **comb. nov.**, but these two species were not observed to be syntopic in any of the sites. A gravid female was recorded in the month of July in Siruvani reserve forest, which hints that pre-monsoon might be a breeding season for this species. No other congeners were found to be syntopically distributed with *M. montanus* **gen. et sp. nov.**

***Psammophilus* Fitzinger, 1843**

Type species: *Agama dorsalis* (Gray, 1845)

Content: *Psammophilus dorsalis*, *Psammophilus blanfordanus* (Stoliczka, 1871)

Etymology: None provided but probably from Latin “Psammo” meaning sand and “Philus” meaning loving.

Diagnosis. The genus *Psammophilus* can be distinguished from the genera *Cophotis*, *Ceratophora*, *Lyriocephalus*, *Ptyctolaemus*, *Phoxophrys*, *Japalura otai* Mahony 2009, *J. planidorsata* Jerdon, 1870, *J. sagittifera* Smith, 1940 and *Otocryptis* by the presence of an external tympanum (Boulenger, 1885; Smith, 1935; Inger, 1960; Pethiyagoda & Manamendra-Arachchi 1998; Schulte II *et al.* 2004; Bahir & Silva 2005; Manamendra-Arachchi *et al.* 2006; Samarawickrama *et al.* 2006); from other members of genus *Japalura* by the absence of heterogeneous dorsal scales and short and thick nuchal scales.

The genus *Psammophilus* can be diagnosed from all other species of draconinae lizards from the Indian subcontinent except *Calotes minor*, in having a dorso-ventrally compressed body. *Psammophilus* differs from *Calotes minor* in having small body scales and higher number of around the body scales 80–150 (vs 48–60). *Psammophilus* are characterized by a medium to large adult body size (SVL mm to mm); body dorso-ventrally compressed; presence of an antehumeral fold; supratympanic spines present, reduced in size; dorsal and lateral scales rows slightly irregular; nuchal and dorsal crest small, reduced; dorsal and lateral scales small, keeled, scale rows directed postero-dorsally. *Psammophilus* can be distinguished from its sister genus *Monilesaurus* **gen. nov.** and *Calotes* in having a dorso-ventrally compressed body (vs dorso-laterally compressed) and higher number of scales on the mid-body scales (more than 80 vs less than 65) and reduced nuchal crest (vs. well developed); and from *Microauris* **gen. nov.** by having a relatively large tympanum (Fig. 9d vs 9b). Scales on head large uniform shield like (vs small, sub-triangular) (Fig. 10c vs 10d). Supratympanic spines are present, in the form of two separated spines vs clusters in *Calotes*. *Psammophilus* are sexually dimorphic, adult males are larger than females and have enlarged cheeks. *Psammophilus* are also sexually dichromatic; during breeding season males acquire bright yellow and orange colors on the dorsum while females remain dull to dark brown with or without orange/yellow spots.

Taxonomic comments. The two species *Psammophilus dorsalis* and *Psammophilus blanfordanus* were earlier placed in the genus *Agama* (Daudin, 1802) and the now obsolete genus *Charasia* (Gray, 1845). Smith (1935) transferred the two species *Charasia dorsalis* and *Charasia blanfordanus* to the genus *Psammophilus*. Most likely due to their dorso-ventrally compressed body, *Psammophilus* was placed among the Agaminae but molecular data suggest that they are nested well within the subfamily Draconinae.

Both *P. dorsalis* and *P. blanfordanus* have been recorded in the Western Ghats (Smith, 1935). Stoliczka (1871) provided a brief description of *P. blanfordanus* without mentioning a type locality and later provided a detailed description (Stoliczka, 1872) based on a large number of samples collected from central India (Udaypore west of Chotanagpur, West of Raipore, West of Ranchi) which are currently recognized as syntypes in ZSI with additional syntypes in NMW and ZMB (Das *et al.* 1998). Stoliczka (1872) also mentions that *P. blanfordanus* is not uncommon in Parisnath (Parasnath) hill. *Psammophilus dorsalis* was described by Gray (1831).

The key character to diagnose this species is number of scales around the body, which overlap with each other (Boulenger, 1885; Smith, 1935). Boulenger (1885) used a combination of specimens from Southern India (Nilgiris, Malabar, Madras and a few specimens with locality “India”) to describe *P. dorsalis*. To describe *P. blanfordanus*, Boulenger (1885) used specimens from Godavari valley and “Jeypore” (Northern Andhra) and Ranchi (now in Jharkhand state). One single specimen collected from Parasnath, Jharkhand that is relatively close to the type locality (Central India) of *P. blanfordanus* had 1–3% genetic divergence in the 16S gene from *P. dorsalis* samples used in this study.

We were unable to find *P. blanfordanus* from the Western Ghats during our fieldwork. Given the amount of morphological variation among the observed individuals and wide distribution of this group, we would suggest a thorough evaluation of this species group from the entire peninsula with detailed sampling. In the present work, we only describe *P. dorsalis* as we were unable to confirm the presence of *P. blanfordanus* in the Western Ghats.

Members. *Psammophilus dorsalis* and *Psammophilus blanfordanus*.

***Psammophilus dorsalis* (Gray, 1831)** (Fig. 8a)

Agama dorsalis—Gray, 1831. In Griffith, E & E. Pidgeon’s Anim. King. ix, 1851: 56

Charasia dorsalis—Gray, 1845. Cat. Liz. Brit. Mus. 1845: 246.

Charasia dorsalis—Boulenger, 1885. Cat. Liz. Brit. Mus. 1845: 450.

Psammophilus dorsalis—Smith, 1935. Fauna of British India, ii, 1935: 209.

Original description. Gray, J. E. 1831. A synopsis of the species of Class Reptilia. In: Griffith, E & E. Pidgeon: The animal kingdom arranged in conformity with its organisation by the Baron Cuvier with additional descriptions of all the species hither named, and of many before noticed [V Whittaker, Treacher and Co., London: 481 + 110 pp. [1830]

Taxonomic comments. Gray (1831) failed to mention which specimens he used to describe *P. dorsalis*. Currently, there are 20 specimens labelled as *P. dorsalis* at the Natural History Museum. Boulenger (1885) used eight specimens at NHM to describe *Charasia dorsalis* collected from Madras, Nilgiris, Malabar and India and labelled these collections as being from Southern India.

There was no precise type locality given in the original description but most of the localities mentioned in older publications suggest collections from different parts of southern India, especially hilly regions (Boulenger 1890; Smith 1935). The chronological collections of the specimens from NHM need to be verified to choose a lectotype from the specimens at NHM. Since there is very little genetic variation (1–2% in 16S mtDNA) in the samples collected from the Western Ghats of Peninsular India, we provide an expanded description of this species based on the largest male collected during this study and compare with other specimens collected during the study.

Topotypic material. CESL 273, adult male collected from a boulder in grassland in Kotavasal, Achankovil reserve forest, Kerala by SPP and MVP on 28th May 2011.

Other material examined. CESL 326 adult male collected from Kolakumbai, Nilgiri hills, Tamil Nadu; CESL 064 adult female collected from sunrise valley, Wayanad reserve forest, Kerala and CESL 181 adult female collected from near Rishi Valley school, Andhra Pradesh; details of collection locality, specimen voucher and GenBank accession number in Appendix 1.

Diagnosis and comparison. A medium to large sized *Psammophilus* characterized by the posterodorsal orientation of lateral scales; antehumeral fold well developed; 94–148 midbody scale rows (vs 115–140 in Boulenger, 1885; 115–150 Smith, 1935); ventral scales 112–152; nuchal crest reduced, composed of 15–18 very small, triangular spines, continuous with almost equal to or even smaller dorsal crest which appears like slightly raised denticulation; dorsal crest absent in females and juveniles; two separated, very small supratympanic spines;

dorsal and lateral scales keeled, ventral scales strongly keeled; paired postmentals, first pair separated by 1–2 scales; 24–28 subdigital lamellae under fourth finger, 26–34 subdigital lamellae under fourth toe; 11–13 supralabials and 10–12 infralabials; adult males with uniform greyish brown to black body, dorsum lighter; indistinct lighter blotches on the sides, lip scales lighter grey or off-white; females and juveniles with a pair of dorsolateral stripes from neck to above tail, dorsum and lateral speckled with lighter spots.

Morphologically, *P. dorsalis* is similar to *P. blanfordanus*, the only other species known from this group, but can be distinguished by a combination of the following characters: 100–140 midbody scale rows (vs 80–100); three samples collected from eastern India close to the type locality of *P. blanfordanus* also had lower number 84–94 (80–100 Boulenger 1885 & Smith, 1935). Midbody scales row counts clearly overlap with *P. dorsalis*. Furthermore, all the meristic characters we checked for few specimens overlap (Appendix 3). There is, therefore a need for more thorough examination of morphological and morphometric characters with a larger sample size to diagnose *P. dorsalis* from *P. blanfordanus*.

Description. Based on CESL 273, a large sized adult male (SVL-107.7 mm), morphometric and meristic data are summarised in Appendix 2 & 3. General habitus moderately depressed. Head moderately large (HL/SVL 0.25), not elongated (HW/HL 1.10), maximum width much more than maximum height; snout rounded; rostral broader than high; nostrils in single nasal shield, which is separated from the rostral by two scales; mental shield broader than rostral; two postmentals, first pair separated by two small scales; genials smooth; gular scales keeled, smaller than genials; scales on top of snout feebly keeled towards the edges; scales on top of head heterogenous in size and shape, keeled; supraorbital scales keeled; canthus-rostralis and supraciliary edge sharp; two separated small, triangular spines on posterior end of head, the anterior midway between nuchal crest and tympanum, posterior above tympanum; orbit diameter 65% of distance between anterior border of orbit and snout tip; tympanum exposed, its greatest diameter 39% horizontal diameter of orbit; few slightly enlarged, smooth scales between tympanum and orbit; posterior region of jaws swollen; supralabials 13/13; infralabials 12/12.

Nuchal crest developed, composed of 15 primary, small, triangular spines, the first being the smallest and the eight longest; nuchal crest continuous with a reduced dorsal crest present in the form of elevated serrated ridge, composed of vertebral scales with a more pronounced median keel continuing till above the vent, on the tail in the form of enlarged strongly keeled median scale; 104 longitudinal scale rows around midbody; dorsal and lateral scales keeled, oriented postero-dorsally; ventrals smooth, irregular, as large as the dorsals, slightly larger than the genial and gular scales; an oblique antehumeral fold present, not extending across the throat.

Limbs strong, robust, covered with uniform keeled scales, slightly larger than laterals forming parallel longitudinal rows; scales under thighs weakly keeled; length of hindlimb 71% SVL; relative length of fingers 4>3>2>5>1; relative lengths of toes 4>3>5>2>1; fourth toe slightly smaller than fifth finger; 15 subdigital lamellae under fourth finger; 19 subdigital lamellae under fourth toe; subdigital lamellae with sharp keels, bicarinate; tail thick, gradually tapering, swollen at the base; scales on dorsal and ventral surface of tail with sharp keels, larger than laterals; median scales on the dorsal surface of tail enlarged, with a pronounced median keel; tail length 147 mm (incomplete, broken at the tip).

Colouration. In life: head and body dull blackish-grey with irregular lighter patches near the flank; a longitudinal thick, lighter buff band from behind the head till above the tail; head laterally darker with indistinct reddish brown speckles behind the orbit, a broken reddish stripe from above the nostril till behind the posterior part of orbit covering the supraorbital region; another pale reddish stipe from the nostril till behind the cheek covering the lip scales and lower margin of tympanum; tympanum pale grey; ventral uniformly lighter, pale grey; gular and genial scales lighter, dirty white; tail with a thick lighter band just at the start, then uniform dark grey followed by indistinct lighter bands, bands more prominent towards the tip. In preservative: colouration pattern mostly similar to that in life, except overall paler; bands on lateral side of head distinct.

Variation and secondary sexual characteristics. The other specimens examined agree with the CESL 273 in general morphology and scalation except for some differences that are summarised in Appendix 2 & 3. The examined female specimen (CESL 064) has slightly smaller nuchal spines compared to the males, dorsal crest almost nonexistent; dorsal and lateral scales feebly keeled; tail base not swollen; overall colouration olive-brown, speckled with irregular lighter blotches, 3–4 triangular darker patches on the mid dorsum from neck to the start of tail and series of whitish spots forming broken parallel dorso-lateral stripes.

Distribution. *Psammophilus dorsalis* is distributed all across the low and medium elevation rocky habitats of central and southern Western Ghats. This species has often been observed on huge rock boulders and sheath rocks

in and around forests but seem to be more common in open, drier habitats. During this study, *P. dorsalis* was recorded in various sites from the southern Western Ghats (See Appendix 1 for details). It is also known from drier habitats throughout peninsular India.

Ecology and natural history. *Psammophilus dorsalis* is a diurnal lizard, chiefly rupicolous in habit, and so far, has been recorded exclusively in and around rocky habitats. Individuals were mostly observed basking on boulders and rock cliffs in the mornings. In some instances, it has also been observed on isolated rocks inside tea estates and plantations. It is a very shy and active species and escapes inside the gaps and crevices among boulders at the slightest hint of an approaching threat. In the breeding season, the adult males of this species develop a thick bright red to vermilion coloured band from the head extending till behind the lower back and the entire remaining body turns black. Adult males have been observed only during summer and pre-monsoon while gravid females were found in the early monsoon seasons.

***Microauris* gen. nov.**

(Fig. 8b)

Type species. *Calotes aurantolabium* (Krishnan, 2008)

Etymology. The genus epithet is derived by adding the word ‘Micro’ as a prefix to the Latin word ‘auris’ meaning ear, referring to the extremely small tympanum of this genus.

Diagnosis. *Microauris* **gen.nov.** differs from all other members of draconinae lizards from the Indian subcontinent in having the smallest tympanum. *Microauris* **gen.nov.** differs from *Mantheyus phuwuanensis* by the absence of femoral pores (Manthey & Nabhitabhata, 1991; Ananjeva & Stuart 2001); from the members of the genus *Bronchocela* by the absence of a fold of skin from angle of jaw to shoulder (Hallermann & Böhme 2000). *Microauris* **gen. nov.** can be easily diagnosed from the genera *Otocryptis*, *Sarada* and *Sitana* by the presence of a well-developed fifth toe (Smith, 1935; Deepak *et al.*, 2016); from *Cophotis*, *Ceratophora*, *Lyriocephalus*, *Ptyctolaemus*, *Phoxophrys*, *Japalura otai*, *J. planidorsata*, *J. sagittifera* and *Otocryptis* by the presence of external tympanum (Boulenger, 1885; Smith, 1935; Inger, 1960; Pethiyagoda & Manamendra-Arachchi 1998; Schulte II *et al.* 2004; Bahir & Silva 2005; Manamendra-Arachchi *et al.* 2006; Samarawickrama *et al.* 2006). *Microauris* **gen. nov.** can be diagnosed from other members of genus *Japalura* by the absence of heterogenous dorsal scales and short and thick nuchal scales; from *Salea* by the absence of enlarged plate like scales between the eye and tympanum (Smith, 1935). *Microauris* **gen. nov.** can be diagnosed from the members of *Psammophilus* and *Monilesaurus* by the absence of a well developed antehumeral fold. *Microauris* **gen. nov.** can be diagnosed from *Complicatus nigrigularis*, *Hypsicalotes kinabaulensis*, *Malayadracon robinsonii*, *Oriocalotes*, *Pseudocophotis* and *Pseudocalotes* by the absence of enlarged row of suborbital scales (Smith, 1935; Taylor 1963; Ota & Hikida, 1991; Manthey & Denzer 1992; Inger & Steubing 1994; Ota & Hikida, 1996; Hallermann & Böhme 2000; Manthey & Denzer, 2000; Hallermann & McGuire 2001; Leong 2001; Manamendra-Arachchi *et al.* 2006; Samarawickrama *et al.* 2006; Ananjeva *et al.* 2007; Hallermann & Böhme 2007; Das & Lakim 2008; Hallermann *et al.* 2010; Mahony 2010; Harvey *et al.* 2014; Denzer *et al.* 2015; Grismer LL *et al.* 2016; Harvey *et al.* 2017).

Microauris **gen.nov.** can be distinguished from the members of the genus *Calotes* (*C. bachae*, *C. bhutanensis*, *C. calotes*, *C. ceylonensis*, *C. chincollium*, *C. desilvai*, *C. emma*, *C. grandisquamis*, *C. hutunwini*, *C. irawadi*, *C. jerdoni*, *C. liocephalus*, *C. liolepis*, *C. versicolor*, *C. manamendrai*, *C. maria*, *C. medgoensis*, *C. minor*, *C. mystaceus*, *C. nemoricola*, *C. nigrilabris*, *C. nigriplicatus* and *C. pethiyagodai*) and *Lophocalotes* (Günther, 1872) in having the smallest tympanum (Hardwicke & Gray, 1827; Duméril and Bibron, 1837; Gray, 1845; Jerdon, 1854; Günther, 1864; Günther, 1870, Günther, 1872, Günther, 1875; Boulenger, 1885; Biswas, 1975; Zhao & Li, 1984; Hallerman, 2000; Vindum *et al.* 2003; Hallerman *et al.* 2004; Bahir & Maduwage, 2005; Zug *et al.* 2006; Manthey, 2008; Krishnan, 2008; Hartmann *et al.* 2013; Amarasinghe *et al.* 2014a,b; Deepak *et al.* 2015).

Suggested English. Small-eared dragon

Holotype. BNHS 1436, an adult female collected from Kalakkad Mundanthurai Tiger Reserve, Tamil Nadu, India; by N. M. Ishwar in 1997.

Referred specimens. CESL 104, an adult female collected from a branch in the canopy of a shola forest tree near Chemunji peak, Peppara Wildlife Sanctuary, Kerala, India; by SPP, SPV, MVP, VTR and ADR in 18th August 2010.

Taxonomic comments. *Microauris aurantolabium* **comb. nov.** was described as *Calotes aurantolabium* in

2008 based on a single specimen (Krishnan 2008). Prior to this, the specimen was wrongly identified and reported as the rediscovery of *Calotes andamanensis*. (Ishwar and Das, 1998). During our fieldwork in the Agasthyamalai hills of Kerala in August 2010, we found a single female specimen sleeping on a branch of a tree in a shola forest. There have been no other reports of this species thereafter and thus all the known specimens are females. There is a clear gap in the knowledge of the morphology of this rare lizard considering that male lizards are known to be better representatives for morphological characterization because of the presence of secondary sexual characters. In spite of this, the two specimens share some common characters, which are unique to this lizard. Based on the presence of unique morphological characters along with the phylogenetic position of this species in the subfamily Draconinae, we designate this species as a new monotypic genus.

Diagnosis. A medium sized light green agamid lizard with a distinct orange streak from above the lip scales till behind the jaw; a moderately broad head with a pointed snout; very small tympanum relative to the orbit diameter (TymD/OrbD = 0.14–0.19); acutely keeled scales over the body and throat; scales on head small, sub-triangular (vs. uniform shield like in members of genus *Calotes*); 3rd and 4th toe almost equal in length; dorsal and lateral body scales oriented backwards and downwards; nuchal crest indistinct, poorly developed; supratympanic and postorbital spines absent and a long and slender tail.

Description of the Holotype. BNHS 1436; a medium sized agamid, adult female (SVL-68.5 mm) Morphometric and meristic data are summarised in Appendix 2 & 3. General habitus moderately compressed. Head moderate (HL/SVL ratio 0.28), broad (HW/HL ratio 0.56), maximum height less than maximum width; snout pointed; rostral broader than high; nostrils in single nasal shield, which is separated from rostral by a single scale; mental shield almost as wide as the rostral; two postmentals; first pair touching each other at the base; genials partially keeled; gular sac small, composed of partially keeled scales, slightly smaller than genials; scales on the snout smooth, unkeeled; scales on top of head heterogenous, keeled, small, subtriangular; supraorbital scales keeled; orbit diameter 95% of distance between anterior border of orbit and snout tip; tympanum very small, exposed, its greatest diameter 11% of horizontal diameter of orbit; slightly keeled scales between tympanum and orbit; posterior region of jaws partially swollen; supralabials 10/10; infralabials 11/11.

Nuchal crest poorly developed, composed of 13 small conical spines; the remaining vertebral scales slightly enlarged relative to adjacent rows and possess a more pronounced median keel; 54 longitudinal scale rows around midbody; scales on dorsum keeled; lateral scales smaller than dorsal, keeled, oriented postero-ventrally; ventrals slightly larger than dorsals, genials and gular scales strongly keeled.

Limbs slender and covered with strongly keeled scales, larger than laterals; scales under thighs keeled; length of hindlimb ca. 64% SVL; relative lengths of toes 4≈3>5>2>1; fourth toe and third toe subequal; 20 subdigital lamellae under fourth finger; 21 subdigital lamellae under fourth toe; tail slender, long; scales on dorsal and ventral surface of tail with sharp keels, mucronate, slightly larger than laterals; tail length 117 mm.

Colouration. In life (CESL 104): dorsum and head uniform, light green overall with a distinct reddish orange streak from above the third lip scale covering 2–3 scale rows below the tympanum, ending just at the shoulder. A distinct pale whitish grey band, edged with black speckles from the base of tail till underside of knee. Mid-dorsal scales edged anteriorly with black, which is visible when the body is inflated; gular scales lighter, yellowish green; ventrally brighter, uniform green with a few rows of pale whitish scales towards the lateral side. This lizard was observed to quickly change its body color to dark blackish-brown on disturbance but the orange streak and band on thigh remained unchanged.

In preservative: dorsum and head uniform, overall pale blue with brownish patches above the eyes and neck continuing on the mid-dorsal line, broader towards the tail; tail pale brown; orange lip streak paler turning whitish towards the neck; laterally pale blue with anteriorly black edged scales; ventrally pale whitish grey overall; limbs edged with brown blotches, broader towards the tips.

Distribution. Currently, this lizard is known only from two sites in the high elevation tropical evergreen forests of Agasthyamalai hills. The second locality near Chemunji peak in Peppara wildlife sanctuary is approximately 50 kms northeast of the type locality near Kakachi in KMTR (See Appendix 1 for details). Both these sites are separated by almost contiguous shola grassland mosaic on undulating hills.

Ecology and natural history. Nothing much is known about the ecology and natural history of this species. Ishwar and Das (1998) reported sightings of 3 individuals, all gravid females in the month of August. Two of these lizards laid 4 elliptical eggs each. This suggests that monsoon might be a breeding season for this lizard. Ishwar and Das (1998) also mentioned that this is a canopy dwelling species. The fact that it was only found again 12 years

after its discovery and that too from a fairly well explored habitat suggests that this might be a rare lizard or it may occur high in the canopy of rain forests and thus escape detection.

Revised key to the genera of agamids from Peninsular India

- I. Ribs much prolonged, supporting a wing like expansion *Draco*
- II. No wing like expansion. A, B
- A. Tympanum exposed, large, distinct. 1
- 1a. 5th toe present, 4th toe longest; large uniform shield like head scales 2
- 2a. Dorsal scales large, unequal, strongly imbricate. *Salea*
- 2b. Dorsal scales uniform, regularly arranged; supratympanic spines present; 3
- 3a. Dorso-ventrally compressed body; body scales small, higher number of scale rows; supratympanic spines small, nuchal and dorsal crest reduced. *Psammophilus*
- 3b. Dorso-laterally compressed body; nuchal and dorsal crest well developed 4
- 4a. Well developed antehumeral fold; two separated supratympanic spines; body scales rows directed posteroventrally *Monilesaurus* **gen. nov.**
- 4b. Antehumeral fold absent; supratympanic spines as clusters or in rows; body scales rows directed posterodorsally. *Calotes*
- 1b. 5th toe absent; males with well developed dewlap. 5
- 5a. Enlarged strongly keeled scale on the thigh, flank region and the around tympanum; flank scales heterogeneous. *Sitana*
- 5b. Absence of enlarged strongly keeled scale on the thigh, flank region and around tympanum; flank scales homogeneous. *Sarada*
- B. Tympanum not exposed or if present then very small, less than half of orbit. 6
- 6a. 5th toe not longer than the 1st. *Otocryptis*
- 6b. 3rd and 4th toe sub-equal; supratympanic spines absent; scales on head small, sub-triangular *Microauris* **gen. nov.**

Revised key to the genus *Calotes*

modified from Smith, 1935; Hallermann 2000; Zug et al (2006), Vindum (2003), Amarasinghe (2014a,b, 2015). Geographic distribution Himalayas (H), Indo-Chinese region (IC), Indonesia (I), Sri Lankan Endemic (SLE), Western Ghats Endemic (WGE), Eastern Ghats (EG) and Indian subcontinent (IS). Note the key is not dichotomous.

- 1a. Scales on side of body pointing backwards and upwards (2)
- 1b. Scales on side of body pointing backwards and straight. (17)
- 1c. Scales on side of body pointing backwards and downwards (18)
- 2a. No fold in front of shoulder. (3)
- 2b. An oblique fold or triangle pit in front of shoulder covered with small scales. (11)
- 3a. Enlarged scales/plates between orbit and tympanum present, supratympanic spines two cluster, tail less than or equal to SVL *C. minor* (IS)
- 3b. Enlarged scales/plates between orbit and tympanum absent. (4)
- 4a. Single row of supratympanic spines, tail very long (greater than 320 % of SVL) *C. calotes* (IS)
- 4b. Tail not very long compared SVL (less than 300 %) (5)
- 5a. Two parallel rows of compressed spines above tympanum present, color green in life *C. maria* (IC)
- 5b. Two parallel rows of compressed spines above tympanum absent. (6)
- 6a. Two clusters of supratympanic spines, one erect scale row by the side of the neck present, black variegated patches on the body *C. bhutanensis* (H)
- 6b. Erect scale row by the side of neck absent (7)
- 7a. Two clusters of supratympanic spines, no erect scale row by the side of neck, variably colored, mid-dorsal scales as large as nuchal scales in males. *C. versicolor* (IS)
- 7b. Mid-dorsal scales not as large as nuchal scales in males (8)
- 8a. Scales on the shoulder with similar sized scales relative to the neck scales. (9)
- 8b. Scales on the shoulder very small in size relative to neck scales (10)
- 9a. Scales on side of neck and adjacent shoulder area horizontal, two clusters of supratympanic spines *C. htunwini* (IC)
- 9b. Scales on side of neck and adjacent shoulder area obliquely upwards two clusters of supratympanic spines, adults with narrow dorsal bars middorsally *C. irawadi* (IC)
- 10a. Supratympanic spines single/two cluster, mid-body scale rows 36–43 *C. nemoricola* (WGE)
- 10b. Supratympanic spines two cluster, mid-body scale rows 27–35. *C. grandisquamis* (WGE)
- 11a. Two parallel rows of compressed spines above tympanum (12)
- 11b. No parallel rows of compressed scales above tympanum. (13)
- 12a. Antehumeral pit narrow slit, scales on the lateral body feebly keeled, lateral body with or without dark maroon stripes extend-

	ing in to tail	<i>C. jerdoni</i> (IC)
12b.	Antehumeral pit relatively broad at the base, scales on the lateral body smooth, lateral body without any stripe.	<i>C. medogenensis</i> (IC)
13a.	Post orbital spine present.	<i>C. emma</i> (IC)
13b.	Post orbital spine absent	(14)
14a.	White or yellow stripes above lip extending to shoulder present	(15)
14b.	White or yellow stripes above lip extending to shoulder absent.	(16)
15a.	Relative distance between leg insertions shorter, mid-body scale rows 48–59	<i>C. bachae</i> (IC)
15b.	Relative distance between leg insertions longer, mid-body scale rows 59–74	<i>C. mystaceus</i> (IC)
16a.	Grey stripe above lip extends to tympanum, mid-body scale rows 47–57	<i>C. chincollium</i> (IC)
16b.	No stripe above lip, mid-body scale rows 48–59	<i>C. nigriplicatus</i> (I)
17.	Supratympanic spines two clusters, scales on the ventral thigh smooth.	<i>C. ceylonensis</i> (SLE)
18a.	Scales on the ventral thigh smooth	(19)
18b.	Scales on the ventral thigh keeled	(20)
19.	Supratympanic spines two clusters	<i>C. desilvai</i> (SLE)
20a.	One row of supratympanic spines	<i>C. nigrilabris</i> (SLE)
20b.	Supratympanic spines absent	(21)
20c.	Supratympanic spines two clusters	(22)
21a.	Size of ventral scales smaller than dorsals	<i>C. liocephalus</i> (SLE)
21b.	Size of ventral scales larger than dorsals.	<i>C. pethiyadoda</i> (SLE)
22a.	Females with enlarged pectoral scales	<i>C. liolepis</i> (SLE)
22b.	Females with nonenlarged pectoral scales	<i>C. manamendri</i> (SLE)

Key to the genus *Monilesaurus* gen. nov.

1.	Mid-body scale rows 52–58, small body size	(3)
2.	3–6 nuchal spines, larger body size.	(4)
3a.	3–4 long nuchal spines; long, distinct spine in the posterior corner of orbit present	<i>M. ellioti</i>
3b.	7–8 small nuchal spines; spine in posterior corner of orbit absent	<i>M. rouxii</i>
4a.	Mid-body scale rows 62–64, long, distinct spine in the posterior corner of orbit, long nuchal spines.	<i>M. acanthocephalus</i> sp. nov.
4b.	Mid-body scale rows 46–52, small, indistinct spine in the posterior corner of orbit, small nuchal spines	<i>M. montanus</i> sp. nov.

Discussion

Calotes has been considered as one of the most widely distributed and diverse genera in Agamidae. Overall, the results of our analysis are similar to recent studies with respect to a higher-level phylogeny of South Asian members of Agamidae (Pyron *et al.* 2013) barring a few major exceptions. Additions of the endemic genus *Psammophilus* and other Western Ghats endemic species belonging to the genus *Calotes* to the analysis showed the Western Ghats *Calotes* to be paraphyletic in nature. Here, we assign members of a sister clade from the Western Ghats to a new genus, *Monilesaurus* **gen. nov.** and also describe two new species from this genus adding to the known diversity of agamid lizards from the Western Ghats. In addition, we found that members of the endemic genus *Psammophilus* are sister to *Monilesaurus* **gen. nov.** Most of the earlier known species belonging to the genus *Calotes* from the Western Ghats were described more than a century ago with limited data on type localities and type specimens. Based on extensive spatial sampling across the Western Ghats followed by a multi criteria approach to species delimitation, we were able to identify new lineages.

Monilesaurus rouxii and *M. ellioti* show high intraspecific genetic differentiation. However, phylogeographic studies with extensive sampling are required to address questions related to geographical structuring in these widespread lineages. In *M. montanus* **gen. et sp. nov.**, there is some intraspecific genetic difference, which can be attributed to its distribution. However, owing to low sample size, we treat all the populations as *M. montanus* **gen. et sp. nov.**, but further studies might reveal more lineages. Both the new lineages described here are from high elevation montane forests separated by ancient geographic gaps in the Western Ghats. The new monotypic genus *Microauris* **gen. nov.** recognized here is a montane lizard species restricted to the Agasthyamalai hills. The occurrence of these new lineages in the montane forests of the Southern Western Ghats highlights the significance of these unique habitats (Robin *et al.* 2010; Vijayakumar *et al.* 2016).

Salea is yet another genus of agamid lizard endemic to the high elevation montane forests of the southern Western Ghats (Bhupathy & Kannan, 1997). Both the species belonging to this genus, *S. horsefieldii* and *S. anamallayana* are restricted to the montane forests and grasslands of Nilgiri hills and Anamalai hills respectively. *Salea* and *Calotes* represent the first draconine invasion of India, having diverged from their mainland Asian ancestor approximately 56 million years ago while the diversification of the *Calotes* lineage started much later, around 34 mya (Grismer JL *et al.* 2016). The occurrence of a new monotypic agamid lizard from similar habitats in the Agasthyamalai hills further signifies the role of this ancient mountain range in the evolution of endemic fauna. Adding these new lineages to detailed biogeographic studies with assessment of molecular rates and geological events will help strengthen the understanding of factors responsible for the current diversity and distribution of these lizards.

The only known member from the new genus *Microauris*, *M. aurantolabium*, was earlier considered to be a member of genus *Calotes* (Ishwar & Das 1998; Krishnan 2008). Both the collected individuals differed substantially in morphology from all other members of *Calotes*, with a reduced, indistinct tympanum; lack of supratympanic and orbital spines; 3rd and 4th digits on the hind limbs almost equal in length; a distinct orange stripe above the lip scales and a whitish grey band in the posterior part of the hind limb, a character not found in any other *Calotes* but seen in some other agamids like *Sitana*. It is also deeply genetically divergent from all the other *Calotes* species as well as the peninsular Indian clades, *Psammophilus* and *Monilesaurus*.

Another interesting finding from this study is the phylogenetic relationship of the genus *Psammophilus* with other agamid lizards. The two known species were considered different from *Calotes* based on their overall depressed body shape (Smith 1935). But other than the body shape, almost all key characters of these lizards are similar to members of the genus *Calotes*. Genetically, *Psammophilus* is sister to *Monilesaurus* gen. nov. Species belonging to the *Psammophilus* clade share some characters like the overall scale pattern, spines above tympanum and presence of a crest with members of the sister clade *Monilesaurus* gen. nov., but differ in the overall body size and choice of habitat. The members of genus *Monilesaurus* gen. nov., are arboreal, forest dwelling lizards while *Psammophilus* species are known to prefer rocky outcrops (Radder *et al.* 2005).

Since Smith (1935), there have been several changes to the classification of the Indian and Indo-Chinese agamids. Now all these agamids belong to subfamily Draconinae; Smith's group I: *C. cristatella*, *C. jubatus*, *C. smaragdinus* are all under the genus *Bronchocelela* (Moody, 1980); group II: *C. microlepis*, *C. floweri* are now under the genus *Pseudocalotes* (Moody, 1980) while *C. fruhstorferi* was moved to *Acanthosaura* (Denzer *et al.* 1997); group III: *C. versicolor*, *C. maria*, *C. jerdoni*, *C. emma*, *C. mystaceus*, *C. nemoricola*, *C. grandisquamis* and *C. calotes* remain in the genus *Calotes* while *C. kakhienensis* was moved to the genus *Pseudocalotes* (Mahony, 2010); group IV: *C. liocephalus*, *C. liolepis*, *C. nigrilabris* and *C. ceylonensis* remain in the genus *Calotes* while *C. kingdom-wardi* was moved to the genus *Pseudocalotes* (Mahony, 2010) and *C. andamanensis* was moved to the genus *Pseudocalotes* (Harikrishnan & Vasudevan, 2013) but with a cautionary note that this species has a weak ante-humeral fold which is otherwise present in genera such as *Calotes*, *Psammophilus*, *Gonocephalus*, *Japalura* and *Acanthosaura*; group V: *C. ellioti* and *C. rouxii* have been moved to the new genus *Monilesaurus*. This study has added more stability to the systematics of Draconinae particularly *Calotes* and other endemic agamids from the Western Ghats using comprehensive data on their morphology and genetics.

The presence of distinct new lineages and two new endemic genera from the Western Ghats further signifies the importance of this region in terms of endemism. The addition of endemic lineages like *Psammophilus* to broad-scale agamid phylogeny revealed the paraphyletic nature of the genus *Calotes*. This study thus highlights the importance of sampling endemic lineages while conducting broad level phylogenetic studies. This study also highlights the need for thorough geographic sampling to uncover cryptic lineages of faunal diversity in biodiversity hotspots like the Western Ghats.

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APPENDIX 1. GenBank accession numbers for the agamid species sequences used in this study.

APPENDIX 2. Range and mean of meristic characters counted/verified for the studied specimens of agamid lizards from the Western Ghats.

APPENDIX 3. Morphometric measurements for the studied specimens of agamid lizards from the Western Ghats.

APPENDIX 4. Bayesian tree for Draconinae showing relationship of most of the Indian genera with other draconine genera distributed in Sri Lanka, South-east Asia, Indo-china and Indo-Burma. Dark circles indicate posterior probability >95% and light circles indicate bootstrap support <95%

APPENDIX 5. Uncorrected p sequence divergence (16S data set) for genetic samples included in this study. Names arranged alphabetically.

APPENDIX 6. Ratio of morphometric measurements for the studied specimens of agamid lizards from the Western Ghats.

Comparative material examined in this study:

Calotes jerdonii: BMNH 1946.8.11.50–51, BMNH 1946.8.11.54–53, BMNH 1946.8.11.56

Calotes emma: BMNH 1946.8.11.26

Calotes maria: BMNH 1946.8.11.24

Calotes grandisquamis: BMNH 1946.8.11.44–47, CESL 035, CESL120 & CESL191.

Calotes nemoricola: BMNH 74.4.29.224–225s, CESL 038, CESL 406, CESL 545, CESL 555, BNHS 1778, BNHS 373 & ZSI 6560.

Calotes cf. *versicolor*: CESL 036, CESL 041, CESL 182, CESL 190, CESL 046, CESL 049, CESL 055, CESL 071, CESL 048, CESL 163, CESL 073, CESL 306, CESL 454 & BNHM 374.

Calotes calotes: CESL 037, CESL 374 & BNHS 378.

Calotes bhutanensis: ZSI 22480 type images only.

Monilesaurus acanthocephalus **gen. et sp. nov.**: BNHS 2409, CESL 001, CESL 112 & BNHS 2410.

Monilesaurus ellioti **comb.nov.**: CESL 045, CESL 042, CESL 060, CESL 047, CESL 057, CESL 059, CESL 061, CESL 058, CESL 060, CESL 077, CESL 033, CESL 162, CESL 204, CESL 369 & BNHS 1033.

Bronchocela indica (Junior synonym of *Monilesaurus ellioti*): ZSI 4325 & ZSI 4328.

Monilesaurus montanus **gen. et sp. nov.**: BNHS 2411, BNHS 2412, BNHS 2413, CESL 131, CESL 133, CESL 330, CESL 331 & CESL 529.

Monilesaurus rouxii: CESL 129, CESL 523, CESL 554, CESL 669, CESL 834, CESL 678, CESL 875, CESL 095, CESL 072, CESL 123, CESL 153, CESL 215, CESL 581, BNHS 1033 & MNHN-RA- 0.6894 (type images only).

Psammophilus blanfordanus: ZSI 6592-93, ZSI 6595-97, ZSI 6604, ZSI 6609 & ZSI 6611-13.

Psammophilus dorsalis: CESL 273, CESL 326, CESL 132, CESL 064, CESL 180, CESL 181, CESL 179

Psammophilus sp.: CES P_JNC.

Microauris aurantolabium **comb. nov.**: BNHS 1436 & CESL 104.

Salea horsfieldii: CESL173, CESL 289, CESL 325, CESL 174, CESL 004 & CESL 005.

Salea anamallayana: CESL 373, CESL 411, CESL 241 & CESL 242.

Draco dussumierii: CESL 034, CESL 021 & CESL 183.

Sitana marudhamneydhal: CESL407.

Otocryptis beddomii: CESL 025, CESL 032, CESL 099, CESL 268 & CESL 703.