



## A review of the genus *Bronchocela* Kaup, 1827 (Reptilia: Agamidae) in the Nicobar Archipelago with the description of two new species

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### Abstract

Species of the agamid genus *Bronchocela* Kaup, 1827 in the Andaman and Nicobar Islands are reassessed based on newly collected specimens from different parts of the Nicobar Archipelago. An assessment based on morphology and distribution of the identified groups reveal two new, unnamed populations, one allied to *B. cristatella* and the other allied to *B. danieli*. These two populations are described as new species, and *Bronchocela cristatella* is redescribed based on Sundaic specimens. The remaining species, *B. danieli* and *B. rubrigularis* are redescribed. Distributions of all of these four species are mapped and recommendations on their conservation status are suggested.

**Key words:** Long-tailed agama, Sundaland, cryptic species, endemic, allopatry, Southeast Asia, Taxonomy

### Introduction

The diurnal, arboreal agamid genus *Bronchocela* Kaup, 1827 currently comprises thirteen species ranging from the Nicobar Islands in the west to the Maluku Islands, west of Papua New Guinea in the east (Uetz *et al.* 2022). The records of *Bronchocela* in the Nicobar Islands date back to Fitzinger (in Steindachner 1867) who reported a purported taxon under the name *Pseudocalotes archidussicae*. This was later identified as *B. cristatella* and the former name was shown to be a *nomen nudum* by Das and Gemel (2000). The second species to be reported from the Nicobar Islands was *B. jubata* (Theobald 1876; Stoliczka 1870; Boulenger 1885; 1890; Smith 1935: 186), which has recently been reassessed and described as a new species, *B. rubrigularis* by Hallermann (2009) (see Amarasinghe *et al.* 2022a). The third species, *B. danieli* was described by Tiwari & Biswas (1973) under the genus *Calotes* from which *Bronchocela* was shown to be a distinct genus and hence, revalidated by Moody (1980). Thus, the Nicobar Islands lying at the western periphery of the range of *Bronchocela*, are known to harbor these three species, namely, *B. danieli* Tiwari & Biswas, 1973, *B. rubrigularis* Hallermann, 2009 and *B. cristatella* (Kuhl, 1820) *sensu lato* (Hallermann 2009). Another tentative, unidentified species was reported by Vijayakumar (2005) as “*Bronchocela* sp. 2 UI”. *Bronchocela cristatella* although currently considered to be widely distributed through peninsular Malaysia and the Philippines (Hallermann 2005), has been shown to comprise unnamed, cryptic species, some of which have been identified and described recently (Grismer *et al.* 2015).

In our study, *B. cristatella* is redescribed based on samples from Java. The composition of the genus *Bronchocela* in the Nicobar archipelago is examined, resulting in the reassessment of the ‘*B. cristatella*’ population of the Nicobars, leading to the description of a new species. The other one of the unidentified species, allied to *B. danieli* reported earlier (Vijayakumar 2005) is reassessed and described as a new species. Furthermore, the redescrptions of *B. danieli* and *B. rubrigularis* are added based on new material.

## Material and methods

Two specimens of *B. rubrigularis*, two of *B. danieli*, two unidentified specimens of the Car Nicobar population and three unidentified specimens of *Bronchocela* sp. from Little Nicobar were collected, preserved and deposited in the collections of the Department of Ocean Studies and Marine Biology, Pondicherry University, Port Blair. Four specimens (three from Car Nicobar and one *B. rubrigularis* from Nancowry) deposited at the BNHS museum were also studied. Thirteen specimens of the Javan population of *B. cristatella* were examined in the collections of the Museum of Zoology Universitas Indonesia (UIMZ), Research Center for Climate Change, Depok and Museum Zoologicum Bogoriense (MZB), Cibinong, Indonesia.

Live specimens of the genus *Bronchocela* encountered in the Nicobar Islands were captured, gently restrained and the following measurements (in mm) and scale counts were taken. Snout-vent length (SVL), measured from the snout tip to the anterior edge of the cloaca; tail length (TAL), measured from the posterior edge of the cloaca to the tail tip; trunk length (AG), measured between the axilla and groin; head length (HL), measured from the snout tip to the jaw angle; head width (HW), measured at the broadest point on the head; head depth (HD), measured from the top of the head to the ventral margin of the mandible, ventrally; horizontal diameter of the orbit (ED), anterior margin of orbit-nostril distance (EN), snout length (ES), measured from the anterior margin of the orbit to the snout tip; distance from the posterior margin of the orbit to anterior margin of tympanum (ETY), tympanum diameter (TYD), measured at the widest point of the tympanum; upper arm length (UAL), measured from the axilla to the elbow when flexed; lower arm length (LAL), measured from the elbow to the wrist; palm length (PAL), measured from the wrist to the tip of finger III; thigh length (FEL), measured from the point of insertion of the hindlimb to the trunk to the knee; tibia length (TBL), measured from the knee to heel when flexed; foot length (FOL), measured from heel to the tip of toe IV; length of fingers (F1-F5) and toes (T1-T5) measured from the fork to the tip excluding claw.

Supralabials and infalabials were counted along the upper and lower lips between rostral and mental to the angle of the mouth, respectively. Ventrals were counted along a longitudinal series along the underside between the mental and cloacal scales; internasals were counted between the nasal scales; mid-body scale-rows were counted at the middle of SVL around the body; number of nuchal crest scales from the foremost scale behind the occiput and the largest distinguishable scale at the level of the neck; number of canthals; number of supra-oculars and supra-ciliaries; subdigital lamellae were counted on the ventral surface of digits on fingers and toes. Geo-coordinates of the localities where the individuals were encountered were recorded with a Garmin GPS MAP 78s and mapped with ARC MAP v. 10. Photographs of the types of *B. danieli* (ZSI 22455) and *B. rubrigularis* (ZMH R09271) and the specimens of *Pseudocalotes archidussisae* (NMW 21002:1-2) collected during the Novara expedition were also studied.

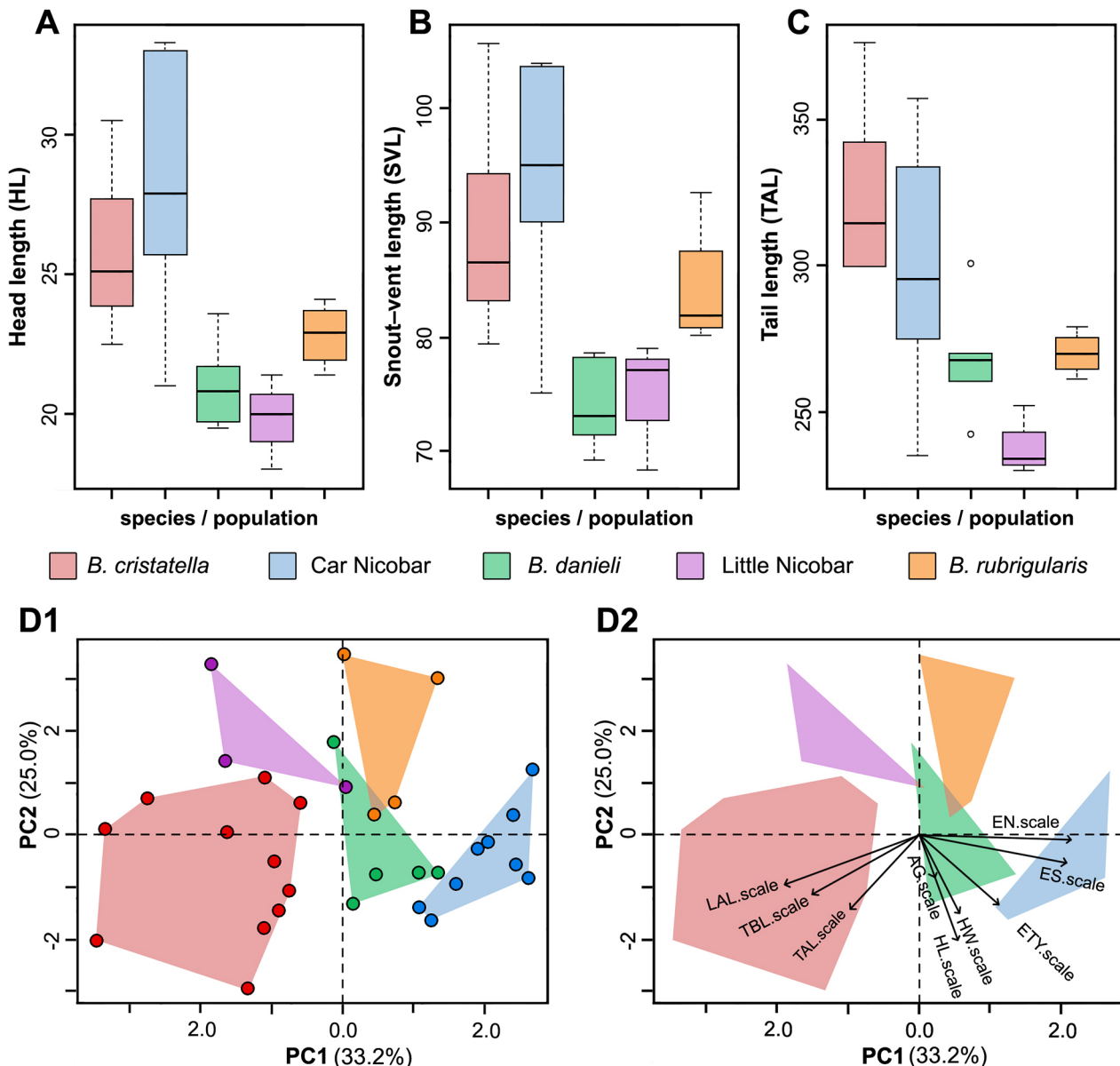
The following Statistical analyses were carried out to test the hypothesis that the two unidentified Nicobar populations of *Bronchocela* from Car Nicobar ( $n=9$ ) and Makachua ( $n=3$ ) are morphologically distinct from *Bronchocela rubrigularis* ( $n=4$ ), *B. danieli* ( $n=5$ ), and *B. cristatella* from Java, Indonesia ( $n=12$ ; type locality). Statistically informative tests could not be performed on separate sexes due to the smaller sample sizes of females representing the different species/populations, insufficient for this purpose. Juveniles were excluded to avoid the bias of allometry for statistical analysis. Kruskal–Wallis univariate analysis of variance tests on mensural data ( $n=33$ ) with statistically similar variances to search for the presence of statistically significant mean differences ( $p < 0.05$ ) among species/populations across the data set. We used this test due to the small sample size (Zar 2010). Boxplots were generated for HL, SVL, and TAL in order to visualize the range, mean, median, and degree of differences between species /populations bearing statistically different mean values. Each morphometric ratio was treated as the dependent variable and the population as the predictor variable. All statistical analyses were performed in the R statistical software program (v4.0.4; R Core Team 2021).

The morphospacial clustering of the sampled individuals was visualized using Principal Component Analysis (PCA) using the `prcomp` function in the R statistical software program (v4.0.4; R Core Team 2021). Additionally, variation in adult size was normalized using the following equation:  $\log X_{\text{adj}} = \log(X) - \beta[\log(\text{SVL}) - \log(\text{SVL}_{\text{mean}})]$ , where  $X_{\text{adj}}$  = adjusted value;  $X$  = measured value;  $\beta$  = unstandardized regression coefficient for each population; and  $\text{SVL}_{\text{mean}}$  = overall average SVL of all populations (Leonart *et al.* 2000; Chan & Grismer 2022). The metrics (i.e. 10 morphometric characters: SVL, AG, TAL, HL, HW, EN, ES, ETY, LAL, TBL) of each species were normalized separately to avoid conflating intra- with interspecific variation (Reists 1986). All data were scaled to their standard

deviations to insure they were analyzed on the basis of correlation and not covariance. The scaled morphometric was treated as the dependent variable and the population as the predictor variable. A biplot of the first two principal component scores was used to examine the morphometric differentiation between the species / populations. All statistical analyses were conducted using the R statistical software program (v4.0.4; R Core Team 2021).

## Results

The body metric comparisons between the species/populations showed significant differences. Among these species, the Javan *B. cristatella* and the Car Nicobar populations have significantly longer heads (HL;  $\chi^2=18.31$ ,  $P=0.001$ ;  $n=33$ ), tails (TAL;  $\chi^2=17.63$ ,  $P=0.001$ ;  $n=33$ ), and bodies (SVL;  $\chi^2=17.57$ ,  $P=0.001$ ;  $n=33$ ) compared to *B. danieli* and Little Nicobar populations (Fig. 1A–C).



**FIGURE 1.** Boxplots of (A) head length, (B) snout–vent length, and (C) tail length indicating differences between *Bronchocele* species/populations in Nicobar and *B. cristatella* in Java (note that both sexes were mixed); Principal Component Analysis (PCA): (D1) biplot of morphometric variation in combined sexes between *Bronchocele* species/populations in Nicobar and *B. cristatella* from Java in Java, Indonesia; (D2) 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.

The results of the analyses support our initial hypothesis that the two unidentified *Bronchocela* populations from Car Nicobar and Little Nicobar are morphologically distinct from the other Nicobarese and Sundaic species. The PCA of the mensural data shows that all the Nicobar populations are well-separated from the Javan *Bronchocela cristatella* along both principal components PC 1 and PC 2 (Fig. 1D). PC1 accounts for 33.2% of the variation in the data set and loads most heavily for EN, ES, LAL, and TBL (Table 1), while PC2 accounts for 25.0% of the variation and loads most heavily for HL, HW, TAL, and ETY. The PCA demonstrated very little overlap between the *B. rubrigularis* and *B. danieli*. Based on the data presented above, we believe there is sufficient evidence to formulate a robust, testable hypothesis indicating the Car Nicobar and Little Nicobar populations are distinct species, and as such, are described below. We also provide a redescription of *B. cristatella* based on specimens from Java (see below).

**TABLE 1.** Factor loadings and proportion of variance explained by the principal components

	PC1	PC2	PC3	PC4	PC5	PC6	PC7
Standard deviation	1.7290	1.4998	1.2484	0.82795	0.7422	0.64532	0.48548
Proportion of Variance	0.3322	0.2499	0.1732	0.07617	0.0612	0.04627	0.02619
Cumulative Proportion%	33.2%	58.2%	75.5%	83.1%	89.3%	93.9%	96.5%
AG	0.0561	-0.2219	0.6432	-0.2581	0.3414	-0.5110	0.0368
TAL	-0.2303	-0.3873	0.3069	0.5201	0.2586	0.5411	0.1897
HL	0.1313	-0.5515	-0.1301	0.2739	-0.2479	-0.4417	0.3384
HW	0.1337	-0.4166	-0.3431	-0.6324	0.2022	0.3115	0.3716
EN	0.5097	-0.0235	-0.2742	0.1876	0.1254	-0.0574	-0.2241
ES	0.4936	-0.1465	-0.0951	0.2221	0.4509	0.0268	-0.3125
ETY	0.2657	-0.3644	0.3425	-0.1910	-0.6066	0.2885	-0.4351
LAL	-0.4515	-0.2632	-0.1296	-0.1969	0.3126	-0.0368	-0.5789
TBL	-0.3615	-0.3145	-0.3729	0.1676	-0.1708	-0.2555	-0.1942

## Systematics

### *Bronchocela cristatella* (Kuhl, 1820)

*Agama cristatella* Kuhl, 1820

**Material studied:** Java ( $n=13$ ): UIMZ 0247–48; MZB 196, 304, 995, 1668, 3036, 4895, 6989, 8885–88, 9811

**Differential diagnosis and comparisons:** A species of *Bronchocela* occurring in the Greater Sunda Islands and southern Peninsular Malaysia characterized by: medium body size (79.4–105.6 mm SVL); relative tail length (357.5 % SVL); 61–79 scale rows around mid-body, of which, the first 4–8 rows on the dorsum oriented posterodorsally, the next two rows oriented posteriorly, followed by 20–30 rows oriented posteroventrally; 10–15 enlarged, elongated and backwardly curved scales forming the nuchal crest; dorsal crest rudimentary; three postmentals; 9–10 supralabials; 9–10 infralabials; 5 or 6 canthals; 6–7 supraciliaries; 31–34 subdigital lamellae under toe IV; 60–86 ventrals; bright bluish green dorsal colouration with bright yellow eyes in both sexes (Table 2).

**Description and variation:** A medium sized species of *Bronchocela* (mean SVL 89.2 mm), with a long, tapering tail (TaL:SVL 3.57). Body relatively short and robust (AG:SVL 0.51). Head large (HL:SVL 0.29); longer than broad (HL:HW 1.91) and about as broad as deep. Snout less than half as long as the head (ES:HL 0.38) with a blunt, narrow and rounded tip. Canthus rostralis sharply defined, with five or six canthal scales. Orbit relatively large, a little more than 1/4<sup>th</sup> the length of the head (ED:HL 0.32); tympanum ovoid, relatively smaller, a little smaller than half the eye diameter (TYH:ED 0.40) and green in colour. Scales between the eye and tympanum fairly enlarged. Nasal large and ovoid in shape. Scales on the cheek below the tympanum slightly enlarged; keeled. Mental

semicircular, bounded by three small postmentals and nine or ten infralabials on either sides. Rostral relatively small, bounded by nine to ten supralabials on each side. Nostrils separated from each other by seven to nine small internasals. Nuchal crest composed of eight to ten shortened, lanceolate scales. Dorsal body scales not enlarged, feebly keeled and non-homogeneous in size, with the lateral scales being slightly larger, in 50–53 rows around the mid-body. Of the dorsal scales, the first row on the dorsum on either sides oriented posteriorly and slightly upwards; the next three to seven rows of scales oriented posterodorsally, with the rest of the scales on the lateral body oriented posteroventrally. Ventrals 60–86 in a longitudinal series; 3–5 times larger than the dorsal scales, bearing a strong median keel, projecting posteriorly towards the lower vertex. Limbs relatively robust and elongate; upper arm short; lower arm nearly as long as the upper arm; palm about as long as the lower arm (LAL:PAL 0.98). Fingers long and slender, relative length of fingers IV>III>V>II>I. Thigh long and robust (FEL:SVL 0.28); tibia slightly longer than thighs (FEL:TBL 1.07); foot elongated, distinctively longer than thigh (FEL:FOL 1.37). Hindlimbs almost the size of body length (HLL:SVL 0.95). Relative lengths of toes IV>III>V>II>I; 31–34 subdigital lamellae under toe IV.

Dorsal and ventral coloration bluish green throughout the body; distal half of the tail brownish. Head yellowish green both dorsally and ventrally. Sides of the lips, cheeks yellow and orbits brownish or bluish. Tympanum green and chin uniform yellowish green in males.

**Distribution and Natural history:** This species is widely distributed in Great Sunda Islands and southern Peninsular Malaysia. The outranged populations of *B. cristatella* sensu lato represent several other distinct species and the work is currently in progress (Amarasinghe *et al.* in press). Following Figueroa (2021), here we restrict the type locality of *B. cristatella* to Java and we do not designate a neotype for the nomen as a systematic revision is in progress (*vide* Amarasinghe *et al.* 2022a, b). Amarasinghe *et al.* (2022b) pointed that the northern and western Sumatran population of *B. cristatella* sensu lato is close to *B. shenlong* Grismer, Wood, Lee, Quah, Anuar, Ngadi & Sites, 2015 described from Peninsular Malaysia. *Bronchocela cristatella* sensu stricto mostly utilizes closed canopy primary forests compared to its sympatric congener, *B. jubata* which uses open canopy forests (see Amarasinghe *et al.* 2022a). *Bronchocela cristatella* is a rare species in Java compared *B. jubata*, but it is common in other Greater Sundaic islands while *B. jubata* is rarer on those islands.

### ***Bronchocela cyanopalpebra* sp. nov.**

(Fig. 2)

*Pseudocalotes archiducissae* (*nomen nudum*)—Fitzinger in Steindachner (1867)

*Calotes cristatellus* (non Kuhl, 1820)—Biswas & Sanyal (1977), (1980); Biswas (1984) part

*Bronchocela cristatella* (non Kuhl, 1820)—Das (1999); Das & Gemel (2000) part

*Bronchocela* sp.—Vijayakumar (2005)

*Bronchocela* cf. *cristatella* (non Kuhl, 1820)—Harikrishnan *et al.* (2009) part; Chandramouli (2020) part

**Holotype:** DOSMB 05054, an adult male collected from Chukchuka (9.21358°N, 92.79647°E, 33 m asl.) Car Nicobar, Nicobar Islands, India by S.R. Chandramouli in June 2017.

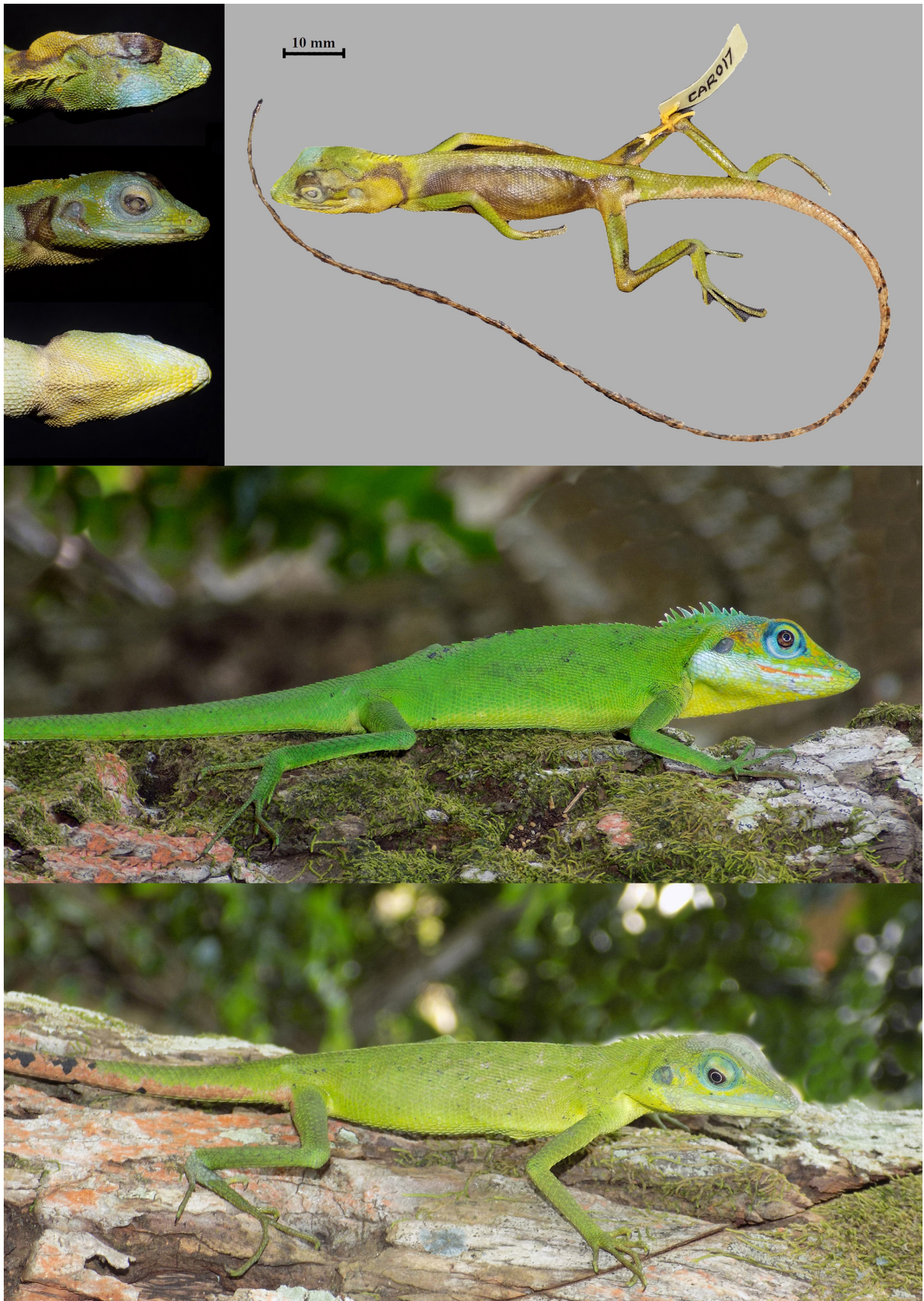
**Paratype:** DOSMB 05089, an adult male collected along with the holotype from the same locality.

**Referred material:** BNHS 1610 (adult male), BNHS 1662 (adult female) collected from Air-force station, Car Nicobar by S. Krishnan in 2004; BNHS 961 (adult male) collected from Car Nicobar by Humayun Abdulali & party in 1966.

**Etymology:** The specific epithet *cyanopalpebra* is a noun in apposition referring to the bright blue (=cyan) coloured eyelid (=palpebra), a diagnostic character of this species.

**Nomenclatural note:** As the name *Pseudocalotes archiducissae*, attributed to the Car Nicobar population by Fitzinger in: Steindachner (1867) has been shown to be a *nomen nudum* (Das & Gemel, 2000), it cannot be applied to this species as it is not an available nomen (ICZN Art. 11.6).

**Differential diagnosis and comparisons:** A species of *Bronchocela* endemic to the northern group of Nicobar Islands characterized by: moderate to large body size (81.23–103.6 mm SVL); relative tail length (336 % SVL versus 330–390 % SVL in *B. cristatella* sensu stricto); 56–78 scale rows around mid-body (versus 61–79 in *B. cristatella*), of which, the first 3–4 rows on the dorsum oriented posterodorsally, the next 1–3 rows oriented posteriorly, followed by 17–22 rows oriented posteroventrally; 7–12 enlarged and elongated scales forming the nuchal crest; dorsal crest merely a serrated ridge; three postmentals; 9–10 supralabials; 8–10 infralabials; 5–6 canthals;



**FIGURE 2.** *Bronchocela cyanopalpebra* sp. nov. (top: Holotype DOSMB 05054, middle: live male, below: live female).

6–8 supraciliaries; 32–43 subdigital lamellae under toe IV (*versus* 31–34 in *B. cristatella*); 76–85 ventrals (*versus* 60–86 in *B. cristatella*); bright grass green dorsal colouration with a distinctly cyan coloured ring around the eyes (*versus* absent in *B. cristatella*) in both sexes (Table 2).

**Description of the Holotype:** An adult male, measuring 81.23 mm SVL; with a very long tail (TaL:SVL 3.39) with a short and robust body (AG:SVL 0.45). Head large (HL:SVL 0.28); longer than broad (HL:HW 1.75) and about as broad as deep (HW:HD 1.04). Snout long (ES:HL 0.45) with a rounded tip. Canthus rostralis sharply defined, with five canthal scales. Eyes relatively small, about 1/5<sup>th</sup> the length of the head (ED:HL 0.21); tympanum circular, relatively small, about half as large as the orbit (TYH:ED 0.51) and black in colour. Scales between the eye and tympanum slightly enlarged and keeled. Nasal relatively large, with a pointed anterior and rounded posterior ends. Scales on the check below the tympanum slightly enlarged and keeled. Mental semicircular, bounded by three small postmentals and nine infralabials on either sides. Rostral relatively small, bounded by nine supralabials on each side. Nostrils separated from each other by nine small internasals. Nuchal crest composed of nine slightly enlarged, triangular scales projecting posterodorsally. Dorsal body scales relatively small, feebly keeled and homogeneous, in 68 rows around the mid-body. Of the dorsal scales, the first two rows on the dorsum on either sides oriented posteriorly; the next three rows of scales below oriented posterodorsally, with the rest of the scales on the lateral body oriented posteroventrally. Ventrals 80 in a longitudinal series; much larger (about twice) than the dorsal scales, bearing a strong median keel, projecting posteriorly towards the lower vertex. Limbs relatively robust and elongate; upper arm short and slender (UAL:SVL 0.19); lower arm nearly as long as the upper arm (UAL:LAL 1.05); palm about as long as the lower arm (LAL:PAL 1.06). Fingers long and slender, relative length of fingers IV>III>V>II>I. Thigh long and slender (FEL:SVL 0.25); tibia slightly longer than thighs (FEL:TBL 0.95); foot elongated, slightly longer than thigh (FEL:FOL 0.87). Hindlimbs much longer than half the body length (HLL:SVL 0.82). Relative lengths of toes IV>III>V>II>I; 35 subdigital lamellae under toe IV.

Dorsal coloration verdant green throughout the body; tip of the tail reddish. Ventral side of the head and body of a lighter shade of green than the dorsum. Sides of the lips, cheeks and eyelids bright aqua blue in color. Lips with an orange-red streak; tympanum black. Upper portion of the head slightly more bluish. In preservation, overall body colouration bright green with trunk and posterior edge of the neck being dark grey; tail brownish. Venter greenish brown without any specific pattern on the throat.

**Variation:** Measurements and scale-counts of the male paratype and the referred specimens are presented in Table 3. Females slightly smaller than males, with a weakly developed nuchal crest and less legible blue shade around the eyes on the face.

**Distribution and Natural history:** This species is endemic to Car Nicobar and possibly, the smaller southern island of Batti Malv. It is arboreal and diurnal in habit and is a fairly common species found in an array of habitats ranging from evergreen forests, secondary forests and plantations to home gardens (Fig. 8).

### ***Bronhocela rubrigularis* Hallermann, 2009** (Fig. 3)

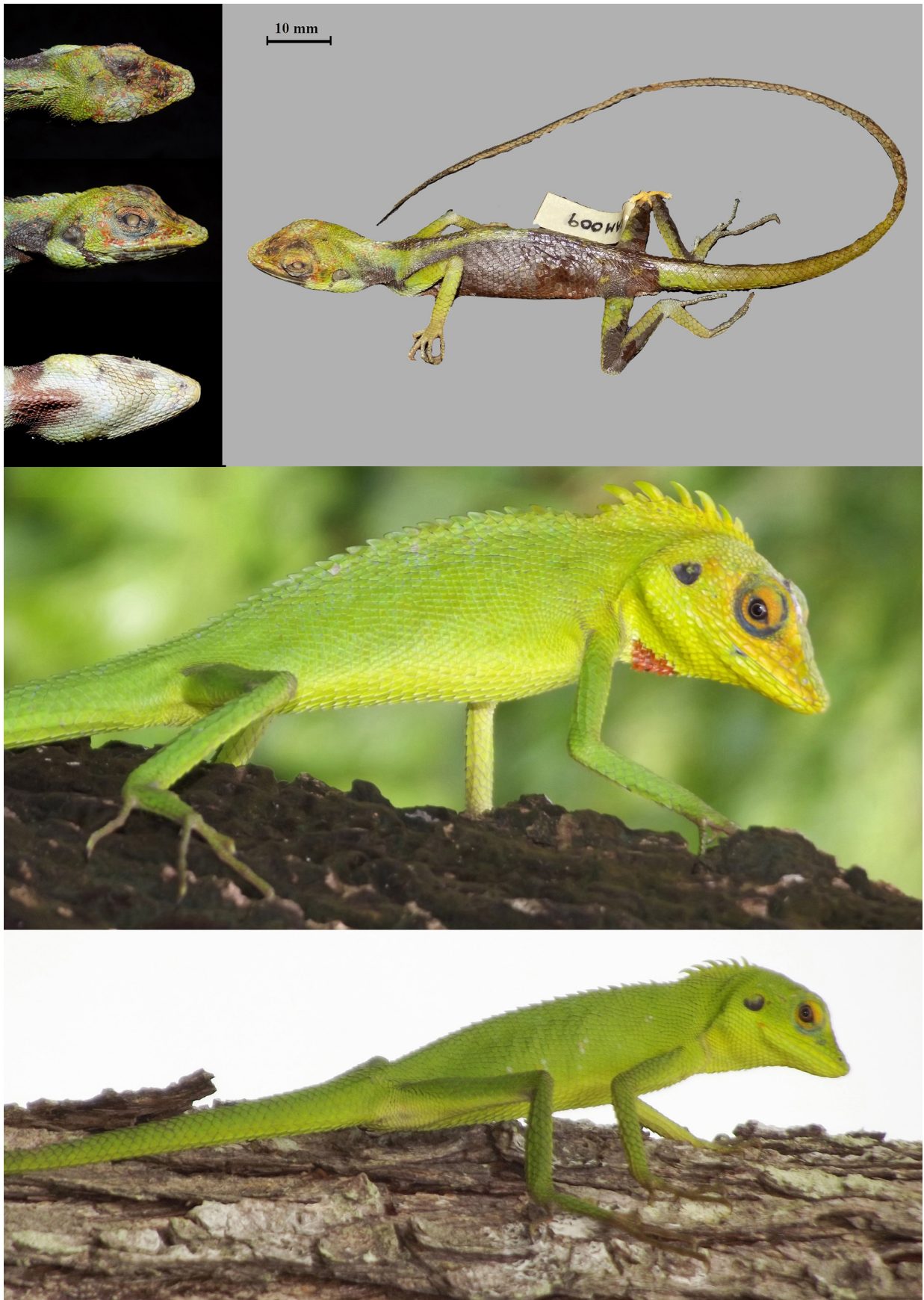
*Bronhocela jubata* (non Duméril & Bibron, 1837)—Stoliczka (1870); Theobald (1876) part

*Calotes jubatus* (non Duméril & Bibron, 1837)—Boulenger (1885; 1890); Annandale (1905); Smith (1935) part

**Material studied:** DOSMB 05086, an adult male and DOSMB 05087, an adult female, from near the APWD guest house, Camorta (8.03792°N, 93.54263°E, 28 m asl.), BNHS 1609, an adult female from Nancowry.

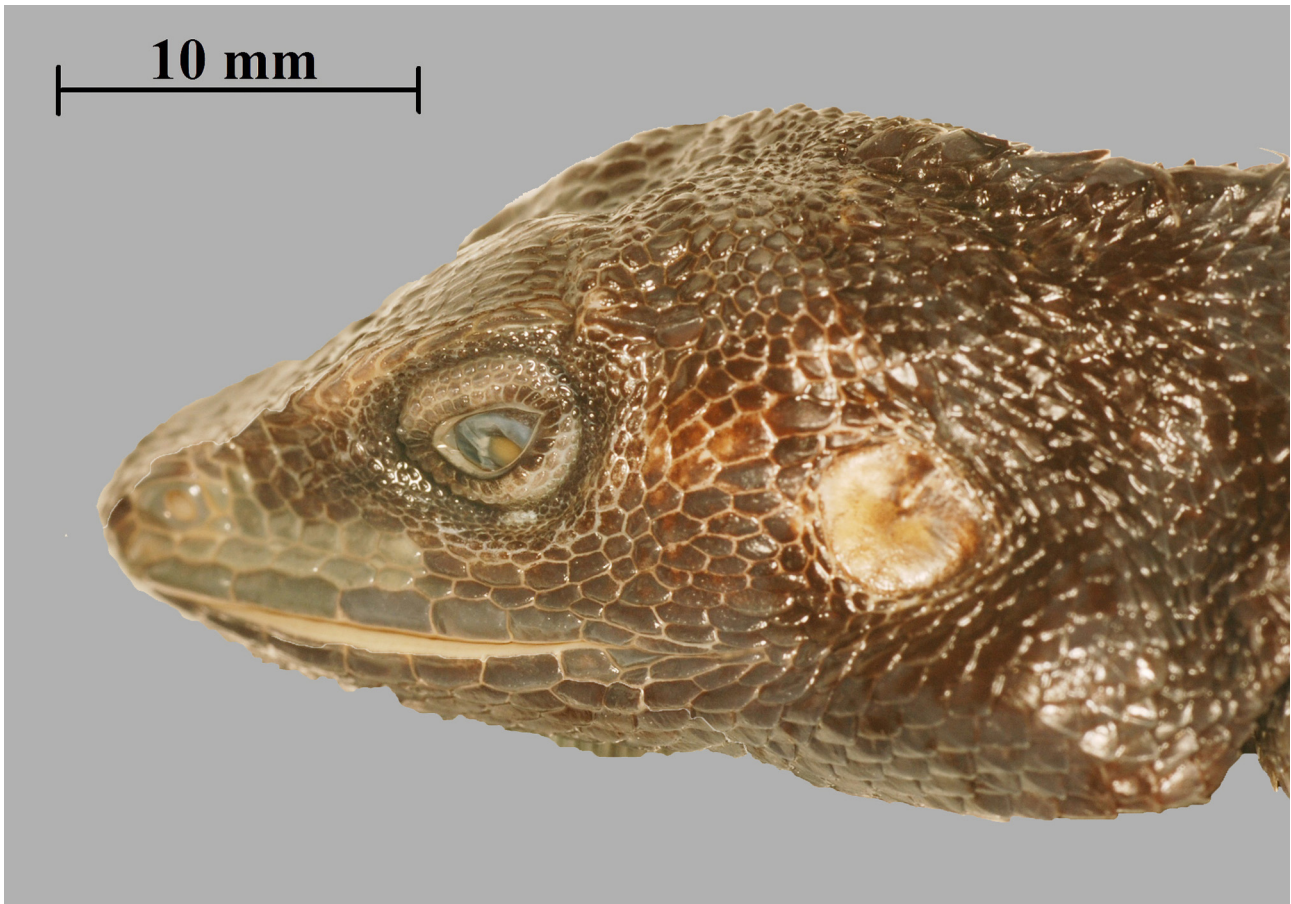
**Holotype:** ZMH R09271, an adult male collected from Triket Island, Central Nicobar Islands (Fig. 4).

**Differential diagnosis and comparisons:** A species of *Bronhocela* endemic to the Central group of Nicobar Islands characterized by: large body size (82.3–106.4 mm SVL); relative tail length (338 % SVL); 50–58 scale rows around mid-body, of which, the first two to three rows on the dorsum oriented posterodorsally, the next 4–5 rows oriented posteriorly, followed by 10–11 rows oriented posteroventrally; 10–11 enlarged, elongated and backwardly curved scales forming the nuchal crest; dorsal crest relatively well developed, composed of enlarged scales in the form of a well-defined serrated ridge; three postmentals; 7–10 supralabials; 7–10 infralabials; six canthals; 6–7 supraciliaries; 27–32 subdigital lamellae under toe IV; 68–77 ventrals; bright grass green dorsal colouration with a bright yellow and black coloured ring around the eyes in both sexes and a red, triangular gular patch in males (Table 2).



**FIGURE 3.** *Bronchocela rubrigularis* (top: DOSMB 05086, middle: live male, below: live female).





**FIGURE 4.** Head of the holotype of *Bronchocela rubrigularis* (ZMH R09271) (Photo: J. Hallermann).

**Description and variation:** A large bodied species of *Bronchocela* (mean SVL 86.95 mm; n=10), with a long, tapering tail (TaL:SVL 3.37, n=7). Body relatively short and robust (AG:SVL 0.44, n=3). Head large (HL:SVL 0.27); longer than broad (HL:HW 1.83) and about as broad as deep (HW:HD 0.99, n=3). Snout less than half as long as the head (ES:HL 0.44) with a blunt, broadened and rounded tip. Canthus rostralis sharply defined, with six canthal scales. Orbit relatively large, a little less than 1/4<sup>th</sup> the length of the head (ED:HL 0.20); tympanum circular, relatively slightly large, a little larger than half the orbit diameter (TYH:ED 0.72) and black in colour. Scales between the eye and tympanum fairly enlarged. Nasal relatively large and ovoid in shape. Scales on the check below the tympanum slightly enlarged; the first two rows smooth and those below keeled. Mental semicircular, bounded by three small postmentals and nine infralabials on either sides. Rostral relatively small, bounded by seven to ten supralabials on each side. Nostrils separated from each other by seven small internasals. Nuchal crest composed of seven to eight elongated, backwardly curved scales projecting posterodorsally. Dorsal body scales fairly enlarged, feebly keeled and homogeneous, in 50-58 (n=11) rows around the mid-body. Of the dorsal scales, the first row on the dorsum on either sides oriented posteriorly; the next two to three rows of scales oriented posterodorsally, with the rest of the scales on the lateral body oriented posteroventrally. Ventrals 60-68 in a longitudinal series; much larger (about twice) than the dorsal scales, bearing a strong median keel, projecting posteriorly towards the lower vertex. Limbs relatively robust and elongate; upper arm short and slender (UAL:SVL 0.18, n=3); lower arm nearly as long as the upper arm (UAL:LAL 1.06, n=3); palm about as long as the lower arm (LAL:PAL 1.03, n=3). Fingers long and slender, relative length of fingers IV>III>V≥II>I. Thigh long and robust (FEL:SVL 0.24, n=3); tibia slightly shorter than thighs (FEL:TBL 0.93, n=3); foot elongated, slightly longer than thigh (FEL:FOL 0.84, n=3). Hindlimbs longer than half the body length (HLL:SVL 0.98, n=10). Relative lengths of toes IV>III>V>II>I; 24-27 subdigital lamellae under toe IV.

Dorsal and ventral coloration verdant green throughout the body; tip of the tail reddish. Head yellowish green both dorsally and ventrally. Sides of the lips, cheeks yellow and eyelids with a black ring around. Tympanum black and the throat with a bright red triangular patch in males. In preservation, dorsal green colouration present in the

recently collected samples while the old ones uniform dark throughout. Trunk and belly dark grey. The red throat-patch grey in preservation.

**Distribution and Natural history:** Endemic to islands of the central group of Nicobars and recorded during the present study from Camorta, Katchall, Teressa and Nancowry Islands. Has been reported from Trinkat, Bompoka, Chowra and Tillanchong Islands (Hallermann 2009). Arboreal and diurnal in habit. A fairly common species found in a variety of habitats ranging from evergreen forests, secondary forests and plantations to home gardens (Fig. 8).

### ***Bronchocela danieli* (Tiwari & Biswas, 1973)**

(Fig. 5)

*Calotes danieli* Tiwari & Biswas, 1973

*Bronchocela danieli*—Moody (1980); Hallermann (2005, 2009)

**Material Studied:** DOSMB05025, an adult male from Shastri Nagar (6.80821°N, 93.8859°E, 0 m asl.), Great Nicobar and DOSMB05026, an adult female from East-West Road, (7.01893°N, 93.92333°E, 12 m asl.) Campbell Bay, Great Nicobar.

**Holotype:** ZSI 22455 from Campbell Bay, Great Nicobar (Fig. 6)

**Differential diagnosis and comparisons:** A species of *Bronchocela* endemic to Great Nicobar Island, in the southern group of Nicobar archipelago, characterized by: small body size (72.62–79.00 mm SVL); relative tail length (331–343 % SVL); 65–71 scale rows around mid-body, of which, the first three to six rows on the dorsum oriented posterodorsally, the next four rows oriented posteriorly, followed by 12–13 rows oriented posteroventrally; upto 10 slightly enlarged, relatively short scales forming the nuchal crest; dorsal crest rudimentary; three postmentals; 8–9 supralabials; 8–9 infralabials; 4–5 canthals; 6–7 supraciliaries; 25–27 subdigital lamellae under toe IV; 71–77 ventrals; pale green dorsal colouration with a distinct, black coloured patch behind the eye with two bright yellow or white spots (Table 2).

**Description and variation:** A small species of *Bronchocela* (mean SVL 76.61 mm; n=3), with a long, tapering tail (TaL:SVL 3.31). Body rather long and slender (AG:SVL 0.45–0.54, n=3). Head large (HL:SVL 0.27); much longer than broad (HL:HW 1.91–1.93) and about as broad as deep (HW:HD 1.01). Snout less than half as long as the head (ES:HL 0.40) with a blunt, rounded tip. Canthus rostralis sharply defined, with four to five canthal scales. Eyes relatively large, a little larger than 1/4<sup>th</sup> the length of the head (ED:HL 0.27); tympanum circular, relatively slightly large, a little larger than half the eye diameter (TYH:ED 0.43) and black in colour. Scales between the eye and tympanum small. Nasal slightly larger than the adjacent scales and ovoid in shape. Scales on the check below the tympanum small and keeled. Mental triangular, bounded by two large and one small postmentals and eight infralabials on either side. Rostral bounded by eight to nine supralabials on each side. Nostrils separated from each other by nine to ten small internasals. Nuchal crest composed of up to twelve short scales projecting posterodorsally. Dorsal body scales small, feebly keeled and homogeneous, in 65 rows around the mid-body. Of the dorsal scales, the first four rows on the dorsum on either sides oriented posteriorly; the next three rows of scales oriented posterodorsally, with the rest of the scales on the lateral body oriented posteroventrally. Ventrals 71–77 in a longitudinal series; about five times larger than the dorsal scales, bearing a strong median keel, projecting posteriorly towards the lower vertex. Limbs relatively slender and elongate; upper arm short and slender (UAL:SVL 0.17); lower arm slightly longer than the upper arm (UAL:LAL 0.93); palm about as long as the lower arm (LAL:PAL 0.99). Fingers long and slender, relative length of fingers IV~III>II>IV>I. Thigh long and slender (FEL:SVL 0.24); tibia nearly as long as the thighs (FEL:TBL 0.98); foot elongated, longer than thigh (FEL:FOL 0.84). Hindlimbs longer than half the body length (HLL:SVL 0.73–0.89). Relative lengths of toes IV>III>II>V>I; 25–27 subdigital lamellae under toe IV.

Dorsum pale green throughout the body; tip of the tail reddish. Ventral surfaces of the head, lips and body white. Head greyish with a black ring around the eye. Tympanum black and males with a black patch behind the eye up to the tympanum, with a distinct yellow or white patch, which is absent in females. In preservation, overall dorsal body grey in color, with patches of black along the sides of the trunk. Venter pale white.

**Distribution and Natural history:** It is endemic to Great Nicobar and was recorded during the present study from several sites within this island. It is arboreal and diurnal in habit, and is a common species found in evergreen forests (Fig. 8).



**FIGURE 5.** *Bronchocelea danieli* (top: DOSMB 05025, middle: live males, below: live female).

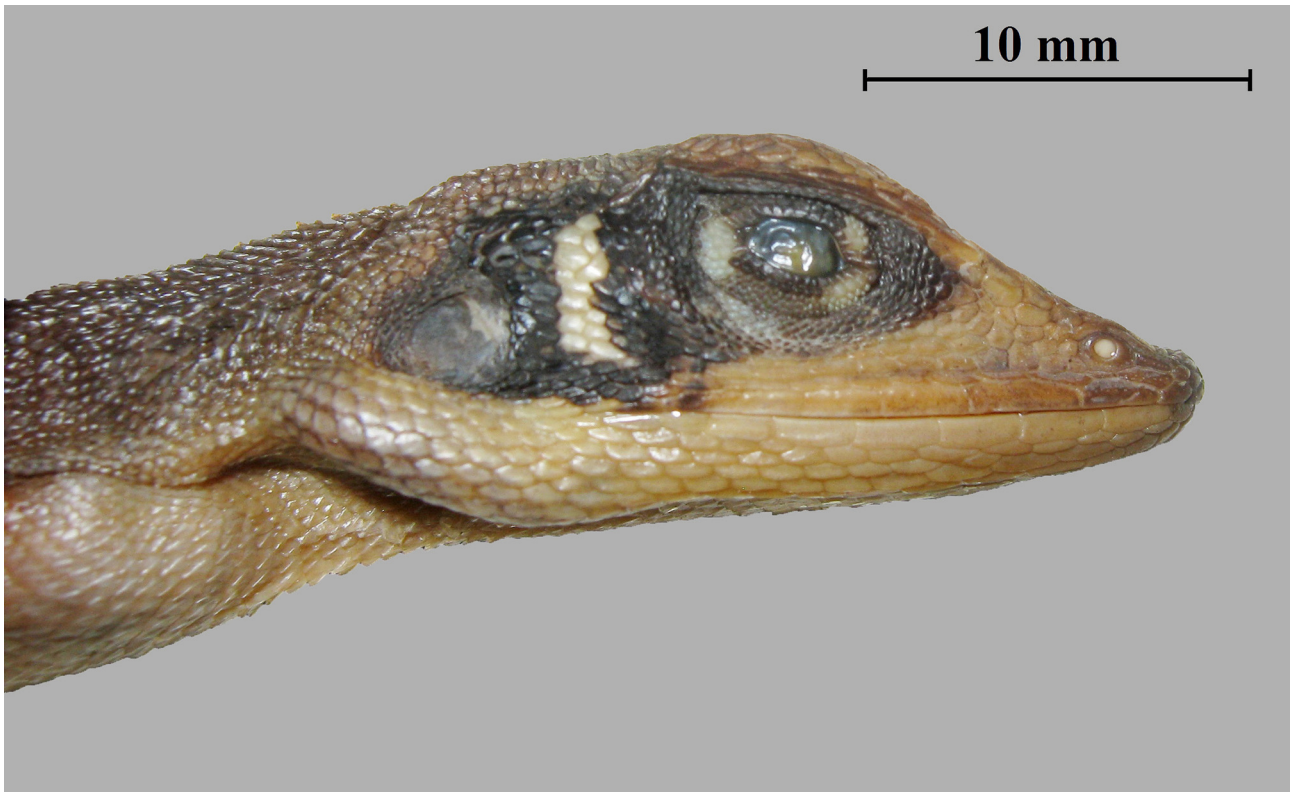


FIGURE 6. Head of the holotype of *Bronchocela danieli* (ZSI 22455).

***Bronchocela nicobarica* sp. nov.**

(Fig. 7)

*Bronchocela* sp. 2—Vijayakumar (2005)

**Holotype:** DOSMB 05070, an adult male, collected from Makachua, (7.40637°N, 93.70894°E, 23 m asl.), Little Nicobar, Nicobar Islands, India by S.R. Chandramouli in April 2017.

**Paratypes:** DOSMB 05055, an adult male, collected from Makachua, Little Nicobar Island; DOSMB05056, an adult female collected from Pulo Ulon (7.29238°N, 93.68415°E, 36 m asl.), Little Nicobar Island in April 2017 (coll. as above).

**Etymology:** The specific epithet is a toponym, in feminine gender, referring to the distribution (Nicobar Islands) of the new species.

**Differential diagnosis and comparisons:** A species of *Bronchocela* endemic to the Southern group of Nicobar Islands, excluding Great Nicobar, characterized by small body size (68.32–79.04 mm SVL); relative tail length comparatively shorter (319 % SVL in *B. nicobarica* sp. nov. versus 331% in *B. danieli*); 62–63 scalerows around mid-body (versus greater, 65–71 in *B. danieli*), of which, the first three rows on the dorsum oriented posterodorsally, the next two rows oriented posteriorly (versus four in *B. danieli*), followed by 10–11 rows oriented posteroventrally; 10–12 slightly enlarged, relatively short scales forming the nuchal crest; dorsal crest rudimentary; three postmentals; eight supralabials; 7–9 infralabials; four canthals; 7–9 supraciliaries; 30–33 subdigital lamellae (versus 25–27 in *B. danieli*) under toe IV; 76–80 ventrals; pale green dorsal colouration with a black coloured ring around the eyes in males, but males lacking the characteristic dark patch behind the eye (versus always present in *B. danieli*) (Table 2).

**Description of the holotype:** An adult male, measuring 79.04 mm SVL; with a short, incomplete tail and a long and slender body (AG:SVL 0.45). Tail 134 mm, broken and incomplete. Head large (HL:SVL 0.27); longer than broad (HL:HW 1.67) and broader than deep (HW:HD 1.21). Snout long (ES:HL 0.43) with a blunt, rounded tip. Canthus rostralis sharply defined, with four canthal scales. Eyes fairly large, more than 1/4<sup>th</sup> the length of the head

(ED:HL 0.27); tympanum nearly triangular, relatively small, less than half as large as the eye (TYH:ED 0.46) and black in colour. Scales between the eye and tympanum slightly enlarged and keeled, in four rows. Nasal relatively large, with a pointed anterior and rounded posterior ends. Scales on the check below the tympanum elongated and feebly keeled. Mental triangular, bounded by three small postmentals; two larger ones on the sides with a small scale in between and seven infralabials on either sides. Rostrum with a small bulge above the rostral scale, bounded by eight supralabials on each side. Nostrils separated from each other by nine small internasals. Nuchal crest composed of twelve slightly enlarged, triangular scales projecting posterodorsally. Dorsal body scales relatively small, feebly keeled and homogeneous, in 62 rows around the mid-body. Of the dorsal scales, the first two rows on the dorsum on either sides oriented posteriorly; the next three rows of scales oriented posterodorsally, with the rest of the scales on the lateral body oriented posteroventrally. Ventrals 76 in a longitudinal series; much larger and broader than the dorsal scales, bearing a strong median keel, projecting posteriorly towards the lower vertex. Limbs relatively slender and elongate; upper arm long and slender (UAL:SVL 0.21); lower arm nearly as long as the upper arm (UAL:LAL 1.07); palm shorter than the lower arm (LAL:PAL 1.21). Fingers long and slender, relative length of fingers IV>III>V>II>I. Thigh long and slender (FEL:SVL 0.27); tibia nearly as long as the thighs (FEL:TBL 0.99); foot elongated, slightly longer than thigh (FEL:FOL 0.92). Hindlimbs much longer than half the body length (HLL:SVL 0.85). Relative lengths of toes IV>III>V>II>I; 30 subdigital lamellae under toe IV.

**TABLE 2.** Comparison of morphological characters of *Bronchocele* spp. of the Nicobar Islands and *B. cristatella*

	<i>B. cristatella</i> sensu stricto	<i>B. cyanopalpebra</i> <b>sp. nov.</b>	<i>B. rubrigularis</i>	<i>B. nicobarica</i> <b>sp. nov.</b>	<i>B. danieli</i>
Sample size	13	9	11	3	5
SVL	79.4–105.6	75.1–103.6	82.3–106.4	68.32–79.04	72.62–79.0
Relative tail length	330–390 %	334 %	343 %	319 %	331–343 %
Midbody scalerows	61–79	56–78	50–58	62–63	65–71
Dorsally oriented	1–2	3	2–3	3	3
Posteriorly oriented	3–7	1–3	4–5	2	4
Ventrally oriented	24	14–22	10–11	10–11	12–13
Crest scales	10–15	7–12	10–11	10–12	10
Postmentals	3	3	3	3	3
Supralabials	10	9–10	7–10	8	8–9
Infralabials	9	8–10	7–10	7–9	8–9
Canthals	4–5	5–6	6	4	4–5
Toe IV lamellae	31–34	32–43	27–32	30–33	25–27
Eyelids	green	blue	yellow	grey	black
Eye patch in males	absent	absent	absent	absent	present
Hindlimb L:SVL	0.95	0.86	0.77–0.93	0.88	0.87–0.89

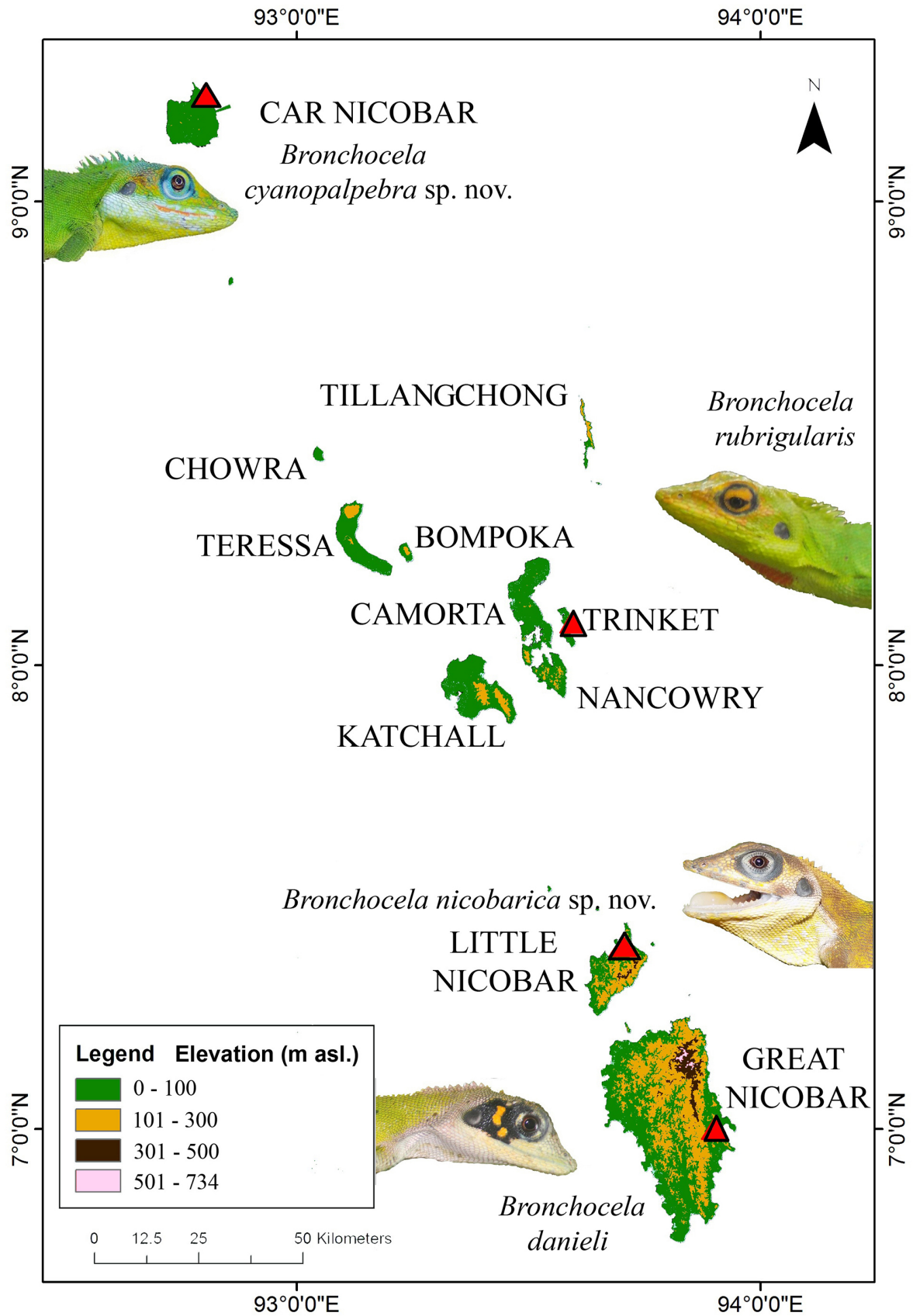
Dorsal coloration (in life) dull green throughout the body, head pale brown; tip of the tail brownish. Ventral side of the head and body of a lighter shade of green than the dorsum. Tympanum black, lacking a dark eye-patch. Upon preservation, much of the green body colouration decolorized to uniform grey on the head and body. Venter uniform pale white.

**Variation:** Measurements and scale-counts of the paratypes are presented in Table 3. Female slightly smaller than males, uniform green dorsally, lacking nuchal crest.

**Distribution and Natural history:** Recorded only on Little Nicobar during the present study. However, it has been reported from other smaller islands in the southern Nicobar Islands such as Menchal, Kondul and Pilo Milo (Vijayakumar, 2005). It is arboreal and diurnal in habit and is a fairly common species found in evergreen forests and plantations (Fig. 8).



**FIGURE 7.** *Bronchocela nicobarica* sp. nov. (top: Holotype DOSMB 05070, middle: live male, below: live female).



**FIGURE 8.** Map, showing the distribution of the four *Bronchocela* species in the Nicobar Archipelago (red triangles indicate type localities).

**TABLE 3.** Measurements and scale counts of *Bronchocele* spp. of the Nicobar Islands and *B. criatata*

Species	<i>Bronchocele rubrigularis</i>						<i>Bronchocele cyanopalpebra</i> sp. nov.					
	DOSMB 05086	DOSMB 05087	BNHS 1609	DOSMB 05054	Chuckchuka	DOSMB 05089	BNHS 1610	BNHS 1662	BNHS 961	Car Nicobar	Car Nicobar	
Loc.	Camorta	Camorta	Nancowry	Chuckchuka	Chuckchuka	CarNicobar	Car Nicobar	Car Nicobar	Car Nicobar	Car Nicobar		
Lat	8.03792	8.03792	-	9.21358	9.21358	-	-	-	-	-		
Long	93.54263	93.54263	-	92.79647	92.79647	-	-	-	-	-		
Alt (m asl.)	28	28		33	33							
SVL (mm)	92.6	82.3	80.1	81.24	81.23	103.6	92.0	92.0	75.1	75.1		
Trunk length	41.66	35.21	41.5	36.36	32.57	55.3	49.0	49.0	41.0	41.0		
Tail length	268	272	279	275	275	357	347	347	193+	193+		
Tail/Total length	0.87	0.89	0.8	0.88	0.89	0.8	0.8	0.8	0.7	0.7		
Head length	24.12	21.43	23.3	22.61	22.18	33.2	31.9	31.9	21.0	21.0		
Head width	13.41	11.82	11.2	12.9	12.15	15.7	19.5	19.5	11.7	11.7		
Head depth	13.41	12.15	10.0	12.41	11.7	15.3	15.3	15.3	9.3	9.3		
Eye diameter	5.94	5.07	7.0	4.76	5.52	7.9	7.6	7.6	7.0	7.0		
Tympanum dia	3.75	3.17	3.2	2.42	2.28	5.1	4.0	4.0	3.1	3.1		
Eye-nostril dist	5.67	5.87	5.5	5.99	5.66	7.4	7.8	7.8	5.3	5.3		
Eye-snout dist	9.75	10.26	9.6	10.15	10.08	13.9	13.3	13.3	9.3	9.3		
Eye-tympanum dist	5.43	3.77	4.1	5.1	4.35	6.9	6.2	6.2	4.3	4.3		
Inter-orbital dist	12.04	11.06	9.7	11.32	11.04	13.4	11.9	11.9	7.2	7.2		
Inter-narial dist	5.03	5.04	4.4	5.78	5.03	6.8	7.2	7.2	4.4	4.4		
Midbody scalerows	50	53	53	68	72	63	78	78	56	56		
Posteriorly oriented	1	1	1	2	1	3	3	3	3	3		
Dorsally oriented	3	3	3	3	3	4	4	4	4	4		
Ventrally oriented	11	10	13	19	20	17	22	22	14	14		
Nuchal crest scales	9	8	8	11	7	9	12	12	8	8		
Supalabials	9	10	9	9	9	9	9	9	9	9		
Infralabials	9	9	8	9	8	9	9	9	9	9		
Post-mentals	3	3	3	3	3	3	3	3	3	3		
Ventrals	68	60	65	80	76	85	82	82	80	80		
Canthals	6	6	5	5	6	6	6	6	5	5		

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TABLE 3. (Continued)

Species	<i>Bronchocelea rubrigularis</i>					<i>Bronchocelea cyanopalpebra</i> sp. nov.				
	DOSMB 05086	DOSMB 05087	BNHS 1609	DOSMB 05054	DOSMB 05089	BNHS 1610	BNHS 1662	BNHS 961		
Catalogue No:										
Supraoculars	7	6	7	7	6	8	8	7		
Intermasal	8	8	8		10	10	10	12		
Upper arm length	16.51	14.73	13.0		16.62	20.2	22.1	15.7		
Lower arm length	15.22	14.28	15.7		14.76	17.5	20.8	15.4		
Palm length	14.03	14.75	4.2		15.17	7.6	7.1	4.1		
Femur length	21.38	19.85	21.0		22	22.3	25.5	21.4		
Tibia length	23.8	20.45	21.4		23.78	27.2	27.6	21.1		
Foot length	26.43	22.63	-		27.35	-	-	-		
T4 lamellae	27	24	32		32	38	40	43		
F1	4.09	3.85	3.8		4.17	7.2	7.3	5.3		
F2	5.37	5.13	7.5		5.99	9.9	11.4	7.5		
F3	7.55	8.75	11.9		11.12	13.8	15.4	11.6		
F4	7.88	8.97	13.4		10.97	15.4	16.2	13.1		
F5	5.56	5.03	7.9		5.57	9.5	9.9	7.8		
T1	3.88	3.7	8.1		4.46	7.6	9.5	7.9		
T2	6.1	6.68	13.8		8.86	15.1	15.6	11.7		
T3	11.57	12.12	17.4		14.4	17.6	19.0	15.4		
T4	16.31	15.73	25.7		16.24	31.6	31.6	25.3		
T5	10.11	8.08	11.8		10.88	13.31	11.7	11.3		
Sex	m	f	M		m	m	m	f		

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**TABLE 3. (Continued)**

Species	<i>Bronchocelea danieli</i>			<i>Bronchocelea nicobarica</i> sp. nov.			<i>Bronchocelea cristatella</i> (mean±SD)	
	Catalogue No:	DOSMB 05025	DOSMB 05026	DOSMB 05070	DOSMB 05055	DOSMB 05056	See Material examined (n=13)	
Loc.	Shastri Nagar	Campbell Bay	Makachua	Makachua	Pulo Ulon	Java		
Lat	6.80821	7.01893	7.40637	7.40637	7.29238			
Long	93.8859	93.92333	93.70894	93.70894	93.68415			
Alt (m asl.)	0	12	23	23	36			
SVL (mm)	78.21	72.62	79.04	77.12	68.32			89.2±8.12
Trunk length	35	32.42	35.87	33.84	31.02			45.4±4.31
Tail length	270	230	134+	234	230			318.2±34.12
Tail/Total length	0.89	0.88	-	0.87	0.88			0.8±0.02
Head length	20.81	19.43	21.36	20.01	18.01			25.8±2.47
Head width	10.67	10.22	12.79	10.57	9.39			13.5±1.51
Head depth	10.86	9.84	10.58	9.09	9.68			-
Eye diameter	5.66	5.36	5.68	6.76	5.47			8.3±0.81
Tympanum dia	2.56	2.2	2.63	2.71	2.04			-
Eye-nostril dist	5.63	5.05	5.27	4.73	4.63			5.4±0.41
Eye-snout dist	9.28	6.97	9.2	8.3	7.02			9.8±0.78
Eye-tympanum dist	3.68	4.62	3.46	3.06	2.96			5.0±0.49
Inter-orbital dist	9.06	10.04	9.37	9.04	8.49			-
Inter-narial dist	3.62	4.02	4.58	4.02	4.46			-
Midbody scalerows	65	65	62	63	63			61-79
Posteriorly oriented	4	4	2	2	2			1-2
Dorsally oriented	3	3	3	3	3			3-7
Ventrally oriented	12	13	23	11	11			20-30
Nuchal crest scales	10	0	12	10	0			10-15
Supalabials	9	8	8	8	8			10
Infralabials	8	8	7	8	9			9
Post-mentals	3	3	3	3	3			3
Ventrals	71	77	76	80	77			60-86

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**TABLE 3. (Continued)**

Species	<i>Bronchoceila danieli</i>		<i>Bronchoceila nicobarica</i> sp. nov.		<i>Bronchoceila cristatella</i> (mean±SD)
	DOSMB 05025	DOSMB 05026	DOSMB 05070	DOSMB 05055	
Catalogue No:					See Material examined (n=13)
Canthals	4	5	4	4	4-5
Supraoculars	7	6	9	7	-
Internasal	10	9	9	8	-
Upper arm length	14.43	11.44	16.37	17.46	17.0±0.6
Lower arm length	15	12.71	15.24	14.98	18.2±2.0
Palm length	15.17	12.72	12.62	12.45	17.7±2.06
Femur length	23.07	17.95	21.58	21.48	26.4±3.95
Tibia length	22.68	19.06	21.86	22.2	26.5±3.72
Foot length	27.65	21.78	23.46	25.1	34.2±3.73
T4 lamellae	25	27	30	33	31-34
F1	3.97	3.15	3.01	3.99	-
F2	5.95	4.87	5.65	5.31	-
F3	10.53	8.65	8.87	8.85	-
F4	10.56	8.5	9.17	8.63	-
F5	5.06	5.02	6.9	5.7	-
T1	4.67	4.4	5.2	5.23	-
T2	8.71	8.96	7.53	10.88	-
T3	14.02	12	12.7	14.4	-
T4	18.7	14.68	16.17	16.2	-
T5	9.02	8.35	9.72	10.16	-
Sex	m	f	m	m	m & f
				f	

## Discussion

The present study has revealed an underestimated diversity of *Bronchocela* spp. in the Nicobar Archipelago, which is in line with the new species descriptions and revalidations done recently from other regions of its range (Grismer *et al.* 2015, 2016; Zug *et al.* 2017). Of the four species recognized from the Nicobar Islands in this study, two have been recently described and are hence, free from taxonomic issues. On the other hand, the third species that had been identified as *B. cristatella* (after Das & Gemel 2000), had not been assessed systematically until now. Vijayakumar (2005) recognized it to be distinct from *B. cristatella* and mentioned it as *Bronchocela* sp. Subsequent authors (see chresonymy above) also regarded it to be distinct from *B. cristatella*, pending a formal taxonomic assessment of this population. Figueroa (2021) clarified the information on the type of *B. cristatella* (Kuhl, 1820) and designated Seba's (1734) painted specimen as the lectotype. He also clarified the confusion caused due to the misinformation provided by Das & Gemel (2000) who had indicated that the type(s) of *B. cristatella* could be in the collections of the MNHN, Paris. The three specimens (MNHN 6884, Fig. 9) that were speculated to be the syntypes of *B. cristatella* were collected from "Ambon, Indonesia" (N. Vidal pers. comm. March 2021) and their status as possible syntypes of *B. cristatella* was rejected by Figueroa (2021). Therefore, the population on Car Nicobar does not have any nomenclatural connection to *B. cristatella* and the name given to it (*Pseudocalotes archiducissae*, Fig. 10) has been shown to be a *nomen nudum* that cannot be applied. Hence, it has been given a new name herein. Likewise, the second species, *B. nicobarica* **sp. nov.** described here was recognized as a potentially distinct taxon from *B. danieli* by Vijayakumar (2005), although, no attempt has been made to assess the taxonomic status or name this population formally until now. The present study has resolved these issues and resulted in the description of these two unnamed populations of *Bronchocela* as new species, in addition to providing detailed redescriptions of *B. danieli* and *B. rubrigularis* based on new samples.

Among the four *Bronchocela* species of the Nicobar Islands, the two new species, *B. cyanopalpebra* **sp. nov.** and *B. nicobarica* **sp. nov.** occur in a very narrow geographic range with their distributions restricted to one and four small islands, totaling to 126 km<sup>2</sup> and ~170 km<sup>2</sup> respectively. The other two species, *B. danieli* and *B. rubrigularis* have fairly wide geographic distribution ranges; 1045 km<sup>2</sup> and 603 km<sup>2</sup> respectively. Conservation status has been assessed for *B. danieli* as Least Concern. Based on IUCN criteria B1 and B2, it is recommended that all of the four species of *Bronchocela* in the Nicobar Islands should be considered endangered. It is of concern that the islands occupied by the new species described here are devoid of terrestrial protected areas and hence, are prone to threats that could result in their extinction. The Nicobar Islands, forming the northwestern periphery of the Sundaland biodiversity hotspot is known for its faunal uniqueness and endemism across several faunal groups. Recent studies on reptiles and amphibians in this region have been highlighting the uniqueness of its underexplored herpetofauna (Amarasinghe *et al.* 2020; Chandramouli 2020; Chandramouli *et al.* 2020, 2021; Garg *et al.* 2022).

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**FIGURE 9.** The three specimens (MNHN 6884) wrongly regarded to be the syntypes of *B. cristatella* (courtesy: Nicholas Vidal).



**FIGURE 10.** Specimens of *Pseudocalotes archidussicae* (*nomen nudum*) NMW 21002:1-2 (courtesy: Gernot Vogel).

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**APPENDIX 1. Additional material examined.**

*Bronchocela rubrigularis*: ZSI15033, ZSI2671 two adult males and ZSI15034, ZSI14668 two adult females from ‘Nicobars’.  
*B. danieli*: ZSI22455, ZSI22496 two adult females from Great Nicobar.