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Taxonomy, distribution, and conservation status of a rare arboreal lizard, *Bronchocela hayeki* (Müller, 1928) (Reptilia: Agamidae) from northern Sumatra, Indonesia

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Abstract

Bronchocela hayeki (Müller, 1928) is one of the rarest species of the genus, known only from a handful of museum specimens from five locations in North Sumatra, and often confused with its similar congener, *B. cristatella*, which occurs widely throughout the Indonesian Archipelago and Peninsular Malaysia. Here, we examined the morphology of *B. hayeki* based on museum specimens, and redescribe the species based on a freshly collected series near the type locality, as the condition of its neotype is not in a good state. We studied the characters of *B. hayeki* with a morphometric comparison to its sympatric congener *B. cristatella* and allopatric congener, *B. jubata* from Sumatra Island, Indonesia. Based on the current distribution pattern and the apparent threats, we update the conservation status of *B. hayeki* using IUCN Red List Criteria and propose that it be considered as an Endangered (EN) species endemic of northern Sumatra including Aceh. We also provide a key to the recognized *Bronchocela* species, based on examined material and literature.

Key words: Conservation, Endemic, Indonesia, morphometric characters, Sumatra

Introduction

The morphologically highly variable, arboreal agamid lizard genus, *Bronchocela* Kaup, 1827 has a wide range of distribution from southern Indochina in the west to Papua New Guinea in the east including the Andaman and Nicobar Islands and other transcontinental oceanic islands of the Indonesian and Sulu Archipelagos (Wermuth 1967; De Rooij 1915; Diong & Lim 1998; Hallermann 2005; Manthey 2008; Grismer *et al*. 2015). 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 similarity of some of the species to one another, intraspecific variation, and difficulties of species determination (Hallermann 2005). Currently, the genus *Bronchocela* consists of 13 species and four of them are insular species distributed across the Indonesian Archipelago: *B. cristatella* (Kuhl, 1820); *B. jubata* Duméril & Bibron, 1837; *B. celebensis* Gray, 1845; and *B. hayeki* (Müller, 1928). Among them, the first species is the most widely distributed occurring throughout the

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Sunda-Sahul Convergence Zone, and the fourth is the rarest, known only from nine museum specimens from three localities in North Sumatra. Very little has been published about this species (Hallermann 2005).

Calotes hayeki was described by Müller (1928) based on a single specimen collected from Mount Sibayak Plateau (1,400 m a.s.l.) in Berastagi, North Sumatra, Indonesia. Brongersma (1930) reported the species from Takengon, Aceh. There were no further reports until Manthey & Grossmann (1997) provided field notes based on two males and a juvenile from the type locality and from Bukit Lawang (300 m a.s.l.), North Sumatra. Moody (1980) transferred the species to the genus *Bronchocela*. Hallermann (2005) in a taxonomic review of the genus *Bronchocela*, designated a neotype and redescribed the species along with identifying historical specimens collected by W. Burchard in 1895 from a locality near Lake Toba in Sumatra, which were previously misidentified as *B. cristatella*. Although the condition of the neotype is not as good as that of other specimens from other localities, he selected it because it was found near the type locality (Hallermann 2005). Hallermann (2005) also reported the species from near Rantauprapat, the southernmost known point of its distribution, based on photographic evidence. So far, this species' presence has been reliably reported from only five localities. Here we report the species from additional localities and provide comprehensive details on morphology and morphometry.

Material and methods

During field surveys conducted (by AATA, MK, and CAP) within North Sumatra, Indonesia, we encountered several individuals of *Bronchocela hayeki* (Fig. 1). Natural history observations were made by looking with the naked eye at the animal from a distance of at least 3–4 m, being careful not to disturb it. Latitude, longitude, and elevation of localities of specimens collected were recorded using a Garmin GPSmap 60CSx using WGS 84 map datum. A single adult male individual was collected by hand, from near the type locality (outside the protected areas), euthanized with sodium pentobarbital, and preserved liver and thigh muscle tissue samples for DNA analysis in 95% ethanol. The specimen was fixed in 10% buffered formalin for 24 hours and washed in running water before storage in 70% ethanol. The specimen is deposited at the Museum of Zoology, Research Center for Climate Change, University of Indonesia (UIMZ).

Morphological, morphometric, and meristic characters. We compared the specimen to other relevant historical specimens of *Bronchocela hayeki* (including the neotype), and all the congeners of the genus. The other 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); Museum Zoologicum Bogorienese, 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 Leicawild 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: 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, horizontal largest diameter of orbit), tympanum–eye length (TYE, distance between anterior-most margin of tympanum and posterior-most margin 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, measured entire tail from posterior margin of vent to tail tip).

FIGURE 1. Current distribution map showing the collection/observation localities of *Bronchocela hayeki* (yellow) on Sumatra Island, its sympatric congener, *B. cristatella* sensu lato (blue) and allopatric congener *B. jubata* sensu lato (red) also indicated on the map; sympatric localities filled partially

Meristic characters were taken 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, count number of spinose scales on the dorsal head until the level of axilla; midbody scale rows, count of scales around midbody (across the body); ventrals, counted from first scale posterior to mental (along mid gular) to 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.

TABLE 1. Principal Component Analysis (PCA) and loadings for *B. hayeki*, *B. cristatella*, and *B. jubata* in Sumatra for **(A)** combined sexes and **(B)** males separately. Principal components (PC) 1 and 2 in each analysis collectively explained 49.7% and 46.7% of the variation respectively for combined sexes and males separately.

PCA variable	PC1	PC2	PC3	PC4	PC5	PC6
(A) Combined sexes						
Standard deviation	1.789	1.5038	1.1889	1.0494	0.92796	0.78950
Proportion of variance	0.291	0.2056	0.1285	0.1001	0.07828	0.05666
Cumulative percentage%	29.1	49.7	62.5	72.5	80.3	86.0
Loadings						
HL.scale	-0.4661	0.1422	-0.0741	0.2280	-0.1626	0.1080
HW.scale	-0.3065	0.2339	-0.4889	-0.1989	-0.2028	0.1863
EN.scale	-0.1792	0.4390	0.2195	-0.1828	0.0654	-0.6400
ES.scale	-0.3739	0.3018	0.2750	0.1056	-0.2790	-0.1912
TYE.scale	-0.3800	-0.0054	-0.3410	0.2473	-0.0384	0.1269
ED.scale	0.1464	0.3524	-0.1915	-0.6667	-0.0259	0.1724
TBL.scale	-0.3261	-0.0612	-0.0183	-0.0129	0.8148	-0.0926
AG.scale	0.1593	-0.2782	-0.5187	0.0023	-0.2016	-0.6664
LAL.scale	-0.3169	-0.3565	-0.2224	-0.2941	0.1614	-0.0727
FOL.scale	-0.2495	-0.3115	0.3074	-0.5162	-0.1280	0.0476
PLM.scale	-0.2379	-0.4602	0.2557	-0.0716	-0.3181	-0.0380
PCA variable	PC1	PC2	PC3	PC4	PC5	PC6
(B) Males						
Standard deviation	1.730	1.4651	1.4022	0.99767	0.93307	0.82708
Proportion of variance	0.272	0.1951	0.1787	0.09049	0.07915	0.06219
Cumulative percentage%	27.2	46.7	64.6	73.6	81.5	87.8
Loadings						
HL.scale	0.2684	-0.3805	0.2670	-0.1186	0.2419	-0.5048
HW.scale	0.1665	0.0803	0.5452	0.4092	0.0964	-0.2706
EN.scale	-0.1652	-0.4548	0.3041	-0.0169	0.0252	0.5526
ES.scale	0.0005	-0.6041	0.0232	0.0310	0.2941	0.1499
TYE.scale	0.3215	0.0854	0.3581	-0.3444	-0.0139	0.0155
ED.scale	-0.3251	0.0635	0.2987	0.6191	-0.0694	0.0778
TBL.scale	0.2862	-0.1682	0.2162	-0.1635	-0.7313	0.1417
AG.scale	0.2237	0.3786	0.1983	-0.1542	0.4769	0.5061
LAL.scale	0.4611	0.2053	0.0731	0.2636	-0.0947	0.1572
FOL.scale	0.3655	-0.1879	-0.3334	0.3889	-0.1293	0.1919
PLM.scale	0.4310	-0.1286	-0.3441	0.2100	0.2284	-0.0102

Morphometric analysis. Statistical tests were performed on adult voucher specimens of *Bronchocela hayeki* and its congeners, *B. cristatella* and *B. jubata* for both sexes combined, and separately for males. The smaller number of females of *B. hayeki* would have rendered them insufficient for statistical analysis separately. In total 57 specimens of *B. hayeki* (8 males and 2 females), *B. cristatella* sensu lato (16 males and 17 females), and *B. jubata* sensu lato (10 males and 4 females) from Sumatra Island were used for the statistical analysis. A detailed analysis and systematic revision of *B. cristatella* and *B. jubata* will be discussed elsewhere (Amarasinghe *et al*. in press). 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=57), SVL (n=57), and TAL (n=41 with complete original tails) to see whether these body metrics are significant 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 species. 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) 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 the data associated with the museum specimens examined and 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 these body size metrics significantly separate each species: Higher head (HL, $\chi^{2=}22.59$, P=1.24e-05), body (SVL, $\chi^{2=}23.98$, P=6.19e-06), and tail (TAL, $\chi^{2=}13.33$, P=1.27e-03) lengths of *B*. *jubata* indicated a relatively elongated head, body, and tail than that of *B*. *hayeki* and *B*. *cristatella* sensu lato in Sumatra (Fig. 2). Among the three species, *B*. *cristatella* represented the smallest with shortest head, body, and tail lengths, while *B*. *hayeki* has intermediate body metrics compared to its congeners in Sumatra (Fig. 2, Table 2).

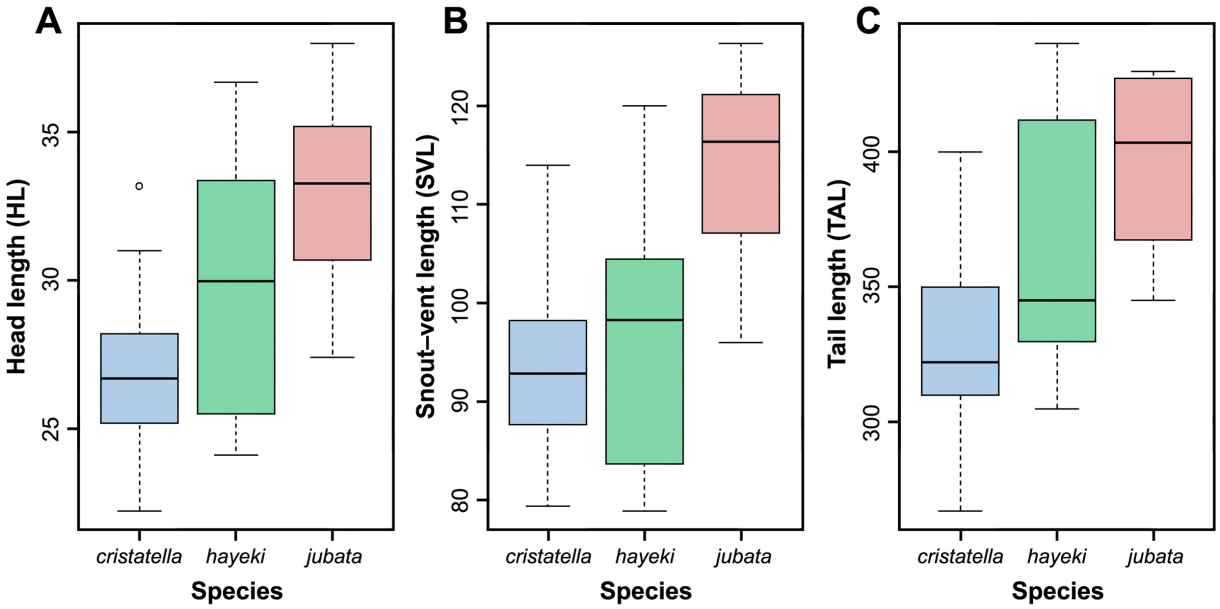

FIGURE 2. Boxplots of **(A)** head length, **(B)** snout–vent length, and **(C)** tail length of *Bronchocela hayeki*, *B*. *cristatella* and *B*. *jubata* in Sumatra, Indonesia; top, middle and bottom lines of the boxes indicate 75th percentile, median and 25th percentile, respectively.

Multivariate analysis by principal components analysis also showed distinct overall differences in morphometric characters between these three species with a distinct non-overlapping cluster for *B*. *hayeki* when sexes were combined (Fig. 3A) as well as for males separately (Fig. 3B). However, *B*. *cristatella* and *B*. *jubata* had largely overlapping clusters in both analyses. Principal components 1 and 2 collectively explained the 49.7% and 46.7% of variation in the morphometric data matrix (Table 1A–B) for combined sexes and males respectively. In both

principal components (PC1 and PC2) TYE.scale and LAL.scale loaded positively for males while for combined sexes it loaded negatively. Among the morphometric characters, scaled HL, PLM, EN, ES, LAL contributed most in both principal components for males as well as combined sexes.

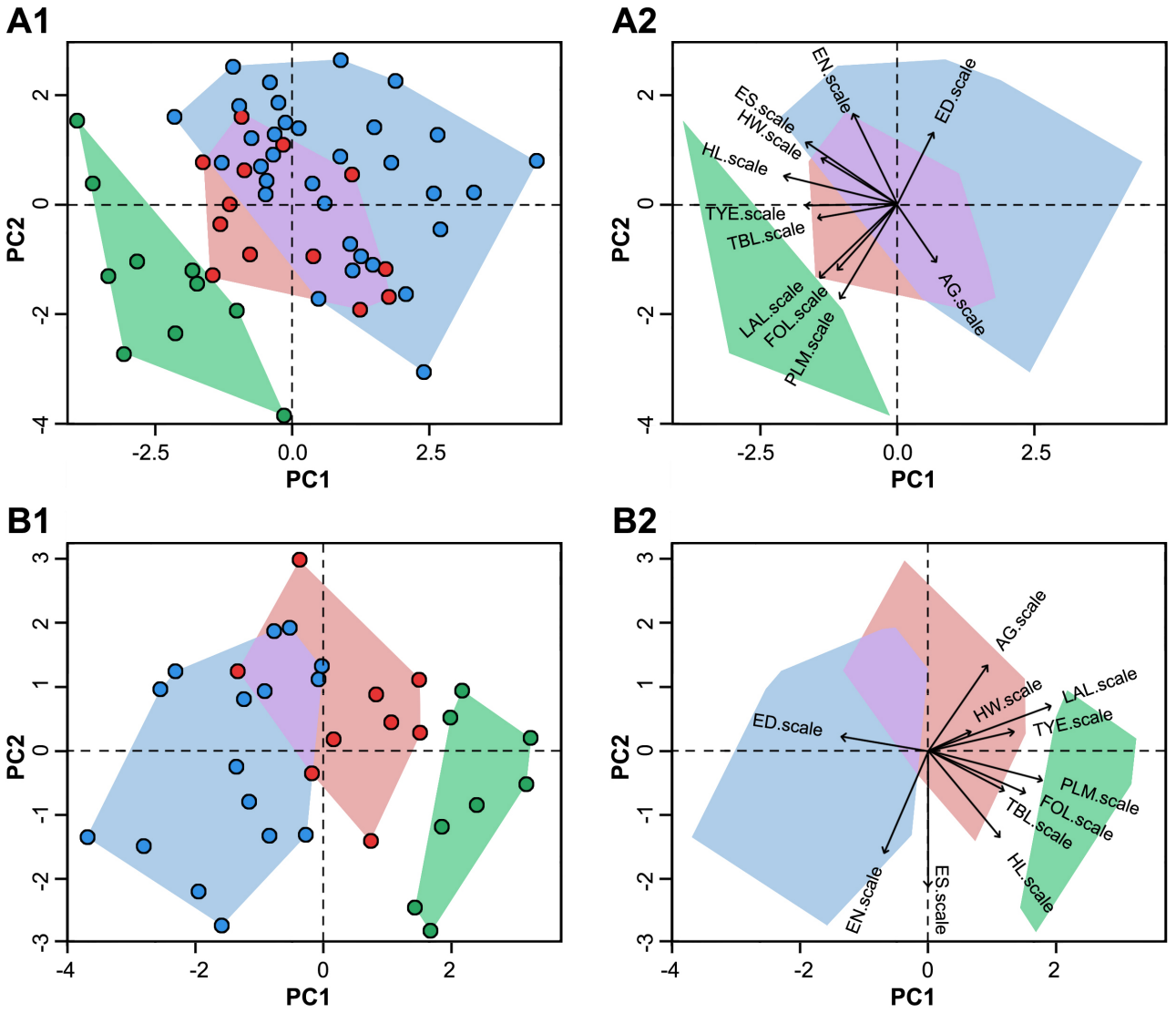

FIGURE 3. Principal Component Analysis (PCA) biplot of morphometric variation between *Bronchocela hayeki* (green), *B. cristatella* (blue) and *B. jubata* (red) in Sumatra, Indonesia with **(A1)** combined sexes and **(B1)** males only, shows the morphological distinctiveness of *Bronchocela hayeki*; **(A2, B2)** 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.

Taxonomy

Bronchocela hayeki (Müller, 1928)

(Fig. 4; Tables 2, 3)

Calotes hayeki Müller, 1928
Calotes hayeki—Brongersma 1931, Wermuth 1967: 38
Bronchocela hayeki—Moody 1980, Manthey & Grossmann 1997: 161, Hallermann 2005, Manthey 2008, Teyni *et al*. 2010

Holotype. ZSM 3/1928, collected from Sibayak Plateau (1,400 m above sea level), Berastagi, North Sumatra, Indonesia, by Prof. H. v. Hayek, on April 1, 1927 (lost, fide Hallermann 2005).

Neotype. ZMB 55931, adult male, collected from the foothills of Sibayak (311'N, 9831'E; 1,450 m), Berastagi, North Sumatra, Indonesia, by Ulrich Manthey, in April 1996 (designated by Hallermann 2005).

TABLE 2. Some morphometric ratios and meristic characters of *B. hayeki* and two congeners of the genus *Bronchocela* in Sumatra, Indonesia, for accession data see Appendix; — not measured / evaluated

Character	*Bronchocela* in Sumatra (Indonesia)					
	B. hayeki		*B. cristatella*		*B. jubata*	
	Male (*n*=8)	Female (*n*=2)	Male (*n*=16)	Female (*n*=17)	Male (*n*=10)	Female (*n*=4)
AG/SVL%	50.4–51.9	52.1–52.3	49.4–50.7	52.1–56.1	52.6–52.9	51.5–52.2
HL/SVL%	30.5–30.6	30.5–30.6	29.1–29.2	28.0–29.1	28.8–30.1	27.6–27.9
HW/HL%	50.2–50.9	46.4–50.2	52.1–54.3	50.9–52.2	54.7–54.8	53.9–56.5
EN/HL%	19.6–20.3	19.5–19.6	20.7–22.9	21.9–22.0	21.0–22.1	22.0–23.5
ES/HL%	37.3–39.8	37.3–37.9	38.6–41.3	38.8–39.6	37.6–38.3	10.5–12.8
ED/HL%	20.7–24.5	23.5–24.0	31.3–32.8	30.9–32.9	28.9–29.0	28.0–28.8
TYE/HL%	17.8–19.6	18.5–19.5	18.2–18.9	19.1–19.4	19.3–21.0	20.9–21.5
LAL/SVL%	19.0–20.1	20.0–20.5	18.6–20.0	19.3–20.4	20.4–21.1	20.0–20.5
PLM/SVL%	21.4–21.5	21.6–21.7	17.8–17.9	19.3–19.7	20.3–21.3	18.5–20.7
TBL/SVL%	28.3–28.6	28.5–28.6	26.7–28.7	28.2–28.7	27.7–27.9	27.2–27.7
FOL/SVL%	36.2–39.6	33.7–36.4	36.1–36.3	35.6–37.3	37.0–38.0	36.8–37.3
TAL/SVL	3.7–3.9 (*n*=6)		3.4–3.5 (*n*=27)		3.4–3.5 (*n*=8)	
supralabials	9, 10		8, 9		10, 11	
infralabials	9, 10		8, 9		11, 12	
scales from eye to tympanum	5–7		8–10		7–9	
nuchal crest scales	8–12		9–13		8–12	
subdigital lamellae on toe IV	30–33		30–34		30–36	
midbody scale rows	64–72	70–75	67–85	62–81	43–53	39–46
ventrals	55–60	50–55	60–85	61–80	65–73	62–70

Other materials examined. UIMZ 243, adult male, collected from Paribuan in the Sibayak Plateau (33'14.04"N, 9837'49.74"E; 1,414 m) near Berastagi, Dolok Silau, Simalungun, North Sumatra, by C.A. Putra, D. Arfianto, and P. Sitorus; MZB 203, adult male collected from Paya Lueng Kalon (1,260 m), Aceh, by Madzud, on 13 September 1930; ZMH R05472 and R05473 (adult males) and ZMH R05470 (adult female) collected from near Lake Toba (235'N, 9850'E; 1,565 m), North Sumatra; RMNH 14916, adult female, collected from Takengon (1,260 m), Aceh; MZB 8892 and 8893, adult males from Paya Lueng Kalon, Aceh; MZB 13839 and 13840, adult males from Rainforest Lodges Kedah (1,225 m), Blang Jerango, Gayo Lues, Aceh.

Diagnosis. A species of *Bronchocela* inhabiting northern parts of Sumatra Island, Indonesia, characterized as follows: morphologically most similar to its congeners on Sumatra Island, *B. cristatella* and *B. jubata* in body colouration, but differs by having the orbital area and the tympanum black (vs. mostly the same as body color in *B. cristatella* and *B. jubata*), enlarged ventral scales arranged in 8 rows (vs. 10–14 slightly-enlarged rows in *B. cristatella* and 10–12 non-enlarged rows in *B. jubata*), well-developed nuchal crest in males (vs. weakly-developed in *B. cristatella* sensu stricto), higher number of mid body scale rows, 64–75 (vs. 33–59 in *B. jubata*). In addition, *Bronchocela hayeki* is distinguished from other congeners by having the following combination of characters: adults reach maximum SVL 120.0 mm in males and 94.0 in females, 9 or 10 supralabials, 8–12 nuchal crest scales, 50–60 ventrals, 30–33 lamellae on fourth toe, third finger longer than the fourth; dwindled lateral scales directed downward anteriorly and upward posteriorly, 5–7 upper dorsal scale rows on the lateral body directed upward along the body, mid gular scales enlarged, abdominal scales acuminated and enlarged compared to pectoral, non-enlarged and keeled temporal scales with 5–7 rows between orbit and tympanum, tympanum diameter 50–60% of orbit diameter.

Redescription based on UIMZ 0243. An adult male, SVL 117 mm. Head moderately large, elongate, HL 28.8% of SVL, narrow, subtriangular in dorsal and ventral aspects, HW 51.2% of HL; distinct from neck; snout elongate, snout length greater than eye diameter, ED 71.9% of ES; interorbital distance broad; eye large, pupil rounded; diameter of eyes greater than eye-tympanum distance, TYE 68.5% of ED; ear opening shallow, its greatest diameter dorsolaterally, tympanum smaller than orbit, half sized; tympanum surrounded by keeled scales; temporal scales not enlarged, keeled, juxtaposed, 5–7 scale rows between orbit and tympanum; forehead convex; scales on interorbital and supercilium area keeled; scales on snout keeled, larger in size than those of occipital region; a developed nuchal crest continue dorsally as a dorso-nuchal crest; dorsal crest rudimentary, consisting of 12 crescent-shaped scales up to the level of axilla, no crest on the tail; rostral scale width greater than its height, ventroposteriorly in contact with first supralabial, contact posteriorly by five more or less equal-sized postrostral scales; around nostrils on each side two supranasals, two or three postnasals, two prenasals, and two subnasals, which separate nasal from supralabials; nostrils round located middle of the undivided nasal plate; canthus rostralis and supraciliary edges sharp; five canthal scales between supranasal and anterior margin of orbit; no distinct parietal plate; mental subtriangular, shorter than wide, posteriorlaterally in contact with two enlarged postmentals separated by a smaller scale; each postmental pair bordered posteriorly by three smooth scales, including the medial scale, but exclusive of infralabial; chin scales smooth; gular pouch present; throat scales and midgular scales keeled, mucronate, and imbricate; three scale rows separate orbit from supralabials; supralabials nine (seventh in midorbit position); infralabials nine, decreasing in size toward gape; ventral scales on the neck granular and keeled.

Body slender; lateral body scales equal, strongly keeled and imbricate; scales on lateral body much smaller (approximately 1/10th of mid ventrals) in size than those of venter at same level, directed backward and downward anteriorly and directed backward and upward posteriorly; lateral body scales on the posterior body slights enlarged and shorter than the anterior body scales; 5–7 upper dorsal scale rows directed backward and upward along the body; 69 scales around the midbody; pectoral scales and abdominal scales keeled, acuminated, imbricate and keels forming regular and parallel continuous ventral ridges; abdominal scales larger than pectoral scales; eight scale rows enlarged ventrally, with clear margin with the lateral scales; ventrals, 57.

Forelimbs moderately short; no oblique fold (pit) present on shoulders, but shoulder scales keeled and granular; 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) 3 > 4 > 2 > 5 > 1; (toes) 4 > 3 > 5 > 2 > 1; all bearing slightly recurved claws, claws are sharp and elongate; subdigital lamellae entire, bicarinate, and regular, subdigital lamellae on toe IV (left) 30.

Tail elongate and complete, 412 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, dorsum pale grayish green; few greyish blue markings on the lateral body; lateral head and nuchal crest scales cream, dorsal head greyish cream; orbit, labial band including the tympanum brown; dorsal crest scales, knee, elbow, wrist, heel grey; dorsal fingers and toes, posterior 2/3rd of the tail brown; ventral body, limbs, anterior tail, and mid gular pale yellowish green; ventral digits light brown.

In life, dorsum bright luminous green; few sky blue markings on the lateral body; lateral head lemon yellow; nuchal crest blonde yellow, dorsal head greyish green; ventral head bluish green; orbit, labial band including the tympanum blackish brown; dorsal crest luminous green; knee, elbow, wrist, heel dark green; dorsal fingers and toes, posterior 2/3rd of the tail greenish brown; ventral body, limbs, anterior tail, and mid gular lighter luminous green; ventral digits light brown.

Habitat, natural history, and distribution. This species is usually found in open canopy areas in primary forests (mostly forest edge) or undisturbed secondary forests, but avoids completely open areas. We often found it at the ecotone of forests and other vegetation (e.g. bamboo forests, coffee and pepper plantations, pine forests, well-maintained home gardens etc.) while basking (from sunrise until midday) on horizontal bamboo sticks or coffee branches, usually 1.5 to 4 meters above the ground. It is usually active during the daytime, mostly around 09:00 hr. At night, the adults prefer higher branches of the tress to sleep, mostly in open canopy areas, while juveniles prefer tiny branches of shrubs. In the Tapanuli area, we sometimes observed this species on Benjamin trees (*Styrax benzoin*; Family Styracaceae) around 7 m above the ground. The species seems sensitive to being disturbed when approached and when in danger quickly jump to the dense undergrowth and disappear.

TABLE 3. Diagnostic characters separating the species of *Bronchocela* (modified after Zug *et al*. 2017);—not measured / evaluated

	B. danieli (*n*=2)	*B. smaragdina* (*n*=6)	*B. vietnamensis* (*n*=2)	*B. celebensis* (*n*=20)	*B. cristatella* s.l. (*n*=90)	*B. marmorata* (*n*=62)	*B. hayeki* (*n*=11)	*B. jubata* (*n*=64)	*B. orlovi* (*n*=1)	*B. rubrigularis* (*n*=2)	*B. shenlong* (Grismer *et al*. 2015)	*B. rayaensis* (Grismer *et al*. 2015)	*B. burmana* (Zug *et al*. 2017)
Maximum SVL in adults (in mm)	80.0	113.0	122.0	119.0	119.7	119.6	120.0	142.0	109.6	106.4	106.0	85.0	94.0
Number of postmentals	3	3	2	3	3	3	3	3	3	3	3	3	3
Gular sac absent (0) or small (1) or large (2) in males	0	0	1	1	1, 2	1	2	2	1	1	2	0	0
Mid gular scales not enlarged (0) or enlarged (1) in males	0	1	1	0	0, 1	0	1	1	0	1	1	0	0
Red gular patch in males absent (0) or present (1)	0	0	0	0	0	0	0	0	0	1	0	0	0
Enlarged ventral scale rows	10–12	10–12	12	10–12	10–14	10–12	8–10	10–12	—	10–12	—	—	—
Ventrals larger than dorsals in × times	5–8	4–5	2–3	1–2	1–5	1–5	8–10	1	2–3	2–3	1–5	1–5	1–5
Ventrals	75–79	64–72	70–73	62–78	52–89	72–74	50–60	56–73	—	54–72	—	—	—
Lateral body scales smooth (0), feebly (1) or strongly (2) keeled	2	0, 1	1	2	1, 2	2	2	2	1	2	2	2	2
Number of upwards pointing upper dorsal scale rows	3, 4	1, 2	0	2–4	4–10	1, 2	5–7	1, 2	0	1–2	4–7	0	0
Supraoculars smooth (0) or keeled (1)	0	1	1	1	1	1	1	1	1	1	1	1	1
Pale/white ventrolateral body stripe absent (0) or present (1)	0	0, 1	1	0	0	0	0	0	0	0	0	0	0
Nuchal crest weakly (0) or well (1) developed	0	0	0	1	0, 1	0	1	1	1	1	1	0	0
Nuchal crest scales crescent-shaped (0) or lanceolate (1)	1	1	0	1	1	1	0	0	0	0	1	1	1
Number of nuchal crest scales to the level of axilla	12–14	10–12	10–12	8–10	8–15	7–11	8–12	10–12	8–10	8–10	10–12	8–10	6–9
Nuchal crest scales shorter (0) or longer (1) than ED	0	1	1	0	0	0	1	1	1	1	0	0	0
Dorsal crest indistinct (0) or distinct (1)	0	1	0	0	0, 1	1	1	1	1	1	0	0	0
Tympanum diameter / ED %	50–60	55–65	45–55	35–45	45–55	50–60	50–60	50–60	53	75–90	38–44	46–49	45–55
Tympanum and orbit pale (0) or dark (1)	1	0	0	0	0, 1	0	1	0	0	1	0	0	0
Temporal scales smooth (0) or keeled (1)	1	1	1	1	1	1	1	1	1	0	1	1	1

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TABLE 3. (Continued)

	B. danieli (*n*=2)	*B. smaragdina* (*n*=6)	*B. vietnamensis* (*n*=2)	*B. celebensis* (*n*=20)	*B. cristatella* s.l. (*n*=90)	*B. marmorata* (*n*=62)	*B. hayeki* (*n*=11)	*B. jubata* (*n*=64)	*B. orlovi* (*n*=1)	*B. rubrigularis* (*n*=2)	*B. shenlong* (Grismer *et al.* 2015)	*B. rayaensis* (Grismer *et al.* 2015)	*B. burmana* (Zug *et al.* 2017)
Enlarged scales on temporal region absent (0) or present (1)	1	0	0	1	0, 1	0	0	1	0	1	1	0	0
Number of temporal scale rows between orbit and tympanum	7, 8	9, 10	12, 13	7, 8	6–10	8–11	7, 8	6, 7	6	6, 7	6, 7	7, 8	7, 8
Prominent white patch on temporals absent (0) or present (1)	1	0	0	0	0	0	0	0	0	0	0	0	0
Pale/dark labial stripe/band absent (0) or present (1)	0	1	0	0	0	1	0, 1	0, 1	0	0	1	0	0
Canthal scales between supranasal and anterior border of orbit	4, 5	4, 5	4, 5	3, 4	4–7	4–6	4, 5	5, 6	3, 4	3, 4	6–11	5–7	5–7
Canthal edges blunt (0) or sharp (1)	0	0	0	0	1	1	1	0, 1	1	0	1	1	1
Midbody scale rows	55–71	43–53	47–54	50–76	50–106	47–73	64–75	33–59	43	52–58	71–92	67–71	55–67
3rd finger shorter (0) or longer (1) than 4th finger	0	1	1	1	0, 1	—	1	0	—	1	0	1	1
4th finger shorter (0) or longer (1) than 5th toe	1	1	1	0	0, 1	0	0	0, 1	—	0	0	0	0
Tail colouration uniform (0) or banded (1)	0	0	1	0	0, 1	0	0	1	0	0	1	1	1

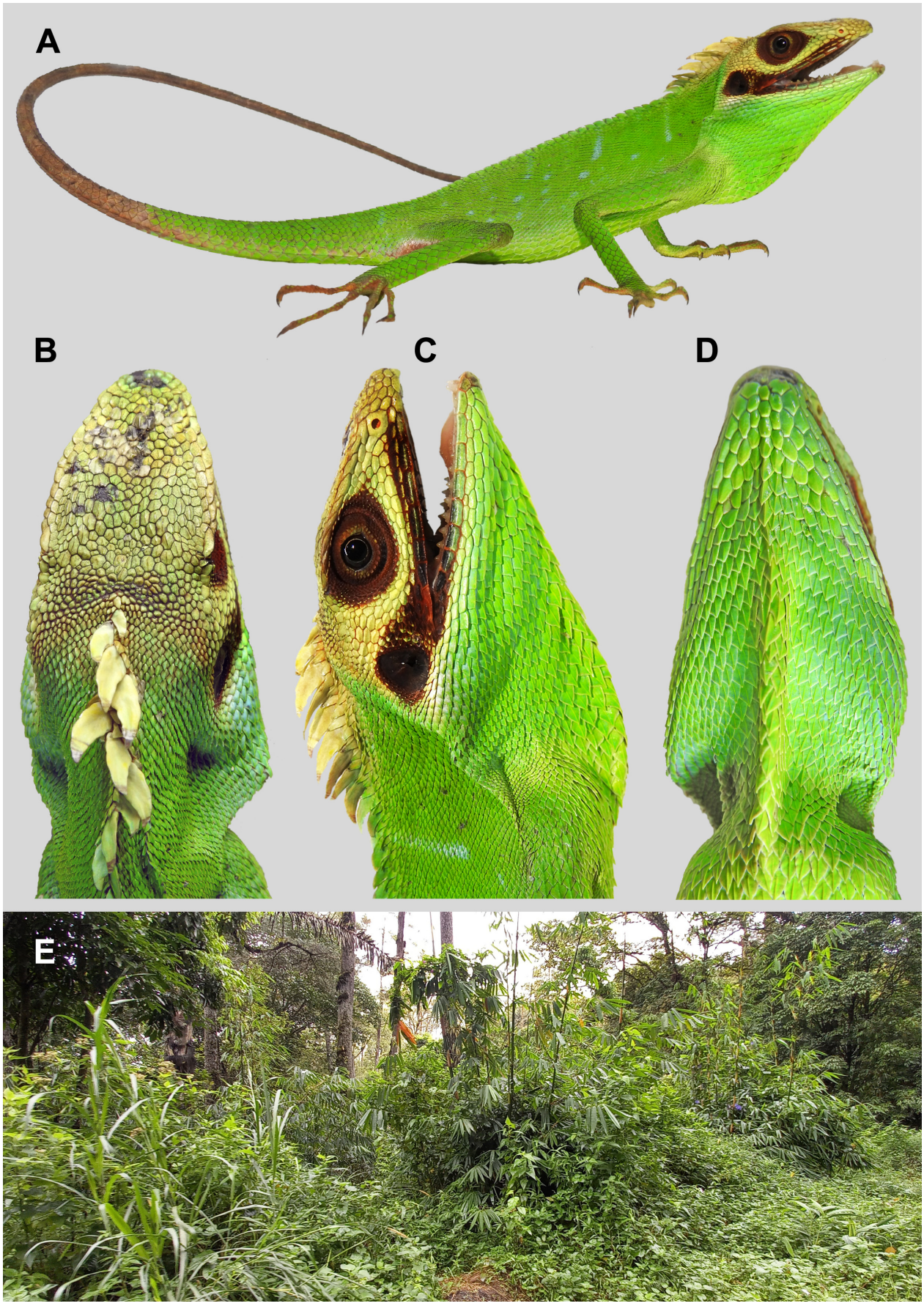

FIGURE 4. *Bronchocela hayeki* in life (UIMZ 0243, adult male): **(A)** lateral view of the full body, **(B)** dorsal head, **(C)** lateral head, **(D)** ventral head, and **(E)** secondary forest habitat collected from near the type locality.

The species is sympatric with other arboreal agamids such as *Dendragama boulengeri*, *Gonocephalus lacunosus*, and *Bronchocela cristatella*. We always found several individuals close together at elevations of 900–1600 m above sea level, and never at elevations lower than 600 m. Most of the individuals were observed at Mt. Paribuan (Simalungun Regency), Mt. Meriah (Deli Serdang Regency), and Mt. Sinabung and Mt. Sibayak (Karo Regency) in North Sumatra. The southern margin of the distribution of this species is the southern parts of Lake Toba, and it seems the distribution records are scattered (Fig. 1) due to forest fragmentation, but always confined to forested uplands. The northernmost distribution is in the Jantho Panorama Park (600 m a.s.l) mostly at the ecotone of the forest and pine plantation.

Conservation status. The forest habitat fragments are further threatened by encroaching agricultural lands, especially large-scale vegetable plantations. We have observed large scale humus soil extraction inside the forest areas around Mt. Paribuan, probably for agricultural use. Such disturbances directly impact the forest system and the population status of the species as they lay their eggs in the humus. Based on our observations, illegal pet trade has been identified as one of the major threats. The application of the IUCN Red List criteria (IUCN Standards & Petitions Subcommittee 2019) with the updated distribution data shows that *B. hayeki* is restricted to an area of occupancy (AOO) of 144 km^2 recorded from 13 localities (eight locations) within 52, 857 km^2 extent of occurrence (EOO). Given the low area of occupancy, the scattered distribution of severely fragmented forests, *B. hayeki* should be considered as an "Endangered" (EN) species.

Discussion

Bronchocela hayeki has been mistaken (e.g. Nugraha *et al*. 2020) for some northern Sumatran and northern parts of West Sumatran populations of *B*. cf. *shenlong* which has a more prominent nuchal crest than typical *B. cristatella* on Java Island. Although *B. hayeki* populations from the northern areas (mostly in Aceh Province) have a very prominent and thick black labial band, most of the southern populations around Toba Lake (mostly in North Sumatra Province) have no labial bands, and the dark colouration is confined to the orbit scales and the tympanum. This colour variation has led to *B. hayeki* being mis-identified as *B. cristatella* and our re-examination of some *B. cristatella* specimens (MZB 203, 8892, 8893, 13839, and 13840) at MZB turned out to be *B. hayeki*. Therefore, to distinguish *B. hayeki* and *B. cristatella* the comparative size of ventral scales is the ideal character because the nuchal crest of juveniles and subadult females of *B. hayeki* may still be difficult to distinguish from *B. cristatella*. Although, *B. cristatella* has been reported from northern Sumatra utilizing the same forested areas, and some areas the same habitat, but only coexist syntopically. *Bronchocela cristatella* mostly utilize the closed canopy primary forests compared to *B. hayeki*, which prefers open habitats similar to habitat preferred by *B. jubata*. Interestingly, *B. hayeki* shares a few unique morphological characters of both *B. cristatella* and *B. jubata*, but *B. hayeki* is allopatric with *B. jubata*. A systematic revision of *B. cristatella* (including a neotype designation) and *B. jubata* (including a lectotype designation) will be published elsewhere (Amarasinghe *et al.* in press). Details on the ecology, habitat, population, and breeding biology of *B. hayeki* are still sparse and further studies are needed.

Key to the species of the genus *Bronchocela* (modified after Hallermann, 2005)

1.(a) Nuchal crest well-developed 2
(b) Nuchal crest weakly-developed 7
2.(a) Nuchal crest scales shorter than ED 3
(b) Nuchal crest scales longer than ED 4
3.(a) Pale labial band absent, gular sac small and midgular scales not enlarged in males, 2–4 upper dorsal scale rows pointing upwards, 8–10 nuchal crest scales to the level of axilla, canthal edges blunt, 3 or 4 canthal scales between supranasal and anterior border of orbit, 50–76 midbody scale rows, tail colouration uniform . . . . . *B. celebensis*
(b) Pale labial band present, gular sac large and midgular scales enlarged in males, 4–7 upper dorsal scale rows pointing upwards, 10–12 nuchal crest scales to the level of axilla, canthal edges sharp, 6–11 canthal scales between supranasal and anterior border of orbit, 71–92 midbody scale rows, tail colouration banded . . . . . *B. shenlong*
4.(a) Mid gular scales enlarged, lateral body scales strongly keeled, 1–7 upper dorsal scale rows pointing upwards 5
(b) Mid gular scales not enlarged, lateral body scales feebly keeled, 1–7 upper dorsal scale rows pointing upwards . . . . *B. orlovi*
5.(a) Temporal scales keeled, no gular patch in males, 10–12 nuchal crest scales to the level of axilla, gular sac large in males, tympanum diameter 50–60% of ED 6
(b) Temporal scales smooth, red gular patch in males, 8–10 nuchal crest scales to the level of axilla, gular sac small in males,

tympanum diameter 75–90% of ED . . . . . *B. rubrigularis*

6.(a) 33–59 midbody scale rows, ventrals and dorsals equal in size, 10–12 enlarged ventral scale rows, 3rd finger shorter than 4th finger, enlarged temporal scales present, 1 or 2 upper dorsal scale rows pointing upwards, tympanum and orbit pale in color, tail colouration banded . . . . . *B. jubata*

(b) 64–75 midbody scale rows, ventrals 8–10 times larger than dorsals, 8–10 enlarged ventral scale rows, 3rd finger longer than 4th finger, enlarged temporal scales absent, 5–7 upper dorsal scale rows pointing upwards, tympanum and orbit dark in color, tail colouration uniform . . . . . *B. hayeki*

7.(a) Three postmentals, nuchal crest scales lanceolate, less than 11 temporal scale rows between orbit and tympanum 8

(b) Two postmentals, nuchal crest scales crescent-shaped, 12 or 13 temporal scale rows between orbit and tympanum . . . . . *B. vietnamensis*

8.(a) No white colour patch on temporals, Supraoculars keeled, ventrals larger than dorsals in less than five times 9

(b) Prominent white colour patch present on temporals, Supraoculars smooth, ventrals 5–8 times larger than dorsals . . . . . *B. danieli*

9.(a) Nuchal crest scales shorter than ED, canthal edges sharp 10

(b) Nuchal crest scales longer than ED, canthal edges blunt . . . . . *B. smaragdina*

10.(a) Gular sac absent in males, no upper dorsal scale rows pointing upwards 11

(b) Gular sac present in males, several upper dorsal scale rows pointing upwards 12

11.(a) 55–67 midbody scale rows . . . . . *B. burmana*

(b) 67–71 midbody scale rows . . . . . *B. rayaensis*

12.(a) 1 or 2 upper dorsal scale rows pointing upwards, pale labial band present . . . . . *B. marmorata*

(b) 4–10 upper dorsal scale rows pointing upwards, pale labial band absent . . . . . *B. cristatella* sensu stricto

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APPENDIX 1. Other specimens examined

***Bronchocela celebensis*: Indonesia:** Sulawesi: NHMUK 1946.8.11.48 (holotype), 72.4.6.126–127, ZMB 688, 8801, 36898, RMNH 3021a–e, 3023a–d, 7419a–e.

***B. cristatella*: Indonesia:** Borneo: RMNH 7371a–c, 7374a–b, ZMH R04639–43, 5586–91, 5593–99, 6081–2, ZMB 51019, 53634, ZFMK 50529–30; Java: ZFMK 20783, RMNH 2848a–b, ZMH R00608, 5602–3, 5623; Maluku: RMNH 3030–1, 3034a–b, 3035, 3036a–b, 3037a–c, ZMUC R98502– 4, ZMH R04891–2, 6083– 4, ZSM 366a–b; Sulawesi: ZSM 365; Sumatra: MZB 187, 653, 1569, 1679, 1872, 2163, 4390, 4594, 4730, 4993, 4995, 5292, 7463–64, 9803–5, 9807–8, 9810, 9812, 9907, 13407, 13409, 14732, 14733–4, 15062, 15064, ZMB 57217, ZSM 333.1999, 376.1978.d, ZMH R04928; Papua: ZMH R04927.

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

***B. jubata*: Indonesia:** Borneo: ZMH R06163; Java: MNHN 2543 (syntype), 1911.142, ZFMK 48897–906, 48917–21, 27099–101 (syntypes of *B. intermedia*), ZMH R4934–6, 7066–9, 7070, 7074–9, 7080–7, RMNH 7304, 7417a–b, 35930, ZMUC R98500, TCWC 73121, ZMB 14438, Sumatra: MZB 6612–6, 6638, 6656–7, 9757, 9758, 9761–4.

***B. marmorata*: Philippines:** NHMUK 1946.8.11.16 (holotype), 72.8.20.25–26, RMNH 3022a–d, ZMH R04882, MNHN 5775, 1900.341, 1999.8131, ZFMK 43702–13, ZMB 681 (syntype of *C. philippinus*), 5433, 5642, 49761–6 (syntypes of *C. philippinus*), 54507, USNM 36167–8, 58838, 77133–5, 140839, 318692, 318694–5, 498716, 498783, 513564–71, 513836, FMNH 251691, CAS 15457, 20338, 61705, 62398–99, 131925, ZMUC 148.

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

***B. rubrigularis*: India:** Nicobar: ZMH R09271 (holotype), R09272 (paratype).

***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).