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Taxonomy, distribution, and conservation status of a rare arboreal lizard, *Bronchocela celebensis* Gray, 1845 (Reptilia: Agamidae) endemic to Sulawesi, Indonesia

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Abstract

Bronchocela celebensis Gray, 1845 is one of the rarest species of the genus, known only from less than 20 museum specimens collected from northern Sulawesi. It is often confused with its similar congener, *B. cristatella*, which occurs widely throughout the Indonesian Archipelago and Peninsular Malaysia, except on the Sulawesi mainland. Here, we examine the morphology of *B. celebensis* based on 46 museum specimens including freshly collected individuals, and redescribe the species based on the holotype (by monotypy). We studied the characters of *B. celebensis* with morphometric comparison to its allopatric congener *B. cristatella* from the adjacent islands of southern Sulawesi in Indonesia. Based on the current distribution pattern and the apparent threats, we update the conservation status of *B. celebensis* using the IUCN Red List Criteria and propose that it be considered as a Vulnerable (VU) species endemic to Sulawesi.

Key words: Conservation, Endemic, Indonesia, morphometric, Celebes, taxonomy

Introduction

The agamid lizard genus, *Bronchocela* Kaup, 1827, has a wide range from southern Sundaland in the west to Papua New Guinea and other transcontinental oceanic islands of the Indonesian and Sulu Archipelagos (De Rooij 1915; Wermuth 1967; Diong & Lim 1998; Hallermann 2005; Manthey 2008; Grismer *et al*. 2015; Amarasinghe *et al*. 2022a, b), but excluding the Andaman and Nicobar Islands (Chandramouli *et al*. 2023). All the species are arboreal, diurnal, and colourful lizards inhabiting both forests and anthropogenic habitats up to over 1,600 m above sea level (Grismer 2011). The exact distribution of each species of *Bronchocela* is unknown due to the close similarity of some of the species to one another leading to difficulties of species determination (Hallermann 2005) and intraspecific variation. Currently, the genus *Bronchocela* consists of 15 species, four of which are insular species distributed across the Indonesian Archipelago (Amarasinghe *et al*. 2022a, b): *B. cristatella* (Kuhl, 1820); *B. jubata* Duméril & Bibron, 1837; *B. celebensis* Gray, 1845; and *B. hayeki* (Müller, 1928).

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Bronchocela celebensis was described by Gray (1845) based on a single specimen (holotype by monotypy) collected from "Celebes" (Sulawesi). Boulenger (1885) reported additional specimens of this species specifically from Manado, northern Sulawesi, but listed them under the genus *Calotes* Cuvier, 1817. Moody (1980) transferred the species back to the genus *Bronchocela*. De Rooij (1915) reported the species from Rurukan in northern Sulawesi, from Posso (Poso) in Central Sulawesi and from Bantimurong (Bantimurung) in southern Sulawesi. Hallermann (2005) reported seven additional specimens from Manado, northern Sulawesi. Manthey (2008) reported the species from Lore Lindu National Park, Central Sulawesi and Dumoga-Bone (Bogani Nani Wartabone), northern Sulawesi. Koch (2012) listed a specimen from Maros, Southwestern Sulawesi, and another from North Sulawesi. Previously, this species had only been reliably reported from eight localities. Here we report the species from 10 additional localities and provide comprehensive details on its morphology and morphometry.

Material and methods

During field surveys conducted on Sulawesi Island, Indonesia, we encountered some individuals of *Bronchocela celebensis* (Fig. 1). Natural history observations were made by studying the animals' activity from a distance of at least 3–4 m, carefully without disturbing them. Latitude, longitude, and elevation of observed and/or collected specimens were recorded using a Garmin GPSmap 60CSx using WGS 84 map datum.

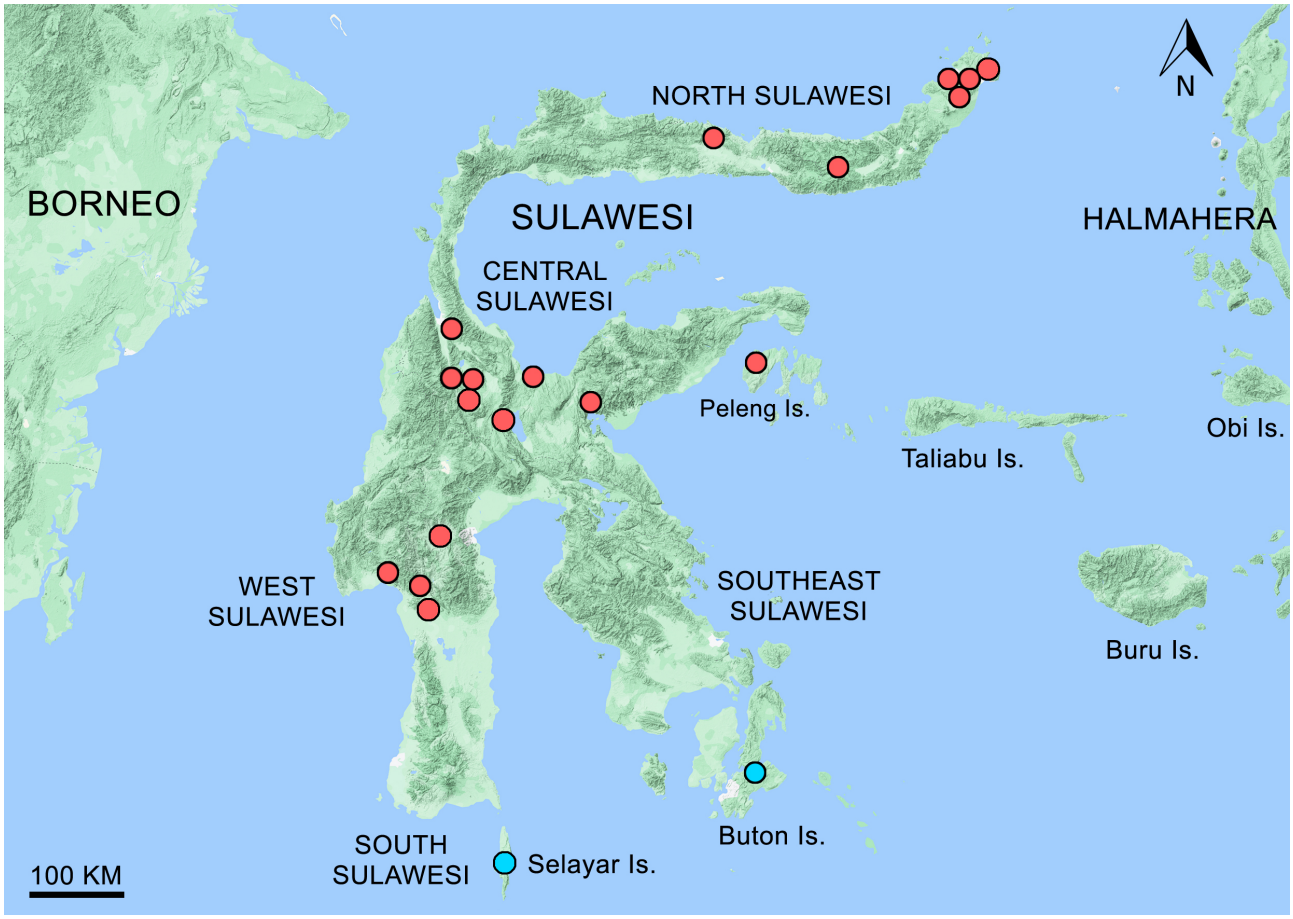

FIGURE 1. Current distribution map showing the collection/observation localities of *Bronchocela celebensis* (red) and its allopatric congener, *B. cristatella* sensu lato (blue) on adjacent islands of southern Sulawesi.

Morphological, morphometric, and meristic characters. We compared museum specimens to the holotype of *Bronchocela celebensis*, and all the congeners included in the genus. The museum specimens of *Bronchocela* were examined at the California Academy of Sciences, San Francisco, USA (CAS); Field Museum of Natural History, Chicago, USA (FMNH); Muséum National d'Histoire Naturelle, Paris, France (MNHN-RA); Museum Zoologicum Bogoriense, Cibinong, Indonesia (MZB); Natural History Museum, London, UK (NHMUK); Naturalis Biodiversity

Center, Leiden, the Netherlands (RMNH); Biodiversity Research and Teaching Collections, Department of Wildlife and Fisheries Sciences, Texas, USA (TCWC); Smithsonian Institution, National Museum of Natural History, Washington DC, USA (USNM); Zoologisches Forschungsmuseum Alexander Koenig, Bonn, Germany (ZFMK); Zoologicheskii Institut, Rossiiskoi Akademii Nauk, St. Petersburg, Russia (ZISP); Museum für Naturkunde, Berlin, Germany (ZMB); Zoologisches Museum Hamburg, Germany (ZMH); Zoologisk Museum, Københavns Universitet, Copenhagen, Denmark (ZMUC); Zoological Survey of India, Kolkata, India (ZSI); and Zoologische Staatssammlung München, Germany (ZSM). Museum acronyms follow Uetz *et al*. (2019). The material examined for morphological comparisons is listed in Appendix I. We used an AmScope SM-1BZ-RL (10–90×; United Scope LLC) and Leica Wild M3Z or ZEISS DCR dissecting microscope to examine the external morphology of specimens and a Canon EOS 7D SLR digital camera to take photographs. The following morphometric characters were taken with a Mitutoyo digital calliper to the nearest 0.1 mm on the left side of the animal: snout–vent length (SVL, measured from tip of snout to anterior margin of vent), axilla–groin length (AG, distance between axilla and groin), head length (HL, distance between posterior edge of mandible and tip of snout), head width (HW, maximum width of head), eye–nostril length (EN, distance between anterior-most point of orbit and posterior border of nostril), snout length (ES, distance between anterior-most point of orbit and tip of snout), orbit diameter (ED, antero-posterior largest diameter of orbit), tympanum–eye length (TYE, distance between anterior-most margin of tympanum and posterior-most point of orbit), lower-arm length (LAL, distance from elbow to wrist with both upper arm and palm flexed), palm length (PLM, distance between wrist (carpus) and tip of longest finger, with both palm and lower arm flexed), tibia length (TBL, distance between knee and heel, with both tibia and tarsus flexed), foot length (FOL, distance between heel and tip of longest toe, with both foot and tibia flexed), tail length (TAL, from posterior margin of vent to tail tip when tail was entire).

Meristic characters were recorded as follows: supralabials and infralabials, counted from first labial scale towards gape up to distinctly larger scale than the granular scales at gape on both sides; scales from eye to tympanum, count scale rows from posterior-most point of orbit to anterior-most point of tympanum; dorso-nuchal crest scales, count number of spiny scales on the dorsal head until the level of axilla; midbody scale rows, count of scales around at midbody (across the body); ventrals, counted from the first scale posterior to mental plate (along mid gular) to the last scale anterior to vent; subdigital lamellae on toe IV, from first proximal enlarged scansor wider than twice the width of the largest palm scale, to distalmost lamella at tip of digit.

Morphometric analysis. Statistical tests were performed only on adult voucher specimens of *Bronchocela celebensis* and its allopatric congener, *B. cristatella* for both sexes combined. In total 20 specimens of *B. celebensis* (5 males and 15 females) and 16 specimens of *B. cristatella* sensu stricto from Java (8 males and 8 females), and 7 specimens of *B. cristatella* sensu lato (2 males and 5 females) from the adjacent islands of southern Sulawesi were used for the statistical analysis. A systematic revision of the *B. cristatella* complex will be published elsewhere (Amarasinghe *et al*. in preparation). Juveniles were excluded to avoid the bias of allometry for the statistical analysis. We performed Kruskal–Wallis univariate analysis of variance tests on HL (n=43), SVL (n=43), and TAL (n=32 with complete original tails) to see whether these body metrics were significant enough in separating the species. We used this test due to the small sample size (Zar 2010). Boxplots were generated for above body metrics in order to visualize the range, mean, median, and degree of differences between the above three phenotypes. Each morphometric ratio was treated as the dependent variable and the population as the predictor variable.

Additionally, variation in adult size was normalized using the following equation: $\log X_{adj} = \log(X) - \beta[\log(SVL) - \log(SVL_{mean})]$, where X_{adj} = adjusted value; X = measured value; β = unstandardized regression coefficient for each population; and SVL_{mean} = overall average SVL of all populations (Lleonart *et al*. 2000; Chan & Grismer 2022) prior to multivariate analyses on twelve morphometric characters, HL, HW, EN, ES, TYE, ED, TBL, AG, LAL, FOL, PLM. The scaled morphometric was treated as the dependent variable and the population as the predictor variable. Multivariate analysis was conducted using Principal Component Analysis (PCA) on the scaled morphometrics above to reduce the highly correlated multidimensional data matrix into a few uncorrelated variables [i.e., principal components (PC)]. We used the princomp function in the R statistical software program (v4.0.4; R Core Team 2021). A biplot of the first two principal component scores was used to examine the morphometric differentiation between the populations. All statistical analyses were conducted using the R statistical software program (v4.0.4; R Core Team 2021).

Conservation status assessment. All the distribution records are based on data associated with the examined museum specimens and our field observations. The conservation status of the species was evaluated using the IUCN Standards and Petitions Subcommittee (2019) to assess their risk of extinction.

Results

Morphometric analysis. The head (HL), snout–vent (SVL), and tail (TAL) length comparison of Kruskal–Wallis test showed that only the head length metrics significantly separate each species: Higher head (HL, χ^2=11.6, *P*=0.003) lengths of *B. celebensis* indicated a relatively elongated head compared to that of *B. cristatella* in both Java and adjacent islands of southern Sulawesi (Fig. 2). Among the two populations of *B. cristatella* the population on adjacent islands of southern Sulawesi represented the smallest median with shortest head, while *B. cristatella* sensu stricto from Java has intermediate head length metrics compared to its population on adjacent islands of southern Sulawesi and *B. celebensis*.

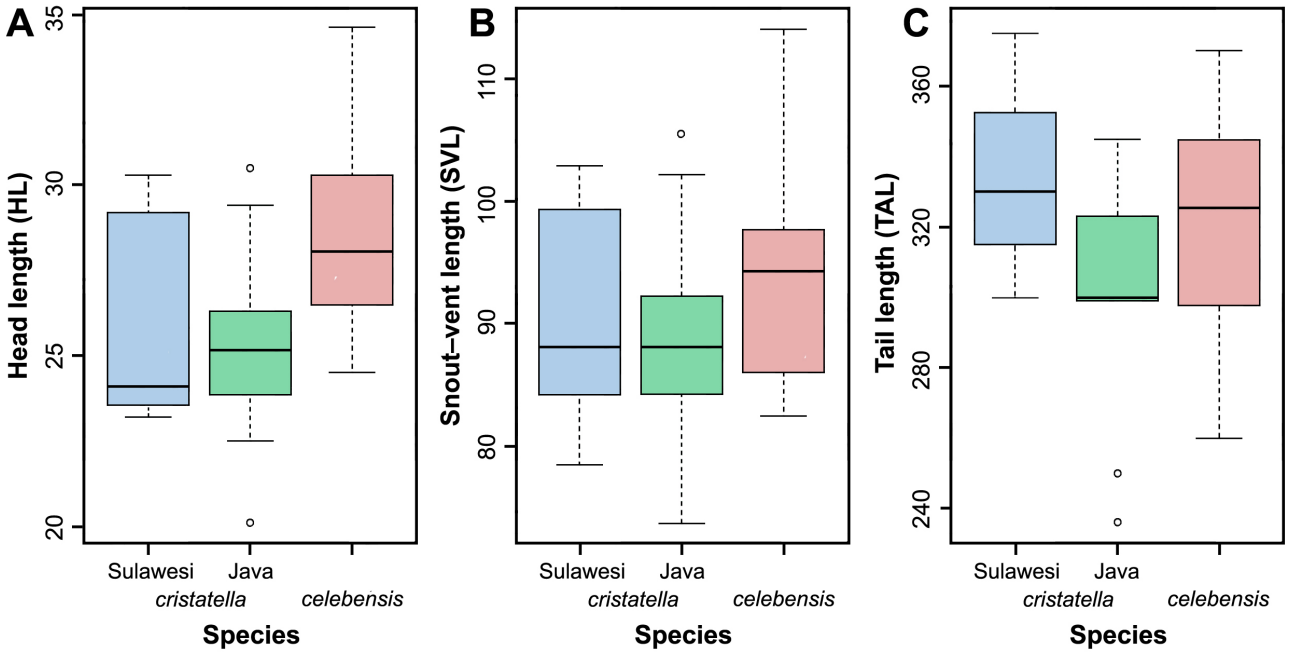

FIGURE 2. Boxplots of **(A)** head length, **(B)** snout–vent length, and **(C)** tail length of *Bronchocela celebensis*, *B. cristatella* sensu stricto from Java, and sensu lato from adjacent islands of southern Sulawesi; top, middle and bottom lines of the boxes indicate 75th percentile, median and 25th percentile, respectively.

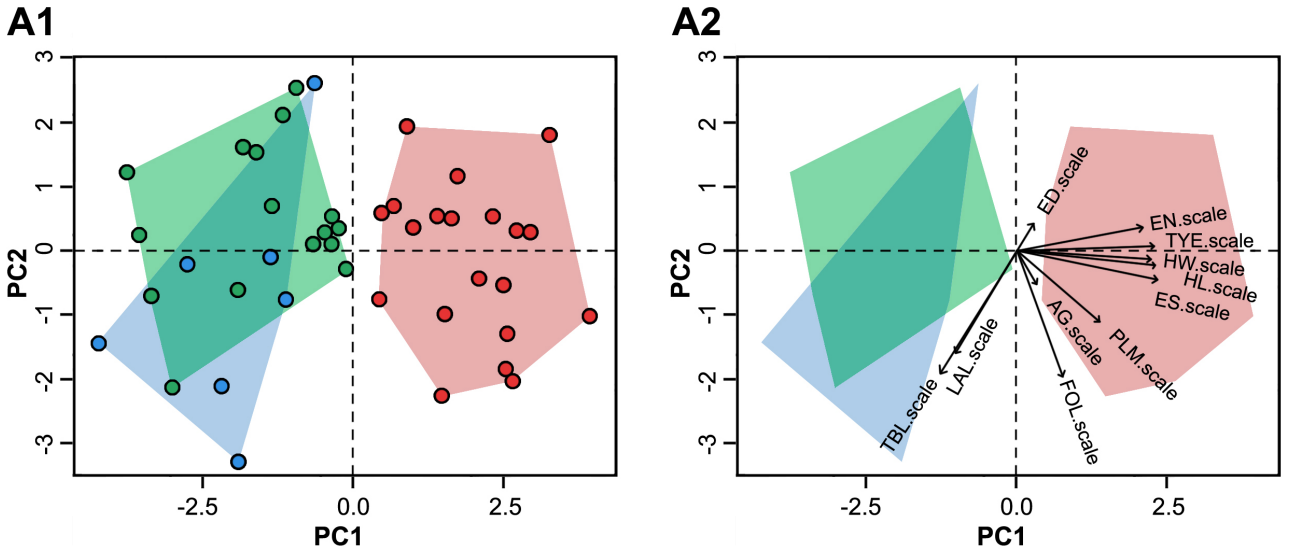

FIGURE 3. Principal Component Analysis (PCA) biplot of morphometric variation between *Bronchocela celebensis* (red), *B. cristatella* sensu stricto from Java (green) and sensu lato from adjacent islands of southern Sulawesi (blue), with **(A1)** combined sexes showing the morphological distinctiveness of *B. celebensis*; **(A2)** the same base biplots with vectors associated with species clusters. Each point represents an individual specimen, and the relative distance between two points is equivalent to the amount of dissimilarity.

Principal components analysis also showed distinct overall differences in morphometric characters between *B. celebensis* and *B. cristatella* with a distinct non-overlapping cluster (Fig. 3). However, the *B. cristatella* populations on Java and adjacent islands of southern Sulawesi had largely overlapping clusters implying that both populations represent a single species. Principal components 1 and 2 collectively explained 59.2% of variation in the morphometric data matrix (Table 1) for combined sexes. In both principal components (PC1 and PC2) TBL.scale and LAL.scale loaded negatively while EN.scale, TYE.scale, and ED.scale loaded positively. Among the morphometric characters, scaled PLM and TBL contributed most to both principal components.

TABLE 1. Principal Component Analysis (PCA) and loadings for *Bronchocela celebensis*, *B. cristatella* sensu stricto from Java, and adjacent islands of Sulawesi. Principal components (PC) 1 and 2 in each analysis collectively explained 59.2% of the variation for combined sexes.

PCA variable	PC1	PC2	PC3	PC4	PC5	PC6
(A) Combined sexes						
Standard deviation	2.1649	1.3505	1.2395	1.0239	0.7856	0.6608
Proportion of variance	0.4261	0.1658	0.1397	0.0953	0.0561	0.0397
Cumulative percentage%	42.6	59.2	73.1	82.7	88.3	92.3
Loadings						
HL.scale	0.4139	-0.0598	0.2504	-0.0473	0.0849	-0.0145
HW.scale	0.4038	-0.0432	0.1336	-0.1096	-0.2129	-0.3666
EN.scale	0.3758	0.1017	-0.0179	-0.1714	0.5324	0.0323
ES.scale	0.4234	-0.1287	0.0924	0.0015	0.1954	0.0470
TYE.scale	0.4133	0.0142	0.0878	0.2076	-0.0925	-0.1496
ED.scale	0.0507	0.1171	0.6833	-0.0393	-0.4675	0.4354
TBL.scale	-0.2279	-0.5545	0.2191	-0.1151	0.0236	-0.1216
AG.scale	0.0608	-0.1488	-0.0104	0.9364	0.0118	0.0243
LAL.scale	-0.1871	-0.4579	0.4075	0.0151	0.4737	0.0864
FOL.scale	0.1395	-0.5618	-0.2339	-0.1241	-0.4091	-0.2628
PLM.scale	0.2482	-0.3142	-0.4087	-0.0776	-0.0794	0.7471

Taxonomy

Bronchocela celebensis Gray, 1845

(Fig. 4; Tables 2, 3)

Bronchocela celebensis Gray, 1845
Calotes celebensis — Boulenger 1885, Müller 1895, De Rooij 1915, Wermuth 1967
Bronchocela celebensis — Moody 1980, Malkmus 2000, Barts & Wilms 2003, Hallermann 2005, Manthey 2008, Wanger *et al*. 2011, Koch 2012

Holotype. NHMUK 1946.8.11.48, collected from Celebes (Sulawesi), Indonesia, and entered to the museum registry on 22 February 1844 (received from Leyden Museum).

Diagnosis. A species of *Bronchocela* inhabiting Sulawesi Island, Indonesia, characterized as follows: morphologically most similar to its congener *B. cristatella* in body colouration, but differs by having non-enlarged (*vs*. slightly enlarged), developed (*vs*. rudimentary) nuchal crest in males, 2–4 (*vs*. 8–10) upper dorsal scale rows on the lateral body directed upward along the body, relatively small tympanum with less than half diameter of orbit (*vs*. relatively large with more than half diameter of orbit). In addition, *Bronchocela celebensis* is distinguished from other congeners by having the following combination of characters: adults reach maximum SVL 119.0 mm in males and 105.9 in females, orbital area and tympanum with the same colour as body, ventral scales arranged in 10–12 rows, 50–76 mid body scale rows, 10–12 lanceolate nuchal crest scales, 62–78 ventrals, 33–35 lamellae on fourth toe, third finger longer than the fourth; mid gular scales not enlarged, abdominal scales acuminated and enlarged compared to pectoral, non-enlarged and keeled temporal scales with 7 or 8 rows between orbit and tympanum.

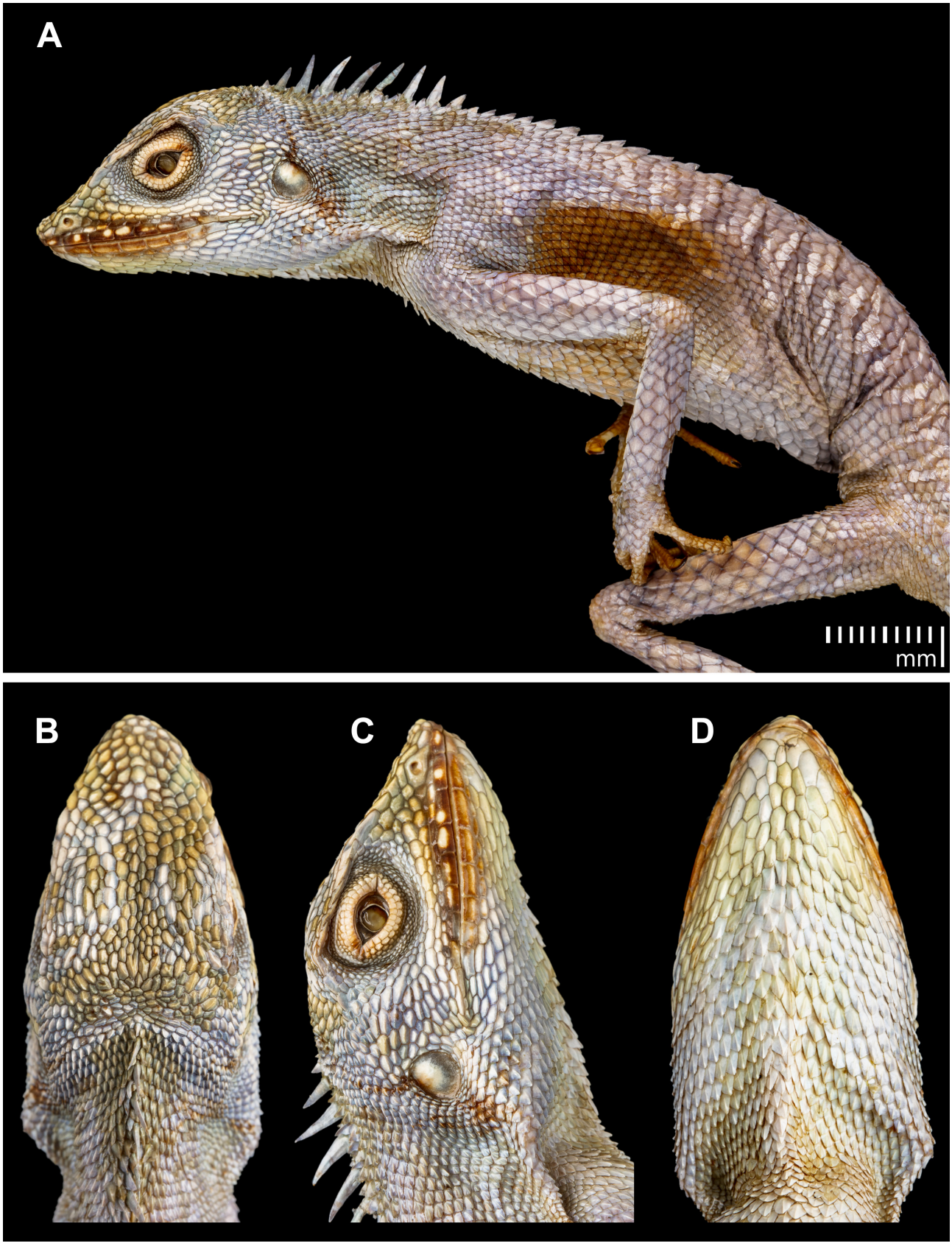

FIGURE 4. *Bronchocela celebensis* holotype (NHMUK 1946.8.11.48, adult female) from Sulawesi, Indonesia: **(A)** lateral view of the anterior body, **(B)** dorsal head, **(C)** lateral head, **(D)** ventral head.

TABLE 2. Some morphometric ratios and meristic characters of *Bronchocela celebensis* and its allopatric congener, *B. cristatella* on adjacent islands of Sulawesi, Indonesia (for accession data see Appendix).

Character	Mainland Sulawesi		Adjacent islands of Sulawesi	
	B. celebensis		*B. cristatella*	
	Male (*n*=5)	Female (*n*=15)	Male (*n*=2)	Female (*n*=5)
AG/SVL%	47.5–54.1	48.3–54.9	48.7–51.4	46.1–52.8
HL/SVL%	30.3–31.6	29.1–31.3	28.5–28.7	26.4–30.1
HW/HL%	50.9–56.0	51.4–56.6	51.6–52.3	48.7–54.8
EN/HL%	21.0–22.0	19.6–23.3	20.3–20.6	19.3–21.0
ES/HL%	39.5–40.6	39.2–41.4	39.1–39.4	38.0–41.2
ED/HL%	26.6–30.4	26.9–31.3	28.6–30.2	29.7–34.5
TYE/HL%	19.6–22.3	19.6–22.4	17.8–18.5	18.5–21.1
LAL/SVL%	19.0–20.1	18.7–20.3	20.4–21.0	18.4–21.6
PLM/SVL%	20.3–22.7	18.1–22.7	19.6–21.3	18.7–20.3
TBL/SVL%	26.8–30.2	26.5–30.1	29.8–32.7	27.1–32.7
FOL/SVL%	37.4–41.4	36.7–44.2	36.4–41.4	35.6–39.4
TAL/SVL	3.0–3.6 (*n*=3)	3.2–3.7 (*n*=13)	Tail broken	3.3–3.6 (*n*=3)
supralabials	9–10		9, 10	
infralabials	8–10		9, 10	
scales from eye to tympanum	7, 8		7, 8	
nuchal crest scales	8–10		8–10	
subdigital lamellae on toe IV	32–34		31–33	
midbody scale rows	50–62	52–76	54–56	57–60
ventrals	64–72	62–78	78–80	75–79

Redescription of holotype. An adult female, SVL 102.4 mm. Head moderately large, elongate, HL 28.0% of SVL, narrow, subtriangular in dorsal and ventral aspects, HW 58.9% of HL; distinct from neck; snout elongate, snout length greater than eye diameter, ED 77.1% of ES; interorbital distance broad; eye large, pupil rounded; diameter of eyes slightly greater than eye-tympanum distance, TYE 92.6% of ED; ear opening shallow, its greatest diameter horizontally, tympanum smaller than orbit, nearly 40% of orbit diameter; tympanum surrounded by keeled scales; four or five temporal scales enlarged, keeled, juxtaposed, seven or eight scale rows between orbit and tympanum; forehead concave; scales on interorbital and supercilium area keeled; scales on snout feebly keeled, larger in size than those of occipital region; a developed nuchal crest continuing dorsally as a dorso-nuchal crest; dorsal crest rudimentary, consisting of 10 scales up to the level of axilla, no crest on the tail; rostral scale width greater than its height, ventro-posteriorly in contact with first supralabial, contacting posteriorly four more or less equal-sized postrostral scales; around nostrils on each side two supranasals, two postnasals, a single prenasal, and two subnasals, which separate the nasal from the supralabials; nostrils round located in the middle of the undivided nasal plate; canthus rostralis and supraciliary edges blunt; three canthal scales between supranasal and anterior margin of orbit; no distinct parietal plate; mental subtriangular, flat posteriorly, shorter than wide, posterior-laterally in contact with two enlarged postmentals separated by a smaller scale; each postmental pair bordered posteriorly by three or four smooth scales, including the medial scale, but exclusive of infralabials; chin scales keeled; gular pouch present, midgular scales not enlarged; throat scales and midgular scales keeled, mucronate, and imbricate; three scale rows separate orbit from supralabials; supralabials nine (seventh in midorbit position); infralabials eight, decreasing in size toward gape.

Body slender; lateral body scales large, equal, strongly keeled and imbricate; scales on lateral body slightly smaller than on the venter at same level, directed backward and downward anteriorly and directed straight backward posteriorly; lateral body scales on the posterior body slightly larger than the anterior body scales; 2–4 upper dorsal scale rows directed backward and upward along the body; 50 scales around the midbody; pectoral scales and

abdominal scales keeled, mucronate, imbricate and keels forming regular and parallel continuous ventral ridges; abdominal scales slightly larger than pectoral scales; 10–12 rows enlarged ventrally, without clear margin with the lateral scales; 70 ventrals.

Forelimbs moderately short; no oblique fold (pit) present on shoulders, but shoulder scales keeled and smaller; dorsal scales on fore- and hind limbs keeled, enlarged, imbricate and mucronate; ventral scales on upper arm and lower arm keeled, imbricate, and mucronate; hind limbs relatively longer than forelimbs; scales on ventral surface of thigh keeled, enlarged, imbricate and mucronate; tibia comparatively longer than femur; keels on tibia forming a series of continuous parallel ridges; digits elongate, slender; relative length of digits (fingers) 4 > 3 > 2 > 5 > 1; (toes) 4 > 3 > 5 > 2 > 1; all bearing slightly recurved, sharp and elongate claws; subdigital lamellae entire, bicarinate, and regular, 34 (left) subdigital lamellae on toe IV.

FIGURE 5. *Bronchocela celebensis* in life (adult female, not collected) from Pangana Village, Central Sulawesi, Indonesia (Photo © J.A. McGuire).

Tail elongated and complete, 355.0 mm. Ventral scales on tail base keeled and imbricate, smaller in size than on dorsal tail; dorsal scales on tail enlarged, imbricate, keeled, mucronate, and keels forming continuous parallel ridges; tail with subcaudals on median row not enlarged, subequal, imbricate, keeled, and mucronate.

Colouration.—In preservative, colours faded and dorsum pale purplish gray due to colour having been bleached with time.

In life, dorsum dull green; mostly uniform body colour with scales edged dark, some individuals with few brown markings on the lateral body; nuchal spines yellowish or brownish; orbit and labials pale, tympanum whitish; knee, elbow, wrist, heel dark brownish; dorsal fingers and toes, posterior 2/3rd of the tail brown; ventral head, body, limbs, anterior tail, and mid gular lighter green.

Habitat, natural history, and distribution. This species is usually found in closed canopy areas in primary forests (mostly forest edge) or rarely in undisturbed secondary forests, but avoids open areas. We often found it at the ecotone of forests and other vegetation (e.g., plantations, well-maintained home gardens etc.) while basking (from sunrise until midday), usually 1.5 to 4 meters above the ground. Like other *Bronchocela* species, it is usually active during the daytime, mostly around 0900 hr. At night, the adults prefer higher branches of the trees to sleep, mostly in open canopy areas, while juveniles prefer tiny branches of shrubs at lower heights.

TABLE 3. Diagnostic characters separating the species of *Bronchocela* (modified after Amarasinghe *et al*. 2022b); **(1)** maximum SVL in adults (in mm); **(2)** number of postmentals; **(3)** gular sac absent (a), small (s), or large (l) in males; **(4)** mid gular scales not enlarged (n) or enlarged (e) in males; **(5)** red gular patch in males absent (a) or present (p); **(6)** number of enlarged ventral scale rows; **(7)** ventrals × times larger than dorsals**; (8)** number of ventrals; **(9)** lateral body scales smooth (sm), feebly (fk) or strongly (sk) keeled; **(10)** number of upwards pointing upper dorsal scale rows; **(11)** supraoculars smooth (s) or keeled (k); **(12)** pale/white ventrolateral body stripe absent (a) or present (p); **(13)** nuchal crest weakly (wk) or well (wl) developed; **(14)** nuchal crest scales crescent-shaped (c) or lanceolate (l); **(15)** number of nuchal crest scales to the level of axilla; **(16)** nuchal crest scales shorter (s) or longer (l) than ED; **(17)** dorsal crest indistinct (i) or distinct (d); **(18)** tympanum diameter / ED%; **(19)** tympanum and orbit pale (p) or dark (d); **(20)** temporal scales smooth (s) or keeled (k); **(21)** temporal scales not enlarged (n) or enlarged (e); **(22)** number of temporal scale rows between orbit and tympanum; **(23)** prominent white patch on temporals absent (a) or present (p); **(24)** pale/dark labial stripe/band absent (a) or present (p); **(25)** number of canthal scales between supranasal and anterior border of orbit; **(26)** canthal edges blunt (b) or sharp (s); **(27)** number of midbody scale rows; **(28)** 3rd finger shorter (s) or longer (l) than 4th finger; **(29)** 4th finger shorter (s) or longer (l) than 5th toe; **(30)** tail colouration uniform (u) or banded (b); — not measured / evaluated.

Character	*B. burmana* (Zug *et al*. 2017)	*B. celebensis* (*n*=46)	*B. cristatella* s.l. (*n*=119)	*B. cyanopalpebra* (*n*=7)	*B. danieli* (*n*=2)	*B. hayeki* (*n*=11)	*B. jubata* (*n*=170)	*B. marmorata* (*n*=62)	*B. nicobarica* (*n*=3)	*B. orlovi* (*n*=1)	*B. rayaensis* (Grismer *et al*. 2015)	*B. rubrigularis* (*n*=6)	*B. shenlong* (Grismer *et al*. 2015)	*B. smaragdina* (*n*=6)	*B. vietnamensis* (*n*=2)
(1)	94.0	119.0	119.7	103.6	80.0	120.0	142.0	119.6	79.0	109.6	85.0	106.4	106.0	113.0	122.0
(2)	3	3	3	3	3	3	3	3	3	3	3	3	3	3	2
(3)	a	s	s, l	s	a	l	l	s	l	s	a	s	l	a	s
(4)	n	n	n, e	n	n	e	e	n	n	n	n	e	e	e	e
(5)	a	a	a	a	a	a	a	a	a	a	a	p	a	a	a
(6)	—	10–12	10–14	10–12	10–12	8–10	10–12	10–12	8–10	—	—	10–12	—	10–12	12
(7)	1–5	1–2	1–5	2	5–8	8–10	1	1–5	1–2	2–3	1–5	2–3	1–5	4–5	2–3
(8)	—	62–78	52–89	76–85	75–79	50–60	56–73	72–74	76–80	—	—	54–72	—	64–72	70–73
(9)	sk	sk	fk, sk	fk	sk	sk	sk	sk	fk	fk	sk	sk	sk	sm, fk	fk
(10)	0	2–4	4–10	3, 4	3, 4	5–7	1, 2	1, 2	3, 4	0	0	1–2	4–7	1, 2	0
(11)	k	k	k	k	s	k	k	k	k	k	k	k	k	k	k
(12)	a	a	a	a	a	a	a	a	a	a	a	a	a	a, p	p
(13)	wk	wl	wk	wl	wk	wl	wl	wk	wk	wl	wk	wl	wl	wk	wk
(14)	l	l	l	c	l	c	c	l	l	c	l	c	l	l	c
(15)	6–9	8–10	8–15	7–12	12–14	10–12	10–12	7–11	10–12	8–10	8–10	8–10	10–12	10–12	10–12
(16)	s	s	s	s	s	l	l	s	s	l	s	l	s	l	l

.....Continued on the next page

TABLE 3. (Continued)

Character	*B. burmana* (Zug *et al*. 2017)	*B. celebensis* (*n*=46)	*B. cristatella* s.l. (*n*=119)	*B. cyanopalpebra* (*n*=7)	*B. danieli* (*n*=2)	*B. hayeki* (*n*=11)	*B. jubata* (*n*=170)	*B. marmorata* (*n*=62)	*B. nicobarica* (*n*=3)	*B. orlovi* (*n*=1)	*B. rayaensis* (Grismer *et al*. 2015)	*B. rubrigularis* (*n*=6)	*B. shenlong* (Grismer *et al*. 2015)	*B. smaragdina* (*n*=6)	*B. vietnamensis* (*n*=2)
(17)	i	i	i, d	i	i	d	d	d	i	d	i	d	i	d	i
(18)	45–55	35–45	45–55	50–55	50–60	50–60	50–60	50–60	45–50	53	46–49	75–90	38–44	55–65	45–55
(19)	p	p	p, d	d	d	d	p	p	d	p	p	d	p	p	p
(20)	k	k	k	k	k	k	k	k	k	k	k	s	k	k	k
(21)	n	e	n, e	e	e	n	e	n	e	n	n	e	e	n	n
(22)	7, 8	7, 8	6–10	6, 7	7, 8	7, 8	6, 7	8–11	4–6	6	7, 8	6, 7	6, 7	9, 10	12, 13
(23)	a	a	a	p	p	a	a	a	a	a	a	a	a	a	a
(24)	a	a	a	p	a	a, p	a, p	p	a	a	a	a	p	p	a
(25)	5–7	3, 4	4–7	4, 5	4, 5	4, 5	5, 6	4–6	3, 4	3, 4	5–7	3, 4	6–11	4, 5	4, 5
(26)	s	b	s	s	b	s	b, s	s	s	s	s	b	s	b	b
(27)	55–67	50–76	50–106	56–78	65–71	64–75	33–59	47–73	62–63	43	67–71	50–58	71–92	43–53	47–54
(28)	l	l	s, l	s	s	l	s	—	s	—	l	l	s	l	l
(29)	s	s	s, l	l	l	s	s, l	s	s	—	s	s	s	l	l
(30)	b	u	u, b	u	u	u	b	u	u	u	b	u	b	u	b

The species is sympatric with other arboreal agamids such as *Draco iskandari*, *D. spilonotus*, and *D. supriatnai*, but allopatric with *Bronchocela cristatella*. We always found several individuals of *B. celebensis* close together at higher elevations (usually above 900m above sea level), and never at lower elevations where *B. cristatella* sensu lato is usually distributed on the adjacent islands of southern Sulawesi. Most of the individuals were observed at Donggala Regency and Sigi Regency in Central Sulawesi, and Mt. Klabat, Minahasa regency in North Sulawesi. However, we have observed a lower number of adult males (male:female ratio = 1:4), and this is an unusual phenomenon compared to other *Bronchocela* species. It is probably due to the impact that the illegal pet trade which accelerates the removal of healthy adult males from their natural habitats. Because the males have prominent nuchal crests and brighter colours compared to females. The southern margin of the distribution of this species is Polewali Regency in West Sulawesi, and it seems the distribution records are scattered (Fig. 1) due to forest fragmentation, but always confined to forested uplands. This species has never been reported from Southeastern parts of Sulawesi.

Conservation status. The habitats of *Bronchocela celebensis* are highly fragmented. The application of the IUCN Red List criteria (IUCN Standards & Petitions Subcommittee 2019) with the updated distribution data shows that *B. celebensis* is restricted to an area of occupancy (AOO) of 224 km^2 recorded from 13 localities (10 locations) within 92,520 km^2 extent of occurrence (EOO). Given the low area of occupancy, the scattered distribution of severely fragmented forests, considerable number of individuals available in local pet trade (wild catch) for low price (IDR 400,000 = USD 27), consequence lower number of adult males observed in the natural habitat, *B. celebensis* should be considered as a "Vulnerable" (VU) species.

Discussion

Bronchocela celebensis has often been mistaken with *B. cristatella* on the adjacent islands of southern Sulawesi which has a more prominent nuchal crest than typical *B. cristatella* on Java Island. Although *B. celebensis* specimens have a prominent small tympanum and lanceolate crest scales, among juveniles these characters are weak. Therefore, juveniles of *B. celebensis* may still be difficult to distinguish from *B. cristatella* for specimens with imprecise collection localities. In that case, to distinguish *B. celebensis* and *B. cristatella*, the comparative shape of the head is an ideal character because the head of *B. celebensis* is elongated compared to *B. cristatella* populations on the adjacent islands of southern Sulawesi. An integrative taxonomic approach might clarify whether the population on the adjacent islands of southern Sulawesi is conspecific with the Javan population. A systematic revision of the *B. cristatella* complex (including a neotype designation) will be published elsewhere (Amarasinghe *et al.* in preparation). However, our morphometric analysis (Table 1, Fig. 3) highlights the higher probability of Javan and adjacent southern Sulawesi populations of *B. cristatella* being one species. Although, *B. cristatella* has been reported from historical collections as "celebes", the same area where *B. celebensis* has also been reported, they have never been observed sympatrically, mostly showing allopatric distribution patterns. Although the Javan population of *B. cristatella* mostly inhabits the closed canopy primary forests, the *B. cristatella* populations on adjacent islands of southern Sulawesi mostly utilize secondary forests; this could probably be related to the lack of larger forested areas on smaller islands adjacent to southern Sulawesi.

Details on the ecology, habitat, population, and breeding biology of *B. celebensis* are still sparse and further studies are needed. The reptile fauna of Sulawesi is one of the least known in Southeast Asia. According to Koch (2012) approximately 60% of the known snake fauna from Sulawesi is endemic, although this is likely to be underestimated. Sulawesi is a geological composite island exhibiting substantial geographic variation across its landscape, so several species may be restricted to isolated areas of endemism (Amarasinghe *et al*. 2015). Given the biogeographical complexity of Sulawesi and the presence of large tracts of poorly known upland rainforest in the island's interior portion, the discovery of many new species can be expected in the future (Amarasinghe et al. 2021).

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Appendix 1. Specimens examined

***Bronchocela celebensis*: Indonesia:** Sulawesi: NHMUK 1946.8.11.48 (holotype), 1872.4.6.126–127, 1871.7.20.161–165, 1927.4.20.27, ZMB 688, 8801, 36898, RMNH 3021a–e, 3023a–d, 7419a–e, MZB 6991–6, 6998–7006, 7008–12.

***B. cristatella*: Indonesia:** Borneo: RMNH 7371a–c, 7374a–b, ZMH R04639–43, 5586–91, 5593–99, 6081–82, ZMB 51019, 53634, ZFMK 50529–30; Java: ZFMK 20783, RMNH 2848a–b, ZMH R00608, 5602–03, 5623, MZB 196, 304, 705, 767, 995, 1668, 3036, 4895, 6989, 7751, 8885–88, 9649, 9811, 11888, 14124–25; Maluku: RMNH 3030–31, 3034a–b, 3035, 3036a–b, 3037a–c, ZMUC R98502–04, ZMH R04891–92, 6083–84, ZSM 366a–b; Sulawesi (probably adjacent island): ZSM 365; Sumatra: MZB 187, 653, 1569, 1679, 1872, 2163, 4390, 4594, 4730, 4993, 4995, 5292, 7463–64, 9803–05, 9807–08, 9810, 9812, 9907, 13407, 13409, 14732, 14733–34, 15062, 15064, ZMB 57217, ZSM 333.1999, 376.1978.d, ZMH R04928; Papua: ZMH R04927.

***B. cyanopalpebra*: Car Nicobar:** DOSMB 5054 (holotype), DOSMB 5089 Paratype), BNHS 961, 1610, 1662, ZSI 2671, 15033–34.

***B. danieli*: India:** Nicobar: ZSI 22455 (holotype), 22496.

***B. hayeki*: Indonesia:** Sumatra: ZMB 55931 (neotype), UIMZ 243, ZMH R05470, R05472–3, RMNH 14916, MZB 203, 8892–93, 13839–40.

***B. jubata*: Indonesia:** Bali: MZB 4393, 13988; Borneo: ZMH R06163; Java: MNHN-RA 2542 (lectotype), 1911.0142, ZFMK 48897–906, 48917–21, 27099–101 (syntypes of *B. intermedia*), ZMH R4934–36, 7066–69, 7070, 7074–79, 7080–87, RMNH 7304, 7417a–b, 35930, ZMUC R98500, TCWC 73121, ZMB 14438, UIMZ 0001–2, MZB 197, 198, 223, 637, 639, 996, 997, 1342, 1462, 1465, 1484, 1649, 1671, 2629, 2916, 2963, 3023–32, 3034–35, 3037, 3543, 3678, 3733–34, 3791–92, 3898, 3911, 4191–93, 4885–87, 4896–99, 5442–43, 6224–25, 6639, 6988, 7053, 7057, 7488, 7632, 7754–55, 7765, 8010, 8013, 8439, 9423, 9787, 9789, 9916, 9921, 9925, 10284, 12081–86, 13194–95, 13245–47, 13775, 13898–900, 13902–03, 13971, 13973, 14008–10, 14681–84, 14687, 14699; Sumatra: MZB 6612–16, 6638, 6656–57, 9757, 9758, 9761–64, RMNH 8646. **India (?)**: Pondicherry: RMNH 3849, MNHN-RA 2543 (paralectotype). **Philippines (?)**: ZMB 16305. **Thailand (?)**: MNHN-RA 1895.0460, ZSM 552, 559. **Cambodia (?)**: RMNH 26743–44, RMNH 26746.

***B. marmorata*: Philippines:** NHMUK 1946.8.11.16 (holotype), 72.8.20.25–26, RMNH 3022a–d, ZMH R04882, MNHN-RA 5775, 1900.0341, 1999.8131, ZFMK 43702–13, ZMB 681 (syntype of *C. philippinus*), 5433, 5642,

49761–66 (syntypes of *C. philippinus*), 54507, USNM 36167–68, 58838, 77133–35, 140839, 318692, 318694–95, 498716, 498783, 513564–71, 513836, FMNH 251691, CAS 15457, 20338, 61705, 62398–99, 131925, ZMUC 148.

***B. nicobarica*: Little Nicobar:** DOSMB 5070 (holotype), 5055–56 (paratypes).

***B. orlovi*: Vietnam:** ZISP 22827 (holotype).

***B. rubrigularis*: Nicobar:** ZMH R09271 (holotype), R09272 (paratype), DOSMB 5086–87, BNHS 1609, ZSI 14668.

***B. smaragdina*: Cambodia:** NHMUK 1946.8.11.35–36 (syntypes), FMNH 262309; **Vietnam:** USNM 90392, 144202, 146163.

***B. vietnamensis*: Vietnam:** FMNH 252295 (holotype), ZISP 22845 (paratype).