Bonn zoological Bulletin 70 (1): 141–171
2021 · Wagner P. et al.
https://doi.org/10.20363/BZB-2021.70.1.141

ISSN 2190–7307
http://www.zoologicalbulletin.de

Research article
urn:lsid:zoobank.org:pub:4E7B4E14-7682-465D-A2D9-A26EA04AB3FD

Integrative approach to resolve the *Calotes mystaceus* Duméril & Bibron, 1837 species complex (Squamata: Agamidae)

Philipp Wagner[1, *], Flora Ihlow[2], Timo Hartmann[3], Morris Flecks[4], Andreas Schmitz[5] & Wolfgang Böhme[6]

[1] *Allwetterzoo Münster, Sentruper Straße 315, D-48161 Münster, Germany*
[1] *Department of Biology and Center for Biodiversity and Ecosystem Stewardship, Villanova University, 800 Lancaster Avenue, Villanova, Pennsylvania 19085, USA*
[2] *Museum of Zoology Senckenberg, Dresden, Königsbrücker Landstraße 159, D-01109 Dresden, Germany*
[3, 4, 6] *Zoologisches Forschungsmuseum Alexander Koenig, Adenauerallee 160, D-53113 Bonn, Germany*
[5] *Natural History Museum of Geneva, UREC-Herpetology & Ichthyology, Route de Malagnou 1, CH-1208 Genève, Switzerland*

[*] *Corresponding author: Email: wagner@allwetterzoo.de*

[1] urn:lsid:zoobank.org:author:0575CE45-AB5C-4493-A8AD-DD399E18284A
[2] urn:lsid:zoobank.org:author:10DB565B-DA19-484E-AE50-ED29945658E8
[3] urn:lsid:zoobank.org:author:A911B13A-B364-424E-8579-AE23820F1DC1
[4] urn:lsid:zoobank.org:author:974BF839-926B-4039-9617-135F5CEC2596
[5] urn:lsid:zoobank.org:author:5B1146D2-B9A6-48E6-9E4E-EB1C8ED1AE7A
[6] urn:lsid:zoobank.org:author:FFAC2972-9F52-404B-BA9C-489C7793FF8D

Abstract. The genus *Calotes* Cuvier, 1816 "1817" currently contains 25 species, which are widely distributed in Asia and have been introduced in Africa and America. The genus includes several species complexes, for example, *Calotes versicolor* and *Calotes mystaceus*. The latter was partly resolved by describing *Calotes bachae* as a distinct species, but it became obvious that *C. mystaceus* still consists of several lineages. This study was done to resolve those lineages and we herein restrict *Calotes mystaceus* to southern coastal Myanmar, while describing three new species occurring in Cambodia, China, Laos, Myanmar, Thailand, and India. The new species are distinguishable from each other by male coloration with *C. goetzi* sp. n. having prominent dark brown dorsolateral blotches, *C. geissleri* sp. n. having orange to light brown blotches and a whitish stripe from snout-tip to hind limb insertion and *C. vindumbarbatus* sp. n. having a whitish stripe from tip of snout continuing to beyond limb insertion. Mean uncorrected p-distances for COI between *C. mystaceus* and other taxa are: *C. goetzi* sp. n. (=0.0603); *C. vindumbarbatus* sp. n. (=0.0656) and *C. bachae* (=0.1415). Mean uncorrected p-distances for 12S between *C. mystaceus* and other taxa are: *C. goetzi* sp. n. (=0.0291), *C. vindumbarbatus* sp. n. (=0.0375), *C. bachae* (=0.0548) and *C. geissleri* sp. n. (=0.0457).

Key words. *Calotes bachae*, *Calotes goetzi* sp. n., *Calotes geissleri* sp. n., *Calotes vindumbarbatus* sp. n., Indochina.

INTRODUCTION

To date, 25 species of the genus *Calotes* Cuvier, 1816 "1817" (=journal issued in 1816, but published in 1817) (Squamata: Agamidae: Draconinae) are recognized (Uetz et al. 2020). They are mainly distributed across continental Asia, but also occur on, for example, Sri Lanka, Sumatra, and the Moluccas. With the exception of *C. versicolor* (Daudin, 1802) and *C. mystaceus* Duméril & Bibron, 1837, species of this genus occupy small geographic ranges in India, Sri Lanka, and Myanmar (Hallermann 2000), while *Calotes versicolor* in particular has been introduced on several Asian islands (e.g., Sulawesi and Borneo). Indochina, the focal area of this study, harbors eight *Calotes* species: *C. bachae* Hartmann, Geissler, Poyarkov, Ihlow, Galoyan, Rödder & Böhme, 2013; *C. chincollium* Vindum, 2003; *C. emma* Gray, 1845; *C. htunwini* Zug & Vindum in Zug et al., 2006; *C. irawadi* Zug, Brown, Schulte & Vindum, 2006; *C. jerdoni* Günther, 1870; and the widespread species *C. mystaceus* and *C. versicolor*. *Calotes rouxii* Duméril & Bibron, 1837 and *C. ophiomachus* Duméril & Bibron, 1837, previously mentioned in early faunal publications (Morice 1875; Tirant 1885; Bourret 1927) to occur in Southeast Asia, are based on misidentifications or synonyms. The latter is today recognized as synonym of *C. calotes*, whereas *C. rouxii* was transferred to the recently described genus *Monilesaurus* (Pal et al. 2018), which is restricted to the Indian subcontinent.

Despite the widespread distribution of the genus, no complete review has been done, but several publications demonstrate that some taxa represent species complexes (e.g., Zug et al. 2006; Hartmann et al. 2013). One of these is the spectacularly colored Blue Forest Lizard

Received: 20.01.2021
Accepted: 15.04.2021
Corresponding editor: A. Bauer
Published: 07.05.2021

Calotes mystaceus Duméril & Bibron, 1837. Originally described from "Pays de Birmans" (=Myanmar), the putative range of *C. mystaceus* extends from China (e.g., Bain & Hurley 2011) through Southeast Asia (e.g., Cambodia: Hartmann et al. 2013, Laos & Myanmar: Das 2015; Thailand: Chan-Ard et al. 2015; to India e.g., Das 2015; see also Figure 1). Previous records from Vietnam (e.g., Pham et al. 2018) refer to the recently described *C. bachae.* A record from Sri Lanka by Flower (1899) was not confirmed by Somaweera & Somaweera (2009) and reports from peninsular Malaysia (Das 2015) and the Andaman and Nicobar Islands (Chan-Ard et al. 2015) lack references to specific records and are likely also based on misidentifications. According to Enge & Krysko (2004), *C. mystaceus* is introduced in Florida, USA.

Previous studies (e.g., Hartmann et al. 2013; Saijuntha et al. 2017) revealed high levels of morphological and genetic differentiations within *C. mystaceus*. Furthermore, geographic variation of the color pattern of different populations was recognized from both sides of the Mekong (e.g., Smith 1921; Bourret 2009), which was later resolved by the description of *Calotes bachae* (Hartmann et al. 2013). Therefore, the aim of this study is a range wide analysis of the morphological variance and genetic relationships of *C. mystaceus* s. str. and *C. bachae*, to implement respective taxonomic results and discuss potential geographic barriers.

MATERIAL AND METHODS

Institutional abbreviations

The specimens used in this study (see Appendix I) have been obtained from the following collections:

- BMNH = (now NHM) Natural History Museum, London, UK
- CAS = California Academy of Sciences, San Francisco, CA, USA
- MNHN = Muséum national d'Histoire naturelle, Paris, France
- NME = Naturkundemuseum Erfurt, Erfurt, Germany
- ZFMK = Zoologisches Forschungsmuseum Alexander Koenig, Bonn, Germany
- ZMB = Museum für Naturkunde, Berlin, Germany
- ZMMU = Zoological Museum, Moscow State University, Moscow, Russia

Genetic analysis

Fragments of the two mitochondrial genes 12S rRNA and COI were sequenced to assess genetic differentiation and to determine phylogenetic relationships between different populations of *Calotes mystaceus*. Samples of thigh muscle tissue were extracted from 54 ethanol-preserved museum collection specimens. DNA was extracted using the peqGold tissue DNA mini kit (peqLab). The primers 12sL1091 (light chain; 5′–AAACTGGGATTAGATACCCCACTAT—3′) and 12sH1478 (heavy chain; 5′–AAACTGGGATTAGATACCCCACTAT—3′) of Kocher et al. (1989) as well as COIVF1d (light chain; 5′–TTCTCAACCAACCACAARGAYATYGG—3′) and COIVR1d (heavy chain; 5′– TAGACTTCTGGGTGGCCRAARAAYCA—3′) of Nazarov et al. (2012) were used for amplification of 388 bp of 12S rRNA and 600 bp of COI, respectively. PCR cycling conditions follow Schmitz et al. (2005) and Nazarov et al. (2012). PCR products were purified using the QIAquick PCR purification kit (Qiagen) and sequenced by an external vendor (Macrogen). Sequences were checked using the original electropherograms in PhyDE (http://www.phyde.de). The dataset was supplemented with sequences from previous studies (Hartmann et al. 2013; Saijuntha et al. 2017), resulting in a total of 63 sequences (see Table 1 for sampled taxa and GenBank accession numbers). We included only three sequences from Saijuntha et al. (2017), carefully chosen to best represent each of the three lineages of *C. mystaceus* detected by their study, since including all sequences showed no alteration in topology, but resulted in drawbacks concerning the overall support statistics of trees during preliminary analyses. Sequences were aligned with MAFFT (Katoh et al. 2009), refined using the MUSCLE algorithm (Edgar 2004), and manually corrected where necessary. To account for the phylogenetic information of indels, gaps were coded using the 'simple method' of Simmons & Ochoterena (2000) as implemented in FastGap 1.2 (Borchsenius 2009). Both gene fragments were analyzed separately as well as using a concatenated data set for phylogenetic reconstruction by Bayesian inference (BI). Model parameters were estimated separately for each gene and codon position by partitioning the data set. Models of nucleotide substitution (GTR+G+I for 12S rRNA; K80+I for the 1st, HKY for the 2nd, and GTR+G for the 3rd codon position of COI) were chosen by the Akaike information criterion (AIC) using Modeltest (Posada & Crandall 1998) as implemented in the package 'phangorn' (Schliep 2011) for Cran R (R Core Team 2020). Bayesian trees were calculated with MrBayes 3.2.6 (Ronquist et al. 2012) with four independent runs (10 million generations each, sampled every 1000, random starting tree). Runs were stopped when the average standard deviation of split frequencies had reached 0.01. Convergence of the Markov chains was checked with Tracer v1.7.1 (Rambaut et al. 2018) and the initial 25% of generations were discarded prior to building a consensus tree.

Morphological comparison

A total of 109 specimens belonging to the *Calotes mystaceus* complex (including *Calotes bachae*) were examined (see Appendix I). Measurements were taken to the nearest 0.1 mm using digital calipers. Twenty-three mensural and eleven meristic characters were obtained according to Hartmann et al. (2013; Table 2). Specimens were grouped according to the genetically resolved operational taxonomic units (OTUs). Juveniles were defined as specimens with a snout-vent length (SVL) less than 50% of the SVL of the largest specimen of the same OTU and excluded from the statistical analyses. Analyses of (co-)variance (AN(C)OVA) were performed to identify morphological characters that show significant differences between the OTUs. OTU and sex were considered as factors for the two-way ANOVA and SVL was added as covariate for the two-way ANCOVA. Due to sexual dimorphism, males and females were analyzed separately. All metric data were log-transformed to assure normal distribution. Regression residuals were calculated on the morphometric variables using SVL as a covariable to account for allometry, i.e., to avoid size dependent intercorrelation effects, prior to conducting a principal component analysis (PCA) to assess the overall morphological variation between the putative taxa without making a priori assumptions about groupings. PCAs were computed using the 'ade4'package (Dray & Dufour 2007) for Cran R retaining only principal components (PCs) with an eigenvalue > 1. Outliers in the PCs were identified using Mahalanobis distances and removed from the analyses. As previous authors demonstrated that coloration is an important character to distinguish distinct evolutionary lineages in agamid lizards (see, e.g., Stuart-Fox & Ord 2004; Chen et al. 2012; Quah et al. 2012; Wagner 2014) we also compared coloration patterns of the genetically distinct lineages.

RESULTS

The phylogenetic analysis of the concatenated 12s rRNA and COI gene fragments (Fig. 2) reveals differentiation within the *Calotes mystaceus* complex, including *C. bachae*. Based on the type locality ("Pays de Birmans"), *Calotes mystaceus* s. str. is referable to Clade D, the sister to Clade A. This latter includes two lineages (A1 and A2) from Central Indochina. Clades A and D together form the sister to Clade C which includes specimens from northern Myanmar. Basal to these clades is one lineage including the sister Clades B and E. The latter includes the holotype of *Calotes bachae*, while Clade B includes specimens from western Myanmar. According to our analysis the valid species *Calotes mystaceus* s. str. (Clade D) and *Calotes bachae* (Clade E) are clearly not sister lineages as *C. bachae*, along with specimens of Clade B, constitutes a distinct lineage to the clade that contains *C. mystaceus* s. str. *Calotes bachae* (Clade E) shows geographic variation between specimens from Cambodia and Vietnam and one distinct specimen from Vietnam without precise locality. Clade A shows a differentiation (Clade A1 and A2) roughly along the border between Thailand and Myanmar. None of the other clades show geographic separation.

Mean uncorrected p-distances between species for COI and 12s rRNA are shown in table 3.

A PCA (Figs 3–4, Table 4, Appendix II–III) computed for all morphological characters of males grouped according to genetic OTUs revealed that morphospaces of the distinct genetic lineages overlap. However, Clade C is only partly overlapping with Clades B and E, whereas Clades B, D and E are largely overlapping with Clade A. The currently valid taxa *Calotes bachae* (Clade E) and *C. mystaceus* (Clade D) also overlap in their morphospaces. In females, most of the morphospaces are overlapping as well, except for one specimen of Clades B and C, respectively, and the two specimens representing Clade D (Figs 3–4, Table 4, Appendix II). Females of Clade E are almost completely embedded in the morphospace of Clade A. None of the examined morphological characters was significantly different between OTUs in the ANOVA and only two characters ("Head width" and "Interorbital width") showed differences in the ANCOVA (Table 5, Appendix II). According to these results, the valid species *C. mystaceus* and *C. bachae* as well as the unnamed lineages within the complex are supported by our genetic data. However, despite the non-discriminatory results of the AN(C)OVA, the clades are clearly identifiable and have diagnosable characters. Differences in coloration support the genetic data and distinguish the lineages from one another. Neither the valid species nor the cryptic lineages as groups are monophyletic. Therefore, this complex of lineages, including the above-mentioned taxa is herein revised and the genetically supported clades are described as new species according to their diagnostic morphological characters.

Taxonomic Revision of the *Calotes mystaceus* species complex

Calotes bachae Hartmann, Geissler, Poyarkov, Ihlow, Galoyan, Rödder & Böhme 2013: 252
(Fig. 2, Clade E)

Hartmann, T., Geissler, P., Poyarkov, N. A. J., Ihlow, F., Galoyan, E. A., Rödder, D. & W. Böhme (2013). A new species of the genus *Calotes* Cuvier, 1817 (Squamata: Agamidae) from southern Vietnam. Zootaxa 3599 (3): 246–260.

Holotype. ZFMK 88935 (adult male, Fig. 5A-B, Clade E) from "Vietnam, Dong Nai Province, Cat Tien National Park (11.6344444° N 107.456667° E), 104 m elevation," collected by Peter Geißler on May 10th 2009.

Original Diagnosis. A medium-sized *Calotes* with a maximum SVL of 97 mm. It can be distinguished from all taxa of the *C. mystaceus* complex by the combination of the following characters: 1) head and body robust; 2) body scales homogeneous, relatively small, feebly keeled and arranged in regular rows;

Table 1. Specimens included in the phylogenetic analyses and respective GenBank accession numbers.

					GenBank Accession		
Species	**Voucher/Sample ID**	**Type**	**Country**	**Locality**	**12s rRNA**	**COI**	**Reference**
Calotes bachae	ZFMK 94395		Cambodia	Ratanakiri Province: Banlung	MW817233	MW817626	This study
	ZFMK 94396			Ratanakiri Province: Banlung	MW817234	MW817627	This study
	ZFMK 94397			Ratanakiri Province: Banlung	MW817235	MW817628	This study
	ZFMK 96231		Vietnam	[no precise locality]	MW817236		This study
	ZMMU NAP00301			Binh Phuoc Province: Bu Gia Map National Park: Phuoc Hoa		HM425545	Hartmann et al. 2013
	ZFMK 92028			Cao Bang Province: Trung Khanh	MW817232	MW817625	This study
	IEBR A.2012.23	paratype		Dong Nai Province: Cat Tien National Park		KC016062	Hartmann et al. 2013
	ZFMK 88935	holotype		Dong Nai Province: Cat Tien National Park	MW817231	KC016061	This study
C. geissleri sp. n.	ZFMK 97991	paratype	Myanmar	Chin State: Falam District: Simggial village	MW817238		This study
	CAS 243332			Chin State: Falam District: Tonzang Township: Natzang village	MW817213		This study
	CAS 243028	paratype		Magway Division: Gangaw District: Gangaw Township: Mauk village	MW817211		This study
	CAS 243050	paratype		Magway Division: Gangaw District: Gangaw Township: Mauk village	MW817212		This study
	CAS 210270	paratype		Sagaing Division: Alaungdaw Kathapa National Park: Log Cabin Camp	MW817187		This study
	CAS 215539	holotype		Sagaing Division: Alaungdaw Kathapa National Park: Thabake Sae Camp	MW817189		This study
C. goetzi sp. n.	ZFMK 90413		Cambodia	Preah Vihear Province: Kulen Promtep Wildlife Sanctuary		KC016060	Hartmann et al. 2013
	ZFMK 88341			Siem Reap Province: Phnom Kulen National Park: Kbal Spean		KC016063	Hartmann et al. 2013
	CAS 242463		China	Yunnan: Baoshan: Longling: Longling-Liuku road S of Baihualing turnoff	MW817210	MW817616	This study
	CAS 242457			Yunnan: Baoshan: Longyang	MW817209	MW817615	This study
	CAS 242455			Yunnan: Baoshan: Longyang	MW817208	MW817614	This study
	CAS 228144			Yunnan: Nujiang: 18 km S of Liuku bridge on Liuku-Longling road	MW817191	MW817597	This study
	CAS 228143			Yunnan: Nujiang: 13 km N of Liuku bridge on Liuku-Fugong road	MW817190	MW817596	This study
	CAS 207489			Yunnan: Nujiang: Nujiang (= Salween River) just downriver of Liuku	MW817186	MW817594	This study
	ZFMK 49243		Laos	Sainyabuli Province: Muang Pak Lay	MW817228		This study
	ZFMK 47080			Vientiane Province: Muang Phon Hong	MW817226		This study
	CAS 204849		Myanmar	Mandalay Division: 96 km S of Mandalay on Mandalay-Yangon road	MW817184	MW817592	This study
	CAS 231404			Mandalay Division: Myin Gyan District: Nwa Htoe Gyi Township: Minsontaung Wildlife Sanctuary: Pan Taw Yoe Dam	MW817195	MW817601	This study

Table 1. (continued)

Species	Voucher/Sample ID	Type	Country	Locality	12s rRNA	COI	Reference
	CAS 231231			Mandalay Division: Nyaung U District: Kyaukpadaung Township: Popa Mountain Park: Le Gwa village	MW817194	MW817600	This study
	ZFMK 45498			Mon State: Mawlamyine: Mudon	MW817224		This study
	ZFMK 45499			Mon State: Mawlamyine: Mudon	MW817225		This study
	CAS 235883			Shan State: Kyaitong Township: between Mine Wa and Panhope village	MW817201	MW817607	This study
	CAS 235517			Shan State: Kyaitong Township: Kyaiphaung to Win Bo village	MW817200	MW817606	This study
	CAS 241577			Shan State: Inle Lake Wetland Sanctuary: Maing Thouk Village	MW817207	MW817613	This study
	CAS 235469			Shan State: Tachileik Township: Parsar Wildlife Sanctuary: near Mine Phone Monastery	MW817199	MW817605	This study
	CAS 230654			Shan State: Inle Lake Wetland Sanctuary: Maing Thouk Village village	MW817193	MW817599	This study
	CAS 230624			Shan State: Ywangan Ngan Township: Panlaung and Padalin Cave Wildlife Sanctuaryy: Ma Au Bin Camp to Kinta Dam	MW817192	MW817598	This study
	NME R 0584/09a		Thailand	Chiang Mai	MW817216	MW817618	This study
	NME R 0584/09j			Chiang Mai	MW817217	MW817619	This study
	CMf1			Chiang Mai: Fang		KX388084	Saijuntha et al. 2017
	CNb1			Chon Buri: Ban Bueng		KX388061	Saijuntha et al. 2017
	ZFMK 84867			Kanchanaburi: Kwai River bridge	MW817230	MW817624	This study
	ZFMK 49164			Lopburi: Dilang	MW817227		This study
	NME R 0581/09			Nakhon Ratchasima	MW817215	MW817617	This study
	NME R 0785/13			Nakhon Ratchasima	MW817220	MW817621	This study
	ZFMK 55610			Nan Province	MW817229	MW817623	This study
	PTk1			Pathum Thani: Khlong Luang		KX388066	Saijuntha et al. 2017
	NME R 0751/12			Sakon Nakhon	MW817219	MW817620	This study
	NME R 0786/13			Sakon Nakhon	MW817221	MW817622	This study
	ZFMK 40561			Ubon Ratchathani: Phibun: Lam Dom Noi River	MW817222		This study
C. mystaceus	CAS 239398		Myanmar	Ayeyarwady Division: Pathein District: Ngapudaw Township: between Htan-thabin village and Youngyin forest camp	MW817204	MW817610	This study
	CAS 239276			Ayeyarwady Division: Pathein District: Ngapudaw Township: Ngayokekaung village	MW817203	MW817609	This study
	CAS 240287			Mon State: Kyaikhto Township: along the trail Kinmon to Kyaiktiyo Pagoda	MW817205	MW817611	This study

3) 44–50 midbody scale rows; 4) upper dorsolateral scales pointing backwards and upwards; 5) two short and well separated spines, surrounded by three to four scales on either side of the upper head above the tympanum; 6) nuchal and dorsal crest continuous, composed of erected compressed scales, directed posteriorly; 7) vertebral spines and scales in males 35–42 and in females 43–46; 8) oblique fold of skin in front of fore limb insertion distinct, covered with small granular dark scales; 9) extremities and tail relatively long and slender (see comparison with *C. mystaceus* for details); 10) bluish to turquoise head and anterior body part, this coloration not well exceeding front limb insertion; 11) yellowish light stripe at upper lip reaching from below anterior corner of eye to posterior end of head; 12) no dorsolateral brownish blotches, sometimes faint medial brownish blotches across the vertebral crest.

Male coloration. The brilliant coloration of adult males is characterized by a brightly colored bluish to turquoise head, with bluish coloration continuing posteriorly to fore limb insertion. There is a relatively faded light (bright yellowish, when under acute distress, a character typical for *C. bachae* only) stripe at the upper lip crossing the tympanum from beneath the eye to end of head. Gular pouch colored in darker blue, interscale skin black. A triangular to crescent-shaped patch of small black scales is present in front of shoulder. Very faint brownish blotches extending mid-dorsally over the vertebral crest, from above fore limb insertion on to tail; posterior to fore limb insertion brownish orange in color on trunk and tail; hind limb in a slightly darker brown; venter cream.

Distribution. *Calotes bachae* is known from southern Vietnam, with two specimens reported from the Vietnam-China border in northern Vietnam, and from eastern Cambodia (Fig. 1).

Ecology. *Calotes bachae* is a diurnal, semi-arboreal lizard, often observed climbing on tree trunks at a height of 5–10 meters above the ground. The species mainly inhabits dipterocarp lowland forests and cultural landscapes up to 700 m a.s.l. The species seems to be quite heliophilic, preferring more open habitats without closed canopies (Hartmann et al. 2013), but was also observed in dense tropical monsoon forests with closed canopy, in open gallery forest, and anthropogenic habitats like roadsides within the forest or open park landscapes within the headquarters of the park. In these anthropogenic habitats *C. bachae* occurs in syntopy with *Calotes versicolor* (Hartmann et al. 2013). According to Hartmann et al. (2013) *C. bachae* feeds on numerous arthropods including Formicidae, Coleoptera, Orthoptera, and Myriapoda. Males acquire their breeding coloration at the end of February, while gravid females have been found mid-April and egg-laying of a clutch of five eggs was observed in April and May. Juveniles hatched after 56 days while incubated at 22 to 25° C in captivity.

Table 1. (continued)

Species	Voucher/Sample ID	Type	Country	Locality	12s rRNA	COI	Reference
	CAS 240296			Mon State: Kyaikhto Township: along the trail Kinmon to Kyaiktiyo Pagoda	MW817206	MW817612	This study
	CAS 213300			Yangon Division: Hlawga National Park: Mingalardon Township	MW817188	MW817595	This study
	CAS 206548			Yangon Region: Letpein village	MW817185	MW817593	This study
C. vindumbarbatus sp. n.	CAS 232387	paratype	Myanmar	Kachin State: Myitkyina: Gat Shang Yang village	MW817197	MW817603	This study
	CAS 232388	holotype		Kachin State: Myitkyina: Gat Shang Yang village	MW817198	MW817604	This study
	ZFMK 97990	paratype		Kachin State: Myitkyina: Gat Shang Yang village	MW817237	MW817629	This study
	CAS 239206	paratype		Sagaing Division: Hkanti District: Hkanti Township: Linpha village	MW817202	MW817608	This study
	CAS 232247	paratype		Sagaing Division: Homalin Township: N of Swekawngaw	MW817196	MW817602	This study
C. emma	NME R 0590/09		Laos	Phongsali	MW817218		This study
	NME R 0577/09		Thailand	Chiang Mai	MW817214		This study
	ZFMK 44016			Surat Thani	MW817223		This study
C. versicolor	-		-	-	AB183287	AB183287	Amer & Kumazawa 2007

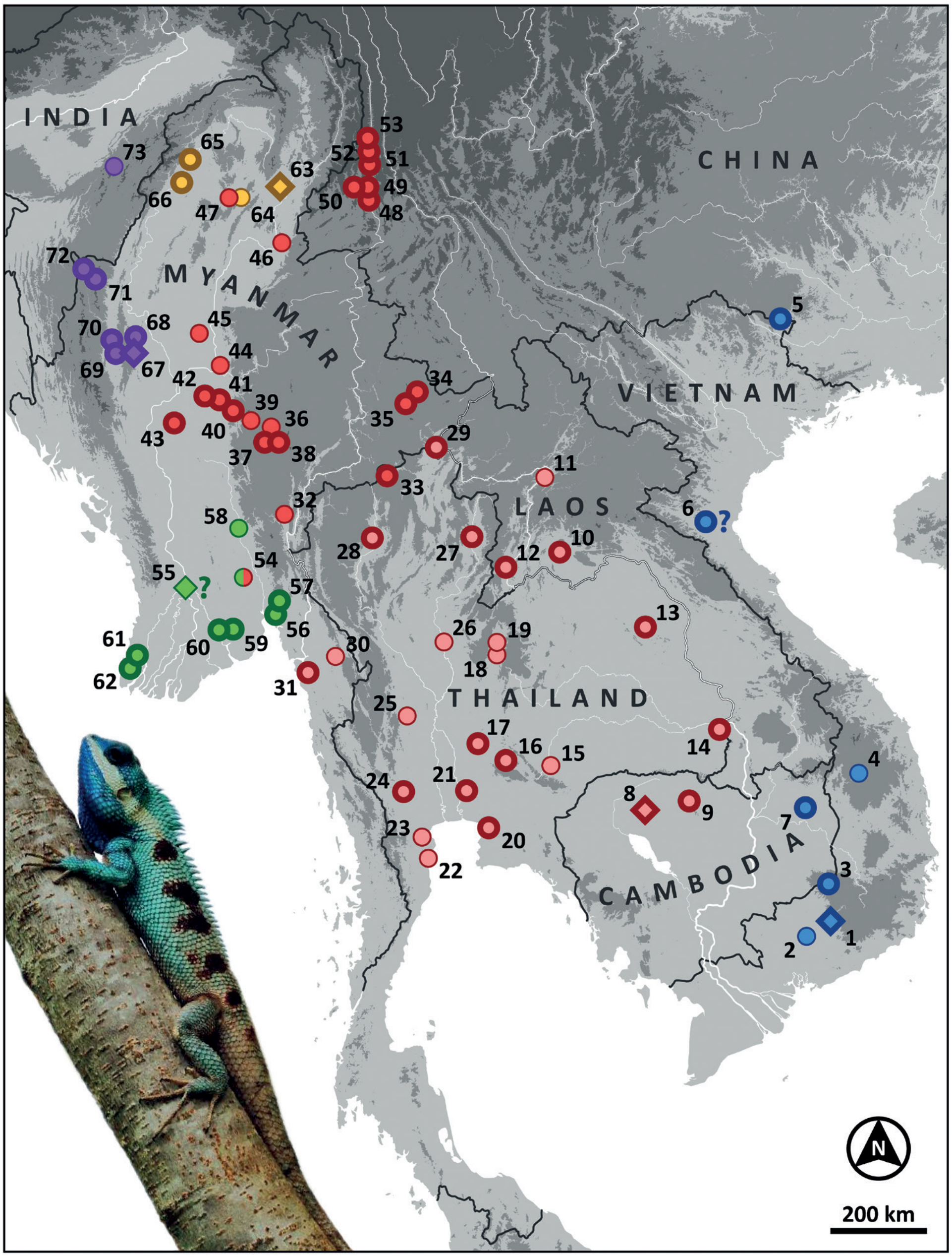


Fig. 1. Geographic distribution of examined specimens of the *Calotes mystaceus* complex. Colors correspond to the identified OTUs. Diamonds mark the type localities of the species described herein. Records with a bold margin were also included in the phylogenetic analyses. Imprecise (i.e., country-level) records are marked with a question mark. Detailed localities are: ***Calotes bachae***: Vietnam: Dong Nai Prov.: Cat Tien National Park (**1**); Dong Nai Nature Reserve (**2**); Bu Gia Map National Park (**3**); Kon Tum (**4**); Trung Khanh (**5**); Cambodia: Banlung (**7**); ***Calotes goetzi* sp. n.**: Cambodia: Phnom Kulen National Park (**8**); Kulen Promtep Wildlife Sanctuary (**9**); Laos: Muang Phon Hong (**10**); Luang Prabang (**11**); Muang Pak Lay (**12**); Thailand: Sakon Nakhon Prov. (**13**); Lam Dom Noi River (**14**); Khon Buri (**15**); Nakhon Ratchasima (**16**); Dilang (**17**); Ban Nam Len (**18**); Lom Sak (**19**); Ban Bueng (**20**); Khlong Luang (**21**); Cha-am (**22**); Ban Phai (**23**); Kwai River bridge (**24**); Ban Dong Noi (**25**); Phitsanulok Prov. (**26**); Nan Prov. (**27**); Chiang Mai Prov. (**28**); Fang (**33**); Myanmar: Kawkareik (**30**); Mudon (**31**); Karen Hills (**32**); Parsa Wildlife Sanctuary (**29**); Kyaitong Township (**34**, **35**); Inle Lake Wetland Sanctuary (**36**, **37**); Taunggyi (**38**); Pindaya (**39**); Panlaung and Padalin Cave Wildlife Sanctuary (**40**); Mandalay-Yangon road (**41**); Minsontaung Wildlife Sanctuary (**42**); Popa Mountain Park (**43**); Mandalay (**44**); Shwebo (**45**); Bhamo (**46**); Indawgyi Lake (**47**); "Pegu" (**54**, see discussion in text); China: Baihualing (**48**); Longyang (**49**, **50**); Liuku-Longling road (**51**); Liuku (**52**); Liuku-Fugong road (**53**); ***Calotes mystaceus***: Myanmar: "Pegu" (**54**; see discussion in text); Kyaiktiyo Pagoda (**56**, **57**); Taungoo (**58**); Letpein village (**59**); Hlawga National Park (**60**); Ngapudaw township (**61**); Ngayokekaung village (**62**); ***Calotes vindumbarbatus* sp. n.**: Myanmar: Gat Shang Yang village (**63**); Hepu village (**64**); Linpha village (**65**); Swekawngaw (**66**); ***Calotes geissleri* sp. n.**: Myanmar: Alaungdaw Kathapa National Park (**67**, **68**); Mauk village (**69**, **70**); Natzang village (**71**); Simggial village (**72**); India: Nagaland: Kohima (**73**).

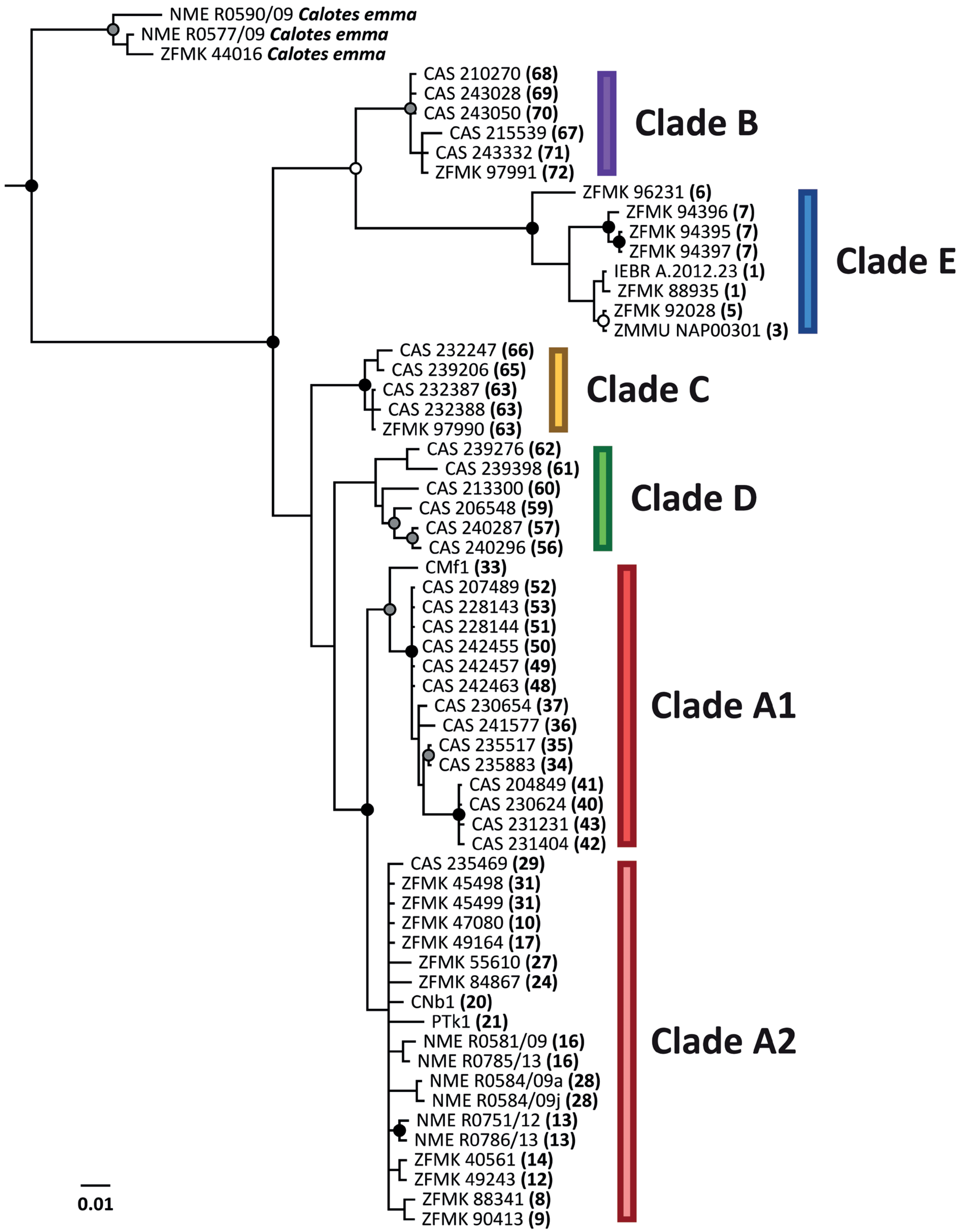


Fig. 2. The Bayesian consensus tree based on 988 bp of mitochondrial DNA (12S rRNA and COI) shows six distinct lineages within *Calotes mystaceus*. Node support in terms of Bayesian posterior probabilities is indicated by circles at nodes (nodes with a BPP ≥ 0.90 are white, BPP ≥ 0.95 are grey, BPP ≥ 0.99 are black, values < 0.90 are not marked). Outgroup (*Calotes versicolor*) not shown for clarity. Numbers in parentheses behind taxa refer to localities mapped in Fig. 1.

Table 2. Description of the morphological characters and respective abbreviations used in this study.

Character	Abbreviation	Description
Mensural characters		
4th finger	**4thFingL**	Distance from juncture of 3rd and 4th digits to distalmost extent (outer/distalmost surface of claw) of 4th finger.
4th toe	**4thToeL**	Distance from juncture of 3rd and 4th digits to distal end of 4th digit on hindfoot.
Crus length	**CrusL**	Length of tibia from knee to heel.
Eye-ear length	**EyeEar**	Distance from anterior edge of tympanum to posterior of orbit (not pupil opening).
Forefoot length	**ForefL**	Distance from proximal end of forefoot to tip of fourth digit.
Head height	**HeadH**	Dorsoventral distance from top of head to underside of jaw at transverse plane intersecting angle of jaws.
Head length	**HeadL**	Distance from anterior edge of tympanum to tip of snout.
Head width	**HeadW**	Distance from left to right outer edge of temporal or jaw muscles at their widest point without compression of soft tissue.
Hindfoot length	**HindfL**	Distance from proximal end (heel) of hindfoot to distalmost surface of fourth toe.
Interorbital width	**Interorb**	Transverse distance between anterodorsal corners of left and right orbits.
Jaw width	**JawW**	Distance from left to right outer edge of jaw angles; this measurement excludes jaw musculature broadening of head.
Lower arm length	**LoArmL**	Distance from elbow to distal end of wrist, or just before underside of forefoot.
Naris-eye length	**NarEye**	Distance from anterior edge of orbit to posterior edge of naris.
Snout-eye length	**SnEye**	Distance from anterior edge of orbit to tip of snout (rostral scale).
Snout-forelimb length	**SnForeL**	Distance from anterior of forelimb, or shoulder, to tip of snout.
Snout width	**SnW**	Internasal or internarial distance; transverse distance between left and right nares.
Snout-vent length	**SVL**	
Tail height	**TailH**	Distance from dorsal to ventral surface of tail base measured just posterior to vent.
Tail length	**TailL**	Distance from vent to distal end of tail; noting completeness or regeneration of tail.
Tail width	**TailW**	Distance from left to right side of tail base just posterior to vent.
Trunk length	**TrunkL**	Body length or axilla-groin length of others; distance between posterior edge of forelimb insertion (axilla) to anterior edge of hindlimb insertion (inguen).
Upper arm length	**UpArmL**	Distance from anterior insertion of forelimb, or shoulder, to elbow.
Upper leg length	**UpLegL**	Distance from anterior edge of hindlimb insertion to knee.
Meristic characters		
Forefoot lamellae	**4FingLm**	Number of 4th digit lamellae; from 1st lamella at digits' cleft that is wider than deep and touches dorsal digital scale (on at least one side) to most distal lamella; fragmented proximal scales are excluded.
Hindfoot lamellae	**4ToeLm**	Analogous to **4FingLm** at 4th toe.
Canthus rostralis	**CanthR**	Number of elongate scales along 'dorsolateral snout ridge' from above posterodorsal corner of nasal scale to and including posteriormost supraciliary scale.
Dorsal eyelid scales	**Eyelid**	Number of scales found along dorsal edge of eyelid.
Dorsal head scales	**HeadSLn**	Number of scales longitudinally on midline between interparietal and rostral scale.
Head scales	**HeadSTr**	Number of scales in transverse line between posteriormost left and right supraciliary scales, just anterior of interparietal.
Infralabials	**Inflab**	Posterior end defined by posteriormost enlarged scales that touches with Suplab at rear corner of mouth.
Midbody scale rows	**MidbS**	Number of scale rows around trunk at midbody.
Snout scales	**SnS**	Number of scales on line transversally between left and right nasal scales (single scale surrounding naris).
Supralabials	**Suplab**	Posterior end defined by posteriormost enlarged scales that touches Inflab at rear corner of mouth.
Vertebral scales or spines	**VertS**	Number of middorsal scales (spines or not), beginning with first enlarged spine-like scale on nape to above vent.

Table 3. Mean uncorrected p-distances between species for COI (above diagonal) and 12S rRNA (below diagonal). [NA = not available, *C. geissleri* sp. n. missing in COI data set]

	bachae	*geissleri* sp. n.	*goetzi* sp. n.	*mystaceus*	*vindumbarbatus* sp. n.
bachae		NA	0.1465	0.1415	0.1391
geissleri sp. n.	0.0610		NA	NA	NA
goetzi sp. n.	0.0603	0.0486		0.0603	0.0647
mystaceus	0.0548	0.0457	0.0291		0.0656
vindumbarbatus sp. n.	0.0615	0.0476	0.0326	0.0375	

Calotes geissleri sp. n.
(Fig. 2, Clade B)
urn:lsid:zoobank.org:act:EC4DA90A-417D-48E6-8EA2-FA073D168425

Holotype. CAS 215539 (adult male, Fig. 6A-B, Clade B) from Myanmar, Sagaing Division, Mon Ywa District, AK Park, Thabake Sae Camp [22.316806° N, 94.475556° E], collected by H. Win, T. Thin, S.L. Oo and H. Tun on June 9th 2000.

Paratypes. CAS 210270 from Myanmar, Alaungdaw Kathapa National Park, Thabakesay (Log Cabin Camp) [22.318194° N, 94.475722° E]; ZFMK 97991 (formerly CAS 243200) from Myanmar, Chin State, Phalum District, Simggial village [23.762583° N, 93.546167° E, 1362 m.]; CAS 243028, CAS 243050 both from Myanmar, Magway Division, Gangaw District, Gangaw Township, Mauk village [22.335861° N, 94.144583° E, 205 m.].

Diagnosis. A large sized *Calotes* species with a known maximum SVL of 122 mm in males and 114 mm in females. Tail relatively short, up to 270 mm in males and 223 mm in females. The new species can be distinguished from other species of the complex by the combination of the following characters: 1) head and body very robust; 2) nuchal and dorsal crests continuous, composed of erect compressed scales, directed posteriorly, larger on the nuchal crest than on the dorsal crest, becoming smaller towards the tail; 3) 50–62 scale rows around midbody; 4) 35–45 vertebral spines and scales in males, 49–50 in females; 5) body scales small, homogeneous, feebly keeled and arranged in regular rows; 6) a short row of separated spines on both sides of the head, directing from the tympanum to the first scale of the nuchal crest; 7) extremities relatively short and robust; 8) oblique skin fold in front of the fore limbs, 9) head and body bluish, with a white band from the tip of the mouth along the upper lip, the tympanum and prominently continuing between the dorsolateral brownish orange body blotches on the body reaching the hind limbs, band as broad as the height of the tympanum on the head and above the front legs, becoming gradually narrower until the insertion of the hindlimbs; 10) three or more large distinct brownish orange blotches on both sides of the body between the limbs.

Description of the holotype. Moderately large male of 110 mm SVL. Tail relatively short (201 mm), extremities robust. Head large, distinct from the neck and lateral sides flat. Posterior parts of jaw angle swollen. Snout-tip blunt. Nostril in a single scale, separated from the labial scale by a single scale. Rostral and mental scales small. Canthus rostralis sharp and straight from the nostril to the posterior part of the eye, including six scales between the nostril and the eye and 12 supraciliary scales. Eleven supralabial scales on both sides of the head, separated from the orbit by five rows of small scales. Nine infralabial scales. Seven scales between the orbit and the tympanum, tympanum distinct, with a row of spiny scales from above the tympanum to the first scale of the nuchal crest. Scales on chin and throat keeled. Nuchal crest with 14 scales, dorsal crest with 21 scales. Spines of the nuchal crest larger than those of the dorsal crest, relatively uniform in height at the nuchal crest but gradually decreasing from posterior of the neck to the hind limbs. Dorsal and lateral body scales keeled, pointing upwards and backwards. Caudal scales keeled, directed backwards. Fore and hind limbs relatively robust, forth finger and fourth toe longest.

Male coloration. Males in breeding color with blue head and body (Fig. 6C). A white band is present from the tip of the snout along the upper lips and the tympanum, predominantly continuing between the dorsolateral blotches on the lateral sides of the body to the hind limbs. The band is as broad as the height of the tympanum on the head and above the fore legs, becoming gradually narrower towards the insertion of the hind limbs. Three or more large distinct brownish-orange blotches on the lateral sides of the body between the limbs. Non-display coloration unknown.

Variation. Body measurements and meristic characters for adult individuals are given in Table 4. Specimens ranged in size from the smallest female with a SVL of 92 mm (CAS 210270) and the largest female with a SVL of 114 mm (CAS 243200) to the largest male with a SVL of 120 mm (CAS 243028). In general, adult males are larger than females, and have greater SVLs, tail lengths and head lengths and widths and fewer vertebral scales, including crest scales. While proportionally the heads of adult males and females are equal, males have propor-

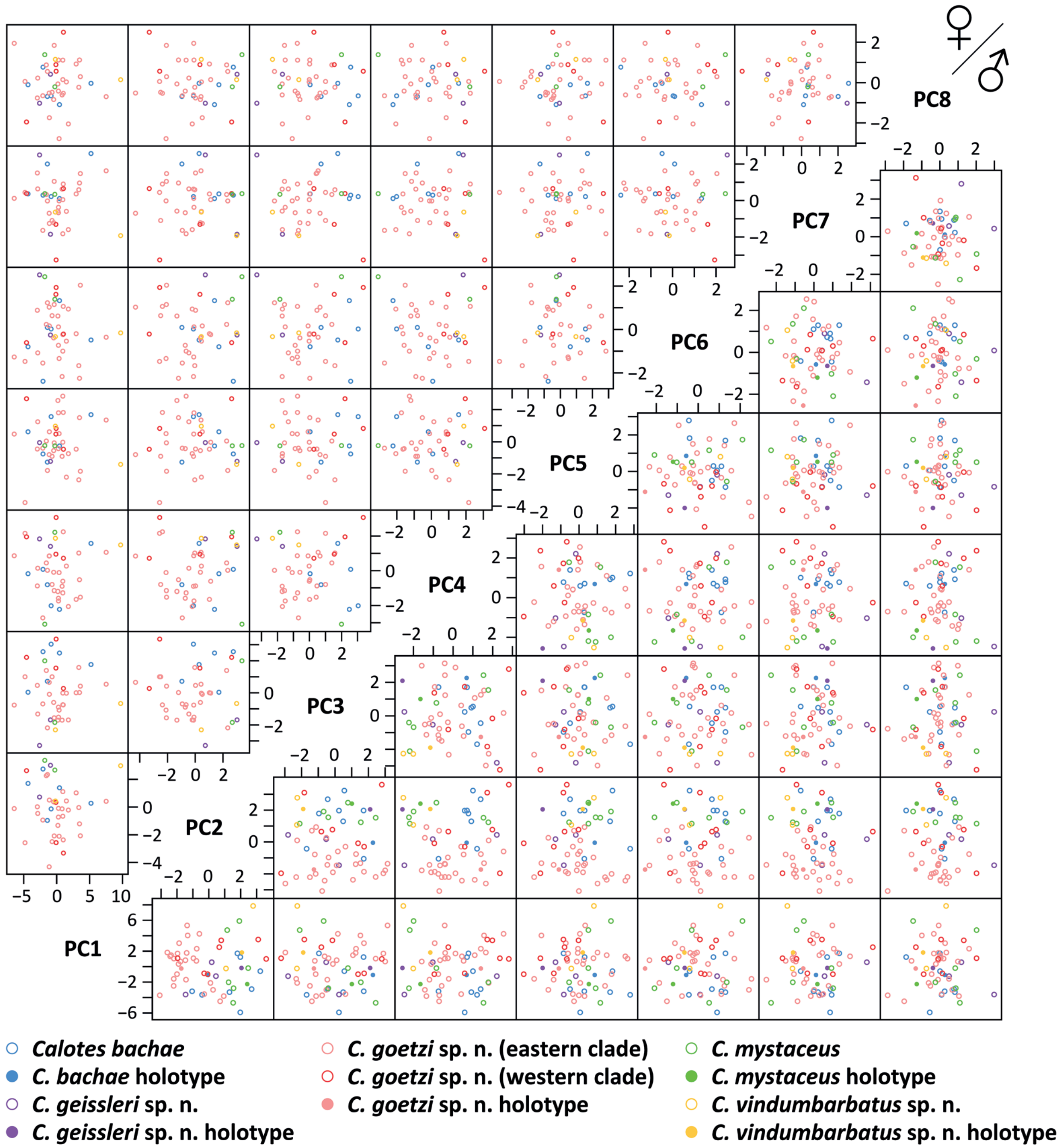


Fig. 3. Principal component analyses results for the morphologically examined specimens. Details of Eigenvalues and explained variance are given in Table 3.

tionally wider heads than females, probably because of the swollen jaw angle. Dorsal coloration differs between sexes and both sexes are able to change coloration. Coloration characters (lateral stripe, blotches) are lighter or sometimes absent in females. Blue coloration on head and body. The stripe is distinctly present between the mental and the shoulder, becoming more indistinct between the blotches on the lateral sides of the body, and extending to above the hindlimbs. Irregular whitish dots of several scales are present on the lateral sides of the body in females.

Etymology. The specific epithet is a patronym formed in the genitive singular honoring Dr. Peter Geißler, Museum Natur und Mensch, Freiburg, Germany, in recognition of his work on the Southeast Asian herpetofauna in general, and his collection of *Calotes bachae* specimens in 2009 in particular, which initiated research on the *Calotes mystaceus* complex.

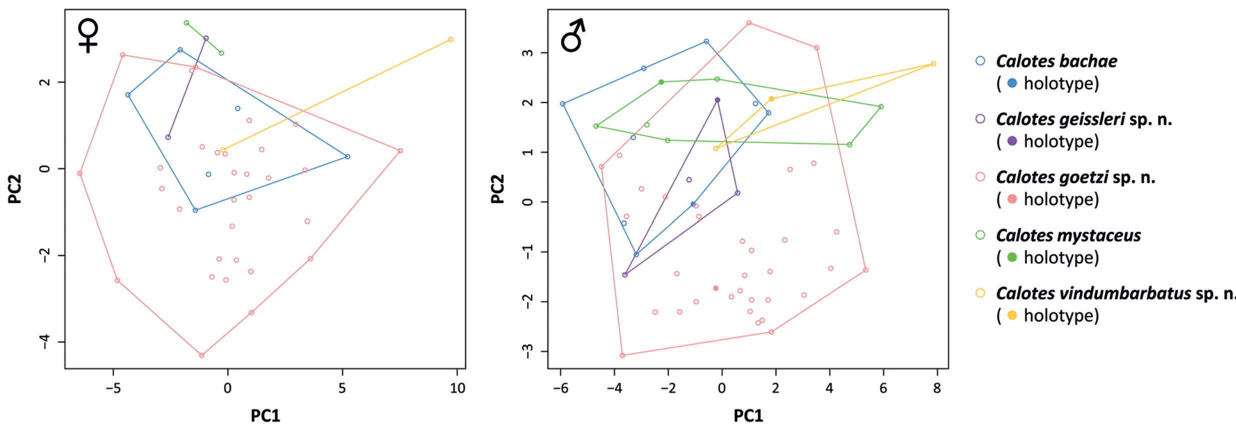


Fig. 4. Principal component analysis results for the morphologically examined specimens, colored according to to the genetic clades. Details of Eigenvalues and explained variance are given in Table 3.

Table 4. Eigenvalues and percent of explained variance per principal component of mensural and meristic data of males and females as shown in Figs 3–4.

Females	**PC1**	**PC2**	**PC3**	**PC4**	**PC5**	**PC6**	**PC7**	**PC8**
Eigenvalue	8.97458	3.36167	2.39687	2.23517	1.94366	1.50995	1.49041	1.16296
Explained variance	0.29915	0.11206	0.07990	0.07451	0.06479	0.05033	0.04968	0.03877
Males	**PC1**	**PC2**	**PC3**	**PC4**	**PC5**	**PC6**	**PC7**	**PC8**
Eigenvalue	8.36195	3.14874	2.78013	2.03641	1.53439	1.34330	1.23076	1.06270
Explained variance	0.27873	0.10496	0.09267	0.06788	0.05115	0.04478	0.04103	0.03542

Distribution. The new species is documented only from Myanmar and India (e.g., BMNH 1956.1.11.98, specimens mentioned by Lalremsanga et al. [2010]).

Ecology. *Calotes geissleri* sp. n. is diurnal and semi-arboreal. Preferred habitats are unknown. Lalremsanga et al. (2010) collected one individual on a branch of *Pinus kesiya*, about 3m above the ground, in a secondary forest. The specimen was kept and remained greyish brown in coloration in captivity, but changed the color of the head and anterior portion of the trunk to bright blue minutes after exposure to the sun. Like other *Calotes* species, *C. geissleri* sp. n. feeds on arthropods like Coleoptera, Formicidae and others. In India (see Lalremsanga et al. 2010) the species occurs in sympatry with *Calotes jerdoni* and *C. versicolor*.

Calotes goetzi sp. n.
(Fig. 2, Clade A)
urn:lsid:zoobank.org:act:7827D48E-E121-4904-9636-3A46AE42B369

Holotype. ZFMK 92606 (adult male, Fig. 7A-C, Clade A) from Cambodia, Siem Reap Province, near Kbal Spean within the Phnom Kulen National Park [13.699167° N, 103.998611° E].

Paratypes. ZFMK 88341 (adult male), ZFMK 92607 (adult female) from the same locality as the holotype.

Diagnosis. A large species of *Calotes*, with a maximum SVL of 143 mm in males and 122 mm in females. It can be distinguished from other species of the group by the combination of the following characters: 1) head, body and limbs robust, tail long but not as long as in *C. mystaceus*; 2) body scales mid-sized, homogeneous, keeled, arranged in regular rows; 3) upper dorsolateral scales pointing up- and backwards; 4) body scales arranged in 45–60 rows around midbody; 5) two short and separated spines, surrounded by a ring of scales between the tympanum and the vertebral crest on both sides of the head; 6) vertebral crest continuous from above the tympanum to the hind limbs, composed of erected scales, directed posteriorly, highest slightly in front of the insertion of the front limbs, becoming gradually shorter towards the hind limbs; 7) vertebral scales, including vertebral spines, 37–52 in males and 43–60 in females; 8) oblique skin fold in front of the fore limbs; 9) head, body, and limbs bluish in males; 19) males with a white stripe from between nostril and orbit along the upper lip and the tympanum to the front limb insertion; 11) three to five distinct dark brown dorsolateral blotches.

Description of the holotype. Large male (SVL 118 mm). Body robust, tail relatively short, 236 mm long. Fore- and hind limbs relatively slender, fourth finger and toe longest. Head distinct from the neck, posterior jaw angles heavily swollen. Tip of the snout blunt, rostral small. Nostril large, in a single scale, separated from the rostral by one elongated scale and from the first two supralabial scales by two rectangular scales. Canthus

Fig. 5. *Calotes bachae* Hartmann et al., 2013. **A**. Holotype (ZFMK 88935, adult male), general view from above. **B**. Holotype, lateral view. **C**. Living holotype from Cat Tien National Park, Vietnam.

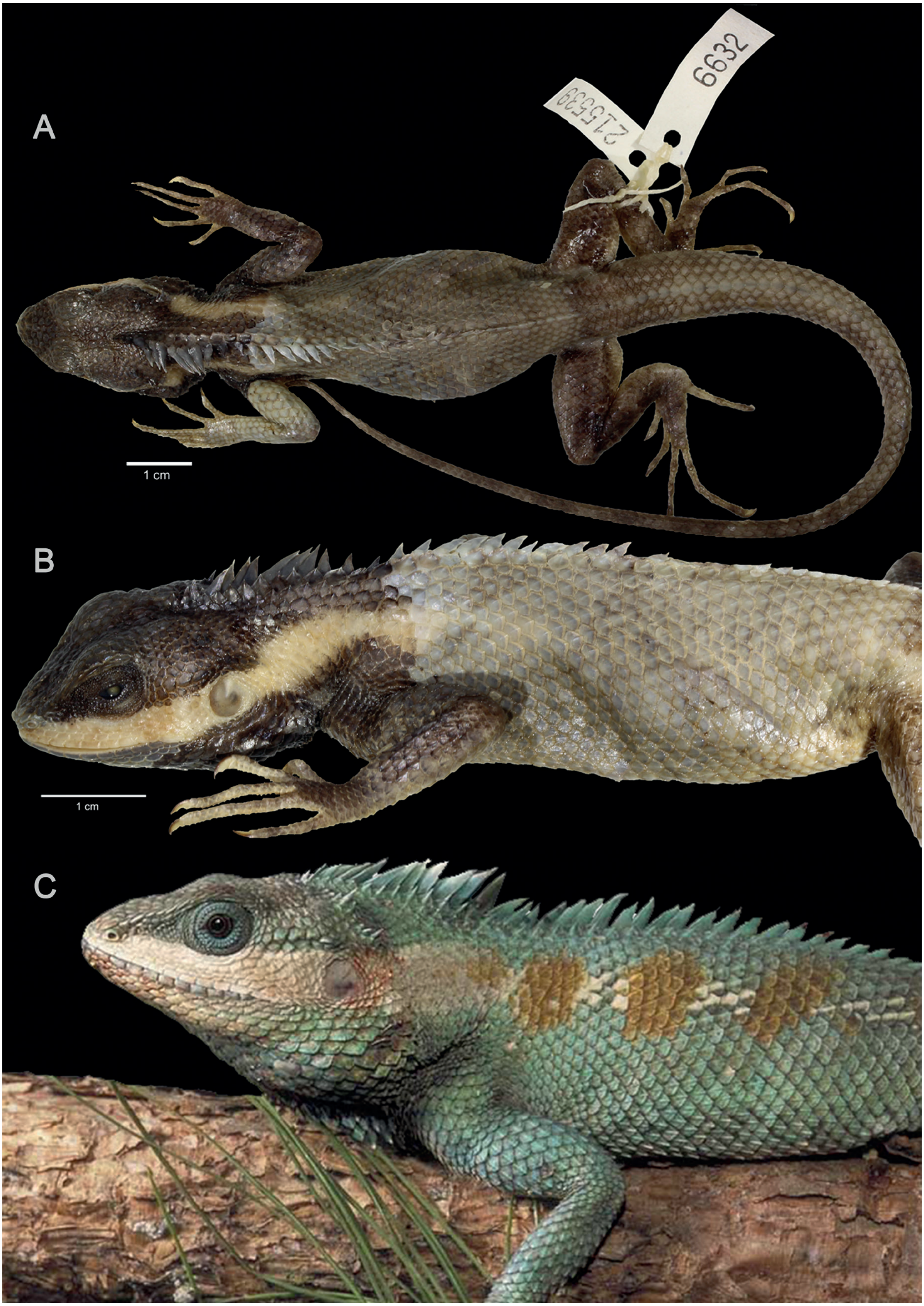


Fig. 6. *Calotes geissleri* sp. n. **A**. Holotype (CAS 215539, adult male), general view from above. **B**. Holotype, lateral view. **C**. Living adult male (CAS 220586), from Nat Ma Taung National Park, Htin Chaun Village, Chin State, Myanmar.

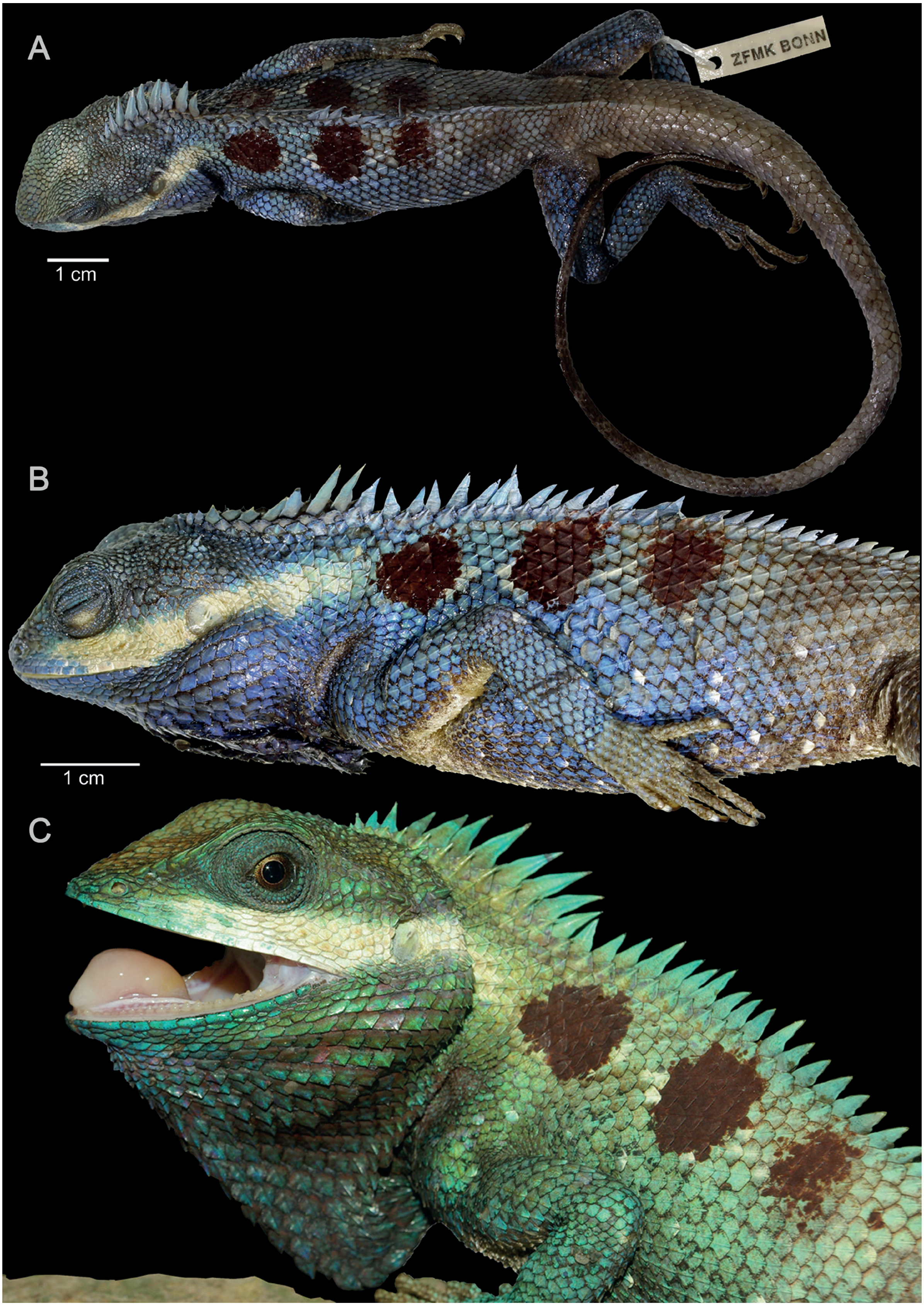


Fig. 7. *Calotes goetzi* sp. n. **A**. Holotype (ZFMK 92606, adult male), general view from above. **B**. Holotype, lateral view. **C**. Living holotype from Kbal Spean, Cambodia.

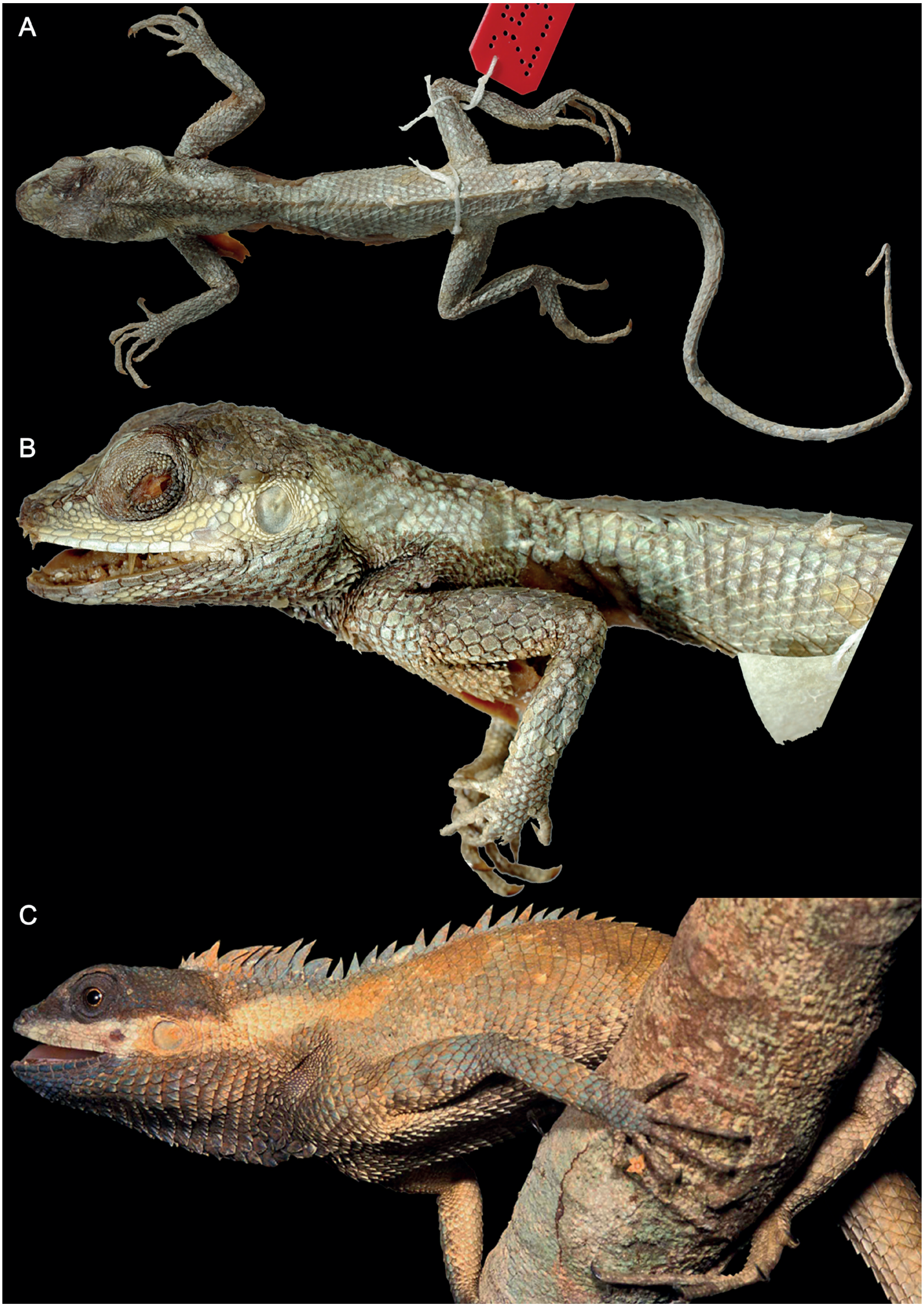


Fig. 8. *Calotes mystaceus* Duméril & Bibron, 1837. **A**. Holotype (MNHN 2557, juvenile male), general view from above. **B**. Holotype, detailed lateral view. **C**. Adult male from Yangon, eastern Irrawaddy delta, coastal Myanmar, which is within the type locality "pays de Birmans [=Myanmar]."

rostralis distinct, formed by nine scales from the nostril to above the orbit and continuous with supraciliary scales. Lateral sides of the head flat. Supralabial scales 9/9, infralabial scales 10/10. Supralabial scales separated from the orbit by four rows of small scales. Eight scales between the orbit and the tympanum, two of them slightly ridged. Tympanum distinct, two spines, surrounded by a ring of scales, between the tympanum and the vertebral crest. Mental scale small, bordered by two postmental scales which are separated from each other. First pair of the postmental scales in contact with the infralabial scale. Scales on the dorsal part of the chin smooth to feebly keeled, becoming strongly keeled towards the throat. Vertebral crest continuous from above the tympanum to the tail, spines highest above the insertion of the front limbs and gradually decreasing towards the tail. Dorsal and lateral scales strongly keeled, pointing up- and backwards. Ventral scales parallelly keeled. Caudal scales smooth to feebly keeled, directed backwards. Subcaudal scales parallel and strongly keeled.

Male coloration. Head, body and limbs bluish. A white stripe, as high as the tympanum, is present from between nostril and orbit along the upper lip and the tympanum to the insertion of the front limb. The stripe is followed by three to five large reddish-brown to dark-brown blotches, with the first above the insertion of the fore limbs and the latest at around midbody or above the insertion of the hindlimbs, sometimes continuing on the tail. Throat coloration darker than the chin and the head coloration. From Thailand, males are known to have bright blue hindlimbs and crest scales. Intermediate males with a blue head and a white stripe, but body coloration brownish-black with indistinct light brown blotches. Non-brilliant coloration in males from Thailand reddish-brown, with a white non-continuous stripe from the orbit to above the hindlimbs. Blotches brownish, darker than the body coloration.

Variation. Body measurements and meristic characters for adult individuals are given in Tables 4. Specimens ranged in size between the smallest adult with a SVL of 84 mm (MNHN 1884.548) and the largest female with a SVL of 126 mm (ZFMK 44893) to the largest male measuring 145 mm (MNHN 1884.546). In general, adult males are larger than females, because of longer SVLs, tail lengths, head lengths, and widths and slightly fewer vertebral scales including the crest scales. Heads of adult males and females are proportionally equal in length, but male heads are wider than those of females, probably because of the swollen jaw angle. Dorsal coloration differs between sexes and both sexes are able to change the coloration. Coloration characters being lighter in females; head and body blue. Lateral stripe from between the nostril and orbit along the upper lips and the tympanum to the first blotch. Sometimes the first two brownish blotches are framed by scales in the same coloration as the lateral stripe. Three to five blotches present, from above the insertion of the fore limbs to about mid-body or even hindlimb insertion. Non-display coloration of females with lateral parts of the body gray and dorsal parts brown, with three to four darker crossbands between the lateral stripes on both sides of the body. Lateral stripe white, from the mental scale along the upper lips and the tympanum to the hindlimbs. Head light blue.

Etymology. The specific epithet is a patronym formed in the genitive singular honoring Dr. Stephan Goetz, Munich, Germany, in recognition of his longtime support of species conservation efforts in Cambodia.

Distribution. *Calotes goetzi* sp. n. is distributed in a large area of Indochina and inhabits most of the previous range of *C. mystaceus*. The new species is documented by museum specimens and photo vouchers from Cambodia, China (Yunnan province), Laos, Myanmar, and Thailand.

Ecology. *Calotes goetzi* sp. n. is diurnal and semi-arboreal to arboreal and can easily climb on tree trunks at a height of 5–10 meters or above. The species is known from dipterocarp lowland forests, cultural landscape and secondary forest. At its type locality the species was observed in more open habitats with a closed canopy, but also within dense monsoon tropical forests and solitary trees in rather open areas. Here it occurs sympatrically with *Calotes versicolor*. Hawkeswood & Sommung (2018) report it from farmland with e.g., rice, coconut, banana, and durian plantations. Chan-Ard et al. (2015) report the species from a wide range of forest types in Thailand, including tree-lined agricultural lands and grasslands. Similar to other *Calotes* species, *C. goetzi* sp. n. feeds on a variety of arthropods. Chan-Ard et al. (2015) report from Thailand, that mature individuals are territorial, chasing away possible intruders. Eggs are buried in soft soil and later guarded by the males. Amber et al. (2017) recognized a possible ontogenetic shift in defense strategies of *C. goetzi* sp. n. (*C. mystaceus* at the time of their publication), with older individuals utilizing color change, while juveniles do not.

Calotes mystaceus Duméril & Bibron, 1837: 408
(Fig. 2, Clade D)

Duméril, A. M. C. & G. Bibron (1837). Erpétologie Générale ou Histoire Naturelle Complète des Reptiles. Vol. 4. Libr. Encyclopédique Roret, Paris, 570 pp.

Holotype. MNHN 2557 (juvenile male, Fig. 8A-B), from “Indes orientales (…) pays de Birmans [=Myanmar].”

Original Diagnosis. “Deux petites épines places l’une après l’autres de chaque côte de la nuque. Un pli oblique en longueur devant l’épaule. Écailles des côtes du tronc grandes; celles du ventre moitié plus petites. Dessus de la base de la queue subanguleux, garni d’écailles seulement un peu plus grandes que celles qui les avoisinent. Fauve en dessus; sous l’oeil une bande jaune qui se prolonge jusque sur l’épaule.”

Table 5. Morphological variation in the examined specimens of the *Calotes mystaceus* complex. Values are given are as mean ± standard deviation and minimum – maximum. Characters marked with an asterisk were significantly different between species in the AN(C)OVA.

	C. bachae		***C. geissleri* sp. n.**		***C. goetzi* sp. n.**		***C. mystaceus***		***C. vindumbarbatus* sp. n.**	
	females (*n* = 6)	males (*n* = 10)	females (*n* = 2)	males (*n* = 4)	females (*n* = 33)	males (*n* = 38)	females (*n* = 2)	males (*n* = 7)	females (*n* = 2)	males (*n* = 3)
SVL	80.5 ± 6.35 71–86	88.6 ± 14.06 56–102	103 ± 15.56 92–114	114.5 ± 7.72 106–122	101.33 ± 10.32 83–126	114.16 ± 16.34 84–145	87 ± 16.97 75–99	82.29 ± 17.58 58–101	60 ± 18.38 47–73	67 ± 14 51–77
EyeEar	4.82±0.58 3.91–5.61	5.92 ± 1.21 3.56–7.15	6.84 ± 1.36 5.88–7.8	8.11 ± 1.25 6.95–9.45	6.01 ± 0.76 4.66–7.73	7.88 ± 1.64 5.33–11.46	5.61 ± 0.86 5–6.21	5.09 ± 1.18 3.49–6.56	3.51 ± 1.56 2.41–4.61	4.35 ± 0.79 3.44–4.89
HeadH	14.88 ± 1.85 12.19–17.35	16.2 ± 2.95 11.7–19.55	17.43 ± 3.3 15.1–19.76	20.75 ± 3.88 17.45–26.35	17.81 ± 2.13 13.74–22.38	21.85 ± 4.18 13.55–31.79	15.14 ± 3.73 12.5–17.78	14.64 ± 3.57 9.87–20.03	10.05 ± 2.97 7.95–12.15	11.02 ± 2.07 8.64–12.33
HeadL	19.82 ± 1.94 16.92–21.5	21.97 ± 3.53 14.71–25.72	24.71 ± 4.65 21.42–28	28 ± 2.71 24.89–31.07	23.75 ± 2.15 20.14–28.39	27.18 ± 5.44 7.8–36	21.12 ± 3.85 18.4–23.85	20.4 ± 4.13 14.59–24.73	15 ± 4.49 11.83–18.18	16.28 ± 3.47 12.28–18.43
HeadW*	15.01 ± 1.04 14.12–16.93	16.89 ± 3.22 11.21–20.54	19.66 ± 2.62 17.81–21.52	24.87 ± 3.86 20.81–30	17.97 ± 2.16 14.92–22.73	23.84 ± 5.2 12.75–37.13	15.82 ± 1.95 14.44–17.2	15.79 ± 3.65 11.19–21.36	12.66 ± 3.85 9.94–15.39	13.12 ± 2.59 10.19–15.12
Interorb*	8.96 ± 0.73 7.85–9.73	9.92 ± 1.67 6.7–11.69	14.16 ± 1.92 12.8–15.52	12.3 ± 1.99 9.92–14.69	11.12 ± 0.99 9.2–12.7	12.48 ± 1.85 8.75–16.65	10.39 ± 1.77 9.13–11.64	8.9 ± 1.6 6.62–10.87	7.16 ± 2.22 5.59–8.73	7.74 ± 1.43 6.08–8.57
JawW	13.92 ± 0.93 12.82–15.56	15.07 ± 2.5 10.74–18.36	17.77 ± 1.79 16.5–19.03	20.98 ± 1.53 19.32–22.44	16.54 ± 1.44 14.2–19.65	20.01 ± 4.06 12.03–37.39	14.91 ± 1.53 13.83–16	14.09 ± 2.73 10.44–17.6	11.84 ± 3.34 9.47–14.2	11.89 ± 2.47 9.13–13.9
NarEye	5.35 ± 0.85 3.75–6.19	6.15 ± 1.04 4.34–7.62	7.31 ± 1.55 6.22–8.41	7.89 ± 0.69 7.38–8.9	6.86 ± 0.73 5.25–8.44	7.76 ± 1.31 5.31–10.71	6.62 ± 2.05 5.17–8.07	5.99 ± 1.43 3.61–7.41	4.23 ± 1.03 3.5–4.96	4.69 ± 0.86 3.72–5.33
SnEye	9.19 ± 1.26 7.58–10.56	10.08 ± 1.85 6.32–11.96	12.01 ± 2.23 10.43–13.59	12.44 ± 0.78 11.71–13.5	11.39 ± 1.13 8.74–14.22	12.97 ± 2.19 8.64–17.54	10.14 ± 2.67 8.26–12.03	9.54 ± 2.2 6.44–11.72	6.97 ± 1.82 5.69–8.26	7.69 ± 1.5 5.96–8.63
SnW	5.04 ± 0.62 4.06–5.83	5.53 ± 0.75 3.94–6.56	6.33 ± 0.49 5.98–6.68	6.92 ± 0.45 6.49–7.48	6.56 ± 1.52 5.11–14.39	7.78 ± 2.88 5.1–18.43	5.42 ± 0.59 5–5.84	5.37 ± 0.66 4.48–6.3	4.45 ± 0.69 3.96–4.93	4.64 ± 0.81 3.7–5.15
4FingL	10.04 ± 1.05 8.56–10.93	10.67 ± 1.47 7.44–12.04	12.35 ± 0.64 11.89–12.8	13.69 ± 0.46 13.41–14.37	12.14 ± 1.12 9.99–14.14	13.15 ± 1.64 9.82–16.03	10.27 ± 1.89 8.93–11.6	10.2 ± 1.74 7.63–12.08	7.45 ± 1.34 6.5–8.4	8.09 ± 1.41 6.46–8.91
4ToeL	13.38 ± 0.93 11.83–14.59	15.03 ± 1.95 11.04–16.92	16.22 ± 0.76 15.68–16.76	17.68 ± 0.71 16.88–18.59	15.12 ± 1.57 12.75–20.31	17.43 ± 2.19 13.71–21.89	14.91 ± 2.5 13.14–16.68	14.07 ± 2.92 10.31–18.19	10.46 ± 2.64 8.6–12.33	11.84 ± 1.4 10.25–12.86
CrusL	17.22 ± 1.66 14.58–18.55	18.46 ± 2.92 12.65–21.57	20.91 ± 3.43 18.49–23.34	23.41 ± 0.94 22.39–24.22	20.57 ± 2.25 17.11–27.25	23.31 ± 2.91 17.55–28.98	17.35 ± 3.44 14.92–19.78	17.08 ± 3.81 11.83–21.83	12.59 ± 4.19 9.62–15.55	13.89 ± 2.96 10.48–15.81
ForefL	13.35 ± 0.79 12.11–14.17	14.62 ± 2.22 10.29–17.73	15.9 ± 1.09 15.13–16.67	18.25 ± 0.4 17.67–18.56	15.95 ± 1.68 13.98–22.19	17.71 ± 2.03 13.16–21.4	13.36 ± 1.34 12.41–14.3	13.88 ± 2.75 9.97–17.8	10.39 ± 2.64 8.53–12.26	11.39 ± 1.73 9.39–12.43
HindfL	23.75 ± 1.94 20.34–25.3	25.69 ± 3.18 19.75–28.7	28.39 ± 2.74 26.46–30.33	30.88 ± 0.81 29.94–31.58	27.31 ± 2.22 23.74–33.62	30.82 ± 3.25 23.36–37.41	25.34 ± 3.85 22.62–28.07	24.22 ± 4.89 17.24–29.07	17.89 ± 4.4 14.78–21	19.95 ± 3.35 16.09–22.12
LoArmL	14.45 ± 1.51 11.95–15.75	15.49 ± 2.93 9.6–18.64	17.39 ± 2.81 15.4–19.38	20.09 ± 1.31 18.48–21.57	17.5 ± 2.22 13.64–24.14	19.78 ± 3.3 13.64–27.73	15.42 ± 3.44 12.99–17.85	13.98 ± 3.27 8.99–17.38	10.1 ± 3.68 7.5–12.7	11.12 ± 2.17 8.62–12.51
SnForeL	27.83 ± 3.43 23–32	30.3 ± 11.23 2–39	32 ± 2.83 30–34	42 ± 5.6 37–50	35.21 ± 4.54 29–45	40.17 ± 7.61 27–59	31.5 ± 6.36 27–36	29.29 ± 8.04 20–41	21 ± 5.66 17–25	22.61 ± 4.1 18–25.83
TailH	6.72 ± 0.97 5.12–8.06	9.74 ± 2.07 6.02–12.29	10 ± 2.67 8.11–11.89	14.56 ± 1.31 13.44–16.43	9.79 ± 1.44 7.46–12.69	14.41 ± 3.26 6.6–21	9.27 ± 3.52 6.78–11.76	9.04 ± 2.95 5.18–13.07	4.88 ± 1.92 3.52–6.23	6.91 ± 2.69 3.81–8.61

Table 5. (continued).

	C. bachae		*C. geissleri* sp. n.		*C. goetzi* sp. n.		*C. mystaceus*		*C. vindumbarbatus* sp. n.	
	females (*n* = 6)	males (*n* = 10)	females (*n* = 2)	males (*n* = 4)	females (*n* = 33)	males (*n* = 38)	females (*n* = 2)	males (*n* = 7)	females (*n* = 2)	males (*n* = 3)
TailL	178.33 ± 21.86 157–203	174.4 ± 63.54 13.6–215	206 ± 24.04 189–223	222.67 ± 41.04 197–270	193.77 ± 23.48 127–237	219.96 ± 29.55 161–272	158 ± NA 158–158	169.33 ± 37.56 119–210	113 ± 38.18 86–140	115 ± 24.04 98–132
TailW	7.15 ± 1.43 5.27–9.15	9.04 ± 1.85 5.3–12.38	11.25 ± 1.53 10.17–12.33	12.43 ± 0.67 11.75–13.35	10.49 ± 1.14 8.31–12.9	12.42 ± 2.18 5.56–16.39	8.1 ± 1.51 7.03–9.17	8.04 ± 2.31 4.98–11.03	6.38 ± 3.84 3.67–9.1	6.62 ± 1.75 4.61–7.82
TrunkL	38 ± 2.83 34–41	37.65 ± 13.2 2.5–47	54 ± 7.07 49–59	55 ± 2.45 52–57	48.52 ± 5.75 38–62	52.39 ± 6.28 39–65	40 ± 4.24 37–43	38.57 ± 6.58 29–47	29 ± 7.07 24–34	30.67 ± 5.13 25–35
UpArmL	13.15 ± 1.37 11.67–14.78	14.76 ± 2.26 9.69–16.94	16.05 ± 0.11 15.98–16.13	18.38 ± 1.41 16.64–20.09	15.61 ± 1.73 12.59–20.53	17.56 ± 1.97 13.46–21.64	14.1 ± 0.52 13.73–14.47	14.34 ± 3.09 9.91–17.87	10.25 ± 2.17 8.72–11.79	9.95 ± 1.33 8.44–10.96
UpLegL	17.92 ± 1.85 14.85–20.14	19.23 ± 3.13 12.86–21.83	21.12 ± 2.67 19.23–23.01	23.51 ± 1.39 22.31–25.17	20.12 ± 1.81 17–25.2	23.19 ± 3.01 18.47–29.1	18.71 ± 4.84 15.29–22.14	17.51 ± 3.9 11.96–22.18	13.1 ± 3.14 10.88–15.32	13.82 ± 1.7 11.85–14.85
CanthR	8.83 ± 0.75 8–10	8.7 ± 1.34 6–11	6 ± 0 6–6	7 ± 2 6–10	8.55 ± 0.79 7–10	8.89 ± 0.8 8–11	7 ± 2.83 5–9	6.57 ± 2.07 5–10	5.5 ± 0.71 5–6	5 ± 0 5–5
Eyelid	13.17 ± 0.75 12–14	12.6 ± 0.7 12–14	11.5 ± 0.71 11–12	13 ± 1.15 12–14	13.33 ± 1.05 11–16	13.11 ± 0.92 11–15	11.5 ± 0.71 11–12	12.29 ± 0.95 11–14	12.5 ± 0.71 12–13	11.33 ± 1.15 10–12
HeadSLn	15 ± 2.19 12–18	15.8 ± 1.55 14–19	16 ± 2.83 14–18	15.5 ± 1.29 14–17	16.18 ± 1.33 14–19	16.29 ± 2.22 11–21	16 ± 0 16–16	16.71 ± 2.43 13–20	15.5 ± 2.12 14–17	15.67 ± 1.15 15–17
HeadSTr	15.67 ± 1.63 14–18	15.6 ± 1.58 13–18	16 ± 1.41 15–17	15.5 ± 1 14–16	17.3 ± 1.79 13–21	16.86 ± 1.46 13–20	14.5 ± 0.71 14–15	16.29 ± 1.11 15–18	16 ± 1.41 15–17	16.33 ± 0.58 16–17
Inflab	10.33 ± 0.52 10–11	10.2 ± 0.79 9–11	10.5 ± 0.71 10–11	10 ± 1.41 9–12	10.64 ± 0.93 9–13	10.61 ± 1.1 8–13	9.5 ± 0.71 9–10	10.14 ± 0.38 10–11	10.5 ± 0.71 10–11	10 ± 0 10–10
SnS	8.33 ± 1.03 7–10	7.6 ± 1.35 6–10	6.5 ± 0.71 6–7	7 ± 0 7–7	8.36 ± 1.29 6–10	7.89 ± 1.25 6–10	7.5 ± 0.71 7–8	6.57 ± 0.98 5–8	6.5 ± 0.71 6–7	6.67 ± 0.58 6–7
Suplab	10.5 ± 0.55 10–11	10 ± 0.82 9–11	10.5 ± 0.71 10–11	11 ± 0.82 10–12	10.7 ± 0.81 9–12	10.42 ± 1.06 8–13	9.5 ± 0.71 9–10	10 ± 1.15 8–11	10.5 ± 0.71 10–11	10 ± 1 9–11
4FingLm	19.33 ± 1.63 18–22	20.71 ± 0.95 20–22	19 ± 1.41 18–20	22.33 ± 2.08 20–24	20.33 ± 1.22 18–23	20.42 ± 1.29 19–24	22 ± NA 22–22	21.6 ± 1.95 20–25	20.5 ± 0.71 20–21	21.33 ± 0.58 21–22
4ToeLm	23.83 ± 1.17 22–25	24 ± 1 23–25	25 ± 0 25–25	26.33 ± 3.79 22–29	23.97 ± 1.98 21–28	24.19 ± 1.78 22–30	28 ± NA 28–28	26 ± 1.22 25–28	25 ± 0 25–25	26.67 ± 0.58 26–27
VertS	44.5 ± 1.22 43–46	37.4 ± 3.63 32–42	49.5 ± 0.71 49–50	41.5 ± 4.51 35–45	48.88 ± 4.01 43–60	45.16 ± 3.64 37–52	43 ± 7.07 38–48	41.86 ± 3.67 38–49	46 ± 2.83 44–48	44.33 ± 3.79 40–47
MidbS	48.17 ± 2.04 46–51	47.6 ± 2.76 44–53	52 ± 2.83 50–54	55 ± 5.29 50–62	51.82 ± 2.81 46–59	51.68 ± 3.32 45–60	49.5 ± 4.95 46–53	47.57 ± 4.54 44–56	54 ± 0 54–54	50.67 ± 1.15 50–52

Revised Diagnosis. A small sized *Calotes* with a maximum known SVL of 101 mm in males and 99 mm in females. Distinguished from all other species of the group by the combination of the following characters: 1) Head and body slender, with long tail and extremities; 2) body scales relatively large in respect to the body size, homogeneous, strongly keeled and arranged in regular rows; 3) upper dorsolateral scales pointing back- and upwards; 4) 44–56 scale rows around midbody; 5) no spines above the tympanum; 6) Vertebral crest, composed of erected spiny scales, directed posteriorly, continuous from above the tympanum to about the insertion of the hindlimbs, but spines becoming abruptly shorter above the insertion of the front limbs; 7) Vertebral scales, including crest spines 38–49 in males and 38–48 in females; 8) oblique skin fold in front of the fore limbs; 10) Head, chest, front limbs, and anterior dorsal crest turquoise; 11) whitish lateral stripe from the snout along the upper lip and the tympanum to behind the insertion of the fore limbs, behind tympanum becoming brownish beige and fusing with

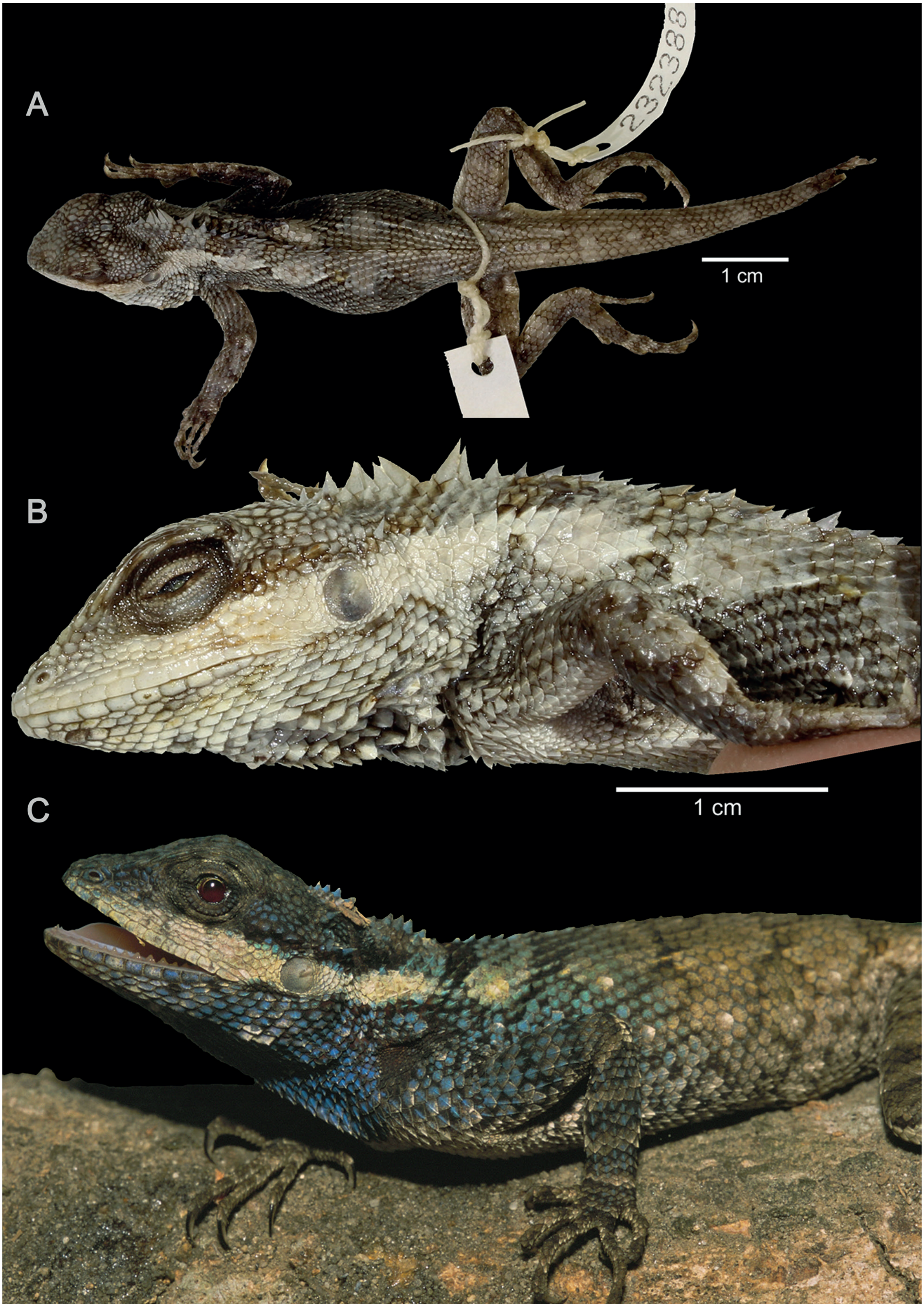


Fig. 9. *Calotes vindumbarbatus* sp. n. **A**. Holotype (CAS 232388, adult male) from Myanmar, Kachin State, Gat Shang Yang Village, general view from above. **B**. Holotype, lateral view. **C**. Living adult male (CAS 232819) from Myanmar, Kachin State, Mohnyin Township, Hepu village [25.094528° N, 96.401833° E, alt. 243 m.].

beige dorsolateral blotches above front limb insertion; 12) four faint beige dorsolateral blotches.

Male coloration. According to the original description ventral and dorsal parts of the body, tail and limbs brownish. Upper parts of the head olive, chest and throat brownish to yellow. Orange-yellowish stripe from the upper lip crossing the tympanum to the shoulders. More recently collected males (Figure 8C) show the head and the anterior of body to the shoulders blue, with a yellowish stripe from the mental towards the upper lips and the tympanum to above and in front of the insertion of the front limbs, followed by indistinct orange blotches.

Variation. Body measurements and meristic characters for adult individuals are given in Table 4. Specimens ranged in size between the smallest juvenile male with a SVL of 58 mm (CAS 239398) to the largest male with a SVL of 101 mm (BMNH 1891.11.26.18) and the largest female measuring 99 mm (BMNH 1868.4.3.62). In general, adult males and females have the same body proportions. Dorsal coloration differs between sexes with coloration characters generally being lighter in females. Both sexes are able to change their color. Turquoise coloration is restricted to the throat, other parts of the head and body brownish. White lateral stripe present, extending from the mental along the upper lips, becoming beige posterior to tympanum, ending in the first lateral blotch of the same coloration, followed by three blotches of the same color but lighter.

Distribution. With the description of the new species of the group, the distribution of *Calotes mystaceus* is restricted to the Irrawaddy delta region of coastal southern Myanmar. However, further research is needed to fully clarify the species distributional boundaries.

Ecology. *Calotes mystaceus* is diurnal and arboreal. The species inhabits forests and more open landscapes with a closed canopy. Mating was observed in September 2014 in a public garden within Yangon (pers. comm. Andreas Hellmann). As in other species of the genus the diet mainly consists of arthropods.

Calotes vindumbarbatus sp. n.
(Fig. 2, Clade C)
urn:lsid:zoobank.org:act:202D3652-BF04-464E-87A2-E1A4611C0CA1

Holotype. CAS 232388 (adult male, Fig. 9A-B, Clade C) from Myanmar, Kachin State, Myitkyina Township, Gat Shang Yang village [25.373421° N, 97.37475° E], collected by T.Z. Min on April 8th 2003.

Paratypes. CAS 232247 from Myanmar, Sagaing Division, Homalin Township, North of Swekawngaw [25.371694° N, 95.369028° E, 205 m.]; CAS 232387 from Myanmar, Kachin State: Myitkyina, Gat Shang Yang village; CAS 239206 from Myanmar, Sagaing Division, Hkanti District, Hkanti Township, Linpha village [25.803389° N, 95.528778° E, 155 m.]; CAS 232819 from Myanmar, Kachin State, Mohnyin Township, Hepu village [25.094528° N, 96.401833° E, 254 m.]; ZFMK 97990 (formerly CAS 232389) from Myanmar, Kachin State: Myitkyina, Gat Shang Yang village.

Diagnosis. A small *Calotes* species of the complex, males with a known maximum SVL of 77 mm, females with a SVL of 73 mm. Tail length short, up to 140 mm. It can be distinguished from the other species of the complex by the combination of the following characters: 1) head slender, not as distinct from the body as in other species of the complex; 2) body scales small and homogeneous, smooth, and arranged in regular rows around the body. 3) Upper dorsolateral scales pointing backwards; 4) body scales arranged in 50–54 rows around midbody; 5) 40–47 vertebral spines and scales in males, 44–48 in females; two short and well separated spines above the tympanum; 6) low nuchal and dorsal crest continuous to the midpoint between the limbs, composed of erect compressed scales, which are larger on the nuchal and smaller on the dorsal crest, gradually decreasing towards the end of the crest; 7) oblique skinfold in front of the fore limb; 8) extremities and tail long, but shorter than in *C. mystaceus*; 9) bluish head and chest; 10) whitish stripe from about the nostril, along the upper lip to about the insertion of the fore limb, posteriorly the whitish stripe is laterally intersected by a dark reticulate pattern across vertebrae; 11) brownish blotches missing.

Description of the holotype. Small male (SVL 77 mm). Extremities relatively slender with the fourth finger and toe longest, tail incomplete. Head slightly distinct from the neck, area posterior of jaw angle slightly swollen. Tip of the snout blunt, rostral small, nostril in a single scale, separated from the rostral and the first supralabial scale by two scales in a row. Canthus rostralis of five scales, distinct and straight, canthus scales continuous with supraciliary scales. Lateral sides of the head flat with 9/9 supralabial scales separated from the orbit by three rows of small scales. Five feebly ridged scales from the orbit to above the tympanum. Tympanum distinct, one spiny scale posteriorly above the tympanum. Mental scale small, bordered by two postmental scales which are separated from each other, only the first pair is in contact with the infralabial scales; 10/10 infralabial scales. Lateral scales on the chin and throat smooth, becoming keeled towards the ventral part. A continuous vertebral crest of elevated spiny scales from above the tympanum to about mid-body, spine height gradually decreasing posterior of the neck, in total 40 vertebral scales from the nape to above the cloaca. Dorsal and lateral scales keeled, pointing back- and upwards, in 50 rows around midbody. Caudal scales parallel keeled, directed backwards. Ventral scales parallel keeled.

Male coloration. Brilliant coloration unknown (Fig. 9C). Head most probably blue, with a whitish stripe, less broad than in the other species of the *C. mystaceus* complex, from behind the nasal scale along the upper lips and the tympanum to the shoulders. Followed

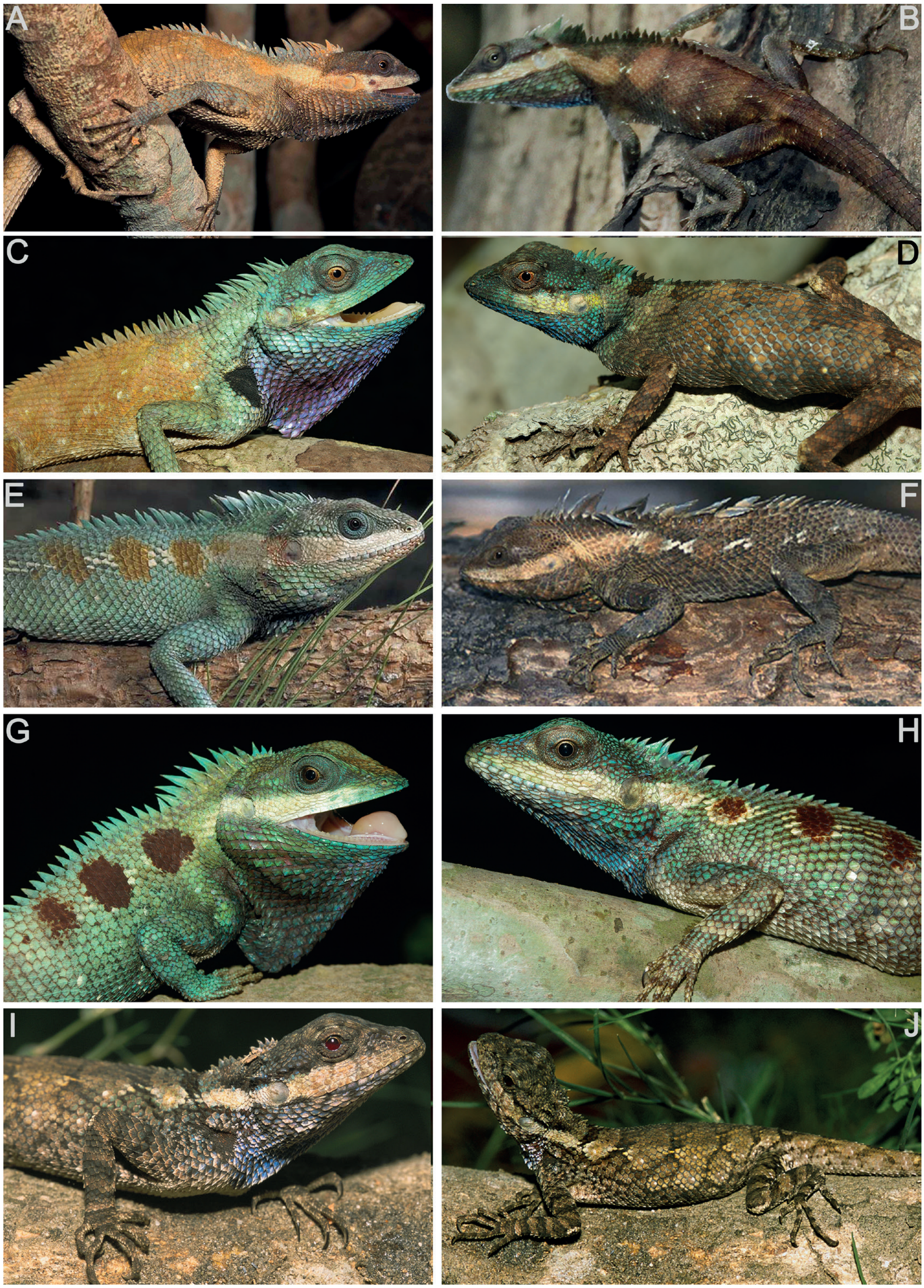


Fig. 10. Overview of the distinct taxa of the *Calotes mystaceus* complex. **A**. *Calotes mystaceus*, male from Mingalardon Township, Hlawga Wildlife Park, Yangon Divison, Myanmar (CAS 213300). **B**. *Calotes mystaceus*, female from Yangon, Myanmar. **C**. *Calotes bachae*, holotype from Cat Tien National Park, Vietnam (ZFMK 92028). **D**. *Calotes bachae*, female paratype from Cat Tien National Park, Vietnam (ZFMK 88936, now IEBR A.2012.23). **E**. *Calotes geissleri* sp. n., male from Chin, Myanmar (CAS 220586). **F**. *Calotes geissleri* sp. n., female from Magwe, Myanmar (CAS 221593). **G**. *Calotes goetzi* sp. n., male from the type locality Kbal Spean, Cambodia (ZFMK 92606). **H**. *Calotes goetzi* sp. n., female from the type locality Kbal Spean, Cambodia (ZFMK 92607). **I**. *Calotes vindumbarbatus* sp. n., male from Kachin, Myanmar (CAS 232819). **J**. *Calotes vindumbarbatus* sp. n., male from Kachin, Myanmar (CAS 232819).

by one distinct and one or more indistinct lateral blotches of the same color.

Variation. Body measurements and meristic characters for adult individuals are given in Table 4. Specimens ranged in size from the smallest female with a SVL of 47 mm (CAS 232247) and the largest female with a SVL of 73 mm (CAS 232387) to the largest male with a SVL of 77 mm (CAS 232388). Adult males are slightly larger than females, because of longer SVLs and tail lengths, and have fewer vertebral scales including the crest scales. However, proportionally males and females are equal. Dorsal coloration of females unknown, but most probably similar to other taxa of the species group with females having lighter coloration characters (lateral stripe, blotches) than males. Most probably, both sexes are able to change their coloration.

Etymology. The specific epithet is a patronym honoring Jens Vindum, retired staff of the California Academy of Sciences, in respect of his outstanding contributions to the herpetology of Myanmar and SE Asia. The patronym of his family name was used, in recognition of his impressive beard which has a direct link to "mystaceus" [Greek for bearded], together with the Latin word "barbatus" for bearded.

Distribution. This new species is so far only known from northern Myanmar.

Ecology. *Calotes vindumbarbatus* sp. n. is diurnal and arboreal to semi-arboreal. It inhabits forests and more open habitats with a dense canopy, but detailed habitat preference is unknown. As in other *Calotes* species the diet most likely consists predominantly of arthropods, but details are not known.

Identification key

Key to the species using the characters of male coloration:

Key to the species using the characters of male coloration

1. Brownish dorsolateral blotches 2
– No brownish dorsolateral blotches............................. 4
2. Prominent dark brown dorsolateral blotches............ .... ***Calotes goetzi*** sp. n.
– Brownish orange/tan/light brown dorsolateral blotches 3
3. Whitish stripe from snout-tip to hindlimb insertion continuous between orange to light brown blotches, body robust with relatively short limbs.................... .... ***Calotes geissleri*** sp. n.
– Whitish stripe from snout-tip to front limb insertion, posterior to tympanum becoming brownish beige and fusing with faint brownish dorsolateral blotches, body slender with relatively long limbs .... ***Calotes mystaceus***
4. Yellowish stripe from below eye to posterior end of head .... ***Calotes bachae***
– Whitish stripe from tip of snout continuing to beyond limb insertion ....***Calotes vindumbarbatus*** sp. n.

Genetically the clades (Fig. 2) refer to the following taxa: Clade A1+A2=*Calotes goetzi* sp. n.; Clade B=*C. geissleri* sp. n.; Clade C=*C. vindumbarbatus* sp. n.; Clade D=*C. mystaceus*; Clade E=*C. bachae*. The morphological variation within the type specimens is given in Appendix IV. In general, PCAs demonstrated that the species are not distinguishable by their morphospaces. However, they are identifiable by their coloration (Fig. 10) and by the combination of single characters (Appendix. V, Table 5). In *Calotes vindumbarbatus* sp. n. both males and females are distinctly shorter than the other species of the complex but have comparably high numbers of vertebral scales and scales around midbody. The largest species with the highest scale counts are *C. geissleri* sp. n. and *C. goetzi* sp. n., whereas *C. bachae* usually has low scale counts.

DISCUSSION

Duméril & Bibron (1837) gave as type locality for *Calotes mystaceus* "Indes orientales (…) pays de Birmans," which corresponds to Myanmar today. The type specimen, a juvenile male (MNHN 2557), morphologically resembles material from the Irrawaddy delta in southern Myanmar. Specimens from this region also form a distinct genetic lineage (Clade D) referable to *Calotes mystaceus.* Since no specimens from other regions could be assigned to *C. mystaceus*, the species' distribution might be restricted to the Irrawaddy delta in southern Myanmar. More research in this area is required to corroborate this assumption. In addition to *C. mystaceus* and *C. bachae*, we revealed the *C. mystaceus* complex to harbor three genetically distinct lineages which are further supported by both morphological characters and coloration of adult males. Several authors have demonstrated, that coloration is an important character to distinguish distinct evolutionary lineages in agamid lizards, especially in taxa with sexually dimorphic coloration but without body ornamentations like horns (see, e.g., Stuart-Fox & Ord 2004; Chen et al. 2012; Quah et al. 2012; Wagner 2014). Within the *C. mystaceus* complex, two lineages (*Calotes bachae*, *C. vindumbarbatus* sp. n.) are clearly distinct in coloration from all other lineages. The genetic distinctness of *Calotes bachae* was also supported by Saijuntha et al. (2017). The remaining three lineages (*Calotes mystaceus*, *C. geissleri* sp. n., *C. goetzi* sp. n.) are more similar to each other in coloration, but distinct to each other according to the phylogenetic results. However, all unnamed lineages are distinct enough in coloration from the recognized species *C. bachae* and *C. mystaceus* to identify them as new species. The former is a distinct genetic lineage within the *C. mystaceus* complex, which would render *C. mystaceus* polyphyletic if these new species were not recognized.

Mean uncorrected p-distances for COI are overall relatively similar between *C. mystaceus* and its close related species (*C. mystaceus* to *C. goetzi* sp. n.: 0.0603; *C. mystaceus* to *C. vindumbarbatus* sp. n.: 0.0656) and similar between *C. goetzi* sp. n. to *C. vindumbarbatus* sp. n. (0.0647), but are higher between *C. mystaceus* to *C. bachae* (0.1415). This is similar to the mean uncorrected p-distances for 12S, where *C. mystaceus* is closely related to *C. goetzi* sp. n. (0.0291) and to *C. vindumbarbatus* (0.0375), but less related to *C. bachae* (0.0548) and *C. geissleri* sp. n. (0.0457). The p-distances are similar between other closely related taxa within the *C. mystaceus* clade: *C. goetzi* sp. n. vs. *C. vindumbarbatus* sp n. (0.0326) while *C. bachae* vs. *C. geissleri* sp. n. (0.0610) has similar p-distances than *C. bachae* vs. *C. goetzi* sp. n. (0.0603) and *C. bachae* vs. *C. vindumbarbatus* sp n. (0.0615). These distances are similar to those shown by Wagner et al. (2009) for recognized taxa at the species level within the genus *Agama*. Therefore, these lineages have been described as new species rather than synonymizing the recently described *Calotes bachae* with *C. mystaceus* and producing a taxonomy which underestimates diversity.

This taxonomic act restricts *C. mystaceus* to Myanmar, while the most widespread taxon of the group, *C. goetzi* sp. n., is distributed nearly across entire central Indochina, excluding Vietnam. While our study also revealed two lineages (A1 & A2) within *C. goetzi* sp. n. (Fig.2), their geographic distribution does not match the phylogeographic pattern previously proposed by Saijuntha et al. (2017). Using the mitochondrial COI gene, Saijuntha et al. (2017) studied 238 *C. goetzi* sp. n. (*C. mystaceus* at that time) from 43 localities across Thailand and Cambodia and found two major lineages. The first of their lineages corresponds to northeast Thailand and adjacent Cambodia and the second to central and northern Thailand respectively. The authors suggested these lineages to be separated by mountain ranges. Our study incorporated three sequences from Saijuntha et al. (2017; table 2), two from the first lineage (CNb1 [20], PTK1 [21]) corresponding to our lineage A2, and one (CMf1 [33]) that matched neither lineage of Saijuntha et al. (2017) but corresponds to our lineage A1. Therefore, the structuring observed by Saijuntha et al. (2017) reveals a fine scale structure within our lineage A2 while the sole sample representing our lineage A1 only found in Myanmar and extreme northwestern Thailand, was suggested to represent a distinct taxon.

The present study supports the Lower Mekong as a distributional boundary separating *C. bachae* from the other taxa as suggested by Hartmann et al. (2013) and Geissler et al. (2015). However, our study demonstrates the distributional range of *C. bachae* to be much larger than assumed, as specimens from northern Vietnam can also be assigned to this species which was previously only known from southern Vietnam and adjacent Cambodia. Myanmar appears to represent a hotspot of species diversity, as all species, except for *C. bachae,* occur in this country. However, further studies are necessary to clarify distributional boundaries, potential contact zones, and speciation processes that led to the diversity of *Calotes* species in Myanmar.

The discovery of so far unrecognized species within the *C. mystaceus* complex in Indochina is not surprising considering the geological history of the region and the large river systems functioning as potential barriers to dispersal. As a result, several new species have been described from the area in recent years (see, e.g., Zug et al. 2006; Bohlen et al. 2016; Zemlemerova et al. 2016). Bain & Hurley (2011) found the Red River in northern Indochina to act as or coincide with an apparent dispersal barrier, but they have not found any evidence that the Mekong River limits dispersal of the regional herpetofauna. In contrast, Geissler et al. (2015) have demonstrated that, at least for amphibians, the Lower Mekong serves as or at least coincides with a biogeographical barrier. Moreover, the distribution pattern of *C. bachae* versus the other taxa of the *C. mystaceus* complex shows that the Lower Mekong represents a barrier for these lizard species.

On the western side of the distributional range of the *C. mystaceus* complex, the Irrawaddy (=Ayeyarwady River) could have acted earlier as a geographic barrier separating *C. goetzi* sp. n. and *C. vindumbarbatus* sp. n. from *C. geissleri* sp. n. leading to speciation. However, for specimens of *C. goetzi* sp. n. (Fig. 1, locality 47) and *C. vindumbarbatus* sp. n. (Fig. 1, locality 64) both collected from the vicinity of "Lake Indawgyi" we are missing more detailed information but suggest that these taxa are already co-occurring in this area, probably due to anthropogenic diversion. According to the known distributional range, dispersal of *C. goetzi* sp. n. could have been restricted by the two large river systems of the Mekong and Irrawaddy resulting in speciation within this geographically isolated area. This is supported by the extreme southern parts of the Salween River marking the genetic split within *C. goetzi* sp. n. as an intraspecific geographic barrier. However, *Calotes mystaceus* is recognized from "Pegu" (Fig. 1, locality 54), referring to the town "Bago" or the "Bago-Division", but not to the borders of the former Pegu Empire, because the latter had ceased to exist long before the specimen was collected. This division encompasses large parts of the supposed distribution area of *C. mystaceus* but in its northern and eastern boundaries as indicated by sample site 54 (see Fig. 1) might overlap with the distribution range of *C. goetzi* sp. n. and therefore it is possible that both species occur sympatrically in this area.

Acknowledgments. We are grateful to the following curators and collection managers: Patrick Campbell (NHM), Lauren

Scheinberg and Jens Vindum (CAS); Ivan Ineich (MNHN), Ulrich Scheidt (NME), Frank Tillack and Mark-Oliver Rödel (ZMB). All of them gave not only access to their collections and material, but also provided help and amicable hospitality. We are grateful to the Ministry of Environment of the Kingdom of Cambodia, the staff of the Angkor Centre for Conservation of Biodiversity (ACCB) for their help during field studies in Cambodia and to the Allwetterzoo Münster (Germany) for the financial support of the ACCB and the field studies. Natalia Ananjeva and Thomas Ziegler helped us with valuable comments on the manuscript and we are thankful to Aaron Bauer who handled it as editor.

REFERENCES

Amber ED, Waengsothorn S, Strine CT (2017) *Calotes mystaceus* (Moustached Crested Lizard). Defensive behaviors. Herpetological Review 48: 640

Bain RH, Hurley MM (2011) A biogeographic synthesis of the amphibians and reptiles of Indochina. Bulletin of the American Museum of Natural History 360: 1–138. https://doi.org/10.1206/360.1

Bohlen J, Petrtyl M, Chaloupkova P, Borin C (2016) *Schistura kampucheensis*, a new species of loach from Cambodia (Teleostei: Nemacheilidae). Ichthyological Exploration of Freshwaters 26 (4): 353–362

Borchsenius F (2009) FastGap 1.2. Department of Biosciences, Aarhus University, Denmark. Online at http://www.aubot.dk/FastGap_home.htm [last accessed 19 Apr. 2021]

Bourret R (1927) La Faune de l'Indochine, Vértébres. Société de Géographie de Hanoi, Hanoi

Bourret R (2009) Les Lézards de l'Indochine. Edition Chimaira, Frankfurt am Main

Chan-Ard T, Parr JWR, Nabhitabhata J (2015) A Field Guide to the Reptiles of Thailand. Oxford University Press, New York

Chen IP, Stuart-Fox D, Hugall AF, Symonds MRE (2012) Sexual selection and the evolution of complex color patterns in dragon lizards. Evolution 66: 3605–3614. https://doi.org/10.1111/j.1558-5646.2012.01698.x

Das I (2015) A Field Guide to the Reptiles of South-east Asia, Myanmar, Thailand, Laos, Cambodia, Vietnam, Peninsular Malaysia, Singapore, Sumatra, Borneo, Java, Bali. Bloomsbury, London, UK

Dray S, Dufour A (2007) The ade4 Package: Implementing the duality diagram for ecologists. Journal of Statistical Software 22 (4): 1–20. https://doi.org/10.18637/jss.v022.i04

Edgar RC (2004) MUSCLE: multiple sequence alignment with high accuracy and high throughput. Nucleic Acids Research 32 (5): 1792–1797. https://doi.org/10.1093/nar/gkh340

Enge KM, Krysko KL (2004) A new exotic species in Florida, the bloodsucker lizard, *Calotes versicolor* (Daudin 1802) (Sauria: Agamidae). Florida Scientist 67: 226–230

Evan SH, Quah CTC, Mohd AM, Shahrul AMS (2012) Color changes during courtship and mating of the green crested lizard *Bronchocela cristatella* (Kuhl, 1820) (Squamata: Agamidae) with a discussion of its behavioral and evolutionary significance. Russian Journal of Herpetology 19: 303–306

Flower SS (1899) Notes on a second collection of reptiles made in the Malay Peninsula and Siam, from November 1896 to September 1898, with a list of the species recorded from those countries. Proceedings of the Royal Zoological Society of London 1899: 600–697

Geissler P, Hartmann T, Ihlow F, Rödder D, Poyarkov NA. Jr, Nguyen TQ, Ziegler T, Böhme W (2015) The Lower Mekong: an insurmountable barrier to amphibians in southern Indochina? Biological Journal of the Linnean Society 144: 905–914. https://doi.org/10.1111/bij.12444

Grismer LL (2011) Lizards of Peninsular Malaysia, Singapore and their Adjacent Archipelagos. Edition Chimaira, Frankfurt am Main, Germany

Hallermann J (2000) A new species of *Calotes* from the Moluccas (Indonesia), with notes on the biogeography of the genus (Sauria: Agamidae). Bonner zoologische Beiträge 49 (1–4): 155–163

Hammer O, Harper DAT, Ryan PD (2001) PAST: Paleontological statistics software package for education and data analysis. Palaeontologia Electronica 4 (1): 1–9

Harikrishnan S, Vasudevan K, Choudhury BC (2010) A review of herpetofaunal descriptions and studies from Andaman and Nicobar Islands, with an updated checklist. Pp 387–398 in: Ramakrishna, Raghunathan C., Sivaperuman C. (eds) Recent trends in biodiversity of Andaman and Nicobar Islands. Zoological Survey of India, Kolkata

Hartmann T, Ihlow F, Edwards S, Sovath S, Handschuh M, Böhme W (2013) A preliminary annotated checklist of the Amphibians and Reptiles of the Kulen Promtep Wildlife Sanctuary in Northern Cambodia. Asian Herpetological Research 4: 36–55. https://doi.org/10.3724/SP.J.1245.2013.00036

Hawkeswood TJ, Sommung A (2018) First record of the Blue Forest Lizard, *Calotes mystaceus* Duméril & Bibron, 1837 (Reptilia: Agamidae) from Ubon Ratchathani Province, Thailand, with a review of literature on the biology and distribution of the species in Thailand. Calodema 607: 1–8

Katoh K, Asimenos G, Toh H (2009) Multiple alignment of DNA sequences with MAFFT. Methods in Molecular Biology 537: 39–64. https://doi.org/10.1007/978-1-59745-251-9_3

Kocher TD, Thomas WK, Meyer A, Edwards SV, Pääbo S, Villablanca FX, Wilson AC (1989) Dynamics of mitchondrial DNA evolution in animals: Amplification and sequencing with conserved primers. Proceedings of the National Academy of Sciences, USA 86: 6196–6200. https://doi.org/10.1073/pnas.86.16.6196

Lalremsanga HT, Khawlhring L, Lalrotluanga (2010) Three additional lizard (Squamata: Sauria) records for Mizoram, India. Journal of Threatened Taxa 2 (2): 718–720. https://doi.org/10.11609/JoTT.o2246.718-20

Manthey U (2008) Agamid Lizards of Southern Asia, Draconinae 1, (Terralog 7a). Edition Chimaira, Frankfurt am Main

Morice A (1875) Coup d'oeil sur la faune de la Cochinchine Française. Association Lyonnaise des Amis des Sciences Naturelles 1875: 25–121

Nazarov R, Poyarkov NA, Orlov NL, Phung TM, Nguyen TT, Hoang DM, Ziegler T (2012) Two new cryptic species of the *Cyrtodactylus irregularis* complex (Squamata: Gekkonidae) from southern Vietnam. Zootaxa 3302: 1–24. https://doi.org/10.11646/zootaxa.3302.1.1

Pal S, Vijayakumar SP, Shanker K, Jayarajan A, Deepak V (2018) A systematic revision of *Calotes* Cuvier, 1817 (Squamata: Agamidae) from the Western Ghats adds two genera and reveals two new species. Zootaxa 4482 (3): 401–450. https://doi.org/10.11646/zootaxa.4482.3.1

Pham AV, Hoang VT, Nguyen TV, Ziegler T, Nguyen TQ (2018) New records and an updated list of lizards from Son La Province, Vietnam. Herpetology Notes 11: 209–216

Posada D, Crandall KA (1998) Modeltest: testing the model of DNA substitution. Bioinformatics 14: 817–818. https://doi.org/10.1093/bioinformatics/14.9.817

R Core Team (2020) R: A language and environment for statistical computing. R Foundation for Statistical Computing,

Vienna, Austria. Online at https://www.R-project.org/ [last accessed 19 Apr. 2021]
Rambaut A, Drummond AJ, Xie D, Baele G, Suchard MA (2018) Posterior summarization in Bayesian phylogenetics using Tracer 1.7. Systematic Biology 67: 901–904. https://doi.org/10.1093/sysbio/syy032
Ronquist F, Teslenko M, van der Mark P, Ayres DL, Darling A, Höhna S, Larget B, Liu L, Suchard MA, Huelsenbeck JP (2012) MrBayes 3.2: efficient Bayesian phylogenetic inference and model choice across a large model space. Systematic Biology 61: 539–542. https://doi.org/10.1093/sysbio/sys029
Saijuntha W, Khumkratok S, Wongpakam K, Thanonkeo S, Senakhun C, Appamaraka S, Yodsiri S, Thongnetr W, Pilap W, Kongbuntad W, Tawong W, Agatsuma T, Petney TN, Tantrawatpan C (2017) Genetic diversity and population structure of blue-crested lizard, *Calotes mystaceus* Duméril & Bibron, 1837 (Squamata: Agamidae) in Thailand. Journal of Genetics 96 (2): 377–382. https://doi.org/10.1007/s12041-017-0767-x
Schliep KP (2011) phangorn: phylogenetic analysis in R. Bioinformatics 27 (4): 592–593. https://doi.org/b2rv94
Schmitz A, Ineich I, Chirio L (2005) Molecular review of the genus *Panaspis* sensu lato in Cameroon, with special reference to the status of the proposed subgenera. Zootaxa 863: 1–28. https://doi.org/10.11646/zootaxa.863.1.1
Simmons MP, Ochoterena H (2000) Gaps as characters in sequence-based phylogenetic analyses. Systematic Biology 49: 369–381. https://doi.org/10.1093/sysbio/49.2.369
Smith, MA (1921) New or little-known reptiles and batrachians from southern Annam (Indo-China). Proceedings of the Zoological Society of London 29: 423–440. https://doi.org/10.1111/j.1096-3642.1921.tb03271.x
Somaweera R., Somaweera N. (2009) Lizards of Sri Lanka: A Colour Guide with Field Keys. Edition Chimaira, Frankfurt am Main
Stuart-Fox DM, Ord TJ (2004) Sexual selection, natural selection and the evolution of dimorphic coloration and ornamentation in agamid lizards. Proceedings of the Royal Society of London B 271: 2249–2255. https://doi.org/dfwvnd
Tirant P (1885) Notes sur les Reptiles et les Batraciens de la Cochinchine et du Cambodge. Excursions et Reconnaissance, Saigon
Uetz P, Freed P, Hošek J (2020) The Reptile Database. Online at http://www.reptile-database.org [last accessed 29 Nov. 2020]
Wagner P, Barej MF, Schmitz A (2009) Studies on African *Agama* VII. A new species of the *Agama agama*-group (Linnaeus, 1758) (Sauria: Agamidae) from Cameroon & Gabon, with comments on *Agama mehelyi* Tornier, 1902. Bonner zoologische Beiträge 56 (4): 285–297
Wagner P (2014) A new cryptic species of the *Agama lionotus* complex from south of the Ngong Hills in Kenya. Salamandra 50 (4): 187–200
Zemlemerova ED, Bannikova AA, Lebedev VS, Rozhnov VV, Abramov AV (2016) Secrets of the underground Vietnam: An underestimated species diversity of Asian moles (Lipotyphla: Talpidae: *Euroscaptor*). Proceedings of the Zoological Institute RAS 320 (2): 193–220. https://doi.org/f9nr
Zug GR, Brown HHK, Schulte II JA, Vindum JV (2006) Systematics of the garden lizards, *Calotes versicolor* group (Reptilia, Squamata, Agamidae), in Myanmar: Central dry zone populations. Proceedings of the California Academy of Sciences 57 (2): 35–68

APPENDIX I. List of specimens examined for morphological analyses. See text for acronyms of museum collections (BMNH numbers refer to the Natural History Museum, London, UK, now NHM).

Calotes bachae (*n* = 17): BMNH 1927.5.20.30, BMNH 1927.5.20.31, BMNH 1927.5.20.32, MNHN 1927.44, MNHN 1927.46, ZFMK 88935, ZFMK 88936 (now IEBR A.2012.23), ZFMK 88937, ZFMK 92028, ZFMK 92029, ZFMK 94395, ZFMK 94396, ZFMK 94397, ZMMU NAP 01509, ZMMU NAP 01512, ZMMU NAP 02910, ZMMU NAP 02911. ***Calotes geissleri* sp. n.** (*n* = 6): BMNH 1856.1.11.98, CAS 210270, CAS 215539, CAS 243028, CAS 243050, CAS 243200 (now ZFMK 97991). ***Calotes goetzi* sp. n.** (*n* = 71): BMNH 1868.4.3.61, BMNH 1868.4.3.63, BMNH 1891.11.26.29, BMNH 1914.4.25.1, BMNH 1929.12.1.11, BMNH 1933.3.10.1, BMNH 1933.3.10.2, MNHN 1884.546, MNHN 1884.547, MNHN 1884.548, MNHN 1893.335, MNHN 1893.336, NME R0581/09, NME R0584/09, NME R0585/09, NME R0686/11, NME R0751/12, NME R0783/13, NME R0784/13, NME R0785/13, NME R0786/13, NME R0787/13, NME R0790/14, ZFMK 16640, ZFMK 16641, ZFMK 40561, ZFMK 43906, ZFMK 43930, ZFMK 43931, ZFMK 43932, ZFMK 44893, ZFMK 44894, ZFMK 45490, ZFMK 45491, ZFMK 45492, ZFMK 45493, ZFMK 45494, ZFMK 45495, ZFMK 45496, ZFMK 45497, ZFMK 45498, ZFMK 45499, ZFMK 45500, ZFMK 45501, ZFMK 45502, ZFMK 45553, ZFMK 45554, ZFMK 47080, ZFMK 47081, ZFMK 49164, ZFMK 49202, ZFMK 49219, ZFMK 49220, ZFMK 49221, ZFMK 49242, ZFMK 49243, ZFMK 49244, ZFMK 49245, ZFMK 49246, ZFMK 55610, ZFMK 55611, ZFMK 55612, ZFMK 84867, ZFMK 88341, ZFMK 92606, ZFMK 92607, ZMB 11603A, ZMB 30186, ZMB 30188A, ZMB 30197, ZMB 6034. ***Calotes mystaceus*** (*n* = 9): BMNH 1868.4.3.60, BMNH 1868.4.3.62, BMNH 1891.11.26.18, CAS 206548, CAS 213300, CAS 239398, CAS 240287, CAS 240296, MNHN 2557. ***Calotes vindumbarbatus* sp. n.** (*n* = 6): CAS 232247, CAS 232387, CAS 232388, CAS 232389 (now ZFMK 97990), CAS 232819, CAS 239206.

APPENDIX II. Results of the analyses of (co-)variance.

	ANOVA (Species*Sex)					ANCOVA (Species*Sex+SVL)				
	Df	**Sum Sq**	**Mean Sq**	**F value**	**Pr(>F)**	**Df**	**Sum Sq**	**Mean Sq**	**F value**	**Pr(>F)**
EyeEar	4	9.8948	2.4737	1.5780	0.1863	4	1.8177	0.4544	1.8669	0.1225
HeadH	4	52.8725	13.2181	1.2188	0.3079	4	13.4904	3.3726	0.9480	0.4398
HeadL	4	30.9982	7.7496	0.4756	0.7536	4	0.7392	0.1848	0.0398	0.9969
HeadW	4	110.3601	27.5900	1.8957	0.1173	4	40.9293	10.2323	2.6634	0.0371
Interorb	4	22.8385	5.7096	2.4167	0.0538	4	13.5416	3.3854	5.1825	0.0008
JawW	4	47.4540	11.8635	1.4079	0.2371	4	13.8597	3.4649	1.1385	0.3431
NarEye	4	3.5544	0.8886	0.7383	0.5681	4	0.4279	0.1070	0.3667	0.8318
SnEye	4	9.0886	2.2721	0.7153	0.5835	4	1.2831	0.3208	0.6036	0.6610
SnW	4	4.5220	1.1305	0.2793	0.8907	4	4.0574	1.0144	0.2483	0.9101
4FingL	4	2.3127	0.5782	0.2894	0.8842	4	0.5621	0.1405	0.3025	0.8757
4ToeL	4	15.4688	3.8672	1.0240	0.3989	4	2.8556	0.7139	0.4292	0.7872
CrusL	4	19.1150	4.7787	0.6483	0.6294	4	1.5220	0.3805	0.3354	0.8535
ForefL	4	3.7860	0.9465	0.2603	0.9027	4	1.4872	0.3718	0.3248	0.8607
HindfL	4	36.3682	9.0920	1.0157	0.4032	4	3.7463	0.9366	0.4704	0.7574
LoArmL	4	24.4185	6.1046	0.7766	0.5431	4	1.6210	0.4052	0.2291	0.9214
SnForeL	4	138.3759	34.5940	0.7310	0.5730	4	42.8073	10.7018	0.7989	0.5288
TailH	4	43.2840	10.8210	1.7550	0.1442	4	9.9255	2.4814	1.7805	0.1390
TailL	4	2929.8532	732.4633	0.6505	0.6283	4	1616.6444	404.1611	0.7285	0.5753
TailW	4	8.8285	2.2071	0.6745	0.6113	4	2.6875	0.6719	0.5411	0.7059
TrunkL	4	91.0978	22.7744	0.4831	0.7481	4	30.3159	7.5790	0.5770	0.6800
UpArmL	4	9.7110	2.4277	0.6430	0.6331	4	3.7578	0.9394	1.0160	0.4031
UpLegL	4	35.9759	8.9940	1.2683	0.2878	4	6.3605	1.5901	0.8706	0.4846
CanthR	4	2.8504	0.7126	0.6347	0.6390	4	1.9353	0.4838	0.4558	0.7679
Eyelid	4	6.9810	1.7452	1.9294	0.1116	4	7.3572	1.8393	2.0673	0.0911
HeadSLn	4	2.5589	0.6397	0.1826	0.9470	4	2.7415	0.6854	0.1938	0.9411
HeadSTr	4	7.6648	1.9162	0.7963	0.5305	4	6.6723	1.6681	0.6886	0.6017
Inflab	4	1.2920	0.3230	0.3560	0.8393	4	1.2709	0.3177	0.3466	0.8458
SnS	4	2.3226	0.5806	0.3999	0.8083	4	2.2272	0.5568	0.3804	0.8221
Suplab	4	1.9375	0.4844	0.5645	0.6890	4	1.7392	0.4348	0.5079	0.7300
4FingLm	4	15.6652	3.9163	2.2782	0.0677	4	15.5661	3.8915	2.2371	0.0721
4ToeLm	4	8.0602	2.0151	0.6241	0.6466	4	8.5495	2.1374	0.6771	0.6098
VertS	4	77.0790	19.2698	1.3790	0.2470	4	74.8883	18.7221	1.3456	0.2588
MidbS	4	30.3863	7.5966	0.7433	0.5648	4	34.1770	8.5443	0.8404	0.5029

APPENDIX III. PCA loadings showing the correlations of the variables with each principal component.

	Females								Males							
	PC1	**PC2**	**PC3**	**PC4**	**PC5**	**PC6**	**PC7**	**PC8**	**PC1**	**PC2**	**PC3**	**PC4**	**PC5**	**PC6**	**PC7**	**PC8**
EyeEar	-0.75525	0.16989	-0.22269	-0.01294	0.24323	0.00700	-0.04300	0.11053	-0.49448	-0.02133	-0.44625	0.06837	0.03929	0.06267	0.31731	0.13505
HeadH	-0.67424	0.02346	0.15873	-0.04942	-0.27829	-0.22727	0.08993	0.19408	-0.54832	-0.40647	-0.24104	0.19018	0.23031	0.17456	-0.28018	-0.06276
HeadL	-0.86595	0.05108	-0.05904	-0.24969	0.21947	0.03273	-0.01811	0.09272	-0.77265	-0.07336	-0.15015	0.20683	0.16099	-0.15454	0.19897	0.15761
HeadW	-0.60811	0.34174	-0.08501	0.32551	0.48056	-0.10907	-0.07130	0.14145	-0.48326	-0.13349	-0.62878	-0.01647	-0.22370	0.10301	0.05942	0.01572
Interorb	-0.59644	0.11476	-0.47778	-0.01772	0.09550	0.27685	0.11750	-0.09362	-0.53248	-0.15727	-0.34010	0.21315	0.30224	-0.01767	-0.30404	-0.06344
JawW	-0.70201	0.21499	-0.24915	0.23554	0.45903	0.00286	-0.01674	-0.02673	-0.54572	-0.29901	-0.45650	-0.07679	-0.14994	0.01496	-0.12911	0.16814
NarEye	-0.55888	0.10090	-0.02613	-0.28023	-0.42155	0.25182	-0.33016	0.26470	-0.63474	0.17902	-0.17293	0.13905	0.08910	-0.22567	-0.08849	0.35082
SnEye	-0.70519	-0.06856	-0.22104	-0.43262	-0.12481	0.00138	-0.09491	0.09595	-0.70986	0.02333	-0.03465	0.14698	0.33054	-0.28926	-0.21731	-0.13810
SnW	-0.35463	-0.21067	-0.47750	-0.22143	-0.06374	0.13042	-0.23115	-0.09282	-0.25000	-0.25742	-0.19629	-0.12475	-0.33731	0.39429	-0.23871	0.04083
X4FingL	-0.38443	-0.31922	0.19819	-0.05155	-0.19096	0.36051	0.01694	-0.55210	-0.52555	0.10494	0.57245	-0.09094	-0.13827	-0.22248	-0.01199	0.16279
X4ToeL	-0.69787	0.04033	0.36659	0.28480	-0.24105	0.21365	0.15823	0.07841	-0.50561	0.24765	0.49917	0.15975	-0.39533	0.23919	-0.18324	-0.03572
CrusL	-0.85104	-0.18965	0.16945	0.07265	-0.12514	-0.10511	0.11699	-0.03772	-0.80714	-0.18595	0.30386	-0.18112	-0.11203	-0.15885	0.04568	-0.07284
ForefL	-0.66583	-0.27931	0.27745	0.37895	-0.22584	-0.19237	-0.02880	-0.06696	-0.72394	0.07031	0.27142	0.03083	-0.17620	0.34152	0.00254	0.07634
HindfL	-0.85521	-0.08047	0.29367	-0.00698	-0.26403	0.09581	0.11081	-0.02399	-0.74190	-0.06006	0.51220	-0.10618	-0.19790	-0.03208	-0.08698	-0.04896
LoArmL	-0.82898	-0.18214	0.21096	0.09452	-0.10009	-0.07696	0.16949	-0.02846	-0.82194	-0.08915	0.15888	-0.11019	0.03200	-0.24464	-0.02479	-0.04130
SnForeL	-0.17538	-0.26259	0.10331	-0.19321	0.63065	0.35282	-0.17874	-0.32135	-0.32402	0.51756	-0.08928	-0.25167	0.23200	0.49388	0.04105	0.08881
TailH	-0.64347	0.18157	-0.09635	-0.16504	-0.03693	-0.10019	-0.21686	0.09744	-0.71715	-0.20001	-0.15575	-0.18595	-0.07670	-0.00060	0.05789	-0.17193
TailW	-0.60269	-0.16016	-0.55652	-0.17410	-0.04155	-0.17064	0.03768	-0.02758	-0.69643	-0.28763	-0.09897	-0.28503	-0.11902	0.09819	0.15706	-0.31878
TrunkL	-0.30761	0.07998	-0.55369	-0.06031	-0.19381	-0.36406	0.40744	-0.34864	-0.35213	0.11127	0.09077	-0.72006	0.21148	0.17127	-0.08173	-0.20439
UpArmL	-0.43331	-0.06371	-0.07085	0.40439	0.15450	0.02603	0.48463	-0.01337	-0.59939	-0.01912	0.31731	-0.03996	0.15214	-0.08263	0.27742	0.08373
UpLegL	-0.70564	0.15285	0.46822	-0.12682	0.21040	0.16618	-0.03706	0.02772	-0.64429	0.00180	0.17486	0.04809	0.27442	0.09823	0.30656	0.31426
CanthR	-0.23477	-0.39123	0.51004	-0.40430	0.38986	-0.18081	-0.03345	0.13267	-0.14721	-0.37221	0.18127	0.70641	-0.14171	0.22109	-0.00282	-0.10976
Eyelid	0.11221	-0.43959	0.16014	-0.15034	0.29433	-0.58140	0.20952	0.01400	0.03388	-0.40134	0.14306	0.45892	-0.24158	-0.00807	0.43340	-0.19650
HeadSLn	0.10498	-0.55602	-0.26430	0.18548	0.09349	0.43481	0.39520	0.26326	0.34793	-0.22163	0.53327	0.00820	0.21020	0.18253	-0.16753	0.38285
HeadSTr	0.16085	-0.79420	-0.10576	0.03352	-0.03726	0.14819	0.18963	0.16826	0.20249	-0.54805	0.26218	-0.08652	0.39470	-0.07070	-0.10593	-0.11181
Inflab	-0.02711	-0.70759	-0.11644	-0.01106	0.22691	-0.00926	-0.06686	0.32044	0.13877	-0.57709	0.12324	0.01809	0.09956	0.31839	-0.18659	0.23510
SnS	0.07648	-0.48978	-0.08728	-0.65324	-0.16930	-0.09119	0.07348	-0.01296	0.06954	-0.67905	0.19148	0.05743	0.30968	0.09565	0.05075	-0.09419
Suplab	-0.33310	-0.42133	0.00313	0.24329	0.05218	-0.32409	-0.45256	-0.37246	0.38437	-0.44679	0.02271	-0.36597	0.12892	0.19758	0.48938	0.03290
VertS	0.06534	-0.62521	-0.06376	0.38778	-0.06164	0.10847	-0.28200	-0.12152	0.34780	-0.57617	0.04991	-0.33670	-0.23357	-0.30235	-0.17845	-0.05054
MidbS	-0.10086	-0.28365	-0.28425	0.56212	-0.16698	-0.13425	-0.44121	0.24713	0.14780	-0.49523	-0.19489	-0.28996	-0.35693	-0.21622	-0.01141	0.48185

APPENDIX IV. Morphological variation in the type specimens of the *Calotes mystaceus* complex. Values given as mean ± standard deviation and minimum – maximum.

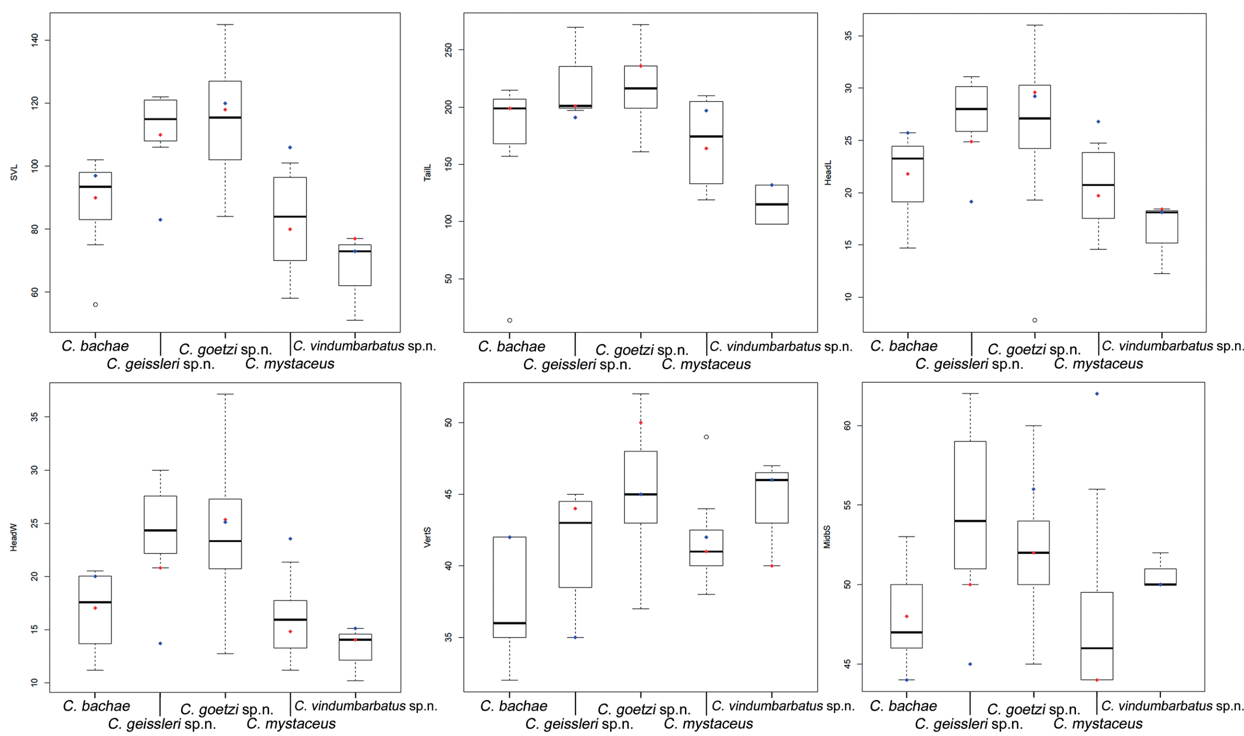
	C. bachae		*C. geissleri* sp. n.		*C. goetzi* sp. n.		*C. mystaceus*	*C. vindumbarbatus* sp. n.	
	holotype	paratypes (*n* = 5)	holotype	paratypes (*n* = 4)	holotype	paratypes (*n* = 2)	holotype	holotype	paratypes (*n* = 4)
SVL	90	85 ± 8.22 74–97	110	108 ± 12.11 92–120	118	97.5 ± 9.19 91–104	80	77	61 ± 13.95 47–73
EyeEar	5.30	5.19 ± 1.2 3.91–7.15	6.95	7.57 ± 1.49 5.88–9.45	8.20	5.55 ± 0.80 4.99–6.12	4.68	4.89	3.79 ± 1.09 2.41–4.71
HeadH	14.88	14.44 ± 2.24 12.19–18.22	17.45	18.51 ± 2.29 15.10–19.85	26.81	17.55 ± 1.07 16.80–18.31	13.56	12.33	10.21 ± 2.23 7.95–12.15
HeadL	21.80	20.84 ± 3.26 16.92–25.72	24.89	26.36 ± 3.44 21.42–29.22	29.60	24.27 ± 1.32 23.33–25.20	19.72	18.43	15.11 ± 3.53 11.83–18.18
HeadW	17.04	15.57 ± 2.57 13.71–20.02	20.81	22.00 ± 3.15 17.81–25.11	25.35	18.34 ± 3.38 15.95–20.73	14.83	14.05	12.66 ± 3.00 9.94–15.39
Interorb	10.09	9.31 ± 1.45 7.85–11.69	9.92	13.22 ± 1.60 11.8–15.52	12.73	10.98 ± 1.00 10.27–11.69	8.20	8.56	7.24 ± 1.64 5.59–8.73
JawW	15.00	14.40 ± 2.06 12.62–17.94	19.32	19.50 ± 2.46 16.50–22.44	20.02	17.34 ± 1.63 16.19–18.50	13.73	12.63	11.68 ± 2.75 9.13–14.20
NarEye	6.16	5.54 ± 1.21 3.75–6.97	7.38	7.47 ± 0.92 6.22–8.41	7.95	6.51 ± 0.39 6.23–6.78	5.88	5.33	4.30 ± 0.81 3.50–5.03
SnEye	10.44	9.54 ± 1.46 7.58–11.54	11.71	12.14 ± 1.31 10.43–13.59	13.76	11.40 ± 0.51 11.04–11.76	9.90	8.63	7.10 ± 1.48 5.69–8.48
SnW	5.45	5.37 ± 0.92 4.06–6.56	6.49	6.59 ± 0.46 5.98–7.09	7.23	6.17 ± 0.49 5.82–6.52	4.98	5.15	4.41 ± 0.68 3.70–5.06
4FingL	11.79	10.28 ± 0.84 8.88–10.94	13.56	13.12 ± 1.04 11.89–14.37	13.30	12.12 ± 0.30 11.90–12.33	10.40	8.89	7.57 ± 1.27 6.46–8.91
4ToeL	15.08	13.47 ± 1.09 11.83–14.59	18.59	16.70 ± 0.75 15.68–17.47	16.62	14.58 ± 0.40 14.30–14.86	14.07	12.42	11.01 ± 1.96 8.60–12.86
CrusL	19.21	17.38 ± 2.07 14.58–19.83	22.83	22.11 ± 2.53 18.49–24.22	24.48	20.88 ± 1.33 19.94–21.82	16.42	15.81	12.75 ± 3.14 9.62–15.55
ForefL	13.74	13.59 ± 1.35 12.11–15.59	17.67	17.14 ± 1.57 15.13–18.44	17.43	15.00 ± 0.28 14.80–15.19	13.59	12.43	10.63 ± 1.96 8.53–12.35
HindfL	26.14	24.34 ± 2.45 20.34–26.97	31.58	29.70 ± 2.22 26.46–31.53	30.61	27.39 ± 0.33 27.16–27.62	24.22	21.64	18.5 ± 3.61 14.78–22.12
LoArmL	15.59	14.95 ± 2.51 11.95–18.64	19.73	18.46 ± 2.22 15.40–20.60	20.82	17.75 ± 0.88 17.12–18.37	13.41	12.23	10.33 ± 2.66 7.50–12.70
SnForeL	30	30.40 ± 4.67 25.00–37.00	40	35.50 ± 4.65 30.00–41.00	30	32.00 ± 1.41 31–33	24	24	21.46 ± 4.6 17.00–25.83
TailH	8.71	7.49 ± 2.02 5.12–10.35	13.44	12.09 ± 2.87 8.11–14.42	15.1	9.48 ± 1.67 8.30–10.66	9.33	8.61	5.47 ± 2.25 3.52–8.31
TailL	199	188.25 ± 21.53 157–203	201	203 ± 17.78 189–223	236	214 ± 0 214–214	164	NA	114 ± 26.08 86–140
TailW	8.44	7.41 ± 1.68 5.27–9.57	11.75	11.78 ± 1.08 10.17–12.35	13.38	9.82 ± 0.03 9.80–9.84	8.25	7.42	6.3 ± 2.58 3.67–9.1
TrunkL	42	37.60 ± 2.97 34–41	54	54.25 ± 4.57 49–59	54	47.00 ± 1.41 46–48	43	35	28.75 ± 4.99 24–34
UpArmL	14.73	13.66 ± 1.62 11.77–15.78	16.64	17.64 ± 1.97 15.98–20.09	17.13	15.77 ± 1.48 14.72–16.81	16.33	10.96	9.85 ± 1.57 8.44–11.79
UpLegL	20.24	18.51 ± 2.78 14.85–21.83	22.42	22.43 ± 2.46 19.23–25.17	23.26	19.91 ± 0.11 19.84–19.99	16.52	14.75	13.22 ± 2.19 10.88–15.32
CanthR	9	8.8 ± 0.84 8–10	6	6 ± 0 6–6	9	8.5 ± 0.71 8–9	6	5	5.25 ± 0.5 5–6
Eyelid	14	13.2 ± 0.45 13–14	12	12.25 ± 1.26 11–14	14	12.5 ± 0.71 12–13	12	12	11.75 ± 1.26 10–13
HeadSLn	17	15 ± 1.73 14–18	14	16 ± 1.83 14–18	14	16 ± 0 16–16	13	15	15.75 ± 1.5 14–17
HeadSTr	16	16.4 ± 1.34 15–18	16	16 ± 0.82 15–17	16	17.5 ± 0.71 17–18	15	16	16.25 ± 0.96 15–17
Inflab	11	10.2 ± 0.45 10–11	9	10.5 ± 1.29 9–12	10	10.5 ± 0.71 10–11	10	10	10.25 ± 0.5 10–11

APPENDIX IV. (continued).

	C. bachae		*C. geissleri* sp. n.		*C. goetzi* sp. n.		*C. mystaceus*	*C. vindumbarbatus* sp. n.	
	holotype	paratypes (*n* = 5)	holotype	paratypes (*n* = 4)	holotype	paratypes (*n* = 2)	holotype	holotype	paratypes (*n* = 4)
SnS	9	8.6 ± 0.89 8–10	7	6.75 ± 0.5 6–7	7	7.5 ± 0.71 7–8	7	7	6.5 ± 0.58 6–7
Suplab	10	10.2 ± 0.45 10–11	11	11 ± 0.82 10–12	9	10 ± 0 10–10	10	9	10.5 ± 0.58 10–11
4FingLm	21	20 ± 1.41 18–22	24	20.25 ± 2.06 18–23	19	20 ± 1.41 19–21	20	21	21 ± 0.82 20–22
4ToeLm	23	23.8 ± 1.3 22–25	28	25.25 ± 2.87 22–29	22	22.5 ± 0.71 22–23	25	26	26 ± 1.15 25–27
VertS	42	42 ± 4.18 35–46	44	46.5 ± 3.7 42–50	50	47.5 ± 4.95 44–51	41	40	46.25 ± 1.71 44–48
MidbS	48	45.8 ± 1.48 44–48	50	55.5 ± 5 50–62	52	52 ± 4.24 49–55	44	50	52.5 ± 1.91 50–54

APPENDIX V. Boxplots of selected characters of examined specimens of the different described species. **A**. Males. **B**. Females.

A: Males



B: Females