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TAXONOMIC REVIEW AND MORPHOMETRIC DESCRIPTION OF *BRONCHOCELA CRISTATELLA* (KUHL, 1820) (SQUAMATA: AGAMIDAE) WITH NOTES ON OTHER SPECIES IN THE GENUS

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ABSTRACT. - The agamid genus *Bronchocela* is represented by seven species distributed in the southeastern corner of south Asia, the Sundaland, the Lesser Sunda Islands, Sulawesi, Philippines, and the Moluccan islands and northwest New-Guinea east of the Lydekker's Line. The taxonomic status of *Bronchocela cristatella,* once considered a member of the speciose genus *Calotes,* is reviewed. Egg shape and the ratio of tail length to snout-vent length are two characters that are useful to delimit the genus *Bronchocela* from other agamid genera allied to it. Of 10 morphometric variables studied in 32 museum specimens, tail length (TL) and snout-vent length (SVL) were the main variables which accounted for body size and shape variation respectively. No sexual dimorphism for body size and shape was detected. *Bronchocela cristatella,* like other members in the genus, has the longest tail among arboreal agamids. A diagnosis for the species is proposed.

KEYWORDS. - Agamidae, taxonomy, *Bronchocela cristatella*, *Calotes*, distribution, morphometrics.

INTRODUCTION

The green crested lizard, *Bronchocela cristatella* (Kuhl, 1820), was first recorded from Singapore Island in 1847 (Cantor, 1847; Flower, 1896). Members in the genus *Bronchocela* are true arboreal lizards with a long head, slender body, elongated hind limbs, and a long tail. The species, *B. cristatella,* is closely allied with members in the speciose *Calotes* group and is the most widely distributed and the best known agamid in the *Bronchocela* group in the Far East (Fig. 1). Although first named by Kuhl in 1820 from Java as *Agama cristatella*, it was Johann J. Kaup (as Johann J. Caup) who in 1827 placed the species in his newly created genus *Bronchocela* as *B. cristatella.* Early Europeans in the Far East called the lizard a "chameleon" because of its ability to change its natural body colour rapidly.

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Bronchocela cristatella is common in Singapore and the Malay Peninsula, but in parts of its range near urban areas, the species is largely replaced by a more adaptable agamid, the oriental garden lizard, *Calotes versicolor.*

The present paper reviews the taxonomic status of *Bronchocela cristatella as* well as provides a description of the species inclusive of morphometric analyses. A diagnosis for the species is proposed.

MATERIALS AND METHODS

Material examined. - Thirteen male and 19 female specimens in the Zoological Reference Collection, Department of Biological Sciences, National University of Singapore. Only specimens with intact tails were used in this study: Singapore – ZRC 2.351-353 (C. C. Kuhl, Botanic Gardens, 1896), 2.356 (Botanic Gardens, 1921), 2.355 (C. C. Kuhl, Fort Canning, 1916), 2.368 (G. H. Sworder, Pulau Ubin, 1921), 2.359 (Pulau Ubin, 1921), 2.357 (Pulau Ubin, 1921), 2.361 (Pulau Ubin, 1921), 2.367 (Pulau Ubin, 1921), 2.364 (Pulau Ubin, 1921), 2.360 (Pulau Ubin, 1921), 2.369 (1952), 2.363 (Pulau Ubin, 1921), Indonesia – 2.381, 2.384 (Anambas & Natuna Islands, 1911 -1928), Malaysia – 2.336, 2.336a

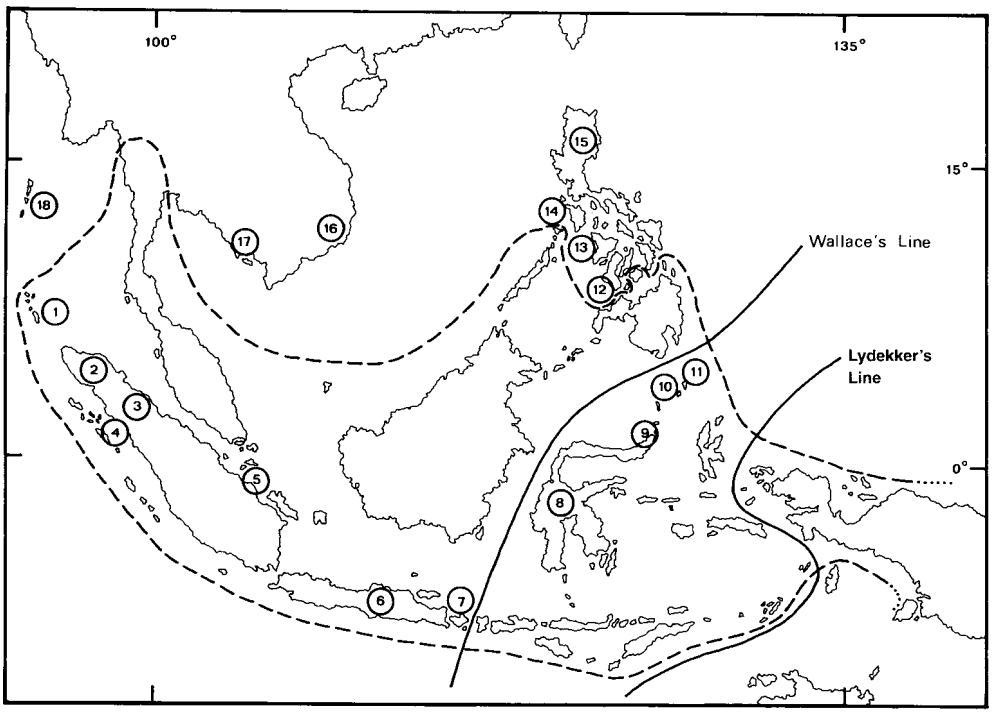

Fig. 1. Distribution of *Bronchocela cristatella* and other species in the genus. Dotted line indicates range of *B. cristatella,* the most widely distributed species, ranging from south Burma, south Peninsular Thailand, Peninsular Malaysia, Borneo, Indonesia, southern Phillipines, to north-west New Guinea. Selected known locality records of other *Bronchocela* species:- *B. danieli*: (1) Campbell Bay, Great Nicobar, Nicobar Islands; *B. hayeki*: (2) Takengon, Lake Tawar, Acheh Province; (3) Bukit Lawang & Mt. Sibayak, North Sumatra Province; *Bronchocela jubata*: (1) Nicobar Islands, (4) Nias Island, (5) Singkap Island, (6) Java - whole island, (7) Bali Island, (9) Manado (Sulawesi), (10) Salibabu, Sangihe Islands), (11) Karakelong, Talaud Islands, (18) Andaman Islands; *B. celebensis*: 8 (Sulawesi); *B. marmorata*: (12) Negros Island, (13) Panay Island, (14) Mindoro Island, (15) Luzon Island, including offshore Polillo Island); *B. smaragdina*: (16) Dalat, Langbian Plateau, South Vietnam, (17) Cambodia, locality unknown, probably the Elephant Mts., near Kampot).

(Maxwell Hill, 1908, 2921 ft), 2.334 (Penang, 1896), 2.333 (Penang, 1896), 2.335 (Perak, ?), 2.3392.341 (Kuala Teku, Pahang, 1921 -1927), 2.345-2.348, 2.350 (Johore, 1904 -1921), 2.33X (Penang, 1896), uncatalogued, 1, 2 (localities unknown), 2.433 (Ipoh, 1892).

Measurement of morphometric parameters. - Ten linear body measurements (after Ota & Hikida, 1989), accurate to the nearest 0.1 mm, were recorded from each of the specimens (n = 32): snout-vent length (SVL), tail length (TL), jaw length (JL), head length (HL), head width (HW), head depth (HD), fore leg length (FLL), fore foot length (FFL), hind leg length (HLL), and hind foot length (HFL). JL, HL, HW, and HD were measured with a pair of digital calipers (Mitutoyo); the other measurements were recorded with a ruler. Sex was determined by dissection of the specimens.

Statistical analyses. - A principal components analysis (PCA) was applied to the morphometric data for all the lizards to determine which of variables were important in contributing to body size and shape. A regression analysis was then performed separately for each sex on the main morphometric variables associated with each of the two important principal components (PC) scores. An analysis of covariance (GLM in MINITAB, 1991) was used to test for difference in the covariation of morphometric variables between the sexes.

TAXONOMY

The 19th century experienced a great curiosity in reptiles of which many oriental specimens of lizards were brought to Europe by travellers and collectors. Many specimens were described and named by leading herpetologists of that period but it was G.A. Boulenger (1858-1937), Keeper of Zoology at the British Museum, London, who attempted to place the many new discoveries into convenient categories. In *Catalogue of Lizards*, Boulenger (1885) "lumped" together 19 species into the genus *Calotes*, dismissing the genus *Bronchocela* as a junior synonym. It is therefore appropriate to review the wide ranging genus *Calotes*.

Calotes (sensu Boulenger) is widely distributed throughout the Oriental region and the Sunda Islands. Smith (1935) divided the 23 then known species of *Calotes* into four subgroups, namely: the *Calotes cristatellus* subgroup (*C. smaragdinus, C. jubatus, C. cristatellus),* the *Calotes microlepis* subgroup [*C. floweri, C. fruhstorferi* (= *C. brevipes,* fide Wermuth 1967), (see also Günther, 1864; Denzer & Manthey, 1991; Manthey & Grossmann, 1997), *C. tympanistriga, C. flavigula,* including the aberrant *C. kakhienensis* (= *Salea kakhiensis,* fide Moody 1980)], the *Calotes versicolor* subgroup (C. *nemoricola, C. grandisquamis, C. maria, C. jerdoni, C. emma, C. mystaceus, C. calotes),* and the *Calotes liocephalus* subgroup *(C. liolepis, C. ceylonensis, C. nigrilabris, C. andamanensis,* as well as the two dwarf species, *C. rouxi,* and *C. elliotti),* but did not make any name changes. Taxonomic difficulties in general are compounded by the fact that there are insufficient data as a few species come from very remote regions with vague or ambiguous locality records or have been described from only one specimen, e.g., *C. andamanensis, C. (inc. sed.) kinabaluensis, C. nigrigularis* (= *Complicitus* gen. n. *nigrigularis,* see Manthey & Grossmann, 1997), *C. kingdonwardi,* and *C. flavigula.* Ten more species since 1935 have been added to the genus (Wermuth, 1967; Tiwari & Biswas, 1973; Biswas, 1976; Zhao & Li, 1984; Ota & Hikida, 1991), bringing the total number of species to 33 (see also Welch et al., 1990).

Moody (1980) reviewed the validity of Smith's taxonomic groupings and separated the many species assembled by Boulenger under the speciose *Calotes* into four genera, namely: *Calotes, Bronchocela, Dendragama, and Pseudocalotes*. He removed seven *species, C. celebensis, C. cristatellus, C. danieli, C. hayeki, C. jubatus, C. marmoratus, and C. smaragdinus,* from *Calotes* and re-assigned them to the genus *Bronchocela* KAUP, 1827 which is approximately equivalent to Smith's (1935) *cristatellus* subgroup, while his *Pseudocalotes* species group agrees with Smith's *microlepis* group. *Calotes boulengeri* (Doria) was also removed from *Calotes* and reverted to *Dendragama boulengeri* Doria, 1888 as a monotypic genus. The *Calotes versicolor* and the *Calotes liocephalus* subgroups are not very homogeneous, but Moody (1980), in his revision of the Agamidae, left them in the genus *Calotes* Cuvier, 1817 without further subdivision. In doing so, Moody thus resurrected the genus *Bronchocela* Kaup, 1827 from synonymy mainly on the basis of phylogenetic analysis of a total of 122 phenotypic characters and not on the description of diagnostic characters.

The terra typica of *B. cristatella* was not given by Kuhl (1820) when he first described the species as *Agama cristatella*; the type specimen was not listed in the Paris Museum (Brygoo, 1988). The first locality record for the species was given by Kaup (1827) as Java, the precise location is however unknown. Given this anomaly and the existence of two different populations of *B. cristatella* in Java (Manthey, pers. comm.), a new type specimen from the terra typica is necessary for a new description against which all other future studies of the species can be compared.

Several recent taxonomists, notably Ota & Hikida (1991), and others (e.g., Frost & Etheridge, 1989; Ota & Hikida, 1989) preferred to use the junior synonym *Calotes* (sensu Smith 1935) instead of *Bronchocela,* pending further work on the genus. Although members in the two genera are closely allied, Günther (1864: 139) taxonomically defined the main difference of *Bronchocela* KAUP as having body scales that are directed posteriorly and downwards and *Calotes* CUVIER as having scales that are directed posteriorly and upwards, but this character seems insufficient to denote phyletic relationship as other characters have to be considered.

Only *Bronchocela* species have a lateral fold of skin that stretches from the posterior edge of the jaw to the shoulder which can be erected by the hyoid apparatus. They have long tails to suit their arboreal habits and are particularly agile in flitting from branches of one tree to another tree or to the ground. Tail length (TL) to snout-vent length (SVL) ratio expressed as a percentage ranges between 300% to 372% (Table 1). All other species grouped by Boulenger (1885) in the genus *Calotes* have a smaller tail length to snout-vent length (TL/SVL) ratio, the exception being, *Calotes calotes* which has a TL/SVL ratio that is comparable to *B. cristatella*. Unlike *Calotes* species which lay ellipsoidal eggs, *B. cristatella, B. jubata, B. hayeki* and *B. marmorata,* all lay long, tapered, fusiform eggs; no records on egg shape are, however, available for eggs in the other three *Bronchocela* species. The fusiform egg shape, unique to *Bronchocela*, is not found in other saurian species. Unfortunately De Rooij (1915) wrote erroneously that in *B. cristatella* "the eggs are long and oval", and further illustrated, wrongly, in Fig. 42c, p. 121, an oval egg as that of *B. cristatella*. This mistake was repeated in Smith (1935), and Taylor (1963). Brongersma (1930) refuted De Rooij's accounts on egg shape in the species. He examined fully-shelled oviductal eggs in *B. cristatella* and reported that they were fusiform, just like eggs of *B. jubata* and *B. hayeki*. Hendrickson (1966) also reported that eggs of *B. cristatella* were distinctly fusiform, not oval. Clutch size in *B. cristatella* is small, usually two eggs or more, rarely just one (Mocquard, 1890; Taylor, 1922; Brongersma, 1930; Ota & Hikida, 1991; Inger & Greenberg, 1966).

Selected list of synonyms and names used for *Bronchocela cristatella*.-

Agama cristatella Kuhl, 1820: 108, terra typica: unknown.
Agama gutturosa Merrem, 1820: pl. 89, figs. 1 & 2.
Bronchocela cristatella – Kaup (Caup), 1827: 619; Duméril & Bibron, 1837: 395; Gray, 1845: 241; Cantor, 1847: 636; Günther, 1864:138; Peters, 1867: 17; Steindachner, 1867: 27; Stoliczka, 1870: 178.
Agama moluccana Lesson, 1830: 34.
Calotes gutturosa Wagler, 1830: 152.
Bronchocela moluccana – Peters, 1867: 17.
Pseudocalotes archiducissae Steindachner, 1867: 27, terra typica: Nicobar Islands.
Bronchocela burmana Blanford, 1878: 127, terra typica: Tavoy (Htawei), in Tenasserim, Burma.
Bronchocela intermedia Peters & Doria, 1878: 374.
Calotes cristatellus – Boulenger, 1885: 316; Boulenger, 1890: 134-135; Mocquard, 1890: 129; Flower, 1896: 871; Ridley, 1899: 191; Shelford, 1901: 52; Boulenger, 1912: 70 -71; Barbour, 1912: 86; Fry, 1915: 88.
Calotes octospinosus Baumann, 1913: 266, fig. B.
Calotes cristatellus – De Rooij, 1915: 121 -122, fig. 53; 1917: 334; Taylor, 1918: 264; De Jong, 1927: 309.
Calotes cristatellus moluccanus – Kopstein, 1927: 439.
Calotes cristatellus – Sworder, 1925: 66; De Jong, 1927: 309; Smith, 1930: 27; 1935: 184 -185; Smedley, 1931: 48; Brongersma, 1934: 179; Taylor, 1963: 886, Fig. 50; Hendrickson, 1966: 64; Inger & Greenberg, 1966: 1017; Wermuth, 1967: 36; Ota & Hikida, 1991: 180.
Bronchocela cristatella – Malkmus, 1989: 179-200; Lim & Chou, 1990: 55; Denzer & Manthey, 1991: 309 -322; Manthey & Schuster, 1992: 27; Tan, 1993: 18; Gaulke, 1994: 21; Das, 1996: 43, 69; Manthey & Grossmann, 1997: 160, fig. 103.

DESCRIPTION

Head. - forehead concave; upper head scales small, unequal, keeled, slightly enlarged, on supraorbital region, nasal angular separate from labial series by one scale row; canthus rostralis and supraciliary edge sharp; 3 - 5 erect, compressed scales, behind supraciliary edge directed outwards, forming a small longitudinal crest; scales on snout keeled or ridged, subequal, a little smaller than keeled scales above orbits; 2 or 3 enlarged scales in occipital region, 8 - 10 upper and as many lower labials, snout distinctly longer than orbit; forehead concave. ***Tympanum.*** - round, large, blackish, greater than half -diameter of orbit, nearly as large as the diameter of the eye. ***Gular sac.*** - a small pouch in males, gular scales keeled, smaller than ventrals which are distinctly larger than latero-dorsal scales; skin-fold extending from behind jaw to above shoulder always present, prominent, but sometimes not obvious in preserved specimens, erectable by the hyoid apparatus, a diagnostic character shared by members of the whole genus (Manthey, 1997 - pers. comm.); oblique fold in front of shoulder absent. ***Nuchal crest.*** - cervical crest, 6 - 10 erect, flattened scales, reaching greatest height (5 mm) at middle of series, the longest, shorter than diameter of orbit. ***Dorsal crest.*** - very low, serrated ridge or absent; when present, crest continues from nuchal crest without a gap; size of last nuchal scale compared to first dorsal distinctly marks the boundary. ***Body.*** - strongly compressed; dorsal scales mucronate, keeled, homogenous, smaller than ventrals; upper 5 - 10 rows, directed backwards and upwards, gradually changing downwards and backwards on the flanks; ventral scales largest, strongly keeled, 1 - 5 times larger than dorsals, mucronate, 60 - 120 scales round middle of body. ***Limbs.*** - arms slender and legs long; adpressed hind limb reaches beyond eye or tip of snout; (in *Calotes* species, adpressed hind limb only reaches the axilla or a little beyond); 4th toe much longer than 3rd; digits long, 3rd and 4th fingers subequal, the 3rd finger not twice the length of 2nd finger; 5th toe shorter than 3rd; subdigital lamellae usually with double keels; scales on arms and legs enlarged,

keeled. ***Tail.*** - long, round, compressed and subtriangular at base, covered with regular scales; subcaudal scales moderately keeled, those ventral largest. ***Eggs.*** - distinctly elongate and fusiform with "puckered" tapering ends (Mocquard, 1890: pl. 7, fig. 3; Ota & Hikida, 1991, fig. 3, p. 185) (cf. Kopstein, 1927 pl. xxvi, figs. 65 & 66, photographs of eggs of *B. jubata* Duméril & Bibron, 1837; see also Brongersma, 1930); definitely not cylindrical or ellipsoidal as in eggs of the *Calotes* species complex; clutch size 1 - 2; at least three other species, *B. hayeki, B. jubata and B. marmorata,* also lay long fusiform eggs with similar egg shape (but egg shape of *B. celebensis*, *B. danieli*, and *B. smaragdina* is unknown). See also Cantor (1847: 636), Boulenger (1890: 134), De Rooij (1915: 121), Smith (1935: 184), Taylor (1963: 886), and Ota & Hikida (1991: 99) for descriptions of the species.

Colour in life. - Natural body colour, bright grass or jade-green, nearly uniform, dull white lighter underneath, sometimes with thin widely spaced transverse bars on flanks; these light whitish green bars are formed by indistinct spots are parallel with the light coloured bars on tail. This lizard readily changes its natural body colour to grey, greyish olive, greenish brown, or black rapidly when handled or stressed, but occasionally some individuals remain in their natural body colour even when in captivity; indistinct black network sometimes forms during colour change from green to black; large blackish ring around orbit; tympanum almost black; transverse dark blackish-brown bands on tail; pupil circular; iris brown with narrow golden ring.

Variation. - Taylor (1922) noted that specimens from Mindanao may "have spines forming the nuchal crests strongly overlapping at the base and curving backward, not making a serrated crest". The specimens from Panaon Island, Philippines, have much higher nuchal crest than specimens from other Philippine localities, e.g., Sulu Archipelago and Calamian Island group (Gaulke, 1994). In some populations, there is a distinct interruption between the nuchal and dorsal crest, in others, there is no gap, but the boundary between the crests is clearly visible due to the difference in scale size. It would be reasonable to expect variation in scale count at mid-body and minor variation in size and shape of nuchal crest as the species has a very wide geographic distribution.

Ecological note. - An active, diurnal, insectivorous, arboreal lizard often seen perched in a head-up or head-down "survey posture", on tree trunks. It is a swift runner up and down tree trunks as well as on the forest floor and often scurries or leaps across branches of trees or bushes; the force of a fall during landing is broken by the long legs and long total body length which exceeds half-meter in large adults. The preferred habitat is the forest edge, but the species also occurs in secondary forests, cultivated areas such as fruit orchards, and is occasionally seen in country gardens.

Distribution of **Bronchocela cristatella.** - The extreme southern part of Burma (below 16° N lat.); Peninsular Thailand up to Kanchanaburi province; Nicobar Islands; Peninsular Malaysia, including Penang, Pulau Tioman; Singapore; Sumatra, Java, Natuna Island; Borneo Island; Amboyna, Buru Island, Ceram Island, Tanibar Islands, Halmahera Islands, Misol Island, and the Lesser Sunda Islands (Smedley, 1931; Boulenger, 1885, 1890, 1912; Smith, 1930, 1935; De Rooij, 1915; Das, 1996); Bohol Island and Mindanao in the Philippine as well as the smaller islands to the west, namely, Palawan, Calamain, Cagayan Islands, and the Sulu Archipelago (Taylor, 1922; Brown & Alcala, 1970).

In 1889, 10 specimens of the lizard collected from "North West New Guinea" were presented by Captain Strachan to the Museum of Comparative Zoology, Harvard (Fry, 1915: 88). In his Herpetological Notes, Fry (in litt.) examined Barbour's (1912) long list of locality records for *B. cristatella*, in the East Indies, and wrote that "Dutch New Guinea" must now be added to the species range. This is the first definitive record of *B. cristatella* from New Guinea. De Rooij (1917: 363), vaguely added New Guinea as a new locality, when she wrote in her "ADDENDA AND CORRIGENDA", "add to the list of New Guinea: *Calotes cristatellus* (Kuhl)". De Jong (1927) referred to the one specimen collected by W.K.H. Feuilleton De Bruyn from "North New Guinea" (precise locality unknown) and wrote, mistakenly, that the species was not yet known from New Guinea. Brongersma (1934), doubted the natural occurrence of *B. cristatella* in New Guinea (see Hennig 1936:169, 194) stated that if the localities Misol and New Guinea should prove to be correct, then the lizard had been imported there. With a recent discovery of another New Guinean specimen in the Amsterdam Museum, probably of *B. cristatella moluccana* Peters (Manthey, pers. comm.), and Fry's (1915) earlier locality record, it now appears confirmed that the distributional range *B. cristatella* extends as far east into New Guinea, west of Lydekker's Line (see also Manthey & Grossmann, 1977: 161). More field studies are necessary to ascertain the extent of this the species range extension.

Note on distribution of other* Bronchocela *species. - *Bronchocela marmorata* has a fairly wide range in the Philippines, occurring in Luzon, Polillo Mindoro, Negros, and Panay Islands (Taylor 1922; Brown & Alcala, 1970). De Rooij (1915) recorded *B. jubata* from Java and Bali where it is common, Singkap Island in the Riau-Lingga Archipelago, and Nicobar Islands. She mentioned "Celebes (Manado?)", but the specimen referred to was probably the same male specimen from Manado, Celebes in Boulenger (1885), contributed by Dr. A. B. Meyer who had similarly deposited specimens of *B. celebensis* and *B. marmorata* in the British Museum, London. De Rooij further recorded as localities the little known Karakelang and Salibubu Islands which are about half-way between Manado (Sulawesi) and Mindanao Island. Locality records of *B. jubata* specimens in the Zoological Museum, Berlin (now Institut für Systematische Zoologie im Museum für Naturkunde der Humboldt-Universität zu Berlin) shows that the species range includes Pulau Nias and "Celebes" (Manthey, pers. comm.). Das (1994) reported *B. jubata* from Andaman Islands and Nicobar Islands, with *B. danieli* endemic to the Nicobar Islands. It is not known if the three *Bronchocela* species, *cristatella*, *jubata*, and *danieli*, range in different islands or whether their ranges overlap on some of the islands of the Nicobar group.

Bronchocela celebensis is known from four localities in Sulawesi (Celebes) (De Rooij, 1915). *Bronchocela hayeki* has been recorded from Berastagi (1,400 m), Bukit Lawang in North Sumatra Province, and Takengon on the shore of Lake Tawar in Acheh Province, Sumatra (Manthey & Grossmann, 1997). Little is known about *B. smaragdina.* Smith (1935, pp. 185) wrote , "Three specimens are known. The types (females) were obtained by Mouhot in Cambodia. I (Smith) obtained a third specimen at Dalat, Langbian Plateau, south Annam (south Vietnam), altitude 5,000 feet". According to Boulenger's (1885) *Catalogue of Lizards*, two female specimens were deposited in the British Museum by M. Mouhot from Camboja (sic) and these were probably the same two specimens in Günther's Systemic Index (1864) p. 83 in which Günther wrote, "...two specimens have been collected by Mouhot in Gamboja (Cambodia)." The ravages of war and political turmoil made the collections of more specimens impossible for many decades, and it is hoped herpetologists can now explore that region again.

RESULTS AND DISCUSSION

Body-size and shape. - Table 2 summarises the mean values of 10 morphometric variables and TL/S VL ratios of male and female *B. cristatella* examined in this study. Mean SVL was 100.91 ± 10.78 mm (n=32, range: 83 - 120 mm). Mean TL was 341.97 ± 35.57 mm (n = 32, range: 270 - 412 mm). The smallest specimen (ZRC2.345) examined was 366 mm long (SVL = 96 mm), TL = 270 mm); the largest (ZRC 2.367) was 527 mm (SVL = 115, TL = 412 mm). Mean total length (i.e., SVL + TL) of all 32 specimens was 442.87 ± 43.49 mm (range: 366 - 527 mm). The ratio of TL to SVL for all lizards averaged 3.403 ± 0.288 with a spread of 2.491 - 3.831; this ratio was slightly higher in females than males (Table 2).

The ratio of TL to SVL in the both sexes obtained in this study compares favourably with similar data reported by Ota & Hikida (1991) for 17 specimens of the species and also with earlier records in De Rooij (1915), Smith (1935), Boulenger (1885), and Taylor (1963) (Table 1). The species has the longest tail in relation to body length among arboreal agamids with a tail length varying between 3.2 to 3.5 times that of the SVL; this character (with the exception of *Calotes calotes* from southern India and Sri Lanka where a TL/SVL ratio of 3.64 and 3.84 was reported from 2 individuals) is shared by 3 other *Bronchocela* species, namely, *B. hayeki* (TL/SVL = 3.5, Manthey & Grossmann 1997: 152), *B. jubata* (TL/SVL = 3.38, Table 1), *B. celebensis* (TL/SVL = 3.53, Table 1).

Table 1. Summary of published snout-vent length (SVL) and tail length (TL) measurements of *Bronchocela cristatella* and other selected agamids. Tail length to snout vent length ratio (TL/SVL) is derived from measurements in the literature, and expressed as a percentage. (sex.- U = unknown; M = male; F = female)

Species	n	sex	SVL (mm)	TL (mm)	Ratio (TL/SVL) in %	Reference
Bronchocela cristatella	19	F	97 (83-120)	335 (270-396)	345 (281-383)	THIS STUDY
	13	M	105 (84-118)	352 (274-412)	333 (249-366)	THIS STUDY
	1	U	130	440	338	De Rooij (1915)
	1	U	122	454	372	Taylor (1963)
	1	U	110	374	340	Taylor (1963)
	1	U	120	400	333	Boulenger (1885)
	9	M	102 (86-109)	331	325 (301-352)	Ota & Hikida (1991)
	8	F	91 (82-95)	321	352 (291-342)	Ota & Hikida (1991)
Bronchocela celebensis	1	U	92	325	353	De Rooij (1915)
Bronchocela danieli	1	U	79	271	343	Tiwari & Biswas (1973)
Bronchocela hayeki	8	M	(81-108)	(272-385)	(320-374)	Brongersma (1930)
	2	F	(74-80)	(253-265)	(330-344)	
Bronchocela jubata	1	U	150	450	300	Smith (1935)
	1	U	130	440	338	De Rooij (1915)
Bronchocela marmorata	1	U	122	390	319	Boulenger (1885)
	1	M	125	425	340	Taylor (1922)
Bronchocela smaragdina	1	U	95	300	315	Smith (1935)

Table 1. Continued

Species	n	sex	SVL (mm)	TL (mm)	Ratio (TL/SVL) in %	Reference
Calotes ceylonensis	1	U	70	165	235	Smith (1935)
Calotes calotes	1	U	130	500	384	Smith (1935)
	1	U	140	510	364	Boulenger (1885)
Calotes grandisquamis	1	U	138	325	235	Boulenger (1885)
	1	U	145	330	227	Smith (1935)
Calotes elliotti	1	U	70	170	242	Smith (1935)
Calotes emma	1	U	97	249	256	Taylor (1963)
	1	U	90	240	266	Boulenger (1885)
	1	U	115	290	252	Smith (1935)
Calotes jerdoni	1	U	100	285	285	Smith (1935)
	1	U	92	270	293	Boulenger (1885)
Calotes (inc. sed.) kinabaluensis	1	M	133	315	236	Ota & Hikida (1991)
Calotes liocephalus	1	M	90	250	277	Smith (1935)
	1	U	90	270	300	Boulenger (1885)
Calotes liolepis	1	U	85	210	247	Smith (1935)
	1	U	76	180	236	Boulenger (1885)
Calotes mystaceus	1	U	132	278	210	Taylor (1963)
	1	U	122	233	190	Taylor (1963)
	1	M	140	280	200	Smith (1935)
Calotes maria	1	U	120	370	308	Smith (1935)
Calotes nemoricola	1	U	145	330	227	Smith (1935)
	1	U	140	330	235	Boulenger (1885)
Calotes nigrilabris	1	M	105	310	295	Smith (1935)
Calotes rouxii	1	U	77	170	220	Smith (1935)
Calotes versicolor	1	U	98	260	265	Taylor (1963)
	1	U	120	285	237	Boulenger (1885)
Complicitus nigrigularis	1	M	70	155	221	Ota & Hikida (1991)
Dendragama boulengeri	1	U	73	160	219	De Rooij (1915)
Gonocephalus grandis	1	M	154	396	257	Taylor (1963)
	1	F	100	194	194	Taylor (1963)
	1	U	155	405	261	De Rooij (1915)
Oriocalotes paulus	1	U	70	130	185	Smith (1935)
Pseudocalotes flavigula	1	M	68	127	186	Smith (1930)
Pseudocalotes floweri	1	U	95	175	184	Smith (1935)
	1	U	98	180	183	Taylor (1963)
Pseudocalotes microlepis	1	U	85	185	217	Smith (1935)
Pseudocalotes tympanistriga	1	U	79	185	234	Boulenger (1885) De Rooji (1915)

Table 2. Mean lengths ± s.d., range of the measurements of 10 morphometric variables, and TL/SVL ratio in museum specimens of *Bronchocela cristatella*. See text for details.

Morphometric variable	mean ± s.d	Range of data (mm)	
		Minimum	Maximum
Female lizards: (n=19)			
SVL	97.47 ± 10.14	83.00	120.00
TL	335.21 ± 38.72	270.00	396.00
HL	24.96 ± 2.64	20.28	29.26
HW	15.99 ± 2.11	12.50	21.23
HD	15.32 ± 1.88	12.55	19.66
JL	29.12 ± 3.71	24.20	35.85
FFL	19.84 ± 3.08	16.00	26.00
FLL	34.58 ± 3.39	29.00	40.00
HFL	36.32 ± 4.12	30.00	44.00
HLL	53.00 ± 5.46	42.00	62.00
TL/SVL	3.45 ± 0.28	2.81	3.83
Male lizards: (n=13)			
SVL	105.92 ± 10.00	84.00	118.00
TL	341.90 ± 59.10	166.00	412.00
HL	27.48 ± 3.50	20.42	33.44
HW	17.43 ± 2.04	12.66	20.02
HD	16.81 ± 1.43	13.64	19.30
JL	31.64 ± 4.02	21.15	37.27
FFL	20.92 ± 3.64	15.00	28.00
FLL	35.23 ± 3.54	25.00	40.00
HFL	37.77 ± 2.98	33.00	42.00
HLL	57.15 ± 4.20	47.00	64.00
TL/SVL	3.32 ± 0.29	2.49	3.65

Table 3. Two main principal components vectors for PCA on morphometric variables for all specimens of *Bronchocela cristatella* examined. See text for details.

Variable	PC1	PC2
SVL	-0.209	0.779
TL	-0.962	-0.267
HL	-0.059	0.194
JL	-0.085	0.235
HW	-0.038	0.139
HD	-0.031	0.127
FFL	-0.014	0.157
FLL	-0.054	0.142
HFL	-0.068	0.126
HLL	-0.096	0.365
Sex	-0.003	0.016
% total variance explained	91.8	6.0

Principal components analysis of morphometric variables (PCA) and analysis of covariance (ANCOVA). - The PCA of 10 morphometric variables and the sex variable yielded 2 important PC scores which cumulatively accounted for 97.8 % of the total variability of the data (Table 3). The first score (PC 1) accounted for 93.3 % of the morphometric variance with the highest loading on TL. Hence, TL accounted for most, if not all (96.2%), of the variability in body size in *B. cristatella.* The PC2 score accounted for 6 % of the morphometric variance, with the heaviest loading on SVL (77.9%). This indicates that body shape variability in *B. cristatella* was due to variability of SVL. It was evident from the results of the PCA that TL and SVL were the main morphometric variables which contribute to body size and shape variation in this lizard.

The sex variable accounted for 0.3 % and 1.6 % of PC 1 and PC2 respectively, suggesting that body size and shape variation was not sexually dimorphic. ANCOVA of TL vs SVL [ln (TL) = a + ß(ln SVL)] showed no significant difference in slopes ($p > 0.05$) between sexes. Therefore, the covariation between TL and SVL did not differ significantly between the sexes (Fig. 2). The test of intercepts in the regression lines for males and females showed a significant difference between the intercepts, indicating that at any given size below 107.2 mm, female lizards seem to have longer tails than males, with the reverse being so above this intercept point. This trend was similarly reflected in Ota & Hikida's (1991) TL/SVL data for female *B. cristatella* specimens, although the authors did not make reference to this pattern in their paper. Further work with a larger sample size is necessary to confirm the observed pattern of size trend changes in the sexes.

Proposed diagnosis for *Bronchocela cristatella.* - **Head:** narrow, without swollen cheeks; forehead concave, head scales small; scale that arise as sharp spines absent; snout acute;

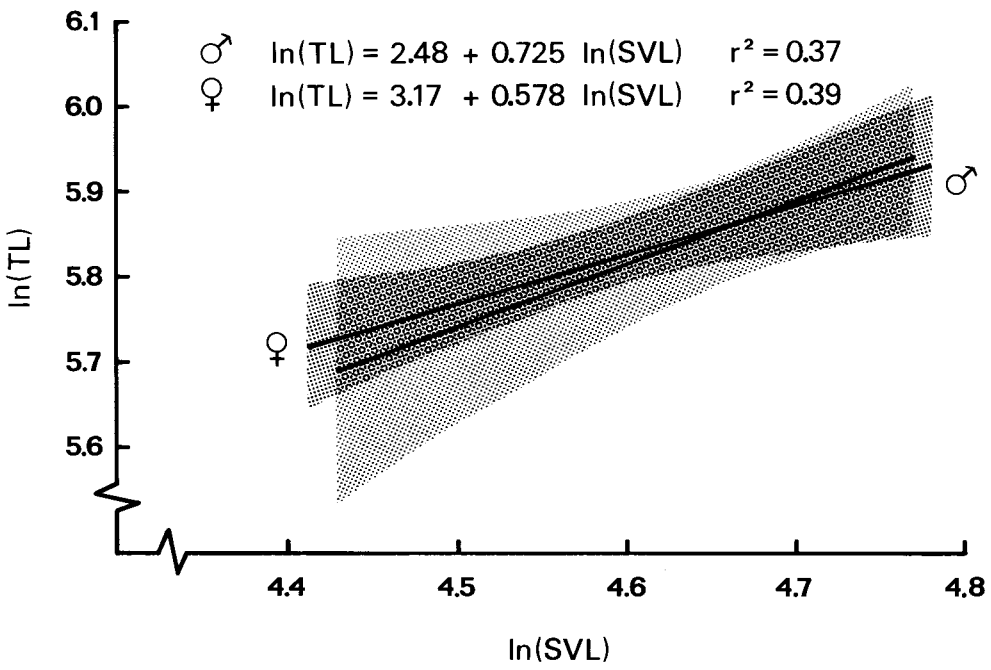

Fig. 2. Least squares regression lines for ln(tail length) (TL) against ln(snout-vent length) (SVL) of male and female *Bronchocela cristatella.* The 95% confidence bands as well as equations and r^2 values of the regressions are shown. Fitted lines are only drawn to cover the range of data used.

canthus rostralis moderately sharp; distinct lateral skin fold from angle of jaw to top of shoulder. **Gular sac:** small to medium in males, much smaller or absent in females, scales keeled, mucronate. **Nuchal crest:** medium to small in males, smaller or almost absent in females. **Dorsal crest:** usually a low serrated ridge. **Tympanum:** distinct, usually dusky in colour not all species. **Teeth:** clearly differentiated; molars compressed, acrodont; incisors and canines semi-thecodont. **Body:** compressed, slender to suit arboreal habits; dorsal scales about size of head scales; ventral scales larger; 1 - 2 rows dorsals at base of nuchal crest point upwards, turning gradually to point backwards and slightly downwards, same as the flankscales; scale count at mid-body, 43 - 97. **Femoral or preanal pores:** absent. **Limbs:** forelimb shorter than hindlimb; adpressed hindlimb reaches at least between eye and snout. **Tail:** round at base, not swollen in adult males; tail tapers gradually to a pointed scale terminally, percent ratio of tail length to snout-vent length mostly at least 300, more often 310 % - 360 %. **Eggs:** distinctly long, fusiform, slightly curved, tapering to narrow blunt ends; clutch size, mostly 2. **Sex dimorphism:** males larger with small to medium-sized gular sac; otherwise, sexes look alike, male natural body colour always green during breeding and non-breeding season. **Distribution:** Southern Burma, Peninsular Thailand, Peninsular Malaysia, Borneo Island, Indonesian Archipelago, the Philippines, and New Guinea.

Though *Bronchocela* may seem superficially similar to *Calotes, Pseudocalotes, and Dendragama,* Moody's (1980; figs., 31, 32, 33) phylogenetic hypothesis shows that *Bronchocela* is closer to *Dendragama and Gonocephalus,* coming from the same branch. *Pseudocalotes and Calotes* on the contrary, are far distant on the evolutionary scale. This study supports the view that *Bronchocela* is a valid genus and *B. cristatella* is the nominate species of the genus since *cristatella* is the first species of the genus to be named and described.

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