



Molecular phylogenetics and taxonomic reassessment of the widespread agamid lizard *Calotes versicolor* (Daudin, 1802) (Squamata, Agamidae) across South Asia

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Abstract

The genus *Calotes* Cuvier, 1817 (Agamidae: Draconinae) is highly diverse, with species occurring in South and Southeast Asia, and Oceania. Most species of the subfamily except *C. versicolor* have narrow geographic distributions. *Calotes versicolor* is distributed from western Iran in the west to south China and Indonesia in the east and has been introduced to parts of Africa and North America. The species has had a complicated taxonomic history; multiple species and subspecies related to *C. versicolor* were described from India and adjoining regions, which were synonymized in subsequent revisions. However, a study of Burmese *C. versicolor* yielded two new species, *C. htunwini* and *C. irawadi*, indicating that *C. versicolor* is a species complex. Such integrative taxonomic studies have not been carried out in India, the supposed type locality of *C. versicolor*. Hence, we studied *C. versicolor* sensu lato from the Indian subcontinent and generated sequences of mitochondrial 16S and COI fragments from tissues sampled from multiple localities in the region, including the type localities of its synonyms. Phylogenetic analyses revealed four well-supported, deeply-divergent lineages, supported by morphological data. These lineages represent (i) *C. versicolor* sensu stricto, from South India and parts of the east coast, (ii) *C. irawadi* sensu lato from northeast India and Southeast Asia, (iii) a synonym from the eastern Indo-Gangetic Plains which we resurrect here, and (iv) a subspecies from Pakistan which we elevate to species level. We provide re-descriptions for the resurrected or elevated species, and a diagnostic key to the species of the *C. versicolor* complex. The study shows that *C. versicolor* sensu stricto is endemic to parts of southern and eastern India, and not widely distributed, though it may have been introduced to other parts of the world.

Key words

16S, COI, distribution, mtDNA, phylogenetics, species complex, species delimitation, systematics

Introduction

Widely distributed species often display intraspecific molecular and morphological variation (Zug et al. 2007; Gonçalves et al. 2012; Deepak et al. 2016; Saijuntha et al. 2017). When the levels of intraspecific variation are sufficiently high, and the variants compose distinct, phylogenetic lineages, multiple cryptic species need to be recognized using an integrated approach (Agarwal et al. 2011, 2019a; Priti et al. 2016; Mirza et al. 2017, 2018). The high intraspecific genetic diversity could be attributed to factors including, but not restricted to, vicariance (Matthee and Flemming 2002; Oliver et al. 2010; Vijayakumar et al. 2014, 2016), climate change or upheaval (Swart et al. 2009), ecological factors (Vijayakumar et al. 2016; Priti et al. 2016), sea-level changes (Oliver et al. 2010; Huang et al. 2013), or in some cases, non-physical putative barriers (Mirza et al. 2018). Examples of widely distributed reptilian species representing species complexes are common and have been encountered in different reptile groups, including lizards (Zug et al. 2007; Huang et al. 2013; Agarwal et al. 2014; Deepak et al. 2016; Saijuntha et al. 2017; Mirza et al. 2018; Pal et al. 2018; Wagner et al. 2021, and literature therein).

The genus *Calotes* includes species which are characterized by the presence of largely homogeneous, regularly arranged dorso-lateral scales and an exposed tympanum. Until recently, the genus included more than 25 species, with the greatest species diversity occurring in the Western Ghats of India, Sri Lanka, and Indo-Burmese biodiversity hotspots (Pal et al. 2018). The genus was then shown to be paraphyletic with respect to the Indian endemic, predominantly ground-dwelling genus *Psammophilus* Fitzinger, 1843. Subsequently, two new genera of the subfamily Draconinae were described from the Western Ghats of India (Pal et al. 2018). Most of the species of the genus *Calotes* sensu stricto show restricted distributions (Hallermann 2000), with the exception of *C. versicolor*, which is a widely distributed species, occurring throughout the Oriental realm (Smith 1935; Hallermann 2000). The other species of the genus with an exceptionally wide distribution was *C. mystaceus* Duméril and Bibron, 1837; however, recently, that species was shown to be composed of multiple lineages, with the recognition of multiple new species (Hartmann et al. 2013; Saijuntha et al. 2017; Wagner et al. 2021).

The Oriental Garden Lizard, *Agama versicolor*, was described based on two specimens housed at the MNHN, Paris, collected by an unknown collector and also from an unknown locality, probably in India (Daudin 1802). The types were subsequently lost, misplaced, or stolen (*vide* Amarasinghe et al. 2009; Gowande et al. 2016). Further, the diagnosis provided in the original description (Daudin 1802) was largely based on coloration data and is not detailed enough to diagnose the species. Kuhl (1820) provided additional diagnostic features for the species described by Daudin (1802) based on the specimens housed at MNHN, which Kuhl believed were sent to the museum by Leschenault from Pondicherry (now Puducherry),

which led to his consideration of Puducherry as the type locality of *A. versicolor*. Following Kuhl (1820), numerous authors treated Puducherry as the type locality of *C. versicolor* (Gowande et al. 2016). However, the specimens examined by Kuhl (1820) likely did not represent the type material of *C. versicolor*, since Leschenault visited Puducherry only after 1816 (*vide* Amarasinghe et al. 2009), indicating that the specimens sent to the museum by Leschenault likely were not present at the museum at the time of Daudin's investigation. The lack of knowledge of the collector and the type locality and the subsequent misplacement of the name-bearing types have been the reason for the taxonomic turmoil and uncertainty with regards to the taxon (Gowande et al. 2016; Chaitanya et al. 2017). This has further resulted in the description of additional species resembling *C. versicolor* by subsequent authors (Kuhl 1820; Harlan 1825; Jacquemont 1844; Gray 1846; Blyth 1853), which were synonymized during later revisions (see Duméril and Bibron 1837; Smith 1935). Kuhl (1820) also described another similar species, *Agama tiedemanni* Kuhl, 1820 from the same locality which he claimed was the place of origin of the specimens examined by Daudin (1802), Puducherry, based on a specimen which was likely sent to MNHN by Leschenault. Gowande et al. (2016), following Amarasinghe et al. (2009) accepted that currently, MNHN hosted only three specimens of taxa resembling *C. versicolor*, and of these, the one collected by Leschenault is most probably the syntype of *A. tiedemanni*, and not of *C. versicolor*, and the species *C. versicolor* lacked a name-bearing type.

Therefore, as per the provisions of ICZN (1999), Gowande et al. (2016) designated a freshly collected specimen from Pondicherry as neotype for *A. versicolor*, with the objective of stabilizing the taxon, with a recognized type specimen. The consideration of Puducherry as the type locality of *A. versicolor* implied that Gowande et al. (2016) treated *A. tiedemanni* as a synonym of *C. versicolor*. Gowande et al. (2016) also discussed the validity of other junior synonyms of the taxon and listed the following names as available for taxonomic consideration, sensu the Principle of Priority (ICZN 1999): *Calotes vultuosa* (Harlan, 1825: Kolkata, West Bengal), *Calotes viridis* (Gray, 1846: Chennai, Tamil Nadu) and *Calotes versicolor farooqi* Auffenberg and Rehman, 1993 (Manshera, Pakistan). However, Chaitanya et al. (2017) stated that Puducherry was the type locality of *A. tiedemanni*, a junior synonym of *C. versicolor*, and suggested that the specimen MNHN-RA-2548 (MNHN 2548 sensu Chaitanya et al. 2017) from Pondicherry had to be considered the syntype of *A. tiedemanni*, and not that of *C. versicolor* sensu stricto, following Amarasinghe et al. (2009). Chaitanya et al. (2017) further stated that Gowande et al. (2016) provided neither a diagnosis to differentiate their neotype from the other related taxa nor a morphological comparison with the original description of Daudin (1802) and with that of the syntype of *A. tiedemanni*. Furthermore, Chaitanya et al. (2017) also stated that given that *C. versicolor* is a widespread species complex, the neotype should have been fixed from an unambiguous type locality. Therefore, Chaitanya et al. (2017) tentative-

ly invalidated the neotype designation, leaving *C. versicolor* without a type locality or a type specimen.

Following Chaitanya et al. (2017), inquiries with MNHN for the examination of the syntype of *A. tiedemanni* MNHN 2548 were made during this study, which would have enabled comparisons of the neotype with the syntype of *A. tiedemanni*, for better diagnosis of the two taxa. However, the inquiries revealed that the specimen MNHN-RA-2548 has been on loan since 1999, and could not be located in the collections of MNHN, and is therefore considered lost (Z. Mirza pers. comm., Ivan Ineich pers. comm. to A.A.T. Amarasinghe, August 2020). This has rendered the morphological comparison of the neotype designated by Gowande et al. (2016) with the syntype of *A. tiedemanni* not possible at this time. Additionally, a review of the herpetofaunal species described by Daudin (1801–1802) from India revealed that the type localities of a majority of these species were along the east coast of India (Coromandel Coast), especially the localities Tranquebar, Puducherry, Vishakhapatnam, or rarely Bengal (Uetz et al. 2020). Historically, these localities were parts of, or located in the vicinity of, the French colonies in India. It thus seems reasonable to consider Puducherry as the type locality of the species. Furthermore, the designated neotype agrees with the available original description of Daudin (1802), except for the characters that are bound to sex, given that Daudin's specimens were most likely subadults or females (Amarasinghe et al. 2009). In the light of this knowledge and to stabilize the taxon, we consider that the neotypification by Gowande et al. (2016) is in accordance with Article 75 of the ICZN (1999), and thus, the neotype NCBS AT102 stands valid and is considered here as the name-bearing type for comparisons. Further diagnosis and comparisons are included herein.

Calotes versicolor has been shown to be a species complex. Two species of the complex, *C. htunwini* Zug and Vindum, 2007 and *C. irawadi* Zug, Brown, Schulte and Vindum, 2007 were described from the Burmese regions adjoining northeast India (Zug et al. 2007) using an integrated morphological-molecular approach. Recently, high levels of genetic diversity and the potential existence of cryptic species were reported in *C. versicolor* from Thailand and Lao PDR (Tantrawatpan et al. 2021). It should be noted though that the species Tantrawatpan et al. (2021) dealt with most likely represents *C. irawadi* and not *C. versicolor*. However, there has not been a similar, comprehensive, integrative taxonomic investigation into the other populations of *C. versicolor* sensu lato including in Peninsular India, where the type locality of the taxon lies. The only available study on this taxon from India is that of Tiwari and Aurofilio (1990), who examined the morphometry of multiple *C. versicolor* individuals from the southern Indian state of Tamil Nadu. While the authors made comparisons of their data with those from other regions of India, the characters examined were limited, these comparisons were largely based on secondary literature, and the study did not focus on resolving the systematics of the complex.

Presently, only one species of the *C. versicolor* complex is known to occur in the Indian subcontinent with

certainty, namely *C. versicolor*. Literature (Das et al. 2009) and photographic records (Anonymous 2020) hint at the presence of the largely Burmese *C. irawadi* in adjoining northeast India; however, these need confirmation using integrative taxonomic approaches. Given the widespread nature of the species, we hypothesized that multiple cryptic lineages are embedded within the *C. versicolor* complex across South Asia. We used a combination of literature review, morphological data obtained from the examination of freshly collected as well as museum specimens, and molecular phylogenetics to revise the species complex using an integrated approach. In this study, we confirm the type locality for *C. versicolor* sensu stricto as Puducherry, based on the neotype designation by Gowande et al. (2016), provide a diagnosis for *C. versicolor* sensu stricto and clarifications on the systematic positions of *Agama vultuosa* Harlan, 1825 and *A. tiedemanni*, which are currently synonymized under *C. versicolor*, the subspecies *C. v. farooqi*, and other available synonyms of *C. versicolor*. We also briefly discuss the distribution of the apparently widespread *C. versicolor* and the other species of this species complex hereby dealt with and provide a diagnostic key for the species of the complex.

Materials and Methods

Taxon Sampling

Systematic sampling was carried out throughout Peninsular India, the adjoining Indo-Gangetic Plains of India, the Indian deserts and northeast India (Fig. 1), and the hilly areas of northern Pakistan. The sampling strategy was designed so that maximum variation between populations was captured. Accordingly, one to three samples were captured from the various landscapes of Peninsular India, including the Western Ghats, the Eastern Ghats, and the intervening dry regions, the Southern Granulite Terrain, the extra-peninsular regions including the deserts, the central highlands, the Indo-Gangetic Plains of India, and northeast India. The sampling strategy was also designed to include the type locality of *C. versicolor* and its synonyms and subspecies whose type localities are known: Pondicherry (*A. tiedemanni*), Kolkata (*A. vultuosa*, *C. indica*), Madras (*C. viridis*) and Manshera (*C. v. farooqi*). This resulted in the collection of 93 tissue samples in the form of tail/toe clips which were stored in 95% to 99.9% ethanol. A few specimens were also collected and euthanized with halothane following Leary et al. (2013), after which they were fixed with a 4–8% formaldehyde solution for 24–36 hours, for use in morphological analysis. All efforts were taken to minimize animal suffering from euthanasia. The specimens were then washed with water to remove traces of formaldehyde, and transferred to 70% ethanol for long-term preservation. All the tissues were stored at –20°C at CES, while the specimens were deposited at the collections facility at CES.

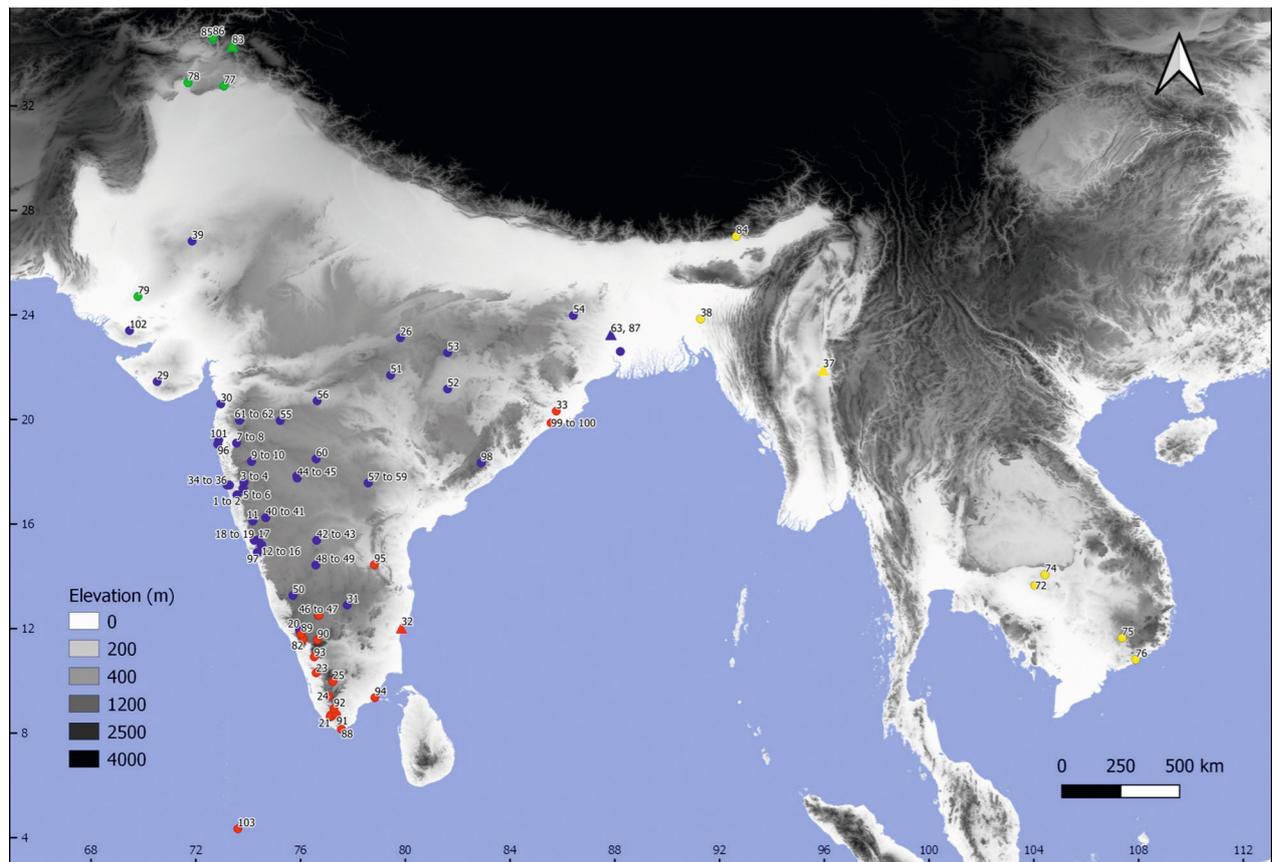


Figure 1. A map of south and Southeast Asia representing the localities from which morphological and/or primary or secondary genetic data were collected. Red circles indicate the localities from which *C. versicolor* sensu stricto (Clade1) originate, yellow samples indicate those of *C. irawadi* sensu lato (Clade2), blue circles represent the localities of *C. vultuosus* **comb. nov.** (Clade3), green circles indicate Clade4, with *C. farooqi* **stat. nov.** (77, 83, 85, 86) and *C. aff. farooqi* (78, 79). A single sequence of *Calotes irawadi* from Huanan Province, China (locality 73) is not marked on the map, since it was very distant to all other localities, as also those whose precise localities were unknown. Triangles indicate type localities of the respective species. See supplementary Table S1 for details on molecular and/or morphological vouchers used, and their respective localities.

Molecular phylogenetics

Total genomic DNA was extracted from the collected tissue samples using the Phenol-Chloroform-Isoamyl Alcohol method (Sambrook and Russell 2001), dissolved in 50 μ l of 0.1% TE buffer (pH 7.6–8.0, 10mM Tris-HCL, 0.1mM EDTA), and stored at 4°C. The quality and the length of the extracted DNA fragments were checked on 1% agarose gel, electrophoresed at 70V.

A fragment of the mitochondrial 16S rRNA gene (16S) was amplified using PCR, using 16Sar (5'-CGCC-TGTTTATCAAAAACAT-3') and 16Sbr (5'-CTCCGG-TTTGAACTCAGATCA-3') (Simon et al. 1991) primers for all the extracted DNA samples. PCR was carried out in 25 μ l reaction volume containing 2.5 μ l of 1X Taq Buffer, 2.5 μ l of 2.5 mM MgCl₂, 0.25 μ l each for the forward and reverse primers, 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. Initial denaturation was 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. For a subset of the collected tissue samples ($n=19$), the cytochrome c

oxidase subunit 1 (COI) region of the mitochondrial genome was also amplified, using the primer pairs VF1-d (5'-TTCTCAACCAACCACAARGAYATYGG-3') and VR1-d (5'-TAGACTTCTGGGTGGCCRAARAAYC-A-3') and LCO1490 (5'-GGTCAACAAATCATAAAG-ATATTGG-3') and HCO2198 (5'-TAAACTTCAGGG-TGACCAAAAATCA-3'). The PCR conditions were similar to the 16S gene, however, the annealing temperature was at 54.5°C.

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. Sequencing was performed using a 3130xl Genetic Analyzer. This resulted in the generation of 67 16S sequences, and 19 COI sequences. Additionally, 16S and COI sequences were generated for one *C. calotes* Linnaeus, 1758 sample from south India, which was used as an outgroup. Laboratory work was largely carried out at CES and sequencing was outsourced to Barcode Biosciences (Bengaluru, India), except for Pakistani samples, which were processed by DJ in Slovakia and their sequencing of PCR products was outsourced to the MacroGen Europe (Amsterdam, The Netherlands). The generated sequences were checked manually in

Table 1. A summary of the models of sequence evolution used for each partition in the ML and BI molecular phylogenetic analyses. *COI 2nd was combined with 16S in BI, as per the output of PartitionFinder analysis.

Partition	Codon position	Model	
		ML	BI
1	16S	TPM+F+I+G4	HKY+I
2	COI 1 st	TN+F+G4	GTR+G
3	*COI 2 nd	TIM3e+G4	–
4	COI 3 rd	F81+F	F81

Table 2. Table representing the least and the greatest un-corrected percent pairwise genetic p-distances within and between species recovered in this study. Values above the diagonal represent divergence on COI, whereas those below the diagonal represent divergence on 16S. Values in bold along the diagonal represent distance within species, written as COI/16S. *Does not include *Calotes* aff. *farooqi*.

Species	<i>Calotes farooqi</i> stat. nov.*	<i>Calotes irawadi</i>	<i>Calotes versicolor</i>	<i>Calotes vultuosus</i> comb. nov.	<i>Calotes calotes</i>
<i>Calotes farooqi</i> stat. nov.*	–/0.2–0.4	16.9–17.5	17.1–17.9	15.5–16.9	19.2–20.3
<i>Calotes irawadi</i>	3.3–6.0	0.0–4.5/0.2–2.4	12.6–15.1	12.8–15.9	17.2–18.1
<i>Calotes versicolor</i>	3.5–5.2	2.7–4.7	0.2–7.6/0–1.5	13.0–15.5	17.0–18.7
<i>Calotes vultuosus</i> comb. nov.	3.9–5.1	2.7–4.7	3.3–4.6	0.0–9.5/0–2.0	16.1–17.4
<i>Calotes calotes</i>	4.9–6.3	5.9–6.9	5.1–6.1	5.3–6.9	–/0.8

MEGA v.6 (Tamura et al. 2013), using the chromatograms visualized in CHROMAS v.2.6.5 (Technelysium Pty. Ltd. 2018). The sequences were aligned using MUSCLE (Edgar 2004) implemented in MEGA v.6, using default parameters, and manually corrected, wherever necessary. To this alignment, 16S and COI sequences available on GenBank (Benson et al. 2017) were downloaded and added for use in molecular phylogenetic analyses. The final 16S+COI concatenated 1130 bp alignment consisted of 83 individuals, including two sequences of *C. calotes*. A sequence each of *C. grandisquamis* Günther, 1875 and *C. nemoricola* Jerdon, 1853 was used as outgroup. Congruence between the gene trees was tested for, before concatenation. The concatenated alignment was used for molecular phylogenetic analyses.

Maximum Likelihood (ML) and Bayesian Inference (BI) methods of phylogenetic analyses were implemented to determine the clustering pattern of the sequences of the *C. versicolor* complex generated in this study, as well as those of the related species, including *C. calotes* and *C. irawadi*. The non-coding 16S region (522 bp) was not partitioned by codon positions, whereas the coding COI region (608 bp) was partitioned by codon position. COI sequences were translated to their protein products using the vertebrate mitochondrial code table to check for premature stop-codons in the alignment and to rule out the possibility of having sequenced pseudogenes. Maximum Likelihood trees were analysed using W-IQ-TREE (Trifinopoulos et al. 2016), the web implementation of IQ-TREE (Nguyen et al. 2015). Branch support was assessed using ultrafast bootstrap (UFboot) analysis (Minh et al. 2013), performing 1000 bootstrap alignments. Models of sequence evolution to be implemented were tested using MODELFINDER (Kalyaanamoorthy et al. 2017). The best substitution model for BI phylogenetic analy-

ses was determined using PartitionFinder v. 1.1.1 (Lanfear et al. 2012), model search was performed using the Akaike Information Criterion (AIC), with a greedy search algorithm. Bayesian Inference trees were generated using MRBAYES v.3.2.6 (Ronquist et al. 2012). Two simultaneous, independent analyses were run starting from different random trees. Three heated and one cold chains were used in the analyses, Markov chains were sampled every 1000 generations, for 20 million generations. At the end of the run, the standard deviation of the split frequencies was less than 0.01, and the analyses were not continued further. A total of 25% trees were discarded as burn-in, and convergence was tested with Tracer v.1.7 (Rambaut et al. 2018). The Effective Sample Size (ESS) values were sufficiently higher than 200, and the Potential Scale Reduction Factor values were very close to 1.00, further indicating convergence. The tree representing the best evolutionary hypothesis for the dataset was selected using a 50% majority consensus rule. The ML and BI tree topologies were visualized in FIGTREE v. 1.4.4. The substitution models used for ML and BI analyses across partitions are represented in Table 1.

The uncorrected genetic “p-distances” were calculated separately for 16S (522 bp) and COI (608 bp) in MEGA v.6 (Table 2). We employed a sequence pair-wise deletion of gaps while calculating the pairwise genetic distance. The list of sequences used in this study, their GenBank® accession numbers, and sampling localities are summarized in Supplementary Table S1.

We further retained one or two representative sequences of each of the species which we here delimit as distinct from the *C. versicolor* complex revealed by the analyses, and inserted these into the larger 16S dataset used in Pal et al. (2018), to elucidate the positions of these distinct lineages within Draconinae. The COI sequences were not

included in these analyses due to the absence of COI sequences of species related to the ingroup taxa, especially those of the genera *Calotes*, *Microauris* Pal, Vijayakumar, Shanker, Jayarajan and Deepak, 2018, *Monilesaurus* Pal, Vijayakumar, Shanker, Jayarajan and Deepak, 2018 and *Psammophilus* Fitzinger, 1843. Maximum Likelihood phylogenetic trees were constructed on this dataset following the above methodology. We comment on the phylogenetic positions of the species of the *C. versicolor* complex based on ML tree analysed using only the 16S gene.

Morphology

Mensural and meristic data from the sampled specimens as well as those deposited at museums in India and abroad, including the available type material of the species under the synonymy of *C. versicolor*, were recorded for use in systematics. Published literature (Zug et al. 2007; Pal et al. 2018) was also referred to for morphological data for *C. irawadi* and *C. versicolor* sensu lato respectively. Since males were present in greater proportions than females in our collection, and in those of the museums, morphological comparisons and descriptions were largely based on male specimens. Wherever possible, female specimens were also included in diagnosis and comparisons. Only adult specimens were used for diagnosis and comparisons.

Data for the following characters were recorded following Zug et al. (2007): Eye-ear length (EyeEar – distance between anterior edge of the tympanum to posterior of the orbit), Head height (HeadH – distance from top of the head to underside of the jaw at transverse plane intersecting the jaw, measured dorsoventrally), Head length (HeadL – distance between the anterior edge of the tympanum and the tip of the snout), Head width (HeadW – distance between the edges of the right and left jaw muscles or edge of temporal ridge, measured at the widest point, without compression of the soft tissue), Interorbital width (Interorb – distance between the antero-dorsal corners of the orbits), Jaw width (JawW – transverse distance between the outer edges of jaw angles, excluding the jaw musculature broadening the head), Naris-eye length (NarEye – distance between the anterior edge of the orbit and the posterior edge of the naris), Snout-eye length (SnEye – distance between the anterior edge of the orbit and the rostral scale, or the snout tip), Snout width (SnW – distance between the left and the right nares), 4th finger (4FingLng – length of the fourth finger, starting at the bifurcation of third and fourth finger, to the distal-most surface of the claw), 4th toe (4ToeLng – length of the fourth finger, starting at the bifurcation of third and fourth toe, to the distal-most surface of the claw), Crus length (CrusL – length of the tibia from knee to heel), Forefoot length (ForefL – distance from the proximal end of forefoot to the tip of the fourth digit), Lower arm length (LoArmL – distance from elbow to the distal end of the wrist), Pectoral width (PectW – distance between the left and the right forelimb insertion, measured transversely, posterior to the insertion), Pelvic width (PelvW – distance between the left and the right forelimb insertion, mea-

sured transversely, posterior to the insertion), Snout-vent length (SVL – distance from rostral scale, or the snout tip, to the vent), Snout-forelimb length (SnForeL – distance from the anterior of the forelimb or shoulder to the snout), Tail height (TailH – dorsoventral distance of the tail base measured just posterior to the vent), Tail length (TailL – distance from vent to the distal end of the tail), Tail width (TailW – transverse distance of the tail, just posterior to the vent), Trunk length (TrunkL – distance between the posterior edge of forelimb insertion and anterior edge of hindlimb insertion), Upper arm length (UpArmL – distance between shoulder and elbow), Upper leg length (UpLegL – distance between anterior edge of hindlimb insertion and knee). We also calculated the total length of both the limbs and recorded those as ForeLimbL (the sum of UpArmL+LoArmL+ForefL) and HindLimbL (the sum of UpLegL+CrusL+HindfL). Following meristic data was taken: Canthus rostralis (CanthR – number of flattened, elongated scales of the canthal edge, from above the posterodorsal corner of the nasal scale to and including the posteriormost supraciliary scale), dorsal eyelid scales (Eyelid – scales of the dorsal edge of eyelid), dorsal head scales (HeadSLn – counted longitudinally between the rostral and interparietal scales), head scales (HeadSTr – counted transversely between the posteriormost left and right supraciliary scales, just anterior of to the interparietal), infralabials (Inflab – lower lip scales), snout scales (SnS – counted transversely between the left and the right nares), supralabials (Suplab – upper lip scales), temporal spines (TempSp – number of distinctly enlarged spine-like scales above and posterior to the tympanum), 4th finger lamellae (4FingLm – starting from the first lamella that is wider than deep, touches the dorsal digital scale on at least one side, to the distalmost lamella), 4th toe lamellae (4ToeLm – same as for fourth toe), dorsal scales or spines (Dorsal – number of mid-dorsal scales, beginning from the first enlarged spine-like scale to the top of the vent), mid-body scale rows (Mid-body – number of scale rows at trunk around the mid-body). We counted the scales of the loreal region in a single row between the nasal shield and the orbit, calling the character as NarEyeS. Further, we recorded the carination condition (UnKl – smooth, PKl – partially keeled and Kl – keeled) of the scales of the snout, head, mid-body, ventrals and limbs. The condition of the first post-mental pair (joined – J or, separated – SP), was also noted, and if separated, the number of scales separating the post-mental pair. The coloration details of the specimens in life and preservation were recorded separately. All measurements were recorded in mm, and are mentioned in the same unit in the taxonomic accounts. Measurements were taken with the help of Mitutoyo digital caliper to the nearest of 0.1 mm, except the SVL and the TailL, which were measured using a thread and a ruler.

Species delimitation

We followed a modified version of species delimitation strategy employed by Vijayakumar et al. (2014; see also Shanker et al. 2017). Individually clustered distinct hap-

lotypes with strong support (ultrafast bootstrap value > 90, posterior probabilities > 0.9) were identified from the analysed ML and BI trees and were treated as Operational Taxonomic Units (OTUs) in the context of this study. The pairwise genetic divergence within and between the identified OTUs was calculated following the methodology mentioned above. The genetic distance between *C. versicolor* sensu stricto (this study) and *C. irawadi* was used as the threshold to identify the OTUs which could be delimited as distinct species. OTUs which showed genetic divergences as high as, or exceeded, the genetic divergence values between *C. versicolor* and *C. irawadi* were designated as species. We then carried out detailed morphological comparisons of the specimens representing the distinct haplotype clusters. This species delimitation approach revealed lineages that could be differentiated with the integration of morphology and phylogenetics, and are discussed in the systematics account.

Repositories (following Sabaj 2020)

ANSP = The Academy of Natural Sciences of Philadelphia (also known as The Academy of Natural Sciences of Drexel University), Philadelphia, United States of America.

BNHS = Bombay Natural History Society, Mumbai, Maharashtra, India.

BMNH = (now NHM) Natural History Museum, London, United Kingdom.

CES = Centre for Ecological Sciences, Indian Institute of Science, Bengaluru, Karnataka, India.

CM = Carnegie Museum of Natural History, Pittsburgh, United States of America.

CUDZ = Comenius University, Department of Zoology (collection of Daniel Jablonski).

FLMNH/UF = Florida Museum of Natural History, University of Florida, Gainesville, Florida, United States of America.

MNH = Muséum National d'Histoire Naturelle, Paris, France.

PMNH = Pakistan Museum of Natural History, Islamabad, Pakistan.

USNM = National Museum of Natural History, Smithsonian Institute, Washington D.C., United States of America.

Results

Molecular phylogenetics

Maximum Likelihood and Bayesian Inference (Fig. 2) phylogenetic analyses based on the combined 16S+COI dataset, including only the sequences of the *C. versicolor* complex and the closely related species *C. calotes*, *C. grandisquamis*, and *C. nemoricola* were useful in discerning the clustering pattern of the sequences generated. The ML and the BI analyses generated trees with similar topologies, except that the relationships between the species were slightly poorly resolved on the BI tree. Nonetheless, the trees revealed the existence of four deeply divergent OTUs, of which, three obtained strong support (ML bootstrap values > 90, BI posterior probabilities > 0.9) except Clade2, which we here label as Clade1, Clade2, Clade3,

and Clade4 (see Fig. 2). The recovered clades were observed to show high geographic affinity (Fig. 1).

Clade1 included samples from south India, largely from the Southern Granulite Terrain, roughly to the south of 12°N latitude, including the southern Central and the Southern Western Ghats, along with the samples from the east coast of India (Puducherry and Bhubaneswar). A single sequence from Huraa Islands, Maldives also belonged to this clade. This clade includes genetic sequences (MW901307: 16S, MZ489209: COI) from the type locality (discussed below) of *C. versicolor*, and hence we designate this clade as *Calotes versicolor* sensu stricto. Within the clade, the *p*-distance was up to 1.5% at 16S and between 0.2%–7.5% at COI, whereas the clade was at least 2.7% and 12.6% divergent from the other three clades at 16S and COI respectively.

Clade2 was composed of samples from northeast India and the adjoining Southeast Asian regions, including samples from Cambodia, China, Myanmar, and Vietnam. This clade contained the topotypic sequence of *C. irawadi*. Thus, we confirm the presence of this taxon in India and refer to this clade as *Calotes irawadi* sensu lato. This clade was the most heterogeneous at 16S, as the within clade *p*-distance ranged between 0.2%–2.4%; however, at COI, the within clade *p*-distance was not as high due to the absence of COI sequences from localities where 16S sequences were most divergent. The clade was at least 2.7% and 12.6% divergent from other clades at 16S and COI respectively. This clade likely contains additional undescribed species distributed across Southeast Asia. Given the heterogeneous nature of this clade, the clade was comparatively poorly supported in the phylogenetic analyses (ML bootstrap values 88, BI posterior probabilities 0.82).

Clade3 included samples from the Indian deserts (Jaisalmer), the Gangetic Plains (West Bengal), the Central Highlands (Bhedaghat, Chhattisgarh), and parts of Peninsular India (Deccan Volcanic Province) to the north of Southern Granulitic Terrain. The within clade divergence for Clade3 was up to 2.0% on 16S and up to 9.5% at COI, whereas the clade was at least 2.7% and 12.8% divergent from all other clades at 16S and COI respectively. This clade included a sequence from Burdwan near Kolkata, West Bengal, the type locality of *Agama vultuosa* (MW901298: 16S). Since this clade represents a genetically and morphologically distinct lineage, we resurrect *Agama vultuosa* from the synonymy of *C. versicolor*, provide diagnosis, and re-describe the taxon. Clade2 and Clade3 appear to be separated by the rivers Ganga and Brahmaputra, with Clade2 distributed on the eastern side of the rivers, whereas Clade3 occurs on the western side (Fig. 1).

Lastly, the samples from the northern hilly regions and southern plains of Pakistan formed a distinct clade, Clade4, which was at least 3% divergent on 16S from all the other clades recovered in this study. Within this clade, the genetic distance was between 0.8–2.7% at 16S and 11.5% at COI, whereas the clade was at least 3.7% and 15.5% divergent from all other clades at 16S and COI respectively. This clade included sequences from

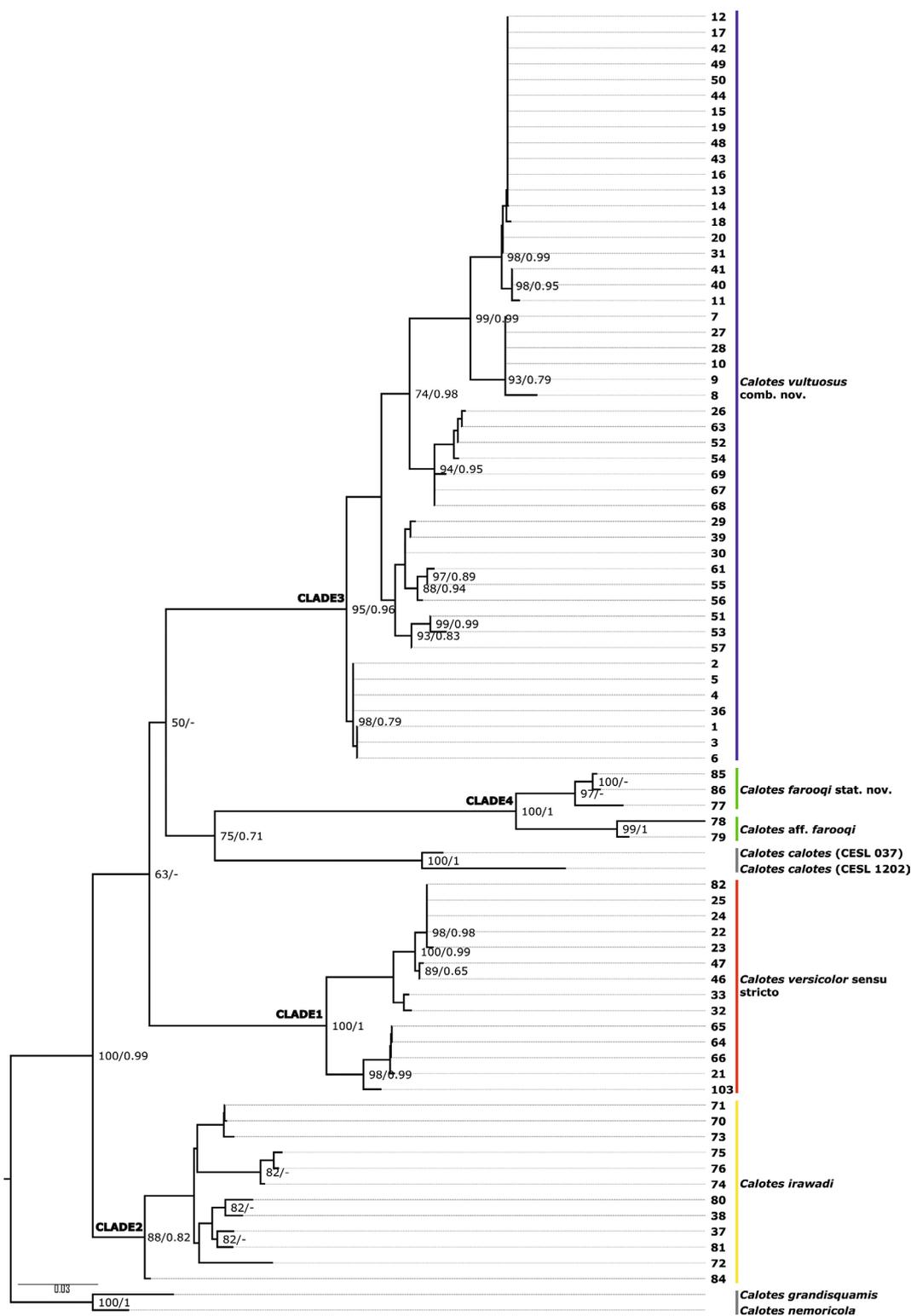


Figure 2. The ML phylogenetic output representing the ML+BI phylogeny based on the 1130 bp long 16S+COI combined dataset representing the clustering pattern of the sequences of the *Calotes versicolor* species complex. Values at the nodes indicate ultrafast ML bootstrap values/BI posterior probabilities. Colour code follows that of Figure 1. *Calotes grandisquamis* and *Calotes nemoricola* were used as the outgroup to root the trees.

near the type locality of the subspecies *C. v. farooqi* (MW901312–14: 16S, MZ489214: COI; Khyber Pakhtunkhwa and Punjab Provinces, Pakistan). Our results revealed that the population in the hilly regions of northern Pakistan is genetically and morphologically highly divergent from *C. versicolor sensu stricto*, *C. irawadi*

and Clade3. Additionally, our analyses revealed the existence of yet another lineage (referred here as *Calotes aff. farooqi*, *p*-distance up to 2.7% at 16S and 11.5% at COI) distributed in the southern hilly regions as well as the southern plains (localities 78, 79 in Fig. 2) of Pakistan. For morphological comparisons, specimens of *C.*

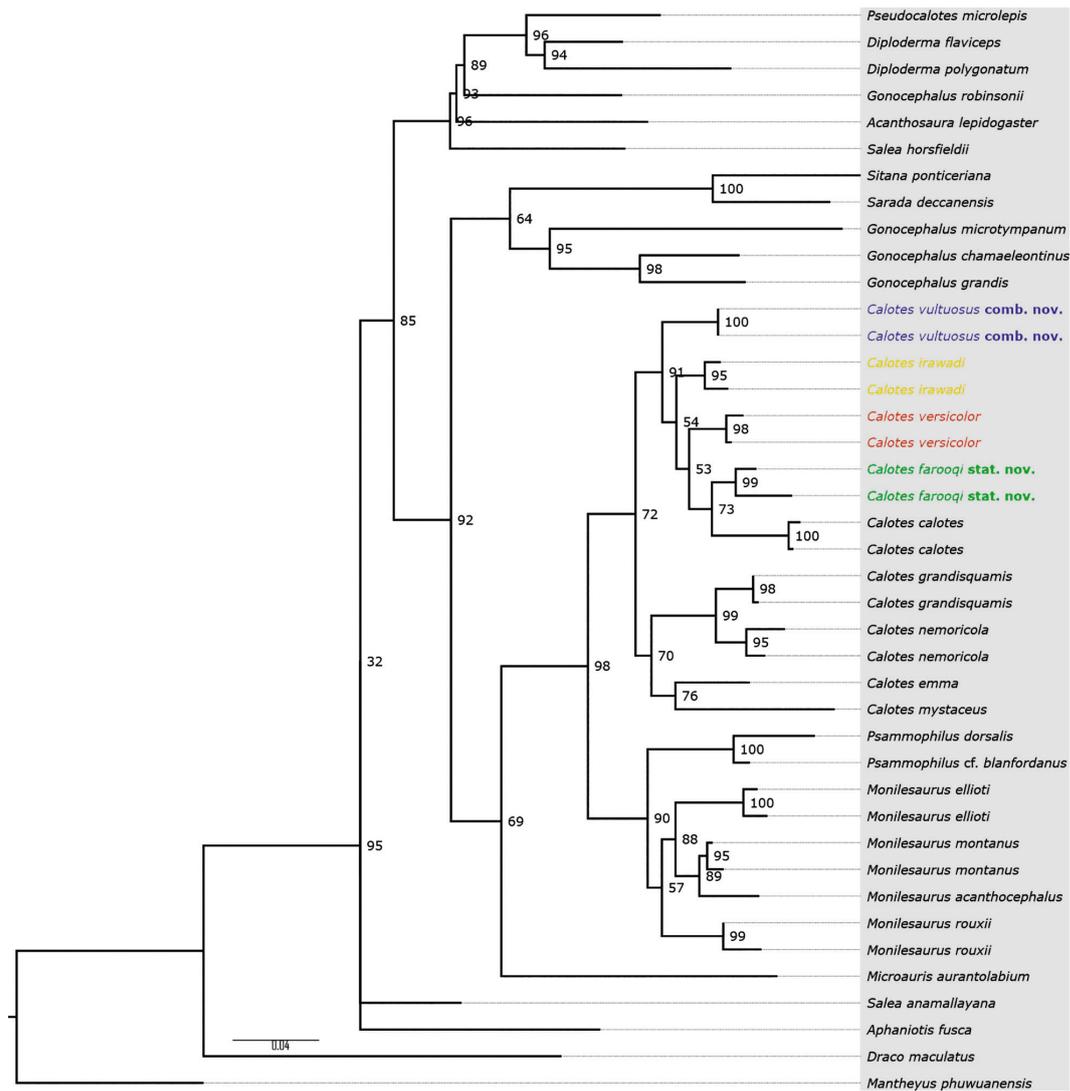


Figure 3. Maximum Likelihood 16S gene tree based on the ~416 base pair sequence data revealing the position of the species of the *Calotes versicolor* complex within the genus *Calotes*. Numbers at the nodes indicate bootstrap values. The tree was rooted using the *Mantheyus phuwanensis* (Manthey and Nabhitabhata, 1991) as the out group. The tree was analysed under the TIM2+F+I+G4 model of sequence evolution, implementing 1000 ultrafast bootstraps on the web platform of IQ-TREE. Species delimited in this study are colour coded: Green – *C. farooqi* stat. nov.; Yellow – *C. irawadi*; Red – *C. versicolor*; Blue – *C. vultuosus* comb. nov.

aff. *farooqi* were not included, as this lineage requires taxonomic attention, and is not dealt with here.

Three of the four phylogenetically distinct clades, Clade1, Clade2, and Clade3, fulfilled our species delimitation criteria with the integration of morphology and geography, and the identity of these clades as distinct species is established here. Clade4, on the other hand, included two divergent lineages, of which, the one from northern hilly regions of Pakistan, including the sequences from near the type locality of *C. v. farooqi*, is dealt with herein.

The 16S gene tree analysed using the sequences of representative species of the subfamily Draconinae suggested the relationships of the recovered lineages within the subfamily (Fig. 3). *Calotes calotes* was recovered as a phylogenetic sister of Clade4, and *C. versicolor* (Clade1) was sister to the clade comprising *C. calotes* and Clade4. *Calotes irawadi* (Clade2) was sister to the clade comprising of *C. calotes*, Clade4 and Clade1, whereas Clade3

was sister to a clade comprising *C. calotes*, Clade4, *C. versicolor* and *C. irawadi*.

Systematics

Calotes versicolor (Daudin, 1802)

Figs 4–5; Table 3; Clade1

Agama versicolor Daudin, 1802

Agama tiedemanni Kuhl, 1820

Calotes versicolor – Duméril and Bibron, 1837: 405

Calotes cristatus Jaquemont, 1844

Calotes viridis Gray, 1846: 429

Calotes gigas Blyth, 1853: 648 (*nomen dubium* fide Gowande et al. 2016)

Calotes versicolor major Annandale, 1921: 321 (*nomen nudum fide* Gowande et al. 2016)

Calotes versicolor – Smith 1935; Taylor 1963; Manthey and Grossmann 1997; Cox et al. 1998; Manthey and Schuster 1999; Amarasinghe et al. 2009

Calotes cf. versicolor versicolor Manthey 2008: 86 (in part)

Calotes cf. versicolor – Mahony et al. 2009; Pal et al. 2018 (in part)

Neotype (designated by Gowande et al. 2016). INDIA • 1 ♂; Puducherry, Kalapet, Pondicherry University Campus; 12.02909°N, 79.85034°E; 34 m a. s. l.; 20 Mar. 2016; Anurag Mishra and Zeeshan Mirza leg.; GenBank: MW901307 (16S), MZ489209 (COI); NCBS AT102.

Note. The neotype designation by Gowande et al. (2016) stands valid *sensu* Article 75, and we reject the invalidation suggested by Chaitanya et al. (2017). Further comparisons and justifications are included herein.

Other material (morphological vouchers). All from INDIA • 1 ♂; Kerala, Thiruvananthapuram, Peppara Wildlife Sanctuary; 8.62448°N, 77.13646°E, 132 m a. s. l.; 15 Apr. 2010; Saunak Pal and Mrugank Prabhu leg.; GenBank MH844713 (16S), MZ489207 (COI); CESL 036; • 1 ♂; Kerala, Periyar Wildlife Sanctuary, Ranni Forest Division, Sabarimala; 9.40692°N, 77.06780°E, 181 m a. s. l.; 21 Feb. 2011; Saunak Pal and Mrugank Prabhu leg.; GenBank MH844729 (16S); CESL 182 • 1 ♂; Kerala, Pooppara, Mathikettan Shola National Park; 9.97136°N, 77.23283°E, 1088 m a. s. l.; 27 Mar. 2011; Saunak Pal leg.; GenBank MH844730 (16S); CESL 190 • 1 ♂; Kerala, Kottappadi part, Chembra; 11.55390°N, 76.08328°E, 1085 m a. s. l.; 10 Jun. 2010; Saunak Pal and Mrugank Prabhu leg.; CESL 046; • 1 ♂; Tamil Nadu, Thiruchitrambalam, Aranya Forest and Sanctuary; 11.96644°N, 79.76334°E, 28 m a. s. l.; 14 May 2017; Gaurang Gowande, Zeeshan Mirza and Vishal Verma leg.; CESL 1072 • 11 ♂; Puducherry; 11.93°N, 79.88°E; 1 m a. s. l.; Shekhar Dattatri leg.; CMNH152047–CMNH152051, CMNH152053, CMNH152054, CMNH152066, CMNH152068, CMNH152069, CMNH152071 • 1 ♂; Kerala, Palakkad District; Jan. 1961; DN Mathew leg; BNHS 362 • 1 ♂; Tamil Nadu, Masinagudi; Jun. 1975; Rezakhan leg; BNHS 1260 • 1 ♂, 3 ♀; Tamil Nadu, Jamestown; May–Jun. 1965; RB Grubb leg; BNHS 728, BNHS 810, BNHS 811, BNHS 813 • 1 ♂; Tamil Nadu, Courtallam; 19 Jun. 1966; JC Daniel leg; BNHS 858 • 2 ♂; Odisha, Chilika Lake; Jan. 1967; BNHS 779, BNHS 781 • 1 ♂; Tamil Nadu, Papanasam Wildlife Sanctuary; 3 Apr. 1978; H Abdulali leg; BNHS 1257 • 1 ♀; Kerala, Mananthavady; 1 May 1975; PBSL Mahadik leg; BNHS 1129.

Genetic diagnosis. The within species genetic divergence across all the examined sequences is up to 1.6% at 16S and 0.2–7.6% at COI. The species is at least 3.3% and 13.0% divergent from Clade3, at least 2.7% and 12.6% divergent from *C. irawadi* and at least 3.5% and 17.1% divergent from Clade4 at 16S and COI respectively. From *C. calotes*, the species differs by sequence divergence of at least 5.1% at 16S and 16.7% at COI (Table 2). The species was recovered as sister to a clade comprising of *C. calotes* and Clade4 in the phylogenetic analyses (Fig. 3).

Diagnosis and comparison. A medium to large sized species of *Calotes*, adult males averaging 108 mm in SVL, females averaging 90 mm in SVL; body compressed;

head relatively long; dorso-lateral scales posterodorsally oriented, large, weakly to strongly keeled, homogeneous; ventral scales smaller than the dorso-lateral scales, strongly keeled, mucronate; 36–46 scales around the mid-body; anti-humeral fold absent; two distinct, elongated spines in the supratympanic region on each side of the head, anterior spine longer and more prominent; nuchal and dorsal crest continuous, distinct, slightly recurved; scales of the nuchal crest long, those of dorsal crest slightly shorter, ending at the top of the base of the tail; nuchal, dorsal and supratympanic spines more pronounced in males; limbs slender, dorsal surface strongly keeled, ventral surface moderately keeled.

The species can be separated from all the members of Smith's *C. versicolor* group, which includes the species *C. calotes*, *C. emma* Gray, 1845, *C. grandisquamis*, *C. jerdoni* Günther, 1870, *C. maria* Gray, 1845, *C. minor* (Hardwicke and Gray, 1827), *C. mystaceus* Duméril and Bibron, 1837, *C. nemoricola* by a combination of characters: absence of crescent-shaped patch of granular scales at the insertion of the forelimbs (vs. present in *C. emma*, *C. grandisquamis*, *C. jerdoni*, *C. mystaceus* and, and *C. nemoricola*), 36–46 Mid-body scale rows (vs. 49–65 in *C. emma*, 27–35 in *C. grandisquamis*, 45–57 in *C. jerdoni*, 58–63 in *C. maria*, 48–60 in *C. minor* and 45–58 in *C. mystaceus*); nuchal and dorsal crest scales well developed, nuchal crest scales slightly larger than the dorsal crest scales (vs. nuchal spines much longer, dorsal spines reduced in *C. maria* and *C. nemoricola*; nuchal spines much longer than dorsal spines in *C. calotes*, *C. emma*, *C. grandisquamis*); two well-separated supratympanic clusters of spine-like conical scales, one scale from each cluster enlarged, prominent to form a spine (vs. row of 3–4 compressed supratympanic spines in *C. grandisquamis* and *C. nemoricola*, 8–9 compressed spines above tympanum in *C. calotes*; two parallel rows of supratympanic scales in *C. jerdoni* and *C. maria*, single well-developed postorbital spine in *C. emma*). The species differs from *C. paulus* (Smith, 1935) and *C. zolaiking* Giri, Chaitanya, Mahony, Lalrunga, Lalrinchhana, Das, Sarkar, Karanth and Deepak, 2019 primarily by the homogeneous scalation on the dorsolateral region (vs. heterogeneous) and a comparatively well-developed dorsal crest. From the dubious species *C. bhutanensis* Biswas, 1975, the species differs in possessing longer head, concave orbital region, and by the absence of a row of erect scales on the sides of the neck. From *C. chincolium* Vindum, 2003, *C. nigriplicatus* Hallermann, 2000 and other members of the *C. mystaceus* complex (*C. bachae* Hartmann, Geissler, Poyarkov, Ihlow, Galoyan, Rödder and Böhme, 2013, *C. geissleri* Wagner, Ihlow, Hartmann, Flecks, Schmitz and Böhme, 2021, *C. goetzi* Wagner, Ihlow, Hartmann, Flecks, Schmitz and Böhme, 2021, *C. mystaceus*, *C. vindumbarbatus* Wagner, Ihlow, Hartmann, Flecks, Schmitz and Böhme, 2021, *sensu* Wagner et al. (2021)) *C. versicolor* differs by the absence of an oblique fold of skin in front of forelimbs or shoulder (vs. present). From the Sri Lankan congeners (*C. ceylonensis* Müller, 1887, *C. desilvai* Bahir and Maduwage, 2005, *C. liocephalus* Günther, 1872, *C. liolepis* Boulenger, 1885, *C. manamendrai* Am-

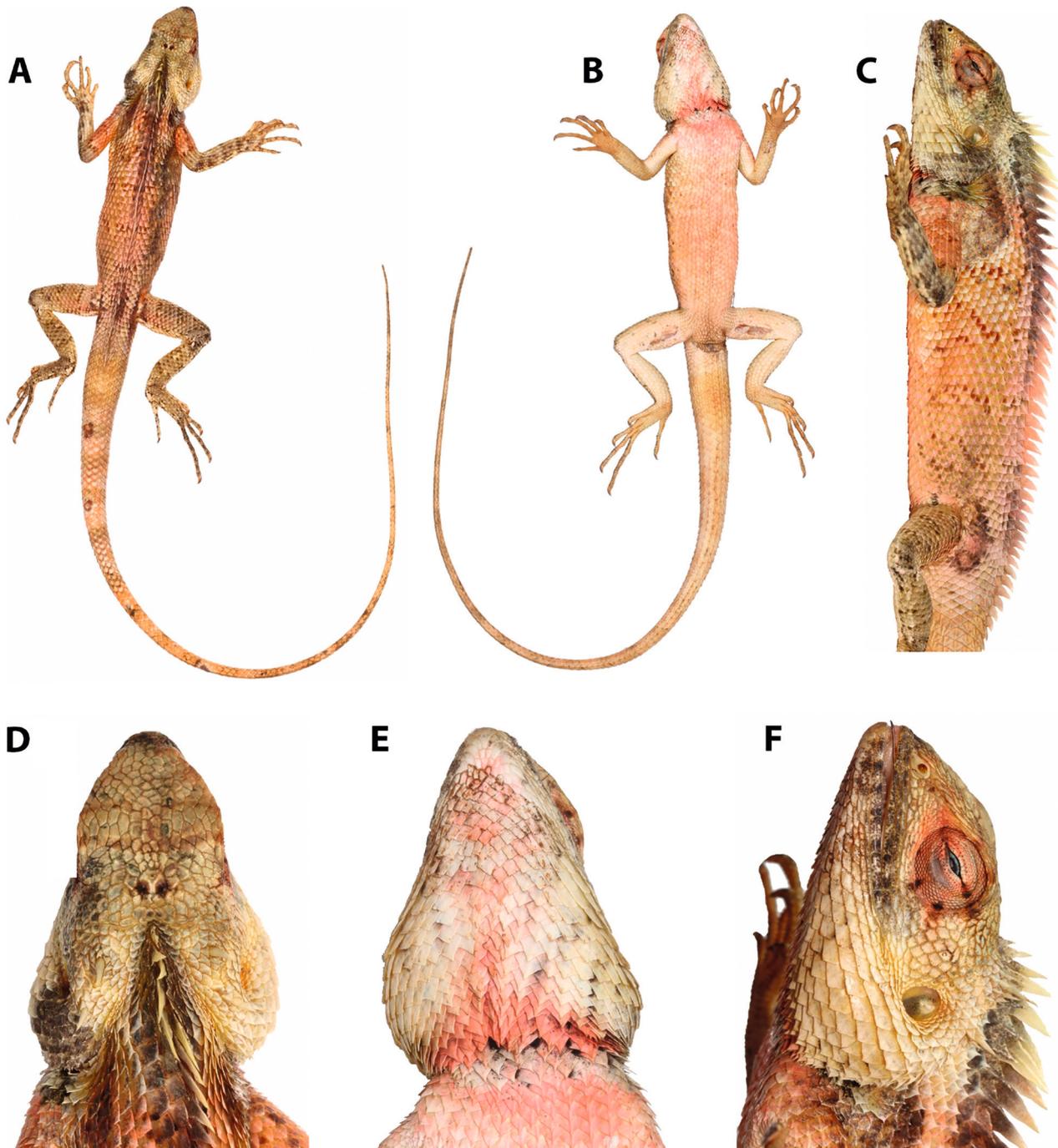


Figure 4. Neotype of *Calotes versicolor* NCBS AT102. **A.** full body dorsal, **B.** full body ventral, **C.** full body lateral, **D.** head dorsal, **E.** head ventral, **F.** head lateral. Photographs by Zeeshan Mirza.

arasinghe and Karunarathna, 2014, *C. nigrilabris* Peters, 1860, *C. pethiyagodai* Amarasinghe, Karunarathna and Hallermann, 2014) the species differs by its posterodorsal orientation of lateral body scales (vs. posteroventral) and absence of shoulder pit (vs. present). The species most closely resembles, and differs from *C. irawadi* by its much larger adult male body size (average SVL 108 mm in *C. versicolor*, vs. 82.4 mm, in *C. irawadi*), lesser number of dorsal crest scales (average 39.8 in *C. versicolor* vs. 48.9 in *C. irawadi*); from *C. htunwini* by the posterodorsal or vertical orientation of scale rows on the sides of the neck and supra-axillary area (vs. horizontal in *C. htunwini*). Detailed comparison with the species resur-

rected and elevated in this communication is presented in the respective diagnosis and comparison sections of those species.

Original description. Daudin (1802). Histoire naturelle, générale et particulière des reptiles, ouvrage faisant suite, a l'histoire naturelle, générale et particulière composée par Leclerc de Buffon, et redigée par C.S. Sonnini, vol. III. Paris, F. Dufart, 452 pp.

Etymology. The specific epithet is an adjective in Latin referring to variable or to turn (*versi*, derived from *versare*) and color (*color*) of the species in life.



Figure 5. *Calotes versicolor* (CESL 036), Peppara WLS, Thiruvananthapuram, Kerala, India, in life. Photograph by Saunak Pal.

Variation in the material examined. Twenty-three male specimens were examined. The means for the mensural characters in mm are: HL 26.5; HW 26.2; HH 19.6; JawW 21.3; SnEye 10.3; NarEye 5.8; EyeEar 8.6; SnW 6.6; Interorb 12.5; SVL 110; TrunkL 49.0; TailL 280.4; TailH 16.8; TailW 13.6; PectW 19.3; PelvW 13.7; SnForeL 45.0; UpArmL 19.2; LoArmL 20.2; ForefL 18.9; 4FingLng 12.8; UpLegL 24.6; CrusL 26.4; HindfL 34.5; 4ToeLng 19.9; ForeLimbL 58.6; HindLimbL 85.2. The means for meristic characters are: SnS 7; HeadSTr 13; HeadSLn 15; CanthR 8; Eyelid 12; Suplab 11; Inflab 11; TempSp 2; Dorsal 40; Mid-body 42; 4FingLm 21; 4ToeLm 27. Seven female specimens were examined. The means for the mensural characters in mm are: HL 21.4; HW 17.1; HH 14.7; JawW 15.3; SnEye 9.0; NarEye 5.2; EyeEar 6; SnW 5.3; Interorb 10.5; SVL 90; TrunkL 42.3; TailL 228; TailH 10.3; TailW 9.6; PectW 15.6; PelvW 10.8; SnForeL 33.2; UpArmL 17.7; LoArmL 16.4; ForefL 15.2; 4FingLng 11.5; UpLegL 20.4; CrusL 21.4; HindfL 27.2; 4ToeLng 16.6; ForeLimbL 44.5; HindLimbL 64. The means for meristic characters are: SnS 7; HeadSTr 15; HeadSLn 13; CanthR 8; Eyelid 13; Suplab 11; Inflab 9; TempSp 2; Dorsal 45; Mid-body 42; 4FingLm 18; 4ToeLm 25. The ranges for each of these characters are given in Table 3.

Distribution. The species appears to be endemic to India, occurring largely on the Southern Granulite Terrain and the eastern coast of India. The species was found in the Southern Western Ghats, the south-west coast of India, the southern Eastern Ghats, the eastern coast of India till Mahanadi basin in the north, and in the low-elevation areas of Peninsular India between the Eastern and the Western Ghats during this study. The species also has been introduced to the Maldives (Figs 1–3).

Calotes htunwini Zug and Vindum, 2007

Taxonomic comments. We did not include this species in our analyses; however, the species is distinct from members of the *C. versicolor* group due to the horizontal orientation of the scale rows of the neck and the supra-axillary region. The species occurs throughout the lower elevations of Myanmar's Central Dry Zone (Zug et al. 2007).

Holotype. MYANMAR • 1 ♀; Sagaing Division, Chatthin Wildlife Sanctuary; 23.5743°N, 95.7376°E; ca. 110 m a. s. l.; 22 May 1998; Htun Win leg.; USNM 524044.

Original description. Zug et al. (2007). Proceedings of the California Academy of Sciences 57(2): 35–68.

Calotes irawadi Zug, Brown, Schulte and Vindum, 2007

Clade2

Taxonomic comments. The species can be diagnosed by its posteriorad or vertical orientation of the scale rows of the neck and the supra-axillary region, this separates the species from *C. htunwini*; detailed comparisons with *C. versicolor*, the species resurrected and elevated in this communication are provided in the diagnoses and comparisons sections of those species. The species was thought to have a narrower distribution in the Central Dry Zone of Myanmar, in comparison to *C. htunwini* (Zug et al. 2007). It was subsequently reported from the northeast Indian states of Assam and Tripura (Das et al. 2009, Anonymous 2020), and has recently been reported from

Table 3. Mensural and meristic characters of the type and non-type specimens of *Calotes versicolor* and its synonym *Agama tiedemanni*, mensural characters recorded as a ratio of SVL. Note that the morphometric data for the types of other synonyms of *C. versicolor* were not available.

Species	<i>Calotes versicolor</i>		
	Neotype <i>Calotes versicolor</i> NCBS AT102	Syntype <i>Agama tiedemanni</i> (<i>vide</i> Kuhl 1820)	Other morphological vouchers (<i>n</i> =29)
Mensural characters			Range
HeadL/SVL	0.23	0.22	0.22–0.28
HeadW/SVL	0.23	0.20	0.15–0.28
JawW/SVL	0.17	–	0.15–0.21
HeadH/SVL	0.17	–	0.14–0.21
SnEye/SVL	0.10	–	0.08–0.11
NarEye/SVL	0.05	–	0.04–0.07
EyeEar/SVL	0.07	–	0.06–0.09
Snw/SVL	0.07	0.06	0.05–0.07
InterOrb/SVL	0.13	0.13	0.10–0.14
TrunkL/SVL	0.46	–	0.38–0.50
PectW/SVL	0.19	–	0.11–0.23
PelvW/SVL	0.11	–	0.09–0.16
SnForeL/SVL	0.35	–	0.34–0.41
UpArmL/SVL	0.21	–	0.14–0.23
LoArmL/SVL	0.20	–	0.16–0.20
ForefL/SVL	–	–	0.14–0.21
4fingLng/SVL	0.11	–	0.10–0.18
UpLegL/SVL	0.24	–	0.17–0.25
CrusL/SVL	0.26	–	0.19–0.28
HindfL/SVL	0.31	–	0.28–0.39
4toeLng/SVL	0.18	–	0.15–0.26
ForeLimbL/SVL	–	–	0.48–0.59
HindLimbL/SVL	–	–	0.69–0.91
ForeLimbL/HindLimbL	–	–	0.61–0.73
PelvW/PectW	0.60	–	0.5–1.0
Meristic characters			
SnS	7	–	6–8
HeadSTr	13	–	11–17
HeadSLn	17	–	11–18
CanthR	8	–	6–9
Eyelid	13	–	10–15
Suplab	11	–	9–14
Inflab	12	12	8–12
TempSp	2	2	2
Dorsal	44	–	31–51
Midbody	42	–	36–46
4FingLm	21	–	15–24
4ToeLm	28	–	21–30

Western Yunnan, China (Liu et al. 2021). Our samples from northeast Indian states of Arunachal Pradesh and Tripura belonged to Clade2 (Fig. 2), thus confirming the occurrence of the species in northeast India.

Holotype. MYANMAR • 1 ♂; Sagaing Division, Chathin Wildlife Sanctuary; 23.5743°N, 95.7376°E; ca. 110 m. a. s. l.; 17 Jul. 1997; USNM 520543.

Original description. Zug et al. (2007). Proceedings of the California Academy of Sciences 57(2): 35–68.

***Calotes vultuosus* comb. nov. (Harlan, 1825)**

Figs 6–7; Table 4; Clade3

Agama vultuosa Harlan 1825: 296*Agama indica* Hardwicke and Gray 1827: 217*Calotes* cf. *versicolor versicolor* Manthey 2008: 88 (in part)*Calotes* cf. *versicolor* – Pal et al. (2018) (in part)**Holotype.** INDIA • 1 ♂; West Bengal, Kolkata; 20.55°N, 88.36°E, 10 m a. s. l.; Dr R. Coates leg.; ANSP 7296

Other material (morphological vouchers). All from INDIA • 1 ♂, 1 ♀; Maharashtra, Satara, Koyna WLS; Soman and Thakar leg; BNHS 356 (both); • 1 ♂; Maharashtra, Solapur, Kurduwadi; 18.09°N, 75.43°E, 516 m a. s. l.; BNHS 368; • 2 ♂; Maharashtra, Satara, Thoseghar; 17.58880°N, 73.83805°E, 1119 m a. s. l.; 06 Jun. 2015; Gaurang Gowande and Pushkar Phansalkar leg.; GenBank MW901288–89 (16S); CESL 1004–05; • 1 ♂; Maharashtra, Satara, Patan; 17.35397°N, 73.80288°E, 587 m a. s. l.; 10 Jun. 2015; Gaurang Gowande and Pushkar Phansalkar leg.; GenBank MW901290 (16S); CESL 1007; • 1 ♂; Maharashtra, Pune, Taleghar; 19.04670°N, 73.55370°E, 925 m a. s. l.; 13 Jun. 2015; Gaurang Gowande and Pushkar Phansalkar leg.; GenBank MW901255 (16S); CESL1009; • 2 ♂; Maharashtra, Pune, Waghapur; 18.39990°N, 74.12400°E, 762 m a. s. l.; 11 Oct. 2015; Gaurang Gowande and Pushkar Phansalkar leg.; CESL 1042–43; • 1 ♂; Maharashtra, Chiplund, Guhagar; 17.49495°N, 73.18475°E, 11 m a. s. l.; 24 Oct. 2016; Gaurang Gowande and Pushkar Phansalkar leg.; CESL 1036; • 1 ♂; Rajasthan, Pali; 26.82485°N, 71.85335°E, 230 m a. s. l.; 2 Jul. 2017; Vishal Varma leg.; GenBank MW901284 (16S); CESL 1041 • 1 ♂; Maharashtra, Mumbai, Bandra; 8 May 1959; H. Abdulali leg.; BNHS 350 • 1 ♂; Karnataka, Kadra; Dec. 1914; S. Prater leg.; BNHS 354 • 1 ♂; Maharashtra, Mumbai; Sir Norman Kinnear leg.; BNHS 343 • 1 ♂; Gujarat, Kutch; P. Soman leg.; BNHS 316 • 1 ♂; Maharashtra, Aurangabad; Gaurang Gowande and Pushkar Phansalkar leg.; CESL 1065 • 3 ♂; Telangana, Hyderabad; 14 Apr. 2017; Gaurang Gowande and Pushkar Phansalkar leg.; GenBank MW901282 (16S); CESL 1068–70 • 1 ♂; Maharashtra, Latur; 16 Apr. 2017; Gaurang Gowande and Pushkar Phansalkar leg.; CESL 1071 • 1 ♀; Maharashtra, Mumbai, Borivali; 6 Jun. 1971; BNHS 1027.

Genetic diagnosis. The least within species divergence at 16S and COI was 0%, while the greatest within species distance recorded was 2.0% and 9.5% at 16S and COI respectively. The species was at least 3.3% and 13.0% divergent from *C. versicolor*, 2.7% and 12.8% divergent from *C. irawadi*, and 3.9% and 15.5% divergent from Clade4 at 16S and COI respectively (Table 2). The species differed from *C. calotes* by sequence divergence of > 5% at 16S and 16.3% at COI from *C. calotes*. Phylogenetically, the species was recovered as sister to a clade comprising of *C. calotes*, *C. versicolor*, and Clade4 (Fig. 3).

Diagnosis and comparison. A medium to large sized species of *Calotes*, adult males averaging 106 mm in SVL, females averaging 78 mm in SVL; body compressed; head relatively short; dorso-lateral scales posterodorsally oriented, large, weakly to strongly keeled, homogeneous; ventral scales smaller than the dorso-lateral scales, strongly keeled; 37–45 scales around the mid-

body; anti-humeral fold absent; two distinct spines in the supratympanic region, posterior spine as long as the anterior spine, at times longer, more prominent; nuchal and dorsal crest continuous, distinct, slightly recurved; scales of the nuchal crest large, those of dorsal crest reduced to mere denticulation towards the base of the tail, generally ending in the region between the mid-body and the tail, rarely continues to the base of the tail; nuchal, dorsal and supratympanic spines more pronounced in males; limbs slender, dorsal surface of the limbs strongly keeled, ventral surface weakly keeled, that of the thighs smooth.

The species can be separated from the members of Smith's *C. versicolor* group (as defined above), by a combination of characters: absence of crescent-shaped patch of granular scales at the insertion of the forelimbs (vs. present in *C. emma*, *C. grandisquamis*, *C. jerdoni*, *C. mystaceus*, and *C. nemoricola*), 37–45 Mid-body scale rows (vs. 49–65 in *C. emma*, 27–35 in *C. grandisquamis*, 45–57 in *C. jerdoni*, 58–63 in *C. maria* Gray, 48–60 in *C. minor*, and 45–58 in *C. mystaceus*); nuchal and dorsal crest scales well developed, nuchal crest scales slightly larger than the dorsal crest scales, dorsal crest scales become progressively smaller towards the base of the tail (vs. nuchal spines much longer, dorsal spines reduced in *C. maria* and *C. nemoricola*; nuchal spines much longer than dorsal spines in *C. calotes*, *C. emma*, *C. grandisquamis*); two well-separated supratympanic clusters of spine-like scales, one from each cluster enlarged, prominent to form a spine (vs. row of 3–4 compressed supratympanic spines in *C. grandisquamis* and *C. nemoricola*, 8–9 compressed spines above tympanum in *C. calotes*; two parallel rows of supratympanic scales in *C. jerdoni* and *C. maria*). The species differs from *C. paulus* and *C. zolaiking* primarily by the homogeneous scalation on the dorsolateral region (vs. heterogeneous) and a comparatively well-developed dorsal crest. From the dubious species *C. bhutanensis*, the species differs in possessing longer head, concave orbital region, and by the absence of a row of erect scales on the sides of the neck. From *C. chincolium*, *C. nigriplicatus*, and other members of the *C. mystaceus* complex (*C. bachae*, *C. geissleri*, *C. goetzi*, *C. mystaceus*, *C. vindumbarbatus*, sensu Wagner et al. (2021)) the species differs by the absence of an oblique fold of skin in front of forelimbs or shoulder (vs. present). From the Sri Lankan congeners (*C. ceylonensis*, *C. desilvai*, *C. liocephalus*, *C. liolepis*, *C. manamendrai*, *C. nigrilabris*, *C. pethiyagodai*) the species differs by its posterodorsal orientation of lateral body scales (vs. posteroventral) and absence of shoulder pit (vs. present). The species differs from *C. irawadi* by its much larger adult male body size (average SVL 106 mm, vs. 82.4 mm), lesser number of scales around the mid-body (average 42, vs. 47 in *C. irawadi*); from *C. htunwini* by the posterodorsal or vertical orientation of scale rows on the sides of the neck and supra-axillary area (vs. horizontal in *C. htunwini*). For comparison with the subspecies elevated to species rank in this communication, see the diagnosis and comparison section for that species.

The species can be further differentiated by its southern congener *C. versicolor* by its slightly smaller adult

body size (average male SVL 106 mm vs. 108 mm in *C. versicolor*, female SVL 77.5 vs. 92.2 mm in *C. versicolor*), dorsal crest composed of comparatively smaller scales, which become progressively smaller to the base of the tail in both sexes (vs. dorsal crest composed of large scales, which continues to the base of the tail in *C. versicolor*), supratympanic spines shorter in both sexes (vs. longer in *C. versicolor*). The species has shorter crus than *C. versicolor* (average male CrusL 22.7 vs. 26.6 in *C. versicolor*). The species differs in the overall shape of the trunk, which tapers to a lesser extent in *C. vultuosus* **comb. nov.** (average PectW/PelvW 0.81) vs. trunk tapers to a greater extent in *C. versicolor* (average PectW/PelvW 0.70 in *C. versicolor*).

Besides, the species differs from *C. versicolor* in adult male coloration during the breeding season. *Calotes vultuosus* **comb. nov.** males generally attain a cream to brown body coloration, the head and the anterior two-thirds of the trunk attain orange color, which at times extends to the forelimbs; the posterior parts of the trunk and the hind limbs remain dull, whereas *C. versicolor* males attain yellowish overall coloration, the trunk and the orbital region turns bright orange, forelimbs and hind limbs turn dark to black. Further, the black patches under the throat extend anteriorly onto the jaw musculature, at times running along the lower jaw margin on each side, before terminating posterior to the post-mental scales, whereas, in *C. versicolor*, the black patches under the throat do not extend anteriorly onto the jaw muscles.

Description of the holotype ANSP 7296 (based on photographic data, Fig. 6). A medium sized male, SVL ~77 mm. Tail complete, TailL ~160 mm. The specimen is in a damaged condition, there are multiple openings on the mid-body and near the vent, all artefacts of preservation. Further, the specimen has developed randomly distributed white patches on the scales of the head and the body. The description is based on the images of the specimen and modified from the original description; hence the mensural details should be treated with caution.

Head moderately large (HL/SVL ~0.19), snout tip blunt, rounded in dorsal perspective; loreal region between the nasals and the orbit slightly concave, acute, covered by heterogeneous, juxtaposed scales, some of which are ridged; the area comprising the loreal region and nasal shield triangular from the lateral perspective; eight CanthR scales, elongate, with their ends overlapping; supraciliary and canthal edge sharp, giving the head a flat appearance laterally from the dorsal perspective; large supraocular scales do not form shields, become parallel to convergent at the supraocular region; edges of the head divergent bordered by scales of the canthus rostralis and supraciliary; rostral broader than high; nasal shields single on each side, subtriangular, pointed anteriorly, rounded posteriorly, separated from the first Suplab by one prenasal scale, from rostral by two scales, from each other by seven SnS; nostrils round, in a single large nasal shield each, centrally placed; scales between rostral and SnS small, juxtaposed; SnS heterogeneous, the median SnS smallest, the pair bordering the median scale elon-

gate; scales of the forehead posterior to SnS sub-imbriate, very irregular in shape and size, some rugose; Head-SLn 12 bordered anteriorly by the rostral scale, posteriorly by a single, large interparietal shield; orbit encased in a sock of granular scales, separated from the nasal shield by 6–8 scale rows, from Suplab by 3–4 scale rows; Head-Str 14, between the posteriormost supraciliary scales on each side, just anterior to the interparietal; eye opening bordered dorsally and ventrally by two rows of non-granular scales, outer row composed of larger, square-shaped scales, inner row similar in shape, slightly smaller; eyelid scales (Eyelid) 13; pupil round, large; region between the orbit and the tympanum covered by rows of 6–9 smooth, roughly hexagonal scales; tympanum large, round, naked; its greatest diameter roughly 42% of horizontal diameter of the orbit; supratympanic scales weakly keeled; two enlarged supratympanic spines, subequal in size, separated from each other by four scales; anterior spine slender, bent parallel to the horizontal plane, posterior spine erect, prominent, its apex bent; scales in a row connecting the enlarged supratympanic spines give the posterior region of the head a serrated appearance; posterior region of the jaws swollen, bulging out, covered by subtriangular, mucronate, imbricate, postero-ventrally directed scales, upper border of the jaw muscles conceal the lower portion of the tympanum; labial scales large, sub-rectangular; Suplab 10; Inflab 10; two parallel rows of scales border the upper margin of the Suplab, lower originates above the second Suplab, separating the nasal shield and the second Suplab, terminates near the last Suplab; the upper row originates slightly posteriorly, terminates abruptly above the sixth Suplab; interparietal large, irregularly pentagonal, posterior border straight, tapers toward the anteriority, anterior border nearly pointed; interparietal bordered by 10 smooth, heterogeneous scales; nuchal crest starts 3–4 scales behind the interparietal; mental shield large, single, subtriangular, narrower than rostral; two pairs of elongate postmentals, anterior pair joint, in contact with mental, narrow; posterior pair broader, separated by two small chin scales; chin scales behind the postmental scales small, progressively become larger towards the throat, median row of gular scales enlarged, mucronate, and form a longitudinal fold.

First nuchal scale smallest, size of the nuchal scale progressively increases towards the median nuchal scale, nuchal scales beyond the median nuchal scale roughly the same size as, or slightly smaller than the median nuchal scale; nuchal crest composed of ~10 long, conical spines, scales recurved, continue into dorsal crest scales; dorsal crest composed of spines that progressively become smaller towards the middle of the back; continues as an obsolete row of vertebral scales to the base of the tail, beyond which the mid-dorsal crest row terminates at the keeled tail scale rows; paravertebral scales recurved, strongly keeled, mucronate; dorso-lateral scales sub-triangular, imbricate, moderately keeled, posterodorsally oriented; those in the supra-axillary region mostly dorsally oriented, slightly smaller than those of the mid-body; body at the mid-body to the pelvic region damaged; ventrals strongly keeled, smaller than the dorso-later-

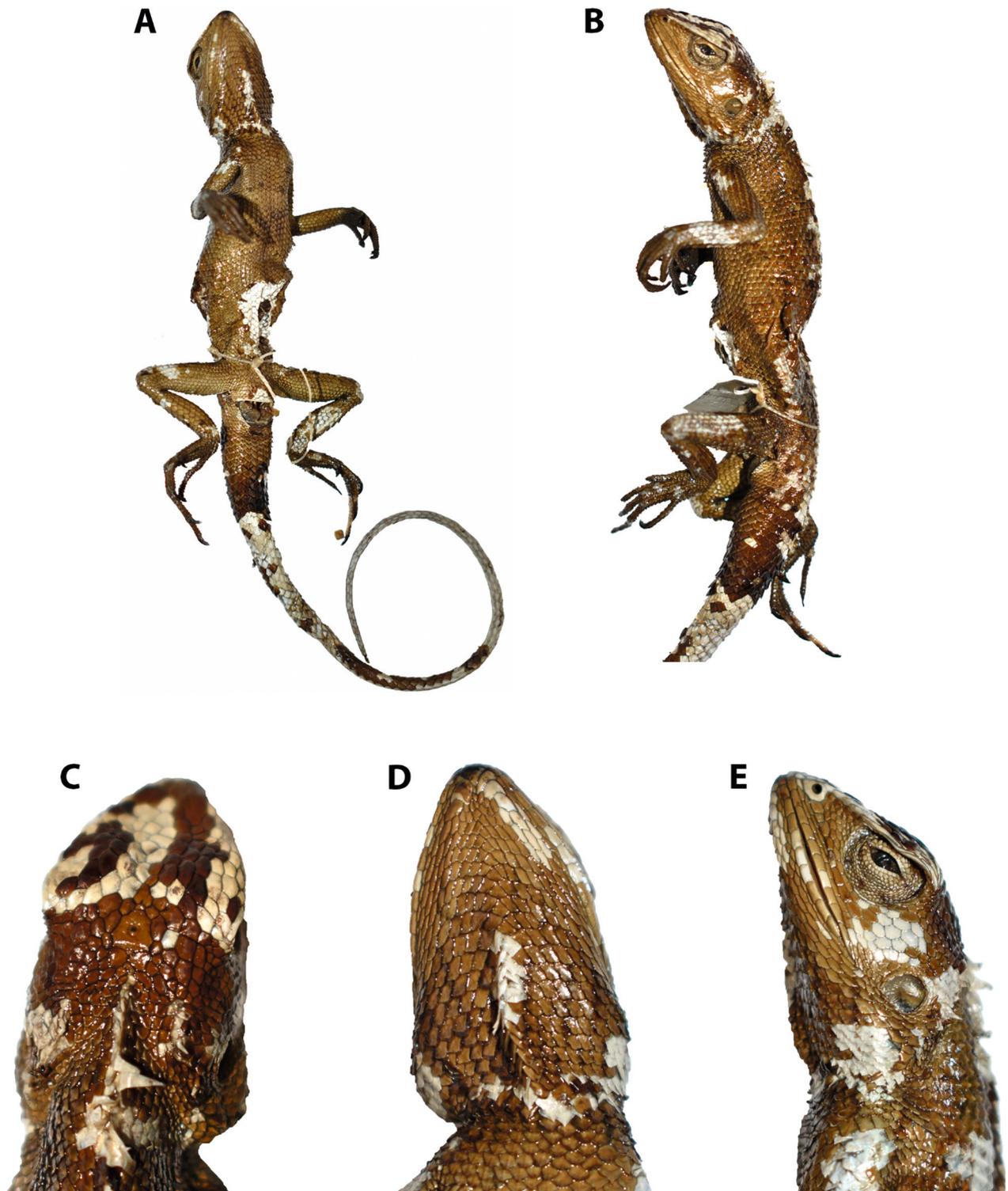


Figure 6. Holotype of *Calotes vultuosus* **comb. nov.** ANSP 7296. **A.** full body ventro-lateral, **B.** full body lateral, **C.** head dorsal, **D.** head ventral, **E.** head lateral. Photographs by Ned Gilmore.

al scales, mucronate, imbricate; ventral scales between the insertion of the forelimbs weakly keeled, some with rounded apices.

Limbs long and slender, covered with keeled scales, similar to dorso-laterals in shape and size, forming parallel longitudinal rows; scales on the dorsal surfaces of the thigh weakly keeled, ventral surfaces smooth, those on the crus and sole strongly keeled; hindlimbs longer, almost 80% of SVL; relative length of fingers $4 > 3 > 2 > 5 > 1$,

fourth slightly longer than third; relative length of toes $4 > 3 > 5 > 2 > 1$; subdigital lamellae bicarinate, keels sharp; digits and subdigital lamellae slender, digits swollen at base; tail damaged ventrally near the vent, exposing the hemipenis; tail scales large, imbricate, strongly keeled on dorsal and ventral aspects, mucronate; TailL ~160 mm.

Coloration in preservation: Dorsum generally dark brown, venter paler, light yellow; head dark brown dorsally, throat paler; orbit whitish, nasal shield, canthals and



Figure 7. An uncollected male of *Calotes vultuosus* **comb. nov.**, from Burdwan, West Bengal, India, in life. Photograph by Ayan Mondal.

supraciliary region almost white; irregularly distributed white patches on the labials, throat, jaw muscles, axillary region, on the scales between the tympanum and the ear, the supratympanic region, and on the nuchal crest scales; the white patches continue on to the upper arm, lower arm, dorso-laterals, supraxillary region, and on the dorsal crest; white patches also present on the venter, the hindlimbs and the tail; tail scales show marks of corrosion due to preservative near the vent.

Original description. Harlan R (1825). Journal of the Academy of Natural Sciences of Philadelphia 4(1): 296–305.

Etymology. The specific epithet ‘*vultuosa*’ could refer to the grim or frowning look of the species when viewed frontally, which it gets due to the flattened scales of the CanthR and the supercilium. The specific epithet *vultuosa* is feminine singular and is here changed to the masculine gender *vultuosus* in agreement with the generic epithet, *Calotes*, which is masculine in gender.

Variation in the material examined. Eighteen male specimens were examined. The means for the mensural characters in mm are: HL 21.2; HW 25.3; HH 19.9; JawW 19.9; SnEye 10.9; NarEye 5.7; EyeEar 8.6; SnW 6.5; Interorb 11.1; SVL 106.0; TrunkL 47.1; TailH 16.4; TailW 13.1; PectW 18.4; PelvW 15.1; SnForeL 41.2; UpArmL 19.8; LoArmL 19.5; ForefL 19.2; 4FingLng 12.7; UpLegL 25.1; CrusL 23.1; HindfL 30.8; 4ToeLng 19.0; ForeLimBL 58.5; HindLimBL 79.1. The means for meristic characters are: SnS 7; HeadSTr 13; HeadSLn 14; CanthR 7; Eyelid 12; Suplab 11; Inflab 11; TempSp 2; Dorsal 48; Mid-body 42; 4FingLm 21; 4ToeLm 26. Additionally,

two female specimens were examined. The means for the mensural characters in mm are: HL 17.4; HW 13; HH 12.4; JawW 13; SnEye 8.1; NarEye 4.1; EyeEar 4.8; SnW 4.5; Interorb 8.7; SVL 77; TrunkL 36.8; TailH 6.3; TailW 5.9; PectW 11.5; PelvW 9.6; SnForeL 28.9; UpArmL 16.6; LoArmL 13.5; ForefL 14.7; 4FingLng 10.7; UpLegL 17.6; CrusL 17.9; HindfL 23.7; 4ToeLng 16.3; ForeLimBL 44.3; HindLimBL 59.3. The means for meristic characters are: SnS 6; HeadSTr 13; HeadSLn 13; CanthR 7; Eyelid 10; Suplab 10; Inflab 10; TempSp 2; Dorsal 45; Mid-body 40; 4FingLm 18; 4ToeLm 25. The ranges for each of these characters are given in Table 4.

Distribution. The species appears to be widely distributed, occupying parts of the Dharwar Craton till Brahmagiri, Deccan Volcanic Province, the Central Highlands, the Gangetic Plains, and the Indian Deserts (Fig. 1).

Calotes farooqi Auffenberg and Rehman, 1995 **stat. nov.**

Figs. 8–9; Table 4; Clade4, in part

Calotes versicolor nigrigularis Auffenberg and Rehman, 1993

Calotes versicolor farooqi Auffenberg and Rehman, 1995 (nom. nov. for *C. v. nigrigularis*)

Holotype. Pakistan • 1 ♂; Khyber Pakhtunkhwa, Mansehra, Shargal (corrected to Sarhan); 34.3°N, 73.4°E, 1077 m a.s.l.; 15 Jun. 1990; PMNH field crew leg.; FLMNH/UF 79470.

Other material (morphological vouchers). All from Pakistan • 1 ♂; Punjab, Kotli Syedan; 32.7604°N, 73.0736°E, 834 m a. s. l.; 16 Sept. 2018; Daniel Jablonski leg.; GenBank MW901312 (16S), MZ489214 (COI); CUDZ DJ 7902; • 2 ♀; Khyber Pakhtunkhwa, Mansehra; 34.5610°N, 73.2635°E, 834 m a. s. l.; PMNH 414, PMNH 1355.

Genetic diagnosis. The analysis included a total of three samples (MW901312–14: 16S, MZ489214: COI) from the localities Tangora, Gulbandi Buner (localities 85 and 86 in Figure 2, both west of the Indus River in Buner District, ca. 60 km. by airline from the type locality Mansehra) and Kotli Syedan (locality 77 in Figure 2) from the northern hilly regions of Pakistan, representing *C. farooqi* **stat. nov.** The maximum within species divergence (not including the divergent lineage from the southern hilly and southern plains regions) was 0.4% at 16S. The species is at least 3.5% and 17% divergent from *C. versicolor*, 3.6% and 16.9% divergent from *C. irawadi*, 3.9% and 15.5% from *C. vultuosus* **comb. nov.**, and 4.9% and 20.4% from *C. calotes* at 16S and COI respectively (Table 2). The species was recovered as sister to *C. calotes* (Fig. 3).

Diagnosis and comparison. A medium to large species of *Calotes*, adult males ranging from 94–99 mm in SVL, body moderately compressed; head relatively long; dorso-lateral scales posterodorsally oriented, large, weakly to strongly keeled, homogeneous; ventral scales smaller

than the dorso-lateral scales, strongly keeled, mucronate; anti-humeral fold absent; two distinct spines in the supratympanic region; nuchal and dorsal crest continuous, distinct; scales of the nuchal crest large, those of dorsal crest slightly smaller, slightly recurved, ending at the top of the base of the tail, males with distinct black patches on both sides of the lower jaw, extending into the forebody, in the breeding season.

The species can be separated from all the members of the *C. versicolor* group by a combination of characters: absence of crescent-shaped patch of granular scales at the insertion of the forelimbs (vs. present in *C. emma*, *C. grandisquamis*, *C. jerdoni*, *C. mystaceus*, and *C. nemoricola*), 41–51 Mid-body scale rows (vs. 49–65 in *C. emma*, 27–35 in *C. grandisquamis*, 58–63 in *C. maria* Gray, 48–60 in *C. minor* Hardwicke and Gray, and 45–58 in *C. mystaceus*); nuchal crest scales well-developed, dorsal crest scales much smaller, more or less equal in size (vs. nuchal spines much longer, dorsal spines reduced in *C. maria* and *C. nemoricola*; nuchal spines much longer than dorsal spines in *C. calotes*, *C. emma*, *C. grandisquamis*); two well-separated supratympanic spines (vs. row of 3–4 compressed supratympanic spines in *C. grandisquamis* and *C. nemoricola*, 8–9 compressed spines above tympanum in *C. calotes*; two parallel rows of supratympanic scales in *C. jerdoni* and *C. maria*, single well developed postorbital spine in *C. emma*). The species differs from *C. paulus* and *C. zolaiking* primarily by the homogeneous scalation on the dorsolateral region (vs. heterogeneous) and a comparatively well-developed dorsal crest. From the dubious species *C. bhutanensis*, the species differs in possessing longer head, concave orbital region, and by the absence of a row of erect scales on the sides of the neck. From *C. chincolium*, *C. nigriplicatus*, and members of the *C. mystaceus* complex (*C. bachae*, *C. geissleri*, *C. goetzi*, *C. mystaceus*, *C. vindumbarbatus*, sensu Wagner et al. (2021)) by the absence of an oblique fold of skin in front of forelimbs or shoulder (vs. present). From the Sri Lankan congeners (*C. ceylonensis*, *C. desilvai*, *C. liocephalus*, *C. liolepis*, *C. manamendrai*, *C. nigrilabris*, *C. pethiyagodai*) the species differs by its posterodorsal orientation of lateral body scales (vs. posteroventral) and absence of shoulder pit (vs. present). The species differs from *C. irawadi* by its larger adult male body size (average male SVL 96.5 mm in *C. farooqi* **stat. nov.**, vs. 82.4 mm in *C. irawadi*), lesser number of dorsal crest scales (41 in *C. farooqi* **stat. nov.** vs. 48.9 in *C. irawadi*); from *C. htunwini* by the posterodorsal or vertical orientation of scale rows on the sides of the neck and supra-axillary area (vs. horizontal in *C. htunwini*).

The species is most similar in appearance to *C. versicolor* and *C. vultuosus* **comb. nov.**, however, can be differentiated from *C. versicolor* by its smaller adult male body size (average male SVL 97 mm, vs. 108 mm in *C. versicolor*, female SVL 82 vs. 92 in *C. versicolor*), dorsal crest scales composed of comparatively shorter scales, which become shorter progressively to the base of the tail (vs. dorsal crest composed of longer scales, dorsal crest continues to the base of the tail in *C. versicolor*), lesser number of eyelid scales, Eyelid 9–11 (vs. 10–15 in *C.*

versicolor, 11–14 in *C. vultuosus* **comb. nov.**), the shape and the size of the scales between the nasal shield and the orbit (large, <6 in a row between the nasal shield and the orbit in *C. farooqi* **stat. nov.**, vs. small, >6 in *C. versicolor* and *C. vultuosus* **comb. nov.**), by the acuteness of the region between the nostril and the orbit (more acute in *C. farooqi* **stat. nov.**, less acute in *C. vultuosus* **comb. nov.** and *C. versicolor*). *C. farooqi* **stat. nov.** also has slightly lower number of SnS (6), in comparison to *C. versicolor* and *C. vultuosus* **comb. nov.** (generally 7).

The species also differs from *C. versicolor* and *C. vultuosus* **comb. nov.** in terms of breeding coloration of the adult males. The head and the forebody of the males of *C. farooqi* **stat. nov.** attain grey to black colour, except the vertebral region and the parts of the head above the jaw muscles; the lower portion of the orbit turns black, the black colour extends to the outer surfaces of the forelimbs, the inner surfaces of the forelimbs and the region of the venter intervening the limbs turn greyish black. In contrast, *C. versicolor* males attain a yellowish colour, trunk and orbital region turn orange, forelimbs and hind limbs turn dark to black, the black patches under the throat do not extend anteriorly onto the jaw muscles; *C. vultuosus* **comb. nov.** males attain a cream to brown body colour, the head and the anterior two-thirds of the trunk attain orange colour, which may extend on to the forelimbs, the posterior parts of the body remain duller.

Description of the holotype FLMNH/UF 79470 (Fig. 8). A large-sized male, SVL 94 mm, tail complete, 245 mm. The specimen is in a mediocre condition, the head is bent to the left, tail to the right; forelimbs adpressed to the body. A vertical incision on the ventral surface between the insertion of the forelimbs.

Head large (HL/SVL 0.27), snout tip pointed in dorsal perspective; region between the nasals and the orbit slightly concave, acute, covered by heterogeneous, juxtaposed scales; loreal region from the nasal shield triangular, the anterior border of the nasal shield at the vertex of the triangle; eight CanthR scales, elongate, with their ends overlapping; supraciliary and canthal edge sharp, giving the head a flat appearance laterally from the dorsal perspective; large supraocular scales do not form shields; become parallel to convergent at the supraocular region; dorsal edges of the forehead divergent, bordered by scales of the canthus rostralis and supraciliary region, rostral broader than high; nasals single on each side, subtriangular, pointed anteriorly, rounded posteriorly, separated from the first Suplab by one prenasal scale, from rostral by two scales, from each other by six SnS; nostrils round, in a single large nasal shield each, centrally placed; scales between rostral and SnS small, juxtaposed; SnS heterogeneous, the median SnS smallest; scales of the forehead posterior to SnS sub-imbriate, very irregular in shape and size, some rugose; HeadSLn 12, bordered anteriorly by the rostral, and posteriorly by the single, large interparietal shield; orbit large, encased in a sock of granular scales, separated from the nasal shield by rows of 4–5 scales, from Suplab by three scale rows; HeadSTr 14, between the posteriormost supracili-

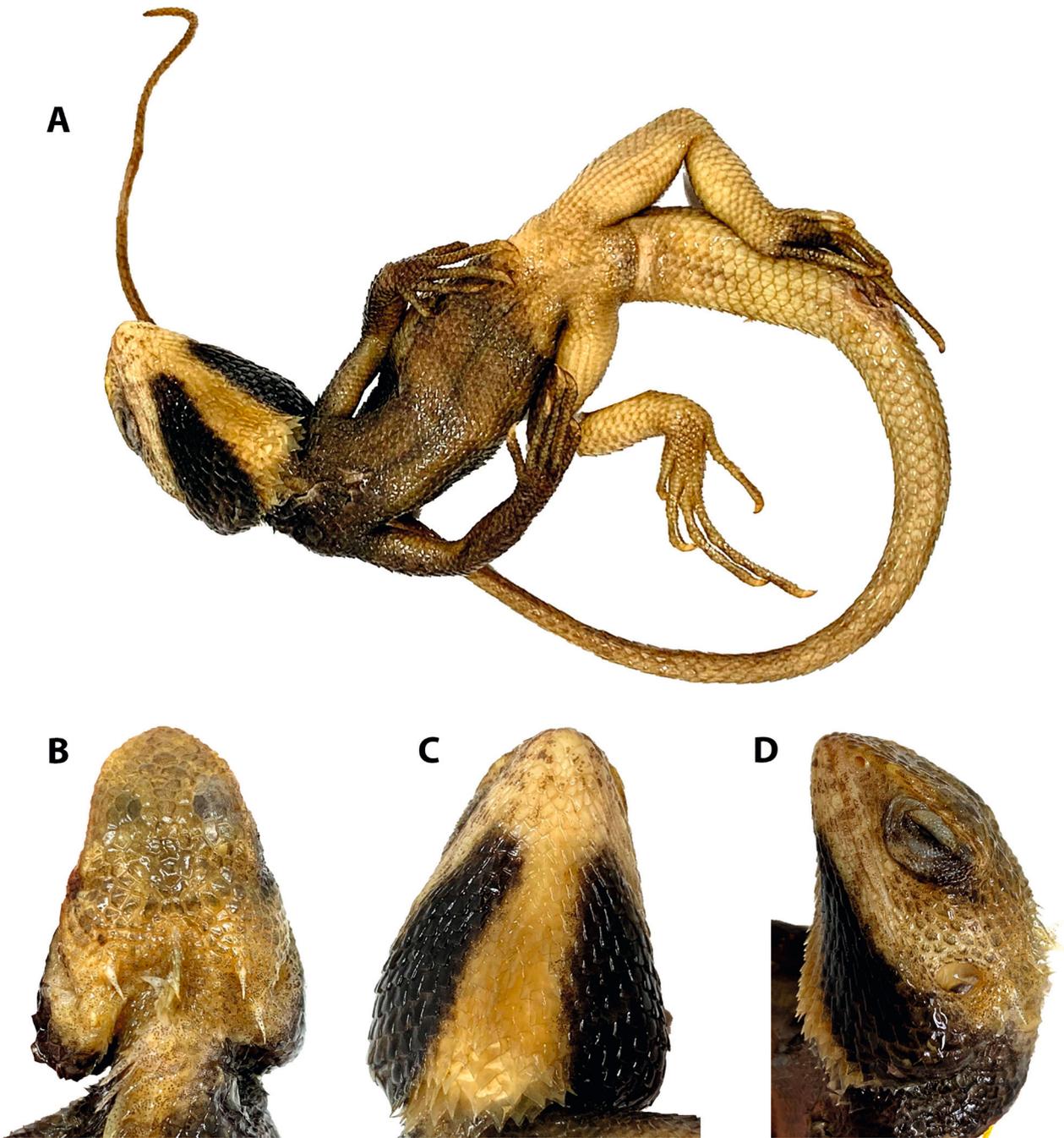


Figure 8. Holotype of *Calotes farooqi* stat. nov. FLMNH/UF 79470. **A.** full body ventral, **B.** head dorsal, **C.** head ventral, **D.** head lateral. Photographs by Coleman Sheehy.

ary scales on each, just anterior to the interparietal; eye opening bordered by two rows of non-granular scales, outer row composed of larger, square-shaped scales, inner row similar in shape, slightly smaller; eyelid scales (Eyelid) 13; region between the orbit and the tympanum covered by rows of 6–7 smooth, irregular in shape; tympanum large, round, naked; 3.1 mm at its greatest height; supratympanic scales smooth to weakly keeled; two enlarged supratympanic spines, separated from each other by 3–4 scales; anterior spine slender, shorter, posterior spine prominent; posterior region of the jaws swollen, bulges out, covered by subtriangular, imbricate, postero-ventrally directed scales, some of these mucronate; upper border of the jaw muscles conceal the lower por-

tion of the tympanum; labial scales large, sub-rectangular; Suplab 12; Inflab 11; two parallel rows of scales border the upper margin of the Suplab, lower originates above the upper margin of the second Suplab, separating the nasal shield and the second Suplab, terminates near the last Suplab; the upper row originates slightly posteriorly, terminates abruptly above the ninth Suplab; interparietal large, irregularly pentagonal, bordered by 9–10 smooth, heterogeneous scales; nuchal crest starts 3–4 scales behind the interparietal; mental shield large, single, subtriangular, , mental narrower than rostral; two pairs of elongate postmentals, anterior pair narrow, separated by a single small chin scale posterior to the mental; posterior pair broader, separated by three small scales; chin scales posterior to



Figure 9. *Calotes farooqi* stat. nov. (CUDZ DJ 7902), from Kotli Syedan, Punjab, Pakistan, in life. Photograph by Daniel Jablonski.

the postmental scales small, progressively become larger towards the throat; scale rows of the posterior region of the throat large, mucronate.

First nuchal scale smallest, size of the nuchal scale increases modestly towards the median nuchal scale; beyond which, the size reduces slightly, nuchal crest composed of lanceolate, recurved spines, which continue into dorsal crest scales; dorsal crest scales slightly smaller than nuchal crest scales, composed of spines that progressively become smaller towards the middle of the back; continues to the base of the tail, beyond which the mid-dorsal crest row terminates at the keeled tail scales; paravertebral scales recurved, strongly keeled, mucronate; dorso-lateral scales sub-triangular, imbricate, distinctly keeled, posterodorsally oriented; those in the supra-axillary region slightly smaller than those of the mid-body; ventrals strongly keeled, smaller than the dorso-lateral scales, mucronate, imbricate; ventral scales between the insertion of the forelimbs weakly keeled.

Limbs long and slender, covered with keeled scales, similar to dorso-laterals in shape and size, forming parallel longitudinal rows; scales on the dorso-ventral surfaces of the thigh weakly to moderately keeled, those on the crus and sole strongly keeled; first finger shortest, third and fourth almost equal, fifth longer than first; relative length of toes $4 > 3 > 5 > 2 > 1$; subdigital lamellae bicarinate, keels sharp, 20 under the fourth finger, 24 under the fourth toe; tail slender, swollen at base, TailL 245 mm.

Coloration in preservation: Anterior two-thirds of the body generally greyish-tan, dorsum distinctly black till mid-body, black coloration fades away in the posterior half, vertebral and paravertebral row of scales paler; venter greyish black at the pectoral region, slightly

duller towards the vent, colour abruptly changes to greyish-cream; a dark ventral midline runs from the pectoral region to the vent; dorsal surface of the forelimbs dark, lower surfaces slightly paler; hindlimbs and tail greyish-cream; supra-axillary region greyish-black, the black patches continue anteriorly along the lower surface of the jaws and gular region, except the mid-gular region which is strikingly lighter, pinkish in colour; head generally greyish above, paler laterally and posteriorly; eyelids light grey anteriorly, a small black patch near the anterior corner of the eye, a large black patch near the posterior corner of the eye.

Original description. Auffenberg W, Rehman H (1993). *Asiatic Herpetological Research* 5: 14–30.

Etymology. The specific epithet is a patronym in genitive singular case, dedicated to Farooq Ahmed, former Director, Zoological Survey Department, Pakistan.

Variation in the material examined. One male specimen (CUDZ DJ7902) was examined. The mensural characters in mm are: HL 28.1; HW 21.0; HH 16.9; SVL 99.0; TrunkL 49.2; UpArmL 16.6; The meristic characters are: SnS 6; HeadSTr 11; HeadSLn 13; CanthR 8; Eyelid 9; Suplab 11; Inflab 12; TempSp 2; Mid-body 41; 4FingLm 17; 4ToeLm 24. Additionally, two female specimens were examined. The means for the mensural characters in mm are: HL 20.2; HW 16.8; HH 12.4; JawW 15.7; SnEye 8.6; NarEye 3.6; EyeEar 5.6; SnW 5.1; Interorb 11.8; SVL 82; TrunkL 41.3; TailH 7.3; TailW 7; PectW 14; PelvW 10.5; SnForeL 17.6; UpLegL 17.5; CrusL 17.9; HindfL 25.3; 4ToeLmg 13.4; HindLimbL 60.5. The means for meristic

Table 4. Mensural and meristic characters of the type and non-type specimens of *Calotes vultuosus* **comb. nov.** and *Calotes farooqi* **stat. nov.**, mensural characters recorded as a ratio of SVL. Note that the morphometric data for the types of *A. indica* were not available, whereas those for *C. farooqi* have been sourced from Auffenberg and Rehman (1993). – indicates that measurements/counts could not be taken.

Species	<i>Calotes vultuosus</i> comb. nov.		<i>Calotes farooqi</i> stat. nov.	
	Specimens measured	Holotype ANSP 7296	Other morphological vouchers (n=20)	Holotype FLMNH/UF 79470
Mensural characters		Range		Range
HeadL/SVL	0.19	0.16–0.30	0.27	0.23–0.25
HeadW/SVL	–	0.16–0.26	0.24	0.19–0.21
JawW/SVL	–	0.17–0.21	–	0.17–0.20
HeadH/SVL	–	0.16–0.21	0.20	0.14–0.16
SnEye/SVL	–	0.08–0.11	–	0.09–0.11
NarEye/SVL	–	0.04–0.06	–	0.04–0.05
EyeEar/SVL	–	0.06–0.09	–	0.07
Snw/SVL	–	0.05–0.08	–	0.06
InterOrb/SVL	–	0.09–0.13	–	0.12–0.15
TrunkL/SVL	0.49	0.37–0.50	0.50	0.48–0.52
PectW/SVL	–	0.12–0.20	–	0.14–0.20
PelvW/SVL	–	0.09–0.17	–	0.11–0.13
SnForeL/SVL	–	0.34–0.45	–	0.31–0.35
UpArmL/SVL	–	0.14–0.23	0.20	0.13–0.18
LoArmL/SVL	–	0.16–0.23	–	0.16–0.17
ForefL/SVL	–	0.14–0.20	–	0.17–0.18
4fingLng/SVL	–	0.10–0.15	–	0.12–0.13
UpLegL/SVL	–	0.18–0.29	–	0.21–0.22
CrusL/SVL	–	0.19–0.25	–	0.22
HindfL/SVL	–	0.28–0.34	–	0.30–0.35
4toeLng/SVL	–	0.15–0.23	–	0.13–0.20
ForeLimbL/SVL	–	0.47–0.59	–	–
HindLimbL/SVL	–	0.68–0.85	–	–
ForeLimbL/Hind-LimbL	–	0.65–0.81	–	–
PelvW/PectW	–	0.74–1.0	–	0.60–0.86
Meristic characters				
SnS	7	5–7	6	6
HeadSTr	14	10–16	14	11
HeadSLn	12	12–17	12	13–14
CanthR	7	7–8	8	8
Eyelid	13	11–14	9	9–11
Suplab	10	9–13	13	11–13
Inflab	10	9–13	13	12
TempSp	2	2	2	2
Dorsal	–	35–62	–	40–44
Midbody	–	37–45	51	41–44
4FingLm	–	19–22	21	17–18
4ToeLm	–	23–28	23	24–25

characters are: SnS 6; HeadSTr 11; HeadSLn 14; CanthR 8; Eyelid 11; Suplab 12; Inflab 12; TempSp 2; Dorsal 42; Mid-body 43; 4ToeLm 25. The ranges for each of these characters are given in Table 4.

Distribution. The species has been reported from the northern hilly regions of Pakistan, while the samples from the southern plains represent a hitherto undescribed species (localities 78, 79 in Fig. 1, 2). One of us (DJ) collected samples from the northern mid-elevation, hilly

regions of Pakistan. *Calotes farooqi* **stat. nov.** has not been reported from within the political boundaries of India, although surveys in the hilly regions of north India adjoining Pakistan would be necessary to further comment on the presence of the species in India. Similarly, populations probably resembling *C. farooqi* **stat. nov.** have been reported from parts of Afghanistan (provinces Kabul, Laghman, Nangarhar, Paktia) adjoining Pakistan (Wagner et al. 2016); however, their systematic status needs further morphological and genetic investigation.

Key to the species of *Calotes* allied to *C. versicolor*

- 1a Orientation of the scale rows on the neck and the supra-axillary region lateral, Southeast Asia *C. htunwini*
 1b Orientation of the scale rows on neck and supra-axillary region oblique or vertical 2
 2a Average adult male SVL < 90 mm, supratympanic or temporal spines and crest scales short, average number of mid-dorsal scales ~49, northeast India and Southeast Asia *C. irawadi*
 2b Average adult male SVL > 90 mm, average number of mid-dorsal scales < 49 3
 3a Nuchal and dorsal crest scales long, dorsal crest continues to the base of the tail; supratympanic spines long, slender, southern Peninsular India and east coast, males in breeding season yellowish, trunk and orbital region orange, limbs dark to black, a black patch across the neck *C. versicolor*
 3b Nuchal and dorsal crest scales short, dorsal crest shortens progressively at mid-body; supratympanic spines short 4
 4a Scales between the nasal shield and the orbit large, < 6; Eyelid 9–11; head long, northern hilly regions of Pakistan, males during breeding season grey to black, except the vertebral region and upper head, orbits, inner and outer surface of forelimbs and anterior and venter between the forelimbs dark to black *C. farooqi stat. nov.*
 4b Scales between the nasal shield and the orbit small, > 6; Eyelid 11–14; head short, Peninsular India to the north of 13° latitude, Indian deserts, males during breeding season cream to brown, head and anterior two-thirds of trunk orange *C. vultuosus comb. nov.*

Discussion

Integrated investigations into the south Asian “*Calotes versicolor*” demonstrate that *C. versicolor* is not a widely distributed single species, as was previously considered, but harbours multiple lineages. Molecular phylogenetic analyses revealed the existence of four distinct species distributed across South Asia: (i) *Calotes versicolor sensu stricto*, (ii) *C. irawadi*, (iii) *C. vultuosus comb. nov.* and, (iv) *C. farooqi stat. nov.*, which allowed us to revise its taxonomy. This study also addressed the taxonomic predicaments in revising the nomenclature of the species complex.

Daudin’s illustration of *C. versicolor* as well as the measurements of one of the syntypes presented in the original description (Daudin 1802) suggests that the specimen examined by Daudin was most likely a female or a subadult (based on French inches converted to mm by Amarasinghe et al. (2009)). Further, the diagnosis and the description provided by Daudin was inadequate and was based largely on the characters that vary with age, sex, dominance status, and season. Except for the characters which are bound to sex and life stage, the neotype NCBS AT102 designated by Gowande et al. (2016) is in general agreement with the original description provided by Daudin (1802), and although the neotype designate is of different sex and life stage, the designation still qualifies as per the Article 75.3.5 of the ICZN (1999). The type locality of the species has been a matter of debate since its description. Kuhl (1820) mentioned that Daudin (1802) believed that the species came from Brazil based on the illustration of Seba (1734). Kuhl (1820), in his account of *C. versicolor*, stated that *Agama versicolor* was not from Brazil, as Daudin believed, but from Pondicherry, from where Leschenault sent five specimens to MNHN. Even Kuhl’s description of *Agama tiedemanni* was based on specimens sent to MNHN by Leschenault (*vide* Kuhl 1820). However, Amarasinghe et al. (2009) argued that

Seba’s illustration could be an Amazonian iguanid and Daudin’s (1802) description and illustration correctly refer to the Asian Agamid, *C. versicolor*. We know that Leschenault visited Puducherry only after 1816 (*vide* Amarasinghe et al. 2009), after the species was described. Nonetheless, multiple authors regarded Puducherry as the type locality following Kuhl’s suggestion (e.g. Smith 1935; Zug et al. 2007).

It is impossible to comment with objectivity on where the specimens of *Agama versicolor* were collected from; nevertheless, a review of the herpetofaunal species described by Daudin (from 1801 to 1803) suggests that almost all the species described by him were based on the material collected from along the east coast of India (Coromandel Coast), especially from the localities Tranquebar, Puducherry, Vishakhapatnam, or rarely from Bengal (Uetz et al. 2020). It is, thus, highly likely that the specimens examined by Daudin (1802) came from the French colonies located along the east coast of India. It thus makes sense to retain Puducherry as the type locality of the species, in accordance with the Article 75.3.6 of ICZN (1999). Furthermore, the neotype is currently housed safely in the collections facility at NCBS, with open access to any researcher to examine, thus meeting all the conditions of the Article 75.3 of the ICZN (1999). Chaitanya et al. (2017) tentatively invalidated the designation until “comparative data with the syntype of *C. tiedemanni* (*sic*) are provided, and the designation is in complete accordance with Article 75 (ICZN 2000)”. Unfortunately, the syntype of *A. tiedemanni* is currently untraceable at MNHN, hence making morphological comparison of the neotype with the syntype of *A. tiedemanni* impossible. Furthermore, the morphological and molecular analyses including the neotype and other samples from south India and the adjoining east coast revealed reasonable homogeneity, and thus warrants the retention of *A. tiedemanni* under the synonymy of *C. versicolor*. The description of *A. tiedemanni* by Kuhl (1820) matches closely with that of *C. versicolor*, except for difference that are bound to

sex and life stage. Additionally, the neotype designation by Gowande et al. (2016) is in accordance with the provisions of Article 75 (ICZN 1999), and thus, the neotype designation stands valid, and *A. tiedemanni* is to be retained in the synonymy of *C. versicolor*.

The study led to the revalidation of *C. vultuosus* **comb. nov.**, which represents a lineage genetically and morphologically distinct from *C. versicolor* sensu stricto. *Agama vultuosa* was described based on a specimen brought by Dr R. Coates from Calcutta (now Kolkata), West Bengal, which according to the original description (Harlan 1825), differed from *C. calotes* by the absence of lateral stripes, the difference in the form and shape of the dorsal crest scales, by the spines behind the ears, the form of the eye, the presence of supraciliary ridge and the longitudinal fold of skin beneath the throat. However, the species was not compared morphologically with *C. versicolor* by Harlan (1825). A closer examination of the holotype of *A. vultuosa*, along with the specimens obtained from the Deccan Volcanic Province, the Central Highlands, the Gangetic Plains, and the Indian deserts, which are in agreement with the holotype of *A. vultuosa*, differed from *C. versicolor* sensu stricto in terms of morphology. Similarly, the aforementioned populations formed a clade distinct from *C. versicolor* sensu stricto in the phylogenetic reconstruction.

Thus, we here resurrect the nomen *Agama vultuosa* Harlan, 1825 from its synonymy as *Calotes vultuosus* **comb. nov.** (Harlan, 1825). A related species *A. indica* Hardwicke and Gray, 1827 (type locality Kolkata) was described, from the same locality as *C. vultuosus* **comb. nov.** The species was diagnosed on the basis of its green coloration, dimensions of the scales of the head, body, tail and limbs, two bundles of spines above the ears, and a crest composed of simple, compressed spines that extends only to the middle of the back, and tail that is nearly thrice as long as the body. A majority of these characters, such as the dimensions of scales of the head, body, tail and limbs, and the extension of the dorsal crest, overlap with those of *C. vultuosus* **comb. nov.** Similarly, Harlan's description of *A. vultuosa* precedes that of *A. indica*, and thus, the name *C. vultuosus* **comb. nov.** is prioritized, and *A. indica* is transferred to the synonymy of *C. vultuosus* **comb. nov.** *Calotes vultuosus* **comb. nov.**, the northern Peninsular Indian representative of the complex, was observed to be phenotypically variable during the study, at least in terms of coloration and a select few mensural and meristic characters. For example, the specimen CESL 1041 from the deserts differs from the other examined specimens of the species in certain morphological aspects, such as the length of the head and the size of the dorso-lateral body scales; however, it clusters phylogenetically with members of *C. vultuosus* **comb. nov.**, with very shallow genetic divergence from other examined sequences of the species. Similarly, there is a certain variation in the sexual characters such as the size and the number of nuchal and dorsal crest scales and the extent and the brightness of the orange patch in breeding males. But, as Zug et al. (2007) pointed out, these characters could be ontogenetically variable. Nonetheless, we do not

rule out the possibility that the species recognized in this study could still be split into additional cryptic species with finer sampling, especially from the geographic gaps in this research.

Gray (1846) described another agamid species related to *C. versicolor* from India, *C. viridis*, based on specimens sent to BMNH (now NHM) by Jerdon from Madras (Gray 1846). BMNH currently houses 28 specimens from India (NHM 2021), of which four specimens are from Madras; however none of these specimens were collected by Jerdon. Of the three specimens collected by Jerdon that the museum currently hosts, two were collected from Khasia (Khasi Hills, Assam), whereas the locality of origin of the third specimen could not be determined. Smith (1935) mentioned that the types of *C. viridis* were lost. The specimen sent to Gray by Jerdon from Madras (Gray 1846) most likely originated from the localities Tiruchirappalli, Nilgiris or Nellore, where Jerdon was posted, and which then were a part of the Madras Presidency. Given that we obtained fair homogeneity in the morphology and genetic make-up of samples from the Southern Granulite Terrain (Clade1), and since these populations represent *C. versicolor* sensu stricto, we follow previous authors (Boulenger 1885, Smith 1935, Gowande et al. 2016) in retaining *C. viridis* in the synonymy of *C. versicolor*.

Auffenberg and Rehman (1993) examined numerous specimens of *C. versicolor* sensu lato from Pakistan and India which were deposited across multiple museums in order to revise the taxonomy of *C. versicolor* from Pakistan. The authors assigned a subspecific epithet for the population from the high elevation regions of Pakistan as *C. versicolor nigrigularis* Auffenberg and Rehman, 1993 while restricting the nominate subspecies to Peninsular India. However, it was later realized that *C. v. nigrigularis* was a junior homonym of *C. nigrigularis* (currently *Complicitus nigrigularis* (Ota and Hikida, 1991)). Auffenberg and Rehman (1995) thus proposed a new substitute name, *C. v. farooqi*. Although the holotype is in a mediocre preservation condition, morphological comparisons with the neotype of *C. versicolor* were possible. Our morphological data of the holotype and three other specimens, and the molecular data from near the type locality of *C. v. farooqi* revealed that the subspecies is significantly divergent (Clade4) from *C. versicolor* sensu stricto, and deserves a species level recognition. Therefore, here, we propose to elevate the subspecific status of *C. v. farooqi* to species level as *C. farooqi* **stat. nov.** Amongst the species allied to *C. versicolor*, *C. farooqi* **stat. nov.** is the most distinct in terms of breeding male body coloration, due to the characteristic grey-black colour on the anterior regions of the trunk. Furthermore, our results show the existence of another divergent lineage affiliated to *C. farooqi* from the southern, mid to low elevation regions of Pakistan which needs further attention and taxonomic investigation. So, tentatively we assign *C. farooqi* **stat. nov.** to the north Pakistani and, most probably, Afghan populations, with Mansehra as the type locality of this species.

Results from molecular phylogenetic analyses revealed that the sequences generated from Southeast Asia,

including those from northeast India, Myanmar, Vietnam, Cambodia and far eastern China fell into the *C. irawadi* clade (Clade2). We tentatively assign the Southeast Asian populations morphologically resembling *C. versicolor* in terms of the obliquely posteriorad or vertical orientation of the neck and the supra-axillary area to *C. irawadi*, pending further investigation, and suggest that records from Southeast Asia labelled as *C. versicolor* should be treated with caution. The within clade *p*-distance for this clade was high, the greatest recorded being 2.4% at 16S and 4.5% at COI (Table 2), indicating that *C. irawadi* from Southeast Asia is itself a species complex. This is also apparent from Zug et al. (2007) and the recently published Tantrawatpan et al. (2021), and projects similar to this one, Zug et al. (2007) and Tantrawatpan et al. (2021) should be implemented in areas of Southeast Asia outside the central dry province of Myanmar. This is also true to a lesser extent of the other species of the *C. versicolor* complex recognized in this study, such as *C. farooqi* **stat. nov.**, and *C. vultuosus* **comb. nov.**, since these species too showed considerable levels of genetic variability. Although Tantrawatpan et al. (2021) regard their specimens as *C. versicolor*, these most likely represent *C. irawadi*.

The *p*-distances between the species recognized in this study ranged between 2.7% (between *C. versicolor* and *C. irawadi*; and *C. vultuosus* **comb. nov.** and *C. irawadi*) and 6.0% (between *C. farooqi* **stat. nov.** and *C. irawadi*) at 16S, and between 12.6% (between *C. versicolor* and *C. irawadi*) and 20.4% (between *C. calotes* and *C. farooqi* **stat. nov.**) at COI. Comparable genetic divergences were observed in the other, previously defined species, such as those in the genus *Monilesaurus*, between the species pair *C. grandisquamis*-*C. nemoricola* (*p*-distance 3.7%–5.1%), and species of the *C. mystaceus* complex (Wagner et al. 2021).

The ML tree analysed using additional representatives of the subfamily Draconinae based on the 16S dataset revealed the tentative positions of the species of the *C. versicolor* species complex (Fig. 3). *Calotes farooqi* **stat. nov.** was recovered as sister to *C. calotes*, whereas *C. versicolor* was sister to this (*C. farooqi* **stat. nov.** + *C. calotes*) clade. Further, *C. irawadi* was recovered as the phylogenetic sister of the (*C. farooqi* **stat. nov.** + *C. calotes* + *C. versicolor*) clade, while *C. vultuosus* **comb. nov.** was obtained as sister to the clade containing (*C. farooqi* **stat. nov.** + *C. calotes* + *C. versicolor* + *C. irawadi*). However, we maintain some restraint while commenting on the phylogenetic positions of the species, given that the tree was analysed using ~416 bp sequence of the 16S gene, and the Burmese species *C. htunwini* is missing from the analyses. The phylogenetic relationships obtained using this larger matrix, including numerous species of the subfamily Draconinae, are different from the relationships obtained in the trees analysed using the sequences of the species of the *C. versicolor* complex alone, which included all the sequences generated in this study (Figs 2–3). Hence, we suggest that the addition of other nuclear and mitochondrial markers to the dataset would be necessary to infer their phylogenetic relationships with confidence.

With the recognition of *C. farooqi* **stat. nov.** and *C. vultuosus* **comb. nov.**, the genus *Calotes* now includes 30 species (Uetz et al. 2020), including *C. minor*, *C. paulus*, *C. zolaiking*, the recently described members of the *C. mystaceus* species complex (Wagner et al. 2021), and the ambiguous species *C. bhutanensis*. Of these, five species are currently derived from the *C. versicolor* complex, namely, *C. farooqi* **stat. nov.**, *C. htunwini*, *C. irawadi*, *C. versicolor* and *C. vultuosus* **comb. nov.** Almost all the species of the genus *Calotes* appeared to occupy relatively narrow distribution ranges (Hallermann 2000). This study shows that *C. versicolor* occupies a smaller geographic area than earlier believed, and is tentatively found to be confined to southern Peninsular India and the east coast of India till Bhubaneswar. This is a significant reduction in the distribution range of *C. versicolor*. Photographic data hints towards the presence of the *C. versicolor* and *C. cf. vultuosus* **comb. nov.** in Sri Lanka (A.A. Thasun Amarasinghe pers. comm.); however, that remains to be confirmed based on an integrative taxonomic study. Similarly, our analyses confirm that *C. versicolor* *sensu stricto* has been introduced to Maldives, similar to other lizards of this archipelago (Agarwal et al. 2019b) and could have been introduced to other parts of the world as well. *Calotes htunwini* and *C. irawadi* are the Southeast Asian representatives, with *C. irawadi* being reported from northeast Indian localities in Assam (Das et al. 2009) and Tripura (Anonymous 2020), and more recently from Western Yunnan in China (Liu et al. 2021). *Calotes vultuosus* **comb. nov.**, on the other hand, appears to be distributed in the deserts of India, the Gangetic Plains, the Central Highlands, northern Peninsular India, as well as the Northern and parts of the Central Western Ghats, the Eastern Ghats and the intervening dry plateau. The distribution of the species of the *C. versicolor* complex in Peninsular India resembles that of the species of *Sitana* Cuvier, 1829, in that the distribution of *C. versicolor* resembles that of the members of the *S. ponticeriana* clade of Deepak and Karanth (2018), whereas *C. vultuosus* **comb. nov.** appears to be distributed in a fashion similar to the species of the *S. spinaecephalus* clade (Deepak and Karanth 2018).

This study provides further evidence to support the hypothesis that many widely distributed species represent species complexes (Agarwal et al. 2011, 2019a; Priti et al. 2016; Mirza et al. 2017, 2018, Wagner et al. 2021), warranting urgent taxonomic revision. Such taxonomic studies are important for the thorough documentation of biodiversity on the planet. Another significant outcome of the study is that it focuses on the relatively frequently occurring, commonly encountered species of lizards. The *C. versicolor* complex has often been largely overlooked and has been treated as a non-charismatic member of the genus. As Zug et al. (2007) point out, in addition to multiple species described from India getting synonymized with *C. versicolor*, taxonomists' attitude of labelling a specimen in hand as *C. versicolor* without detailed examination of the specimen, irrespective of the biogeographic location at which the specimen was encountered, had left the species with a very large geographic range. This pri-

marily stems from the assumption that *C. versicolor* is a widely distributed reptilian species. We suggest that the practice of labelling specimens of apparently widely distributed species as the nominate form must be curtailed. Further, we also suggest that projects focusing on the systematics of widely distributed species must be promoted as these may harbor many cryptic species. This is a modest effort at the resolution of *C. versicolor* complex, and there were many geographic regions which could not be adequately sampled, including parts of western and central Asia, Indochina and other regions of Southeast Asia, as well as localities such as USA, Oman, Mauritius and others where the species has been introduced. With the availability of the molecular and morphological data presented here and in Zug et al. (2007), we urge taxonomists in these regions to ascertain the status of the respective populations of *C. versicolor*.

Conclusion

An integrated molecular-morphological investigation demonstrates that *C. versicolor* on the Indian subcontinent is composed of multiple lineages. It is not as widely distributed as was earlier believed, but occurs in southern India and on the east coast, with the possibility of its occurrence on the island of Sri Lanka. The study led to the revalidation of the species *C. vultuosus* **comb. nov.**, a species potentially endemic to the Deccan Volcanic Province, Central Highlands, arid and semi-arid regions of India and Gangetic Plains, which was under the synonymy of *C. versicolor*; and the promotion of the subspecies *C. versicolor farooqi* from Pakistan to species rank, as *C. farooqi* **stat. nov.** We further confirm the presence of *C. cf. irawadi* in northeast India. The taxonomic status of the populations introduced to Maldives was also resolved. Our results lend further support to the argument that many widely distributed species represent species complexes, demanding urgent taxonomic attention.

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Supplementary material 1

Table S1

Authors: Gowande G, Pal S, Jablonski D, Masroor R, Phansalkar PU, Dsouza P, Jayarajan A, Shanker K (2021)

Data type: .csv

Explanation note: The table represents localities from where the samples were included for molecular and morphological comparisons, and the GenBank accession numbers of the sequences used in the analysis. Also includes accession numbers of the sequences used in the larger Draconinae 16S tree.

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