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Taxonomy and distribution of a common arboreal lizard, *Bronchocela jubata* Duméril & Bibron, 1837 (Reptilia: Agamidae), with designation of its lectotype from Java, Indonesia

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Abstract

Bronchocela jubata Duméril and Bibron, 1837 is one of the commonest species of the genus, known mostly from Java Island and southern parts of Sumatra. It is rare in Bali and Borneo. The juveniles are often confused with its morphologically similar congener, *B. cristatella*, which occurs widely throughout the Indonesian Archipelago and Peninsular Malaysia. We examined the morphology of *B. jubata* based on museum specimens including its two available syntypes, and redescribed the species based on the lectotype designated herein. We highlight the characters of *B. jubata* with a morphometric comparison to its sympatric congener *B. cristatella* from Java Island, Indonesia. Based on the current distribution pattern and the apparent threats, we update the conservation status of *B. jubata* using IUCN Red List Criteria, and propose that it be considered as a species of Least Concern (LC), endemic to the Greater Sundaic Islands.

Key words: Conservation, endemic, Indonesia, lectotype, morphometric, Java, taxonomy

Introduction

Green agamid lizards of the genus *Bronchocela* Kaup, 1827 have a wide range extending from India, Peninsular Malaysia to south-east Asia (Myanmar, Thailand, Cambodia, Vietnam), Philippines, Sulawesi, southern Sundaland in the west, to Papua New Guinea in the east including the Andaman and Nicobar Islands and some 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; Zug *et al*. 2017; Amarasinghe *et al*. 2022). 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 these, *B. cristatella* is the most widespread species, occurring throughout the Sunda-Sahul Convergence Zone. Very little has been published about other *Bronchocela* species (Hallermann 2005; Amarasinghe *et al*. 2022).

Bronchocela jubata was described by Duméril and Bibron (1837: 397–399) based on four specimens (syn-

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types—see discussion) from Java (Indonesia) and Pondichéry (India). Stoliczka (1870) suggested that the locality "Pondichéry" might be an error and may have really come from the French Missionaries on the way to Nicobar *via* Pondicherry, which is incorrect—see discussion. Although, Stoliczka (1870) and Theobald (1876) recognized that the Nicobar and Java specimens are morphologically different, Boulenger (1885, 1890) mistakenly identified the *Bronchocela* specimens from Nicobar (now identified as the endemic *B. rubrigularis* Hallermann, 2009) and some *B. cristatella* specimens from the Malay Archipelago as *B. jubata*, but he noticed the exceptional high midbody scale row counts of *B. cristatella* specimens he examined which are out of the range for *B. jubata*. De Rooij (1915) reported the species from several locations in Sumatra, Java, Bali, and Sulawesi Islands. Mertens (1957) also reported the species from Bali Island. Smith (1935) restricted the type locality of *B. jubata* to Java.

Berthold (1842) described another closely matching species, *Bronchocele* (sic) *intermedia* [Note. *Calotes intermedia* Peters and Doria, 1878 is a different taxon, currently a junior synonym of *B. cristatella*; *fide* Hallermann 2005] from the Sunda Islands, but without a more precise locality. Berthold (1842) considered *Bronchocele* (sic) as a subgenus of *Calotes*, and in his later paper (Berthold 1846), where he only used *Calotes*, gave Java as the origin of the specimen. Moody (1980) reassigned the species in the genus *Bronchocela*. Berthold (1842) identified his species as an intermediate form between *B. cristatella* and *B. jubata*, but more closely allied to *B. jubata*. He however provided several minor characters to highlight the distinctiveness of his species. Therefore, Hallermann (2005) considered it as a junior synonym of *B. jubata*. Here we examine all the historical specimens (including types and supposed types) involved with the nomen *B. jubata* and its junior synonyms and report the species from additional localities including freshly collected specimens to reassess the taxonomic status and distribution pattern of *B. jubata*. We also provide comprehensive taxonomic details on morphology and morphometry based on all our examined museum specimens (including types).

Material and methods

During field surveys conducted (by AATA and AR) within the Greater Sunda Islands, Indonesia, we encountered plentiful individuals of *Bronchocela jubata* (Fig. 1) on Sumatra and Java Islands. Natural history observations were made by looking with the naked eye at the animal's activity from a distance of at least 3–4 m, being careful not to disturb them. Latitude, longitude, and elevation of observed and/or collected specimens were recorded using a Garmin GPSmap 60CSx using WGS 84 map datum. Two adult male individuals were collected by hand, from Depok and Bogor, West Java (outside the protected areas), euthanized with sodium pentobarbital, and liver and thigh muscle tissue samples were preserved in 95% ethanol for DNA analysis. The specimens were fixed in 10% buffered formalin for 24 hours and washed in running water before storage in 70% ethanol. The specimens are deposited at the Museum of Zoology, Research Center for Climate Change, University of Indonesia, Depok (UIMZ).

Morphological, morphometric, and meristic characters. We compared voucher specimens to other relevant historical specimens of *Bronchocela jubata* (including its available syntypes), syntypes of *B. intermedia*, and all the other congeners of the genus. 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-RA); 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 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: 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, measured entire tail from posterior margin of vent to tail tip).

FIGURE 1. Current distribution map showing the collection/observation localities of *Bronchocela jubata* (red) and its sympatric congener, *B. cristatella* sensu lato (blue) on Java and Bali Islands; sympatric localities filled partially; for the distribution of *B. jubata* on Sumatra Island, see Amarasinghe *et al*. 2022.

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 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 on adult voucher specimens of *Bronchocela jubata* and its sympatric congener *B. cristatella* for both sexes combined. We choose to combine both sexes since the smaller number of *B. cristatella* would have rendered them insufficient for a statistical analysis for separate sexes. In total 116 specimens [*B. jubata* (*n*=98) and *B. cristatella* sensu stricto (*n*=18)] from Java Island were used for the statistical analysis. A systematic revision of *B. cristatella* complex will be published elsewhere (Amarasinghe *et al*. in press). Juveniles were excluded from the statistical analysis to avoid the bias of allometry. We performed Kruskal–Wallis univariate analysis of variance tests on HL (*n*=116), SVL (*n*=116), and TAL (*n*=85 with complete original tails) to see whether these body metrics are significant in separating the two often mixed species. We used this test due to the small sample size following Zar (2010). Boxplots were generated for the above body metrics in order to visualize the range, mean, median, and degree of differences between the two species. Each morphometric 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 eleven 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 fewer 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 our distribution records are based on the combined data obtained from examined museum specimens and our recent field observations. The conservation status of the species was evaluated using the IUCN Standards and Petitions Subcommittee (2019) to assess its risk of extinction.

Results

Morphometric analysis. The head (HL), snout–vent (SVL), and tail (TAL) lengths comparison of Kruskal–Wallis test showed that these body size metrics significantly separate the two species: Higher head (HL, $\chi^{2=}$35.67, *P*=2.339e-09), body (SVL, $\chi^{2=}$38.38, *P*=5.807e-10), and tail (TAL, $\chi^{2=}$26.57, *P*=2.547e-07) lengths of *B. jubata* indicated a relatively elongated and larger head, body, and tail than that of *B. cristatella* on Java Island (Fig. 2A–C). However, Multivariate analysis by principal components analysis showed an indistinct overlapping cluster including both species (Fig. 3). Principal components 1 and 2 collectively explained only 55.7% of the variation in the morphometric data matrix (Table 1) for combined sexes. In both principal components (PC1 and PC2) scaled AG loaded negatively while all other limbs related metrics, scaled LAL, PLM, TBL, FOL loaded positively. Among the morphometric characters, scaled TBL contributed most to the separation of both species in both principal components.

TABLE 1. Principal Component Analysis (PCA) and loadings for *B. jubata* and *B. cristatella* in Java only. Principal components (PC) 1 and 2 in each analysis collectively explained 55.7% of the variation for combined sexes.

PCA variable	PC1	PC2	PC3	PC4	PC5	PC6
Standard deviation	2.0591	1.3748	1.0449	0.9833	0.8896	0.8009
Proportion of variance	0.3854	0.1718	0.0992	0.0879	0.0719	0.0583
Cumulative percentage%	38.5	55.7	65.6	74.4	81.6	87.5
Loadings						
HL.scale	0.4419	-0.1500	-0.0471	0.0361	-0.0062	0.0150
HW.scale	0.3955	-0.1660	-0.1250	0.1599	0.0390	-0.2218
EN.scale	0.3152	-0.2671	0.2235	-0.3554	-0.0376	0.4802
ES.scale	0.4083	-0.1798	0.1265	-0.1043	-0.1758	0.2299
TYE.scale	0.2939	-0.2510	0.3379	0.0260	-0.1706	-0.6389
ED.scale	0.2988	-0.0074	-0.4254	0.2575	0.3904	0.3145
TBL.scale	0.3134	0.3188	-0.2451	0.1251	0.2791	-0.2873
AG.scale	-0.1403	-0.2791	0.4818	0.0512	0.7980	-0.0285
LAL.scale	0.0651	0.1998	0.4406	0.7922	-0.2143	0.2669
FOL.scale	0.2460	0.5380	0.1668	-0.1922	0.1505	-0.0438
PLM.scale	0.1549	0.5238	0.3268	-0.2935	0.0373	0.0588

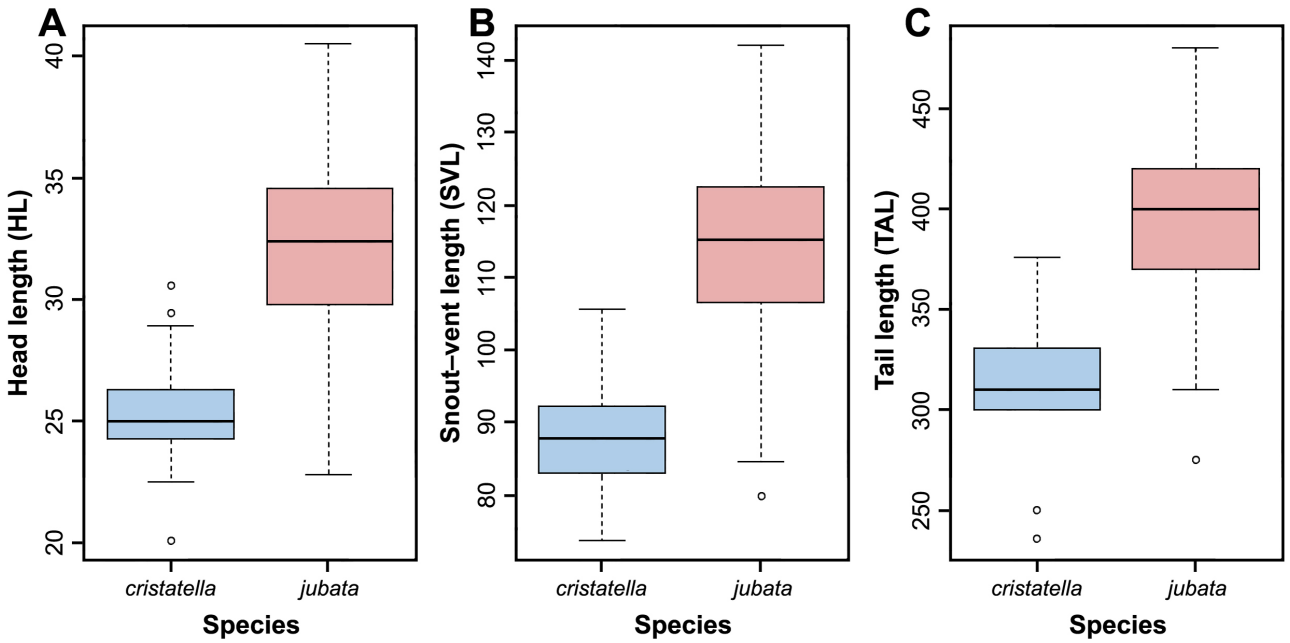

FIGURE 2. Boxplots of **(A)** head length, **(B)** snout–vent length, and **(C)** tail length indicating differences between *Bronchocela jubata* and *B. cristatella* in Java, Indonesia (note that both sexes were mixed); top, middle and bottom lines of the boxes indicate 75th percentile, median and 25th percentile, respectively.

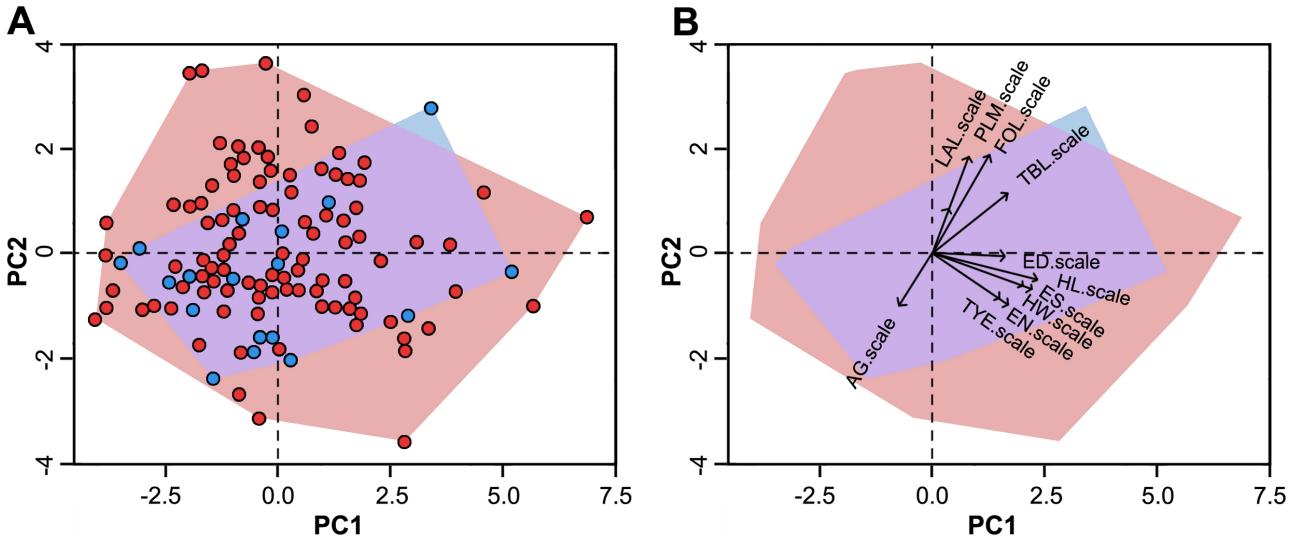

FIGURE 3. Principal Component Analysis (PCA): **(A)** biplot of morphometric variation in combined sexes between *Bronchocela jubata* (red) and *B. cristatella* (blue) in Java, Indonesia; **(B)** the same base biplots with vectors associated with species clusters. Each point represents an individual specimen, and the relative distance between two points is equivalent to the amount of dissimilarity.

Taxonomy

Bronchocela jubata Duméril and Bibron, 1837

(Figs. 4, 5; Tables 2, 3)

Bronchocela jubata Duméril & Bibron, 1837
Bronchocele (sic) *intermedia* Berthold, 1842 (not *Calotes intermedia* Peters & Doria, 1878)
Calotes intermedius—Berthold 1846
Calotes jubatus—Boulenger 1885, de Rooij 1915, Smith 1935
Bronchocela jubata—Moody 1980, Manthey & Schuster 1992, Hallermann 2005, Manthey 2008, Amarasinghe *et al*. 2022

Lectotype (designated herein). MNHN-RA 2542, adult male (SVL 130 mm), collected from Java, Indonesia by Jean-René Constant Quoy and Joseph-Paul Gaimard in 1828. Note: The original syntypes were composed of four specimens: (i) MNHN-RA 2541 and (ii) MNHN-RA 2541A from Java, Indonesia (donated from the Leyden Museum) labelled as *Calotes gutturosus* on the original tag of Leyden, currently lost; (iii) MNHN-RA 2542 from Java, Indonesia (collected by Quoy and Gaimard); and (iv) MNHN-RA 2543 from Pondichéry, India (collected by Leschenault). Only the latter two syntypes are present at MNHN, and here we designate the one from Java as the lectotype. For the justification for lectotype designation see discussion.

Diagnosis. A species of *Bronchocela* inhabiting the Greater Sunda Islands (Sumatra, Java, Borneo, and Bali), characterized as follows: morphologically most similar to its allopatric congener on Sumatra Island, *B. hayeki* (see Amarasinghe *et al.* 2022) and sympatric congener, *B. cristatella*, but differs by having a comparatively larger gular sac (smaller in *B. hayeki* and *B. cristatella*), ventral scales arranged in 10–12 non-enlarged rows (vs. 8–10 enlarged rows in *B. hayeki* and 10–14 slightly-enlarged rows in *B. cristatella*), lower number of mid body scale rows, 33–59 (vs. 64–75 in *B. hayeki* and 50–106 in *B. cristatella*), 1 or 2 upper dorsal scale rows directed upward (vs. 5–7 rows in *B. hayeki* and 4–10 in *B. cristatella*), well-developed nuchal crest (weakly-developed in *B. cristatella*) with crescent-shaped scales longer than ED (vs. lanceolate and shorter than ED in *B. cristatella*), enlarged scales on temporal region (vs. absent in *B. hayeki*), 3rd finger shorter than fourth (vs. longer in *B. hayeki*), the orbital area and the tympanum mostly pale (vs. mostly black in *B. hayeki*), and tail colouration banded (vs. uniform in *B. hayeki*).

In addition, *Bronchocela jubata* is distinguished from other congeners by having the following combination of characters: adults reach a maximum SVL of 141.0 mm in males and 142.0 in females, 9–11 supralabials, 10–12 nuchal crest scales to the level of axilla, 56–73 ventrals, 30–37 lamellae on fourth toe, third finger shorter than the fourth; large lateral scales directed downward anteriorly and straight backwards posteriorly, 1 or 2 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, keeled temporal scales with some enlarged scales and 6 or 7 rows between orbit and tympanum, tympanum more than half the size of orbit.

Description of lectotype. MNHN-RA 2542, an adult male, SVL 130 mm. Head moderately large, elongate, HL 27.3% of SVL, narrow, subtriangular in dorsal and ventral aspects, HW 52.2% of HL; distinct from neck; snout elongate, snout length greater than eye diameter, ED 48.8% of ES; interorbital distance broad; eye large, pupil rounded; diameter of eyes slightly shorter than eye-tympanum distance, ED 98.7% of TYE; ear opening shallow, its greatest diameter dorsolaterally, tympanum smaller than orbit, nearly 60% of orbit diameter; tympanum surrounded by keeled scales; several temporal scales enlarged, keeled, juxtaposed, six scale rows between orbit and tympanum; forehead concave; scales on interorbital and supercilium area keeled; scales on snout keeled, larger in size than those of occipital region; a well-developed nuchal crest continuing dorsally as a dorso-nuchal crest; dorsal crest rudimentary, consisting of 12 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 five more or less equal-sized postrostral scales; around nostrils on each side two supranasals, three postnasals, a single prenasal, and two subnasals, which separate the nasal from the 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, flat posteriorly, shorter than wide, posterior-laterally in contact with two enlarged postmentals separated by a smaller scale; each postmental pair bordered posteriorly by four smooth scales, including the medial scale, but exclusive of infralabials; chin scales keeled; gular pouch present, midgular scales enlarged; throat scales and midgular scales keeled, mucronate, and imbricate; three scale rows separate orbit from supralabials; supralabials eleven (ninth in midorbit position); infralabials eleven, 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; 1 or 2 upper dorsal scale rows directed backward and upward along the body; 37 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; 10–12 rows enlarged ventrally, without clear margin with the lateral scales; 64 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 claws, claws are sharp and elongate; subdigital lamellae entire, bicarinate, and regular, 30 (left) subdigital lamellae on toe IV.

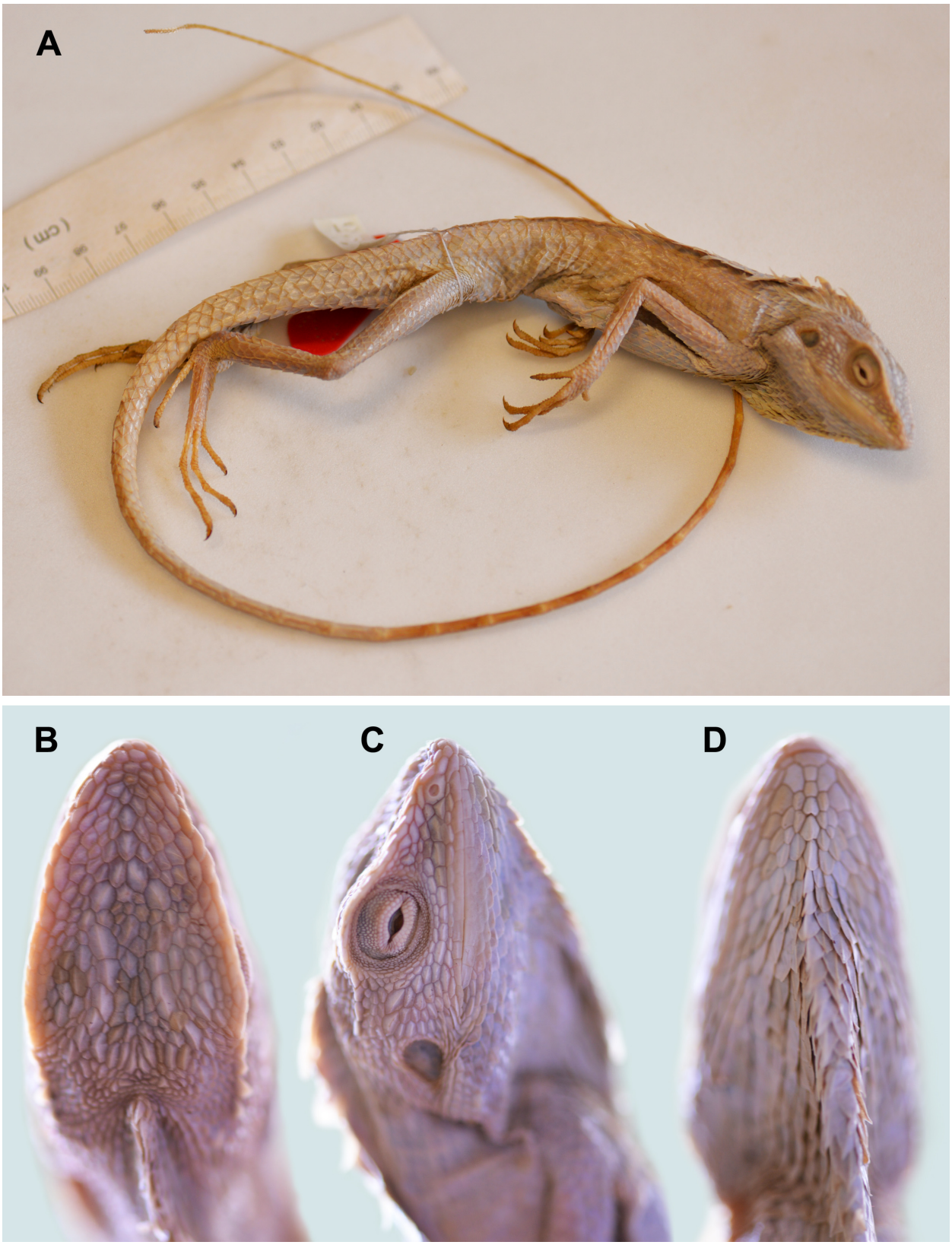

FIGURE 4. *Bronchocela jubata* lectotype (MNHN-RA 2542, adult male) from Java: **(A)** lateral view of the full body, **(B)** dorsal head, **(C)** lateral head, **(D)** ventral head.

Tail elongated and complete, 447 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 cream due to colour having been bleached.

In life, based on field observations, dorsum bright luminous green to dark olive green; few sky blue markings on the lateral body; lateral head lemon green; nuchal crest scales blonde yellow, green or cream, dorsal head greyish or brownish green; ventral head bluish green or pale green; orbit, labial band including the tympanum same as body colours or sometimes pale or whitish; dorsal crest scales luminous green or same colour as body; knee, elbow, wrist, and heel darker; 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. In some populations, especially in males, prominent white patch below the tympanum (sometimes this patch may extend to the lips as a labial band), lateral neck (below the nuchal crest), and the lateral sky blue markings may be visible as whitish stripes across lateral body (similar to *Calotes calotes* in Sri Lanka).

Dentition. Based on our examination of three *B. jubata* specimens (MZB 2963, 3791, and 3898) from Java, all have two *premaxillary teeth*, 13 *maxillary teeth*, and 15 *dentary teeth.*

Hemipenes. Based on MZB 6639 (Fig. 6), the hemipenis of *B. jubata* is well developed, single, width of the organ greater than its length; hemipenial lobes slightly divided for approximately 10% of its length; apex divided into four segments, two short dorsal segments and two long ventral segments by lateral and medial sulcus; calyculate ornamentation present on each lobe; thick-walled smooth calyces forming deep oval pits; apical calyces smaller than ventral and dorsal calyces; sulcus spermaticus converged and narrowly open at apex, proximal half deep, distal half shallow; sulcal lips smooth; a fleshy cardioid structure at the base of the ventral sulcus.

TABLE 2. Some morphometric ratios and meristic characters of *Bronchocela jubata* and its sympatric congener, *B. cristatella* in Java, Indonesia (for accession data see Appendix).

Character	*Bronchocela* in Java (Indonesia)			
	B. jubata		*B. cristatella*	
	Male (*n*=54)	Female (*n*=44)	Male (*n*=10)	Female (*n*=8)
AG/SVL%	49.1–52.8	47.9–49.8	48.0–49.6	50.7–52.3
HL/SVL%	28.7–28.9	26.5–28.5	28.9–30.9	27.3–28.4
HW/HL%	52.2–55.1	53.5–54.1	53.4–54.2	51.7–52.5
EN/HL%	21.3–23.2	21.0–23.1	20.2–20.3	20.4–22.2
ES/HL%	37.0–38.3	37.7–40.3	38.0–39.4	43.3–43.8
ED/HL%	28.6–31.6	28.4–31.6	31.8–32.2	37.3–38.7
TYE/HL%	19.3–22.7	17.5–20.7	19.0–19.9	19.1–19.4
LAL/SVL%	20.3–20.9	19.4–19.8	21.8–22.7	19.7–19.9
PLM/SVL%	21.8–22.4	20.2–20.9	20.2–20.3	19.9–20.4
TBL/SVL%	28.9–29.3	26.8–28.2	30.7–31.9	28.9–30.0
FOL/SVL%	36.2–41.3	34.0–38.9	38.9–41.7	37.3–37.4
TAL/SVL	2.4–3.4 (*n*=36)	3.3–3.4 (*n*=34)	3.1–3.6 (*n*=9)	3.4–3.5 (*n*=6)
supralabials	9–11		9, 10	
infralabials	9–11		9, 10	
scales from eye to tympanum	6, 7		8–10	
nuchal crest scales	10–14		10–15	
subdigital lamellae on toe IV	30–37		31–34	
midbody scale rows	35–55	33–49	64–80	61–72
ventrals	56–73	56–70	63–86	60–75

TABLE 3. Diagnostic characters separating the species of *Bronchocela* (modified after Amarasinghe *et al*. 2022);—not measured / evaluated

	B. danieli (*n*=2)	*B. smaragdina* (*n*=6)	*B. vietnamensis* (*n*=2)	*B. celebensis* (*n*=20)	*B. cristatella* s.l. (*n*=119)	*B. marmorata* (*n*=62)	*B. hayeki* (*n*=11)	*B. jubata* (*n*=170)	*B. orlovi* (*n*=1)	*B. rubrigularis* (*n*=6)	*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	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	10–12	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
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

.....continued on the next page

TABLE 3. (Continued)

	B. danieli (*n*=2)	*B. smaragdina* (*n*=6)	*B. vietnamensis* (*n*=2)	*B. celebensis* (*n*=20)	*B. cristatella* s.l. (*n*=119)	*B. marmorata* (*n*=62)	*B. hayeki* (*n*=11)	*B. jubata* (*n*=170)	*B. orlovi* (*n*=1)	*B. rubrigularis* (*n*=6)	*B. shenlong* (Grismer *et al.* 2015)	*B. rayaensis* (Grismer *et al.* 2015)	*B. burmana* (Zug *et al.* 2017)
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 5. *Bronchocela jubata* **(A)** in life (adult male, not collected) from Cibinong near Bogor, West Java.

Habitat, natural history, and distribution. *B. jubata* is usually found in areas of open canopy in primary forests (mostly forest edge) or undisturbed secondary forests, forests ecotones, other vegetation (e.g. coffee and pepper plantations) and in well-maintained home gardens. This could be an artefact since the species will be more visible in such areas and probably more difficult to observe in true dense forest where it also occurs. They usually forage on tree trunks and branches at 1.5 to 4 meters above the ground during the daytime, especially when basking, mostly around 0900 hr. At night, the adults prefer the highest branches of trees to sleep, mostly in open canopy areas, while juveniles prefer tiny branches of shrubs. Puruhita (2014) observed insects of the orders Hymenoptera, Lepidoptera, Odonata, Hemiptera, Orthoptera, and Coleoptera in the gut contents of *B. jubata* populations in Central Java which highlights its insectivorous feeding habit.

This species is mostly distributed in the western parts of Java Island and southern parts of Sumatra Island (most frequently in Lampung Province). It is comparatively rare on the eastern part of Java and Bali Island. It seems extremely rare on Borneo Island and the only occurrence available to us was a couple of museum specimens collected from eastern Kalimantan. As we have noticed it seems that the abundance of *B. jubata* is correlated with the abundance of its sympatric congener *B. cristatella*. *B. jubata* is usually distributed in higher abundance when sympatric in areas where *B. cristatella* shows low abundance, probably in order to reduce the interspecific competition.

In addition, the species is sympatric with several other arboreal agamids such as *Gonocephalus chamaeleontinus*, and *Pseudocalotes tympanistriga.* We always found several *B. jubata* close together at elevations below 1,300 m above sea level. Most of the individuals were observed at 300–800 m elevations. The reports from the Malay Peninsula, northern parts of Sumatra, the Philippines, and Wallacea are doubtful and we remove them from its distribution range—see discussion.

Conservation status. Distribution of this species is scattered (Fig. 1) due to forest fragmentation. Forest habitat fragments are further threatened by encroaching agricultural and industrial lands on Java Island. The application of the IUCN Red List criteria (IUCN Standards & Petitions Subcommittee 2019) with our updated distribution data

(excluding the single specimen reported from Borneo, ZMH R06163) shows that *B. jubata* is restricted to an area of occupancy (AOO) of 2752 km^2 and recorded from nearly 200 localities within 169,604 km^2 extent of occurrence (EOO). Although the species shows scattered distribution in severely fragmented forests patches in highly populated islands, given its wider area of occupancy, *B. jubata* should be considered as a Least Concern (LC) species.

FIGURE 6. Sulcate view of the left hemipenis of *Bronchocela jubata* (MZB 6639) from Sukamantri, Bogor, West Java.

Discussion

The original description of *Bronchocela jubata* by Duméril & Bibron (1837) was based on four syntypes: two from Java, Indonesia, originally deposited at Leyden Museum (MNHN-RA 2541 and 2541A) with no collector indicated; one from Java collected by Jean-René Constant Quoy and Joseph-Paul Gaimard (MNHN-RA 2542); and the fourth syntype from Pondichéry, India, collected by Jean-Baptiste Leschenault de la Tour (MNHN-RA 2543). Duméril and Bibron (1837) provided measurements for only one specimen: total length 560 mm and tail length 430 mm. Among the four syntypes, MNHN-RA 2541 and 2541A were evidently present in 1954 since they were cited in Guibé's (1954) MNHN-type catalogue with a total length of about 270 and 670 mm. Guibé (1954) clearly stated that he has not really measured the specimens and only gives an approximate total size, thus the sizes he indicated have only to be considered as an approximate indicative of total size—see Table 4. Later, in the MNHN agamid type-catalogue, Brygoo (1988) clearly indicate that these two Leyden specimens could not be found and that they have to be regarded as lost or misplaced between 1954 and 1988. Our recent attempt to trace those syntypes again in 2021 was also unsuccessful. We could not locate them in MNHN collections. Thus, both syntypes (MNHN-RA 2541 and 2541A) which also have no precise collector and collector dates can be excluded as potential lectotypes. Brygoo (1988) has precisely measured the available syntypes (MNHN-RA 2542 and 2543)—see Table 4 and our measurements more less match Brygoo's.

TABLE 4. The measurements (in mm) of syntypes of *Bronchocela jubata* given in historical publications and this study; TL, total length; TAL, tail length; SVL, snout–vent length; (?) doubtful measurement

Syntypes (MNHN-RA)	Duméril & Bibron (1837)	Guibé (1954)	Brygoo (1988)	This study
2541 (Java)	(measurements provided for one specimen only) TL = 560 TAL = 430 [SVL = 130] [Note: not indicated Pondichéry in the unpublished catalogue (1857) of MNHN]	TL = 270–670	Lost	Lost
2541A (Java)				
2542 (Java) [lectotype designate here]		TL = 660 (?)	TL = 572 TAL = 447 [SVL = 125]	TL = 577 TAL = 447 SVL = 130
2543 (Pondichéry)		TL = 560 (?)	TL = 418 TAL = 313 [SVL = 105]	TL = 428 TAL = 318 SVL = 110

The syntype (MNHN-RA 2543) from Pondichéry is still present, but despite the fact that it has a collector name, "Leschenault", its origin is wrong since the species *B. jubata* does not occur in India—see below. Also Leschenault visited Java for at least three years and his "Pondichéry" specimen most likely originate from there. In the 1857 unpublished "Catalogue des Reptiles de la collection du Muséum d'histoire naturelle de Paris" of A.H.A. Duméril, on page 18, under *Calotes jubata* (sic) is only indicated as "Java, Batavia" and there is no indication of "Pondichéry". That specimen, erroneously labelled as from India, can thus also be excluded as a potential lectotype. Finally only MNHN-RA 2542 remains as a potential lectotype and this is the one we chose for the following reasons: because it (1) has precise names for its two collectors, (2) has a precise collect locality, Java, Indonesia where the species occurs and is abundant, (3) is the only specimen for which precise size indications are given in the original description. Thus, there is no possible doubt that the only specimen for which measurements are indicated in the original description of Duméril and Bibron (1837) is MNHN-RA 2542, the syntype that we here select and designate as lectotype. The Astrolabe corvette (formerly called the Coquille), led by Jules Sébastien César Dumont d'Urville, left Toulon (France) on April 25, 1826 and returned to Marseille (France) on February 24, 1829. It only made a four-day stopover in Batavia (now Jakarta, Java, Indonesia) that it reached on August 29, 1828. Not obtaining victuals in Batavia, on September 1st it had to make another stopover for supplies in the port of Anyer (Banten Province, West Java) which it left on September 7 to reach Mauritius (Duyker 2021: 276–278). The lectotype that we here designate (MNHN-RA 2542) was collected during that short period on Java in one of those two localities.

Gray (1845) synonymised *B. jubata* with *B. gutturosus* (sic) Merrem, 1820. Berthold (1842) also considered that true *B. jubata* are conspecific with *A. gutturosa* when he described *B. intermedia*. However, in the taxonomic revision of the genus *Bronchocela*, Hallermann (2005) considered *B. gutturosa* as a junior subjective synonym of *B. cristatella*. Figueroa (2021) synonymised it as an objective synonym of *B. cristatella*. Therefore, to uphold the taxonomic stability of a long standing nomen, *B. jubata*—which is junior to *B. gutturosa* sensu Article 23 of the Code (ICZN 1999)—we follow Figueroa (2021) and consider *B. gutturosa* as a junior synonym of *B. cristatella*, and not of *B. jubata*. A systematic revision of *B. cristatella* complex including a neotype designation will be published elsewhere (Amarasinghe *et al*. in press). Günther (1864) recognized *B. jubata* as a distinct species mostly distributed in Java. Stoliczka (1870) and Theobald (1876) recognized that the Nicobar and Java specimens are morphologically different, and Boulenger (1890) and Annandale (1905) further reported *Calotes jubatus* from the Malay Archipelago in addition to Nicobar Island, most probably mixing up some specimens of *B. cristatella* sensu lato, as he stated outranged mid body scale counts (65) for the species. de Rooij (1915) excluded Malay Peninsula, but extended the distribution of the species to Singkep, Bali, Sulawesi, Karakelang, and Salibabu Islands as well as to the Philippines. However, he accepted that *C. jubatus* is common on Java Island and reported it from several locations throughout the Island: Anjer (Anyer), Gadok (Gadog), Krawang, Batavia (Jakarta), Weltevreden (Sawah Besar, Jakarta), Buitenzorg (Bogor), Sukabumi, Tjibodas (Mt. Cibodas), Mt. Salak, Depok, Bantam (Banten), Nusa Kembangan, Semarang, Wonosobo, Salatiga, Surakarta, Willis mountains (Mt. Wilis), Tengger mountains (Bromo), Prigan (Pasuruan), and Surabaia (Surabaya). Smith (1935) considered the species distributed on Nicobar, Java, and the Philippines. In the recent publications, *B. jubata* has been reported from several locations on Java, Sumatra, and Bali islands (e.g. Mumpuni 2001; Kurniati 2005; McKay 2006; Riyanto 2010, 2011; Riyanto & Trilaksono 2012; Riyanto & Mumpuni 2013; Puruhita 2014; Gunawan & Sugiarti 2015; Eprilurahman *et al*. 2016; Findua *et al*. 2016;

Janiawati *et al*. 2016; Kurniawan *et al*. 2016; Khatimah 2018; Septiadi *et al*. 2018; Yudha *et al*. 2018; Cahyadi & Arifin 2019; Priambodo *et al*. 2019; Riyanto *et al*. 2019; Ayu *et al*. 2020; Mustari 2020; Erawan *et al*. 2021; Kusrini *et al*. 2021; Maharani *et al*. 2022), but never reported in the studies conducted in Kalimantan (e.g. Amri *et al.* 2015; Sari *et al.* 2017; Kwatrina *et al.* 2018; Setiadi & Rahayu 2021; Tajalli *et al.* 2021).

In a taxonomic review of the genus *Bronchocela*, Hallermann (2005) confirmed that the species occurs on Borneo based on a specimen (ZMH R06163) collected in 1925 and another specimen from Kalimantan collected by Indraneil Das (Das 2004). Hallermann (2005) further reported the species from Sumatra based on a single specimen (RMNH 8646) collected from Lampung Province. However, we cannot confirm the species occurrence on Borneo because we were unable to locate any recent specimen of *B. jubata* from there (Kalimantan, Indonesia). We found several live and museum specimens from southern Sumatra (see Appendix), thus confirming its occurrence there. However, we have never observed this species in the central and northern parts of Sumatra; probably its northern most extension is located around Bengkulu Province. Hallermann (2005) also reported *B. jubata* from Cambodia evidenced by five specimens in a series labelled formerly as *B. cristatella* in the collection of the Leiden Museum (RMNH) and which are definitively *B. jubata.* Note, however, that *Pseudocalotes tympanistriga*, which inhabits Sumatra and Java and *B. cristatella* were also presented in the same collection series and thus this composition makes that origin of Cambodia doubtful. No other Cambodian record has ever been published. Records from the islands of Salibabu (Sangihe), Karakelong and Talaud, southeast of Mindanao (Philippines) cited by de Roij (1915:123) could not be verified by Hallermann (2005); they might be misidentified individuals of *B. marmorata*. In the same way a series of 14 RMNH specimens formerly labelled as *B. jubata* from Sulawesi were also re-determined as *B. celebensis* (see Hallermann 2005). *Bronchocela jubata* has also been incorrectly reported from the Nicobar Islands by de Rooij (1915) and Smith (1935) but no voucher specimens exist according to Das (1999). In this study we rediscovered those specimens from the Zoological Survey of India (ZSI 2671, 14668, 15033–34), which were presumably collected in the late 1800s by Major A.R. Anderson from the Indian Medical Services, and we identified them as *B. rubrigularis*. Therefore, the occurrence of *B. jubata* in eastern India at Pondicherry is questionable and most probably the syntype MNHN-RA 2543 (now paralectotype) is a mislabelled specimen from Java. This is most likely since the collector, Jean-Baptiste Leschenault de La Tour (1773–1826), was a botanist and he visited Java where he lived for several years between 1803 and 1807 and returned in September 1820. He visited many parts of the island making important natural history collections that he sent to Paris.

A single specimen record (MNHN-RA 1895.0460) from "Province de Pashim", ("Siam") Thailand collected by Jean-Marc Bel around 1895 is definitely *B. jubata*. The locality "Pashim" is another spelling of "Pachim" or "Prachim," and corresponds to the present city of Prachin Buri (or Prachinburi) in southern-central Thailand, along the Bang Pakong River, just northeast of Bangkok. Another two juvenile specimens (ZSM) near Korat (Nakhon Ratchasima Province) probably belong to the same relict population. Pauwels *et al.* (2003) and Bauer *et al.* (2004) discussed the biogeographical significance of that region for endemism and relict forms with strong Sundaic affinities. Furthermore, Guilbert (2009) mentioned that *B. jubata* does not occur in Northern Thailand and the species in Doi Inthanon is clearly different from *B. jubata* that is depicted in the book of Das (2004). As *B. jubata* has not been reported in northern Sumatra and Peninsular Malaysia, the localities on the labels of those historical specimens are doubtful. Regarding the reports of *B. jubata* from the Philippines they also need further confirmation as we have noticed a population of *B. cf. marmorata* with well-developed nuchal crests, and which probably represent a distinct unnamed species. Therefore, here we restrict the distribution of *B. jubata* to the Greater Sunda Islands. Details on breeding biology of *B. jubata* are reported in Kopstein (1938), but the data on ecology, habitat, and populations of *B. jubata* are still sparse and further studies are needed to properly refer observations to unequivocally identified specimens.

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APPENDIX 1. 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, 6081–82, 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: 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. 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. orlovi*: Vietnam:** ZISP 22827 (holotype).

***B. rubrigularis*: India:** Nicobar: ZMH R09271 (holotype), R09272 (paratype), ZSI 2671, 14668, 15033–34.

***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).