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On the systematic status of the genus *Oriocalotes* Günther, 1864 (Squamata: Agamidae: Draconinae) with the description of a new species from Mizoram state, Northeast India

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Abstract

The montane agamid lizard genus *Oriocalotes* is currently considered monotypic, represented by the species, *O. paulus*. The systematic status of this taxon has remained questionable since its initial descriptions in the mid-1800s. A detailed molecular and morphological study was carried out to assess the validity of this genus, and its systematic position within the Asian agamid subfamily, Draconinae. Freshly collected and historical museum specimens from the type locality of *O. paulus* were examined morphologically, along with additional samples collected from localities in Mizoram state, Northeast India. Utilising newly generated molecular sequences (two mitochondrial and three nuclear genes), combined with those previously published for representative genera from the subfamilies Draconinae and Agaminae, Maximum Likelihood and Bayesian phylogenetic trees were constructed. Phylogenetic results suggest that *Oriocalotes* is part of the widespread South and Southeast Asian radiation of *Calotes*. Comparative morphological studies (including external morphology, hemipenis and osteology) between *Oriocalotes* and related genera further support this systematic placement. *Oriocalotes* is herein regarded as a junior subjective synonym of *Calotes*. *Calotes paulus* **comb. nov.** is also assigned a lectotype and given a detailed redescription based on the lectotype, paralectotypes and additional topotypic material. Furthermore, the specimens collected from Mizoram populations are found to be morphologically and genetically distinct from *Calotes paulus* **comb. nov.**, and are described herein as a new species, *Calotes zolaiking* **sp. nov.**

Key words: Agamids, biodiversity, *Calotes*, Khasi Hills, Meghalaya, taxonomy

Introduction

A new agamid lizard, *Agama minor* Hardwicke and Gray, 1827, was described based on an unpublished color sketch in the collection of Thomas Hardwicke (Hardwicke NHMUK archives No. 82) of a specimen from Chittagong [now in Bangladesh]. Subsequently, *Calotes minor* Gray, 1845 was described based on three specimens from “Afghanistan” and one from “Khasia hill” (currently in Meghalaya state, Northeast India), under which Gray (1845) included, and thus inadvertently synonymised, *Agama minor* Hardwicke and Gray (Smith 1935; Deepak *et al.* 2015). Günther (1864) created the monotypic genus *Oriocalotes* Günther, 1864 for the species *Calotes minor* Gray. Günther (1864) used the following suite of characters to diagnose his new genus “Tympanum naked, back and sides covered with scales of moderate size, between which larger ones are intermixed; their tips are directed backwards and upwards; a spine behind the supraciliary edge. Dorsal crest present, formed by non-united spines, less distinct in the female than in the male. Gular sac none. Tail rounded, with keeled scales below, which are as broad as long.”

He also provided a brief redescription of the species based on the type series of *Calotes minor* Gray (but not *Agama minor* Hardwicke and Gray), and included an additional specimen collected by “Messrs. v. Schlagintweit” from Sikkim (Günther 1864).

Subsequently, three additional species were added to the genus: *Oreocalotes*[sic] *major* Jerdon, 1870 described from the western Himalayas, *O. discolor* Anderson, 1870 which appeared in a specimen checklist from Burma, and *O. kakhienensis* Anderson, 1879 also described from Burma. Theobald (1876) transferred both *Oriocalotes minor* (Gray) and *O. major* Jerdon to the now synonymised (under *Psammophilus* Fitzinger, 1843) genus, *Charasia* Gray, 1845. Theobald’s reclassification was broadly based on characters of the dorsal and lateral part of the body, having small keeled scales interspersed with some larger ones. Boulenger (1885), considered *Oriocalotes* and *Charasia* to be synonyms of *Acanthosaura* Gray, 1831, transferring three of the species, *O. minor*, *O. major* and *O. kakhienensis* by implication. He used characters such as the continuity of the nuchal and dorsal crests and the presence of a spine on each side of the neck to diagnose *Acanthosaura minor* (Gray). Smith (1935), for the first time, addressed the taxonomic heterogeneity of *Calotes minor* Gray where he elevated *Agama minor* Hardwicke and Gray from the synonymy of *Calotes minor* Gray based on its short tail, regular scalation and coloration of the body of the former, as opposed to heterogenous, regularly arranged dorsal scales, and a post orbital spine in the latter species. Smith (1935) also resurrected the genus *Oriocalotes* Günther for *Calotes minor* Gray, citing the validity of its original description. Despite both species being in separate genera, Smith mistakenly assumed that there was an issue of homonymy created by the elevation of *Agama minor* Hardwicke and Gray from *Calotes minor* Gray, and created the replacement species epithet “*paulus*” for *Calotes minor* Gray, in the new combination *Oriocalotes paulus* Smith, 1935. Smith’s replacement name “*paulus*” was therefore unjustified and so *Oriocalotes minor* (Gray) should be the valid name, however Smith’s action has remained unquestioned until now and *Oriocalotes paulus* is the only name in use for this taxon (e.g., Wermuth 1967; Moody 1980; Diong & Lim 1998; Manthey & Schuster 1999; Manthey & Denzer 2000; Zhao *et al.* 2000; Mahony 2010; Venugopal 2010; Ananjeva *et al.* 2011; Huang *et al.* 2011; Deepak *et al.* 2015). Smith (1935) assigned Jerdon’s *O. major* to the genus *Japalura* Gray, 1853 (where it remains today), and *O. kakhienensis* to the genus *Calotes* Cuvier, 1817. The forgotten name, *Oriocalotes discolor*, was recently demonstrated to represent a *nomen oblitum* and a senior objective synonym of *O. kakhienensis*, which is currently assigned to the genus *Pseudocalotes* Fitzinger, 1843 (Mahony 2010), rendering *Oriocalotes* monotypic. *Agama minor* Hardwicke and Gray is now placed in the genus *Calotes* as *C. minor* (Hardwicke & Gray) (Deepak *et al.* 2015). Although the validity of the genus *Oriocalotes* has not been questioned until now (e.g., Wermuth 1967; Moody, 1980; Manthey & Schuster 1999; Ananjeva *et al.* 2011), its systematic relationship within Draconinae Fitzinger, 1826 has remained uncertain (Mahony 2010).

In this study, we resolve the systematic position of the genus *Oriocalotes* within Draconinae, based on an integrated taxonomic approach utilising morphological and molecular data. We provide a detailed description of the herein assigned lectotype of *O. paulus* and include morphological variation for the species. We also determine the taxonomic status of recently discovered populations of *Oriocalotes* from Mizoram that are morphologically and genetically distinct from the type species.

Materials and methods

Specimen collection and preservation: Fieldwork was carried out at Sohra, Meghalaya state, Northeast India from October, 2014 to December, 2018 by Vivek Sarkar, and in Mizoram state, Northeast India from September, 2010 to April, 2018 by C. Lalrinchhana and Samuel Lalronunga. Specimens were located during opportunistic visual searches of sub-tropical forest and surrounding open habitats. Live individuals were collected by hand and photographed in life for documentation of coloration. Tissue samples were extracted after specimen euthanasia, before fixation, and were stored at -20°C in absolute ethanol. Specimens were first fixed in 4% formalin in the field, and later transferred to 70% EtOH for long-term storage.

Abbreviations. Museum acronyms are as follows: NCBS (National Centre for Biological Sciences, Bengaluru, India), BNHS (Bombay Natural History Society Museum, Mumbai, India), NHMUK (Natural History Museum, London, UK: specimens are referred to under the original acronym BMNH, British Museum [Natural History], for comparability with historical literature), ESV and CESG (Centre for Ecological Sciences, Indian Institute of Science, Bengaluru, India). Meters above sea level (m a.s.l.).

Gene sequences. Sampling for this study was carried out in Meghalaya and Mizoram states in Northeast India (Fig. 1). A tissue sample from a Meghalaya (NCBS AQ198) and Mizoram (NCBS AU155) specimen of *Oriocalotes* were used in this study. Additional sequences were generated for one sample of *Calotes calotes* (Linnaeus, 1758) (CESG 554), *Calotes emma* Gray, 1845 and *Calotes mystaceus* Duméril & Bibron, 1837, *Psammophilus* cf. *blanfordanus* (Stoliczka, 1871) (CESG 461), *Salea anamallayana* (Beddome, 1878), *Sarada deccanensis* (Jerdon, 1870), *Sitana ponticeriana* Cuvier, 1829 and *Sitana spinaecephalus* Deepak, Vyas and Giri, 2016 (Table 1). Genomic DNA was extracted from liver and tail tip tissue samples that were stored frozen at -20°C in absolute ethanol. DNeasy® Blood & Tissue Kit (Qiagen®, Germany) following manufacturer's instructions. Partial sequences of the mitochondrial genes, nicotinamide adenine dinucleotide dehydrogenase subunit 2 (ND2: 1059 bp [base pairs]) and partial 16S rDNA (16S: 486 bp), and partial sequences from the nuclear genes, recombination activating gene 1 (RAG1: 1000 bp), prostaglandin E2 receptor gene (PTGER: 470 bp), and G protein-coupled receptor R35 (R35: 665 bp), were PCR amplified and sequenced using published primers (Palumbi *et al.* 1991; Macey *et al.* 1997; Macey *et al.* 2000; Groth & Barrowclough 1999; Leaché 2009, respectively). PCR amplifications were carried out in 25 µl aliquots containing 2.5 µL of 1 X Taq buffer, 2.5 µL of 2.5 mM dNTP, 2.5 µL of 2.5 mM of MgCl₂, 0.25 µl each for the forward and reverse primer, 0.33 µl of 2 units of Taq DNA polymerase, 1 µl of extracted DNA of the sample and 16.67 µl of PCR grade H₂O. We used a S1000™ Thermal Cycler (Bio-Rad, USA) to run the PCR. The PCR conditions were as follows: initial denaturation at 94°C for 3 min, denaturation for 35 cycles at 94°C for 50 s, annealing (at 45°C for 16S, 53°C for ND2 & RAG1, between 53°C and 58°C temperature range for PTGER & R35) for 1 min, and extension at 72°C for 40 s. The final extension was at 4°C for 30 min. Amplified PCR products were ran on 2% agarose gel, viewed in an Essential V4 (UVITEC Cambridge, UK) gel documentation system, and purified using a QIAquick PCR Purification Kit (Qiagen®, Germany). PCR products were Sanger sequenced for the forward and reverse strand at Medauxin Sequencing Services (Bangalore, India). Sequence chromatograms were checked and edited using the program Chromas LITE ver.2.1.1. Sequences were subjected to NCBI nucleotide BLAST search to verify approximate identities.

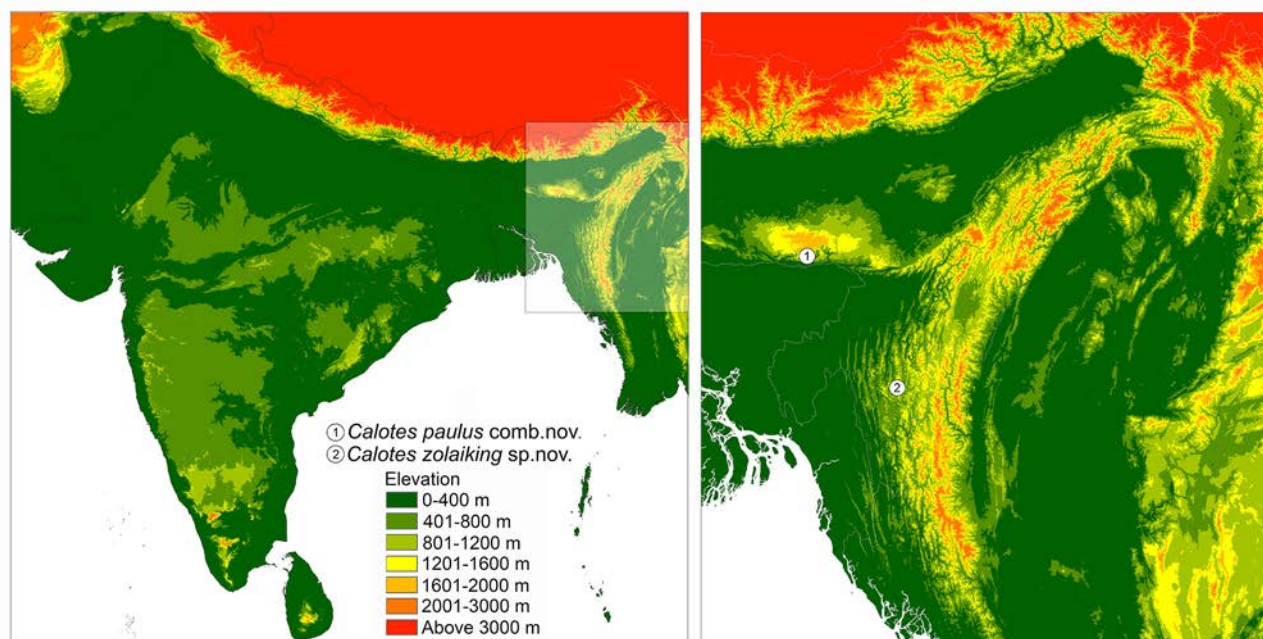


FIGURE 1. Map showing type locality of *Calotes paulus* comb. nov. and *Calotes zolaiking* sp. nov. in North East India.

Phylogenetic analyses. In addition to the sequences generated in this study, sequences for 47 other agamids were downloaded from GenBank (Benson *et al.* 2017), selecting species and vouchers with the maximum gene coverage to correspond with our molecular dataset (Table 1). Species from the sister subfamily Agaminae (Table 1) were selected as outgroup taxa for Draconinae, based on the molecular phylogenetic results of Pyron *et al.* (2013). The per-gene coverage for the 50 sequences used in this study were as follows: ND2 86%, 16S 50%, R35 28 %, PTGER 26% and RAG1 20%. Sequences were aligned using ClustalW in MEGA 5.1 (Higgins *et al.* 1994; Tamura *et al.* 2011). All gene sequences except 16S were adjusted for open reading frames and checked for stop codons. Align-

TABLE 1. Sequences generated and other GenBank sequences used for phylogenetic analysis.

S.no	Taxon	Voucher	Geographic provenance	ND2	16S	R35	PTGER	RAG1
1	<i>Acanthosaura lepidogaster</i>	MVZ224090	Vietnam: Vinh Thu Prov.	AF128499	-	-	-	-
2	<i>Acanthosaura lepidogaster</i>	MD001	China: Hainan Prov.	-	KR092427	-	-	-
3	<i>Acanthosaura lepidogaster</i>	CAS 208426	-	-	-	JF804578	JN880581	-
4	<i>Aphaniotis fusca</i>	TNHC57943	Malaysia: Selangor, outskirts of Kuala Lumpur	AF128497	-	-	-	-
5	<i>Aphaniotis fusca</i>	-	-	-	AB023771	-	-	-
6	<i>Bronchocela cristatella</i>	-	India: Car Nicobar Island	-	EU503023	-	-	-
7	<i>Bufoinceps laungwalaensis</i>	-	-	DQ008214	-	-	-	-
8	<i>Calotes calotes</i>	WHT1679	Sri Lanka: Galle, Navinna	AF128482	-	-	-	AY662584
9	<i>Calotes calotes</i>	-	India: Rameshwaram, Tamil Nadu	-	-	MK792529	MK795777	-
10	<i>Calotes ceylonensis</i>	WHT1624	Sri Lanka: Galle, Yodaganawa	AF128483	-	-	-	-
11	<i>Calotes chincollium</i>	CAS 215505	Myanmar: Sagaing Div.	DQ289459	-	-	-	-
12	<i>Calotes emma</i>	CAS 230941	Myanmar	-	-	-	JN880586	-
13	<i>Calotes emma</i>	CAS 223062	Myanmar: Rakhine State, Sa Byin Village	DQ289460	-	-	-	-
14	<i>Calotes emma</i>	NCBS	India: Cherrapunjee, Meghalaya	-	MK789847	MK792530	MK795778	-
15	<i>Calotes huwini</i>	USNM-GZ 36408	Myanmar: Magwe Div.	DQ289464	-	-	-	-
16	<i>Calotes irawadi</i>	CAS 204862	Myanmar: Sagaing Div.	DQ289468	-	-	-	-
17	<i>Calotes jerdoni</i>	CAS 219992	Myanmar: Chin State, Nat Ma Taung National Park	GQ502783	-	-	-	-
18	<i>Calotes liocephalus</i>	WHT1632	Sri Lanka: Knuckles, Kirimetiakanda	AF128484	-	-	-	-
19	<i>Calotes liolepis</i>	WHT1808	Sri Lanka: Knuckles, Puwakpitiya	AF128485	-	-	-	-
20	<i>Calotes minor</i>	CESG 162	India: Kutch, Gujarat	KT952397	-	-	-	KT952398
21	<i>Calotes mystaceus</i>	CAS: HERP: 204848	Myanmar: Mandalay Div.	AF128488	-	-	-	-
22	<i>Calotes mystaceus</i>	WII	India: Nagaland	-	MK789848	MK792531	MK795779	-
23	<i>Calotes nigrilabris</i>	WHT1680	Sri Lanka: Galle, Sita Eliya	AF128486	-	-	-	-
24	<i>Calotes paulus comb.nov.</i>	NCBSAQ-AC696	India: Cherrapunjee, Meghalaya	MK795773	MK789849	MK792528	MK795780	MK795783
25	<i>Calotes cf. versicolor</i>	CAS 230481	Myanmar: Shan State, Ywa-Ngan Town-ship	DQ289477	-	-	-	-
26	<i>Calotes zolaiking sp. nov.</i>	NCBS-AU155	India: Hmufiang, Mizoram	MK795774	MK789852	MK792527	MK795781	-
27	<i>Ceratophora stoddartii</i>	WHT 1682	Sri Lanka: Colombo	AF364053	-	-	-	-

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TABLE 1. (Continued)

S.no	Taxon	Voucher	Geographic provenance	ND2	16S	R35	PTGER	RAG1
28	<i>Cophotis dumbara</i>	–	Sri Lanka	GQ502785	–	–	–	–
29	<i>Coryphophylax subcristatus</i>	–	India: Nancowry Island	–	EU502989	–	–	–
30	<i>Draco blanfordii</i>	CAS 221153	–	–	–	JF804589	–	–
31	<i>Draco blanfordii</i>	MVZ222156	Vietnam: Gia-Lai Prov.	AF128477	–	–	–	–
32	<i>Gonocephalus grandis</i>	–	–	–	AB031983	–	–	–
33	<i>Gonocephalus grandis</i>	TNHC56500	Malaysia: Selangor, Ulu Gombak	AF128496	–	–	–	–
34	<i>Malayodracon robinsonii</i>	–	–	–	AB070381	–	–	–
35	<i>Diploderma splendidum</i>	CAS: HERP: 194476	China: Sichuan Prov.	AF128501	–	–	–	–
36	<i>Japalura tricarinata</i>	CAS: HERP: 177397	China: Xizang Autonomous region	AF128478	–	–	–	–
37	<i>Diploderma polygonatum</i>	–	–	–	AB031985	–	–	–
38	<i>Laudakia tuberculata</i>	ZISP20697.1	Nepal: Daman	AF128514	–	–	–	–
39	<i>Lyriocephalus scutatus</i>	WHT2196	Sri Lanka: Knuckles Hills	AF128494	–	–	–	–
40	<i>Mantheyus phuvuanensis</i>	–	–	AY555836	AB023772	–	–	–
41	<i>Otocryptis wiegmanni</i>	WHT2262	Sri Lanka	AF128480	–	–	–	–
42	<i>Paralaudakia caucasia</i>	CAS: HERP: 182808	Russia: Dagestan Autonomous republic	AF028687	–	–	–	–
43	<i>Paralaudakia caucasia</i>	–	Iran: Mazandaran Prov.	–	AY053765	–	–	–
44	<i>Phoxophrys nigrilabris</i>	–	–	–	AB031988	–	–	–
45	<i>Phrynocephalus mystaceus</i>	CAS 228621	–	–	–	JF804596	JN880608	–
46	<i>Phrynocephalus mystaceus</i>	CAS179754	Turkmenistan: Ashkabad	AF128518	–	–	–	–
47	<i>Phrynocephalus mystaceus</i>	D74190	Kazakhstan: Kapchagay Dist.	–	–	–	–	GQ242268
48	<i>Phrynocephalus versicolor</i>	–	–	KF691664	–	–	–	–
49	<i>Phrynocephalus versicolor</i>	–	China: Ejinaqi, Neimenggu Prov.	–	AY053857	–	–	–
50	<i>Psammophilus cf. blanfordanus</i>	CESSG 461	India: Parasnath, Jharkhand	MK795775	MH844752	MK792532	MK795782	MK795784
51	<i>Pseudocalotes brevipes</i>	MVZ224106	Vietnam: Vinh Thu Prov., Vinh Yen Dist., Tam Dao	AF128502	–	–	–	–
52	<i>Pseudocalotes flavigula</i>	TNHC58040	Malaysia: Perak, Bukit Larut	AF128503	–	–	–	–
53	<i>Pseudocalotes kakhienensis</i>	CAS 207492	China: Baoshan Pref., Qushi	GQ502784	–	–	–	–
54	<i>Pseudotrapelus sinaitus</i>	BMNH1996.201	United Arab Emirates: Fujjeira	AF128507	–	–	–	–

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TABLE 1. (Continued)

S.no	Taxon	Voucher	Geographic provenance	ND2	16S	R35	PTGER	RAG1
55	<i>Pseudotrappelus sinaitus</i>	–	–	–	HQ901102	–	–	–
56	<i>Pseudotrappelus sinaitus</i>	SBED 11271	–	–	–	JX839168	–	–
57	<i>Phytolaemus gularis</i>	CAS 221515	Myanmar: Kachin State	AY555838	–	–	–	–
58	<i>Salea horsfieldii</i>	BNHS-AMB5739	India: Avalanche, Tamil Nadu	AF128490	–	–	–	–
59	<i>Salea anamallayana</i>	–	India: Munnar, Kerala	MK795776	–	–	–	MK795785
60	<i>Sarada deccanensis</i>	CES 14610	India: Jalna, Maharashtra	KT831315	MK789850	KT831279	–	KT831296
61	<i>Sitana ponticeriana</i>	CES 13657	India: Muttukad, Tamil Nadu	KT831326	MK789851	KT831286	–	KT831304
62	<i>Sitana spinaecephalus</i>	CES 13532	India: Kunauthia, Gujarat	KT831333	MK789853	KT831288	–	KT831306
63	<i>Trappelus agilis</i>	GNHM	Iran: Kerman Prov.	AF128509	–	–	–	–
64	<i>Trappelus agilis</i>	Re.ex.5210	–	–	–	–	–	–
		CAS:	Iran: Semnan Prov.	–	–	–	JN880619	–
		HERP:228565	–	–	–	–	–	–
65	<i>Trappelus ruderatus</i>	MHING2642.35	–	–	HQ901117	–	–	–
66	<i>Trappelus ruderatus</i>	GNHM	Iran: Kermanshahan Prov., Gharaviz Region	AF128508	–	–	–	–
		Re.ex.5212	–	–	–	–	–	–
67	<i>Trappelus ruderatus</i>	CAS 228565	–	–	–	JF804606	–	–
68	<i>Xenagama batillifera</i>	NSMT-H4685	–	AB113825	–	–	–	–
69	<i>Xenagama batillifera</i>	ZFMK 83411	–	–	JX668222	–	–	–

ments were checked and adjusted by eye for the ND2 gene beyond 955 bp and the multiple hypervariable regions in the 16S gene. Uncorrected genetic *p*-distances between taxa were calculated for the ND2 sequences using MEGA 5.1 (Tamura *et al.* 2011). PartitionFinder v1.1.1 (Lanfear *et al.* 2012) was used to find the best partition scheme and model of sequence evolution for each partition. The coding genes were defined before subjecting to PartitionFinder analysis and the optimal partitioning scheme included four partitions for the mitochondrial DNA (mtDNA) dataset and four partitions for the nuclear DNA (nDNA) dataset (Appendix I).

Concatenated mtDNA and concatenated nDNA alignments were analysed separately using a Maximum Likelihood (ML) and a Bayesian (BI) approach. ML trees were generated using the GUI version of RAxML (Silvestro & Michalak 2012; Stamatakis *et al.* 2005) with 1000 bootstrap replicates in ML + rapid bootstrap settings. ML analysis in RAxML permits only one model of sequence evolution in the analysis, therefore we used GTR+ G for all five partitions. We used GTR + G model in RAxML which is recommended over the GTR + G + I because the 25 rate categories account for potentially invariant sites (Stamatakis 2006). Individual ML nuclear gene trees were also generated to determine gene concordance and degree of phylogenetic signal. Bayesian trees were generated using the program MrBayes 3.2 (Ronquist *et al.* 2012) under default prior settings and with all eight partitions assigned their optimum model as determined by PartitionFinder (Appendix. 1). For BI analyses, two separate runs using 4 Markov chains each were initiated from random trees and allowed to run for 1 million generations sampling every 100 generations. Analyses were terminated when the standard deviation of split frequencies were less than 0.005, the first 25% of trees were discarded as “burn-in”, and trees were constructed under 50% majority consensus rule.

External morphology. Measurements (to the nearest 0.1 mm) were taken with digital calipers (Mitutoyo™, Japan), except tail length (TL) which was measured using a string and a ruler. Morphometric characters were measured as follows: snout to vent length (SVL, from tip of snout to anterior border of cloaca), Trunk length (TrL, axilla to groin length), tail length (TL, from posterior border of cloacal opening to tip of tail), tail depth (TaD) and tail width (TW) taken at the highest and widest points respectively, head length (HL, from snout tip to jaw angle), head width (HW, measured at posterior axis of jaw), head depth (HD, dorsoventral distance from top of head to underside of jaw at transverse plane intersecting posterior axis of jaw), snout-eye length (SE, from snout tip to anterior border of orbit), naris to eye (NE, from anterior edge of orbit to posterior edge of naris), eye to ear (EE, from posterior border of orbit to anterior border of tympanum), inter-orbital width (IO, transverse distance between anterodorsal most borders of left and right orbits), tympanum diameter (TD, greatest diameter of tympanum), orbit diameter (OD, greatest diameter of orbit), snout to forelimb insertion (SFI, between tip of snout to anterior insertion of forelimb), upper arm length (UAL, from anterior insertion of forelimb to elbow), lower arm length (LAL, from elbow to distal end of wrist), hand length (HaL, from proximal end of wrist to distal most point of fourth finger, excluding claw), fourth finger length (4FL, distance from juncture of fourth and third finger to distal most point of fourth finger, excluding claw), upper leg length (ULL, length of thigh from groin to knee), lower leg length (LLL, length of crus [tibia] from knee to heel), foot length (FOL, from proximal end of heel to tip of fourth toe, excluding claw), fourth toe length (4TL, distance from juncture of fourth and third toe to distal most point of fourth toe, excluding claw).

The following meristic characters were scored: mid-body scale rows (MSR, number of scale rows around trunk at midbody), scales between superciliaries (SnS, transverse scale count between anterior superciliaries), scales between orbital spines (HeadSTr, transverse scale count between orbital spines), canthal scales (CS, scale row between posterior margin of nasal scale and anterior margin of orbit), supralabials (SL, posterior end defined by last enlarged scale that contacts an infralabial at posterior axis of jaw), infralabials (IL, posterior end defined by posterior-most enlarged scale that contacts a supralabial at posterior axis of jaw), vertebral scales (VS, scales counted from first nuchal spine to level directly above cloacal opening), fourth finger lamellae (4FLam, number of fourth finger lamellae, from 1st transversely enlarged lamella at base of digit to distal most lamella), fourth toe lamellae (4TLam, number of fourth toe lamellae, from 1st lamella at base of digit to distal most lamella), nuchal crest (NC, number of spines that make up the nuchal crest).

Hemipenes morphology and osteology. Hemipenes were everted using 4% formalin during the preservation of two euthanised Mizoram *Oriocalotes* specimens (NCBS-AU156 & NCBS-AU155). Drawings were made using a Leica™ M165C (Leica, Germany) microscope mounted camera lucida. Morphological terminology follows Dowing and Savage (1960). Hemipenial characters of the Mizoram *Oriocalotes* specimen were compared with other draconine lizards (Maduwage *et al.* 2008). After morphological data had been assessed, one adult male (SVL = 62.9 mm) of the Mizoram *Oriocalotes* specimen (NCBS-AU156) was cleared and stained following the protocol of Hanken and Wassersug (1981). Skull was hand prepared, diluted Sodium hypochlorite was used in to remove tissues attached to the bone. Data on skeletal characters followed standard terminology (Moody 1980; Romer 1956;

Oelrich 1956). Diagnostic osteological characters specified by Moody (1980) for *Calotes* and *Pseudocalotes* were compared with *Oriocalotes* for further evidence of systematic association.

Results and discussion

Systematics. The overall ML tree topology of Draconinae obtained using the mtDNA dataset (Fig. 2) was similar to previous studies (see Schulte *et al.* 2004; Pyron *et al.* 2013; Grismer *et al.* 2016) in having *Mantheyus phuwuanensis* (Manthey and Nabhitabhata, 1991) as the sister taxon to all other draconine genera. However, this relationship conflicted with the BI tree of the mtDNA dataset which had a poor node support (Fig. 3). Grismer *et al.* (2016), using next generation sequencing data, identified three problematic relationships within Draconinae, one of which was the placement of *Salea* Gray, 1845 as the sister taxon of *Calotes*. Despite adding more genera and different gene sequences in our study, *Salea* was not sister to *Calotes* in concatenated mtDNA trees. Since *Psammophilus* was not included in Grismer *et al.* (2016) we did not constrain the monophyly of *Salea* + *Calotes*. There are still many gaps in molecular phylogenetic sampling of Draconinae, which is probably one of the reasons why relationships between genera and species remains unresolved. *Psammophilus* was resolved (with high support) as sister to a clade comprising *Calotes* + *Oriocalotes* in both the mitochondrial and nuclear phylogenies, and this arrangement received high support (Figs. 2, 3, & 4). Both ML and BI trees from the concatenated mitochondrial dataset (ND2 + 16S) demonstrated that *Calotes* is paraphyletic with respect to *Oriocalotes* (Figs. 2 & 3). Within the larger *Calotes* clade, *Oriocalotes* was resolved as sister to a subclade comprised of species from Northeast India and Southeast Asia: *C. emma*, *C. chincolium* Vindum, 2003 and *C. mystaceus*. The ML and BI trees for the concatenated nuclear dataset (R35 + PTGER + RAG1) both placed *Oriocalotes* within the *Calotes* radiation but showed conflicting relationships within this radiation. The ML tree placed *Oriocalotes* as sister to *Calotes calotes*, but with weak support (Fig. 4a), whereas in the BI tree *Oriocalotes* samples formed a polytomy with *Calotes calotes* (Fig. 4b). The *Oriocalotes* samples from Mizoram was also consistently resolved as a sister taxon to *Oriocalotes paulus* on all trees, with high support. Since both nuclear and mitochondrial trees supported placing *Oriocalotes* within the *Calotes* radiation, we herein formally synonymise *Oriocalotes* Günther, 1864, with *Calotes* Cuvier, 1817.

The uncorrected genetic *p*-distance for the ND2 sequences between the Mizoram *Calotes* species and *Calotes paulus* **comb. nov.** from Meghalaya was 13% (Appendix 3). This genetic distance is comparable with, or considerably exceeds that observed between other currently recognised *Calotes* species that were resolved as sister taxa on the mtDNA trees (Figs. 2 & 3), e.g., between *C. nigrilabris* Peters, 1860 and *C. liolepis* Boulenger, 1885 (*p* = 13%), between *C. versicolor* (Daudin, 1802) and *C. irawadi* Zug, Brown, Schulte and Vindum, 2006 (*p* = 6%), and only marginally lower than the distance between other closely related species, e.g., between *C. versicolor*/*C. htunwini* Zug and Vindum, 2006 and *C. calotes* (*p* = 15%: Appendix 3). The comparatively high *p*-distance observed between the Mizoram populations of *Calotes* sp. and *Calotes paulus* **comb. nov.** in combination with morphological differences (see comparisons sections) are herein considered sufficient to recognise these genetic haplotypes as distinct species.

Taxonomy

The synonymy of *Oriocalotes* into *Calotes* creates some nomenclatural issues that require explanation. Technically *Oriocalotes paulus* is an unnecessary substitute name for *Calotes minor* Gray, and regardless of its prevailing usage in scientific literature, it is a nomenclaturally invalid name. However, Article 10.6 of the International Code of Zoological Nomenclature (ICZN, 1999) states that invalidity does not affect availability of such names, and Smith's replacement name qualifies as an available (but invalid) junior objective synonym of *Calotes minor* Gray by meeting the requirements of Articles 11 and 13.1. Our proposed synonymy of *Oriocalotes* makes *Calotes minor* Gray an invalid (but available) junior secondary homonym of the older *Calotes minor* (Hardwicke & Gray) that needs to be replaced following Article 60.1: “**Substitute names.** A junior homonym [Art. 53] must be rejected and replaced either by an available and potentially valid synonym [Art. 23.3.5] or, for lack of such a name, by a new substitute name [Art. 60.3].” Following the Principle of Priority, Article 23.3.5 states that “The Principle of Priority requires that if a name in use for a taxon is found to be unavailable or invalid it must be replaced by the next oldest available

name from among its synonyms, providing that that name is not itself invalid. If the rejected name has no potentially valid synonym a new substitute name (see [Article 60.3](#)) must be established in its place”. This means that despite the nomenclatural availability of *Oriocalotes paulus*, its invalidity prevents the application of it as a substitute/replace-ment name. Further, Article 60.3 states “**Junior homonyms without synonyms.** If the rejected junior homonym has no known available and potentially valid synonym it must be replaced by a new substitute name, with its own author and date; this name will then compete for priority with any synonym recognised later”. The purpose of the ICZN is to maintain nomenclatural stability, and favours the avoidance of creating new names that may lead to confusion. Rather than creating a new substitute name, an application will be made to the ICZN to treat the species epithet “*paulus* Smith” as a valid substitute name and *nomen protectum* for *Calotes minor* Gray. Pending a ruling from the ICZN we will continue to use Smith’s species name in the new combination *Calotes paulus* (Smith, 1935) **comb. nov.**

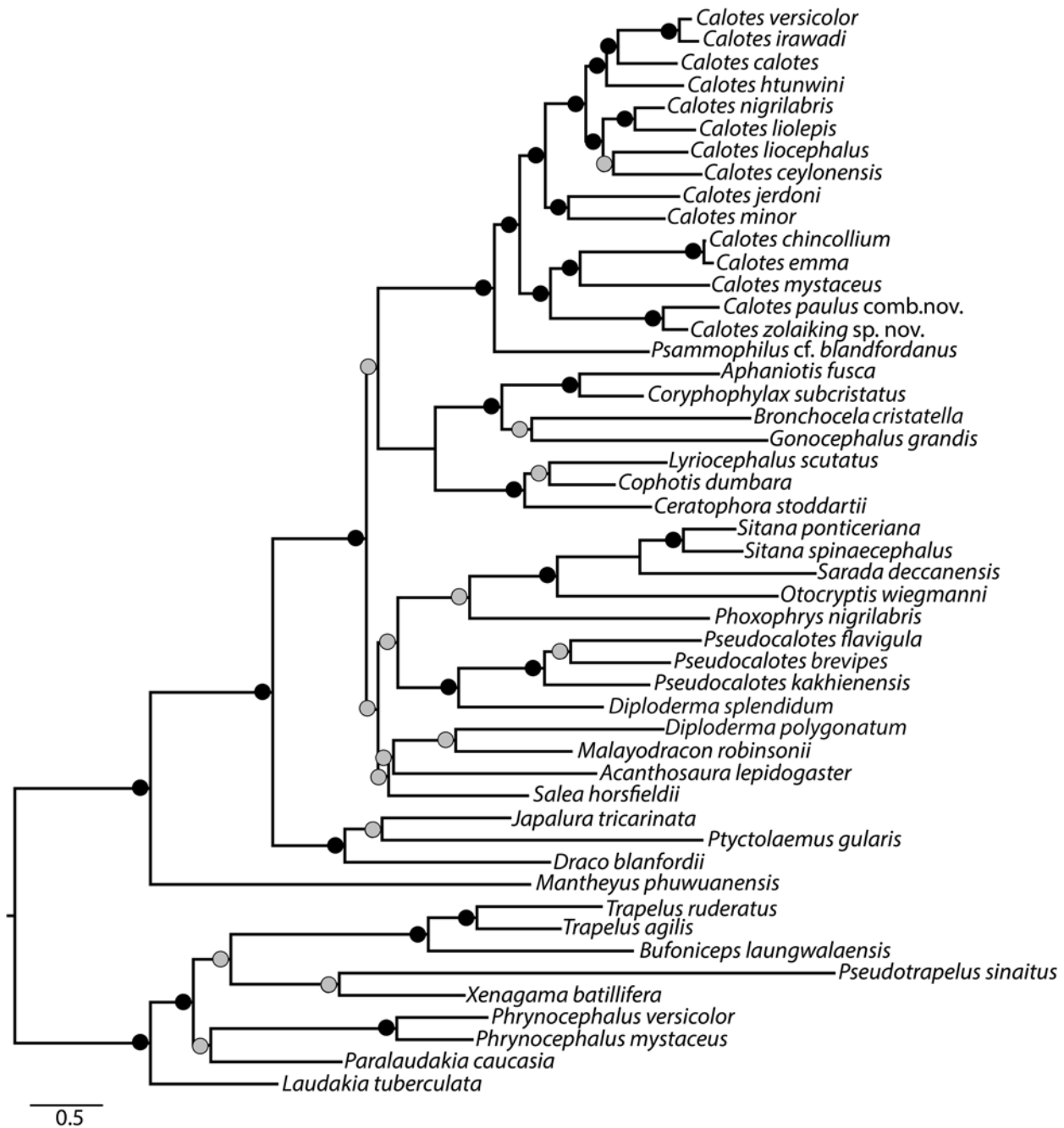


FIGURE 2. ML phylogeny built using the concatenated ND2 + 16S mitochondrial dataset. Bootstrap support > 90 dark circle; < 90 grey circle.

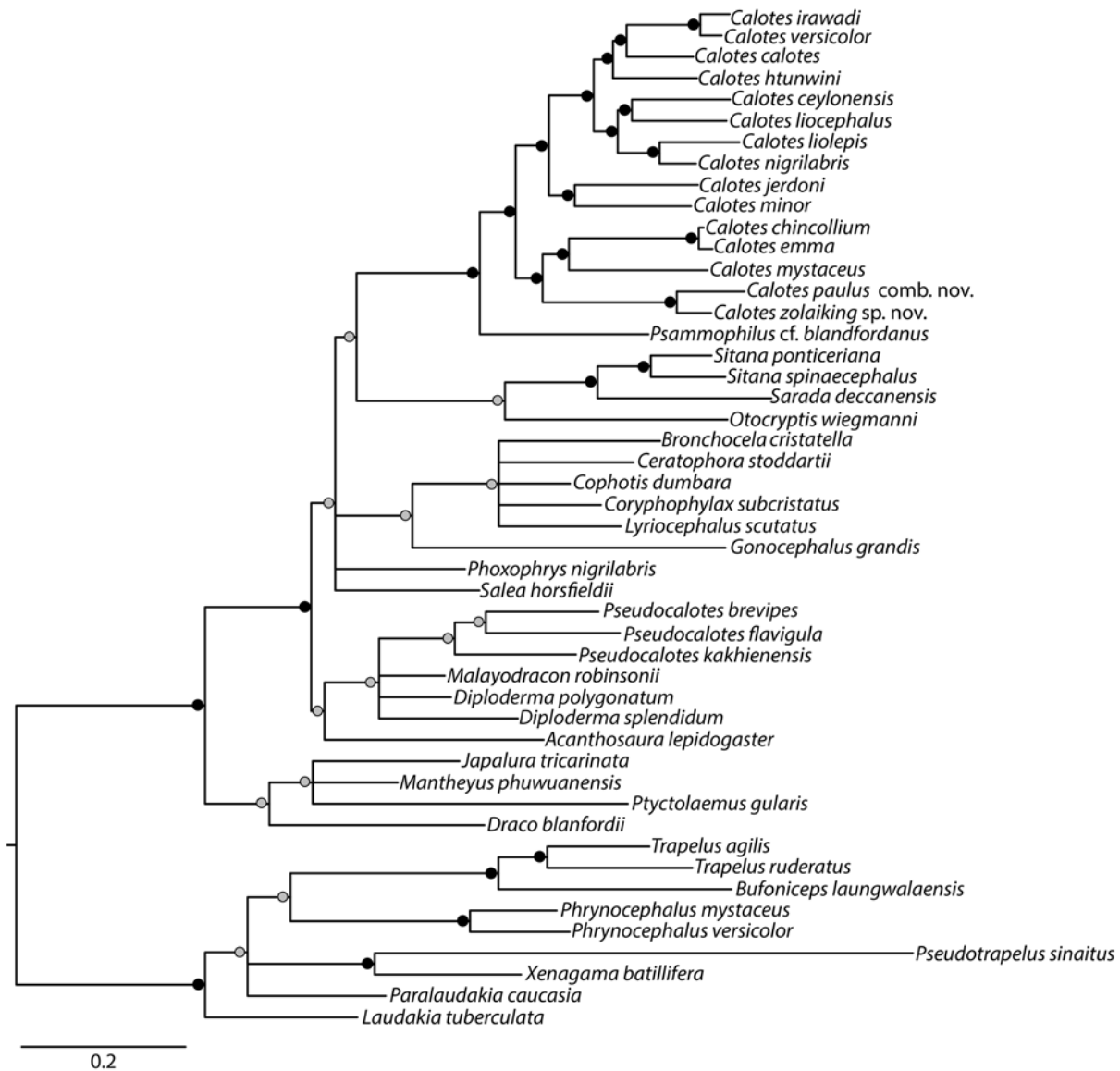


FIGURE 3. BI phylogeny of the mitochondrial (ND2 + 16S) dataset. Posterior probability > 90 dark circle; < 90 grey circle.

The syntype series of *Calotes paulus* **comb. nov.** is comprised of specimens presented from the East India Company from “Affghanistan” and “Khasia hill”, of which the former locality is considered in error. Though we concur with Günther (1864) that the “Affghanistan” specimens were likely to have originated from the Khasi Hills, and our morphological examination of specimens suggests that the syntype series are conspecific, the origin of these specimens is not confirmed at this time (refer to the “Distribution and natural history” section below for further discussion). Considering the discovery presented here of a second, morphologically very similar sister species, we herein designate a lectotype for *Calotes paulus* **comb. nov.** for the purpose of restricting the name bearing type to a single specimen.

***Calotes paulus* (Smith, 1935) comb. nov.**

Figs. 5 and 6; Table 2 and 5.

- Calotes minor* Gray, 1845:244 (partim: “Affghanistan” & “Khasia hill”).
- Oriocalotes minor* Günther 1864:147 (partim: “Afghanistan”, “Khasya” & “Sikkim”).
- Oreocalotes* [sic] *minor* Jerdon 1870:77.
- Charasia minor* Theobald 1876:113 (partim: “Sikkim”).

—*Acanthosaura minor* Boulenger 1885:304–305 (partim: “Afghanistan”, “Khasia” & “Sikkim”).
Oriocalotes paulus Smith, 1935:166–167, 226.

Lectotype by present designation. Adult male, BMNH 1946.8.11.28 (previously BMNH xxiii.30.B), from “Afghanistan” (in error, likely to be Khasi Hills [in Meghalaya state, Northeast India], fide Günther 1864; type locality referred to as “Khasi Hills” by Smith 1935 without discussion), presented by the East India Company.

Paralectotypes by present designation. Adult male, BMNH 1946.8.11.27 (previously BMNH xxiii.30.A), and juvenile, BMNH 1946.8.11.29 (previously BMNH xxiii.30.C), from “Afghanistan” (see comment for lectotype), presented by the East India Company; adult male, BMNH 1946.8.11.35 (previously BMNH xxiii.30.D), from “Khasia hill”, Meghalaya state, Northeast India, presented by the East India Company.

Additional material. Subadult female, NCBS-AQ197, and adult female, NCBS-AQ198, from Sohra (previously known as Cherrapunjee, 25°16′39.38″N; 91°41′48.95″E, 1370 m a.s.l.), East Khasi Hills District, Meghalaya state, Northeast India, collected by Vivek Sarkar on 27 October 2014; an adult female and juvenile, BMNH 70.11.29.43, from ‘Khassya’, Meghalaya state, Northeast India, presented by T.C. Jerdon; adult male, BMNH 60.3.19.1378, from “Himalaya” (given as “Sikkim” [Northeast India] in Boulenger 1885), collected by Messrs. von Schlagintweit; adult male, BMNH 72.4.17.328, and adult female, BMNH 72.4.17.329, from unknown localities (given as “Sikkim, [Northeast India] in Boulenger 1885), presented by T.C. Jerdon; adult male, BMNH 60.3.19.1029, from “Afghan.?” (in error, likely to be “Khasya” [Meghalaya state, Northeast India], fide Günther 1864), presented by Dr. Griffith.

Diagnosis. A medium sized *Calotes*, snout to vent length averaging 57.5 ± 12.5 mm, and maximum to at least 71.0 mm. Body feebly compressed with a weak dorsal crest; scales on top of head highly heterogeneous, keeled, those above orbits are largest, scales surrounding parietal are more or less similar in size; three spines on each side of head, one above orbit, one above tympanum and one on temporal region on each side; dorsal pholidosis heterogeneous, composed of medium sized, weakly pointed, strongly keeled scales intermixed with similar but slightly larger scales which are distinct on flanks; upper rows directed backwards and upwards and a few lower rows directed backwards; 42–46 midbody scale rows; a weakly developed fold anterior to forelimb insertion having granular scales; tympanum small, typically covered by a single large scale; tail rounded; seven to nine supralabials and seven to nine infralabials; lamellae bicarinate, 18–23 on fourth finger and 20–26 on fourth toe. Presence of heterogeneous scales on dorsum and weakly developed dorsal crest of *Calotes paulus* **comb. nov.** distinguish it from all known congeners.

Description of lectotype (BMNH 1946.8.11.28). Adult male. Mensural and meristic data is summarised in Table 2. General habitus slightly laterally compressed. Head relatively long (HL/SVL 0.32), broad (HW/HL ratio 0.66), not depressed (HD/HL ratio 0.55), slightly broader than neck (Fig. 5A). Snout short (SE/HL ratio 0.39), longer than orbital diameter (OD/SE ratio 0.85). Orbit large (OD/HL ratio 0.33); pupil round. Snout bluntly pointed in profile (Fig. 5C), rostral rectangular, approximately two times longer (1.8 mm) than deep (0.8 mm), contacted by first supralabials and four scales dorsally. Nostril oval, laterally positioned, nasal large, pentagonal in shape, bordered by seven scales including supralabials one and two (Fig. 5C). Nine smooth rectangular supralabials, and seven infralabials. Loreal region slightly concave, scales of loreal region small, flat, dominated by a single row of enlarged scales extending from posterior edge of nasals, below orbits, to posteriormost supralabial on each side, enlarged scale row runs parallel with supralabials (though mostly separated from them by a single row of narrow scales; Fig. 5C). A row of four enlarged longitudinally keeled temporal scales extending from posterior edge of orbit to above anterior edge of tympanum. Orbital scales small, rounded, granular. Tympanum covered by a single scale (Fig. 5C). Canthals enlarged, overlapping slightly. Scales on dorsal surface of snout are heterogeneous in size and shape, smaller scales weakly tubercular, larger scales with distinct keels. Supraorbital scales weakly keeled, increase in size from supraciliaries to inner edges of orbits, of which enlarged scales follow curvature of orbits posterolaterally. Two small sized scale rows divide enlarged scales of inner orbits at narrowest point of frontal (Fig. 5B). Posterior mid-dorsal surface of the head (surrounding parietal scale) is dominated by a patch of slightly enlarged scales. Parietal scale moderately enlarged, longitudinally subrectangular without visible pineal eye (but with distinct depression) (Fig. 5B). Temporal spine longer than nuchal spines, orbital spine shorter, and supra-tympanic spine small (Fig. 5B). Mental subtriangular, approximately as wide as long, bordered posteriorly by a ventrolateral row of five elongated chin shields gradually changing shape and size posteriorly to blend with surrounding rows of gular scales. First pair of post-mental chin shields in contact laterally with infralabials, remaining shields are separated from infralabials by one to two rows of small gular scales (Fig. 5D). Remaining gular scales keeled (increasingly

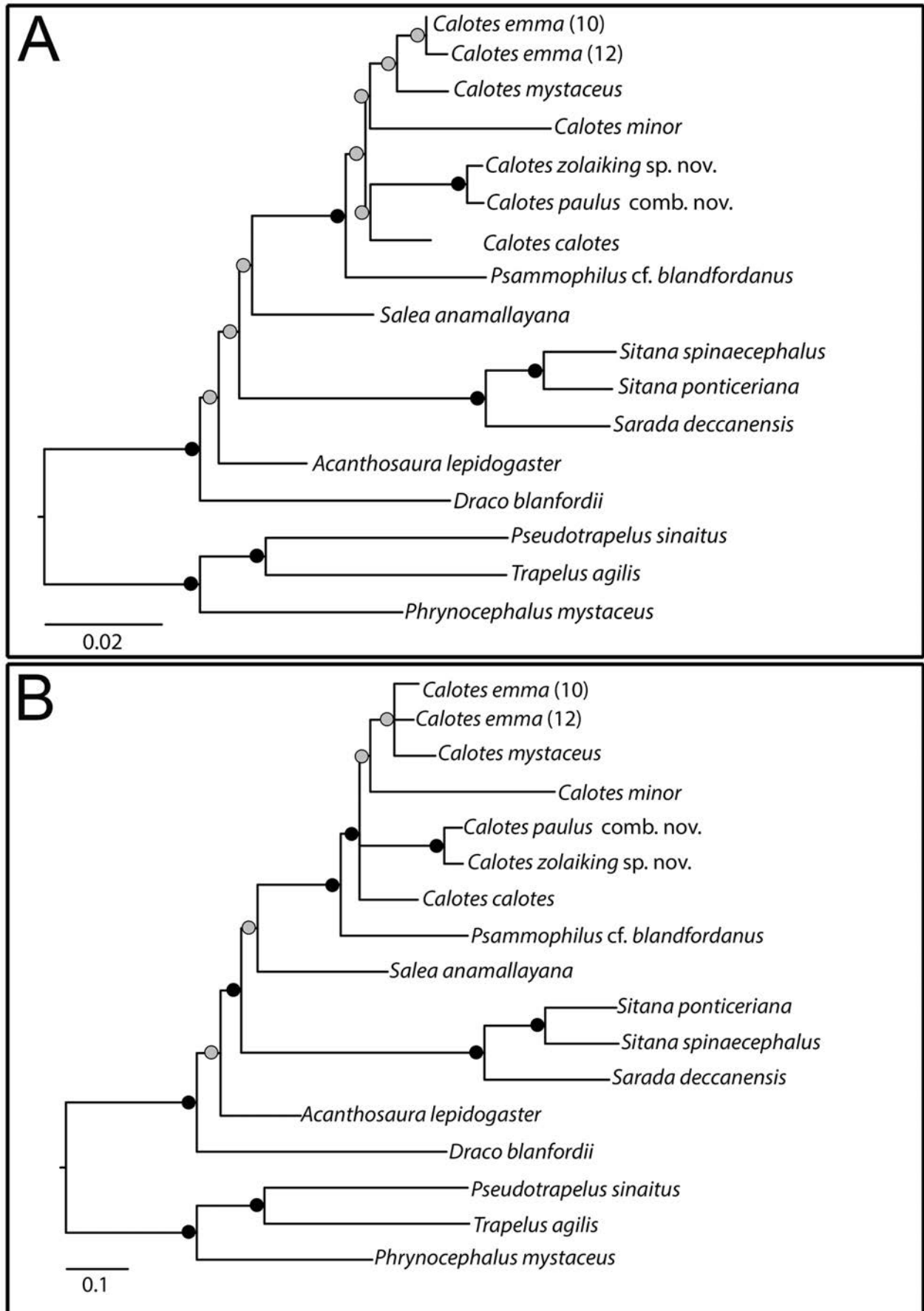


FIGURE 4. Phylogeny constructed using concatenated nuclear dataset (PTGER + R35+RAG1). A. ML phylogeny, bootstrap support: > 90 dark circle; < 90 grey circle. B. BI phylogeny, posterior probability: > 90 dark circle; < 90 grey circle.

posteriorly), subimbricate, mid-gular scales smallest, increasing in size slightly posterolaterally and again decreasing in size dorsally over jowls. No distinct gular pouch present, and transverse gular fold absent (Fig. 5D). Ventral scales imbricate, strongly keeled, heterogeneous in size and arranged in approximate rows, 45 scales around mid-body. Nuchal crest is composed of nine short laterally compressed spines, largest on mid-nuchal region, decreasing in size anteriorly and posteriorly. Remaining vertebral scales are enlarged relative to adjacent rows, and possess a more pronounced median keel providing a serrated appearance in profile, 28 mid-dorsal scales in total. Dorsal and lateral scales are heterogeneous in size and shape (Fig. 5A), all scales with a moderate median keel, arranged into approximate rows, keels on those of upper flanks are mostly oriented obliquely upward, horizontal on mid-flanks, and obliquely downward on lower flanks. A distinct shallow oblique fold in front of and curving around anterior forelimb insertion (Fig. 5C). Scales of forelimbs and ventral hindlimbs form approximate rows, those of dorsal hindlimbs do not form regular rows and are heterogeneous in size. Dorsal scales larger than ventral scales on forelimbs and hindlimbs, all moderately keeled dorsally, and very weakly keeled ventrally. Forelimbs moderately long and thin (Fig. 5A); hindlimbs long and thin. Digits slender, each with a strong, slightly curved claw. Lamellae entire, bicarinate, 23 on fourth finger, and 26 on fourth toe. Tail rounded in cross section, approximately twice as long as SVL (TL/SVL ratio 1.98), slightly enlarged posterior to cloaca; scales on dorsal and ventral surfaces of tail are regularly arranged, strongly keeled, imbricate. Precloacal and femoral pores absent.

Coloration (in preservative). Dorsal surface of head mostly pale grayish/yellowish-brown with dark brown speckling on snout (Fig. 5B); lateral surfaces of snout pale grayish-white with brown blotches on lips; broad brown stripe extends from below eye to slightly posterior of tympanum (Fig. 5C). Dorsal and lateral surfaces of anterior two thirds of body pale grayish-brown, posterior half mostly dark brown mottled with pale grayish-brown (Fig. 5A). Dorsal surfaces of upper forelimbs pale grayish-brown, lower forelimbs mostly dark brown mottled with pale grayish-brown; dorsal surfaces of hindlimbs mottled light and dark brown (Fig. 5A). Tail primarily pale grayish-brown, with faint darker brown bands. Ventral surfaces of head, body and limbs pale grayish-white, with faint irregular stripes radiating from the central gular region (Fig. 5D).

Coloration in life (based on specimens not collected). Head, body, limbs and tail mostly mid to dark brown, with darker brown mottling, and occasionally green mottling. Area on lateral snout white, or white and green. Refer to Figure 6 for finer details of markings and coloration.

Variation. Most specimens examined correspond well with description of lectotype. Females generally larger in size (female SVL 57.9–71.3 mm, $N = 4$ versus male SVL 55.5–66.6 mm, $N = 5$). When hind limb is extended anteriorly along body, it typically reaches between posterior edge of tympanum and posterior edge of orbit on all specimens except BMNH 72.4.17.328 (reaches rear of jaw) and BMNH 72.4.17.329 (reaches anterior forelimb insertion). Transition from nuchal crest spines to strongly keeled dorsal scales is not clearly defined on some specimens (e.g., BMNH 72.4.17.328 and BMNH 60.3.19.1029). Tympanum covered by a single scale on all specimens, bar one (BMNH 60.3.19.137), which possess one to two rows of smaller scales bordering a single large scale anteriorly. Spinose scales in general poorly developed on juveniles. Finer details of coloration and markings vary between individuals, with some specimens having a distinct broad dark brown transverse cross bar on posterior half of dorsum. Further details of morphometric and meristic variation are presented in Table 2.

Suggested common name. Khasi Hills Forest Lizard.

Distribution and natural history. *Calotes paulus* **comb. nov.** is known with certainty only from the the Khasi Hills, Meghalaya state, Northeast India. The syntype series included three specimens with the associated collection locality “Affghanistan”, which has been considered in error by several authors (e.g., Günther 1864; Boulenger 1885), and as such Afghanistan has been omitted from the distribution of the species by others (e.g., Anderson 1879; Smith 1935). Additional specimens in the NHMUK collected by T.C. Jerdon and the Schlagintweit brothers, have the associated collection locality “Sikkim”. These collectors travelled to both the Darjeeling/Sikkim region and the Khasi Hills. Jerdon (1870) notes that he was aware that several of the localities given by the brothers Schlagintweit were erroneous “probably from the displacement of labels”. Furthermore, collection localities associated with some of Jerdon’s specimens from “Sikkim” have also been demonstrated to have been mislabeled for species otherwise found only in the Khasi Hills (Biju *et al.* 2016; Mahony *et al.* 2018). Jerdon (1870) also admits to not having seen this species, despite presenting specimens to the BMNH (NHMUK) soon after. By 1870, Jerdon had completed his tour to Sikkim, thus it is most likely that his specimens were collected from the Khasi Hills postscript. Smith (1935) clearly questioned Sikkim in the distribution of this species, as do we, since it has not been reported since these early specimens. References to the presence of this species in Xizang (Tibet), China by Zhao and Adler (1993) and Li *et al.* (2010, and references therein) require further confirmation.

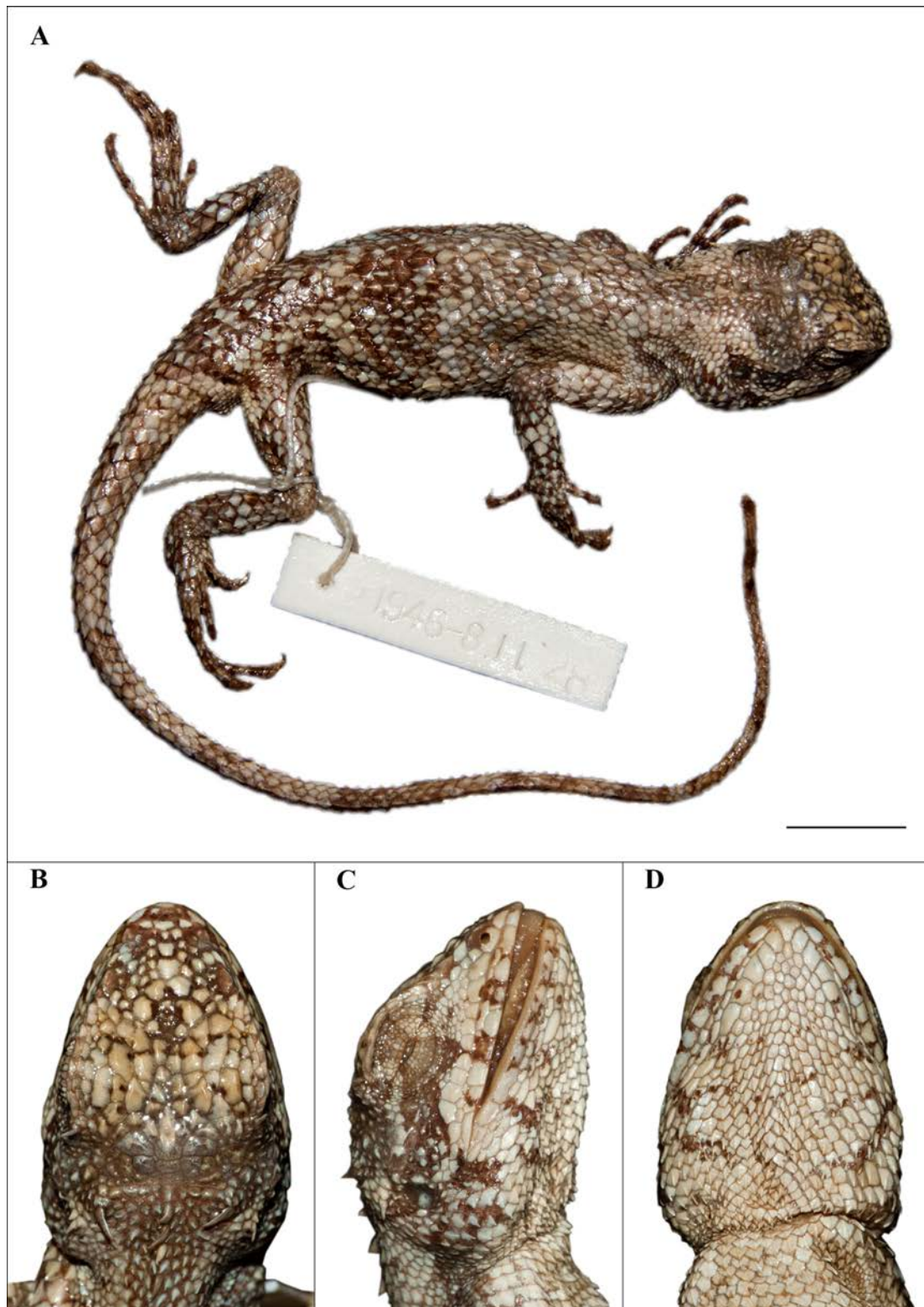


FIGURE 5. Lectotype of *Calotes paulus* **comb. nov.** (BMNH 1946.8.11.28). A. Dorsal view of body. B. dorsal view of head, C. lateral view of head, D. ventral view of head. Scale bar: 10 mm.

Natural history observations of *Calotes paulus* **comb. nov.** were made by one of the authors (VS) over a period of one year at Sohra (previously known as Cherrapunjee), on the Shillong Plateau, East Khasi Hills District, Meghalaya state, Northeast India (Fig. 1). The remaining natural habitat in the vicinity of Sohra predominantly consists of grasslands with isolate trees and small patches of tropical moist evergreen forest (Champion & Seth 1968) on hill slopes and around perennial hill streams (Fig. 7) *Calotes paulus* **comb. nov.** is one of the common agamids found

in this area, where it has been observed along the fringes of forests, or on isolated tree trunks or large bushes. An adult female (BMNH 70.11.29.43) contained six large eggs (two measured, 14.1 X 8.2 mm and 14 X 8.5 mm). One individual of *Calotes paulus* **comb. nov.** was observed feeding on a cicada (*Gudaba* sp.).



FIGURE 6. *Calotes paulus* **comb. nov.** showing live coloration, photographed in-situ from Sohra, East Khasi Hills District, Meghalaya state, Northeast India.

TABLE 2. Morphometric measurements (in mm) of *Calotes paulus* **comb. nov.** specimen in the NHMUK. Refer to the Materials and methods section for morphometric and meristic abbreviations. NM: not mentioned; KH: Khasi Hills; HM: “Himalaya”; M: adult/subadult male; F: adult/subadult female; J: juvenile unsexed; “–” not assessed, ^ lectotype, * paralectotype

Tag no.	BMNH 1946.8.11.28 [^]	BMNH 1946.8.11.27*	BMNH 1946.8.11.29*	BMNH 1946.8.11.35*	BMNH 70.11.29.43	BMNH 70.11.29.43	BMNH 60.3.19.1378	BMNH 72.4.17.328	BMNH 72.4.17.329	BMNH 60.3.19.1029	NCBS AQ198	NCBS AQ197
Location	KH	KH	KH	KH	KH	KH	HM	NM	NM	KH	KH	KH
Sex	M	M	J	M	J	F	M	M	M	M	F	FJ
SVL	58.8	56.8	28.3	58.3	39	69.4	62.1	66.6	71.3	55.5	66	57.9
TrL	28.5	31.9	14.3	32.7	16.5	34.3	28.6	30.4	37.7	26.6	39	31.2
TL	116.7	112.3	50.9	114.7	77	120	127	121.1	140.8	97.8	119	118.3
TaD	3.8	3.9	1.9	3.9	–	4.9	5	5.6	6.2	4.5	5.4	4.5
TW	4.1	4.5	2.1	4.8	–	5.6	5.6	6.5	5.6	5.1	5.2	4.5
HL	19.1	18	10.3	19.3	13.5	20.2	19.8	20.3	22.7	18.4	19.5	17.2
HW	12.7	12	7.7	13.3	9.2	14	13.8	13.8	14.7	12.7	14.3	11.5
HD	10.6	10.4	6.4	10.5	–	11.7	11.6	11	11.7	10.1	11.5	–
SE	7.5	6.8	4.2	7.4	5.1	8.2	7.8	7.6	8.5	6.5	7.1	5.9
NE	4.6	3.8	2.5	4.3	3	5.2	4.9	4.5	5	3.9	4	4.3
EE	4.3	4.1	2.5	4.4	3.3	5.1	4.9	5.1	4.9	3.4	4.7	4.1
IO	8.1	7.7	4.8	7.6	5.9	8.7	8.6	8.6	9.8	7.5	9	7.5
SFI	21.9	19.9	11.6	20.9	16.7	24.3	25.2	26.6	26.5	21.8	24.9	20.5
UAL	8.6	8.2	3.9	7.9	6	9.4	8.9	9.4	9.4	9	11.8	11
LAL	8.3	8.3	4.5	8.5	5.8	9.3	9.3	10.2	9.8	8.7	11	10
HaL	13.2	12.7	6.8	11.2	8	13.6	12.5	12.1	11.5	10.4	12	11.3
4FL	9.5	8.3	4.2	7.3	4.8	8.8	8.1	8.2	7.7	6.7	8.4	8.2
ULL	11.3	12.1	6.7	12	8.4	13.2	13	13.2	13.1	12.6	13.5	12.3
LLL	10.9	11.6	6.2	11.3	7.9	13	12.5	13.1	13.1	11.9	12.7	12.9
FOL	18.1	17.3	9.6	17.6	12.5	20.6	18.3	19	18.7	17.2	18.2	17
4TL	16.1	14.9	5.5	13.3	10.4	16.3	15.3	15.1	15.4	14.1	10.7	10.7
TD	1.9	1.8	1.1	1.5	1.3	1.8	2.1	1.8	2.1	2.1	1.3	1.6
OD	6.4	6.3	3.9	6.5	4.8	7	6.4	6.4	7.5	6.1	6.4	5.8
SnS	9	9	13	11	11	11	11	12	12	10	7	9
HeadSTr	13	12	14	13	12	11	12	14	14	11	12	14
CS	6	5	5	5	6	6	5	5	5	5	5	7
SL(L/R)	9/–	8/–	8/–	7/–	8/–	9/–	7/–	8/8	7/8	8/8	7/8	8/8
IL(L/R)	7/–	8/–	7/–	8/–	8/–	9/–	9/–	8/8	8/8	8/8	8/8	8/8
NC	9	6	–	6	–	5	10	–	6	–	6	4
VS	28	29	27	30	24	31	28	31	32	31	28	29
MSR	45	42	45	44	44	44	45	46	46	43	44	46
4Flam	23	21	19	18	22	21	23	21	21	19	20	23
4TLam	26	22	20	21	25	24	24	26	23	23	27	27

***Calotes zolaiking* sp. nov.**

Figs 8–12; Tables 3–5.

Holotype. Adult female, NCBS-AU152, from Synod Hospital Compound (23°46′19.06″N, 92°43′56.37″E, 1290 m a.s.l.), Durtlang, Aizawl District, Mizoram state, Northeast India, collected by C. Lalrinchhana and Samuel Lalrounga on 10 June 2014.

Paratypes. Two subadult females, NCBS-AU153 and ESV 105, an adult female, NCBS-AU154, and a subadult male, NCBS-AU155, collection data same as holotype; subadult male, BNHS 2327, from Hmuifang (23°27′17.93″N, 92°45′07.05″E, 1478 m a.s.l.), Aizawl District, Mizoram state, Northeast India, collected by C. Lalrinchhana and Samuel Lalrounga.

Referred specimens. Adult male, NCBS-AU156 collection data same as holotype.



FIGURE 7. Habitat where *Calotes paulus* **comb. nov.** were found in Sohra, East Khasi Hills District, Meghalaya state, Northeast India.

Diagnosis. A medium sized *Calotes*, snout to vent length averaging 64.7 ± 8.17 , and maximum to at least 77.0 mm. Body feebly compressed laterally with a weak dorsal crest; scales on top of head highly heterogeneous, keeled, those above orbits are largest, scales surrounding parietal are unequal in size; three spines on each side of head, one above orbit, one above tympanum and one on temporal region; dorsal scales heterogeneous, composed of medium sized, weakly pointed, strongly keeled scales, intermixed with similar but slightly larger scales which are distinct on flanks, upper rows directed backwards and upwards and a few lower rows directed backwards; 49–52 midbody scale rows; a weakly developed fold anterior to forelimb insertion having granular scales; tympanum small; tail rounded; eight to nine supralabials and seven to ten infralabials; lamellae bicarinate, 21–24 on fourth finger and 23–27 on fourth toe.

Calotes zolaiking **sp. nov.** can be easily diagnosed from all congeners except *Calotes paulus* **comb. nov.** in possessing heterogeneous scales on the dorsum and a weakly developed dorsal crest. Based on dorsal pholidosis, the new species is most similar to *Calotes paulus* **comb. nov.**, but differs with respect to the following (*Calotes paulus* **comb. nov.** given in parentheses): greater number of midbody scales rows, 49–52 (*versus* 42–46), greater number of caudal vertebrae, 50 (*versus* 35–45), and fewer caudal vertebrae with transverse processes 12 (*versus* 14).

Description of holotype (NCBS-AU152). Specimen is generally in good condition but slightly dehydrated, tail bent toward left in a sigmoid manner, left manus slightly adpressed with outer three fingers curved, right manus ad-

pressed with fingers directed backwards, eyes sunken, orbital spine on left side broken, tips of supra-tympanic spines on both sides curved, all artefacts of preservation. Mensural and meristic data is summarised in Table 3. An adult female, SVL 77.2 mm. Head relatively long (HL/SVL 0.31), broad (HW/HL ratio 0.65), not depressed (HH/HL ratio 0.52), noticeably broader than neck (Fig. 8A). Snout short (SE/HL ratio 0.37), longer than orbit diameter (OD/SE ratio 0.78). Orbit large (OD/HL ratio 0.29); pupil round, eyelids covered with small rounded scales, a single row of scales bordering eyelids slightly elongate, six supraciliaries on each side, elongate, subimbricate, slightly protruding laterally on supraorbital ridge, similar in size, with single anterior most supraciliary smallest. Snout obtusely pointed; rostral wider (2.1 mm) than deep (0.7 mm), contacted laterally by first supralabial, an elongated large prenasal, and two large scales dorsally. Canthus rostralis and supraciliary edge sharp. Nostril circular, laterally positioned and placed at centre of a large, undivided nasal plate (Fig. 8C), which is bordered by seven scales on both sides, including one prenasal, one supranasal, three postnasals, with two subnasals on left side, and one subnasal and second supralabial on right side; separated on both sides from rostral and first supralabial by prenasal. Supralabials roughly rectangular, more or less equal sized, posterior-most being longest, bordered above by two rows of scales starting behind postnasals and extending to posterior border of orbit; upper row distinctly enlarged consisting of equal sized, roughly rectangular scales; scales on lower row are heterogeneous in shape and size, decreasing in size posteriorly. Loreal region concave, scales of loreal region heterogeneous in shape and size, flat or weakly tuberculate. Scales on postorbital and temporal region heterogeneous in shape and size, subimbricate, mostly tuberculate; a row of five much larger longitudinally keeled scales, fourth being largest, extending from posterior midorbital region to just before anterior edge of tympanum (Fig. 8C). Tympanum covered with single scale (Fig. 8C). Canthals enlarged, overlapping, becoming slightly larger along supraciliaries. Scales on dorsal surface of snout and forehead heterogeneous in shape and size, all weakly pointed anteriorly (Fig. 8B), smaller scales weakly tubercular, larger with distinct keels except those on internarial region which are roughly rounded, uniformly large and smooth. Supraorbital scales weakly keeled, increase in size from supraciliaries to inner edges of orbits, of which enlarged scales follow curvature of orbits posterolaterally (Fig. 8B). Two small scale rows divide enlarged scales of inner orbits at narrowest point of frontal. Scales on occipital region heterogeneous in shape and size; smaller scales weakly tubercular, larger ones with distinct keels. Parietal scale roughly triangular, without visible pineal eye (but with distinct depression) (Fig. 8B). Parietal scale bordered laterally by three enlarged, roughly elongated keeled scales, with much smaller scales anteriorly and posteriorly. Single temporal spine on each side, longer than nuchal spines; shorter orbital spine and a small supra-tympanic spine also present on each side (Fig. 8B). Mental subtriangular, approximately as wide as long, bordered posterolaterally by a row of six elongated postmental chin shields on either side, gradually changing shape and size posteriorly to blend with surrounding rows of gular scales (Fig. 8D). First pair of postmental chin shields in contact laterally with first infralabials, remaining shields separated from infralabials by one to two rows of small gular scales. Posterior gular region with considerably enlarged, flat, strongly keeled, pointed, imbricate scales, those on jowls slightly larger in size; anterior gular scales much smaller, rounded, weakly keeled and subimbricate; all gular scales directed posteromedially except a few median rows which are directed posteriorly. No distinct gular pouch present, transverse gular fold absent (Fig. 8D). Ventral scales are like those on posterior gular region, enlarged, flat, strongly keeled, pointed, imbricate, homogenous in shape but heterogeneous in size, generally increasing in size laterally; arranged in regular longitudinal rows that are directed posteriorly, but those on lateral aspect are directed posteromedially (Fig. 9C). Approximately 49 scales around mid-body. Nuchal crest composed of three short, laterally compressed, equal sized spines. Remaining vertebral scales slightly enlarged relative to adjacent rows (Fig. 9A) but possess a more pronounced median keel providing a serrated appearance in profile (Fig. 9B); 33 mid-dorsal scales from first raised nuchal scale to above level of cloaca. Dorsal scales heterogeneous in size and shape; all scales with a moderate median keel, arranged into approximate rows (Fig. 9A & B); keels on those of upper flanks mostly oriented obliquely upward, horizontal on mid-flanks and obliquely downward on lower flanks (Fig. 9B). A distinct shallow oblique fold in front, and curving around anterior forelimb insertion. Scales of forelimbs and ventral hindlimbs form approximate rows, those on dorsal hindlimbs do not form regular rows and are heterogeneous in size. Dorsal scales larger than ventral scales on forelimbs and hindlimbs, all moderately keeled dorsally, very weakly keeled ventrally. Forelimbs moderately long (UAL+LAL+HaL/SVL ratio 0.45); hindlimbs long (ULL+LLL+FoL/SVL ratio 0.66). Digits slender, elongate and ending in a strong, slightly curved claw. Lamellae entire, bicarinate; 21 on fourth finger, 23 on fourth toe. Relative finger lengths: IV(8.5 mm) > III(7.9 mm) > II(4.6 mm) > V(4.1 mm) > I(3.0 mm) and toes IV(11.9 mm) > III(10.5 mm) > V(8.2 mm) > II(7.2 mm) > I(5.5 mm). Tail entire, rounded, nearly twice head-body length (TL/SVL ratio 1.87), not swollen at base (Fig. 8A); uniformly covered with similar sized, strongly keeled, weakly pointed, regularly arranged, posteriorly directed imbricate scales.

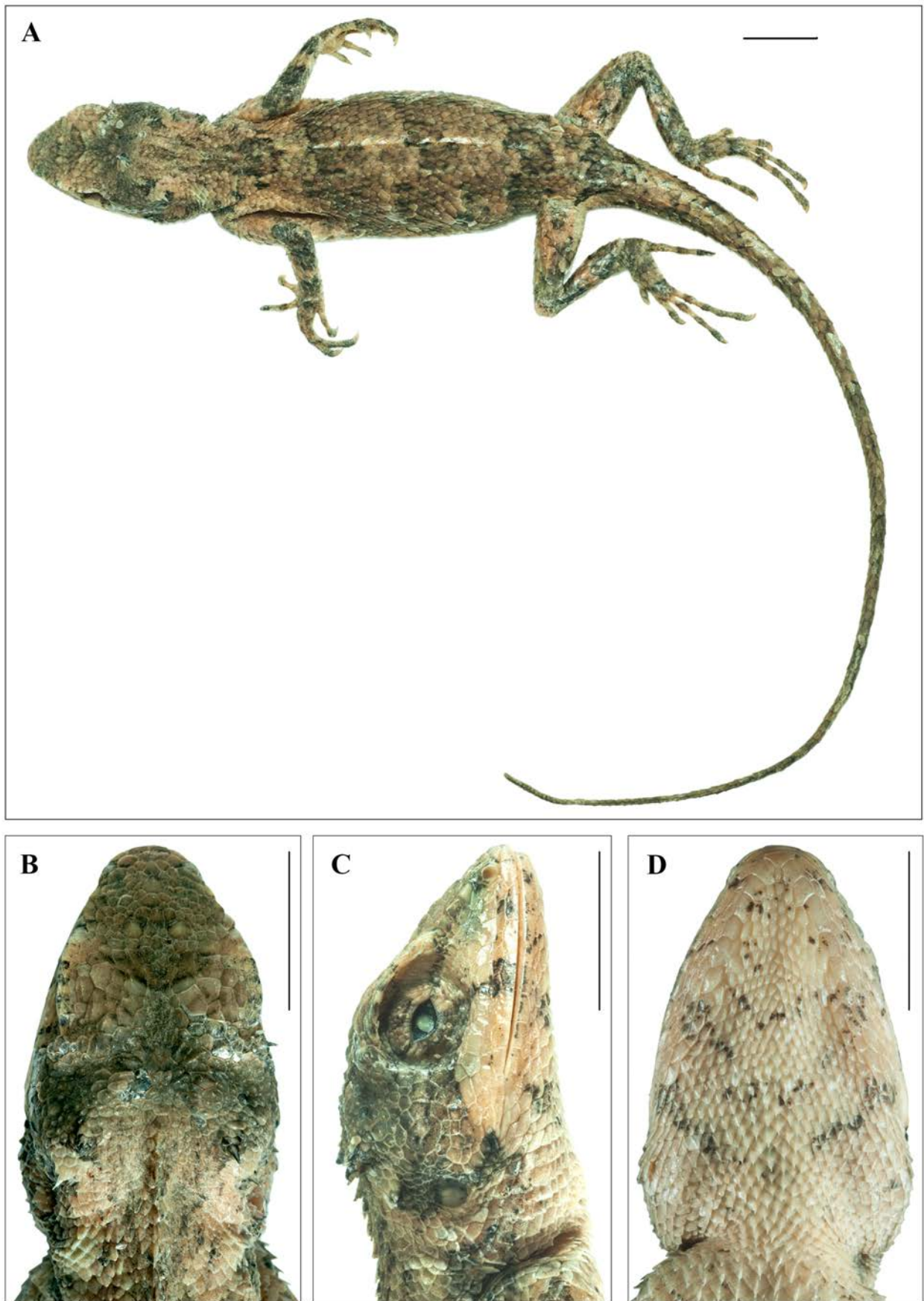


FIGURE 8. Holotype of *Calotes zolaiking* sp. nov. (NCBS-AU152). A. Dorsal view, B. dorsal view of head, C. lateral view of head, D. ventral view of head. Scale bar: 10 mm.

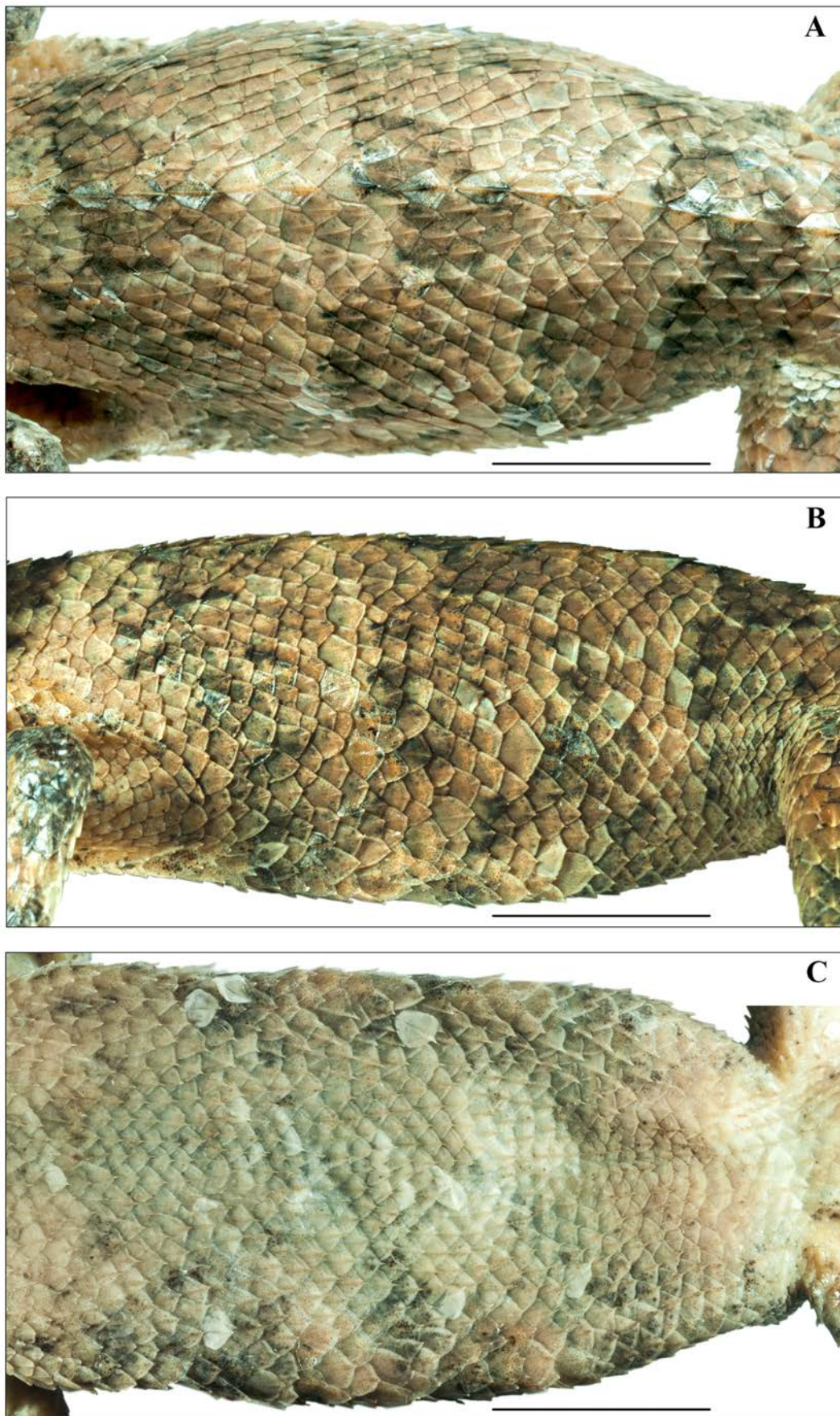


FIGURE 9. Scales on trunk of holotype of *Calotes zolaiking* sp. nov. (NCBS-AU152). A. Dorsal view, B. lateral view, C. ventral view.



FIGURE 10. *Calotes zolaiking* **sp. nov.** showing live coloration, photographed in-situ from Durtlang, Aizawl District, Mizoram state, Northeast India.

TABLE 3. Morphometric measurements (in mm) of *Calotes zolaiking* sp. nov. Refer to the Materials and methods section for morphometric and meristic abbreviations. M: adult/subadult male; F: adult/subadult female; MJ: juvenile male; * tail broken; ^ holotype, # paratype, † preferred material

Tag no.	NCBS-AU156†	NCBS-AU152^	NCBS-AU153#	NCBS-AU154#	ESV 105 #	BNHS 2327#	NCBS-AU155#
Location	Mizoram	Mizoram	Mizoram	Mizoram	Mizoram	Mizoram	Mizoram
Sex(maturity)	M	F	F	F	F	MJ	MJ
SVL	62.9	77.2	71.2	68.6	62.2	52.9	58.5
TrL	33.5	42.7	40.4	36.7	32.3	27.4	29.7
TL	122.1	145.1	123.5*	129.2	112.5*	118.6	120
TaD	6	6.2	5.4	4.7	4.2	4.6	5.1
TW	7.6	6	4.7	5.1	4.4	5.4	5.9
HL	18.4	23.8	21.2	20.2	18.5	16.5	17.7
HW	11.8	15.6	13.6	13.4	12.2	11	11.7
HD	10.9	12.6	11.5	11	10.8	9.1	10
SE	7.1	8.9	8.3	7.7	7.4	6.1	6.5
NE	4.3	6.5	5.4	4.5	4.4	3.8	4.1
EE	4.2	6.2	5	5	4.1	3.7	4
IO	7.5	10	9.6	8.8	8	7.1	8.1
SFI	23.7	27.1	21.5	23.5	23.5	19.6	21.4
UAL	8.5	12.2	9.5	11.8	10.4	9.3	10.9
LAL	8.8	9.7	9.3	9.5	9.5	7.9	9.2
HaL	9.7	13.6	12.3	11.5	10.2	9.4	10.5
4FL	7.1	8.5	8.4	7.4	7.2	6.7	8.1
ULL	13.2	16.7	14.1	13.4	12.6	10.7	13.1
LLL	10.9	15.6	13.5	12.6	12.5	11.1	11.6
FOL	16.8	19.4	18.5	17.6	14	13.5	16.4
4TL	9.8	11.9	11.1	10.4	9.9	8.7	10.6
TD	1.6	2	1.3	1.5	1.5	1	1.2
OD	5.7	7	6.5	6.2	6	6	6.1
SnS	11	12	11	10	8	9	11
HeadSTr	13	15	14	15	13	12	16
CS	5	6	6	7	5	6	7
SL(L/R)	8/8	8/9	8/9	8/8	8/8	9/8	9/8
IL(L/R)	9/9	9/9	9/10	10/10	7/7	9/8	8/8
NC	3	3	3	7	5	4	2
VS	32	33	32	33	34	35	34
MSR	49	49	50	52	51	50	49
4Flam	24	21	23	24	23	22	24
4TLam	26	23	25	27	26	26	26

Coloration (in preservative). Coloration in preservation is more or less similar to live specimens but slightly faded and predominantly light brown. Transverse stripes on body, limbs and tail are darker. Refer to Figures 8 and 9 for further details of coloration and markings.

Coloration in life (based on specimens other than the holotype). Coloration in life varies, but is primarily mottled shades of light and darker brown dorsally, with four distinct lighter transverse stripes on body, two on forelimbs and two on hindlimbs; stripes may be primarily green or light brown (Fig. 10). Two thin white longitudinal stripes on upper flanks extend from rear of head to base of tail. Region below orbit and lateral surface of snout white, with narrow white and brown radial stripes extending from eye. Tail with faint light and darker brown bands. Ventral surfaces whitish, throat with irregularly arranged dark mottling or thin stripes. Refer to Figure 10 for further details of coloration and marking on live animals.

Variation. Paratypes and referred specimen agree with holotype in general morphology and scalation with following exceptions: NCBS-AQ154 has ten infralabials on both sides, and ESV 105 has seven infralabials on both sides; 35 vertebral scales on BNHS 2327; within paratype series, lamellae on fourth finger varies from 22 to 24, and on fourth toe from 25 to 27. Further variation in mensural and meristic characters within paratype series is documented in Table 3.

Hemipenis. Hemipenis single, clavate (divided less than half of length) with length of organ greater than width. Base naked; sulcus spermaticus broad, canal like, shallow at base and deeper at terminal region. Lips of sulcus spermaticus smooth. Calyculate ornamentation present on each lobe. Thick walled smooth calyces form deep oval pits. Fleshy cardioid structure at base of ventral sulcus absent. Apex capitate and divided into four segments (Fig. 11). Hemipenis of *Calotes zolaiking* **sp. nov.** matches with 13 out of 14 characters reported for seven other *Calotes* spp., and 12 out of 14 characters reported for *Calotes ceylonensis* Müller, 1887 (Maduwage *et al.* 2008; Table 4).

Osteology. Skull of *Calotes zolaiking* **sp. nov.** (NCBS-AU156) is subpentagonal in outline (Fig. 12A): raised in parietal region and slopes steeply towards naris (Fig. 12B). Hyoid apparatus broad with a paired ceratobranchial (CB), CB II shorter than CB I. Maxilla has 14 teeth (including one canine-like tooth [on each side]); three premaxillary teeth; thirteen teeth on either side of mandibles (Fig. 12D & E). Twenty presacral vertebrae excluding atlas and axis and 50 caudal vertebrae (Table 5). Sternum with an oval and elongated central foramen. Ten trunk vertebrae have ribs, and an additional five vertebrae near pelvic girdle have ribs replaced by small transverse processes. Shoulder girdle comprises a broad clavicle; interclavicle long and rod like, suprascapula wedge shaped. Humerus with well-developed proximal and distal ends. Phalangeal formula of manus is 2:3:4:5:3 and of pes is 2:3:4:5:4. Many osteological characters checked for *Calotes zolaiking* **sp. nov.** (NCBS-AU156) matched those of *Calotes paulus* **comb. nov.**, except the former had a higher number of caudal vertebrae (Table 5). *Calotes paulus* **comb. nov.** and *Calotes zolaiking* **sp. nov.** differ from other congeners in five different osteological characters (Table 5). *Calotes paulus* **comb. nov.** and *Calotes zolaiking* **sp. nov.** differ from *Pseudocalotes* in three different osteological characters (Table 5). Within the genera *Calotes* and *Pseudocalotes*, there are several variable characters (Table 5).

Etymology. The species is named for its occurrence in high elevation regions. The specific epithet is a noun in apposition, derived from the Mizo language and is a portmanteau word for a lizard that inhabits high elevations (Mizo: Zo = highland/cold region, Laiking = agamid lizard).

Suggested English name. Mizoram Montane Forest Lizard.

Distribution and natural history. *Calotes zolaiking* **sp. nov.** is known only from its type and paratype localities, Durtlang (1290 m a.s.l.) and Hmuifang forest (1480 m a.s.l.) in Aizawl District, Mizoram state, Northeast India. These two localities are approximately 36 km apart [straight line distance]. This species is also suspected to be found in other high elevation areas of Mizoram. However, very few herpetological surveys have been carried out in this state, so the full extent of its distribution and preferred elevational range is currently unknown. The holotype was collected from a residential area where both native and non-native trees were present. It was seen perching on a *Melaleuca citrina* (Curtis) Dum.Cours. (bottlebrush tree), an introduced ornamental species native to Australia. The native trees dominating the locality include *Trema orientalis* Blume, *Callicarpa arborea* Roxb., *Schima wallichii* (DC.) Korth., *Castanopsis tribuloides* Sm., *Albizia chinensis* (Osbeck) Merr. and *Ficus semicordata* Buch.-Ham. ex Sm. The locality where the paratypes were collected is dominated by *Rapanea capitellata* (Wall) Mez., a *Eurya* sp. Korth., *Quercus* spp. L., *Elaeocarpus rugosus* Roxb., *Nyssa javanica* (Blume) Koord., a *Macropanax* sp. Miq., *Schima wallichii* (DC.) Korth. and *Ardisia macrocarpa* Wall., with a small patch of grassland (Fig. 13). According to Champion and Seth (1968), these regions fall under their “Montane Sub-tropical Forest” category. Most of the natural history observations of *Calotes zolaiking* **sp. nov.** were made from Hmuifang where the paratypes were collected. The type series was collected from vegetation at a height of 1.5–4.5 m above ground level. All individuals of

the species were spotted perching on branches, which suggests they are primarily arboreal. In captivity, an adult female (NCBS AU154) laid three large eggs (measuring 14.1 X 8.2 mm, 14.3 X 8.5 mm and 14.5 X 8.5 mm) in July. During fieldwork at the type locality, juveniles were observed in November. Other agamids found in sympatry include *Calotes* cf. *versicolor* and *Cristidorsa otai* (Mahony, 2009).

Phylogenetic relationships and morphology. Based on its phylogenetic position within the subfamily Dracoininae, *Oriocalotes* now becomes the second monotypic genus (after *Brachysaura*: see Deepak *et al.* 2015) in recent years to be subsumed into *Calotes*. The poor support in the nuclear dataset is probably due to incongruence in the individual nuclear genes (Appendix 4–6). So, additional nuclear markers need to be analysed to further resolve its position within the *Calotes* radiation. Our nuclear and mitochondrial trees support a clade encompassing *Calotes* + “*Oriocalotes*” + *Psammophilus*. Members of this radiation are largely confined to India and harbor multiple ecomorphs; *Psammophilus* is a predominantly rock dwelling genus with a dorsoventrally compressed body. *Calotes minor* is completely terrestrial with a relatively short fifth toe (Deepak *et al.* 2015), whereas all other *Calotes* (including *Calotes paulus* **comb. nov.** and *Calotes zolaiking* **sp. nov.**) are predominantly or exclusively arboreal and have a longer fifth toe.

Mahony (2010) noted that *Oriocalotes* shares common external morphological characters with *Calotes* (elongated spines on the post ocular, temporal and supratympanic regions) and *Pseudocalotes* (enlarged subocular scale row and heterogeneous dorsal scalation). Mahony (2010) also noted that no *Calotes* species possessed a noticeably enlarged subocular scale row, however, this character was found to be present or absent in the genus *Diploderma* Hallowell, 1861, so the plasticity of this character within *Calotes* (now including *Oriocalotes*) might not be unusual. The evolutionary relevance of this character is yet to be studied. Hallerman and Böhme (2000) (modified by Deepak *et al.* 2015) attribute the following characters to the genus *Calotes*: a broad head (HW/HL ratio 0.58–0.82), groups of spines from eye to tympanum, cheek often swollen in males, relatively long hindlimbs (hindlimb length/SVL ratio 0.62–1.01) and tail (TL/SVL ratio 0.9–3.0). Presence of regular, uniform dorsal scales, thought to be an important character in the diagnosis of the genus *Calotes* (Smith 1935; Manthey & Denzer 2000), is now demonstrated to have no systematic importance, as observed in the draconine lizards belonging to the genus *Bronchocela* Kaup, 1827 and *Pseudocalotes*.

TABLE 4. Hemipenial morphological characters used for comparison with *Calotes zolaiking* **sp. nov.** Character score “1” for presence and “0” for absence. Numbers on top represent different species of *Calotes*: 1. *C. calotes*; 2. *C. nigrilabris*; 3. *C. versicolor*; 4. *C. ceylonensis*; 5. *C. liolepis*; 6. *C. liocephalus* Günther, 1872; 7. *C. desilvai* Bahir & Maduwage, 2005; 8. *C. minor*; 9. *Calotes zolaiking* **sp. nov.** Sources: Maduwage *et al.* (2008); Deepak *et al.* (2015).

Character	1	2	3	4	5	6	7	8	9
Hemipenis divided for more than half its length	0	0	0	0	0	0	0	0	0
Flounces present	0	0	0	0	0	0	0	0	0
Apex of each lobe divided symmetrically both laterally and medially by sulcus	0	0	0	0	0	0	0	0	0
Sulcus spermaticus bifurcated	1	1	1	1	1	1	1	1	1
Fleshy cardioid structure at base of ventral sulcus	1	1	1	1	1	1	1	1	0
Lateral and medial sulcus distinct throughout length of each lobe	1	1	1	1	1	1	1	1	1
Length of entire organ greater than its width	0	0	0	0	0	0	0	0	0
Minute denticulation on calyces	0	0	0	0	0	0	0	0	0
Sulcus traverses apex	0	0	0	0	0	0	0	0	0
Each lobe with more than 11 flounces	0	0	0	0	0	0	0	0	0
Ventral sulcus with transverse ridges	0	0	0	0	0	0	0	0	0
Transverse ridges along more than half length of ventral sulcus	0	0	0	0	0	0	0	0	0
Calyces subequal along entire length of organ	0	0	0	0	0	0	0	0	0
Entire length of lateral and medial sulcus with calyces	0	0	0	1	0	0	0	0	0

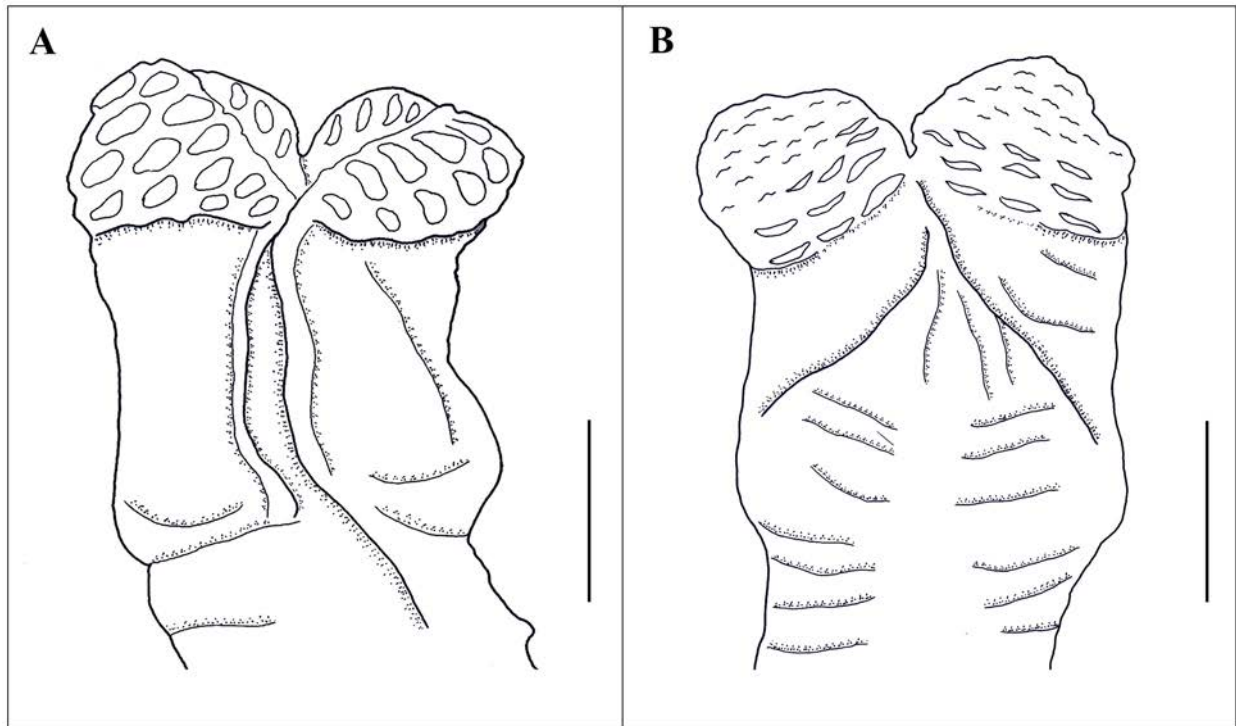


FIGURE 11. Hemipenis of referred specimen of *Calotes zolaiking* **sp. nov.** (NCBS-AU156). A. Sulcal view, B. asulcal view. Scale bar: 1 mm.

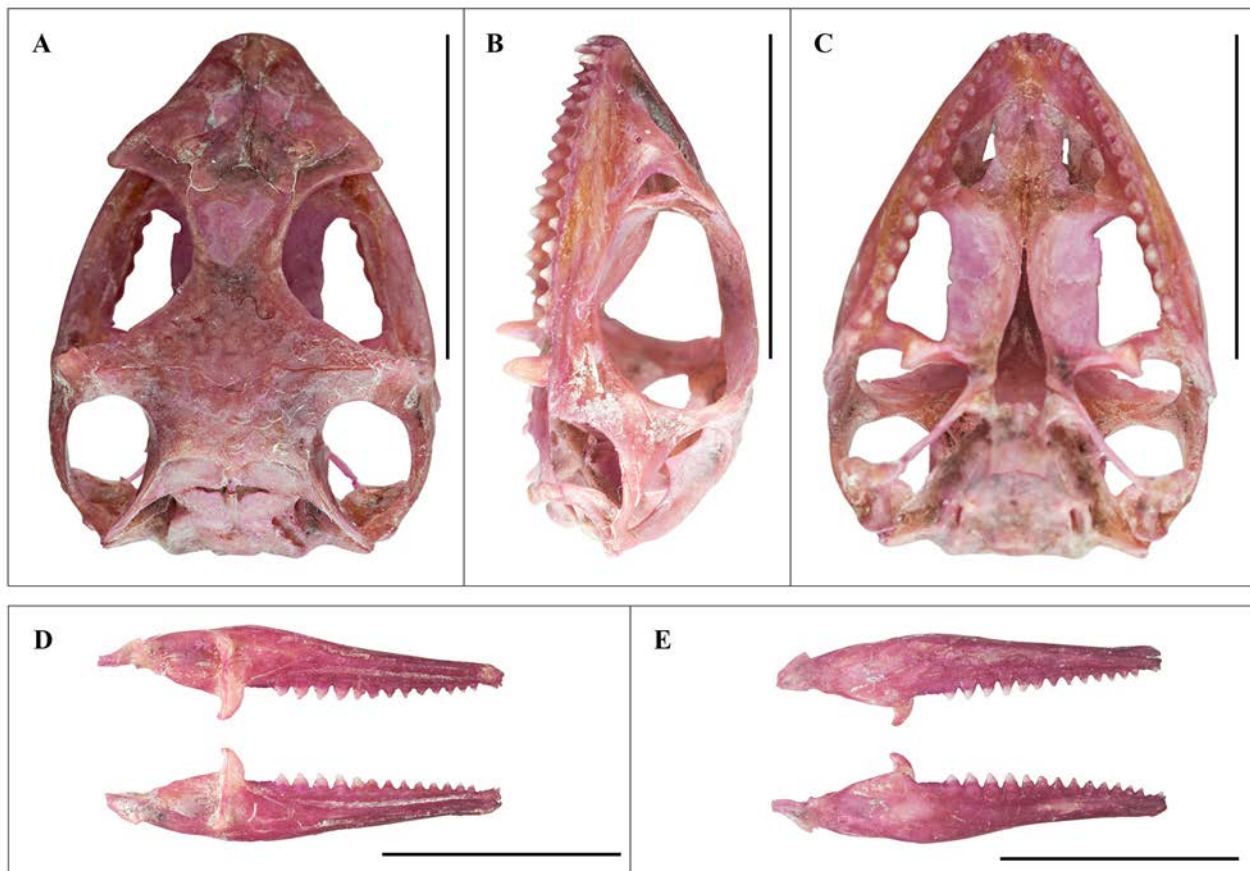


FIGURE 12. Skull of referred specimen of *Calotes zolaiking* **sp. nov.** (NCBS-AU156). A. Dorsal view, B. lateral view, C. ventral view of cranium, D. inner view of mandible, E. outer view of mandible. Scale bar: 10 mm.

TABLE 5. Comparisons of select osteological characters of *Calotes paulus* **comb. nov.** and *Calotes zolaiking* **sp. nov.** with other *Calotes* and *Pseudocalotes*. Sources: Moody (1980); Deepak *et al.* (2015).

Character	Moody's Character No.	<i>Calotes minor</i>	<i>Calotes</i> spp.	<i>Pseudocalotes kakhienensis</i>	<i>Pseudocalotes tympanistriga</i>	<i>Calotes paulus comb. nov.</i>	<i>Calotes zolaiking sp. nov.</i>
Meckelian groove remains on medial surface of dentaries	57	at symphysis < half of maxilla	at symphysis < half of maxilla	rotates to ventral edge < half of maxilla	rotates to ventral edge < half of maxilla	rotates to ventral edge = maxilla	rotates to ventral edge = maxilla
Size of jugal in infraorbital region when viewed laterally	29	< half of maxilla	< half of maxilla	< half of maxilla	< half of maxilla	= maxilla	= maxilla
Ceratobranchial (CB) II of hyoid apparatus	70	> half of CB I	> half of CB I	< half of CB I	> half of CB I	> half of CB I	> half of CB I
External auditory meatus with recessed tympanic membrane	75	absent	absent	absent	absent	absent	absent
Number of acrodont teeth of premaxillae	69	3	3	5	3	3	3
Number of premaxillary acrodont teeth	67	15	13	14–16	13	13	13
Number of sternal ribs	84	2	2	2	3	3	3
Number of mesosternal ribs	85	2	2	2	1	1	1
Caudal vertebrae	88	29	46–65	46–65	46–65	35–45	50
Caudal vertebrae with transverse process	89	11	14	14	15–20	14	12
Number of trunk vertebrae excluding atlas and axis	80	21	21, 22 or 23	21, 22 or 23	21, 22 or 23	18, 19 or 20	20
Width of sternum/pectoral girdle length	96	57%	50–59%	50–59%	40–49%	50–59%	60%
Hypapophyses of the cervical vertebrae sutured/fused with centum	82	fused	fused	sutured	sutured	fused	fused
Phalangeal formula of pes	108	2-3-4-5-4	2-3-4-5-4	2-3-4-5-4	2-3-4-5-4	2-3-4-5-4	2-3-4-5-4
Phalangeal formula of manus	109	2-3-4-5-3	2-3-4-5-3	2-3-4-5-3	2-3-4-5-3	2-3-4-5-3	2-3-4-5-3

Our study reinforces the importance of hemipenial morphology as a generic diagnostic character for agamid lizards. The shape of the hemipenis is largely conserved within draconine genera (Maduwage *et al.* 2008; Maduwage & Silva 2012), however, the absence of the cardioid structure on the hemipenes of *Calotes zolaiking* **sp. nov.** warrants a relook at the usage of this character to diagnose the genus *Calotes* (Maduwage *et al.* 2008; Maduwage & Silva 2012; Deepak *et al.* 2015).

The osteological characters suggested by Moody (1980) to diagnose agamid genera will require revision considering the recent changes in agamid taxonomy, e.g. within the distantly related genus, *Pseudocalotes*, there are multiple osteological characters which are not congruent with Moody's (1980) diagnoses (Table 5). However, osteological comparisons of additional species in the genus *Calotes* is required to better understand homologous osteological characters. The genus-level assignment of draconine species has been historically based on synapomorphic characters. Taxonomic stability for most draconine species will only occur following detailed molecular phylogenetic analysis and a thorough reassessment of morphological characters.



FIGURE 13. Habitat where *Calotes zolaiking* **sp. nov.** were found in Durtlang, Mizoram state, Northeast India.

Conclusions

The draconine agamid taxonomy is currently in a state of flux, however, as more molecular sequence data becomes available, our understanding of the systematic relationships within the subfamily is rapidly improving (Denzer *et al.* 2015; Deepak *et al.* 2015; Deepak *et al.* 2016; Deepak & Karanth, 2018; Grismer *et al.* 2016; Wang *et al.* 2018; Pal *et al.* 2018). The recent generic reallocations (Pal *et al.* 2018, this study), along with the newly described species, *C. manamendrai* Amarasinghe and Karunarathna, 2014, *C. pethiyagodai* Amarasinghe, Karunarathna and Hallermann, 2014 and *C. bachae* Hartmann, Geissler, Poyarkov, Ihlow, Galoyan, Rödder and Böhme, 2013, increase the global *Calotes* diversity to 25 species. After *Cristidorsa otai* (Mahony, 2009) (also endemic to Mizoram state), *Calotes zolaiking* **sp. nov.** becomes the second new agamid species to have been described from Northeast India since the description of *Pseudocalotes austeniana* (Annandale, 1908). Further herpetological exploration of Northeast India is required to better understand the true potential of this biodiversity rich, but poorly studied region.

Acknowledgments

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APPENDIX 1. Partitions and models of sequence evolution used in the Bayesian analyses (BI) for the mitochondrial and nuclear genes.

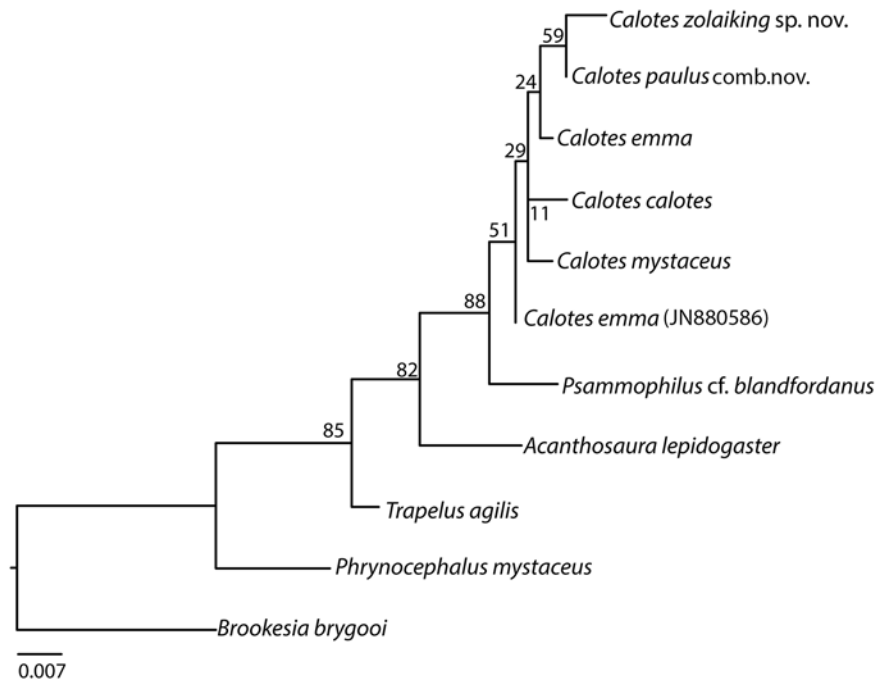
Partitions	Sites	Model
P1	ND2 1 st	GTR+I+G
P2	ND2 2 nd	HKY+I+G
P3	ND2 3 rd	GTR+I+G
P4	16S	GTR+I+G
P1	R35 1 st , RAG1 1 st , RAG12 nd	K80+G
P2	PTGER 2 nd , PTGER 3 rd , R35 2 nd	K80
P3	R35 3 rd , RAG1 3 rd	K80+G
P4	PTGER 1 st	HKY+I

APPENDIX 2. Specimens examined.

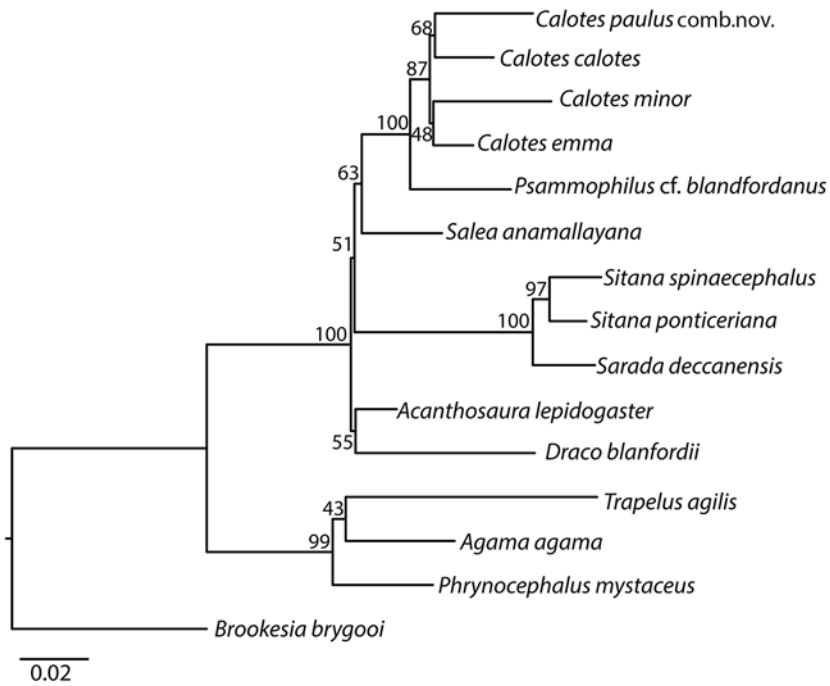
Calotes jerdonii: BMNH 1946.8.11.50–51, BMNH 1946.8.11.54–53, BMNH 1946.8.11.56
Calotes emma: BMNH 1946.8.11.26
Calotes maria: BMNH 1946.8.11.24
Calotes grandisquamis: BMNH 1946.8.11.44–47
Calotes nemoricola: BMNH 74.4.29.224–225
Calotes bhutanensis: ZSI 22480
Calotes nigrilabris: NMI 2007.106.32
Ceratophora aspera: NMI 2007.106.33
Ceratophora tennentii: NMI 2007.106.1
Cophotis ceylanica: NMI 2007.106.36
Pseudocalotes brevipes: BMNH 1946.8.11.22
Pseudocalotes dringi: BMNH 1906.2.28.10 (holotype)
Pseudocalotes flavigula: BMNH 1946.8.11.14
Pseudocalotes floweri: BMNH 1932.8.1.2
Pseudocalotes microlepis: BMNH 1946.8.11.21 (type), BMNH 1921.4.1.118
Pseudocalotes tympanistriga: BMNH 1929.11.2.1; BMNH 1848.5.20.4
Salea anamallayana: BMNH 1964.8.14.84 (type)
Salea horsfieldii: BMNH 1946.8.14.11–12 (types)

APPENDIX 3. Uncorrected genetic *p*-distances for the ND2 gene.

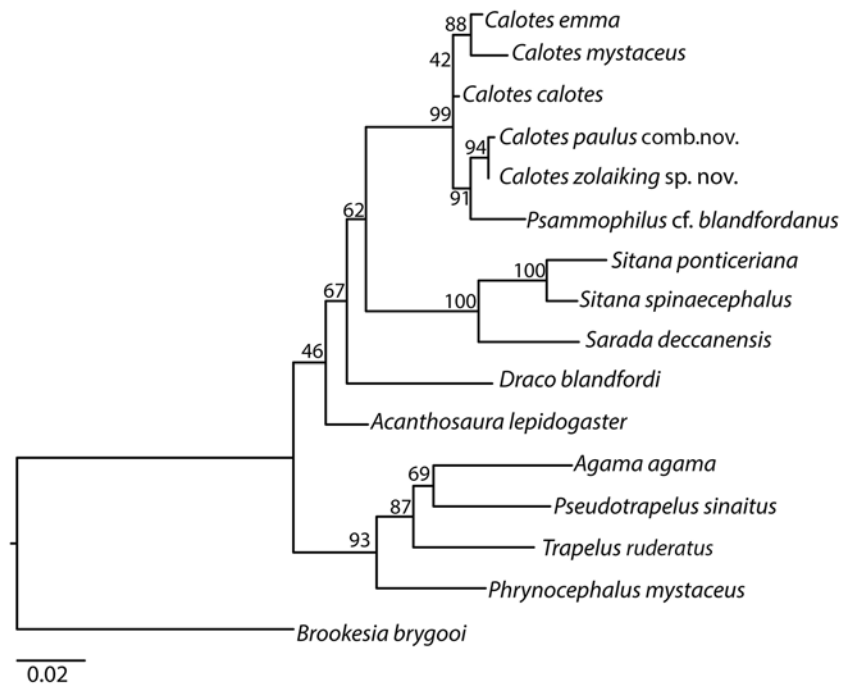
ND2	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16
1 <i>Calotes calotes</i>	-															
2 <i>Calotes ceylonensis</i>	0.20	-														
3 <i>Calotes chincollium</i>	0.28	0.29	-													
4 <i>Calotes emma</i>	0.28	0.29	0.02	-												
5 <i>Calotes htunwini</i>	0.15	0.21	0.26	0.26	-											
6 <i>Calotes irawadi</i>	0.17	0.21	0.28	0.29	0.18	-										
7 <i>Calotes jerdoni</i>	0.23	0.25	0.30	0.31	0.25	0.23	-									
8 <i>Calotes liocephalus</i>	0.19	0.20	0.27	0.28	0.21	0.22	0.24	-								
9 <i>Calotes liolepis</i>	0.20	0.22	0.31	0.32	0.23	0.23	0.28	0.21	-							
10 <i>Calotes minor</i>	0.23	0.27	0.28	0.28	0.23	0.23	0.21	0.24	0.25	-						
11 <i>Calotes mystaceus</i>	0.29	0.31	0.27	0.28	0.29	0.32	0.35	0.28	0.29	0.28	-					
12 <i>Calotes nigrilabris</i>	0.17	0.18	0.28	0.29	0.20	0.20	0.27	0.18	0.13	0.24	0.28	-				
13 <i>Calotes cf. versicolor</i>	0.15	0.21	0.27	0.27	0.18	0.06	0.24	0.21	0.23	0.23	0.31	0.20	-			
14 <i>Calotes paulus comb. nov.</i>	0.30	0.34	0.31	0.32	0.33	0.34	0.29	0.31	0.32	0.31	0.31	0.33	0.32	-		
15 <i>Calotes zolaiking sp. nov.</i>	0.29	0.30	0.30	0.30	0.30	0.32	0.27	0.30	0.30	0.30	0.29	0.30	0.32	0.13	-	
16 <i>Psammophilus cf. blanfordanus</i>	0.29	0.31	0.31	0.32	0.29	0.32	0.30	0.31	0.34	0.30	0.31	0.31	0.32	0.32	0.32	-



APPENDIX 4. Maximum Likelihood phylogeny constructed using PTGER dataset.



APPENDIX 5. Maximum Likelihood phylogeny constructed using RAG1 dataset.



APPENDIX 6. Maximum Likelihood phylogeny constructed using R35 dataset.