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A new species of *Calotes* from the Moluccas (Indonesia), with notes on the biogeography of the genus (Sauria: Agamidae)

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Abstract. A new species of the genus *Calotes* (s. str.) from Ambon Island, Moluccas is described. The new species is most similar to *Calotes mystaceus*, from which it can be distinguished by a black fold in front of the shoulder, by the lack of a white band above the upper lip stretching to the shoulder, and by different nuchal and dorsal crest spines. Distributional and biogeographical notes are given including a key to the species of the genus *Calotes*.

Key words. Reptilia, Squamata, Agamidae, *Calotes*, new species, key to species, Moluccas.

Introduction

The genus *Calotes* Cuvier, 1817 (except *Bronchocela* and *Pseudocalotes* which have formerly been regarded as junior synonyms of *Calotes*) currently contains 19 valid species (Wermuth 1967, Welch 1994, Barts & Wilms 1997, Diong & Lim 1998). Two species of the genus are regarded as taxonomically problematic: *Calotes kingdonwardi* and *Calotes kinabaluensis*. Moody (1980) considered *C. kingdonwardi* as incertae sedis, subsequent authors however did not accept this concept (Ota & Hikida 1991, Welch 1994, Barts & Wilms 1997). *Calotes kinabaluensis* is morphologically different from other *Calotes* species. Only two specimens of this species are known and deposited in museum collections (Ota & Hikida 1996, Inger & Lakim 1998). The holotype formerly deposited in the collection of ZMH is lost (Hallermann 1998). I did not have the opportunity to examine *C. kinabaluensis* and *kingdonwardi* and consequently will leave them in the genus *Calotes* until their status will be resolved. Recently, *Calotes nigrigularis* Ota & Hikida 1991 was placed into the new genus *Complicitor* by Manthey & Grossmann (1997).

The majority of the species of the genus *Calotes* are restricted to relatively small geographical regions in the Indian subcontinent, Sri Lanka and South East Asia, with the exception of *C. versicolor* (see key). This anthropochoric species inhabits a large area from East Iran and East Afghanistan in the northwest through Asia eastwards to Indonesia (Sumatra). None of the species of the genus are found east of the Wallace line (Bali Island, Borneo Island, Philippines) (Smith 1935, Biswas 1975, Zhao & Li 1984). A single undetermined male from the Moluccas is deposited in the herpetological collection of ZFMK. A comparison of this specimen with several specimens of the former genus *Calotes* (*Pseudocalotes*, *Bronchocela*, *Calotes*, *Dendragama*) (see Material, Hallermann 2000, Hallermann & Böhme 2000) confirmed that it belongs to an undescribed species of the genus *Calotes* s. str. The new species is described and its biogeographic and phylogenetic relationships to other species of the genus are discussed. A key to the species of *Calotes* is given.

Material

The material of this study originated from the following institutions (followed by the institutional acronyms in parentheses): The Natural History Museum, London [former British Museum (Natural History)] (BMNH), Muséum National d'Histoire Naturelle, Paris (MNHN), Staatliches Museum für Tierkunde Dresden (MTKD), Zoologisches Forschungsinstitut und Museum Alexander Koenig, Bonn (ZFMK), Zoologisches Museum der Universität Hamburg (ZMH), Zoological Museum University of Copenhagen (ZMUC), Zoologische Staatssammlung München (ZSM).

Specimens examined: *Bronchocela celebensis* Gray, 1845: Indonesia: N Celebes (= Sulawesi) (BMNH 72.4.6.126–127); *B. cristatella*: Moluccas: Bourau (= Pulau Buru) (MNHN 6886+A, syntypes of *Agama moluccana* Lesson, 1830); Halmahera, Patani (ZMH R04891–2), Ille de Amboine (= Pulau Ambon) (MNHN 1962.1111–1127, MNHN 6884 A+B, 6885 A), Ternate (MNHN 1878.184); *Calotes calotes* (Linnaeus, 1758): Sri Lanka: (ZMH R04885), Colombo (ZMH R04914), Vakvella (ZMH R0415–6), Peradeniya (ZMH R04917–8); *Calotes emma* Gray, 1845: Burma (= Myanmar): Mtti. Carin, 800–1000 m asl (ZMH R04615–21); Malaysia: Perak: environs of Kuala-Kangsar (ZMH R04644); *Calotes jerdoni* Günther, 1870: no locality (ZMUC 287); *Calotes liocephalus* Günther, 1872: Sri Lanka: Gammaduwa (ZSM 215/1981/1–5), Corset S Gap (ZSM 258/1979); *Calotes maria* Gray, 1845: India: Uttar Pradesh: Terai: Nishangara ($28^{\circ}15'N$, $81^{\circ}13'E$) (ZMH R00770), Assam: Khasi Hills: Umsaw ($25^{\circ}45'N$, $91^{\circ}52'E$) (ZMH R00771); *Calotes mystaceus* Duméril & Bibron, 1837: Burma (= Myanmar): Kachir Pyinnei: Bhamo (= Banmau) (ZMH R04883), Mtti. Carin, Chialla (1200–1300 m asl) (ZMH R04884), Thailand: Bangkok (ZMH R04886), 6 km SW Ban-Rai (180 m asl) (ZMH R04919–26), 3 km S Nong Rua (250 m asl) (ZMH R04933); Laos: Lowland 20 km N Mekhong River and 30 km E Muang-Pak-Lay (400 m asl) (ZMH R04932); *Calotes nigrilabris* Peters, 1860: Sri Lanka: (ZMH R04887–90, ZMUC R98513, ZMUC R98515); *Calotes nigriplicatus* sp. n.: Indonesia: Moluccas: Amboina (= Amboin Island) (ZFMK 26379); *Calotes rouxi* Duméril & Bibron, 1837: India: North Kanara: Gund ($15^{\circ}10'N$, $74^{\circ}40'E$) (ZMH R00760–1, ZMH R00764–7), Karwar ($14^{\circ}48'N$, $74^{\circ}8'E$) (ZMH R00768–9); *Calotes versicolor* (Daudin, 1802): S Vietnam: Vung tau, at the coast (MTKD 23933); India: (MNHN 2554, holotype of *Calotes cristatus* Jacquemont, 1844).

Methods

For the holotype of the new species and several specimens of *Calotes* spp. (see material and table 1) the following data were recorded: Snout-vent length (SVL), tail length (TL), head length (HL, between tip of snout and occiput), head width (HW, at angle of jaw), number of supralabials (SL) and infralabials (IL), number of scales around midbody (M), number of scales under fourth finger (FI) and fourth toe (TOE), hindlimb length (HLL, from groin to tip of fourth toe), foot length (FL) as well as the ratios TL/SVL, HLL/SVL, HW/HL.

Radiographs were taken at ZMH from specimens of *Calotes nigriplicatus* sp. n. and *C. mystaceus*.

Calotes nigriplicatus sp. n.

Diagnosis: A species of *Calotes* morphologically similar to *C. mystaceus*, with 57 scales around middle of body, ten subralabials and nine infralabials, body compressed, homogeneous scales arranged in regular rows, dorsal and dorsolateral scales larger than ventrals, strongly keeled, pointing backwards and upwards, ventral and gular scales strongly keeled; a small gular pouch is present. In front of the shoulder, there is a distinct oblique fold of skin covered with small granular black-coloured scales. Nuchal and dorsal crest continuously composed of erect triangular scales, the former lower than the latter. Head shape triangular, forehead feebly concave, its length one and a half times its width. No postorbital spines. Limbs slender, moderately long, fourth toe reaching the hind margin of orbit. Fourth toe longer than third, 18 scales under fourth finger, and 25 under fourth toe. *C. mystaceus* differs from the new

Table 1: Morphometrics (in mm) of *Calotes nigriplicatus* sp. n., *C. emma* and *C. mystaceus* (m = male, f = female, j = juvenile, sad = subadult, other abbreviations see under "Methods")

Taxon specimen no	SVL	TL (% of SVL)	sex	M	Fl	TOE	SL/IL	HL	HW	HW/HL	HLL	FL	HLL/SVL %	remarks
<i>nigriplicatus</i> ZFMK 26379	68.9	142.7 (207)	m sad	57	18	25	10 10 / 9 9	19.9	13.0	0.65	50.1	23.1	73.5	
<i>emma</i>														
ZMH R04619	107.7	263.0 (246)	f	66	22	26	11 11 / 11 10	29.9	19.1	0.64	83.4	36.5	77.4	
ZMH R04620	94.5	243.0 (257)	m	62	20	26	11 11 / 10 11	26.7	16.8	0.63	74.3	35.6	78.6	
ZMH R04621	52.0	128.3 (247)	j	60	18	26	10 10 / 9 9	16.5	11.1	0.67	42.1	17.7	80	
ZMH R04644	85.4	207.0 (242)	m	49	19	25	10 10 / 10 10	22.0	14.6	0.66	69.4	29.2	81.2	
ZMH R04616	79.5	210 (264)	f	60	20	25	11 10 / 10 9	23.0	14.6	0.63	65.7	30.0	82.6	
ZMH R04615	98.5	246.0 (?)	f	59	20	25	11 10 / 9 9	27.5	18.7	0.68	75.6	33.6	76.7	
<i>mystaceus</i>														
ZMH R04883	93.3	178.4 (191)	f	56	18	24	9 9 / 10 10	25.3	17.4	0.69	60.3	28.9	64.6	
ZMH R04886	121.0	230.0 (-)	m	56	18	24	10 10 / 9 9	41.0	25.9	0.63	81.5	37.0	67.3	tail incomplete
ZMH R04884	135.3	230 (-)	m	48	18	23	11 12 / 9 11	36.5	23.3	0.64	82.2	36.0	60.7	tail incomplete
ZMH R04919	96.4	193 (200)	m	50	18	24	11 10 / 10 10	25.0	15.8	0.63	64.0	29.6	66.3	
ZMH R04920	105.3	215 (204)	m?	51	18	24	10 10 / 9 9	29.7	18.9	0.63	73.0	31.1	69.3	
ZMH R04921	89.7	196.0 (218)	-	48	18	24	9 9 / 8 9	25.4	15.9	0.62	61.5	27.5	68.5	
ZMH R04922	102.0	220.0 (215)	m	51	18	23	10 9 / 10 11	29.2	18.4	0.63	73.4	32.2	72	
ZMH R04923	104.0	156.0 (-)	m	49	18	23	10 9 / 10 10	29.0	20.2	0.69	68.2	33.0	65.6	
ZMH R04924	122.3	240 (196)	m	50	19	24	11 10 / 11 11	34.3	23.1	0.67	74.5	23.6	61.0	
ZMH R04925	93.4	190.0 (203)	?	50	19	23	11 10 / 10 10	25.5	16.0	0.62	59.7	26.6	63.9	
ZMH R04926	103.8	180.0 (173)	m	50	19	24	10 11 / 10 10	29.1	19.6	0.67	62.4	28.0	60.1	
ZMH 4932	94.0	197.0 (209)	f	48	18	24	11 10 / 10 10	26.0	17.1	0.65	61.7	26.7	65.6	
ZMH 4933	127.0	180.0 (-)	m	52	19	24	10 10 / 11 10	34.3	24.0	0.69	81.0	37.7	63.7	tail incomplete

species in having light brown or uncoloured small scales in the fold in front of the shoulder, a broad white or yellow band stretching over the upper lip and extending to the shoulder, falciform spines of nuchal and dorsal crests and much longer nuchal crest spines than in the new species. *C. emma* with a similar black fold has long postorbital spines. Other species of the genus have body scales pointing backwards (*ceylonensis*) or backwards and downwards (*liocephalus*, *liocephalus*) or dorsal scales equal to ventrals with no spines on head (*andamanensis*), or one row of spines above tympanum (*calotes*, *nigrilabris*) or two rows (*C. jerdoni*). *C. nemoricola*, *C. medogenensis* and *C. grandisquamis* have the fourth toe scarcely longer than third and fewer scales around the body (27 to 43, Smith 1935, and 53–55 in *medogenensis*, Zhao & Li 1984). *C. versicolor*, *C. maria* and *C. bhutanensis* differ from the new species by lacking a fold in front of the shoulder (Biswas, 1975).

Holotype: ZFMK 26379 (figs. 1 & 2), subadult male, gift from Dr. Brock, 1885.

Type locality: Amboina (= Ambon Island), Moluccas, Indonesia.

Etymology: The new species is named after its black fold in front of shoulder, *plica* (lat.) = fold; *niger*, *nigro* (lat.) = black, blackish.

Description of holotype (measurements are reported in table 1): A subadult male (X-Ray shows relatively large gaps between phalanges of fingers and toes) with a SVL of 68.9 mm, TL 142.7 mm, HL 19.9 mm, HW 13.0 mm, and 57 scales around midbody. Canthus rostralis sharp; upper head scales unequal, some keeled, others smooth. The rostral is low, bordered behind by two labials and four postrostrals. On the upper side in the middle of the snout there are two enlarged keeled scales, one behind the other. The two semicircular scale series on the inner borders of the supracocular region are slightly enlarged and keeled. The two semicircular series are separated by a single scale.

Tympanum exposed, its diameter (3 mm) not quite half diameter of orbit (5.0 mm). The scales covering the temporal regions are small enclosing two enlarged scales between orbit and tympanum. Two separated spiny scales situated in a transverse row above the tympanum, between the tympanum and the occiput. Between each spine are three scales. The posterior and lower one of the spines is separated from the tympanum by two or tree scales on each side respectively.

Ten supralabials, nine infralabials on both sides. Gular scales strongly keeled, nearly as large as ventrals, pointing posteriorly and medially. The mental is narrow, about as wide as long and triangular in shape. On each side of the jaw the mental is followed by three enlarged scales, the first is in contact with the first labial laterally. Between the branches of the jaw are many rows of small keeled scales. There is a small gular pouch which may be stretched by hyoid extension. An oblique curved black skin fold in front of the shoulder is covered with small granular scales. The skin area in this fold is triangular in shape.

The nuchal crest is composed of nine erect compressed scales (spines), triangular in shape, the largest 1.8 mm in length, each spine partly overlapped by the following. The nuchal crest is bordered by a row of lower erect scales on each side. The dorsal crest follows the nuchal crest without a gap. The dorsal crest scales are about equal in size to the nuchal crest scales, but do not overlap. Posterior to midbody the crest decreases in height and is reduced to a very low crest over the sacrum. There is no crest on the tail. The strongly keeled dorsal and lateral body scales are arranged in regular transverse series, all directed backwards and upwards. The dorsal and lateral scales are larger than those on the venter. Ventral scales strongly keeled (some are mucronate) in about 21 rows.

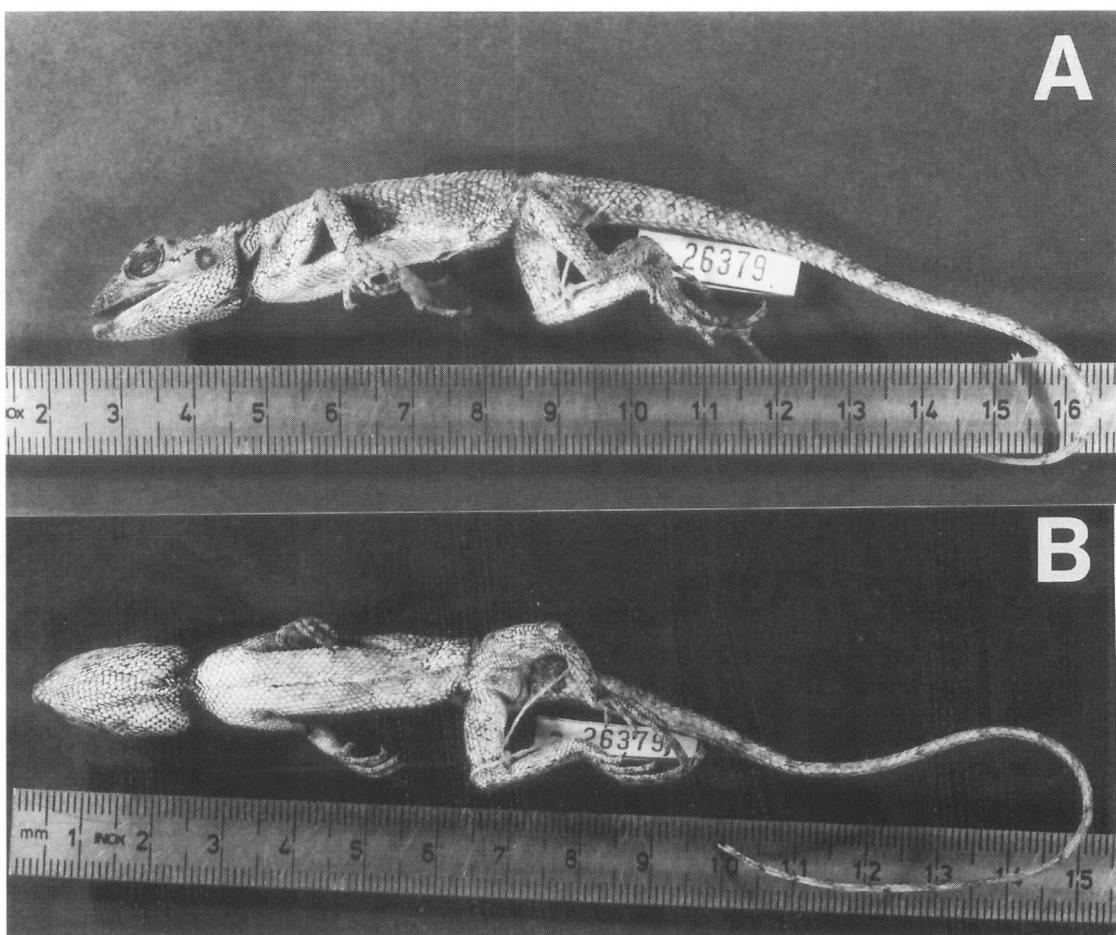


Fig. 1: Holotype of *Calotes nigriplicatus* ZFMK 26379; A lateral view, B ventral view.

Hind legs slender, 50.1 mm in length, reaching with the tip of the fourth toe the hind margin of orbit, forelegs 34.7 mm in length. Forelegs and hindlegs covered with strongly keeled scales, hindfoot 23.1 mm long. Third and fourth finger equal in length, fourth toe distinctly longer than third. Scales under toes are bicarinate, 25 under fourth toe, 19 under fourth finger. Tail compressed, not swollen at its base covered with keeled scales. Scales of the ventral side of tail are more strongly keeled than the others but all have nearly the same size.

Colouration in alcohol: The dorsal body colouration is a light grey with a large brown fleck on each side of body behind insertion of arm, larger on the left side. Tail barred with 21 narrow bands of light brown on a grey ground colour, broader and more indistinct on its base. Venter and lower side of legs whitish; gular pouch blackish. Upper side of legs (like body) with some brown marks. Front part of upper side of head brown, a small brown stripe from behind orbit to above tympanum, upper lip brown, some brown marks on one side of supraocular scales, on supraciliars, above shoulder and on sacrum.

Distribution: Ambon Island, Moluccas. The new species is known only from the single type specimen.



Fig. 2: Head of *Calotes nigriplicatus* ZFMK 26379; holotype in lateral view.

Discussion

Smith (1935) distinguished four groups within the genus *Calotes* by their body scutellation: the *Calotes cristatellus* group (now *Bronchocela*), *C. microlepis* group (= *Pseudocalotes*), *C. versicolor* and the *C. liolepis* group. *C. kingdonwardi*, as well as the dwarfed species *rouxi* and *elliotti* were not assigned to any of Smith's groups. Böhme (1988) found a great conformity of advanced hemipenes structures in the species *C. liolepis*, *C. ceylonensis*, *C. versicolor*, *C. calotes*, *C. emma*, and *C. rouxi*; but a disagreement with *Bronchocela cristatella* and *B. jubata*. Some of the different body scutellations e.g. scales directed upwards or downwards, a row of spines between tympanum and eye, postorbital spine present or absent are characters to differentiate species rather than genera. In contrast to the genera *Bronchocela* and *Pseudocalotes* it is difficult to diagnose the genus *Calotes* by synapomorphic characters (for diagnosis of *Bronchocela* see Diong & Lim 1998, for *Pseudocalotes* see Hallermann & Böhme 2000). It is most likely that the genus *Calotes* is of Indian origin. *C. versicolor* spread out to South East Asia and reached its southernmost point in Singapore and North Sumatra. This species was introduced to several islands (e.g. Réunion, Mauritius) and localities (mountains in the province of Dhofr, Oman) by man (Arnold 1986, Seufer et al. 1999). Only two species of *Calotes* are endemic to South East Asia: *mystaceus* and *emma*. At present I am unable to make statements about the taxonomic status of *Calotes kinabaluensis*.

Unfortunately no other record of the new species exists. The only other species without a postorbital spine, dorsal scales larger than ventrals and directed upwards, and a fold in front of the shoulder covered with small scales and fourth toe distinctly longer than third is *C. mystaceus* (see diagnosis). *C. mystaceus* inhabits Burma (Myanmar) and Thailand, Western Malaysia, and the Andaman and Nicobar Islands (Bourret 1943, Welch et al. 1990). Since no other specimen of *Calotes nigriplicatus* was found on islands of the Indo-Australian Archipelago, the biogeographic relationships of the two related species are still obscure. The large disjunctions in range of the two species cannot be explained by tectonic events (Molengraaf 1921, Weber 1921, Das & Bauer 1998). Most of the Indonesian herpetofauna, especially of the Moluccas is poorly known. For example, large species of new monitor lizards from the Moluccas were discovered by Böhme & Ziegler (1997), Harvey & Barker (1998) and Ziegler et al. (1999). Probably other records of *C. nigriplicatus* from the Moluccas may exist to corroborate the single record of ZFMK. It seems unlikely that the type locality is wrong because the localities of other specimens from the same collector / donator are surely correct (Böhme pers. comm.). However, also an introduction by man to the Moluccas may be possible.

Key to the species of the genus *Calotes*

The following key is modified by own examinations and literature data (Biswas 1975, Zhao & Li 1984) from the key of Smith (1935). Distribution data are included for most species. Note that the key is divided into four major sections (I-IV) and subsections (A, B), and is not dichotomous at all.

- I. Dorsal scales larger than ventrals, scales on side of body pointing backwards and upwards
 - A. No fold in front of shoulder
 - 1. Two separated spines above the tympanum
 - 1 a. No erect scale row by the side of the neck, variably coloured.....*versicolor*
 - 1 b. One erect scale row by the side of the neck, black variegated patches on the body (Bhutan).....*bhutanensis*
 - 2. Two parallel rows of compressed spines above tympanum, colour green in life (Khasi Hills, Assam).....*maria*
 - B. An oblique fold or triangle pit in front of shoulder covered with small scales
 - 1. Two parallel rows of compressed spines above tympanum, colour green in life (NE India, Burma, adjacent China).....*jerdoni*
 - 2. A postorbital spine present (Thailand, W Malaysia, Assam, Burma, Vietnam, S China)
 - 3 a. No postorbital spine, fourth toe much longer than third, relatively large specimens up to 140 mm SVL, pit in front of shoulders light brown or not coloured, white or yellow stripe above lip extending to shoulder (Burma, Thailand, W Malaysia, Andaman, Nicobar Islands).....*mystaceus*
 - 3 b. Pit in front of shoulders black, no white or yellow stripe above lip (Moluccas).....*nigriplicatus*
 - 4 a. Fourth toe scarcely longer than third, lateral scales smooth, 36 to 43 scales around midbody, 12 relatively long lanceolate nuchal spines (Nilgiri Hills, India).....*nemoricola*
 - 4 b. 53 to 55 scales around midbody, 5 short lanceolate nuchal spines (Xizang, Tibet)
 - 4 c. 27 to 35 scales around midbody (Anaimalai and Bramagherry Hills, India).....*medogenensis*
 - 5. Dorsal scales not larger than ventrals, one row of compressed spines above tympanum, tail very long (< 320 % of SVL) (Sri Lanka, S India, Nicobar Islands).....*calotes*

- II. Scales on side of body pointing backwards or backwards and downwards, an oblique fold or pit in front of shoulder present
- 1 a. Two separated spines above the tympanum, lateral scales pointing straight backwards, no dorsal crest..... *ceylonensis*
 - 1 b. Lateral scales almost smooth, pointing backwards and downwards, a dorsal crest present (Sri Lanka)..... *liocephalus*
 - 2 a. No spines on head, ventral scales as large as laterals, 43 to 50 scales around midbody (Sri Lanka)..... *liocephalus*
 - 2 b. Ventral scales smaller than laterals (Burma-Tibetan border)..... *kingdonwardi*
 - 2 c. Ventral scales as large as dorsals, 67 scales around midbody (Andaman Islands)..... *andamanensis*
 3. A row of spines above tympanum, ventral scales larger than dorsals (Sri Lanka)..... *nigrilabris*
- III. A long transversal fold in front of shoulder extending across the throat, two slender spines on back of head
- 1 a. No spine behind supercillium, no white spot below the eye (Bombay to Kerala, India)..... *rouxi*
 - 1 b. A spine behind supercillium, a white spot below the eye (S India)..... *elliotti*
- IV. Dorsal scales inhomogeneous, remarkable enlarged scales in infratympanic region, large spines on gular pouch (Sabah)..... *kinabaluensis*

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Zusammenfassung

Eine neue Art der Gattung *Calotes* s. str. von den Molukken wird beschrieben. Die neue Ar ist *Calotes mystaceus* am ähnlichsten, unterscheidet sich von ihr aber durch den Besitz einer schwarz gefärbten Antehumeralfalte, durch das Fehlen eines weißen Bandes, das sich über die oberen Lippen bis zu den Schultern erstreckt und durch die unterschiedliche Form der Nacken und Rücken-Kammschuppen. Ein Bestimmungsschlüssel zu allen Arten der Gattung, nebst Angaben zur Verbreitung wird vorgestellt. Die biogeographische Sonderstellung der neuen Ar wird diskutiert.

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