## Research article

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

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#### 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 \&
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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

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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 12 S 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 extract-
ed using the peqGold tissue DNA mini kit (peqLab). The primers 12sL1091 (light chain; 5'-AAACTGG-GATTAGATACCCCACTAT- $3^{\prime}$ ) 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; $5^{\prime}-$ TAGACTTCTGGGTGG-CCRAARAAYCA- $3^{\prime}$ ) of Nazarov et al. (2012) were used for amplification of 388 bp of 12 S 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 $\left(G T R+G+I\right.$ for 12 S rRNA; K80+I for the $1^{\text {st }}$, HKY for the $2^{\text {nd }}$, and GTR $+G$ for the $3^{\text {rd }}$ 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 ( $\mathrm{AN}(\mathrm{C}) \mathrm{OVA}$ ) 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 12 s 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 be-
tween Thailand and Myanmar. None of the other clades show geographic separation.
Mean uncorrected p-distances between species for COI and 12 s 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 $\mathrm{AN}(\mathrm{C}) \mathrm{OVA}$, 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 (11.6344444ㅇN $107.456667^{\circ}$ E), 104 m elevation," collected by Peter Geißler on May $10^{\text {th }} 2009$.
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.

Table 1. (continued)


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 Viet-nam-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 $25^{\circ} \mathrm{C}$ in captivity.


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 ( 12 S 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 $\geq$ 0.90 are white, $\mathrm{BPP} \geq 0.95$ are grey, $\mathrm{BPP} \geq 0.99$ 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 |  |  |
| $4^{\text {th }}$ finger | $4^{\text {th }}$ FingL | Distance from juncture of $3^{\text {rd }}$ and $4^{\text {th }}$ digits to distalmost extent (outer/distalmost surface of claw) of $4^{\text {th }}$ finger. |
| $4^{\text {th }}$ toe | $4^{\text {th }}$ ToeL | Distance from juncture of $3^{\text {rd }}$ and $4^{\text {th }}$ digits to distal end of $4^{\text {th }}$ 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 $4^{\text {th }}$ digit lamellae; from $1^{\text {st }}$ 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 $4^{\text {th }}$ 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 12 S 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)

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

Paratypes. CAS 210270 from Myanmar, Alaungdaw Kathapa National Park, Thabakesay (Log Cabin Camp) [22.318194 ${ }^{\circ} \mathrm{N}$, $94.475722^{\circ} \mathrm{E}$ ]; ZFMK 97991 (formerly CAS 243200) from Myanmar, Chin State, Phalum District, Simggial village [23.762583 ${ }^{\circ}$ N, $93.546167^{\circ} \mathrm{E}$, 1362 m.]; CAS 243028, CAS 243050 both from Myanmar, Magway Division, Gangaw District, Gangaw Township, Mauk village [22.335861$N, ~ 94.144583^{\circ} \mathrm{E}$, 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 3 m 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, $\left.103.998611^{\circ} \mathrm{E}\right]$.

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, 3752 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 brown-ish-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 $\pm$ 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 isp. n. |  | C. mystaceus |  | C. vindumbarbatus sp. n. |  |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
|  | females $(n=6)$ | $\begin{gathered} \text { males } \\ (n=10) \end{gathered}$ | females $(n=2)$ | males $(n=4)$ | $\begin{aligned} & \hline \text { females } \\ & (n=33) \\ & \hline \end{aligned}$ | $\begin{gathered} \text { males } \\ (n=38) \end{gathered}$ | females $(n=2)$ | males $(n=7)$ | females $(n=2)$ | males $(n=3)$ |
| SVL | $\begin{gathered} 80.5 \pm 6.35 \\ 71-86 \end{gathered}$ | $\begin{gathered} 88.6 \pm 14.06 \\ 56-102 \end{gathered}$ | $\begin{gathered} 103 \pm 15.56 \\ 92-114 \end{gathered}$ | $\begin{gathered} 114.5 \pm 7.72 \\ 106-122 \end{gathered}$ | $\begin{gathered} 101.33 \pm \\ 10.32 \\ 83-126 \end{gathered}$ | $\begin{gathered} 114.16 \pm \\ 16.34 \\ 84-145 \end{gathered}$ | $\begin{gathered} 87 \pm 16.97 \\ 75-99 \end{gathered}$ | $\begin{gathered} 82.29 \pm 17.58 \\ 58-101 \end{gathered}$ | $\begin{gathered} 60 \pm 18.38 \\ 47-73 \end{gathered}$ | $\begin{gathered} 67 \pm 14 \\ 51-77 \end{gathered}$ |
| EyeEar | $\begin{gathered} 4.82 \pm 0.58 \\ 3.91-5.61 \end{gathered}$ | $\begin{gathered} 5.92 \pm 1.21 \\ 3.56-7.15 \end{gathered}$ | $\begin{gathered} 6.84 \pm 1.36 \\ 5.88-7.8 \end{gathered}$ | $\begin{gathered} 8.11 \pm 1.25 \\ 6.95-9.45 \end{gathered}$ | $\begin{gathered} 6.01 \pm 0.76 \\ 4.66-7.73 \end{gathered}$ | $\begin{aligned} & 7.88 \pm 1.64 \\ & 5.33-11.46 \end{aligned}$ | $\begin{gathered} 5.61 \pm 0.86 \\ 5-6.21 \end{gathered}$ | $\begin{gathered} 5.09 \pm 1.18 \\ 3.49-6.56 \end{gathered}$ | $\begin{gathered} 3.51 \pm 1.56 \\ 2.41-4.61 \end{gathered}$ | $\begin{gathered} 4.35 \pm 0.79 \\ 3.44-4.89 \end{gathered}$ |
| HeadH | $\begin{aligned} & 14.88 \pm 1.85 \\ & 12.19-17.35 \end{aligned}$ | $\begin{aligned} & 16.2 \pm 2.95 \\ & 11.7-19.55 \end{aligned}$ | $\begin{aligned} & 17.43 \pm 3.3 \\ & 15.1-19.76 \end{aligned}$ | $\begin{aligned} & 20.75 \pm 3.88 \\ & 17.45-26.35 \end{aligned}$ | $\begin{aligned} & 17.81 \pm 2.13 \\ & 13.74-22.38 \end{aligned}$ | $\begin{gathered} 21.85 \pm \\ 4.18 \\ 13.55- \\ 31.79 \end{gathered}$ | $\begin{gathered} 15.14 \pm \\ 3.73 \\ 12.5-17.78 \end{gathered}$ | $\begin{gathered} 14.64 \pm 3.57 \\ 9.87-20.03 \end{gathered}$ | $\begin{gathered} 10.05 \pm \\ 2.97 \\ 7.95-12.15 \end{gathered}$ | $\begin{gathered} 11.02 \pm 2.07 \\ 8.64-12.33 \end{gathered}$ |
| HeadL | $\begin{gathered} 19.82 \pm 1.94 \\ 16.92-21.5 \end{gathered}$ | $\begin{aligned} & 21.97 \pm 3.53 \\ & 14.71-25.72 \end{aligned}$ | $\begin{gathered} 324.71 \pm 4.65 \\ 21.42-28 \end{gathered}$ | $\begin{gathered} 28 \pm 2.71 \\ 24.89-31.07 \end{gathered}$ | $\begin{aligned} & 23.75 \pm 2.15 \\ & 20.14-28.39 \end{aligned}$ | $\begin{gathered} 27.18 \pm \\ 5.44 \\ 7.8-36 \end{gathered}$ | $\begin{gathered} 21.12 \pm \\ 3.85 \\ 18.4-23.85 \end{gathered}$ | $\begin{gathered} 20.4 \pm 4.13 \\ 14.59-24.73 \end{gathered}$ | $\begin{gathered} 15 \pm 4.49 \\ 11.83-18.18 \end{gathered}$ | $\begin{aligned} & 16.28 \pm 3.47 \\ & 12.28-18.43 \end{aligned}$ |
| HeadW* | $\begin{aligned} & 15.01 \pm 1.04 \\ & 14.12-16.93 \end{aligned}$ | $\begin{aligned} & 16.89 \pm 3.22 \\ & 11.21-20.54 \end{aligned}$ | $\begin{aligned} & 19.66 \pm 2.62 \\ & +17.81-21.52 \end{aligned}$ | $\begin{gathered} 24.87 \pm 3.86 \\ 20.81-30 \end{gathered}$ | $\begin{aligned} & 17.97 \pm 2.16 \\ & 14.92-22.73 \end{aligned}$ | $\begin{gathered} 23.84 \pm 5.2 \\ 12.75- \\ 37.13 \end{gathered}$ | $\begin{gathered} 15.82 \pm \\ 1.95 \\ 14.44-17.2 \end{gathered}$ | $\begin{aligned} & 15.79 \pm 3.65 \\ & 11.19-21.36 \end{aligned}$ | $\begin{gathered} 12.66 \pm \\ 3.85 \\ 9.94-15.39 \end{gathered}$ | $\begin{aligned} & 13.12 \pm 2.59 \\ & 10.19-15.12 \end{aligned}$ |
| Interorb* | $\begin{gathered} 8.96 \pm 0.73 \\ 7.85-9.73 \end{gathered}$ | $\begin{gathered} 9.92 \pm 1.67 \\ 6.7-11.69 \end{gathered}$ | $\begin{gathered} 14.16 \pm 1.92 \\ 12.8-15.52 \end{gathered}$ | $\begin{aligned} & 12.3 \pm 1.99 \\ & 9.92-14.69 \end{aligned}$ | $\begin{gathered} 11.12 \pm 0.99 \\ 9.2-12.7 \end{gathered}$ | $\begin{gathered} 12.48 \pm \\ 1.85 \\ 8.75-16.65 \end{gathered}$ | $\begin{gathered} 10.39 \pm \\ 1.77 \\ 9.13-11.64 \end{gathered}$ | $\begin{gathered} 8.9 \pm 1.6 \\ 6.62-10.87 \end{gathered}$ | $\begin{gathered} 7.16 \pm 2.22 \\ 5.59-8.73 \end{gathered}$ | $\begin{gathered} 7.74 \pm 1.43 \\ 6.08-8.57 \end{gathered}$ |
| JawW | $\begin{aligned} & 13.92 \pm 0.93 \\ & 12.82-15.56 \end{aligned}$ | $\begin{gathered} 15.07 \pm 2.5 \\ 10.74-18.36 \end{gathered}$ | $\begin{gathered} 17.77 \pm 1.79 \\ 16.5-19.03 \end{gathered}$ | $\begin{aligned} & 20.98 \pm 1.53 \\ & 19.32-22.44 \end{aligned}$ | $\begin{gathered} 16.54 \pm 1.44 \\ 14.2-19.65 \end{gathered}$ | $\begin{gathered} 20.01 \pm \\ 4.06 \\ 12.03- \\ 37.39 \end{gathered}$ | $\begin{gathered} 14.91 \pm \\ 1.53 \\ 13.83-16 \end{gathered}$ | $\begin{gathered} 14.09 \pm 2.73 \\ 10.44-17.6 \end{gathered}$ | $\begin{gathered} 11.84 \pm \\ 3.34 \\ 9.47-14.2 \end{gathered}$ | $\begin{gathered} 11.89 \pm 2.47 \\ 9.13-13.9 \end{gathered}$ |
| NarEye | $\begin{gathered} 5.35 \pm 0.85 \\ 3.75-6.19 \end{gathered}$ | $\begin{gathered} 6.15 \pm 1.04 \\ 4.34-7.62 \end{gathered}$ | $\begin{gathered} 7.31 \pm 1.55 \\ 6.22-8.41 \end{gathered}$ | $\begin{gathered} 7.89 \pm 0.69 \\ 7.38-8.9 \end{gathered}$ | $\begin{gathered} 6.86 \pm 0.73 \\ 5.25-8.44 \end{gathered}$ | $\begin{aligned} & 7.76 \pm 1.31 \\ & 5.31-10.71 \end{aligned}$ | $\begin{gathered} 6.62 \pm 2.05 \\ 5.17-8.07 \end{gathered}$ | $\begin{gathered} 5.99 \pm 1.43 \\ 3.61-7.41 \end{gathered}$ | $\begin{gathered} 4.23 \pm 1.03 \\ 3.5-4.96 \end{gathered}$ | $\begin{gathered} 4.69 \pm 0.86 \\ 3.72-5.33 \end{gathered}$ |
| SnEye | $\begin{aligned} & 9.19 \pm 1.26 \\ & 7.58-10.56 \end{aligned}$ | $\begin{gathered} 10.08 \pm 1.85 \\ 6.32-11.96 \end{gathered}$ | $\begin{array}{r} 12.01 \pm 2.23 \\ 10.43-13.59 \end{array}$ | $\begin{gathered} 12.44 \pm 0.78 \\ 11.71-13.5 \end{gathered}$ | $\begin{gathered} 11.39 \pm 1.13 \\ 8.74-14.22 \end{gathered}$ | $\begin{gathered} 12.97 \pm \\ 2.19 \\ 8.64-17.54 \end{gathered}$ | $\begin{gathered} 10.14 \pm \\ 2.67 \\ 8.26-12.03 \end{gathered}$ | $\begin{gathered} 9.54 \pm 2.2 \\ 6.44-11.72 \end{gathered}$ | $\begin{gathered} 6.97 \pm 1.82 \\ 5.69-8.26 \end{gathered}$ | $\begin{aligned} & 7.69 \pm 1.5 \\ & 5.96-8.63 \end{aligned}$ |
| SnW | $\begin{gathered} 5.04 \pm 0.62 \\ 4.06-5.83 \end{gathered}$ | $\begin{gathered} 5.53 \pm 0.75 \\ 3.94-6.56 \end{gathered}$ | $\begin{gathered} 6.33 \pm 0.49 \\ 5.98-6.68 \end{gathered}$ | $\begin{gathered} 6.92 \pm 0.45 \\ 6.49-7.48 \end{gathered}$ | $\begin{gathered} 6.56 \pm 1.52 \\ 5.11-14.39 \end{gathered}$ | $\begin{gathered} 7.78 \pm 2.88 \\ 5.1-18.43 \end{gathered}$ | $\begin{gathered} 5.42 \pm 0.59 \\ 5-5.84 \end{gathered}$ | $\begin{gathered} 5.37 \pm 0.66 \\ 4.48-6.3 \end{gathered}$ | $\begin{gathered} 4.45 \pm 0.69 \\ 3.96-4.93 \end{gathered}$ | $\begin{gathered} 4.64 \pm 0.81 \\ 3.7-5.15 \end{gathered}$ |
| 4FingL | $\begin{gathered} 10.04 \pm 1.05 \\ 8.56-10.93 \end{gathered}$ | $\begin{gathered} 10.67 \pm 1.47 \\ 7.44-12.04 \end{gathered}$ | $\begin{gathered} 12.35 \pm 0.64 \\ 11.89-12.8 \end{gathered}$ | $\begin{aligned} & 13.69 \pm 0.46 \\ & 13.41-14.37 \end{aligned}$ | $\begin{gathered} 12.14 \pm 1.12 \\ 9.99-14.14 \end{gathered}$ | $\begin{gathered} 13.15 \pm \\ 1.64 \\ 9.82-16.03 \end{gathered}$ | $\begin{gathered} 10.27 \pm \\ 1.89 \\ 8.93-11.6 \end{gathered}$ | $\begin{aligned} & 10.2 \pm 1.74 \\ & 7.63-12.08 \end{aligned}$ | $\begin{gathered} 7.45 \pm 1.34 \\ 6.5-8.4 \end{gathered}$ | $\begin{gathered} 8.09 \pm 1.41 \\ 6.46-8.91 \end{gathered}$ |
| 4ToeL | $\begin{aligned} & 13.38 \pm 0.93 \\ & 11.83-14.59 \end{aligned}$ | $\begin{aligned} & 15.03 \pm 1.95 \\ & 11.04-16.92 \end{aligned}$ | $\begin{aligned} & 16.22 \pm 0.76 \\ & 15.68-16.76 \end{aligned}$ | $\begin{aligned} & 17.68 \pm 0.71 \\ & 16.88-18.59 \end{aligned}$ | $\begin{aligned} & 15.12 \pm 1.57 \\ & 12.75-20.31 \end{aligned}$ | $\begin{gathered} 17.43 \pm \\ 2.19 \\ 13.71- \\ 21.89 \end{gathered}$ | $\begin{gathered} 14.91 \pm 2.5 \\ 13.14- \\ 16.68 \end{gathered}$ | $\begin{aligned} & 14.07 \pm 2.92 \\ & 10.31-18.19 \end{aligned}$ | $\begin{gathered} 10.46 \pm \\ 2.64 \\ 8.6-12.33 \end{gathered}$ | $\begin{gathered} 11.84 \pm 1.4 \\ 10.25-12.86 \end{gathered}$ |
| CrusL | $\begin{aligned} & 17.22 \pm 1.66 \\ & 14.58-18.55 \end{aligned}$ | $\begin{aligned} & 18.46 \pm 2.92 \\ & 12.65-21.57 \end{aligned}$ | $\begin{aligned} & 20.91 \pm 3.43 \\ & 18.49-23.34 \end{aligned}$ | $\begin{aligned} & 23.41 \pm 0.94 \\ & 22.39-24.22 \end{aligned}$ | $\begin{aligned} & 20.57 \pm 2.25 \\ & 17.11-27.25 \end{aligned}$ | $\begin{gathered} 23.31 \pm \\ 2.91 \\ 17.55- \\ 28.98 \end{gathered}$ | $\begin{gathered} 17.35 \pm \\ 3.44 \\ 14.92- \\ 19.78 \end{gathered}$ | $\begin{aligned} & 17.08 \pm 3.81 \\ & 11.83-21.83 \end{aligned}$ | $\begin{gathered} 12.59 \pm \\ 4.19 \\ 9.62-15.55 \end{gathered}$ | $\begin{aligned} & 13.89 \pm 2.96 \\ & 10.48-15.81 \end{aligned}$ |
| ForefL | $\begin{aligned} & 13.35 \pm 0.79 \\ & 12.11-14.17 \end{aligned}$ | $\begin{aligned} & 14.62 \pm 2.22 \\ & 10.29-17.73 \end{aligned}$ | $\begin{gathered} 15.9 \pm 1.09 \\ 15.13-16.67 \end{gathered}$ | $\begin{gathered} 18.25 \pm 0.4 \\ 17.67-18.56 \end{gathered}$ | $\begin{aligned} & 15.95 \pm 1.68 \\ & 13.98-22.19 \end{aligned}$ | $\begin{gathered} 17.71 \pm \\ 2.03 \\ 13.16-21.4 \end{gathered}$ | $\begin{gathered} 13.36 \pm \\ 1.34 \\ 12.41-14.3 \end{gathered}$ | $\begin{gathered} 13.88 \pm 2.75 \\ 9.97-17.8 \end{gathered}$ | $\begin{gathered} 10.39 \pm \\ 2.64 \\ 8.53-12.26 \end{gathered}$ | $\begin{gathered} 11.39 \pm 1.73 \\ 9.39-12.43 \end{gathered}$ |
| HindfL | $\begin{gathered} 23.75 \pm 1.94 \\ 20.34-25.3 \end{gathered}$ | $\begin{gathered} 25.69 \pm 3.18 \\ 19.75-28.7 \end{gathered}$ | $\begin{array}{r} 28.39 \pm 2.74 \\ 26.46-30.33 \end{array}$ | $\begin{aligned} & 30.88 \pm 0.81 \\ & 29.94-31.58 \end{aligned}$ | $\begin{aligned} & 27.31 \pm 2.22 \\ & 23.74-33.62 \end{aligned}$ | $\begin{gathered} 30.82 \pm \\ 3.25 \\ 23.36- \\ 37.41 \end{gathered}$ | $\begin{gathered} 25.34 \pm \\ 3.85 \\ 22.62- \\ 28.07 \end{gathered}$ | $\begin{aligned} & 24.22 \pm 4.89 \\ & 17.24-29.07 \end{aligned}$ | $\begin{gathered} 17.89 \pm 4.4 \\ 14.78-21 \end{gathered}$ | $\begin{aligned} & 19.95 \pm 3.35 \\ & 16.09-22.12 \end{aligned}$ |
| LoArmL | $\begin{aligned} & 14.45 \pm 1.51 \\ & 11.95-15.75 \end{aligned}$ | $\begin{gathered} 15.49 \pm 2.93 \\ 9.6-18.64 \end{gathered}$ | $\begin{gathered} 17.39 \pm 2.81 \\ 15.4-19.38 \end{gathered}$ | $\begin{aligned} & 20.09 \pm 1.31 \\ & 18.48-21.57 \end{aligned}$ | $\begin{gathered} 17.5 \pm 2.22 \\ 13.64-24.14 \end{gathered}$ | $\begin{gathered} 19.78 \pm 3.3 \\ 13.64- \\ 27.73 \end{gathered}$ | $\begin{gathered} 15.42 \pm \\ 3.44 \\ 12.99- \\ 17.85 \end{gathered}$ | $\begin{gathered} 13.98 \pm 3.27 \\ 8.99-17.38 \end{gathered}$ | $\begin{gathered} 10.1 \pm 3.68 \\ 7.5-12.7 \end{gathered}$ | $\begin{gathered} 11.12 \pm 2.17 \\ 8.62-12.51 \end{gathered}$ |
| SnForeL | $\begin{gathered} 27.83 \pm 3.43 \\ 23-32 \end{gathered}$ | $\begin{gathered} 30.3 \pm 11.23 \\ 2-39 \end{gathered}$ | $\begin{gathered} 32 \pm 2.83 \\ 30-34 \end{gathered}$ | $\begin{gathered} 42 \pm 5.6 \\ 37-50 \end{gathered}$ | $\begin{gathered} 35.21 \pm 4.54 \\ 29-45 \end{gathered}$ | $\begin{gathered} 40.17 \pm \\ 7.61 \\ 27-59 \end{gathered}$ | $\begin{gathered} 31.5 \pm 6.36 \\ 27-36 \end{gathered}$ | $\begin{gathered} 29.29 \pm 8.04 \\ 20-41 \end{gathered}$ | $\begin{gathered} 21 \pm 5.66 \\ 17-25 \end{gathered}$ | $\begin{gathered} 22.61 \pm 4.1 \\ 18-25.83 \end{gathered}$ |
| TailH | $\begin{gathered} 6.72 \pm 0.97 \\ 5.12-8.06 \end{gathered}$ | $\begin{aligned} & 9.74 \pm 2.07 \\ & 6.02-12.29 \end{aligned}$ | $\begin{gathered} 10 \pm 2.67 \\ 8.11-11.89 \end{gathered}$ | $\begin{aligned} & 14.56 \pm 1.31 \\ & 13.44-16.43 \end{aligned}$ | $\begin{aligned} & 9.79 \pm 1.44 \\ & 7.46-12.69 \end{aligned}$ | $\begin{gathered} 14.41 \pm \\ 3.26 \\ 6.6-21 \end{gathered}$ | $\begin{aligned} & 9.27 \pm 3.52 \\ & 6.78-11.76 \end{aligned}$ | $\begin{aligned} & 9.04 \pm 2.95 \\ & 5.18-13.07 \end{aligned}$ | $\begin{gathered} 4.88 \pm 1.92 \\ 3.52-6.23 \end{gathered}$ | $\begin{gathered} 6.91 \pm 2.69 \\ 3.81-8.61 \end{gathered}$ |

Table 5. (continued).

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

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 [25.094528º N, $96.401833^{\circ}$ 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 $\mathrm{sp} . \mathrm{n}$.

(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 [ $25.373421^{\circ} \mathrm{N}, 97.37475^{\circ} \mathrm{E}$ ], collected by T.Z. Min on April $8^{\text {th }} 2003$.

Paratypes. CAS 232247 from Myanmar, Sagaing Division, Homalin Township, North of Swekawngaw [25.371694 $\left.{ }^{\circ} \mathrm{N}, 95.369028^{\circ} \mathrm{E}, 205 \mathrm{~m}.\right]$; CAS 232387 from Myanmar, Kachin State: Myitkyina, Gat Shang Yang village; CAS 239206 from Myanmar, Sagaing Division, Hkanti District, Hkanti Township, Linpha village [25.803389ํ $\left.\mathrm{N}, 95.528778^{\circ} \mathrm{E}, 155 \mathrm{~m}.\right] ;$ CAS 232819 from Myanmar, Kachin State, Mohnyin Township, Hepu
village [ $\left.25.094528^{\circ} \mathrm{N}, 96.401833^{\circ} \mathrm{E}, 254 \mathrm{~m}.\right] ;$ 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 $\qquad$

- 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 $\qquad$
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 $\mathrm{A} 1+\mathrm{A} 2=$ Calotes goetzi sp. n.; Clade $\mathrm{B}=C$. geissleri sp. n.; Clade $\mathrm{C}=C$. vindumbarbatus sp. n.; Clade $\mathrm{D}=$ C. mystaceus; Clade $\mathrm{E}=$ 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 12 S , 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.

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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

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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 | $\operatorname{Pr}(>\mathbf{F})$ | Df | Sum Sq | Mean Sq | F value | $\operatorname{Pr}(>\mathbf{F})$ |
| 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 |


| 5818 | Itilo ${ }^{\circ}$ | 229120 | £69s¢0－ | $96687^{\circ}$ | $68661^{\circ}$ | EzS6t＇0 | 08LtI 0 | \＆ILLで0 | てItto 0 | sてtelo | $8699 \mathrm{I}^{\circ} 0^{-}$ | z9S 0 | szt8z | S9¢8z | 9800 | SqP！${ }^{\text {¢ }}$ |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
| ＋SOSO．0－ | St8Lio ${ }^{-}$ | sєzoé0－ | Lธ£Ė0－ | 0＜9¢E0－ | $166+0^{\circ}$ | LI9LS $0^{-}$ | 08LtE 0 | zsizto ${ }^{-}$ | $\mathrm{F}^{-}$ | $80{ }^{\circ} 0$ | ＋919000－ | BLL8E0 | 9LE9000－ | 2sz90－ | ES90 |  |
| 06てE0＇0 | 8668t 0 | 8¢L610 | 268z10 | L69980－ | lızzo | C9tt＇0－ | ¢t8\％ 0 | 9十てLE0－ | ＋0 | $\varepsilon^{\circ}$ | 81250.0 | で0 | 000 | £ยıてt＇0－ | 01¢E¢0－ | dns |
| $61+60^{\circ} 0^{-}$ | sloso 0 | S95600 | 8960¢0 | ¢tLSOO | 8tI610 | 96290－ | tS6900 | $96 \mathrm{zto} 0^{\circ}$ | $0 \cdot 0$ | 160 | $69 \mathrm{I}^{\circ} \mathrm{O}$ | ¢s9 | zL80 | 8268 ＇0＇$^{-}$ | 8t9L0 0 | ${ }^{\text {us }}$ |
| 01s¢ ${ }^{\text {co }}$ | $65981^{\circ} 0^{-}$ | 6 681800 | 95660 0 | $60810^{\circ} 0$ | 七てE | 60LLS | LL8\＆1 | tooze | 98990 | 97600 | 169zz＇0 | 90110 | t911 | 6SLOLO－ | ILL20 |  |
| 18 | ¢6S010 | L0＇0 | $68^{\circ}$ | $80^{\circ}$ | 8129\％0 | S08tS＇0－ | 6 tzoz 0 | $9{ }^{1}$ | £96810 | $618 t \mathrm{I}^{\circ}$ | $0^{\circ}$ | zşE00 | 92SO1＇0－ | $02 \mathrm{t} 6 \mathrm{~L}^{\circ} \mathrm{O}$ | S8091．0 | ${ }^{\text {H }}$ |
| s8z880 | $9 \mathrm{I}^{\circ}$ | £sz810 | ozoız＇0 | $800^{\circ}$ | cs | zz | くte | 9г¢9z＇ | 02S680 | to | $60^{\circ}$ | 8t5810 | ¢t9 | zo9scoo | 6t0 | ${ }^{\text {H }}$ |
| 0S961 $0^{-}$ | 0ャを¢t | L08000 $0^{-}$ | 8SItro－ | 268St＇0 | 90¢trio | เE10か0－ | 88EE00 | 00t100 | で0 | 0ti85 $0^{-}$ | て＇0 | E0S $\mathrm{l}^{0}$ | ＋09100 | 6S6をto－ | IzZİ0 | ${ }^{0} \mathcal{S}_{\text {G }}$ |
| $92600^{\circ} 0^{-}$ | 282000－ | 601でて 0 | ＋10 | It90 ${ }^{\circ} 0$ | $18{ }^{\circ}$ | IZZLE 0 | $\mathrm{H}^{\circ} \mathrm{O}$ | L9zelo | Stexo 0 | $18081^{\circ}$ | 986880 | 0t＇0 | toors | ¢ZI6\％${ }^{\circ}$ | LLter 0 | \％ |
| 9でİ0 | 9s90¢0 | ¢ $2860^{\circ}$ | てt＋LでO | $608+0.0$ | 98tL | $08100^{\circ}$ | $6 \mathrm{t}+9{ }^{\circ} \mathrm{O}$ | zllzo＇o | 90LE0 ${ }^{\circ}$ | $81991^{\circ}$ | 0toIz＇0 | s9210－ | zz89t＇0 | S8z | $0^{-}$ | $\mathrm{d}_{0}$ |
| \＆L¢800 | でLLで0 | £9880 $0^{-}$ | tIzsio | $96680^{\circ} 0^{-}$ | İLI | 216I0．0－ | $68665^{\circ} 0^{-}$ | LEE100－ | ¢9t8t ${ }^{\circ}$ | $0{ }^{\circ}$ | OStstio | － | S8020 $0^{-}$ | ILE900－ | 1 İ |  |
| 6 6toz＇0－ | \＆LI $800^{-}$ | Lzillo | 8turio | 900zL＇0 | LL0600 | Lzı | £Izss $0^{-}$ | t98téo | t＋LOt＇0 | 90t980－ | 1886100－ | 18090 $0^{-}$ | 69¢ss＇0－ | 866L0＇0 | 19L0¢ $0^{-}$ | IL |
| $8 \angle 81$ ¢ $^{-}$ | 90LSİ0 | $61860^{\circ}$ | 206II 0 | ¢0s8z＇0 | L6860 $0^{-}$ | £948200－ | £ャ9690－ | 8SLzo ${ }^{\circ}$ | 89LE00 | t90L | Ssito $0^{-}$ | 01tLIO | zs9ss | 9109 | $69709{ }^{\circ}$ | ${ }_{\text {Item }}$ |
| £6ILİ0－ | 68LSO 0 | 09000 $0-$ | 0L9LO＇0－ | S65810 | slssio | 100020 | SILIL＇0－ | t＋L60 0 | 98912\％${ }^{-}$ | $610010-$ | \＆6980 $0^{-}$ | tos910－ | ¢¢960 $0^{\circ}$ | LSI810 | LtEt90－ | ${ }_{\text {Hel }}^{\text {L }}$ |
| $18880^{\circ} 0$ | S01to 0 | $8886 \mathrm{t}^{\circ}$ | 00z£z＇0 | L91sz | 826 | 9SLIS | zotz | ¢ย1ž＇0－ | ＋ட8L | 282 | S90¢9\％ | 12¢610 | IE\＆or0 | 6sz9rio－ | 8ESLI＇0－ | HS |
| $0 \varepsilon เ+0^{\circ}{ }^{-}$ | 6LLZo\％${ }^{-}$ | t9ttro－ | $00 z$ ¢0 | $61011^{\circ}$ | 888s10 | ¢1680．0－ | ＋6Iz8\％${ }^{-}$ | $9+8700^{-}$ | ${ }^{6} 669 \mathrm{I}^{\circ}$ | 969 $0^{\circ} 0^{-}$ | 600010－ | 2st60 0 | 960120 | ゅız810－ | $86828^{\circ}{ }^{-}$ | ${ }^{\text {T }}$ |
| $968 t 00^{-}$ | $86980^{\circ}$ | 80ZE00 | $06 \mathrm{L6} \mathrm{I}^{\circ}$ | $8190{ }^{\circ} \mathrm{O}$ | 0zzIS 0 | 900900 | 06It＇${ }^{\circ} 0^{-}$ | $66 \mathrm{Ez} 0^{\circ}$ | I80150 | 185600 | ¢0t920－ | $86900{ }^{\circ}-$ | L9¢6て＇0 | く00800－ | IzS580－ | ри！ |
| ＋¢qLO＇0 | tszoo 0 | 2sitco | 0z9く10－ | ¢80¢0\％ | てtILでO | IEOLO 0 | t6ezio－ | $969900^{-}$ | 08820.0 | Lez610－ | ャ8szz＇0－ | S68LE0 | StLlz＇0 | IE6Lで0－ | ¢85990－ | ${ }^{0.0}{ }^{\text {d }}$ |
| ＋8ZLO\％${ }^{-}$ | 89St0 0 | s88S10 ${ }^{-}$ | £oztio | 2lisio | 9880¢0 | S65810－ | til08 $0^{-}$ | てLLE0＇0－ | $66911^{\circ}$ | hisoro－ | diszio－ | s9zlo 0 | St6910 | ¢96810－ | tots8 $0^{-}$ | sn．1 |
| てLSE0．0－ | ＋てE810－ | $6168 z^{\circ} 0$ | £¢S680－ | ¢L6Sİ0 | LI66t＇0 | ¢9L | 19S0S $0^{-}$ | I＋8L0 | £z8s10 | ¢9\＆Iで0 | Soltro ${ }^{-}$ | で0 | $6599 \varepsilon^{\circ} 0$ | EE0t0 | L8L6900－ | ${ }^{\text {PouLt }}$ ¢ |
| 6LZ910 | $661500^{-}$ | $8 \pm$ ¢zzo－ | Lz8E10－ | ＋6060 $0^{-}$ | StLLS 0 | ＋6t010 | ssszs＇0－ | 0izss ${ }^{-}$ | ${ }^{+69100}$ | IS0980 | 960610－ | ¢siso ${ }^{\circ}$ | $61861^{\circ} 0$ | 2z61¢0－ | Ett $8 \varepsilon^{\circ} 0^{-}$ | ¢utat |
| E80to $0^{\circ}$ | LL8EZ＇0－ | 62t6e： 0 | IELE์ $0^{-}$ | sltzio | 6296100 | でくszoo | 000sz＇0－ | 2876000－ | Sıİて＇0－ | ztocio | $t \angle \varepsilon 90^{\circ} 0^{-}$ | £tizz＇0－ | osllt＇o－ | L90ıで0 | £9tsc $0^{-}$ | us |
| $0188 \mathrm{I}^{\circ} 0^{-}$ | İLİ＇0－ | 926820－ | tSosc．0 | 869＋10 | S9＋E00 $0^{-}$ | ££Ez00 | 9860＇${ }^{-}$ | ¢6560 | $16+60^{\circ} 0^{-}$ | 8E1000 | I8tで0－ | 29を¢to ${ }^{-}$ | ャ012て＇0－ | 9589000－ | ${ }^{6} 150 L^{\circ} 0^{-}$ | aus |
| z80s $\varepsilon^{\circ} 0$ | $6+8800^{-}$ | L9szzo－ | 016800 | S06E10 | £6ZLI＇0－ | 206LI＇0 | ャLt¢9\％－ | 0＜taz＇0 | $910 \varepsilon \varepsilon^{\circ} 0^{-}$ | 28Isz＇0 | ssizto－ | £z08z＇0－ | £19z0＇0－ | $0600{ }^{\circ} 0$ | $88855^{\circ} 0^{-}$ | ${ }_{\text {Hen }}$ |
| †18910 | H6zio ${ }^{-}$ | $96+10^{\circ} 0$ | ＋66t10－ | 6L9LO＇0－ | 0s9st＇0－ | 1066て＇0－ | ULStS $0^{-}$ | £ ¢9zo＇0－ | ＋ $2910^{\circ} 0^{-}$ | $98200^{\circ}$ | E06St＇0 | tssczo | Sl6trio | $66 \mathrm{tI} \mathrm{C}^{0}$ | 10zoL＇0－ | mer |
| カ¢¢90 ${ }^{\circ}$ | t0tos： | L9LIOO | †てzǫ 0 | ¢Іદાで0 | 010¢E\％ $0^{-}$ | LILsto－ | 8tてEs $0^{-}$ | 298600－ | osclio | s89Lて 0 | OSS600 | ULLIOO－ | 8LLLt＇0－ | 9とすtio | t＋965 ${ }^{-}$ | ［ |
| zLsio＇o | $27650^{\circ}$ | Losoro | 0L£zz＇0－ | － $4910^{\circ} 0^{-}$ | $8 \angle 8299^{-}$ | $6+\varepsilon$ E10－ | 9288800 | stitio | 0¢LLO＇0－ | L06010－ | 9S08t＇0 | isczeo | 1058000－ | ¢LItE 0 | ${ }^{118090} 0^{-}$ |  |
| 19LSİ0 | L68610 | tStsio ${ }^{-}$ | $6609{ }^{\circ} 0$ | ¢89020 | stostio－ | $9 \varepsilon \varepsilon L 0^{\circ} 0^{-}$ | S9zLL＇0－ | zLz600 | H8100\％ | £Lz¢00 | Lt6İ＇0 | 6962て＇0－ | ＋0650＇0－ | 80150 | ¢65980 $0^{-}$ | ${ }_{\text {¢ }}^{\text {¢ }}$ н |
| $9 \angle 290^{\circ} 0^{-}$ | $8108 \mathrm{C}^{\circ} 0^{-}$ | 9StLI＇0 | 1 E0¢ ${ }^{\text {co }}$ | $81061^{\circ} 0$ | toltro $0^{-}$ | Lt90t＇0－ | 2¢8t5 $0^{-}$ | $80661^{\circ}$ | £6680 0 | Lzlzz＇0－ | 6z8Lて＇0－ | 2t6to $0^{-}$ | EL8sio | $9+\varepsilon z 0^{\circ}$ | tてt＜9 $0^{-}$ | нреэ $^{\text {¢ }}$ |
| Sosel ${ }^{\circ}$ | IELIE＊0 | L92900 | $62680^{\circ}$ | LE8900 | sc9tro－ | ££เz00－ | 8tt6t＇0－ | \＆S0150 | $00 ¢ t 00^{-}$ | 00L00 0 | £てEtで0 | ＋6z1000－ | 69zzz＇0－ | $6869{ }^{\circ} 0$ | szsslo ${ }^{-}$ |  |
| 8．d | LOd | 9 d | s．d | ¢0d | £ ${ }^{\text {d }}$ | 20d | IDd | 8．d | LOd | 9 da | SOd | t．d | £．d | 20d | 10d |  |

APPENDIX IV. Morphological variation in the type specimens of the Calotes mystaceus complex. Values given as mean $\pm$ standard deviation and minimum - maximum.

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

APPENDIX IV. (continued).

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

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


## B: Females



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Zoologisch-Botanische Datenbank/Zoological-Botanical Database
Digitale Literatur/Digital Literature
Zeitschrift/Journal: Bonn zoological Bulletin - früher Bonner Zoologische Beiträge.
Jahr/Year: 2021
Band/Volume: 70
Autor(en)/Author(s): Wagner Philipp, Ihlow Flora, Hartmann Timo, Flecks Morris, Schmitz Andreas, Böhme Wolfgang

Artikel/Article: Integrative approach to resolve the Calotes mystaceus Duméril \& Bibron, 1837 species complex (Squamata: Agamidae) 141-171

