

ZOOLOGISCHE VERHANDELINGEN

UITGEGEVEN DOOR HET RIJKSMUSEUM VAN
NATUURLIJKE HISTORIE TE LEIDEN

(MINISTERIE VAN CULTUUR, RECREATIE EN MAATSCHAPPELIJK WERK)

No. 199

**TAXONOMY OF THE GENUS DRACO L.
(AGAMIDAE, LACERTILIA, REPTILIA)**

by

C. J. M. MUSTERS

Rijksmuseum van Natuurlijke Historie, Leiden, The Netherlands

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E. J. BRILL

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1. INTRODUCTION AND ACKNOWLEDGEMENTS

Studying the lizards of the Greater Sunda Islands, it turned out that the Leiden Museum possessed a large collection of unidentified lizards of the genus *Draco*. It was decided to use this collection to investigate the variation within and the differences between the species. To complete this study, material from other museums was used too.

I would like to thank here Dr. M. S. Hoogmoed, curator of the Rijksmuseum van Natuurlijke Historie and Mr. G. D. E. Povel of the Department of Systematic Zoology of the State University of Leiden for their useful help, Dr. D. Hillenius of the Zoologisch Museum Amsterdam, Dr. J. P. Desmet of the Musée Royal d'Histoire Naturelle de Belgique, Dr. G. Peters of the Zoologisches Museum an der Humboldt Universität zu Berlin, Dr. W. Böhme of the Zoologisches Forschungsinstitut und Museum A. König, Bonn, Dr. K. Klemmer of the Natur-Museum und Forschungs-Institut "Senckenberg", Prof. Dr. E. R. Brygoo of the Muséum National d'Histoire Naturelle, Paris and Dr. F. Tiedemann of the Naturhistorisches Museum, Wien for the loan of material in their care and Miss A. G. C. Grandison of the Reptile Section of the British Museum (Natural History) for allowing me to examine the material of the B. M. and Miss J. Consten and I. Teegelaar for the typewriting.

A grant of the Jan Joost ter Pelkwijk Fonds enabled me to visit the British Museum (Natural History), whereas grants of the Insulinde Fonds and the Stichting ter Bevordering van de Herpetologie provided the financial means for publishing the colour plates.

Finally I would like to thank Dr. R. F. Inger for sending me his manuscript on *Draco* ('Morphological and Ecological Variation in Flying Lizards (Genus *Draco*'). As he stated: "our taxonomic opinions diverge significantly". Let this be a stimulus for future workers.

2. HISTORY

Linnaeus (1758) described in the 10th ed. of the *Systema Natura* only four genera of the "family" Reptilia. One of them was *Draco* with only one species: *D. volans*. This indicates that from the beginning of the use of binominal nomenclature, *Draco* was considered a clearly distinguishable taxon. This is well understandable, knowing that *Draco* is the only group of reptiles in the possession of winglike skin-extensions along the flanks, which enables them to glide. Linnaeus (1766) described two species (viz. *D. volans* and *D. praepos*) and two years later Laurenti (1768) described again two species (viz. *D. major* and *D. minor*). Hardwicke & Gray (1827) placed the genus in the family Agamidae. By that time about ten species had been described.

Wiegmann (1834a) was the first author to split the taxon into two genera: viz. *Draco* and *Dracunculus*, based on the tympanum being visible or not. After him some authors kept on regarding it as one genus, others split it. The most radical splitter undoubtedly was Fitzinger (1843), who considered the taxon to form the family Dracones with two genera: *Draco*, with four subgenera (*Rhacodracon*, *Draco*, *Pterosaurus* and *Pleuropterus*) and *Dracontoides*. He distinguished the genera by the tympanum being covered with scales or not, and the subgenera by the direction of the nostril and the presence of a nuchal crest. One year later Schlegel (1844) pointed out that most of the characters, used till then, are very variable even within one species and he warned against descriptions based on few characters only. After this period, there is a stabilization in the nomenclature: *Draco* is regarded a genus of the family Agamidae. In the following period many new species were described. Günther (1864) discussed 14 species, Boulenger (1885) 21 and De Rooy (1915) 24.

Wandolleck (1900) tried to make a revision of the genus, without much success. The paper by Hennig (1936a) was much better. At that time 64 different names had been used for taxa within *Draco*. Hennig (1936a) was able to reduce these to 16 species, most of them with several subspecies. Since 1936 no revisionary taxonomic work was done on *Draco*, except for that of Taylor (1963) in which two subspecies were added. Therefore Hennig's (1936a) paper was used as a startingpoint for the present study.

3. MATERIAL AND METHODS

About 900 preserved specimens were examined from the collections of the following museums: Rijksmuseum van Natuurlijke Historie (indicated with RMNH); Zoologisch Museum Amsterdam (ZMA); Musée Royal d'Histoire Naturelle de Belgique (IG... reg. ...); Zoologisches Museum an der Humboldt

Universität zu Berlin (ZMB); Zoologisches Forschungsinstitut und Museum A. König, Bonn (ZFMK); Natur-Museum und Forschungs-Institut "Senckenberg" (SMF); British Museum (Natural History) (BM); Muséum National d'Histoire Naturelle, Paris (MHNP) and Naturhistorisches Museum Wien (NMW).

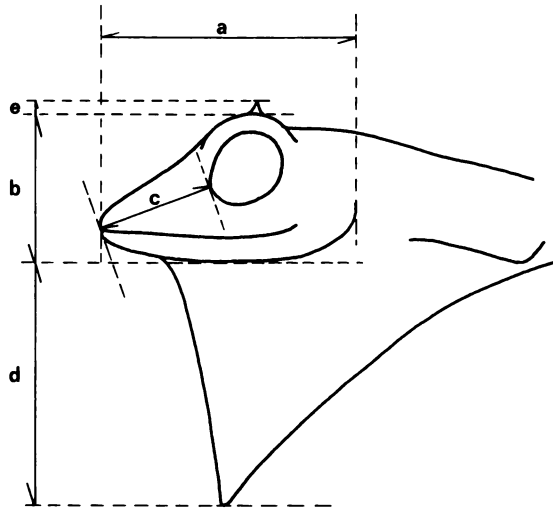


Fig. 1. Head of *Draco*.

Of 770 specimens the following data were noted: subspecies name according to Hennig (1936a); museum number; locality; collector; date of collecting; sex; notes on the colour and markings and the state of the following characters:

- snout-vent length in mm, measured from the tip of the snout to the anterior margin of the vent,
- tail length in mm, measured from the vent to the tip of the tail,
- head length in mm measured from the posterior edge of the corner of the jaw to the tip of the snout (a in fig. 1),
- head depth in mm, measured at the parietal region (where the head is highest, b in fig. 1),
- head width in mm, measured at the level of the tympana,
- snout length in mm, measured from the anterior edge of the orbital cavity to the tip of the snout (c in fig. 1),
- length of the gular pouch in mm, measured in extended state (d in fig. 1), from the ventral edge of the lower jaw to the tip,
- length of both thornlike scales on the supraciliary edge just above and posterior of the centre of the eye (e in fig. 1, not meant is the tubercle at the end of the supraciliary edge). This was noted in micrometer units at a $7 \times$ magnification of the binocular. They had to be multiplied by 0.14 to arrive at mm,

- width of the same thornlike scales, measured in the same way as their length,
- length of both hindlimbs in mm, measured from the pelvis to the tip of the fourth toe,
- distance between the limbs in mm, measured on both sides from the armpit to the groin,
- number of median teeth in the upper jaw, that is, the number of teeth between the two canines minus two (cf. Hennig, 1936a: 161, fig. 6),
- differentiation of the skin, covering the tympanum. Noted was an estimated percentage of covering by small scales, for example 1 = fully covered with small scales (fig. 2c), 1/2 = half covered with small scales (fig. 2b), 0 = completely covered with smooth skin (fig. 2a),
- number of supralabials,

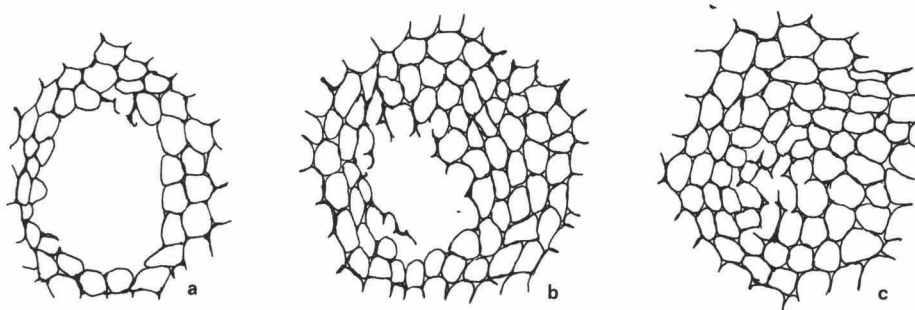


Fig. 2. Skin covering the left tympanum of ♀♀ of *Draco lineatus bourouniensis* (a = RMNH 19746, b = RMNH 19745, c = RMNH 19743).

- number of dorsals, counted along the vertebral line from the posterior edge of the skull, along the left-handed side of the nuchal crest to the line connecting the posterior edges of the ilia. This number sometimes is difficult to define. In species with small dorsal scales it presents no problems, but in species like *D. volans* with very unequal scales, it is difficult to count along a straight line. Yet, when counting consequently in the same manner, it is a useful character. If a specimen was counted twice, the second number of dorsals was always less than 5 % different from the first,
- number of ventrals, counted along the middle of the ventral side of the body, from the posterior edge of the gular pouch to the vent,
- number of subdigital lamellae of fourth finger,
- number of subdigital lamellae of fourth toe,
- number of nuchal crest scales, the last scale of the crest is the last scale that could be distinguished from the dorsals because it was compressed, strongly keeled or distinctly enlarged,
- number of ribs supporting the patagium (= winglike extension) on each side,
- direction of the nostril: upward or outward,
- presence of a caudal crest,
- number of eggs in the oviducts of females.

The following characters were reviewed at the beginning of the investigations, but rejected because they were too difficult to define or had no discriminating value: distance between nostrils, distance nostril-orbit, scales around the tail at a hindlimb length from the base, number of enlarged scales on the border of patagium and body, transverse number of ventrals; number of scales forming the Λ -shaped figure on the snout, forming the canthus rostralis, between the nasals, of the inner edge of the supraocular region, between those two edges, number of tubercles in the ridge between the nuchal crest and the lateral pouches.

The measurements were made with a vernier caliper (wu-I-125, model 183).

The remaining specimens were identified to the species level, but not used further, either because they belonged to *D. volans* of Java, of which there were enough other specimens, or because they had no locality data.

The characters were analysed with the computer-program BIOPAT, a programsystem for biological pattern analysis, written by P. Hogeweg and B. Hesper (Theoretical Biology Group of Utrecht, 1972) (see chap. 5 for more details).

4. RESULTS A. THE SPECIES

4.1. *Draco* Linnaeus

Draco Linnaeus, 1758: 199 (species typica: *Draco volans* L.); Boulenger, 1885: 253; Hennig, 1936a: 173; Wermuth, 1967: 45.

Draconus Rafinesque, 1815: 75 (nomen substitutum pro *Draco* L.).

Dracunculus Wiegmann, 1834a: 14 (species typica: *Draco lineatus* Daudin); Gray, 1845: 235.

Rhacodracon Fitzinger, 1843: 50 (species typica: *Draco fimbriatus* Kuhl).

Pterosaurus Fitzinger, 1843: 51 (species typica: *Draco dussumieri* Duméril & Bibron).

Pleuropterus Fitzinger, 1843: 51 (species typica: *Draco haematopogon* Gray).

Dracontoides Fitzinger, 1843: 51 (species typica: *Draco lineatus* Daudin).

Dracocella Gray, 1845: 234 (species typica: *Draco dussumieri* Duméril & Bibron).

Diagnosis. — The members of the genus can easily be recognized, being the only Agamidae having a large winglike membranous skinfold on each side of the body, between the fore- and hindlimbs, supported by 4-7 elongated ribs. These 'wings', called patagia (Smith, 1935: 135), can be folded parallel to the body or expanded like a fan by ribmovements.

Description. — Body depressed; tail at the base depressed, distally more or less compressed; limbs not very long, hindlimbs about as long as, or shorter than the distance between the fore- and hindlimbs; snout with or without a series of scales forming a Λ -shaped figure; number of supralabials 5-16; a pair of caninelike teeth in both upper and lower jaw; nostril directed upward or outward; with or without a thornlike, compressed scale on the supraciliary edge; a tubercle at the end of the supraciliary edge; tympanum covered with skin which can be unmodified or more or less completely differentiated into granules or small scales (fig. 2); with or without a nuchal crest; with or without a nuchal fold; gular pouch present; on each side of the neck a more or less distinct lateral

pouch; dorsals larger or smaller than ventrals, sometimes keeled; usually with a row of enlarged scales on the border between the body and the patagium; ventral scales subequal, keeled; subdigital lamellae usually keeled, under fourth finger 17-27, under fourth toe 17-34; no femoral or preanal pores; some more or less distinct, fringelike, enlarged scales on the posterior edge of the thigh; males of some species with a caudal crest; tail about 1.5-2.0 times the snout-vent length.

In all species there is a distinct sexual dimorphism. Apart from differences in colour, males have longer gular pouches, usually larger nuchal crests and in some species caudal crests. The females usually are larger than the males (in 70% of the taxa examined). In some subspecies, the studied material suggests that there are differences in the head dimensions too, but since this was never the case in subspecies of which many specimens were examined, it may be a biased observation.

Ecology and behaviour. — No comparative study on the ecology or ethology of the species of *Draco* is available. Apart from some incidental notes, studies are available by Pfeffer (1962) on *D. volans volans*, *D. v. sumatranus*, *D. v. boschmai* (under the name *D. reticulatus*) and *D. lineatus bourouniensis*, on *D. v. reticulatus* (Hairston, 1957; Alcalá, 1967; Reyes, 1968), *D. dussumieri* (John, 1962; 1967a; 1967b; 1970), and on *D. melanopogon* and *D. quinquefasciatus* by Inger & Greenberg (1966). Based on these papers the following abstract, which is probably valid for all the species, has been made.

Strictly diurnal and arboreal lizards, which usually do not leave the trees (except for egg-laying) and live from about 2 m above the ground to the top of the trees. They are accomplished gliders, being able to glide in an angle of about 20% (from horizontal) over a distance of 30 m.

The food of these lizards consists mainly of ants. Other Arthropoda that were found in the stomachs are Hymenoptera, Coleoptera, Isoptera, Dermaptera, Orthoptera, Lepidoptera larvae, Blattidae and Arachnida. Reyes (1968: 354) stated that "availability seems to be the reason for the high frequency of ants as a food item of the lizard".

The animals are only active during the day, usually with a period of inactivity during the hottest hours. On colder days there is no such noon interruption. They do not seem to depend upon direct sunlight as a source of body heat. The periods of inactivity are passed in the top of the trees, between the leaves.

Whether there is a distinct breeding season or not, seems to depend upon local climatological circumstances. On Borneo and in the Philippines breeding takes place all the year round, whereas in Southern India breeding occurs in February, March and April. The clutch-size varies from one to six eggs. The eggs are laid in the ground. Alcalá (1967) found more males than females, but in the complete collections examined by me none of the species had a sex-ratio significantly different from one. The males occupy three-dimensional territories, containing one to several trees.

When another *Draco* of the same species is seen by a male within its territory, it extends its gular pouch, so that it forms a right angle with the jaw. This action

can be repeated. The next action can be a partial unfolding of the patagia. If the intruder is a male, it will react with the extension of its gular pouch. Then head-bobbing may occur (sometimes the whole body is raised and lowered). This is believed to be the peak of the male-male display. Usually one of the males will now glide away. If not, one may chase the other, and even fighting may occur. If the intruder is a female it will remain passive (when it does not escape). The display now performed by the male can be called courtship. It starts with the maximal extension of the gular pouch, which then looks like a 'beak'. The patagia may be unfolded. Sometimes a pushing up and down of the head occurs. If the female remains passive the male will now circle it. When the female escapes, the male will follow her and try to circle her on the new spot. This may go on for hours. Copulation in *Draco* was only described once for *D. dussumieri*. It followed immediately after the circling act (John, 1967).

An investigation of the differences in niches between sympatric species is badly needed.

Distribution of the genus. — Southern India, South-East Asia, the Indo-Australian Archipelago, including the Key Islands, the Moluccas and the Philippines (fig. 3).

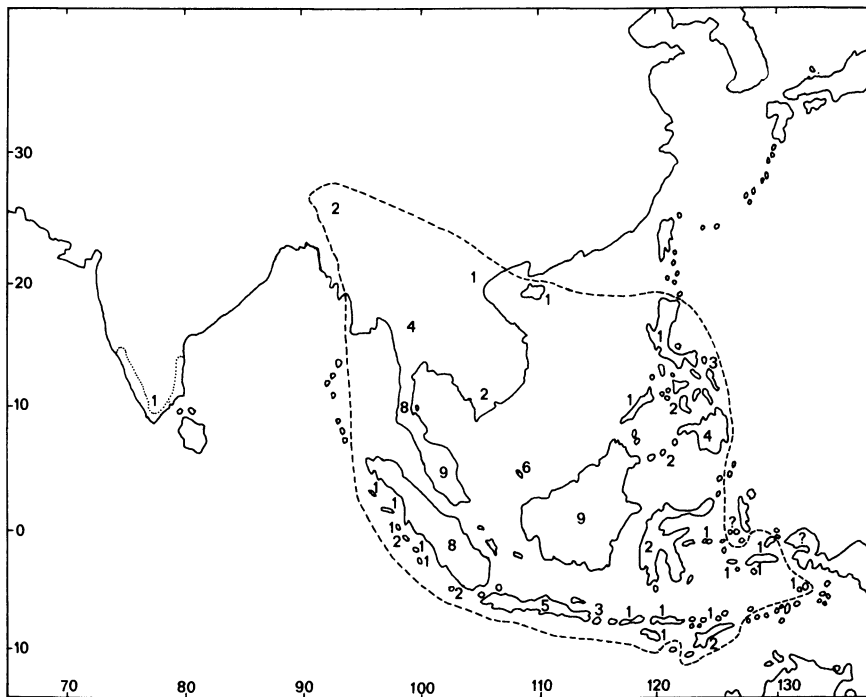


Fig. 3. Distribution of the genus *Draco*. The numerals indicate the number of species found in a certain area.

4.2. KEY TO THE SPECIES EXAMINED

Since no material was available of *D. affinis*, this species does not occur in the key. It is probably closely related to *D. volans* or *D. cornutus*. The only thing known (except for the colour in life) is, that it is “similar to *D. cornutus*, but without the large spinelike scale above the eye (and that the) gular appendage (is) very small” (Bartlett, 1894). It occurs on Borneo (p. 10). Since most characters are highly variable, one must be prepared for exceptional specimens. For example the number of ribs supporting the patagium in 7.4% of the specimens differs from that in other specimens of the same taxon.

1. Nostril directed outward or obliquely upward; a longitudinally enlarged scale, sometimes compressed to a triangular thorn, may be present on the supraciliary edge, just above and posterior of the centre of the eye 2
 Nostril directed upward; no longitudinally enlarged scale on the supraciliary edge 8
2. Number of ribs supporting the patagium six or seven 3
 Number of ribs supporting the patagium five 6
3. Number of dorsals more than 140; thornlike scale on supraciliary edge longer than 0.05 times the head length; hindlimbs always shorter than 0.77 times the distance between the limbs *D. cornutus* (p. 19)
 Number of dorsals usually less than 140; thornlike scale, if present, usually smaller than 0.05 times the head length; hindlimbs may be longer than 0.77 times the distance between the limbs 4
4. Number of median teeth in the upper jaw usually two; tympanum covered with small scales; lateral pouches with slightly enlarged scales; thornlike scale on supraciliary edge smaller than 0.02 times the head length; Philippines *D. spilopterus* (p. 72)
 Number of median teeth in the upper jaw usually three; tympanum completely or partly covered with smooth skin; lateral pouches with or without enlarged scales; specimens from the Philippines with a thornlike scale, which is larger than 0.02 times the head length 5
5. Hindlimbs approximately as long as the distance between the limbs (0.95-1.11 times the distance between the limbs); lateral pouches with slightly enlarged scales; only known from Enggano *D. lineatus modigliani* (p. 45)
 Hindlimbs usually shorter than the distance between the limbs (0.63-1.01 times this distance); lateral pouches with distinctly enlarged scales; not restricted to Enggano *D. volans* (p. 000)
6. Number of dorsals usually more than 160; number of supralabials 8-13; males with a caudal crest *D. fimbriatus* (p. 23)
 Number of dorsals usually less than 160; number of supralabials 5-11; males without a caudal crest 7
7. Lateral pouches with distinctly enlarged scales; number of supralabials 8-11; tail less than 1.65 times the snout-vent length *D. maculatus* (p. 52)
 Lateral pouches without distinctly enlarged scales; number of supralabials 5-10; tail more than 1.65 times the snout-vent length *D. lineatus* (p. 34)
8. Number of ribs supporting the patagium six or seven 9
 Number of ribs supporting the patagium five 11
9. Number of dorsals less than 170; males with a caudal crest; Southern India *D. dussumiers* (p. 21)
 Number of dorsals more than 170; males without a caudal crest; not from Southern India .. 10
10. Number of dorsals more than 220; number of subdigital lamellae of the fourth toe 28-34; hindlimbs about as long as the distance between the limbs *D. maximus* (p. 57)
 Number of dorsals less than 220; number of subdigital lamellae of the fourth toe 17-23; hindlimbs smaller than the distance between the limbs *D. quinquefasciatus* (p. 70)

11. Gular pouch in males and females without enlarged scales; males without a nuchal fold; patagium above usually dark, with light spots 12
 Gular pouch at least in males with enlarged scales; males with a nuchal fold; patagium above usually brown or grey with or without dark markings 14
12. Gular pouch in males without any black markings and in females without grey markings; only known from the Philippines *D. mindanensis* (p. 63)
 Gular pouch in males with black markings and in females with grey markings; not from the Philippines 13
13. Gular pouch in males coal black, in females grey; number of dorsals 164-218; patagium dark brown with distinct, light spots *D. melanopogon* (p. 60)
 A coal black spot at the base of the gular pouch in males; in females a grey brown spot at the base of the gular pouch; number of dorsals 148-184; patagium usually brown with large, light spots, sometimes forming bands *D. haematopogon* (p. 30)
14. Males without a caudal crest; females without enlarged scales on the gular pouch; snout-vent length less than 78 mm *D. taeniopterus* (p. 76)
 Males with a more or less distinct caudal crest; females with enlarged scales on the tip of the gular pouch; snout-vent length in adults more than 75 mm 15
15. Patagium in males brown, sometimes with indistinct bands; in females with distinct bands; specimens from West Malaysia with a black dividing line on the border between the ventral parts of the lateral pouches and the gular pouch; gular pouch not widened distally in males; continental SE. Asia *D. blanfordii* (p. 11)
 Patagium in both sexes brown with dark spots or irregular bandlike markings; no black dividing line between the ventral parts of the lateral pouch and the gular pouch; gular pouch distally widened to a rounded flap in males from West Malaysia; not restricted to continental SE. Asia *D. obscurus* (p. 65)

4.3. DESCRIPTION OF THE SPECIES

Of the (sub)species not examined no description is given, only a diagnosis based on the literature is presented. The names used in the distribution are in agreement with the Times Atlas of the World (Anonymous, 1978, reprint of the 5th ed. of 1967). To find the names of the localities, one has to compare the pertinent distribution map with fig. 4, in which the names of the localities where flying dragons were collected are given. Locality names, that were found in the literature, but could not be located on any of the consulted maps or elsewhere, are not included.

***Draco affinis* Bartlett**

Draco affinis Bartlett, 1894: 80 (terra typica: Borneo); De Rooy, 1915: 88; Hennig, 1936a: 219; Wermuth, 1967: 46.

No material examined.

Diagnosis. — Bartlett (1894) described this species as follows: “Similar to *D. cornutus*, but without the large spinelike scale above the eye. Gular appendage very small; in the female it is almost absent.

Male. — Black dull brown, tinged with green, three distinct greyish white transverse bands on the back; wing membranes above, bright brick red spotted with black, with broad black outer margins, a pale bluish grey line down the cen-

tre of the belly; under side of wing membrane dull brick red tinged with blue, and spotted with blackish brown, margined with blotches of black and greyish white.

Adult female. — Back grey mottled with dark brown and tinged with green; wing-membranes bronze green spotted with black, with a broad black band on the outer margin; gular appendage small, yellowish green; chest blue; a line down the centre of belly and under part of hind limbs pale blue, sides of body greyish white mottled with black, underside of wing-membrane yellowish green, outer margin blue”.

D. affinis may turn out to be a synonym of *D. volans sumatranus*, but the description does not provide enough data to decide upon that.

Draco blanfordii Boulenger

Diagnosis. — Large species (maximum snout-vent length 134 mm); nostril directed upward; indistinct series of enlarged scales forming a **Λ**-shaped figure on the snout; usually two median teeth in the upper jaw; supralabials 7-10, keeled; no thornlike scale on the supraciliary edge; tympanum covered with smooth skin or with small scales; gular pouch and lateral pouches in males and females with enlarged scales; males with a more or less distinct nuchal fold; dorsals 166-224; usually five ribs in the patagium; hindlimbs usually shorter than the distance between the limbs; males with a more or less distinct caudal crest; patagium in males grey-brown with light, longitudinal lines, with or without transverse bands; in females with five distinct, transverse bands.

KEY TO THE SUBSPECIES

1. With a black transverse band running from one lateral pouch, across the posterior part of the gular pouch to the other lateral pouch; Cambodia and Vietnam *D. blanfordii indochinensis* (p. 16)
Without such band; not from Cambodia or Vietnam 2
2. Patagium in males with indistinct, transverse bands; proximal parts of the gular pouch dark with light spots; Assam and Northern Burma *D. blanfordii norvillii* (p. 17)
Patagium in males without transverse bands; black, longitudinal lines on the border between the gular pouch and the lateral pouches; not from Assam or Northern Burma *D. blanfordii blanfordii* (p. 11)

Draco blanfordii blanfordii Boulenger

Draco major Blanford, 1878: 125 (non *Draco major* Laurenti, 1768; terra typica: forest east of Tavoy); Blanford, 1879: 128.

Draco blanfordii Boulenger, 1885: 267 (nomen novum pro *Draco major* Blanford, 1878); Boulenger, 1890a: 112; Boulenger, 1903: 153; Boulenger, 1912: 61; Lönnberg, 1916: 4; Hennig, 1936a: 214, fig. 11f, g, map 13; Taylor, 1963: 855, fig. 44; Wermuth, 1967: 46.

Draco formosus Boulenger, 1900: 190 (partim).

Draco cyanolaemus Boulenger, 1908: 64, pl. 4 fig. 2, 2a (terra typica: Telom (4000 ft.), Perak/Pahang Boundary); Boulenger, 1912: 60, fig. 18; Robinson & Kloss, 1914: 154; Smith, 1916a: 53; Smith, 1930: 22; Taylor & Elbel, 1958: 1042.

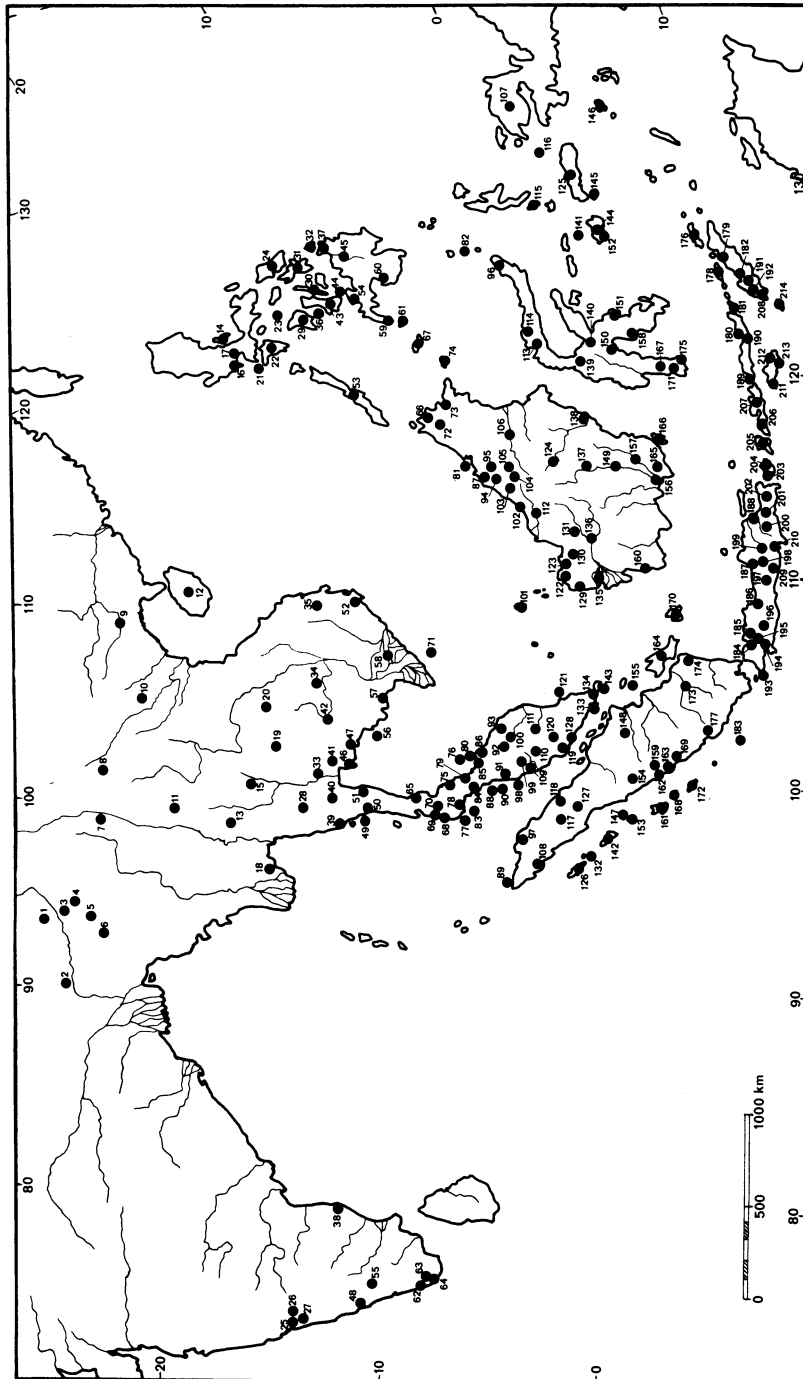


Fig. 4. Localities of *Draco*, arranged from North to South and from West to East. (In = India; Bu = Burma; Th = Thailand; Ca = Cambodia; Vi = Vietnam; Ch = China; WM = West Malaysia; Su = Sumatra; BS = Sarawak; BK = Kalimantan; Sw = Sulawesi; Ja = Java; Ph = Philippines; all the names without an area-abbreviation are islands of Indonesia) 1: Xizang, Ch., 2: Gopalpara, In., 3: Durm Duma, In., 4: Margherita, Patkai Hills, In., 5: Naga Hills, In., 6: Kambiron, In., 7: Sumka Uma, Triangle, Bu., 8: Yunnan, Ch., 9: Guangxi Zhuangzu, Ch., 10: Tonkin, Vi., 11: Chiang Rai, Th., 12: Hainan, Ch., 13: Chiang Mai, Th., 14: Pollilo, Ph., 15: Muang Phrae; Den Chai, Th., 16: Bataan, Ph., 17: Manila; Montalban, Ph., 18: Pegu, Bu., 19: Phu Lom Lo, Th., 20: Muang Song Badan, Th., 21: Lubang, Ph., 22: Mindoro, Ph., 23: Sibuyan, Ph., 24: Samar; Loquilocum, Ph., 25: Karwar, In., 26: Yellapur, In., 27: Gersoppa Falls, In., 28: Khao Wang Hip, Th., 29: Panay, Ph., 30: Cebu, Ph., 31: Leyte, Ph., 32: Dinagat, Ph., 33: Phra Phut-thabati, Th., 34: Phanom Dougrak, Th., 35: Kontum, Vi., 36: Guimaras, Ph., 37: Placer, Ph., 38: Madras, In., 39: Tavoy, Tenasserim, Bu., 40: Kanchanaburi, Th., 41: Muak Lek; Pak Chong, Th., 42: Nakhon Ratchasima, Th., 43: Dumaguete, S. Negros, Ph., 44: Siqunior, Ph., 45: Bunawan, Agusan Valley, Ph., 46: Tung Prong, Th., 47: Chantaburi; Laem Ngop; Kong Yai, Th., 48: Siddapur, In., 49: Kadankyun; Mergui, Bu., 50: Tenasserim, Bu., 51: Nong Kok, Th., 52: Nha Trang, Vi., 53: Palawan, Ph., 54: Dapitan; Datu Anib's place, Malindang Mnt., Ph., 55: Nilgiris, In., 56: Ko Kut, Th., 57: Bokor, Ca., 58: Cochín, Vi., 59: Zamboanga, Ph., 60: Cotabato, Ph., 61: Basilan, Ph., 62: Cochín; Piravam, Ernakulam; Travancore, In., 63: Rathanapuram, Quilon; Kulakulan, Kottayam, In., 64: Trivandrum, In., 65: Pathiu, Th., 66: Paitan, BS., 67: Jolo, Ph., 68: Ko Prayam, Th., 69: Pakchan estr.; Kawthang Victoria Point, Bu., 70: Khao Long, Th., 71: Con Son, Vi., 72: Kina Balu, BS., 73: Sandakan bay; Betotan, BS., 74: Tawitawi; Bongao; Simonor, Ph., 75: Nakhon Si Thammarat, Th., 76: Ko Phangan, Th., 77: Phuket, Th., 78: Kabri; Ko Bot Yai, Th., 79: Phattalung, Th., 80: Ko Samui, Th., 81: Labuan, BS., 82: Kepulauan Sangihe, 83: Ko Phi Phi Don, Th., 84: Trang, Th., 85: Pattani; Yala, Th., 86: Narathiwat; Kwalo Yakong, Th., 87: Brunei, BS., 88: Butang Isl.; Terutau Isl., Th., 89: Pulau Weh, Su., 90: Langhawi Isl., WM., 91: Kedah; S. Menora; Prov. Wellesley, WM., 92: S. Aring; Kelantan, WM., 93: Trengganu, WM., 94: Baram R., BS., 95: Gunung Mulu, BS., 96: Manado; Tomohon; Kana, Sw., 97: Lhokseumawe, Su., 98: Pinang, WM., 99: Padang; Sungai Siput; Kuala Kangsar; Larut Hills; Wray Hills; Perak, WM., 100: Gunung Tahan, WM., 101: Bunguran, 102: Balingian, BS., 103: Gunung Dulit, BS., 104: Lio Matoh, BS., 105: Penambo range, BS., 106: Kayan R., BK., 107: New Guinea, 108: Langka, Su., 109: Dingdings, WM., 110: Sungkai, S. Perak, WM., 111: Pahang; Kuala Tahan; Kuala Tembeling, WM., 112: Kapit; Nanga Tekalit; Akar R., BS., 113: Tolitoli, Sw., 114: Buol, Sw., 115: Bacan, 116: Misool, 117: Batak Hills, Su., 118: Medan; Serdang; Upper Langkat; Sibo Langit; Deli, Su., 119: Kuala Lumpur, Subang estr.; Ulu Langat; Selangor, WM., 120: Gunung Semangko; Gunung Benom, WM., 121: Pulau Tioman, WM., 122: Gunung Gading; Pueh, BS., 123: Kuching; Matang, BS., 124: Longblu; Upper Mahakkam, BK., 125: Wahai; Seram, 126: Simeulue, 127: Bandar, Su., 128: Port Dickson, WM., 129: Singkawang, BK., 130: Peneritan; Banting, BS., 131: Gunung Kenepai, BK., 132: Pulau Babi., 133: Pulau Pisang, WM., 134: Singapore, WM., 135: Pontianak, BK., 136: Sintang, BK., 137: Teweh, BK., 138: Samarinda, BK., 139: Sopo Valley, Sw., 140: Poso, Sw., 141: Pulau Sanana, Kepulauan Sula, 142: Nias, 143: Kepulauan Riau, 144: Rana; Wa Katin; Wa Ehu, Buru, 145: Ambon, 146: Kepulauan Kai, 147: Pini, 148: Indragiri, Su., 149: Buntok, BK., 150: Laowu; Pulau Luha, Sw., 151: Lamontoli, Sw., 152: Leksula, Buru, 153: Batu, 154: Gunung Talakmau; Kajutanam, Su., 155: Singkep, 156: Bandjarmasin, BK., 157: Amuntai, BK., 158: Gunung Mekongga, Sw., 159: Taluk, Su., 160: Maian, BK., 161: Siberut, 162: Padang; Singkarak, Su., 163: Muaralabuh, Su., 164: Bangka, 165: Rantau; Tandjung, BK., 166: Pulau Laut, 167: Tempe; Bantimurong, Sw., 168: Sipora, 169: Lebongtandai, Su., 170: Belitung, 171: Ujung Pandang (= Macassar), Sw., 172: Pulau Pagai, 173: Palembang; Plaju, Su., 174: Serdang, Su., 175: Bonthain, Sw., 176: Wetar, 177: Kepahiang; Bengkulu, Su., 178: Alor, 179: Dili, Timor, 180: Maumere; Sika; Kottling, Flores, 181: Adonara, 182: Atapupu, Timor, 183: Enggaga, 184a: Jakarta; Gamber; b: Depok, Ja., 185a: Krawang; b: Sukamandi, Ja., 186: Cirebon, Ja., 187a: Semarang; b: Salatig; c: Ambarawa, Ja., 188: Surabaya, Ja., 189: Komodo; Rinja, 190: Ende; Waimangura, Flores, 191: Noel toko, Timor, 192: Muais, Timor, 193a: Udjung Kulon; b: Pulau Handeleuleum, Ja., 194: Sukabumi, Ja., 195a: Bogor; b: Gunung Salak; c: Puntjak, Ja., 196a: Bandung; Tjimahi; b: Garut; c: Cimahi; d: Pengalengam; e: Tjikadjar, Ja., 197: Wonosobo, Ja., 198: Gunung Merapi, Ja., 199a: Parang; b: Djugo, Ja., 200a: Kediri; b: Pudjon; c: G. Ardjuno, Ja., 201a: Malang; b: Nongkedjadar; c: Bremi; d: Tengger Mnts., Ja., 202: Ijeh Mnts., Ja., 203: Tjandikesuma, Bali, 204: Gitigit, Bali, 205: Lombok, 206: Sumbawa Besar; Semongkat Atos, Sumbawa, 207: Dompoe, Sumbawa, 208: Kupang; Semau, Timor, 209: Jogyakarta, Ja., 210: Tulungagung, Ja., 211: Koti; Waimangura, Sumba, 212: Melolo; Kambaniru, Sumba, 213: Baing, Sumba, 214: Koti.

Draco blanfordi: Boettger, 1892: 100; Robinson & Kloss, 1914: 154; Smith, 1915: 153; Smith, 1916b: 153; Smith, 1930: 22; Smith, 1935: 141, fig. 41b; Smith, 1937: 75, pl. 8; Taylor & Elbel, 1958: 1093; Anonymous, 1977: 26, fig. 21, tab. 1.

Draco blanfordii blanfordii: Bourret, 1943: 13.

Material examined. — THAILAND. Trang: 1♂, ZFMK 16630, 29.vii.1975, leg. G. Nikolaus. Southern Thailand: 1♂, RMNH 20016. Nakon Sritamarat Mnts.: 1♀, BM 1935.11.5.2, leg. M. A. Smith. Meh Iem, Phrae: 1♀, BM 1921.4.1.93-8, leg. M. A. Smith. BURMA. Tavoy Tenasserim: 1♂, BM 1946.8.26.76 (81.1.14.2)¹⁾ (lectotype), leg. W. T. Blanford; 1♂, BM 1946.8.13.42 (1908.1.29.1) (paralectotype), leg. W. T. Blanford. Tazan & Tapli: 2♀, BM 1921.4.1.87-92, leg. M. A. Smith. WEST MALAYSIA. Telom, Perak/Pahang boundary: 1♀, BM 1946.8.26.35 (1906.2.28.3) (holotype of *D. cyanolaemus* Boulenger), leg. H. C. Robinson. Larut Hills: 1♀, BM 1946.8.26.80 (1900.6.14.4) (paralectotype of *D. formosus* Boulenger), leg. A. L. Butler.

Diagnosis. — Patagium in males usually without dark bands; a black, longitudinal line on the border between the gular pouch and the lateral pouch; gular pouch in males 1.43-1.87 times the head length and in females 0.57-0.63 times the head length.

Description. — Maximum snout-vent length in males 134 mm (Taylor, 1963), 120 mm in material examined ($\bar{x} = 110.3$, $sd = 10.5$, $N = 4$), in females 113 mm ($\bar{x} = 108.2$, $sd = 6.5$, $N = 5$); head length 0.17-0.21 times the snout-vent length (♂: $\bar{x} = 0.18$, $sd = 0.0$, $N = 4$; ♀: $\bar{x} = 0.20$, $sd = 0.01$, $N = 5$); head depth 0.47-0.50 times the head length (♂: $\bar{x} = 0.49$, $sd = 0.01$, $N = 4$; ♀: $\bar{x} = 0.49$, $sd = 0.01$, $N = 5$); head width 0.59-0.66 times the head length (♂: $\bar{x} = 0.64$, $sd = 0.02$, $N = 4$; ♀: $\bar{x} = 0.63$, $sd = 0.03$, $N = 5$); snout length 0.27-0.37 times the head length (♂: $\bar{x} = 0.33$, $sd = 0.02$, $N = 4$; ♀: $\bar{x} = 0.32$, $sd = 0.04$, $N = 5$); nostril directed upward and slightly posteriorly; supralabials 7-10, keeled; usually two median teeth in upper jaw (two teeth: 87.5 %, one tooth: 12.5 %); head scales subequal, keeled, with smaller scales in the supra-orbital region; tympanum covered with smooth skin only (50 %) or partly with small scales; no thornlike scale on the supraciliary edge; a rounded tubercle at the end of the supraciliary edge; a large, keeled scale between the eye and the tympanum; a tubercular scale above and one behind the tympanum; a longitudinal fold instead of a nuchal crest in males; gular pouch in males with distinctly enlarged scales, 1.43-1.87 times the head length ($\bar{x} = 1.63$, $sd = 0.19$, $N = 4$); in females the gular pouch is 0.57-0.63 times the head length ($\bar{x} = 0.61$, $sd = 0.03$, $N = 5$), with enlarged scales at the tip; lateral pouches with enlarged scales; dorsals 183-224 (♂: $\bar{x} = 201.0$, $sd = 15.3$, $N = 4$; ♀: $\bar{x} = 204.0$, $sd = 12.2$, $N = 5$), smooth or faintly keeled, subequal; a few enlarged, keeled scales on the border between body and patagium; ventrals 108-128 (♂: $\bar{x} = 114.3$, $sd = 5.2$, $N = 4$; ♀: $\bar{x} = 121.6$, $sd = 5.0$, $N = 5$), keeled, larger than dorsals; usually five ribs in patagium (five ribs: 94.4 %, six ribs: 5.6 %); 24-32 keeled subdigital lamellae under the fourth finger (♂: $\bar{x} = 26.8$, $sd = 1.6$, $N = 4$; ♀: $\bar{x} = 29.1$, $sd = 2.7$, $N = 5$), 26-33 under the fourth toe (♂: $\bar{x} = 29.4$, $sd = 3.2$, $N = 4$; ♀: $\bar{x} = 30.6$, $sd = 1.6$, $N = 5$); hindlimbs

¹⁾ The numbers given between brackets are the old numbers of the BM-material.

0.49-0.55 times the snout-vent length (σ : $\bar{x} = 0.53$, $sd = 0.02$, $N = 4$; ♀ : $\bar{x} = 0.53$, $sd = 0.02$, $N = 5$), 0.87-0.98 times the distance between the limbs (σ : $\bar{x} = 0.93$, $sd = 0.04$, $N = 4$; ♀ : $\bar{x} = 0.93$, $sd = 0.04$, $N = 5$); fringelike scales on posterior edge of thigh and on base of tail; maximum tail length 256 mm (Taylor, 1963; 215 mm in material examined), 1.71-1.93 times the snout-vent length (σ : $\bar{x} = 1.83$, $sd = 0.07$, $N = 4$; ♀ : $\bar{x} = 1.80$, $sd = 0.07$, $N = 5$); males with a more or less distinct caudal crest.

Colour in preservative. — Above bluish or brownish grey, sometimes with indistinct darker or lighter spots; interorbital spot usually present, sometimes a paired nuchal spot as well; patagium in males dark to light brownish grey, with indistinct lighter spots and distinct light, longitudinal lines; in females the patagium is light grey, usually with distinct dark bands, furcated near the body edge by light spots; chest and belly yellowish or pinkish white; the patagium ventrally yellowish brown, sometimes with a short dark band near the outer edge; chin yellowish or pinkish white, sometimes grey, sometimes with reticulated dark markings; gular pouch in males yellowish white, bluish grey to black at the base; in females the tip of the gular pouch is yellowish white, the rest is bluish grey to dark grey at the base; a more or less broad, black line on the border between the gular pouch and the lateral pouch; lateral pouch yellowish or orangish underneath. Taylor (1963) stated that males with more or less distinct, transverse bands on the patagium occur, but did not state where they occurred.

Colour in life (after RMNH 20016, which died just before receiving it): above grey, patagium brown with light, longitudinal lines; tail with dull red bands; ventral parts of the body whitish grey, of the patagium yellowish; chin and gular pouch whitish grey; ventral parts of lateral pouch red; a black line along the proximal edge.

Ecological notes. — Three females (BM 1946.8.26.80, 1921.4.1.87-92) had four eggs each in the oviducts. Of these females no collecting dates are available.

Distribution. — The subspecies is found from Northern Thailand to the northern part of Malaya (fig. 5). It has been collected at an altitude of 1200 m and not below 750 m in the southern parts of the range (Boulenger, 1912).

Remarks. — Since Boulenger (1885) did not designate a holotype and since BM 1946.8.26.76 is the best preserved specimen of the two syntypes, this latter is selected here as the lectotype. Description: male; snout-vent length: 118 mm; tail length: 209 mm; head length: 21.2 mm; head depth: 10.5 mm; head width: 13.3 mm; snout length: 7.3 mm; gular pouch length: 35.2 mm; hindlimb length: 62/62 mm; distance limbs: 69/65 mm; median upper teeth: 2; tympanum on both sides partly covered with smooth skin; supralabials: 9/9; dorsals: 198; ventrals: 118; subdigital lamellae fourth finger: 28/27; ditto fourth toe: 31/31; ribs patagium: 5/5; low caudal crest; nostril directed upward, slightly back- and outward; gular pouch and lateral pouches with distinct enlarged scales; above brownish grey; distinct dark spots in nuchal region; tail vaguely banded; patagium dark brown, with indistinct light spots and lines, giving it a vaguely reticulated impression; ventral parts yellowish white, of the patagium yellowish

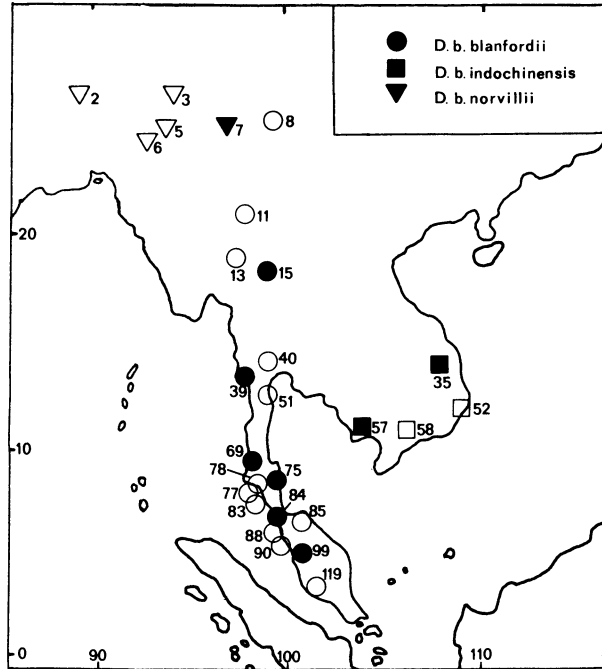


Fig. 5. Distribution of *Draco blanfordii*. Open symbols are localities from the literature.

brown; chin light greyish brown; gular pouch light yellow, bluish grey near the base; a thin dark line along the proximal edge of the lateral pouch ventrally, rest light orangish yellow.

Draco blanfordii indochinensis Smith

Draco indochinensis Smith, 1928: 248 (terra typica: Bockor, Kamchay Mnts., Cambodia (1000 m)); Smith, 1935: 141; Smith, 1937: 76.

Draco taeniopterus indochinensis: Hennig, 1936a: 211, map 11; Wermuth, 1967: 54.

Draco blanfordii indochinensis: Bourret, 1943: 13.

Material examined. — CAMBODIA. Bockor, Kamchay Mnts.: 1 ♀, BM 1946.8.26.77 (1926.6.29.1) (holotype), leg. Delacour & Lowe. VIETNAM. Kontum, Annam: 1 ♀, BM 1946.8.26.78 (1927.5.20.19) (paratype), leg. Delacour & Lowe.

Diagnosis. — Only females are known; a broad, transverse band across the posterior part of the gular pouch, running from lateral pouch to lateral pouch; gular pouch 0.74-0.88 times the head length.

Description. — Females (N = 2): maximum snout-vent length 104 mm (\bar{x} = 102.0); head length 0.20-0.21 times the snout-vent length; head depth 0.47 times the head length; head width 0.63-0.68 times the head length; snout length 0.30-0.33 times the head length; nostril directed upward; supralabials 8-10, keel-

ed; two median teeth in upper jaw; head scales subequal, keeled; tympanum covered with smooth skin; no thornlike scale on the supraciliary edge; a rounded tubercle at the end of the supraciliary edge; no nuchal fold; tip of the gular pouch with enlarged scales, 0.74-0.88 times the head length; lateral pouches with enlarged scales; dorsals 189-210, smooth or faintly keeled, subequal; a few enlarged, keeled scales on the border between body and patagium; ventrals 123-129, keeled, larger than dorsals; five ribs in patagium; 25-26 keeled subdigital lamellae under the fourth finger, 29-32 under the fourth toe; hindlimbs 0.55-0.57 times the snout-vent length, 0.99-1.00 times the distance between the limbs; fringelike scales on posterior edge of thigh and on base of tail; maximum tail length 197 mm, 1.81-1.89 times the snout-vent length.

Colour in preservative. — Females: above brownish grey, with small, dark spots on body; interorbital spot present or not; patagium light- (near body) to dark brown (near outer edge) with six distinct, light bordered, transverse bands; chest and belly yellowish or pinkish white, of the patagium yellowish brown with rests of dark bands; chin light grey with small, darker or lighter spots; tip of the gular pouch yellowish white; frontal parts of the base of the gular pouch bluish grey, the posterior parts black as a part of a transverse band running from the ventral part of one lateral pouch to the other.

Ecological notes. — No eggs were found in the oviducts of the females.

Distribution. — This subspecies occurs in Cambodia and Vietnam (fig. 5). It is found to an altitude of 1000 m.

Remarks. — As Smith (1937) already stated, *indochinensis* is closer related to *blanfordii* than to *taeniopterus*. It differs from *taeniopterus* in length, in relative tail length, in relative gular pouch length, in the fact that females have enlarged gular pouch scales and in colour. It differs from *blanfordii* in colour and possibly in relative gular pouch length and hindlimb length. Therefore it is regarded here as a subspecies of *D. blanfordii*.

***Draco blanfordii norvillii* Alcock**

Draco norvillii Alcock, 1895: 14, pl. 3 (terra typica: Dooma Dooma, Upper Assam); Smith, 1929: 79;

Hennig, 1936a: 219; Wermuth, 1967: 52.

Draco norvilli: Smith, 1935: 142.

Draco blanfordii norvillii: Bourret, 1943: 13.

Draco blanfordi: Biswas, 1967: 374, pl.

Material examined. — BURMA. Sumka Uma, Triangle: 2♂, BM 1940.6.3.34,35, leg. R. Kaulback.

Diagnosis. — Patagium in males with indistinct, dark bands; base of the gular pouch dark grey, with light spots at the border with the lateral pouches; gular pouch in males 1.65-1.67 times the head length.

Description. — Maximum snout-vent length in males 112 mm (\bar{x} = 110.7, sd = 2.3, N = 3, based on Alcock (1895) and on material examined) and in females 96 mm (Biswas (1967) and Smith (1929) mentioned a snout-vent length

of 175 mm, but this must be considered as a printer's error); head length 0.18-0.19 times the snout-vent length (σ : $\bar{x} = 0.19$, $sd = 0.0$, $N = 3$, based on Alcock (1895) and on material examined); head depth 0.50 times the head length (σ : $N = 2$); head width 0.64-0.65 times the head length (σ : $N = 2$); snout length 0.32-0.33 times the head length (σ : $N = 2$); nostril directed upward or slightly oblique (Alcock, 1895); supralabials 9-10, keeled; two median teeth in upper jaw; head scales subequal, keeled; tympanum covered with small scales (Alcock, 1895; Smith, 1929) or smooth skin; no thornlike scale on the supraciliary edge; a rounded tubercle at the end of the supraciliary edge; a large scale between the eye and the tympanum; a more or less developed nuchal fold in males; gular pouch in males and females (Biswas, 1967) with distinctly enlarged scales, 1.65-1.67 times the head length ($N = 2$) in males; lateral pouches with enlarged scales; dorsals 166-183 (σ : $N = 2$), smooth or faintly keeled, subequal; a few enlarged scales on the border between body and patagium; ventrals 114-115 (σ : $N = 2$), keeled, larger than dorsals; five ribs in the patagium; 26-27 keeled subdigital lamellae under the fourth finger, 28-30 under the fourth toe; hindlimbs 0.54-0.56 times the snout-vent length (σ : $\bar{x} = 0.55$, $sd = 0.01$; $N = 3$, based on Alcock, 1895 and on material examined), 0.97-0.98 (σ : $N = 2$) times the distance between the limbs; large fringelike scales on posterior edge of thigh and on base of tail; maximum tail length 197 mm, 1.73-1.76 times the snout-vent length (σ : $\bar{x} = 1.75$, $sd = 0.01$, $N = 3$; ♀ : 1.76, based on Alcock, 1895; Biswas, 1967 and on material examined); males with a caudal crest.

Colour in preservative. — Above bluish or brownish dark grey; interorbital spot sometimes present; head and shoulders with small dark spots; tail banded; patagium rust brown with vaguely recognizable dark bands in males, in females these bands are more distinct (Smith, 1929; Biswas, 1967); chest and belly yellowish; patagium orangish yellow underneath; chin grey with darker and lighter, small spots; gular pouch at least in males yellowish white, dark grey with lighter spots near the base; ventral parts of the lateral pouches orangish grey. In life the bands on the patagium in males and the ventral parts of the lateral pouches are scarlet (Alcock, 1895).

Ecological notes. — No data on this subject are available.

Distribution. — This subspecies occurs in Assam, India and in Northern Burma (fig. 5).

Remarks. — Since the type of this taxon could not be examined, it is not completely certain, that it is a subspecies of *D. blanfordii*. According to Alcock (1895) the type differs from *blanfordii* in the following characters: the tympanum is covered with small scales, the gular pouch of the male is only a little longer than the head, and the patagium has dull red bands. Since specimens of *blanfordii* with a tympanum partly covered with small scales occur and since Taylor (1963) stated that males of *blanfordii* with more or less distinct bands on the patagium occur too, the only character that remains valid is the gular pouch length. Because of lack of exact measurements, this character is difficult to judge. On the other hand there is a great agreement in all other characters between *norvillii* and *blan-*

fordii (nostril directed upward; nuchal fold; gular pouch with enlarged scales; caudal crest (Alcock, 1895: pl. 3); body dimensions; colour of the gular pouch and ventral parts of the lateral pouches). Therefore it seems justified to regard this taxon as a subspecies of *D. blanfordii*. In this case the female, found by Biswas (1967), does belong to this taxon as well.

Draco cornutus Günther

Draco cornutus Günther, 1864: 125 (terra typica: Borneo); Boulenger, 1885: 258, pl. 20 fig. 4; Mocquard, 1890: 128; Van Lidth de Jeude, 1893: 250; Bartlett, 1894: 80; Wandolleck, 1900: 12, fig. 1, 12; Volz, 1903: 425; Werner, 1910: 9; De Rooy, 1915: 72; Taylor, 1922a: 114; Smith, 1925b: 24; Smedley, 1931: 47.

Draco gracilis Barbour, 1903: 59 (terra typica: Sarawak, Borneo); De Rooy, 1915: 73.

Draco spilopterus cornutus: Hennig, 1936a: 183, fig. 10e, map 3; Wermuth, 1967: 53.

Material examined. — BORNEO. 1 ♂, BM 1946.8.27.24 (47.3.4.25) (lectotype), leg. E. Belcher; 1 ♀, BM 1946.8.27.23 (42.9.18.57) (paralectotype), leg. E. Belcher; 2 ♂, 2 ♀, RMNH 2929, 1845, leg. C. A. L. M. Schwaner. MALAYSIA. SARAWAK: 1 ♀, ZMA 12040, 13.vii.1912, leg. v. d. Bergh; 1 ♀, BM 72.2.19.81, leg. Cutter. Balingean, interior Sarawak: 2 ♂, 2 ♀, BM 1904.7.19.33-36, don. Selangor Museum. Labuan: 2 ♂, 2 ♀, BM 95.11.7.2-5, leg. A. Everett. INDONESIA. KALIMANTAN. Rantau: 2 ♂, RMNH 19967-68, v. 1916, leg. F. C. E. v. d. Putten. Bluu, Mahakkam River: 1 ♂, RMNH 19969, leg. A. W. Nieuwenhuis. Upper Mahakkam: 1 ♂, 3 ♀, RMNH 5739, leg. A. W. Nieuwenhuis. JAVA. 1 ♀, ZMB 29701, leg. R. Mertens.

Diagnosis. — Species of small to moderate size (maximum snout-vent length 85 mm); nostril directed outward; series of enlarged, keeled scales forming a **A**-shaped figure on the snout; usually three median teeth in upper jaw; supralabials 8-10, smooth; a thornlike scale on the supraciliary edge; tympanum usually covered with smooth skin; gular pouch without, lateral pouches with enlarged scales; males and females with a short nuchal crest; dorsals 140-177, smooth, subequal; usually six ribs in patagium; hindlimbs short (0.64-0.77 times the distance between the limbs); no caudal crest.

Description. — Maximum snout-vent length in males 78 mm (\bar{x} = 71.5, sd = 4.4, N = 6), in females 85 mm (\bar{x} = 77.4, sd = 6.4, N = 8); maximum head length 13.7 mm in males, 16.4 mm in females, 0.17-0.20 times the snout-vent length (♂: \bar{x} = 0.19, sd = 0.01, N = 6; ♀: \bar{x} = 0.19, sd = 0.01, N = 8); head depth in males 0.58-0.61 (\bar{x} = 0.59, sd = 0.01, N = 6), in females 0.52-0.56 (\bar{x} = 0.55, sd = 0.02, N = 8) times the head length; head width 0.63-0.71 times the head length (♂: \bar{x} = 0.68, sd = 0.02, N = 6; ♀: \bar{x} = 0.65, sd = 0.01, N = 8); snout length 0.27-0.36 times the head length (♂: \bar{x} = 0.30, sd = 0.03, N = 6; ♀: \bar{x} = 0.30, sd = 0.02, N = 8); nostril directed outward; supralabials 8-12 (Hennig, 1936a), smooth; usually three median teeth in upper jaw (three teeth: 92.9 %, two teeth: 7.1 %); head scales unequal, enlarged in the supraocular region, feebly keeled; a series of large, keeled scales forming a **A**-shaped figure on the snout; tympanum usually covered with smooth skin (92.9 %), in one specimen both tympana were completely covered with small scales; a thornlike scale on the supraciliary edge, which is 0.05-0.10 times the head length (♂: \bar{x} = 0.068,

sd = 0.008, N = 6; ♀: \bar{x} = 0.056, sd = 0.007, N = 8); a tubercle at the posterior end of the supraciliary edge; about four large, feebly keeled scales between the eye and the tympanum; sometimes a large scale between the corner of the mouth and the tympanum; two or three tubercular scales above and behind the tympanum; nuchal crest in males and females consisting of 2-8 triangular scales; gular pouch without enlarged scales, in males 0.74-1.31 (\bar{x} = 0.96, sd = 0.20, N = 6) and in females 0.47-0.60 (\bar{x} = 0.54, sd = 0.05, N = 8) times the head length; lateral pouches with enlarged scales; dorsals 140-177 (♂: \bar{x} = 154.5, sd = 13.2, N = 6; ♀: \bar{x} = 153.6, sd = 7.4, N = 8), smooth, subequal; sometimes a few enlarged, keeled scales on the border between body and patagium; ventrals 97-127 (♂: \bar{x} = 108.0, sd = 7.1, N = 6; ♀: \bar{x} = 110.9, sd = 8.7, N = 8), keeled, about as large as the dorsals; usually six ribs in patagium (96.4 %), one specimen with five ribs in its left patagium; 18-24 (♂: \bar{x} = 21.1, sd = 2.1, N = 6; ♀: \bar{x} = 21.3, sd = 1.2, N = 8) keeled subdigital lamellae under the fourth finger, 22-27 (♂: \bar{x} = 24.3, sd = 2.0, N = 6; ♀: \bar{x} = 25.0, sd = 1.3, N = 8) under the fourth toe; hindlimbs about 0.36-0.45 (♂: \bar{x} = 0.40, sd = 0.02, N = 6; ♀: \bar{x} = 0.40, sd = 0.03, N = 8) times the snout-vent length, 0.64-0.77 (♂: \bar{x} = 0.72, sd = 0.04, N = 6; ♀: \bar{x} = 0.71, sd = 0.05, N = 8) times the distance between the limbs; fringelike scales on posterior edge of thigh; maximum tail length 125 mm, 1.39-1.60 (♂: \bar{x} = 1.56, sd = 0.03, N = 5; ♀: \bar{x} = 1.50, sd = 0.08, N = 7) times the snout-vent length; no caudal crest.

Colour in preservative. — Above dark to light brown; males with indistinct, lighter bands on body; interorbital and nuchal spots present; sometimes a distinct lateral spot present in the nuchal region; patagium very variable: uniformly dark brown; light with dark spots forming bands or with dark proximal parts and the light distal parts with dark spots; sometimes with a dark band along the outer edge; chest and belly dark to light brown; sometimes the belly with marble-like, transverse markings; ventral part of the patagium yellowish brown with dark spots (sometimes forming bands); chin in females anteriorly light yellowish, laterally dark brown or bluish; in males with dark and light spots forming a reticulated pattern (indistinct in dark specimens); gular pouch in males yellowish brown with a light, yellowish tip; in females light to dark bluish grey with a light yellowish anterior edge.

Ecological notes. — Seven out of eight females carried eggs in the oviducts, of which four had four and three had three eggs. One of them (ZMA 12040) was collected in July, of the others no collecting dates are available.

Distribution. — The species is known from Borneo, Sumatra, Java, the Bunguran Islands and the Sulu Archipelago (fig. 6).

Remarks. — Being a male, BM 1946.8.27.24 is here selected as lectotype. Description: male; snout-vent length: 74 mm; tail length: 72 mm (broken); head length: 13.4 mm; head width: 9.3 mm; head depth: 7.8 mm; snout length: 4.0 mm; gular pouch length: 17.6 mm; thornlike scale length: 0.94/1.09 mm; thornlike scale width: 0.62/0.62 mm; hindlimb length: 31/31 mm; distance limbs: 44/44 mm; median upper teeth: 3; tympanum on both sides covered with

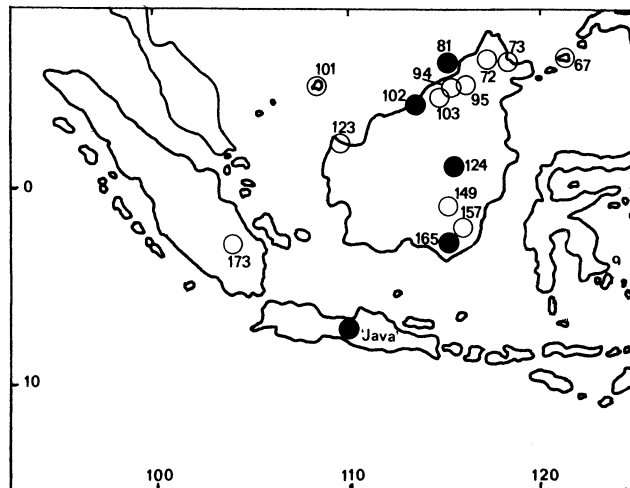


Fig. 6. Distribution of *Draco cornutus*. Open symbols are localities from the literature.

smooth skin; supralabials: 9/9; dorsals: 152; ventrals: 106; subdigital lamellae fourth finger: 23/22; ditto fourth toe: 23/23; nuchal crest scales: 7; ribs patagium: 6/6; nostril directed outward; no caudal crest; gular pouch without and lateral pouches with slightly enlarged scales; above bluish and brownish grey; interorbital and nuchal spots present; body with irregular spots; a distinct spot on each side above the lateral pouch; patagium dark brown (darker spots can be recognized) with light lines near body; ventrally bluish, lateral parts goldish yellow; patagium bluish brown with large, dark spots; chin bluish with large, lighter spots; lateral parts of head with light spots too; gular pouch orangish yellow.

Taylor (1922a) was of the opinion, that the specimens reported from Solo as belonging to *D. cornutus*, might belong to *D. rizali* (= *D. v. reticulatus*), a view that makes sense to me.

Since the present species very much resembles *D. v. volans* and *D. v. sumatranus* the possibility of misidentification in some of the literature references should be taken into consideration.

***Draco dussumieri* Duméril & Bibron**

Draco dussumieri Duméril & Bibron, 1837: 456 (terra typica: Malabar); Fitzinger, 1843: 50; Schlegel, 1844: 95; Günther, 1864: 125, pl. 13 fig. d; Anderson, 1871: 164; Boulenger, 1885: 268; Boulenger, 1890a: 113; Boettger, 1892: 69; Smith, 1935: 143; Hennig, 1936a: 191, fig. 11d, map 5; McCann, 1940: 45; Bourret, 1943: 12; John, 1962; John, 1967a; John, 1967b; Wermuth, 1967: 46; John, 1970.

Draco Duvaucelii Fitzinger, 1843: 50 (nomen nudum).

Dracocella dussumieri: Gray, 1845: 234.

Material examined. — INDIA. Malabar: 1 ♂, RMNH 2954 (syntype), leg. Dussumier. Decan: 1 ♂, 1 ♀, RMNH 5736, 1847, Frank. Kerala prov., Trivandrum: 3 ♂, ZFMK 14098-100, 24.x.1968, leg. S. Peeven. Punakaad (700 ft.), Travancore: 1 ♀, BM 1924.10.13.31, leg. A. F. Abercromby. Madras: 1 ♀, BM 46.11.22.24-25, leg. Jerdon.

Diagnosis. — Species of small to moderate size (maximum snout-vent length 97 mm); nostril directed upward; no Λ -shaped series of enlarged scales on the snout; usually two median teeth in the upper jaw; supralabials 10-13, smooth; no thornlike scale on the supraciliary edge; tympanum covered with smooth skin; gular and lateral pouches with slightly enlarged scales; nuchal fold present; dorsals 142-169, smooth, subequal; six ribs in patagium; hindlimbs about as long as the distance between the limbs; males with caudal crest.

Description. — Maximum snout-vent length in females 97 mm (McCann, 1940), 86 mm in material examined (\bar{x} = 79.7, sd = 5.7, N = 3), in males 86 mm (Hennig, 1936a), 78 mm in material examined (\bar{x} = 70.8, sd = 5.4, N = 5); maximum head length 17.9 mm, 0.18-0.21 times the snout-vent length (♂: \bar{x} = 0.19, sd = 0.01, N = 5; ♀: \bar{x} = 0.20, sd = 0.01, N = 3); head width 0.66-0.71 times the head length in males (\bar{x} = 0.68, sd = 0.02, N = 5), 0.62-0.67 times in females (\bar{x} = 0.65, sd = 0.03, N = 3); head depth 0.49-0.60 times the head length (♂: \bar{x} = 0.54, sd = 0.04, N = 5; ♀: \bar{x} = 0.54, sd = 0.03, N = 3); snout length 0.26-0.32 times the head length (♂: \bar{x} = 0.29, sd = 0.02, N = 5; ♀: \bar{x} = 0.29, sd = 0.02, N = 3); nostril directed upward; supralabials 10-13, smooth; number of median teeth in upper jaw usually two (two teeth: 62.5 %, one tooth: 25.0 %, three teeth: 12.5 %); head scales subequal, small, feebly keeled; only one or two keeled scales on the snout instead of a row or Λ -shaped figure; a tubercle at the end of the supraciliary edge; tympanum covered with smooth skin; two or three enlarged, keeled scales between the eye and the tympanum; two or three tubercles above and behind the tympanum; a longitudinal fold, sometimes with distinct, compressed scales (one male with eight, females with five and four such scales) forming a nuchal crest; a row of small tubercles at each side of the nuchal fold (sometimes very indistinct); gular pouch in males 1.88-2.79 times the head length (\bar{x} = 2.17, sd = 0.37, N = 5), with slightly enlarged scales at the tip; in females 0.61-1.17 times the head length (\bar{x} = 0.90, sd = 0.28, N = 3), without enlarged scales; lateral pouches without or with very slightly enlarged scales; dorsals 142-169 (♂: \bar{x} = 155.3, sd = 12.4, N = 5; ♀: \bar{x} = 152.7, sd = 4.9, N = 3), smooth, subequal; instead of enlarged scales on the border between body and patagium, groups of small, thickened scales; ventrals 98-127 (♂: \bar{x} = 111.0, sd = 9.8, N = 5; ♀: \bar{x} = 127.0, N = 2), keeled, slightly larger than dorsals; six ribs in patagium; 19-23 (♂: \bar{x} = 21.1, sd = 1.2, N = 5; ♀: \bar{x} = 21.2, sd = 1.8, N = 3) keeled subdigital lamellae under the fourth finger, 21-25 (♂: \bar{x} = 22.8, sd = 0.3, N = 5; ♀: \bar{x} = 23.7, sd = 1.9, N = 3) under the fourth toe; hindlimbs 0.52-0.56 times the snout-vent length (♂: \bar{x} = 0.54, sd = 0.02, N = 5; ♀: \bar{x} = 0.54, sd = 0.01, N = 3), 0.83-1.09 times the distance between the legs (♂: \bar{x} = 1.01, sd = 0.02, N = 5; ♀: \bar{x} = 0.97, sd = 0.13, N = 3); thigh and base of tail with fringelike scales; maximum tail length 155 mm (McCann, 1940), 1.58-1.71

times the snout-vent length (σ : $\bar{x} = 1.65$, $sd = 0.04$, $N = 5$; ♀ : 1.58 , $N = 1$); tail of males with a crest, formed by compressed, triangular scales.

Colour in preservative. — Above dark brown, usually without any markings (one female had dark brown bands on head and body); patagium light brown near the body, dark brown on the outer edge, with large, light spots, which give it a reticulated impression; chest and belly dark grey; chin spotted with large, dark grey spots; ventral parts of patagium grey with a dark band along the posterior edge and some (4-6) dark spots on the rest of it; gular pouch yellowish white, with dark spots at the base in males, in females only the tip is yellowish, the rest is dark grey with dark spots; a dark, transverse band between the gular pouch and the shoulders.

In life the colour of the patagium markings is purplish black with yellow spots. The gular pouch is bright yellow (John, 1962; McCann, 1940).

Ecological notes. — One of the females (BM 46.11.22.24-25) had four, another (BM 1924.10.13.31) three eggs. For further ecological data, for bionomics, thermoregulation and behaviour see McCann (1940) and John (1962; 1967a; 1967b; 1970).

Distribution. — This species is restricted to Southern India (fig. 7).

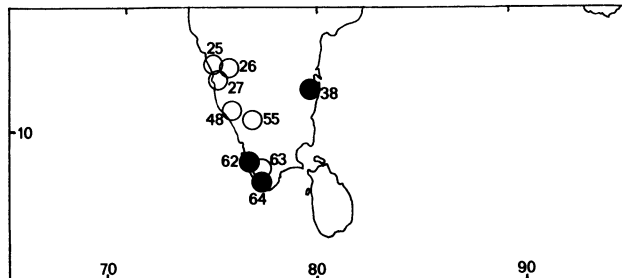


Fig. 7. Distribution of *Draco dussumieri* (Southern India). Open symbols are localities from the literature.

Remarks. — Since RMNH 2954 was collected by Dussumier in Malabar (the type locality) and since the Leiden Museum possesses many specimens that were exchanged with the Muséum National d'Histoire Naturelle, Paris, through Duméril & Bibron, chances are that this specimen formed part of Duméril & Bibron's type series. Consequently this specimen is considered a syntype.

If with the name 'Madras' the state Madras was meant instead of the city, it is possible that the specimen was collected much nearer to the other localities than is suggested now.

***Draco fimbriatus* Kuhl**

Diagnosis. — Species of moderate to large size (maximum snout-vent length 117 mm); nostril directed outward or slightly upward; series of enlarged, keeled

scales forming a Λ -shaped figure on the snout; median teeth in the upper jaw usually two; supralabials 8-13, with several indistinct keels; a low thornlike scale on the supraciliary edge; tympanum usually covered with smooth skin; gular pouch without, lateral pouches with enlarged scales; both sexes with a nuchal crest, in males on top of a nuchal fold; dorsals 155-256, smooth, unequal; usually five ribs in patagium; hindlimbs about as long as the distance between the limbs; males with a caudal crest.

KEY TO THE SUBSPECIES

1. Dorsals 155-226; ventral parts of the patagium usually with dark spots; West Malaysia, Sumatra, Borneo and surrounding islands *D. fimbriatus fimbriatus* (p. 24)
Dorsals 200-256; ventral parts of patagium without any spots; Java and Bali
..... *D. fimbriatus hennigi* (p. 27)

Draco fimbriatus fimbriatus Kuhl

Draco fimbriatus Kuhl, 1820: 101 (terra typica: Malayan Peninsula); Fitzinger, 1826: 48; Schlegel, 1844: 92 (partim); Gray, 1845: 234; Günther, 1864: 123; Stoliczka, 1873: 119; Boulenger, 1885: 265 (partim); Boulenger, 1890b: 33; Günther, 1895: 499; Bartlett, 1894: 81; Flower, 1896: 870; Flower, 1899: 636; Wandolleck, 1900: 14, fig. 5, 9; Lampe & Lindholm, 1901: 202; Boulenger, 1903: 151; Van Lidth de Jeude, 1905: 190 (partim); Boulenger, 1908: 64; Boulenger, 1912: 59; Baumann, 1913: 259; De Rooy, 1915: 79 (partim); Smith, 1916a: 52; Smith, 1916b: 152; Smith, 1922: 268; Smith, 1925a: 24; Lönnberg & Rendahl, 1925: 3; Smith, 1926: 78; Smith, 1930: 21; De Jong, 1930: 115; Smedley, 1931: 47; Taylor, 1934: 289; Taylor & Elbel, 1958: 1042.

Draco abbreviata Hardwicke & Gray, 1827: 219 (terra typica: Singapore); Gray, 1831: 59.

Draco cristatellus Günther, 1872: 592, pl. 35 fig. a (terra typica: Sarawak, Borneo); Boulenger, 1885: 266; Bartlett, 1894: 81; Van Lidth de Jeude, 1905: 190; Baumann, 1913: 260; De Rooy, 1915: 80.

Draco lineatus: Van Lidth de Jeude, 1893: 251 (ex errore).

Draco grandis Bartlett, 1894: 83 (terra typica: Matang, Sarawak, 800 ft.).

Draco punctatus Boulenger, 1900: 189 (terra typica: Larut Hills, Perak); Boulenger, 1903: 151, fig. 1, 1a; Boulenger, 1912: 59; De Rooy, 1915: 75; Smith, 1916a: 53; Smith, 1916b: 153; Smith, 1930: 21; Hennig, 1936a: 182; Bourret, 1943: 12; Taylor, 1963: 841, fig. 40; Wermuth, 1967: 52; Grandison, 1972: 78 (new synonym).

Draco lineatus lineatus: Hennig, 1936a: 192 (partim, ex errore).

Draco fimbriatus fimbriatus: Hennig, 1936a: 202, fig. 10i, map 8 (partim); Bourret, 1943: 13; Taylor, 1963: 838, fig. 38; Wermuth, 1967: 47 (partim); Grandison, 1972: 76.

Material examined. — MALAYSIA. WEST MALAYSIA. Subang: 1 ♀, ZFMK 16492, 25.v.1975, leg. G. Nikolaus. SARAWAK: 1 ♂, BM 72.2.19.4 (holotype of *D. cristatellus* Günther), leg. W. Putter; 1 ♂, BM 1946.8.26.93 (63.3.6.15) (holotype of *D. punctatus* Boulenger), leg. A. Everett. INDONESIA. SUMATRA. Padang: 1 ♂, 1 ♀, RMNH 2920, leg. S. Müller. Siboe Langit: 1 ♀, ZMA 14429 B, 25.v.1916, leg. L. P. le Cosquino de Bussy. Deli: 1 juv., ZMA 15253 Q, leg. L. P. le Cosquino de Bussy. KALIMANTAN. 1 juv., RMNH 19970, leg. J. Büttikofer. Upper Mahakkam: 2 ♂, RMNH 4995, leg. A. W. Nieuwenhuis. Sandakan bay: 1 juv., RMNH 4346, leg. J. Chr. Prakke. Rantau: 1 ♂, 1 juv., RMNH 19974-75, v.1916, leg. F. C. E. v. d. Putten.

Diagnosis. — Dorsals 155-226; ventral parts of the patagium usually with smaller or larger, distinct, dark spots.

Description. — Maximum snout-vent length in males 112 mm (Taylor, 1963), 90 mm in material examined (\bar{x} = 81.5, sd = 5.5, N = 6), in females 117

mm (Taylor, 1963), 102 mm in material examined ($\bar{x} = 89.7$, $sd = 13.7$, $N = 3$) (juv.: 49-56 mm, $\bar{x} = 52.5$, $sd = 4.0$, $N = 4$); maximum head length 26 mm (Taylor, 1963), 0.20-0.23 times the snout-vent length (σ : $\bar{x} = 0.21$, $sd = 0.01$, $N = 6$; φ : $\bar{x} = 0.22$, $sd = 0.0$, $N = 3$; juv.: $\bar{x} = 0.22$, $sd = 0.01$, $N = 4$); head width 0.63-0.75 times the head length (σ : $\bar{x} = 0.69$, $sd = 0.02$, $N = 6$; φ : $\bar{x} = 0.66$, $sd = 0.03$, $N = 3$; juv.: $\bar{x} = 0.72$, $sd = 0.03$, $N = 4$); head depth 0.50-0.60 times the head length (σ : $\bar{x} = 0.56$, $sd = 0.02$, $N = 6$; φ : $\bar{x} = 0.51$, $sd = 0.02$, $N = 3$; juv.: $\bar{x} = 0.58$, $sd = 0.03$, $N = 4$); snout length 0.26-0.37 times the head length (σ : $\bar{x} = 0.31$, $sd = 0.02$, $N = 6$; φ : $\bar{x} = 0.33$, $sd = 0.05$, $N = 3$; juv.: $\bar{x} = 0.28$, $sd = 0.01$, $N = 4$); nostril directed outward, or slightly upward; supralabials 9-13, smooth or faintly keeled; 15.4 % of the specimens with one, 46.1 % with two, 38.5 % with three median teeth in the upper jaw; head scales unequal, keeled; a series of strongly keeled scales forming a Λ -shaped figure on the snout; thornlike scale on supraciliary edge 0.01-0.07 times the head length (σ : $\bar{x} = 0.020$, $sd = 0.013$, $N = 6$; φ : $\bar{x} = 0.018$, $sd = 0.001$, $N = 3$; juv.: $\bar{x} = 0.014$, $sd = 0.003$, $N = 4$); tubercle at end of the supraciliary edge distinct; tympanum usually covered with smooth skin, two specimens with partly differentiated skin on the tympanum; 2-3 enlarged, keeled scales between the eye and the tympanum; the lateral parts of the neck with many, variably distinct tubercles, forming at least two, more or less distinct rows, one above the tympanum and the other behind it; nuchal crest in males on top of a longitudinal fold, consisting of 12-20 slightly enlarged scales ($\bar{x} = 17.0$, $sd = 3.6$, $N = 6$), in females consisting of 3-10 slightly enlarged scales, not on a fold ($\bar{x} = 6.0$, $sd = 3.6$, $N = 3$) (juv.: 0-10; $\bar{x} = 3.7$, $sd = 5.5$, $N = 4$); gular pouch without enlarged scales, 1.06-1.77 times the head length in males ($\bar{x} = 1.44$, $sd = 0.25$, $N = 6$), 0.50-0.99 times in females ($\bar{x} = 0.78$, $sd = 0.26$, $N = 3$) (juv.: 0.75-1.01; $\bar{x} = 0.89$, $sd = 0.12$, $N = 4$); lateral pouches with enlarged scales; dorsals 155-226 (σ : $\bar{x} = 188.0$, $sd = 18.8$, $N = 6$; φ : $\bar{x} = 197.7$, $sd = 37.6$, $N = 3$; juv.: $\bar{x} = 196.3$, $sd = 6.2$, $N = 4$), faintly keeled, unequal; a row of compressed, triangular, thornlike scales on the border between body and patagium; ventrals 97-112 (σ : $\bar{x} = 103.3$, $sd = 4.9$, $N = 6$; φ : $\bar{x} = 104.7$, $sd = 6.4$, $N = 3$; juv.: $\bar{x} = 102.0$, $sd = 6.2$, $N = 4$), keeled, larger than the dorsals; usually five ribs in the patagium (88.5 %), one specimen with four ribs in one of its patagia, another with six ribs in both patagia; 19-25 (σ : $\bar{x} = 21.9$, $sd = 2.0$, $N = 6$; φ : $\bar{x} = 22.3$, $sd = 2.5$, $N = 3$; juv.: $\bar{x} = 21.9$, $sd = 2.6$, $N = 4$) keeled subdigital lamellae under the fourth finger, 21-26 (σ : $\bar{x} = 23.9$, $sd = 1.7$, $N = 6$; φ : $\bar{x} = 25.0$, $sd = 1.0$, $N = 3$; juv.: $\bar{x} = 23.8$, $sd = 2.4$, $N = 4$) under the fourth toe; hindlimbs 0.46-0.59 times the snout-vent length (σ : $\bar{x} = 0.53$, $sd = 0.02$, $N = 6$; φ : $\bar{x} = 0.54$, $sd = 0.07$, $N = 3$; juv.: $\bar{x} = 0.54$, $sd = 0.02$, $N = 4$), 0.83-1.06 times the distance between the limbs (σ : $\bar{x} = 0.94$, $sd = 0.05$, $N = 6$; φ : $\bar{x} = 0.94$, $sd = 0.10$, $N = 3$; juv.: $\bar{x} = 0.98$, $sd = 0.06$, $N = 4$); fringelike scales on posterior edge of thigh and on base of tail; maximum tail length 189 mm (Taylor, 1963), 1.41-1.86 times the snout-vent length (σ : $\bar{x} = 1.61$, $sd = 0.12$, $N = 6$; φ : $\bar{x} = 1.65$, $sd = 0.21$, $N = 3$; juv.: $\bar{x} = 1.75$, $sd = 0.10$, $N = 4$); males with a caudal crest composed of compressed, triangular scales, serried or with a gap of one or two scales.

Colour in preservative. — Above bluish or brownish grey to dark grey, with dark, transverse bands (usually females) or spots (usually males) all over the body; sometimes an interorbital spot is present; patagium dark brown with more or less distinct, lighter lines or rests of these lines; chest and belly bluish or yellowish grey with some minute, dark spots on the shoulders; chin with characteristic white and black spots; ventral parts of the patagium yellowish grey, usually with dark spots at least at the outer edge, sometimes even forming bands; gular pouch in males yellowish grey, in some specimens with dark brown lines and a darker anterior edge, in females bluish grey with a yellowish tip.

For colour in life see Grandison (1972).

Ecological notes. — One female (ZFMK 16492) with three eggs in the oviducts (collected 25.v). Taylor (1963) stated that females carry four eggs.

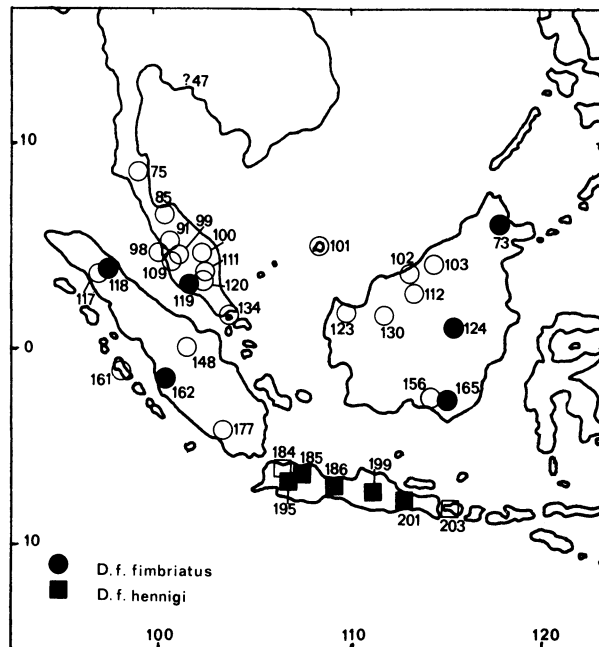


Fig. 8. Distribution of *Draco fimbriatus*. Open symbols are localities from the literature.

Distribution. — The subspecies occurs in West Malaysia, on the greater Sunda Islands Borneo and Sumatra and on some smaller islands in the western malaysian area (fig. 8). Boulenger (1908) stated that the (sub)species is usually found in lowland jungle and that the highest elevation reached by it is probably 900 m.

Remarks. — *D. cristatellus* Günther seems to differ from *fimbriatus* only in its small size and the fact that *cristatellus* has a gular pouch with a dark anterior edge. Except for the type, three specimens with a more or less dark anterior edge of the

gular pouch were present in the material examined: two specimens from Rantau (RMNH 19974-75, one of them a juvenile) and one from Upper Mahakkam (RMNH 4995 B, referred to by Van Lidth de Jeude, 1905). The three adult males (BM 72.2.19.4, RMNH 19974, RMNH 4995 B) have a snout-vent length of 75-81 mm (\bar{x} = 78.0). They do not differ from *fimbriatus* in any other characters. Although the difference in length is remarkable, especially when compared with the measurements given by Taylor (1963) and the values of *D. f. hennigi*, these three specimens do not provide enough arguments to regard *crisatellus* as a distinct species, because it is well possible that the animals are not full-grown. RMNH 4995 B is remarkable because it has a caudal crest continuous with the dorsal crest, which is present on the posterior third of the back.

The type of *D. punctatus* Boulenger differs from *fimbriatus* in snout-vent length (79 mm), gular pouch length (1.06 times the head length) and number of ribs (6). No differences can be found in colour or markings. Taylor (1963) stated that the specimens of *punctatus* he found had five ribs. Therefore the number of ribs of the type can be considered as a not unusual aberration. The other two differences could be due to the fact, that the specimen is not full-grown and, therefore this taxon is considered synonymous with *D. f. fimbriatus*.

Both Van Lidth de Jeude (1893) and Hennig (1936a) considered the juvenile *D. f. fimbriatus* (RMNH 4346) from the Sandakan bay, N. Borneo as a specimen of *D. lineatus*.

All specimens of the material here examined had larger or smaller spots on the ventral parts of the patagium, an observation also made by Hardwicke & Gray (1827), Stoliczka (1873), Baumann (1913), Smedley (1931), and Grandison (1972). Boulenger (1912) and Taylor (1963), however, stated that the (sub)species does not always have spots.

Both specimens from Padang, Sumatra (RMNH 2920) have a remarkably low number of dorsals (155, 166).

Examination of large collections of this subspecies could reveal how to interpret the high variability within this taxon.

***Draco fimbriatus hennigi* nov. subspec.**

(pl. 1 fig. a, pl. 2 fig. a)

Draco fimbriatus: Duméril & Bibron, 1837: 448, Fitzinger, 1843: 50; Schlegel, 1844: 92 (partim); Boulenger, 1885: 265 (partim); Boettger, 1892: 116; Boettger, 1893a: 43; Van Lidth de Jeude, 1905: 190 (partim); Barbour, 1912: 85; De Rooy, 1915: 79 (partim); Mertens, 1929b: 28; De Witte, 1933: 3; Saint-Girons & Saint-Girons, 1956: 137.

Draco fimbriatus fimbriatus: Hennig, 1936a: 202, fig. 10i, map 8 (partim); Wermuth, 1967: 47 (partim).

Holotype. — INDONESIA. JAVA. Soekamandi: 1 ♂, RMNH 19973, ii.1936, leg. F. Kopstein.

Paratypes. — INDONESIA. JAVA. Parang: 6 ♂, 1 ♀, RMNH 2922, leg. H. Boie; 7 ♂, 6 ♀, RMNH 2924, 2925, leg. H. Boie & H. Macklot; 2 ♀, RMNH 2926, leg. S. Müller. Tomo, Cheribon: 1 ♀, RMNH 9019, xii.1930, 100 m, leg. F. Kopstein. Soekamandi: 1 ♀, RMNH 19972, ii.1936, leg. F. Kopstein. Nongkodjadjar: 1 ♂, RMNH 19971, 1934, leg. F. Kopstein. Buitenzorg (= Bogor): 3 ♂, 3 ♀, SMF 23183-88, 1927, leg. R. Mertens. Surroundings Buitenzorg: 2 ♂, ZMA 12103, leg. H. Boschma.

Diagnosis. — Dorsals 200-256; ventral parts of patagium yellowish grey, without any spots.

Description of the holotype. — RMNH 19973: male; snout-vent length: 96 mm; tail length: 168 mm; head length: 21.1 mm; head depth: 11.5 mm; head width: 13.9 mm; snout length: 6.0 mm; gular pouch length: 27.9 mm; hindlimb length: 51/50 mm; distance limbs: 55/54 mm; thorn length: 0.42/0.42 mm; thorn width: 1.12/0.70 mm; two median upper teeth; tympanum covered with smooth skin; supralabials: 11/12; 12 nuchal crest scales on a fold; dorsals: 225; ventrals: 105; subdigital lamellae fourth finger: 24/23; ditto fourth toe: 26/25; ribs patagium: 5/5; nostril directed outward; caudal crest; bluish grey above, with dark spots and rests of bands; patagium dark brown with light, longitudinal lines; ventral parts whitish grey; chin with dark and light spots; gular pouch greyish white.

Description of the typeseries (table 1). — Maximum snout-vent length of females 110 mm, of males 104 mm; maximum head length in females 23.4 mm, in males 22.4 mm, 0.20-0.23 times the snout-vent length; head width 0.64-0.76 times the head length; head depth 0.45-0.57 times the head length; snout length 0.28-0.37 times the head length; nostril directed outward or slightly upward; supralabials 8-13, smooth or faintly keeled; usually two median teeth in upper jaw (two teeth: 76.5%, one tooth: 17.6%, three teeth: 2.9%); head scales unequal, keeled, enlarged in the supraciliary region; a series of enlarged, strongly keeled scales forming a Λ -shaped figure on the snout; thornlike scale on the supraciliary edge to 0.02 times the head length; a distinct tubercle at the end of the supraciliary edge; tympanum covered with smooth skin; two or three enlarged, keeled scales between the eye and the tympanum; many tubercles in the lateral parts of the neck, some arranged in rows, above, behind and under the tympanum; nuchal crest in males on a more or less pronounced fold, consisting of 9-28, triangular, tuberclelike scales; in females 2-13 compressed thornlike scales; gular pouch without enlarged scales, 1.20-1.67 times the head length in males and 0.66-1.09 times the head length in females; lateral pouches with enlarged scales; dorsals 200-256, unequal, smooth or faintly keeled; a row of compressed, thornlike scales on the border between body and patagium; ventrals 94-122, keeled, larger than the dorsals; usually five ribs in the patagium (five ribs: 82.4%, six ribs: 16.2%, four ribs: 1.5%); 21-26 keeled subdigital lamellae under the fourth finger, 22-28 under the fourth toe; hindlimbs 0.48-0.58 times the snout-vent length, 0.87-1.05 times the distance between the limbs; posterior edge of thigh and base of tail with fringelike scales; maximum tail length 191 mm, 1.39-1.85 times the snout-vent length; males with a caudal crest consisting of compressed triangular scales, serried or interrupted by one or two scales.

Colour in preservative. — Above bluish or brownish grey; females usually with dark interorbital spot and transverse bands (64%, remaining specimens with indistinct markings); males usually with dark spots all over the body (71%; 14% with bands and spots, the others with indistinct markings); patagium dark brown with more or less distinct, lighter, longitudinal lines or rests of these lines;

TABLE 1
Morphometric data of *Draco fimbriatus hennigi*

	Males (N=20)		Females (N=14)	
1	97.5 ± 4.3	(85-104)	98.4 ± 12.2	(73-110)
2	167.9 ± 14.0	(136-191)	168.6 ± 20.7	(129-185)
3	20.83 ± 1.13	(17.4-22.4)	21.27 ± 2.73	(15.1-23.4)
4	10.93 ± 0.70	(9.4-12.1)	10.61 ± 1.27	(7.8-11.7)
5	14.00 ± 0.67	(12.7-15.2)	14.36 ± 1.57	(11.0-16.1)
6	6.40 ± 0.46	(5.6-7.4)	6.95 ± 0.97	(4.7-8.1)
7	29.42 ± 2.06	(25.9-33.6)	19.14 ± 4.04	(13.2-24.9)
8	10.7 ± 1.1	(9-13)	10.6 ± 0.9	(8.5-12)
9	222.7 ± 16.1	(200-251)	226.5 ± 15.3	(205-256)
10	108.8 ± 7.7	(94-122)	105.4 ± 5.8	(95-116)
11	23.4 ± 1.3	(21-26)	23.5 ± 1.2	(21.5-26)
12	25.3 ± 1.2	(23.5-27.5)	25.9 ± 1.5	(22-27.5)
13	15.7 ± 5.0	(9-28)	8.1 ± 2.7	(2-13)
14	1.72 ± 0.12	(1.39-1.85)	1.72 ± 0.07	(1.58-1.80)
15	0.21 ± 0.01	(0.20-0.23)	0.22 ± 0.01	(0.20-0.23)
16	0.52 ± 0.02	(0.49-0.57)	0.50 ± 0.02	(0.45-0.54)
17	0.67 ± 0.02	(0.64-0.73)	0.68 ± 0.03	(0.65-0.76)
18	0.31 ± 0.02	(0.28-0.33)	0.33 ± 0.03	(0.29-0.37)
19	1.42 ± 0.12	(1.20-1.67)	0.90 ± 0.13	(0.66-1.09)
20	0.015 ± 0.003	(0.007-0.020)	0.015 ± 0.003	(0.010-0.020)
21	0.042 ± 0.007	(0.025-0.052)	0.043 ± 0.010	(0.031-0.070)
22	0.54 ± 0.02	(0.49-0.58)	0.55 ± 0.02	(0.48-0.58)
23	0.97 ± 0.05	(0.89-1.05)	0.95 ± 0.04	(0.87-1.01)

Means and standard deviations. Between the brackets the lowest and highest values are given. 1 = snout-vent length (mm); 2 = tail length (mm); 3 = head length (mm); 4 = head depth (mm); 5 = head width (mm); 6 = snout length (mm); 7 = gular pouch length (mm); 8 = mean number of supralabials; 9 = number of dorsals; 10 = number of ventrals; 11 = mean number of subdigital lamellae of the fourth finger; 12 = mean number of subdigital lamellae of the fourth toe; 13 = number of nuchal crest scales; 14 = tail length/snout-vent length; 15 = head length/snout-vent length; 16 = head depth/head length; 17 = head width/head length; 18 = snout length/head length; 19 = gular pouch length/head length; 20 = thorn length/head length; 21 = thorn width/head length; 22 = hindlimbs length/snout-vent length; 23 = hindlimbs length/distance limbs.

chest and belly bluish or yellowish light grey with some fine spots on the shoulders; chin very characteristic with white and black spots; ventral parts of patagium yellowish grey, without any spots; gular pouch in males very light yellowish grey, sometimes with indistinct, darker lines, running longitudinally and distally; in females the gular pouch is bluish grey with a yellowish distal part; in the grey parts minute lighter spots and lines may occur.

In life the males have white and the females red ventral parts; gular pouch in males white with a yellow tip and in females bright blue with an orange-yellow tip (Mertens, 1929b).

Ecological notes. — Nine females (64.3%) had eggs in the oviducts: five (55.5%) with four, two (22.2%) with three, one (11.1%) with two and one with one egg. One of these females (RMNH 19972) was collected in February. Of the other females no collecting dates are known.

The subspecies feeds on tree-ants (Mertens, 1929b).

Distribution. — This subspecies occurs on Java and Bali (fig. 8).

Remarks. — The Leiden Museum is in the possession of (a transcript of) the manuscript and the plates of the 'Erpétologie de Java' of H. Boie. *D. fimbriatus* occurs on plate 14 fig. 1 (pl. 1 fig. a) and 2 (pl. 2 fig. a), which were made after RMNH 2924 A. The species was described as follows:

“*Draco fimbriatus*

Draco naribus lateraliter apertis, occipite taberculato, taberculo post superciliari conico utrinque prominulo; squamis dorsalibus laevibus, serie tuberculorum sub hispidorum interrupta in utraque latere dorsi disposita, alis supra fuscis albido lineolatis, infra immaculatis”.

Since the specimen RMNH 2924 A is faded too much, it was not selected as the holotype.

***Draco haematopogon* Gray**

(pl. 1 fig. d, pl. 2 fig. d)

Draco haematopogon (Boie) Gray (in Griffith), 1831: 59 (terra typica: not given, here restricted to Parang, Java); Duméril & Bibron, 1837: 458; Fitzinger, 1843: 51; Schlegel, 1844: 95, pl. 24 fig. 6, 7, 8, 9 (partim); Boulenger, 1885: 267; Mocquard, 1890: 128; Boettger, 1892: 116; Boettger, 1893a: 43; Boulenger, 1894a: 613; Bartlett, 1894: 81; Volz, 1903: 426; Baumann, 1913: 261; De Rooy, 1915: 84; Lloyd et al., 1968: 499.

Dracocella haematopogon: Gray, 1845: 234.

Draco microlepis Boulenger, 1893: 532, pl. 42 fig. 2 (terra typica: Merabah, N. Borneo); Bartlett, 1894: 82; Boulenger, 1912: 62; Robinson & Kloss, 1914: 154; De Rooy, 1915: 86; Smith, 1916a: 53; Smith, 1930: 23; Taylor & Elbel, 1958: 1042.

Draco haematopogon haematopogon: Hennig, 1936a: 204, fig. 10l, map 9; Bourret, 1943: 13; Mertens, 1957: 90; Taylor, 1963: 850; Wermuth, 1967: 48.

Draco haematopogon microlepis: Hennig, 1936a: 206, map 9; Wermuth, 1967: 48 (new synonym).

Material examined. — MALAYSIA. SARAWAK. Baram: 1 ♂, 1 ♀, ZMA 15230, leg. C. H. Merabah, N. Borneo: 1 ♂, BM 1946.8.26.81 (93.3.6) (lectotype of *D. microlepis* Boulenger), xii.1892, leg. A. Everett; 1 ♀, BM 1946.8.26.82 (93.3.6) (paralectotype of *D. microlepis* Boulenger), xii.1892, leg. A. Everett. INDONESIA. SUMATRA. Padang: 1 ♂, 4 ♀, RMNH 2956, leg. S. Müller. Deli: 1 ♂, ZMA 15229, 1908-09, leg. L. P. le Cosquino de Bussy. KALIMANTAN. 1 ♀, RMNH 2957, 1837, leg. S. Müller. Upper Mahakkam: 1 ♂, RMNH 5734 B, leg. A. W. Nieuwenhuis. JAVA. Parang: 1 ♂, RMNH 2958 A (lectotype), 2 ♂, 4 ♀, RMNH 2958 B-E, 2960 (paralectotypes), all leg. H. Boie & H. Macklot. Malang: 2 ♂, RMNH 5733, leg. A. Köller. Bandung: 1 ♂, RMNH 5735, leg. Canngieter. Soekabumi: 1 ♂, ZMA 12042, 1909, leg. W. C. van Heurn. Nongkodjadar: 3 ♂, 2 ♀, RMNH 9024, 1934, ± 1200 m, leg. F. Kopstein. LOCALITY UNKNOWN: 1 ♀, RMNH 2946; 1 ♂, RMNH 19986, leg. J. W. Schoor.

Diagnosis. — A moderately sized species, maximum snout-vent length 94 mm; nostril directed upward; a row of keeled scales on the snout; usually two median teeth in upper jaw; supralabials 9-13, feebly keeled; no thornlike scale on the supraciliary edge; tympanum usually covered with smooth skin; gular pouch at tip with slightly enlarged scales; lateral pouches with slightly enlarged scales; dorsals 148-184, smooth, subequal; usually five ribs in patagium; hindlimbs about as long as the distance between the legs; no caudal crest; in males a large, coal black spot, in females a grey-brown spot at the base of the gular pouch.

Description. — (Data indicated with a B are from specimens collected in Borneo). Maximum snout-vent length in males 87 mm (\bar{x} = 76.1, sd = 8.0, N = 8; B: \bar{x} = 76.3, sd = 2.1, N = 3), in females 94 mm (\bar{x} = 86.0, sd = 10.3, N = 7; B: \bar{x} = 75.7, sd = 3.5, N = 3); maximum head length in males 16.3 mm, in females 17.6 mm, 0.17-0.20 times the snout-vent length (σ : \bar{x} = 0.19, sd = 0.01, N = 8; φ : \bar{x} = 0.19, sd = 0.01, N = 7; σ B: \bar{x} = 0.17, sd = 0.0, N = 3; φ B: \bar{x} = 0.18, sd = 0.01, N = 3); head width 0.64-0.75 times the head length (σ : \bar{x} = 0.68, sd = 0.03, N = 8; φ : \bar{x} = 0.67, sd = 0.02, N = 7; σ B: \bar{x} = 0.68, sd = 0.02, N = 3; φ B: \bar{x} = 0.70, sd = 0.04, N = 3); head depth 0.50-0.56 times the head length (σ : \bar{x} = 0.53, sd = 0.02, N = 8; φ : \bar{x} = 0.50, sd = 0.04, N = 7; σ B: \bar{x} = 0.54, sd = 0.01, N = 3; φ B: \bar{x} = 0.54, sd = 0.03, N = 3); snout length 0.25-0.33 times the head length (σ : \bar{x} = 0.30, sd = 0.02, N = 8; φ : \bar{x} = 0.29, sd = 0.01, N = 7; σ B: \bar{x} = 0.29, sd = 0.02, N = 3; φ B: \bar{x} = 0.27, sd = 0.02, N = 3); nostril directed upward; supralabials 9-13, feebly keeled; usually two median teeth in upper jaw (two teeth: 90.0 %, three teeth: 10.0 %); head scales subequal, faintly keeled; a row of enlarged, keeled scales on the snout; no thornlike scale on the supraciliary edge; a low, rounded tubercle at the end of the supraciliary edge; tympanum usually covered with smooth skin (in one specimen one tympanum was partly covered with small scales); between eye and tympanum sometimes one to three slightly enlarged scales; an enlarged, keeled scale above the tympanum; gular pouch in males sometimes with several more or less distinctly enlarged scales at the tip, 0.59-1.90 times the head length (\bar{x} = 1.42, sd = 0.41, N = 8; B: \bar{x} = 1.36, sd = 0.22, N = 3); in females 0.45-0.82 times the head length (\bar{x} = 0.69, sd = 0.09, N = 7; B: \bar{x} = 0.55, sd = 0.09, N = 3); lateral pouch with slightly enlarged scales; dorsals 148-184 (σ : \bar{x} = 165.8, sd = 11.7, N = 8; φ : \bar{x} = 159.9, sd = 6.5, N = 7; σ B: \bar{x} = 163.3, sd = 17.6, N = 3; φ B: \bar{x} = 171.7, sd = 8.6, N = 3), subequal, smooth or faintly keeled; enlarged, keeled scales on the border between body and patagium; ventrals 89-124 (σ : \bar{x} = 107.9, sd = 12.3, N = 8; φ : \bar{x} = 102.3, sd = 3.6, N = 7; σ B: \bar{x} = 108.3, sd = 11.6, N = 3; φ B: \bar{x} = 107.0, sd = 7.8, N = 3), keeled, slightly larger than dorsals; usually five ribs in the patagium (five ribs: 92.8 %, six ribs: 7.2 %); 20-26 (σ : \bar{x} = 23.8, sd = 1.7, N = 8; φ : \bar{x} = 23.3, sd = 1.8, N = 7; σ B: \bar{x} = 20.8, sd = 0.8, N = 3; φ B: \bar{x} = 21.5, sd = 1.3, N = 3) keeled subdigital lamellae under the fourth finger, 21-29 (σ : \bar{x} = 25.1, sd = 2.2, N = 8; φ : \bar{x} = 25.6, sd = 1.0, N = 7; σ B: \bar{x} = 23.3, sd = 2.3, N = 3; φ B: \bar{x} = 24.8, sd = 1.0, N = 3) under the fourth toe; hindlimbs 0.53-0.63 times the snout-vent length (σ : \bar{x} = 0.59; sd = 0.03, N = 8; φ :

$\bar{x} = 0.58$, $sd = 0.03$, $N = 7$; ♂ B: $\bar{x} = 0.57$, $sd = 0.03$, $N = 3$; ♀ B: $\bar{x} = 0.61$, $sd = 0.03$, $N = 3$), 0.86-1.06 times the distance between the limbs (♂: $\bar{x} = 0.99$, $sd = 0.06$, $N = 8$; ♀: $\bar{x} = 0.96$, $sd = 0.05$, $N = 7$; ♂ B: $\bar{x} = 0.98$, $sd = 0.01$, $N = 3$; ♀ B: $\bar{x} = 1.03$, $sd = 0.04$, $N = 3$); fringelike scales on posterior edge of thigh and on base of tail; maximum tail length 172 mm in males, 179 mm in females, 1.51-1.98 times the snout-vent length (♂: $\bar{x} = 1.83$, $sd = 0.18$, $N = 8$; ♀: $\bar{x} = 1.86$, $sd = 0.09$, $N = 7$; ♂ B: $\bar{x} = 1.77$, $sd = 0.01$, $N = 3$; ♀ B: $\bar{x} = 1.87$, $sd = 0.09$, $N = 3$); no caudal crest.

Colour in preservative. — Above bluish to brownish grey with large, indistinct, lighter and darker spots; indistinct interorbital spot present; sometimes with darker spots in the nuchal region; patagium usually dark brown with dark-centred, light spots, sometimes forming bands; in some specimens the light spots are no longer recognizable and the patagium appears light with dark bands and spots; light, longitudinal lines are present; chest and belly yellowish white; the chin with minute, light and dark grey spots; ventral parts of the patagium yellowish white, usually without any markings, sometimes with some dark brown spots; gular pouch in males yellowish white with a very distinct, large, coal black spot at the base; in females the gular pouch is yellowish or orangish white with an indistinct, large, grey-brown spot at the base.

In life the patagium is black with lemon-yellow spots; chin and base of the gular pouch in males red with a large black spot; tip yellow (after Schlegel, 1844).

Ecological notes. — Three females with eggs in the oviducts; two (RMNH 2956 B, 2958 C) had three and one (RMNH 2958 L) had two eggs. No collecting dates of these females are available.

Distribution. — This species occurs in Southern Thailand, Malaya, Sumatra, Sipora, Borneo and Java (fig. 9). It is found to an altitude of ± 1200 m.

Remarks. — Gray (1831) based the name *haematopogon* on H. Boie, who described the species in the unpublished 'Erpétologie de Java'. In the manuscript of the 'Erpétologie de Java', in the Leiden Museum, the following description occurs:

"*Draco haematopogon*

Draco - naribus horizontaliter apertis, occipite tuberculato, tuberculo post superciliari conico utrinque prominente; paleari longissimo angusto citrino, ad basin utrinque macula nigra rubro marginata, sacculis collaribus subtus rubris, squamis dorsalibus laevibus, serie tuberculorum sub-hispidorum interrupta in utroque latere dorsi; alis ut in *Draco timorensis*".

The table of contents of the plates of this work refers to two plates on which *D. haematopogon* should occur, viz. pl. 17, which has not been found sofar, and pl. 16 fig. 3 (pl. 1 fig. d) and 4 (pl. 1 fig. d). Comparing this latter plate with the material that could have been available to Boie (RMNH 2958, 2960), shows that either the specimens are not the same as on the plate or the material is in too bad a condition to ascertain so. RMNH 2958 A is designated here as lectotype. It is a male, collected by H. Boie & H. Macklot and one of a series of seven specimens,

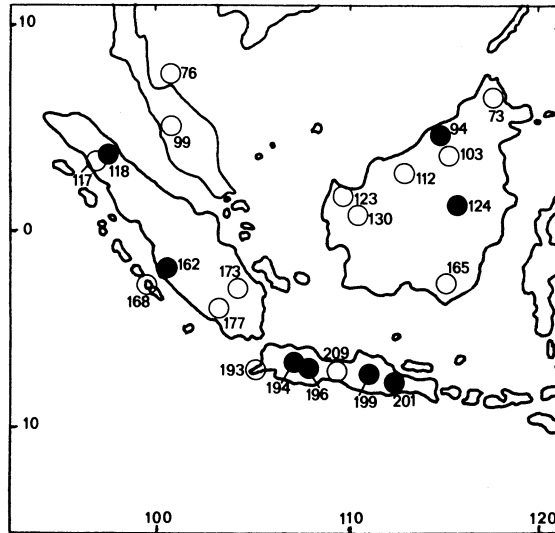


Fig. 9. Distribution of *Draco haematopogon*. Open symbols are localities from the literature.

all collected in Parang, Java. Description of the lectotype: male; snout-vent length: 86 mm; tail length: 155 mm; head length: 15.1 mm; head depth: 7.7 mm; head width: 10.4 mm; snout length: 4.6 mm; gular pouch length: 24.8 mm; hindlimb length: 47/48 mm; distance limbs: 54/53 mm; two median upper teeth; tympanum covered with smooth skin; supralabials: 9/11; dorsals: 166; ventrals: 119; subdigital lamellae fourth finger: 25/25; ditto fourth toe: 26/25; ribs patagium: 5/5; nostril directed upward; no caudal crest; strongly paled; patagium pale with rests of markings; distinct black spot at base of gular pouch.

When Schlegel (1844: 95) under *D. haematopogon* stated that: "Zuweilen geschieht es auch, dass dieser schwarze Fleck sich mehr oder weniger über den Kehlsack selbst verbreitet, oder denselben ganz einnimmt", he is referring to specimens of *D. melanopogon*. Plate 24 fig. 6 of this same work is based on RMNH 2957 (= *D. haematopogon*).

Hennig (1936a) stated that the specimens from Borneo (his subspecies *microlepis*) had a shorter snout and perhaps a shorter tail. However, the differences between specimens from Borneo and those from other areas in these characters or in any other characters (see 'description') do not seem to justify to regard *microlepis* a distinct subspecies of *haematopogon*. *Microlepis* is the name for the colourmorph in which the spots on the patagium are so large that the patagium gives the impression of being light with dark brown bands and spots, at the outer edge forming a reticulated pattern. Intermediate forms do occur and consequently *microlepis* must be regarded a synonym of *haematopogon*. Being the specimen of which a picture was published by Boulenger (1893), BM 1946.8.26.81 is here selected as lectotype of *D. microlepis*. Description: male;

snout-vent length: 78 mm; tail length: 138 mm; head length: 13.6 mm; head depth: 7.4 mm; head width: 9.4 mm; snout length: 4.3 mm; gular pouch length: 16.2 mm; hindlimb length: 45/46 mm; distance limbs: 47/46; number of median upper teeth unknown; tympanum covered with smooth skin on one side, partly with small scales on the other; supralabials: 13/13; dorsals: 158; ventrals: 115; subdigital lamellae fourth finger: 20/23; ditto fourth toe: 26/25; no nuchal crest; ribs patagium: 5/5; nostril directed upward; gular pouch without enlarged scales; grey above; head dark brown; interorbital spot present; body with irregular, large, dark spots; limbs and tail banded; patagium dark-brown with light, dark-centred spots, near the body merging into bands; ventral parts yellowish white, with some dark spots on the outer edge of the patagium; chin dark grey with fine dark and light spots; gular pouch brownish grey, with a light tip and a black spot at the base.

The name *Draco Reinwardtii* (Boie) Fitzinger, 1843 is not a nomen nudum for *Draco haematopogon* Gray, but for *Draco lineatus* Daudin. For arguments see p. 36.

Draco lineatus Daudin

Diagnosis. — Small or moderately sized species (maximum snout-vent length 91 mm); nostril directed outward; series of keeled scales forming a row or A-shaped figure on the snout; usually three median teeth in upper jaw; supralabials 5-10, smooth; thornlike scale on supraciliary edge absent or very small; tympanum covered with smooth skin only, partly with small scales or with small scales only; gular pouch and lateral pouches without enlarged scales or with only slightly enlarged ones; nuchal crest present; dorsals 101-156, smooth or feebly keeled, subequal; six or five ribs in patagium; hindlimbs about as long as the distance between the legs; no caudal crest.

KEY TO THE SUBSPECIES

1. Usually six ribs in patagium; only known from Enggano *D. lineatus modiglianii* (p. 45)
Usually five ribs in patagium; not from Enggano 2
2. Tympanum usually covered with small scales only 3
Tympanum at least partly covered with smooth skin 6
3. Lateral parts of the head and neck in males without distinct, light spots 4
Lateral parts of the head and neck in males with distinct, light spots 5
4. Males with at least one distinct black spot at the front edge of the patagium; females with dark, bluish gular pouch; Kepulauan Banggai *D. lineatus rhytisma* (p. 47)
Males without a black spot at the front edge of the patagium; in females gular pouch white with small black spots, never bluish; Northern Sulawesi *D. lineatus spilonotus* (p. 50)
5. Patagium in males ochre yellow; Kepulauan Kai *D. lineatus ochropterus* (p. 47)
Patagium in males not ochre yellow; Buru, Seram, Amboin and Kepulauan Sula
..... *D. lineatus bourouniensis* (p. 41)
6. A white-centred black spot between the tympanum and the corner of the mouth; Philippines
..... *D. lineatus bimaculatus* (p. 40)
No such a spot between the tympanum and the corner of the mouth; not from the Philippines 6
7. Java and Bali *D. lineatus lineatus* (p. 35)
Middle and Southern Sulawesi *D. lineatus beccarii* (p. 37)

One could regard *D. lineatus* as a superspecies. But since the subtaxa are allopatric and difficult to distinguish, except on the basis of colour, they are regarded here as subspecies. Four subspecies-groups can be recognized: the *lineatus*-group, containing *D. l. lineatus*, *D. l. beccarii* and *D. l. spilonotus*; the *bourouniensis*-group, containing *D. l. bourouniensis*, *D. l. ochropterus* and *D. l. rhytisma*; the *bimaculatus*-group, containing *D. l. bimaculatus* only and the *modiglianii*-group, containing *D. l. modiglianii* only.

Draco lineatus lineatus Daudin

(pl. 3 fig. c, d)

Draco lineatus Daudin, 1802: 298 (terra typica: Java); Kuhl, 1820: 102; Gray, 1831: 59; Wiegmann, 1834a: 14; Wiegmann, 1834b: 217; Schlegel, 1844: 93 (partim); Boulenger, 1885: 264 (partim); Wandolleck, 1900: 12; De Rooy, 1915: 76 (partim); De Witte, 1933: 2 (partim).

Dracunculus personatus Wiegmann, 1834a: 14 (nomen substitutum pro *Draco lineatus* Daudin).

Dracontoides lineatus: Fitzinger, 1843: 51.

Draco Reinwardtii (Boie) Fitzinger, 1843: 51 (nomen nudum); Hennig, 1936a: 205; Wermuth, 1967: 48.

Dracunculus lineatus: Gray, 1845: 235 (partim).

Draco lineatus lineatus: Hennig, 1936a: 195, map 7; Mertens, 1936: 127; Wermuth, 1967: 49.

Material examined. — INDONESIA. JAVA. 2♂, 1♀, RMNH 2965, leg. H. Kuhl & J. C. v. Hasselt; 1♀, ZMA 15244, leg. Kimmel.

Diagnosis. — A subspecies reaching a snout-vent length of 79 mm; supralabials 7-9, smooth; tympanum usually covered with smooth skin; gular pouch and lateral pouches without enlarged scales; dorsals 118-138; five ribs in patagium; patagium brown with light, longitudinal lines and spots forming bands near the body edge; chin and lateral parts of head without distinct spots.

Description. — Maximum snout-vent length in females 79 mm (Hennig, 1936a), 72-75 mm in material examined (N = 2), in males 70 mm (68-70 mm, N = 2); maximum head length 17.3 mm in females and 13.2 mm in males, 0.20-0.24 times the snout-vent length in females (\bar{x} = 0.21, sd = 0.02, N = 3, measurements of Hennig, 1936a and material examined), 0.18-0.19 times in males (\bar{x} = 0.19, sd = 0.01, N = 3, based on Hennig, 1936a and material examined); head width 0.63-0.65 times the head length (♂: \bar{x} = 0.64, sd = 0.01, N = 3; ♀: \bar{x} = 0.63, sd = 0.01, N = 3; based on Hennig, 1936a and material examined); head depth 0.49-0.51 times the head length in females (N = 2), 0.52-0.55 times in males (N = 2); snout length 0.30-0.33 times the head length (♂: 0.30-0.33, N = 2; ♀: 0.31-0.32, N = 2); nostril directed outward; supralabials 7-9, smooth; three median teeth in upper jaw; head scales unequal, enlarged in supraocular region, keeled; a series of enlarged, keeled scales on the snout forming a row or A-shaped figure; no thornlike scale on the supraciliary edge; a low, rounded tubercle at the end of the supraciliary edge; in three specimens the tympanum is covered with smooth skin, in one with small scales only; a row of 3-4 enlarged, faintly keeled scales between the tympanum and the eye; two low tubercles above and behind the tympanum; indistinct nuchal crest in males and females, con-

sisting of 6-15 compressed, triangular scales (σ : 12-13, $N = 2$; φ : 6-15, $N = 2$); gular pouch without enlarged scales, 0.73-1.00 times the head length in males ($\bar{x} = 0.89$, $sd = 0.14$, $N = 3$, based on Hennig, 1936a and material examined), 0.43-0.62 ($N = 2$) times in females; lateral pouches indistinct, without enlarged scales; dorsals 118-138 (σ : 121-123, $N = 2$; φ : 118-138, $N = 2$), subequal, smooth or very faintly keeled; with or without very few enlarged scales on the border between body and patagium; ventrals 85-98 (σ : 85-95, $N = 2$; φ : 91-98, $N = 2$), keeled, about as large as the dorsals; usually five ribs in the patagium (two specimens had six ribs on the left and five on the right side); 24-26 (σ : 24, $N = 2$; φ : 25-26, $N = 2$) keeled subdigital lamellae under the fourth finger, 24-29 (σ : 27-28, $N = 2$; φ : 24-29, $N = 2$) under the fourth toe; hindlimbs 0.53-0.60 times the snout-vent length (σ : $\bar{x} = 0.57$, $sd = 0.03$, $N = 3$; φ : $\bar{x} = 0.57$, $sd = 0.01$, $N = 3$, based on Hennig, 1936a and material examined), 0.98-1.00 ($N = 2$) times the distance between the limbs in males, 0.91-0.96 ($N = 2$) times the distance between the limbs in females; indistinct, fringelike scales on posterior edge of thigh; maximum tail length 162 mm (Hennig, 1936a), 1.61-1.97 times the snout-vent length in males ($\bar{x} = 1.80$, $sd = 0.18$, $N = 3$, based on Hennig, 1936a and material examined), 2.04-2.07 times the snout-vent length in females ($\bar{x} = 2.05$, $sd = 0.02$, $N = 3$, based on Hennig, 1936a and material examined); no caudal crest present.

Colour in preservative. — Above light bluish and brownish grey; distinct nuchal spot; no distinct markings on the body; patagium dark brown with light, longitudinal lines and spots forming bands near the body; chest and belly bluish white; chin with small, but distinct, dark spots, far apart; ventral parts of patagium yellowish white, with some small indistinct, brown spots at the outer edge; gular pouch orangish lightgrey with some distinct, dark spots. (Based on one female (ZMA 15244), the pattern of the other specimens has completely faded).

Ecological notes. — Both females with eggs in the oviducts, one (ZMA 15244) had two and the other (RMNH 2965 A) had three eggs. No collecting dates are available.

Distribution. — This subspecies occurs on Java and Bali (fig. 10).

Remarks. — The name *Draco Reinwardtii* occurs in the afore mentioned manuscript of the 'Erpétologie de Java' of H. Boie. It is described as follows: "*Draco Reinwardtii*.

Draco- naribus lateraliter apertis, occipitis tuberculis nullis prominentibus, nec dorsi; paleari lato triquetro apice prolongato citrino in mare, subrotundo albido ad basin nigro punctato in femina, squamis dorsalibus laevibus; alis supra fuscis in mare ad basin et postice albo lineolatis, margine lattissime atro maculisque duobus atris anterioribus, infra candidis maculis atris duobus magnis; in femina ex aurantiaco nigroque pucherrime variis, infra uti in mare''.

Plate 15 fig. 3, 4 (pl. 3 fig. c, d) of Boie's manuscript shows two specimens of this taxon. Apart from that, the name occurs on three jars in the Leiden Museum, viz. 2965, containing three faded specimens of *D. l. lineatus* from Java,

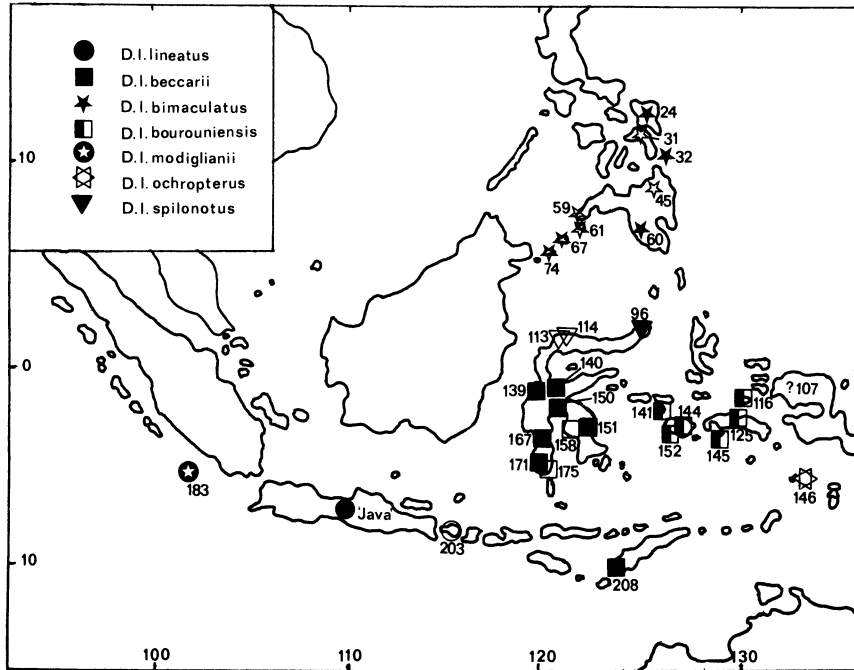


Fig. 10. Distribution of *Draco lineatus*. Open symbols are localities from the literature.

2966, containing six specimens of *D. l. beccarii* from Celebes and 2961, containing two specimens of *D. l. spilonotus* from Manado, Celebes. Comparison of the specimens from Celebes with the plate, shows that certainly none of these lizards served as a model for these figures. The specimens from Java, which are in a bad condition, possibly could have served as a model for these figures and consequently are here regarded as the 'syntypes' of *Draco Reinwardtii* which is a nomen nudum for *D. l. lineatus*.

On the basis of the material examined it is very difficult to find differences between this subspecies and *D. l. beccarii*. Hennig (1936a) however, stated that he thinks that *lineatus* can be distinguished from *beccarii* on the basis of the colour. More material should be examined to confirm this.

***Draco lineatus beccarii* Peters & Doria**

Draco lineatus: Duméril & Bibron, 1837: 459 (? partim); Weber, 1890: 166; De Rooy, 1915: 76 (partim).

Draco beccarii Peters & Doria, 1878: 373 (terra typica: Kandari, Celebes); Boulenger, 1885: 264; Boulenger, 1897b: 206, pl. 9; Wandolleck, 1900: 13, fig. 16; Roux, 1911: 496; De Rooy, 1915: 77; Smith, 1927: 215.

Draco walkeri Boulenger, 1891a: 279 (terra typica: Koepang, Timor); De Rooy, 1915: 75; Smith, 1927: 215.

Draco lineatus beccarii: Hennig, 1936a: 198, map 7; Hennig, 1936b: fig. 4; Wermuth, 1967: 49.

Material examined. — INDONESIA. SULAWESI. 3♂, 3♀, RMNH 2966, leg. G. v. Raalten. Macassar: 1 juv., RMNH 2937, leg. D. M. Piller. Lamontjong: 1♀, ZMA 12038, leg. Sarasin. Loewoe: 1♂, ZMA 15237, 1889, leg. M. Weber. Tempe: 1♂, 1♀, ZMA 15243, leg. Eerdmans. Posso: 2♂, ZMA 15245, 1898, leg. J. A. Kruyt. Sopa Valley, 80 km S. of Palu: 1♂: 1 juv., RMNH 20017-18, iv/v.1979, 1000-1500 m, leg. E. F. de Vogel. TIMOR. Koepang: 1♀, BM 1946.8.26.94 (90.12.2) (lectotype of *D. walkeri* Boulenger); 1♂, 1♀, 1 juv., BM 1946.8.26.95-97 (90.12.2) (paralectotypes of *D. walkeri* Boulenger), leg. J. J. Walker.

Diagnosis. — A subspecies reaching a snout-vent length of 80 mm; supralabials 6-10, smooth; tympanum usually at least partly covered with smooth skin; gular and lateral pouches without enlarged scales; dorsals 101-150; usually five ribs in patagium; patagium in males brown to dark brown with light, longitudinal lines, mainly near the body edge; in females brown with light spots forming bands or reticulated white parts near the edge of the body.

Description. — Maximum snout-vent length in females 80 mm ($\bar{x} = 70.1$, $sd = 6.5$, $N = 7$), in males 70 mm ($\bar{x} = 65.5$, $sd = 2.7$, $N = 8$) (juv.: 41-46 mm, $N = 2$); maximum head length 16.1 mm in females, 14.2 mm in males, 0.18-0.22 times the snout-vent length (♂: $\bar{x} = 0.20$, $sd = 0.01$, $N = 8$; ♀: $\bar{x} = 0.21$, $sd = 0.01$, $N = 7$; juv.: 0.21, $N = 2$); head depth 0.47-0.69 times the head length (♂: $\bar{x} = 0.56$, $sd = 0.02$, $N = 8$; ♀: $\bar{x} = 0.54$, $sd = 0.04$, $N = 7$; juv.: 0.53-0.69, $N = 2$); head width 0.61-0.83 times the head length (♂: $\bar{x} = 0.67$, $sd = 0.02$, $N = 8$; ♀: $\bar{x} = 0.66$, $sd = 0.04$, $N = 7$; juv.: 0.64-0.83, $N = 2$); snout length 0.27-0.39 times the head length (♂: $\bar{x} = 0.32$, $sd = 0.04$, $N = 8$; ♀: $\bar{x} = 0.30$, $sd = 0.02$, $N = 7$; juv.: 0.27, $N = 2$); nostril directed outward; supralabials 6-10, smooth; usually three median teeth in upper jaw (three teeth: 93.8 %, two teeth: 6.2 %); head scales unequal, enlarged in the supraocular and parietal region, smooth or faintly keeled; a row of large, keeled scales on the snout; usually no thornlike scale on the supraciliary edge (one male and one female have very low thornlike scales: 0.01 times the head length); a low rounded tubercle at the end of the supraciliary edge; tympanum usually partly covered with small scales (50.0 %) or with smooth skin only (41.2 %), sometimes with small scales only (8.8 %); six or seven enlarged scales, partly in a double row, between the eye and the tympanum; two low tubercles, one above and one behind the tympanum; nuchal crest in both sexes consisting of 6-20 compressed, triangular (frontal) or enlarged, keeled scales (caudal) (♂: $\bar{x} = 14.1$, $sd = 2.8$, $N = 8$; ♀: $\bar{x} = 12.6$, $sd = 4.2$, $N = 7$); gular pouch without enlarged scales, 0.69-1.09 times the head length in males ($\bar{x} = 0.85$, $sd = 0.13$, $N = 8$) and 0.43-0.75 times the head length in females ($\bar{x} = 0.57$, $sd = 0.11$, $N = 7$) (juv.: 0.55-0.81, $N = 2$); lateral pouches without enlarged scales; dorsals 101-150 (♂: $\bar{x} = 128.6$, $sd = 10.7$, $N = 8$; ♀: $\bar{x} = 122.1$, $sd = 16.2$, $N = 7$; juv.: 101-130, $N = 2$), smooth or faintly keeled, subequal; with or without very few enlarged scales on the border between body and patagium; ventrals 85-112 (♂: $\bar{x} = 98.7$, $sd = 8.5$, $N = 8$; ♀: $\bar{x} = 93.4$, $sd = 5.3$, $N = 7$; juv.: 94-99, $N = 2$), keeled, about as large as, or slightly smaller than dorsals; usually five ribs in the patagium (five ribs: 91.2 %, six ribs: 8.8 %); 21-25 (♂: $\bar{x} = 23.3$, $sd = 1.1$, $N = 8$; ♀: $\bar{x} = 23.2$,

sd = 1.3, N = 7; juv.: 22-23, N = 2) keeled subdigital lamellae under the fourth finger, 22-27 (σ : \bar{x} = 25.4, sd = 1.5, N = 8; φ : \bar{x} = 25.0, sd = 0.8, N = 7; juv.: 24-26, N = 2) under the fourth toe; hindlimbs 0.52-0.61 times the snout-vent length (σ : \bar{x} = 0.57, sd = 0.03, N = 8; φ : \bar{x} = 0.57, sd = 0.03, N = 7; juv.: 0.55-0.61, N = 2) and 0.89-1.04 (\bar{x} = 0.94, sd = 0.05, N = 8) times the distance between the limbs in males, 0.89-1.13 (\bar{x} = 0.99, sd = 0.05, N = 7) times the distance between the limbs in females (juv.: 0.88-1.00, N = 2); indistinct, fringelike scales on posterior edge of thigh; maximum tail length 163 mm in females, up to 135 mm in males, 1.88-1.97 (\bar{x} = 1.92, sd = 0.04, N = 7) times the snout-vent length in males, 1.94-2.04 (\bar{x} = 1.97, sd = 0.07, N = 6) times the snout-vent length in females (juv.: 1.85-1.87, N = 2); no caudal crest.

Colour in preservative. — Above bluish and brownish grey, usually with indistinct, lighter bands; head of females with interorbital spot or thin band, a dark spot on the supraorbital region and a nuchal spot; radial lines around the eyes; in males these markings are absent or vaguely indicated; patagium in males brown to very dark brown at the outer anterior edge, with light, longitudinal lines, mainly near the body edge; patagium in females brown, with light spots forming bands, or with reticulated, white parts near the edge of the body and bands near the outer anterior edge; chest and belly bluish white; chin in males bluish or yellowish with more or less distinct, light spots; in females bluish or yellowish white, sometimes with indistinct, darker spots; ventral parts of patagium either yellowish white with a few (three) dark spots at the anterior edge, completely or nearly completely dark brown in some males; gular pouch in males orangish, usually with lighter or darker spots at the base; in females yellowish white with distinct, dark spots.

For colour in life see Boulenger (1897b: pl. 9).

Ecological notes. — Four of the females had eggs in the oviducts, three of them (ZMA 12038, 15243 A, RMNH 2966 B) had two and the other (RMNH 2966 D) had three eggs. No collecting dates are available.

Distribution. — The subspecies occurs on Southern and Central Sulawesi and on Timor (fig. 10).

Remarks. — From the tail length given by Boulenger (1891a), which is the length of a broken tail, it is clear that he used BM 1946.8.26.94 for these measurements and therefore this specimen is here selected as lectotype of *D. walkeri*. Description: female; snout-vent length: 74 mm; tail length: 115 mm; head length: 15.4 mm; head depth: 7.3 mm; head width: 11.5 mm; snout length: 4.1 mm; gular pouch length: 7.4 mm; hindlimb length: 41/41 mm; distance limbs: 41/42 mm; three median upper teeth; tympanum covered with smooth skin; supralabials: 7/8; dorsals: 105; ventrals: 94; subdigital lamellae fourth finger: 22/22; ditto fourth toe: 25/25; nuchal crest scales: 6; ribs patagium: 5/5; nostril directed outward; gular pouch without enlarged scales; lateral pouches without enlarged scales; no caudal crest; probably two eggs; brownish grey above; nuchal spot and lateral nuchal spot present; lateral parts of the body with small, dark brown spots; patagium dark brown with a light, finely

reticulated pattern, the outer frontal edge with four dark bands; ventral parts yellowish blue; ventral parts of the patagium orangish yellow with two dark brown spots on the frontal edge; chin yellowish; gular pouch yellowish with distinct spots; ventral hind edge of the lateral pouches with dark spot.

Considering the fact that the types of *D. walkeri* are the only specimens of this taxon collected on Timor, and considering that they can not be distinguished from *D. beccarii*, it seems justified to doubt the correctness of the locality Timor.

Kopstein (1927: 439) stated that the specimens of *Draco* he investigated from the Sula Archipelago probably were *D. beccarii*, but since all the material from Sula, investigated by me, clearly belongs to *D. l. bourouniensis*, Kopsteins remark must be considered a misidentification (see p. 42).

***Draco lineatus bimaculatus* Günther**

Draco bimaculatus Günther, 1864: 127 (terra typica: Philippines Isl.); Boulenger, 1885: 263, pl. 20 fig. 6; Boettger, 1886: 97; Taylor, 1918: 246, pl. 2 fig. 1, 2; Taylor, 1922a: 126, pl. 7 fig. 1, 2; Taylor, 1923: 531; Tanner, 1949: 33.

Draco lineatus: De Witte, 1933: 2 (partim).

Draco lineatus bimaculatus: Hennig, 1936a: 197, fig. 11g, map 7; Wermuth, 1967: 49.

Material examined. — PHILIPPINES. 1 ♂, BM 23.1.g, (holotype); 1 ♂, 1 ♀, RMNH 2955 E, F, 1847, Frank; 1 ♂, ZFMK 20899, 1871, leg. G. Semper. MINDANAO. Cotabato Coast: 1 ♂, 1 ♀, ZMA 12039, 1923, leg. E. H. Taylor. SAMAR ISL.: 1 ♂, RMNH 2983, Mus. Berlin. DINAGAT ISL.: 2 ♀, BM 77.10.9.14-15, leg. Higgins (A. Everett).

Diagnosis. — A subspecies reaching a snout-vent length of 73 mm; supralabials 8-10; tympanum usually covered with smooth skin; lateral pouches with slightly enlarged scales; dorsals 122-150; five ribs in patagium; a black, white-centred spot between the tympanum and the corner of the mouth.

Description. — Maximum snout-vent length in females 73 mm (Hennig, 1936a), 69 mm in material examined ($\bar{x} = 64.8$, $sd = 4.7$, $N = 4$), 70 mm in males ($\bar{x} = 66.4$, $sd = 2.3$, $N = 5$); maximum head length 13 mm (Hennig, 1936a), 0.17-0.20 times the snout-vent length (♂: $\bar{x} = 0.18$, $sd = 0.01$, $N = 5$; ♀: $\bar{x} = 0.19$, $sd = 0.01$, $N = 4$); head width in males 0.66-0.71 ($\bar{x} = 0.68$, $sd = 0.02$, $N = 5$) times the head length, in females 0.63-0.68 ($\bar{x} = 0.65$, $sd = 0.02$, $N = 4$) times; head depth 0.52-0.59 times the head length (♂: $\bar{x} = 0.56$, $sd = 0.02$, $N = 5$; ♀: $\bar{x} = 0.56$, $sd = 0.04$, $N = 4$); snout length 0.25-0.32 times the head length (♂: $\bar{x} = 0.27$, $sd = 0.01$, $N = 5$; ♀: $\bar{x} = 0.29$, $sd = 0.03$, $N = 4$); nostril directed outward; supralabials 8-10 (Hennig, 1936a), smooth; number of median teeth in upper jaw usually three (three teeth: 88.9 %, two teeth: 11.1 %); head scales unequal, variably keeled, enlarged in the supraocular region, with smaller ones near the supraciliary edge; a row of enlarged, keeled scales on the snout; no thornlike scale on the supraciliary edge; a low, rounded tubercle at the end of the supraciliary edge; tympanum covered with smooth skin; 4-6 enlarged scales between the tympanum and the eye; 2-3 low tubercles above and behind the tympanum, an enlarged scale between the tympanum and the corner of the

mouth; nuchal crest in males on a low fold, consisting of 17-22 (\bar{x} = 20.2, sd = 2.2, N = 5) small, compressed, triangular scales; nuchal crest in females indistinct (in one specimen six enlarged, keeled scales); gular pouch without enlarged scales, in males 1.10-1.32 times (\bar{x} = 1.25, sd = 0.09, N = 5), in females 0.59-0.86 (\bar{x} = 0.77, sd = 0.12, N = 4) times the head length; lateral pouches with slightly enlarged scales; dorsals 122-150 (σ : \bar{x} = 136.2, sd = 10.3, N = 5; φ : \bar{x} = 133.3, sd = 9.5, N = 4), slightly keeled; with or without a few enlarged, keeled scales on the border between body and patagium; ventrals 79-99, (σ : \bar{x} = 91.0, sd = 7.2, N = 5; φ : \bar{x} = 84.5, sd = 6.0, N = 4), keeled, slightly larger than dorsals; five ribs in patagium; 17-22 (σ : \bar{x} = 19.8, sd = 2.2, N = 5; φ : \bar{x} = 19.5, sd = 1.3, N = 4) keeled subdigital lamellae under the fourth finger, 22-26 (σ : \bar{x} = 24.1, sd = 1.4, N = 5; φ : \bar{x} = 23.7, sd = 1.0, N = 4) under the fourth toe; hindlimbs 0.57-0.66 (σ : \bar{x} = 0.62, sd = 0.03, N = 5; φ : \bar{x} = 0.63, sd = 0.01, N = 4) times the snout-vent length, 0.90-1.15 (σ : \bar{x} = 1.05, sd = 0.09, N = 5; φ : \bar{x} = 1.11, sd = 0.04, N = 4) times the distance between the limbs; fringelike scales on posterior edge of thigh; maximum tail length 131 mm, 1.49-1.94 (σ : \bar{x} = 1.89, sd = 0.05, N = 4; φ : 1.49-1.81, N = 2) times the snout-vent length; no caudal crest.

Colour in preservative. — Above bluish or brownish grey with more or less distinct, dark bands; interorbital spot present; a nuchal spot may be present; black, white-centred spot between the tympanum and the corner of the mouth (the white centre coinciding with the enlarged scale between the tympanum and the corner of the mouth); patagium in males dark brown with lighter grey, longitudinal lines, bands are very vaguely recognizable; patagium in females brown with fine, light spots, giving it a finely, reticulated impression and with light grey lines superimposed on it; chest and belly light, more or less bluish grey, sometimes with brown spots; chin usually with dark lines running from the sublabials to the gular pouch, sometimes these lines are broken up into separate spots; ventral parts of patagium bluish to yellowish grey with distinct, darkbrown spots; gular pouch in males light grey with a lighter, anterior edge, sometimes with dark spots; gular pouch in females coal black with a light, bluish grey anterior and posterior edge, the dark being continued on the underside of the lateral pouches; in females a light bluish grey band behind the gular pouch and behind this, in front of the shoulders, a black band.

For colour in life see Taylor (1922a).

Ecological notes. — Taylor (1922a) stated that females usually lay two eggs.

Distribution. — The subspecies occurs on the Philippines (fig. 10). It is known to occur to an altitude of 600 m above sealevel (Taylor, 1923).

***Draco lineatus bourouniensis* Lesson**

(pl. 1 fig. b, pl. 2 fig. b)

Draco bourouniensis Lesson, 1834: pl. 37 (terra typica: Bourou).

Draco amboinensis Lesson, 1834: pl. 38 (terra typica: Amboine) (new synonym).

Draco lineatus: Duméril & Bibron, 1837: 459 (partim); Schlegel, 1844: 93 (partim), pl. 24 fig. 5;

Peters & Doria, 1878: 373 (partim); Boulenger, 1885: 264 (partim); Boettger, 1892: 149; Lampe & Lindholm, 1901: 202; De Rooy, 1915: 76 (partim); De Jong, 1926: 88; Brongersma, 1933: 18; Pfeffer, 1962: 417.

Dracunculus lineatus: Gray, 1845: 235 (partim).

Draco toxopei De Jong, 1926: 88 (terra typica: Buru).

Draco buruensis De Jong, 1926: 89 (terra typica: Buru).

Draco beccarii: Kopstein, 1927: 439.

Draco lineatus amboinensis: Hennig, 1936a: 199, map 7; Wermuth, 1967: 49.

Draco lineatus bourouniensis: Hennig, 1936a: 201, fig. 11b, map 7; Wermuth, 1967: 49.

Material examined. — INDONESIA. MOLUCCAS. BURU: 1 ♂, RMNH 19740, leg. D. J. Hoedt; 1 juv., RMNH 2945, leg. E. W. A. Ludeking; 1 ♂, 4 ♀, RMNH 5732, 1863, leg. D. J. Hoedt. Hills of M. Buru: 2 ♀, ZMA 15240, 24/25.iii.1921, leg. L. J. Toxopeus. Lesula: 1 ♂, ZMA 10931 (lectotype *D. buruensis* De Jong), 23.ii.1921, leg. L. J. Toxopeus; 2 ♀, ZMA 15232, 1921, leg. L. J. Toxopeus. Ehoe: 2 ♂, ZMA 10932-33 (paralectotypes *D. buruensis* De Jong), 1921, 600-1100 m, leg. L. J. Toxopeus; 3 ♀, ZMA 15241, 20/30.ix.1921, 600-1100 m, leg. Estrin. Wa'katin: 1 ♂, ZMA 10934 (lectotype *D. toxopei* De Jong), 6.vi.1921, leg. L. J. Toxopeus; 2 ♀, ZMA 15239, 25.iii.1921, leg. L. J. Toxopeus. Rana: 1 ♂, ZMA 10935 (paralectotype *D. toxopei* De Jong), 1921, leg. L. J. Toxopeus; 3 ♀, 1 juv., ZMA 15242, 1921, leg. L. J. Toxopeus; 2 ♀, ZMA 15234, 1921, 600 m, leg. L. J. Toxopeus. Wai Eno: 2 ♀, ZMA 15233, 1921, leg. L. J. Toxopeus. KEPULAUAN SULA: 1 ♂, 2 ♀, RMNH 5472, leg. J. W. v. Nouhuys. SULA BES: 2 ♂, 5 ♀, RMNH 19741-47, leg. H. A. Bernstein. SERAM: 1 ♂, RMNH 4998, leg. D. J. Hoedt; 2 ♀, RMNH 19764-65, 1915, leg. J. M. Kampmeindert. East Seram: 1 ♂, 1 ♀, ZMA 15236, leg. Le Cocq d'Armandville. Upper Toeba: 1 ♂, 1 ♀, ZMA 15231, leg. L. F. de Beaufort. Wahaay: 2 ♂, 1 ♀, RMNH 2939, 2941, 1862, leg. J. C. B. Bernelot Moens. Papoetiek bay: 1 ♂, 2 ♀, RMNH 2938, 1863, leg. E. W. A. Ludeking. AMBON: 2 ♂, 7 ♀, RMNH 2963, ix.1828, leg. S. Müller & H. Macklot; 2 ♀, RMNH 2967; 1 ♀, ZMA 15235, ii.1910, leg. Oedien; 11 ♂, 5 ♀, RMNH 199748-63, 1866, leg. D. J. Hoedt. MISOÖL: 2 ♀, BM 70.8.31.133-134, leg. Januack. 'TIMOR?': 1 ♂, ZFMK 20898, 1846, Frank. 'N. CELEBES': 2 ♀, ZMA 15238 B, C, 1884, leg. S. C. J. W. van Musschenbroek. 'JAVA': 1 ♂, BM 51.7.17.65, leg. Parzudake; 1 ♂, 3 ♀, BM 63.7.b-d, leg. E. Belcher. LOC. UNKNOWN: 2 ♀, RMNH 2936; 5 ♂, 2 ♀, RMNH 2964, 1844, leg. E. A. Forsten.

Diagnosis. — A subspecies reaching a snout-vent length of 91 mm; supralabials 5-8, smooth; tympanum usually covered with small scales or partly with smooth skin; gular pouch and lateral pouches without enlarged scales; dorsals 110-156; usually five ribs in patagium; patagium in males dark with indistinct, light spots to completely light with small remains of the dark ground colour; in females dark with light, longitudinal lines; males with distinct, light spots on the lateral parts of the head and the neck; females with indistinct, light spots; gular pouch in males with distinct, yellowish white spots at the base.

Description (table 2). — Maximum snout-vent length 85 mm in males, 91 mm in females (juv.: 50-56, N = 2); maximum head length 16.4 mm in males, 19.5 mm in females, 0.18-0.23 times the snout-vent length (juv.: 0.20-0.22, N = 2); head width 0.57-0.69 times the head length (juv.: 0.66-0.69, N = 2); head depth 0.46-0.60 times the head length (juv.: 0.59, N = 2); snout 0.27-0.39 times the head length (juv.: 0.29, N = 2); nostril directed outward; supralabials 5-8, smooth; usually three median teeth in upper jaw (three teeth: 96.4 %, two teeth: 1.2 %, one tooth: 2.4 %); head scales unequal, enlarged in supraciliary region, keeled; a series of enlarged, strongly keeled scales forming a row or a Λ -shaped figure on the snout; usually no thornlike scale (97.6 %), the rest with a

TABLE 2
Morphometric data of *Draco lineatus bourouniensis*

	A Males N=8	A Females N=22	B Males N=21	B Females N=30
1	69.5 ± 13.0	82.2 ± 5.2	73.2 ± 5.5	77.6 ± 7.0
2	149.1 ± 30.7	175.7 ± 14.6	150.6 ± 12.6	160.4 ± 15.9
3	13.94 ± 2.25	17.39 ± 1.18	14.61 ± 1.16	16.04 ± 1.61
4	6.5 ± 0.5	6.5 ± 0.8	6.3 ± 0.8	6.7 ± 0.6
5	137.9 ± 6.9	137.9 ± 6.4	138.5 ± 9.4	137.1 ± 9.4
6	96.8 ± 3.6	96.2 ± 8.6	97.0 ± 8.7	96.1 ± 6.8
7	24.1 ± 1.3	23.6 ± 1.1	22.7 ± 1.5	23.5 ± 1.3
8	27.8 ± 1.3	26.9 ± 1.3	26.7 ± 1.4	26.8 ± 1.7
9	16.1 ± 2.7	13.7 ± 3.9	15.6 ± 2.7	14.6 ± 4.0
10	2.18 ± 0.11	2.14 ± 0.12	2.07 ± 0.12	2.08 ± 0.10
11	0.20 ± 0.01	0.21 ± 0.00	0.20 ± 0.01	0.21 ± 0.01
12	0.57 ± 0.02	0.53 ± 0.02	0.52 ± 0.02	0.51 ± 0.02
13	0.67 ± 0.02	0.63 ± 0.02	0.63 ± 0.02	0.63 ± 0.03
14	0.30 ± 0.02	0.32 ± 0.02	0.32 ± 0.03	0.32 ± 0.02
15	0.97 ± 0.21	0.68 ± 0.07	1.04 ± 0.20	0.71 ± 0.09
16	0.65 ± 0.08	0.61 ± 0.02	0.61 ± 0.03	0.61 ± 0.02
17	1.09 ± 0.14	1.04 ± 0.04	1.04 ± 0.06	1.03 ± 0.05

Means and standard deviations. A: specimens from Buru and Sula Island; B: specimens from Ambon and Seram; 1 = snout-vent length (mm); 2 = tail length (mm); 3 = head length (mm); 4 = mean number of supralabials; 5 = number of dorsals; 6 = number of ventrals; 7 = mean number of subdigital lamellae of the fourth finger; 8 = mean number of subdigital lamellae of the fourth toe; 9 = number of nuchal crest scales; 10 = tail length/snout-vent length; 11 = head length/snout-vent length; 12 = head depth/head length; 13 = head width/head length; 14 = snout length/head length; 15 = gular pouch length/head length; 16 = hindlimbs length/snout-vent length; 17 = hindlimbs length/distance limbs.

low thorn (up to 0.02 times the head length) on the supraciliary edge; a very low tubercle at the end of the supraciliary edge can be present; tympanum usually covered with small scales only (67.9 %), or with smooth skin and several small scales (28.3 %) (4.9 % completely covered with smooth skin); a few (1-3) more or less distinctly enlarged scales between the tympanum and the eye; a low tubercle above the tympanum and a more distinct one behind it; nuchal crest consists of 4-20 compressed, triangular or strongly keeled scales (juv.: 15-19, N = 2); gular pouch without enlarged scales, 0.33-1.35 times the head length in males and 0.50-0.88 times the head length in females (juv.: 0.68-0.83, N = 2); lateral pouches poorly developed, without enlarged scales; dorsals 110-156 (juv.: 128-140, N = 2), subequal, faintly keeled; with or without a few indistinctly enlarged scales on the border between body and patagium; ventrals 79-117 (juv.:

95-99, N = 2), keeled, about as large as, or slightly larger than dorsals; usually five ribs in patagium (five ribs: 98.2 %, six ribs: 1.8 %); 19-26 (juv.: 25-26, N = 2), keeled subdigital lamellae under the fourth finger, 23-31 (juv.: 27-29, N = 2) under the fourth toe; hindlimbs 0.55-0.84 times the snout-vent length (juv.: 0.61-0.63, N = 2) and 0.96-1.43 times the distance between the limbs (juv.: 1.01-1.07, N = 2); small, indistinct, fringelike scales on posterior edge of thigh; maximum tail length 204 mm, 1.74-2.32 times the snout-vent length (juv.: 2.09-2.14, N = 2); no caudal crest.

Colour in preservative. — Above bluish grey; males with bluish white, transverse bands in nuchal and thoracic region, distinct, light spots on the lateral parts of the head and on the lateral pouches, eye surrounded by a dark and a light band; females with light grey head, sometimes with brownish snout, body with thin, transverse, dark bands, usually as posterior edge of a light band, lateral parts of head with indistinct, lighter spots on light grey background; patagium in males varying from dark grey or brown with light lines and more or less distinct, spots forming bands to completely light with small remains of the dark ground colour, at half unfolded wings, recognizable as remains of dark bands; patagium in females dark brownish or bluish grey with longitudinal, light lines; chest and belly bluish or yellowish white; chin in males with yellowish white, median lines, lateral parts grey with indistinct, yellowish white spots; in females yellowish white anterior part, lateral posterior parts light grey with indistinct, lighter spots; ventral parts of patagium yellowish or bluish grey, sometimes with indistinct, dark markings and lighter, longitudinal lines; gular pouch in males yellowish or orangish white, at the base bluish grey with distinct, yellowish white spots; in females blue grey, at the base grey with indistinct, lighter spots.

Ecological notes. — More than half (59 %) the females had eggs in the oviducts, usually two (92.3 %), sometimes three (7.7 %). Females with eggs were collected in February, March, July and December. For further ecological and ethological data see Pfeffer (1962).

Distribution. — The subspecies occurs on Buru, Ambon, Seram, Kepulauan Sula and Misoöl (fig. 10). De Jong (1926) reported the taxon from New Guinea, but this probably was in error (Brongersma in: Hennig, 1936a).

Remarks. — Since no clear differences can be found between the specimens from Buru and Sula Isl. on the one hand and those from Seram and Ambon on the other (table 2), *D. l. amboinensis* is here regarded as a synonym of *bourouniensis*. Some colour differences between specimens from the different islands are evident (see below), but the distribution of these colourmorphs does not coincide with that of either *amboinensis* or *bourouniensis*.

Males occur in two colourmorphs, although intermediate forms occur: one with a dark patagium with light lines and more or less distinct, spots forming bands and one with a light patagium, with small remains of dark bands (the dark form was described as *D. toxopei*, the light form as *D. buruensis* by De Jong, 1926). On Buru both forms occur together, on the Sula Isl. the light form seems to

dominate, on Seram the dark form dominates and on Ambon the lighter form dominates again. There cannot be found any difference between the females.

Plate 14 figs. 3 (pl. 1 fig. b) and 4 (pl. 2 fig. b) of the manuscript of H. Boie's 'Erpétologie de Java' shows the habitus and the head of a *Draco*, which is clearly *D. l. bourouniensis* under the name of *Draco lineatus*. It is described as follows in the manuscript:

“*Draco lineatus*.

Draco- naribus lateraliter apertis, occipite tuberculato, tuberculis supra tympanum duobus vix prominentibus; paleari lato triquetro ad basin flavido ocellato maris apice angusto producto, citrino feminae parvo rotundato, cijaneo; squamis dorsalibus carinatis tuberculis dorsalibus nullis; alis fuscis, albo longitudinaliter lineolatis”.

It is assumed that the localities ‘Timor?’ (ZFMK 20898), ‘N. Celebes’ (ZMA 15238 B, C) and ‘Java’ (BM 63.7.b-d; 51.7.17.65) are wrong, since the specimens clearly belong to *D. l. bourouniensis*.

Brongersma (in Hennig, 1936a: 169, 194) expressed the view that, if the localities Misoöl and New Guinea should prove to be correct, the animals were imported there.

***Draco lineatus modiglianii* Vinciguerra**

Draco modiglianii Vinciguerra, 1892: 253 (terra typica: Enggano); De Rooy, 1915: 78.

Draco lineatus modiglianii: Hennig, 1936a: 196, map 7; Wermuth, 1967: 50.

Material examined. — INDONESIA. ENGGANO. 1 ♂, BM 1946.8.26.92 (91.11.9) (lectotype), 1 ♀, BM 1946.8.26.91 (19.11.9) (paralectotype), both leg. E. Modigliani; 33 ♂, 22 ♀, 1 juv., RMNH 19766-821, vi.1936, leg. J. K. de Jong.

Diagnosis. — A subspecies reaching a snout-vent length of 71 mm; supralabials 6-9; tympanum usually covered with smooth skin; lateral pouch with slightly enlarged scales; dorsals 110-135; six or seven ribs in patagium; lateral parts of nuchal region in males with light spots.

Description. — Maximum snout-vent length in females 71 mm (\bar{x} = 60.9, sd = 6.5, N = 22), in males 66 mm (\bar{x} = 57.0, sd = 6.9, N = 33) (juv.: 39 mm); maximum head length 15.7 mm in females, 14.3 mm in males, 0.20-0.24 times the snout-vent length (♂: \bar{x} = 0.22, sd = 0.01, N = 33; ♀: \bar{x} = 0.22, sd = 0.01, N = 22; juv.: 0.24); head width 0.61-0.71 times the head length (♂: \bar{x} = 0.65, sd = 0.02, N = 33; ♀: \bar{x} = 0.65, sd = 0.02, N = 22; juv.: 0.66); head depth 0.51-0.60 times the head length (♂: \bar{x} = 0.55, sd = 0.02, N = 33; ♀: \bar{x} = 0.54, sd = 0.02, N = 22; juv.: 0.59); snout length 0.23-0.35 times the head length (♂: \bar{x} = 0.29, sd = 0.02, N = 33; ♀: \bar{x} = 0.30, sd = 0.03, N = 22; juv.: 0.28); nostril directed outward; supralabials 6-9, smooth; usually three median teeth in upper jaw (three teeth: 83.9 %, two teeth: 8.9 %, one tooth: 7.1 %); head scales unequal, keeled, smaller ones near the supraciliary edge; a series of enlarged, keeled scales forming a **Λ**-shaped figure on the snout; thornlike scale usually absent (92.9 %) or very low (up to 0.013 times the head length); tubercle at the end of

the supraciliary edge low, rounded; tympanum covered with smooth skin (94.8 %) or partly with smooth skin (5.2 %); 3-6 enlarged scales between the eye and the tympanum; one, usually indistinct, low tubercle above the tympanum; nuchal crest in males on a low fold, consisting of 9-25 ($\bar{x} = 20.0$, $sd = 3.3$, $N = 33$) small, compressed, triangular scales, in females 7-22 ($\bar{x} = 15.8$, $sd = 4.5$, $N = 22$) such scales (juv.: 16); gular pouch without enlarged scales, in males 0.60-1.24 times ($\bar{x} = 1.00$, $sd = 0.19$, $N = 33$), in females 0.43-0.60 times the head length ($\bar{x} = 0.53$, $sd = 0.05$, $N = 22$) (juv.: 0.68); lateral pouches with slightly enlarged scales; dorsals 110-135 (σ : $\bar{x} = 121.3$, $sd = 6.2$, $N = 33$; φ : $\bar{x} = 120.7$, $sd = 6.0$, $N = 22$; juv.: 128), subequal, smooth or very faintly keeled; sometimes a few scales on the border between body and patagium are slightly enlarged, faintly keeled; ventrals 73-97 (σ : $\bar{x} = 83.7$, $sd = 5.2$, $N = 33$; φ : $\bar{x} = 83.6$, $sd = 5.4$, $N = 22$; juv.: 85), keeled, about as large as the dorsals; patagium usually with six ribs (six ribs: 97.4 %, one specimen with seven ribs in both patagia, another one with seven ribs in one patagium); 19-27 (σ : $\bar{x} = 22.4$, $sd = 1.0$, $N = 33$; φ : $\bar{x} = 23.0$, $sd = 1.6$, $N = 22$; juv.: 20.5) keeled subdigital lamellae under the fourth finger, 23-30 (σ : $\bar{x} = 26.3$, $sd = 1.0$, $N = 33$; φ : $\bar{x} = 26.7$, $sd = 1.5$, $N = 22$; juv.: 26) under the fourth toe; hindlimbs 0.54-0.63 times the snout-vent length (σ : $\bar{x} = 0.58$, $sd = 0.02$, $N = 33$; φ : $\bar{x} = 0.60$, $sd = 0.02$, $N = 22$; juv.: 0.56) and 0.95-1.11 times the distance between the limbs (σ : $\bar{x} = 1.02$, $sd = 0.04$, $N = 33$; φ : $\bar{x} = 1.04$, $sd = 0.05$, $N = 22$; juv.: 1.0); small, fringelike scales on posterior edge of thigh; maximum tail length 155 mm in females, 2.04-2.38 times the snout-vent length ($\bar{x} = 2.21$, $sd = 0.09$, $N = 22$), 148 mm in males, 1.77-2.37 times the snout-vent length ($\bar{x} = 2.13$, $sd = 0.12$, $N = 33$) (juv.: 1.87); no caudal crest.

Colour in preservative. — Above bluish in males, brownish in females; interorbital spot present, sometimes a nuchal spot too; in females body with more or less distinct, dark spots; in males eyes surrounded with a dark and a light band (as in *D. l. bourouniensis*), lateral parts of nuchal region with light spots; patagium in males dark brown with very fine, bluish grey, longitudinal lines; patagium in females dark brown with lighter spots and longitudinal lines; chest and belly yellowish or bluish white; chin in males bluish with lighter spots or with dark and light bands; in females yellowish, sometimes with dark spots forming bands; ventral parts of patagium yellowish or brownish, sometimes with some brown spots at the outer edge; gular pouch in males yellowish white with distinct, grey spots; in females greyish with lighter or darker spots.

Ecological notes. — Half of the females had eggs in the oviducts, usually two (90.9 %), sometimes one (9.1 %). All were collected in June.

Distribution. — Only known from the island of Enggano (fig. 10).

Remark. — The two specimens of this taxon in the BM have the designation 'type' on their labels. Since Vinciguerra (1892) did not state on which specimen he based his description, one of them, the male BM 1946.8.26.92 is selected here as lectotype of *D. modiglianii*. Description: male; snout-vent length: 59 mm; tail length: 127 mm; head length: 13.0 mm; head depth: 7.6 mm; head width: 8.2

mm; snout length: 3.8 mm; gular pouch length: 14.2 mm; hindlimb length: 33/34 mm; distance limbs: 32/32 mm; three median upper teeth; tympanum partly covered with small scales; supralabials: 8/8; dorsals: 119; ventrals: 79; subdigital lamellae fourth finger: 24/22; ditto fourth toe: 27/27; nuchal crest scales: 17; ribs patagium: 6/6; nostril directed outward; gular pouch without enlarged scales; lateral pouches with slightly enlarged scales; no caudal crest; dark brown above; interorbital spot present; lateral parts of the neck with distinct, light spots; patagium dark brown with indistinct, lighter lines; ventral parts yellowish or bluish white; those of the patagium light, yellowish brown with some indistinct, dark spots; chin whitish with bluish grey, reticulated markings; gular pouch pale yellow, near the base with grey spots as on the ventral parts of the lateral pouches.

***Draco lineatus ochropterus* Werner**

Draco ochropterus Werner, 1910: 11 (terra typica: Kei Inseln); De Rooy, 1915: 79.

Draco lineatus: Werner, 1910: 12.

Draco lineatus ochropterus: Smith & Procter, 1921: 354; Hennig, 1936a: 201, map 7; Wermuth, 1967: 50.

Unfortunately no material for examination was available.

Diagnosis. — A subspecies, reaching a snout-vent length of 83 mm; supralabials 5-6; tympanum covered with small scales; lateral pouches indistinct; number of dorsals unknown; five ribs in patagium; lateral parts of head and neck with distinct, light spots in males; patagium in males ochre yellow (after Werner, 1910 and Hennig, 1936a).

Distribution. — Kepulauan Kai (Werner, 1910) (fig. 10).

***Draco lineatus rhytisma* nov. subsp.**

(pl. 4 figs. a, b)

Material examined. — INDONESIA. KEPULAUAN BANGGAI. Pulau Labobo, Lipulalongo: 1♂, RMNH 20993, holotype, 17.xi.1981; 2♂, 4♀, 2 juv., RMNH 20988-92, 20994-96, paratypes, 17.xi.1981, 0-50 m alt.; Pulau Peleng, Bonepuro: 1♂, 1♀, RMNH 20997-98, paratypes, 21.xi.1981, 20-100 m alt., all leg. W. F. Rodenburg.

Diagnosis. — A subspecies reaching a snout-vent length of 85 mm; supralabials 5-8, sometimes feebly keeled; lateral pouches without enlarged scales; dorsals 127-165; usually five ribs in patagium; patagium in males dark brown with more or less distinct lighter spots and at least one distinct large black spot at the front edge; patagium in females dark greyish brown with light lines; gular pouch in females dark bluish grey.

Description of the holotype. — RMNH 20993 (pl. 4 figs. a, b): male; snout-vent length: 82 mm; tail length: 165 mm; head length: 15.4 mm; head depth: 9.4 mm; head width: 10.2 mm; snout length: 4.9 mm; gular pouch length: 15.6 mm; hindlimb length: 45/46 mm; distance limbs: 44/45 mm; no thornlike scale

at the supraciliary edge; three median upper teeth; tympanum covered with small scales; supralabials: 7/8; nuchal crest scales: 14; dorsals: 150; ventrals: 91; subdigital lamellae fourth finger: 24/24; ditto fourth toe: 28/28; ribs patagium: 5/5; nostril directed outward; no caudal crest; head and body dark grey above; patagium near body dark brown with lighter spots that enlarge into light areas near the outer edge; a distinct black spot, covered with parts of three light lines, near the front edge of the patagium; belly and chest bluish yellow; chin grey; ventral parts of the head and base of gular pouch dark grey with small light grey spots; gular pouch yellowish white; in life (after colourslides made by W. F. Rodenburg) the body was bright yellowish green; patagium greenish brown with yellowish brown spots and a black spot near the front edge; belly bluish white; chin greenish grey; patagium ventrally yellowish grey; lateral and ventral parts of head and base of gular pouch green with small yellow spots; gular pouch yellow.

Description of the typeseries. — Maximum snout-vent length in females 85 mm (\bar{x} = 80.6, sd = 4.0, N = 5) and 82 mm in males (\bar{x} = 79.4, sd = 2.1, N = 4) (juv.: 46-53, N = 2); head length to 17.5 mm in females and to 15.7 mm in males, 0.19-0.21 times the snout-vent length (σ : \bar{x} = 0.19, sd = 0.01, N = 4; φ : \bar{x} = 0.20, sd = 0.0, N = 5; juv.: 0.21, N = 2); head width 0.62-0.70 times the head length (σ : \bar{x} = 0.65, sd = 0.01, N = 4; φ : \bar{x} = 0.66, sd = 0.03, N = 5; juv.: 0.63-0.67, N = 2); head depth 0.52-0.61 times the head length (σ : \bar{x} = 0.55, sd = 0.04, N = 4; φ : \bar{x} = 0.53, sd = 0.01, N = 5; juv.: 0.57-0.60, N = 2); snout 0.30-0.35 times the head length (σ : \bar{x} = 0.33, sd = 0.02, N = 4; φ : \bar{x} = 0.32, sd = 0.01, N = 5; juv.: 0.31, N = 2); nostril directed outward; supralabials 5-8, smooth or faintly keeled; usually three median teeth in upper jaw (three teeth: 72.7 %; two teeth: 9.1 %; no teeth: 9.1 %); head scales unequal, keeled, enlarged in the median supraocular and the parietal region, with a row or a Λ -shaped figure of enlarged scales on the snout; no thornlike scale on the supraciliary edge; tubercle at the posterior end of the supraciliary edge very low; tympanum always completely covered with small scales; a few (0-3) more or less distinctly enlarged scales between the eye and the tympanum; one or two small tubercles above and behind the tympanum; nuchal crest in males consisting of 14-18 (\bar{x} = 15.3, sd = 2.3, N = 4), compressed, triangular scales, in females of 6-15 (\bar{x} = 12.2, sd = 3.6, N = 5) such scales (juv.: 5-7, N = 2); gular pouch without enlarged scales, 0.79-1.01 (\bar{x} = 0.90, sd = 0.10, N = 4) times the head length in males, 0.36-0.48 (\bar{x} = 0.42, sd = 0.04, N = 5) times in females (juv.: 0.37-0.48, N = 2); lateral pouches without enlarged scales; dorsals 127-165 (σ : \bar{x} = 140.0, sd = 10.2, N = 4; φ : \bar{x} = 152.4, sd = 11.3, N = 5; juv.: 130-142, N = 2), smooth or faintly keeled, sometimes with a few indistinctly enlarged scales on the border between the body and the patagium; ventrals 85-107 (σ : \bar{x} = 96.0, sd = 4.6, N = 4; φ : \bar{x} = 103.8, sd = 1.9, N = 5; juv.: 85-95, N = 2), keeled, about as large as or slightly larger than dorsals; usually five ribs in patagium (five ribs: 90.5 %; six ribs: 4.8 %; four ribs: 4.8 %); 22-28 (σ : \bar{x} = 24.3, sd = 1.7, N = 4; φ : \bar{x} = 24.3, sd = 1.9, N = 5; juv.: 24-27, N = 2) keeled subdigital lamellae under the

fourth finger; 27-31 (σ : \bar{x} = 29.5, sd = 1.1, N = 4; φ : \bar{x} = 28.7, sd = 0.8, N = 5; juv.: 27-28, N = 2) keeled lamellae under the fourth toe; hindlimbs 0.55-0.63 times the snout-vent length (σ : \bar{x} = 0.58, sd = 0.04, N = 3; φ : \bar{x} = 0.58, sd = 0.02, N = 5; juv.: 0.56-0.59, N = 2) and 0.97-1.11 times the distance between the limbs (σ : \bar{x} = 1.06, sd = 0.05, N = 3; φ : \bar{x} = 1.01, sd = 0.05, N = 5; juv.: 1.00-1.08, N = 2); small fringelike scales on the posterior edge of the thigh; maximum tail length 187 mm, 1.78-2.19 times the snout-vent length (σ : \bar{x} = 1.93, sd = 0.13, N = 3; φ : \bar{x} = 2.12, sd = 0.08, N = 4; juv.: 1.98-2.09, N = 2); no caudal crest.

Colour in preservative. — Above dark, sometimes bluish, grey; females with small, more or less distinct, band-forming darker spots on head and body; patagium in males dark grey with more or less distinct lighter spots, that may enlarge to lighter areas near the outer edge, a distinct large black spot, sometimes (in one specimen) accompanied by a second smaller one, at the front edge; patagium in females dark brownish grey with light longitudinal lines; chest and belly yellowish grey; chin bluish grey, sometimes with a yellowish median part; ventral parts of head and base of gular pouch in males and females grey, usually with small lighter spots; ventral parts of patagium in males and females yellowish blue-grey; gular pouch in males yellowish white, at base grey with small lighter spots, in females bluish dark grey, sometimes with indistinct small lighter spots.

Colour in life (after field notes of W. F. Rodenburg). — Males bright grass-green above, with light bronze green spots along the middorsum from behind the shoulders to the base of the tail; females variegated light, medium and dark bronze green to brown above with a variable amount of black spots especially on the head; tail light bronze-brown, banded with pale grey; limbs in males light green above, with light bronze-brown spots and bands; patagium in males brown with yellow spots of variable size and a big black spot; in females dark grey to black with greenish to brownish lines; chest and belly dirty white with faint bronze sheen; ventral parts of head and neck in males bright green with pale yellow spots, in females greenish or brownish grey with distinct lighter spots; ventral parts of patagium in folded condition with yolk-yellow hue, dark grey when extended; gular pouch in males yellowish, at the base bright green with pale yellow spots, in females bluish grey with light grey spots.

Ecological notes. — All females carried eggs: one had one egg, one had three eggs and the other three had two eggs each. The females were all collected in November.

Distribution. — This subspecies occurs on the Kepulauan (Archipelago) Banggai.

Remarks. — The material of this subspecies was received after the main body of the manuscript was finished. For this reason this taxon does not occur in the analyses of chap. 5, in table 4 or in the distribution maps.

The Banggai Archipelago is situated between Central Sulawesi and the Sula Archipelago, but especially Pulau Peleng lies much nearer to Sulawesi than to

the Sula Archipelago. However, *D. l. rhytisma* differs in many respects from *D. l. spilonotus* and *D. l. beccarii*, respectively from N. and S. Sulawesi. The animals from the Banggai Archipelago are larger, they have relatively longer hindlimbs and a larger number of dorsals. In colour they differ from those of Sulawesi in the absence of a nuchal spot, the presence of the black spot at the front edge of the patagium in males and the bluish gular pouch in females (which is white with small, distinct black spots in the females from Sulawesi). *D. l. rhytisma* seems more closely related to *D. l. bourouniensis*, that occurs on the Sula Archipelago. It does not differ from this latter subspecies in any of the morphometric characters examined. However, the males differ remarkably in colour, again because of the black spot at the front edge of the patagium, but also because of the absence of the large, distinct yellowish white spots on the lateral parts of the head and neck and the absence of the yellowish white and the black band around the eye (compare pl. 1 fig. b with pl. 4 fig. b). The females probably can not be distinguished from those of *D. l. bourouniensis*. Thus, based on *Draco* one could state that the Banggai Archipelago zoogeographically is more related to the Sula Archipelago than to Sulawesi.

Etymology. — The name *rhytisma* is Greek and means “patch, spot” and is used here in reference to the distinct black spot at the front edge of the patagium in males.

***Draco lineatus spilonotus* Günther**

Draco lineatus: Duméril & Bibrion, 1837: 459 (? partim); Peters & Doria, 1878: 373 (partim); De Rooy, 1915: 75 (partim).

Draco spilonotus Günther, 1872: pl. 35 fig. b (terra typica: Manado); Günther, 1873: 167; Boulenger, 1885: 265; Boulenger, 1897b: 206, pl. 8; Wandolleck, 1900: 13, fig. 12; Sarasin & Sarasin, 1901: 67; De Rooy, 1915: 77.

Draco spilopterus Günther, 1872: 592 (ex errore).

Draco lineatus spilonotus: Hennig, 1936a: 199, fig. 11a, map 7; Wermuth, 1967: 50.

Material examined. — INDONESIA. SULAWESI. 1♂, BM 1946.8.27.27 (71.7.20) (lectotype), 1♂, BM 1946.8.27.26 (71.7.20) (paralectotype), both leg. A. B. Meyer; 1♀, ZFMK 20894, 1847, Frank. N. Sulawesi: 4♂, RMNH 4993, 1864, leg. W. F. H. Rosenberg; 1♂, 1♀, ZMA 15238 A, 12046, 1884, leg. S. C. J. W. van Musschenbroek. Manado: 2♂, 1♀, RMNH 2962, leg. E. A. Forsten; 1♂, 1♀, RMNH 2961, leg. P. J. A. v. Delden; 1♂, RMNH 4994, 1865, leg. J. G. F. Riedel.

Diagnosis. — A subspecies reaching a snout-vent length of 80 mm; supralabials 5-8, sometimes feebly keeled; lateral pouches without enlarged scales; dorsals 103-134; usually five ribs in patagium; patagium in males yellowish or orangish white with some dark spots forming bands only near the edge of the body; in females dark brown with light spots forming bands and light grey, longitudinal lines.

Description. — Maximum snout-vent length in females 80 mm (Hennig, 1936a), 73 mm in material examined (\bar{x} = 68.7, sd = 3.1, N = 4), in males 68 mm (\bar{x} = 60.8, sd = 4.7, N = 11); maximum head length in females 18 mm (Hennig,

1936a), 0.21-0.23 times the snout-vent length ($\bar{x} = 0.22$, $sd = 0.01$, $N = 4$); maximum head length in males 14 mm, 0.19-0.21 times the snout-vent length ($\bar{x} = 0.20$, $sd = 0.01$, $N = 11$); head width 0.62-0.70 times the head length (σ : $\bar{x} = 0.65$, $sd = 0.02$, $N = 11$; φ : $\bar{x} = 0.65$, $sd = 0.03$, $N = 4$); head depth 0.49-0.60 times the head length (σ : $\bar{x} = 0.55$, $sd = 0.03$, $N = 11$; φ : $\bar{x} = 0.53$, $sd = 0.01$, $N = 4$); snout 0.24-0.34 times the head length (σ : $\bar{x} = 0.30$, $sd = 0.03$, $N = 11$; φ : $\bar{x} = 0.31$, $sd = 0.03$, $N = 4$); nostril directed outward; supralabials 5-8, smooth or faintly keeled; usually three median teeth in upper jaw (three teeth: 86.7 %, two teeth: 6.7 %, one tooth: 6.7 %); head scales unequal, keeled, enlarged on the supraocular region and on the parietal region; a row or a Λ -shaped figure of enlarged, keeled scales on the snout; usually no thornlike scale on the supraciliary edge (one female with a very low thornlike scale); tubercle at the posterior end of the supraciliary edge very low; tympanum usually completely covered with small scales (73.3 %, in four specimens tympanum covered with smooth skin, in two completely, in the other two partly); 3-5 enlarged scales between eye and tympanum; one or two low, indistinct tubercles above and behind the tympanum; nuchal crest in males consisting of 5-23 ($\bar{x} = 15.9$, $sd = 4.8$, $N = 11$) compressed, triangular scales, in females of 3-17 ($\bar{x} = 10.8$, $sd = 6.1$, $N = 4$) such scales; gular pouch without enlarged scales, 0.75-1.10 times the head length in males ($\bar{x} = 0.98$, $sd = 0.11$, $N = 11$), 0.35-0.58 times in females ($\bar{x} = 0.50$, $sd = 0.10$, $N = 4$); lateral pouches without enlarged scales; dorsals 103-134 (σ : $\bar{x} = 121.3$, $sd = 8.9$, $N = 11$; φ : $\bar{x} = 119.8$, $sd = 9.9$, $N = 4$), smooth or faintly keeled; sometimes a few slightly enlarged, faintly keeled scales are recognizable on the border between the body and the patagium; ventrals 83-105 (σ : $\bar{x} = 90.8$, $sd = 4.8$, $N = 11$; φ : $\bar{x} = 93.8$, $sd = 9.0$, $N = 4$), keeled, slightly smaller than dorsals; usually five ribs in patagium (five ribs: 93.3 %, six ribs: 6.7 %); 22-27 (σ : $\bar{x} = 24.1$, $sd = 1.8$, $N = 11$; φ : $\bar{x} = 23.6$, $sd = 0.9$, $N = 4$), keeled subdigital lamellae under the fourth finger, 25-31 (σ : $\bar{x} = 27.3$, $sd = 1.2$, $N = 11$; φ : $\bar{x} = 27.9$, $sd = 2.4$, $N = 4$) under the fourth toe; hindlimbs 0.53-0.61 times the snout-vent length (σ : $\bar{x} = 0.57$, $sd = 0.01$, $N = 11$; φ : $\bar{x} = 0.56$, $sd = 0.02$, $N = 4$) and 0.91-1.04 times the distance between the limbs (σ : $\bar{x} = 0.96$, $sd = 0.04$, $N = 11$; φ : $\bar{x} = 0.95$, $sd = 0.02$, $N = 4$); small, fringelike scales on posterior edge of thigh; tail length up to 151 mm, 1.69-2.19 times the snout-vent length (σ : $\bar{x} = 2.0$, $sd = 0.14$, $N = 11$; φ : $\bar{x} = 2.03$, $sd = 0.11$, $N = 4$); no caudal crest.

Colour in preservative. — Above bluish or brownish grey with a distinct nuchal spot; males usually with dark and bluish white bands in nuchal region; body uniformly grey or with light bands; patagium in males yellowish or orangish white with some dark spots forming bands only near the edge of the body; patagium in females dark brown with light spots forming bands and covered with light grey, longitudinal lines; chest and belly bluish, sometimes yellowish white; chin in males light blue with white, irregular spots; ventral parts of patagium in males immaculate, yellowish or orangish white; in females brownish with dark spots; gular pouch in males yellowish or orangish white, in females orangish white or grey, with distinct, dark spots.

For colour in life see Boulenger (1897b: pl. 8).

Ecological notes. — Three of the four females had eggs in the oviducts, two females (RMNH 2961 C, 2962 A) had two and one (ZFMK 20894) had three eggs.

Distribution. — This subspecies occurs on Northern Sulawesi (fig. 10).

Remarks. — Being the one that is probably pictured in Günther (1872) BM 1946.8.27.27 is here selected as lectotype. Description: male; snout-vent length: 61 mm; tail length: 121 mm; head length: 12.2 mm; head depth: 6.7 mm; head width: 7.8 mm; snout length: 3.6 mm; gular pouch length: 9.1 mm; hindlimb length: 33/36 mm; distance limbs: 37/36 mm; three median upper teeth; tympanum covered with smooth skin; supralabials: 5/6; dorsals: 124; ventrals: 90; subdigital lamellae fourth finger: 24/24; ditto fourth toe: ?/27; nuchal crest scales: 18; ribs patagium: 5/5; nostril directed outward; gular pouch and lateral pouches without enlarged scales; no caudal crest; grey brown above; distinct nuchal spot; patagium yellowish white with dark spots near the body edge and thin, dark lines; ventral parts bluish yellow; those of the patagium yellowish with small spots near the edge of the body; median parts of the chin yellowish, lateral parts bluish with lighter spots; gular pouch and ventral parts of the lateral pouches yellow.

According to Günther the types were found in Manado, although this locality does not occur on the labels of the types.

***Draco maculatus* (Gray)**

Diagnosis. — A moderately sized species (maximum snout-vent length 87 mm); nostril directed outward and slightly upward; a series of keeled scales forming a **A**-shaped figure on the snout; usually two median teeth in the upper jaw; supralabials 7-11, smooth; a low thornlike scale on the supraciliary edge; tympanum covered with small scales; gular pouch in males with slightly enlarged scales; lateral pouches with enlarged scales; nuchal crest present; dorsals 117-152, some are keeled, unequal; usually five ribs in patagium; hindlimbs about as long as distance between the legs; scales on tail strongly keeled, more or less with a caudal crest in males.

KEY TO THE SUBSPECIES

1. A blue spot on each side of base of gular pouch 2
 No blue spot on each side of base of gular pouch 3
2. Underside of patagia yellowish, usually unmarked or with one to four black spots
 *D. maculatus maculatus* (p. 53)
 Underside of patagia yellow with numerous black spots *D. maculatus divergens* (p. 54)
3. Base of gular pouch yellowish white; patagia below immaculate or with a few (maximum five) spots *D. maculatus haasei* (p. 55)
 Gular pouch brownish near the base; underside of patagium immaculate
 *D. maculatus whiteheadi* (p. 56)

Draco maculatus maculatus (Gray)

Dracunculus maculatus Gray, 1845: 236 (terra typica: Penang).

Draco maculatus: Cantor, 1847: 645; Günther, 1864: 125, pl. 8 fig. c; Anderson, 1878: 802; Boulenger, 1885: 262 (partim ?); Boulenger, 1887c: 492; Boulenger, 1890a: 112; Flower, 1896: 870; Flower, 1899: 636; Werner, 1910: 10; Boulenger, 1912: 58; Robinson & Kloss, 1914: 154; Lönnberg, 1916: 4; Smith, 1916a: 52; Smith, 1916b: 152; Smith, 1929: 79; Smith, 1930: 21; Smith, 1935: 138, fig. 41a, 42 (partim); Taylor & Elbel, 1958: 1089; Pongsapipatana, 1975: 360; Anonymous, 1977: 26, tab. 1 (partim); Inger & Colwell, 1977: 239, tab. 1, 7.

Draco volans: Smith, 1915: 153 (ex errore).

Draco maculatus maculatus: Hennig, 1936a: 211, fig. 11e, map 12; Bourret, 1943: 13; Taylor, 1963: 823, fig. 34; Wermuth, 1967: 50.

Material examined. — ASIA. 2♂, BM 1946.8.27.?,6 (23.9) (paratypes), leg. I. McGregor. THAILAND. Phra Phutabat: 4♂, ZFMK 13171-74, 1972, leg. H. Meyer. Trang: 1♀, BM 1936.6.11.1, 20.vii.1935, leg. Layang Gaddi. Nakon Si Tamarat: 1♀, BM 1961.3.27.8, leg. M. A. Smith. Meh Iem, Phrae: 2♀, BM 1921.4.1.75.9, iv.1916, leg. M. A. Smith. WEST MALAYSIA. Pinang: 1♂, BM 1946.8.27.22 (23.9a) (holotype).

Diagnosis. — Bluish grey spot at the base of the gular pouch; ventral parts of patagium usually unmarked or with 1-4 dark spots.

Description. — Maximum snout-vent length in males 87 mm (Taylor, 1963), 84 mm in material examined (\bar{x} = 78.1, sd = 4.7, N = 7), 80 mm in females (\bar{x} = 73.0, sd = 7.4, N = 4), hatchlings have a snout-vent length of 23.0-24.4 mm (Pongsapipatana, 1975); maximum head length 18 mm (Taylor, 1963), 0.19-0.22 times the snout-vent length (♂: \bar{x} = 0.20, sd = 0.01, N = 7; ♀: \bar{x} = 0.21, sd = 0.01, N = 4); head width 0.62-0.69 times the head length (♂: \bar{x} = 0.63, sd = 0.01, N = 7; ♀: \bar{x} = 0.66, sd = 0.02, N = 4); head depth 0.48-0.54 times the head length (♂: \bar{x} = 0.51, sd = 0.02, N = 7; ♀: \bar{x} = 0.52, sd = 0.02, N = 4); snout length 0.23-0.34 times the head length (♂: \bar{x} = 0.29, sd = 0.03, N = 7; ♀: \bar{x} = 0.29, sd = 0.03, N = 4); nostril directed outward or slightly upward; supralabials 7-11, smooth; usually two median teeth in the upper jaw (two teeth: 80.0 %, three teeth: 20.0 %); head scales subequal, keeled; a series of enlarged, keeled scales forming a Λ -shaped figure on the snout; thornlike scale on supraciliary edge up to 0.04 times the head length; distinct, pyramidal tubercle at the end of the supraciliary edge; tympanum covered with small scales; 2-4 enlarged, keeled scales between the tympanum and the eye; several tubercles in nuchal region, 1-3 above the tympanum, 1-3 behind the tympanum and a more or less distinct, longitudinal row of tubercles between the lateral pouch and the nuchal crest; nuchal crest consisting of 13-25 (\bar{x} = 18.1, sd = 4.3, N = 7) compressed, triangular scales in males and of 3-9 (\bar{x} = 5.0, sd = 2.8, N = 4) scales in females; gular pouch with slightly enlarged scales, 1.47-2.24 times the head length in males (\bar{x} = 1.82, sd = 0.27, N = 7) and without enlarged scales, 0.70-0.79 times the head length in females (\bar{x} = 0.73, sd = 0.04, N = 4); lateral pouches with enlarged scales; dorsals 117-152 (♂: \bar{x} = 136.8, sd = 11.6, N = 7; ♀: \bar{x} = 134.3, sd = 5.0, N = 4), unequal, faintly keeled; a row of thornlike, compressed scales on the border between body and patagium; ventrals 87-117 (♂: \bar{x} = 105.4, sd = 11.1, N = 7; ♀: \bar{x} = 103.0, sd = 5.7, N = 4), keeled, slightly

smaller than the dorsals; usually five ribs in patagium (one specimen had only four ribs in its right patagium); 21-26 (σ : \bar{x} = 23.1, sd = 1.4, N = 7; φ : \bar{x} = 24.1, sd = 1.6, N = 4) keeled subdigital lamellae of the fourth finger, 22-29 (σ : \bar{x} = 25.3, sd = 1.0, N = 7; φ : \bar{x} = 27.3, sd = 2.0, N = 4) under the fourth toe; hindlimbs 0.48-0.56 times the snout-vent length (σ : \bar{x} = 0.51, sd = 0.03, N = 7; φ : \bar{x} = 0.53, sd = 0.03, N = 4) and 0.87-1.05 times the distance between the limbs (σ : \bar{x} = 0.94, sd = 0.07, N = 7; φ : \bar{x} = 0.98, sd = 0.04, N = 4); base of tail and posterior edge of thigh with fringelike scales; maximum tail length 138 mm (Taylor, 1963), 1.32-1.67 times the snout-vent length (σ : \bar{x} = 1.53, sd = 0.12, N = 7; φ : 1.64-1.67, N = 2); males with a caudal crest consisting of strongly keeled or compressed scales.

Colour in preservative. — Above light bluish or brownish grey, sometimes with dark spots; interorbital spot present; sometimes with longitudinal, dark lines in nuchal region; patagium yellowish or orangish light grey with dark spots, sometimes forming indistinct bands or a dark region near the outer edge; chest and belly yellowish, bluish or greyish white; chin sometimes sprinkled with small, dark spots; gular pouch yellowish grey, sometimes with a dark, anterior edge in males, in females yellowish white, a bluish grey spot at the base and orange or yellowish mid- and hindparts; lateral pouches ventrally orange or yellowish white; ventral parts of the patagium yellowish white, sometimes with few (1-4) dark spots or many small spots.

For colour in life see Taylor (1963).

Ecological notes. — One female (BM 1936.6.11.1), collected in July, had four eggs in the oviducts. Pongsapipatana (1975) found females with four and five eggs. Incubation time after deposition 28-29 days.

Distribution. — This subspecies is known from Burma, Western and Southern Thailand and West Malaysia (fig. 11). It is found to 1300 m above sealevel (Hennig, 1936a), mainly in evergreen forest (Inger & Colwell, 1977).

***Draco maculatus divergens* Taylor**

Draco divergens Taylor, 1934: 291, pl. 17, fig. 4 (terra typica: Doi Suthep Mountain, Chiang Mai).

Draco maculatus: Taylor, 1934: 290.

Draco maculatus divergens: Bourret, 1943: 12; Taylor, 1963: 826, fig. 35; Wermuth, 1967: 51.

No material examined.

Diagnosis. — Small bluish spots at the base of the gular pouch; ventral parts of the patagium with numerous black spots (Taylor, 1963).

Distribution. — This subspecies is only known from Chiang Mai, Thailand (fig. 11).

Remarks. — It seems to me that this taxon is synonymous with *D. m. maculatus*. All the discriminating characters, given by Taylor (1963), occur in at least one specimen of the examined material of *D. m. maculatus* in the state that is mentioned for *D. m. divergens* by Taylor (1963). Several specimens have a row of tubercles in the nuchal region; nuchal crest scales in males 13-25; all the males

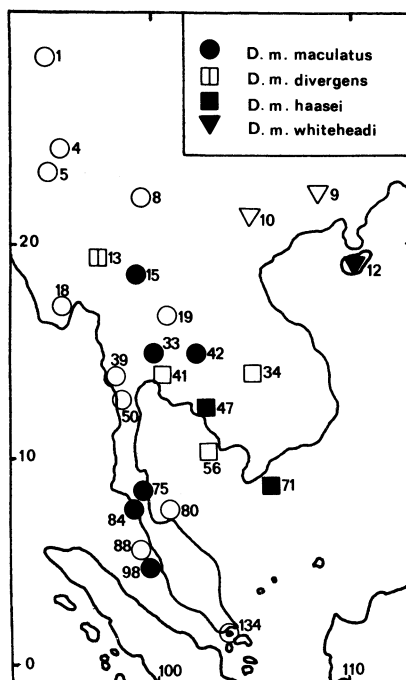


Fig. 11. Distribution of *Draco maculatus*. Open symbols are localities from the literature.

have a more or less distinct caudal crest. There is only one specimen of *D. m. maculatus* collected in Meh Iem (Phrae) with many dark spots on the ventral surface of the patagium. This specimen could belong to *D. m. divergens*, if it were not for an other specimen from the same locality that only had four dark spots underneath the patagium. However, since the types were not examined, I refrain from synonymising it with *maculatus*.

***Draco maculatus haasei* Boettger**

? *Draco maculatus*: Boulenger, 1885: 262 (partim).

Draco haasei Boettger, 1893b: 429 (terra typica: Chantaboon Siam); Taylor, 1934: 288; Taylor & Elbel, 1958: 1088.

Draco haasi: Boulenger, 1894b: 20 (ex errore).

Draco maculatus haasii: Smith & Kloss, 1915: 239; Smith, 1916a: 52; Smith 1921: 93.

Draco maculatus: Smith, 1935: 138 (partim).

Draco maculatus maculatus: Hennig, 1936a: 211 (partim).

Draco maculatus haasei: Taylor, 1963: 829, fig. 38; Wermuth, 1967: 51.

Material examined. — THAILAND. Chantaboon, Kow Sabah: 1 ♂, BM 97.10.8.4, leg. E. Haase. VIETNAM. Pulo Condor: 3 ♂, 1 ♀, BM 1921.4.1.80.3, leg. M. A. Smith.

Diagnosis. — Base of gular pouch yellowish white, without blue spots or markings; ventral parts of patagium without or with a few (to five) black spots.

Description. — Maximum snout-vent length in males 77 mm ($\bar{x} = 73.5$, $sd = 4.0$, $N = 4$), in females 76 mm ($N = 1$); maximum head length 17.0 mm, 0.20-0.23 times the snout-vent length (σ : $\bar{x} = 0.21$, $sd = 0.01$, $N = 4$; φ : 0.22); head width 0.62-0.70 times the head length (σ : $\bar{x} = 0.67$, $sd = 0.04$, $N = 4$; φ : 0.68); head depth 0.51-0.55 times the head length (σ : $\bar{x} = 0.54$, $sd = 0.01$, $N = 4$; φ : 0.51); snout length 0.29-0.33 times the head length (σ : $\bar{x} = 0.32$, $sd = 0.02$, $N = 4$; φ : ?); nostril directed outward or slightly upward; supralabials 8-10, smooth; two median teeth in upper jaw; head scales subequal, keeled; a series of enlarged, keeled scales forming a Λ -shaped figure on the snout; thornlike scale on the supraciliary edge to 0.03 times the head length; a distinct tubercle at the end of the supraciliary edge; tympanum covered with small scales; lateral parts of the nuchal region with or without irregularly arranged tubercles; nuchal crest in males consisting of 9-28 scales ($\bar{x} = 20.3$, $sd = 8.4$, $N = 4$), no nuchal crest in females; gular pouch in males with slightly enlarged scales, 1.33-1.68 times the head length ($\bar{x} = 1.55$, $sd = 0.16$, $N = 4$), in the single available female without enlarged scales, 0.68 times the head length; lateral pouches with enlarged scales; dorsals 120-141 (σ : $\bar{x} = 129.5$, $sd = 8.8$, $N = 4$; φ : 141), unequal, faintly keeled; a row of thornlike, compressed scales on the border between body and patagium; ventrals 91-118 (σ : $\bar{x} = 101.0$, $sd = 14.8$, $N = 4$; φ : 97), keeled, slightly smaller than the dorsals; five ribs in the patagium; 22-26 (σ : $\bar{x} = 24.6$, $sd = 1.4$, $N = 4$; φ : 26) keeled subdigital lamellae under the fourth finger, 27-29 (σ : $\bar{x} = 28.0$, $sd = 0.8$, $N = 4$; φ : 27.5) under the fourth toe; hindlimbs 0.53-0.55 times the snout-vent length (σ : $\bar{x} = 0.54$, $sd = 0.01$, $N = 4$; φ : 0.53) and 0.94-1.05 times the distance between the legs (σ : $\bar{x} = 0.99$, $sd = 0.06$, $N = 4$; φ : 0.96); base of tail and posterior edge of thigh with fringelike scales; maximum tail length 128 mm, 1.60-1.83 times the snout-vent length (σ : $\bar{x} = 1.72$, $sd = 0.12$, $N = 4$; φ : 1.64); a caudal crest present in males.

Colour in preservative. — Above brownish light grey; interorbital spot present; at least in some of the males a paired nuchal spot; patagium yellowish white, with or without some small dark spots near the body edge; chest and belly yellowish or greyish white; chin yellowish or whitish, sometimes with some lighter spots; gular pouch in males greyish at the tip, rest orangish or yellowish, in females yellowish white, without any spots; lateral pouches yellowish white ventrally; ventral parts of patagium without or with a few (up to five) black spots.

For colour in life see Taylor (1963).

Distribution. — This subspecies is known from Eastern Thailand, Cambodia and Southern Vietnam (fig. 11).

Remark. — It is assumed here that the specimens of *D. maculatus* from Cambodia mentioned by Boulenger (1885) belong to this subspecies.

***Draco maculatus whiteheadi* Boulenger**

Draco whiteheadi Boulenger, 1899: 956, pl. 66 fig. 1 (terra typica: Hainan Isl.); Taylor & Elbel, 1958: 1086; Colbert, 1967.

Draco maculatus: Smith, 1935: 138 (partim); Anonymous, 1977: 26, tab. 1 (partim).

Draco maculatus whiteheadi: Hennig, 1936a: 213, map 12; Bourret, 1943: 13; Taylor, 1963: 831, fig. 37; Wermuth, 1967: 51.

Material examined. — CHINA. Hainan, Five Finger Mnts: 1♂, BM 1946.8.26.79 (99.11.30.1) (holotype), leg. I. Whitehead.

Diagnosis. — Base of the gular pouch brownish, without a blue spot; ventral parts of patagium immaculate.

Description. — Maximum snout-vent length 86 mm; head length 16.7 mm, 0.19 times the snout-vent length (0.22 after Taylor, 1963); head width 0.63 times the head length (0.75 after Taylor, 1963); head depth 0.53 times the head length (0.61 after Taylor, 1963); snout length 0.34 times the head length (0.36 after Taylor, 1963); nostril directed outward; supralabials 7-10 (Taylor, 1963), smooth; two median teeth in upper jaw; head scales subequal, keeled; a Λ -shaped figure of enlarged scales on the snout; thornlike scale on the supraciliary edge 0.02 times the head length; a tubercle at the end of the supraciliary edge; tympanum covered with small scales; no distinct row of tubercles on the lateral parts of the nuchal region; nuchal crest consisting of at least 21 scales; gular pouch with only very slightly enlarged scales, 1.57 times the head length (1.50 after Taylor, 1963); lateral pouches with enlarged scales; dorsals 134, unequal, faintly keeled; a row of thornlike scales on the border between body and patagium; ventrals 120, keeled, about as large as the dorsals; five ribs in the patagium; 25-26 keeled subdigital lamellae under the fourth finger, 27-29 under the fourth toe; hindlimbs 0.51 times the snout-vent length (0.52 after Taylor, 1963) and 0.94 times the distance between the legs (1.00 after Taylor, 1963); base of tail and posterior edge of thigh with fringelike scales; tail length 146 mm, 1.70 times the snout-vent length; a caudal crest present (description based on a single male).

Colour in preservative. — Above brownish with dark spots; interorbital and nuchal spots present; a paired spot behind the nuchal spot; patagium whitish with dark spots near the edge of the body; chest and belly yellowish white; ventral surface of the patagium without spots; chin greyish with small dark spots; gular pouch greyish blue at the tip, near the base brownish; ventral parts of the lateral pouches whitish.

Distribution. — This subspecies occurs in Northern Vietnam and on Hainan (fig. 11).

Draco maximus Boulenger

Draco fimbriatus: Schlegel, 1844: 85 (partim).

Draco maximus Boulenger, 1893: 522, pl. 42 fig. 1 (terra typica: Mnt. Dulit (2000 ft.) Borneo); Bartlett, 1894: 82; Günther, 1895: 499; Werner, 1910: 16; Boulenger, 1912: 63; De Rooy, 1915: 81; ? Smith, 1925b: 24; Lloyd et al., 1968: 499.

Draco intermedius Werner, 1910: 14 (terra typica: Bandar Kwala, N.O. Sumatra); De Rooy, 1915: 86.

Draco cryptotis Despax, 1912: 4, fig. (terra typica: Indes Néerlandaises); De Rooy, 1915: 82.

Draco maximus maximus: Hennig, 1936a: 188, fig. 10d, map 4; Bourret, 1943: 12; Wermuth, 1967: 51; Grandison, 1972: 77.

Draco maximus cryptotis: Hennig, 1936a: 190, map 4; Wermuth, 1967: 52 (new synonym).

Material examined. — MALAYSIA. WEST MALAYSIA. Janda Baik, Pahang: 1 ♂, BM 1974.3815, 5.vii.1965, leg. P. Y. Beny. SARAWAK. Mt. Dulit, 2000 ft: 1 ♂, BM 1946.8.13.41 (92.10.4.2) (holotype), leg. C. Hose. Mt. Mulu, alt. < 30 m (4°02'N 114°48'E): 1 ♂, BM 1978.322, 7.viii.1977, leg. I. Dring. INDONESIA. 1 ♀, MHNP 1238 (holotype of *Draco cryptotis* Despax). NATUNA Isl. Paulau Laut: 1 ♂, BM 95.5.1.91, vii.1894, leg. C. Hose. SUMATRA. Padang: 1 ♀, RMNH 2921, leg. S. Müller. Ophir distr., Gng. Talamau: 1 ♀, RMNH 4850, v.1917, 500 m, leg. E. Jacobson. KALIMANTAN: 1 ♀, RMNH 19738, leg. J. Büttikofer.

Diagnosis. — Large species (maximum snout-vent length 145 mm); nostril directed upward; a more or less distinct series of scales forming a Λ -shaped figure on the snout; usually two median teeth in upper jaw; supralabials 13-16, smooth; no thornlike scale on supraciliary edge; tympanum partly covered with small scales or with small scales only; gular pouch without and lateral pouches with slightly enlarged scales; no nuchal crest; males with a nuchal fold; dorsals 226-269, subequal, smooth; six ribs in patagium; hindlimbs approximately as long as the distance between the limbs; no caudal crest.

Description. — Maximum snout-vent length in females 134 mm (\bar{x} = 114.6, sd = 22.9, N = 5), in males 137 mm (\bar{x} = 133.0, sd = 3.4, N = 4) (Boulenger (1912) measured a snout-vent length of 145 mm, but did not state to which sex this animal belonged); maximum head length 28.6 mm in females and 27.3 mm in males, 0.19-0.21 times the snout-vent length (σ : \bar{x} = 0.20, sd = 0.01, N = 4; ϕ : \bar{x} = 0.21, sd = 0.01, N = 5); head width 0.61-0.73 times the head length (σ : \bar{x} = 0.66, sd = 0.05, N = 4; ϕ : \bar{x} = 0.65, sd = 0.02, N = 5); head depth 0.45-0.53 times the head length (σ : \bar{x} = 0.49, sd = 0.01, N = 4; ϕ : \bar{x} = 0.50, sd = 0.04, N = 5); snout length 0.29-0.36 times the head length (σ : \bar{x} = 0.32, sd = 0.02, N = 4; ϕ : \bar{x} = 0.32, sd = 0.03, N = 5); nostrils directed upward; supralabials 13-16, smooth; usually two median teeth in upper jaw (three teeth: 33.3 %, two teeth: 55.6 %, one tooth: 11.1 %); head scales small, subequal, keeled; a more or less distinct Λ -shaped figure, formed by enlarged scales; no thornlike scale on the supraciliary edge; a rounded tubercle at the end of the supraciliary edge; tympanum covered exclusively (66.7 %) or partly (33.3 %) with small scales; 2-4 indistinctly enlarged, keeled scales between the tympanum and the eye; one or two conical tubercles above and one behind the tympanum; males with a nuchal fold; gular pouch without enlarged scales, 1.41-1.62 times the head length in males (\bar{x} = 1.54, sd = 0.12, N = 4) and 0.98-1.17 times the head length in females (\bar{x} = 1.08, sd = 0.09, N = 5); lateral pouches only with slightly enlarged scales along the outer edge; dorsals 226-286 (σ : \bar{x} = 264.0, sd = 26.2, N = 4; ϕ : \bar{x} = 259.6, sd = 12.2, N = 5), subequal, faintly keeled; 1-4 enlarged, thornlike scales on the border between body and patagium; ventrals 124-153 (σ : \bar{x} = 142.3, sd = 8.9, N = 4; ϕ : \bar{x} = 138.0, sd = 9.5, N = 5), keeled, larger than dorsals; six ribs in patagium; 25-29 (σ : \bar{x} = 26.1, sd = 0.5, N = 4; ϕ : \bar{x} = 26.5, sd = 1.5, N = 5) keeled subdigital lamellae under the fourth finger, 28-34 (σ : \bar{x} = 30.3, sd = 1.0, N = 4; ϕ : \bar{x} = 30.6, sd = 2.2, N = 5) under the fourth toe; hindlimbs 0.51-0.63 times the snout-vent length (σ : \bar{x} = 0.54, sd = 0.04, N = 4; ϕ : \bar{x} = 0.59, sd = 0.02, N = 5) and 0.89-1.11 times the distance between the

limbs (σ : $\bar{x} = 0.95$, $sd = 0.05$, $N = 4$; ♀ : $\bar{x} = 1.0$, $sd = 0.07$, $N = 5$); fringelike scales on posterior edge of thigh and on base of tail; maximum tail length 234 mm, 1.63-1.89 times the snout-vent length (σ : $\bar{x} = 1.68$, $sd = 0.04$, $N = 4$; ♀ : $\bar{x} = 1.77$, $sd = 0.07$, $N = 5$); no caudal crest.

Colour in preservative. — Above bluish or brownish grey with small, dark brown spots and more or less distinct, lighter, dark-margined bands; limbs banded; patagium dark brown with light, longitudinal lines or remains of these lines; chest and belly yellowish white; chin with distinct, dark spots; ventral parts of patagium yellowish grey or brown, sometimes with a dark spot or a bandlike marking; gular pouch in males yellowish at the tip, rest greyish brown, at the base grey with lighter spots and some darker lines, in females with a yellow outer edge, remainder black with some light spots; in females even the ventral parts of the lateral pouches are black, in males they are grey with light spots frontally; a dark band in front of the shoulders.

Ecological notes. — Three out of five females had eggs in the oviducts: one female (RMNH 2921) had five eggs, one (RMNH 19738) had four and one had one egg. The latter (RMNH 4850) was collected in May.

Distribution. — This species occurs in West Malaysia, and on Sumatra, Borneo and the Natuna Islands (fig. 12). It is found to an altitude of 600 m.

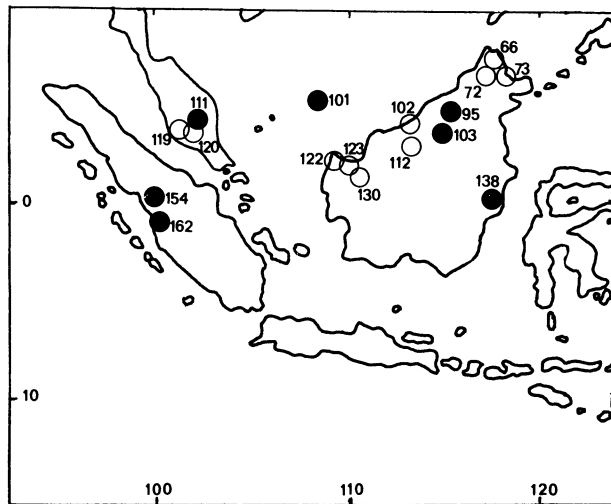


Fig. 12. Distribution of *Draco maximus*. Open symbols are localities from the literature.

Remarks. — Schlegel (1844), when stating: “Ein ungemein grosser Drache von Sumatra, welchen ich für dem alten *Dr. fimbriatus* halte, hat 6 Ribben.” is referring to *D. maximus* (RMNH 2921).

Although in Despax's (1912) paper there is no indication about an exact locality, De Rooy (1915) mentions Java as locality for *Draco cryptotis*. This was copied

by Hennig (1936a), who considered the taxon a subspecies. However, there is no reason to assume it is really found in Java. Examination of the type of *cryptotis* did not reveal any distinct differences between it and *D. maximus*. Therefore it is regarded synonymous with *D. maximus*.

Smith (1925b) stated that "the gular sac of the female is about as long as the distance between the eye and the end of the snout and is yellowish white in colour". Since these characters do not agree with those of the examined material, the specimen of Smith probably belongs to another species, or Smith's description of the gular sac is not completely correct and gives us a false impression about the extent of the yellow element on the gular sac.

The specimen described by Hennig (1936a) as a male, actually is a female (RMNH 4850).

***Draco melanopogon* Boulenger**

(pl. 1 fig. c, pl. 2 fig. c)

Draco haematopogon: Schlegel, 1844: 95 (partim).

Draco melanopogon Boulenger, 1887c: 492 (terra typica: Malacca); Günther, 1895: 499; Flower, 1896: 870; Flower, 1899: 637; Laidlaw, 1901: 307; Lampe & Lindholm, 1901: 202; Boulenger, 1903: 152; Volz, 1903: 425; Boulenger, 1912: 62; Robinson & Kloss, 1914: 154; De Rooy, 1915: 84; Smith, 1916a: 53; Smith, 1916b: 154; Smith, 1922: 268; Smith, 1930: 23; De Witte, 1933: 3; Hennig, 1936a: 207, fig. 10m, map 10; Hennig, 1936b: fig. 1; Bourret, 1943: 13; Tanner, 1953: 4; Taylor & Elbel, 1958: 1093; Taylor, 1963: 848, fig. 42; Inger & Greenberg, 1966: 1007; Wermuth, 1967: 52; Lloyd et al., 1968: 499; Grandison, 1972: 78; Dring, 1979: 232.

Draco nigriappendiculatus Bartlett, 1894: 82 (terra typica: Kuching, Sarawak).

Material examined. — MALAYSIA. WEST MALAYSIA. 1♂, BM 1946.8.26.88 (86.12.28) (lectotype), leg. D. J. A. Hervey; 1♂, 2♀, BM 1946.8.26.87, 89-90 (86.12.28) (paralectotypes), leg. D. J. A. Hervey. Sungei Siput, Saiong, Kledang, Perak: 1♀, RMNH 6215; 1♂, 1♀, ZMA 15247. Ulu Klang: 5♂, 1♀, SMF 58464-69, 22.i.1962, leg. H. Klingel. Johore, Pulau Pisang: 1♀, RMNH 19976, i.1934, leg. G. H. Swoeder. Pulau Tioman: 4♀, ZFMK 25637-40, 1978, leg. D. Kiehlman. Subang: 1♀, ZFMK 16491, 2.v.1975, leg. G. Nikolaus. INDONESIA. SUMATRA. Southern Sumatra: 1♂, ZMA 14682 B, 1930/34, leg. J. van Tuyn. KALIMANTAN. Upper Mahakkam: 1♀, RMNH 5734 A, leg. A. W. Nieuwenhuis. LOC. UNKNOWN: 1♂, RMNH 2959, Péron.

Diagnosis. — Species of small to moderate size (maximum snout-vent length 93 mm); nostril directed upward; no **Λ**-shaped series of scales on snout; two median teeth in upper jaw; supralabials 10-15, faintly keeled; no thornlike scale on supraciliary edge; tympanum covered with smooth skin; gular pouch in males with slightly enlarged scales; lateral pouches with enlarged scales; no nuchal crest nor a nuchal fold; dorsals 164-218, smooth, subequal; usually five ribs in patagium; hindlimbs about as long as the distance between the limbs; no caudal crest; gular pouch coal black in males and grey in females; patagium dark brown with light, dark-centred spots.

Description. — Maximum snout-vent length in females 93 mm (\bar{x} = 80.4, sd = 8.3, N = 12), in males 85 mm (Taylor (1963), 79 mm in material examined; \bar{x} = 72.4, sd = 8.9, N = 10); maximum head length in females 16.7 mm, in males 15 mm (Taylor, 1963), 0.16-0.20 times the snout-vent length (σ : \bar{x} = 0.17,

sd = 0.01, N = 10; ♀: \bar{x} = 0.18, sd = 0.01, N = 12); head width 0.63-0.71 times the head length (♂: \bar{x} = 0.69, sd = 0.02, N = 10; ♀: \bar{x} = 0.67, sd = 0.02, N = 12); head depth 0.51-0.66 times the head length in males (\bar{x} = 0.56, sd = 0.05, N = 10), 0.48-0.56 times in females (\bar{x} = 0.52, sd = 0.02, N = 12); snout length 0.22-0.31 times the head length (♂: \bar{x} = 0.26, sd = 0.02, N = 10; ♀: \bar{x} = 0.27, sd = 0.02, N = 12); nostril directed upward; supralabials 10-15 (Taylor, 1963), keeled; two median teeth in the upper jaw; head scales small, subequal, keeled; a low, longitudinal ridge on the snout, no series of enlarged scales; no thornlike scale on the supraciliary edge; a very low, rounded tubercle at the end of the supraciliary edge; tympanum usually covered with smooth skin, in one specimen the right tympanum is partly covered with small scales; no enlarged scales between the tympanum and the eye; sometimes one enlarged scale above the tympanum; no nuchal crest; gular pouch with slightly enlarged scales in males, 0.86-2.08 times the head length (\bar{x} = 1.73, sd = 0.33, N = 10), in females without enlarged scales, 0.58-0.88 (\bar{x} = 0.77, sd = 0.08, N = 12) times the head length; lateral pouch with enlarged scales; dorsals 164-218 (♂: \bar{x} = 189.6, sd = 14.1, N = 10; ♀: \bar{x} = 201.7, sd = 10.9, N = 12), subequal, smooth or faintly keeled; a row of enlarged, strongly keeled scales on the border between body and patagium; ventrals 108-132 (♂: \bar{x} = 120.0, sd = 6.8, N = 10; ♀: \bar{x} = 120.1, sd = 8.7, N = 12), keeled, larger than dorsals; usually five ribs in patagium (five ribs: 95.5 %, six ribs: 4.5 %); 20-23 (♂: \bar{x} = 21.6, sd = 0.9, N = 10; ♀: \bar{x} = 21.3, sd = 1.3, N = 12) keeled subdigital lamellae under the fourth finger, 22-26 (♂: \bar{x} = 23.6, sd = 0.8, N = 10; ♀: \bar{x} = 23.5, sd = 1.0, N = 12) under the fourth toe; hindlimbs 0.53-0.62 times the snout-vent length (♂: \bar{x} = 0.56, sd = 0.01, N = 10; ♀: \bar{x} = 0.57, sd = 0.03, N = 12) and 0.90-1.12 times the distance between the limbs (♂: \bar{x} = 0.96, sd = 0.04, N = 10; ♀: \bar{x} = 0.97, sd = 0.06, N = 12); posterior edge of thigh and base of tail with fringelike scales; maximum tail length 179 mm in females and 160 mm in males (Taylor, 1963), 1.74-2.03 times the snout-vent length (♂: \bar{x} = 1.87, sd = 0.09, N = 10; ♀: \bar{x} = 1.91, sd = 0.09, N = 12); no caudal crest.

Colour in preservative. — Above bluish to brownish grey with more or less distinct spots and spotlike or bandlike remains of transverse bands; a small, sometimes indistinct, interorbital spot is present; patagium dark brown with light, dark-centred spots, connected near the body by light, longitudinal lines; chest and belly yellowish white, usually with brown spots, especially on the shoulders; chin sprinkled with very small, brown spots; ventral parts of patagium grey, sometimes with larger or smaller, dark brown spots; gular pouch in males coal black, except the upper posterior part which is white, like the ventral parts of the lateral pouches; in females grey, except the posterior parts and the ventral parts of the lateral pouches, which are white.

Patagium in life black with yellow or greenish yellow spots (Taylor, 1963). See also Grandison (1972) for colour in life.

Ecological notes. — Seventy percent of the females had two eggs in the oviducts. No collecting dates are known. See for further notes on the reproduction cycle Inger & Greenberg (1966).

Distribution. — This species occurs in Southern Thailand and West Malaysia, on Sumatra, Borneo and several small islands around these areas (fig. 13). It is known to occur to an altitude of 300 m (Laidlaw, 1901).

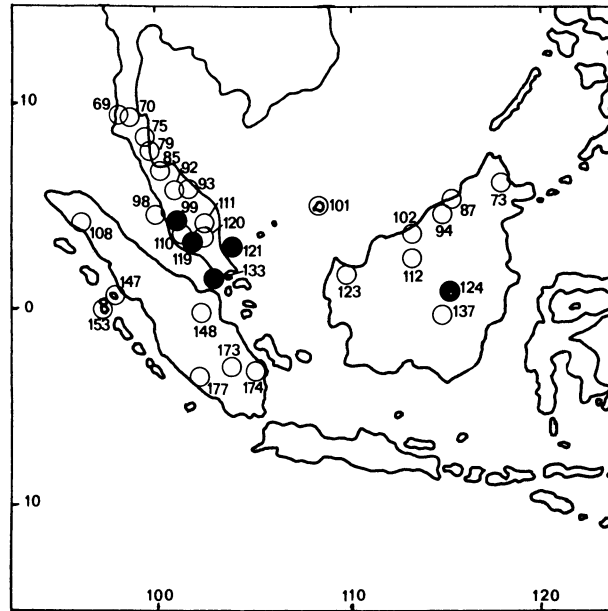


Fig. 13. Distribution of *Draco melanopogon*. Open symbols are localities from the literature.

Remarks. — Schlegel (1844: 95) stated about *D. haematopogon*, that in some of the specimens the black spot at the base of the gular pouch occupies the entire gular pouch. One such specimen was collected by Péron on Timor and pictured by Boie in his 'Erpétologie de Java' under the name *Draco timoriensis*. Plate 16 figs. 1 (pl. 1 fig. c) & 2 (pl. 2 fig. c) of the manuscript of the 'Erpétologie de Java' show a picture of *D. melanopogon* (RMNH 2959) under the name *D. timoriensis*. It is described as follows:

“*Draco timorensis*.

Draco- naribus horizontaliter apertis, occipite laevi, paleari longissimo, angusto, nigro ad basin postice margine albo, extrematibus gracilibus, squamis dorsalibus sublaevibus, serie squamarum majorum interrupta in utroque latere dorsi, alis sub pellucides, postice albo lineolatis, medio ocellis pellucidis nigro nebulosis”.

See also the description of *D. haematopogon* by Boie, cited on p. 32. It is not very probable that the specimen (RMNH 2959) really was collected on Timor.

Because BM 1946.8.26.88 is the animal of which the measurements are given by Boulenger (1887c), this specimen is selected here as lectotype. Description: male; snout-vent length: 79 mm; tail length: 145 mm; head length: 13.3 mm;

head depth: 7.3 mm; head width: 8.9 mm; snout length: 3.8 mm; gular pouch length: 20.9 mm; hindlimb length: 44/45 mm; distance limbs: 47/48 mm; two median upper teeth; one tympanum partly covered with small scales, the other with smooth skin only; supralabials: 12/11; dorsals: 197; ventrals: 129; subdigital lamellae fourth finger: 21/19; ditto fourth toe: 26/24; no nuchal crest; ribs patagium: 5/5; nostril directed upward; gular pouch and lateral pouches with slightly enlarged scales; no caudal crest; grey brown above; small interorbital spot; patagium dark-brown with light, dark-centred spots, near the body connected by light lines; ventral parts yellowish white with brown spots; those of the patagium yellowish brown with spots near the outer edge; chin yellowish brown with many small, brown spots; gular pouch black, posterior parts of the base and ventral parts of the lateral pouches white.

The four examined specimens from Pulau Tioman are all females, which seem to be significantly larger than the females from other parts of the area of distribution (\bar{x} = 85.5 mm, sd = 4.4, N = 4, those from the other parts: \bar{x} = 77.2 mm, sd = 7.6, N = 6). They also differ in having a greyish body colour, whereas the other specimens usually have a brownish body colour, but this could be due to the preservation. More specimens from Tioman should be examined to decide whether they belong to a distinct subspecies or not.

***Draco mindanensis* Stejneger**

Draco mindanensis Stejneger, 1908: 677 (terra typica: Datu Anib's place, near Catagan, northwest Mindanao at base of Malindang Mountain, 1100 ft.); Taylor, 1922a: 128; Taylor, 1922b: 191. *Draco fimbriatus mindanensis*: Hennig, 1936a: 203, fig. 10k, map 8; Wermuth, 1967: 47.

Material examined. — PHILIPPINES. MINDANAO. Cotabato Coast: 1 ♂, ZMA 12043, 1923, leg. E. H. Taylor. Saak, Cotabato: 1 ♂, BM 1965.122, leg. E. E. Williams.

Diagnosis. — Species of moderate size (maximum snout-vent length 90 mm); nostril directed upward; indistinct series of scales forming a Λ -shaped figure on the snout; three median teeth in upper jaw; supralabials 11-15, smooth; no thornlike scale on supraciliary edge; tympanum covered with small scales; gular pouch in males without enlarged scales; lateral pouches with enlarged scales; no nuchal crest; dorsals 202-224, subequal, faintly keeled; five ribs in the patagium; hindlimbs about as long as the distance between the limbs; no caudal crest; gular pouch in males yellowish, at the base grey with light spots; patagium dark brown with lighter spots.

Description. — Maximum snout-vent length in males 90 mm (Stejneger, 1908), 85 mm in examined material (\bar{x} = 86.5, sd = 4.4, N = 4, based on Stejneger (1908), Taylor (1922b) and examined material), 87 mm in females (Taylor (1922b), N = 1); head length to 19 mm (Stejneger, 1908), 0.21-0.22 times the snout-vent length (♂: \bar{x} = 0.21, sd = 0.0, N = 4, based on Stejneger (1908), Taylor (1922b), and examined material; ♀: 0.22, Taylor (1922b)); head width, 0.61-0.74 times the head length (♂: \bar{x} = 0.65, sd = 0.04, N = 4, based on Stejneger (1908), Taylor (1922b), and examined material; ♀: 0.74, Taylor

(1922b)); head depth 0.48-0.52 ($N = 2$) times the head length; snout length 0.28-0.42 times the head length (σ : $\bar{x} = 0.35$, $sd = 0.07$, $N = 3$, based on Taylor (1922b), and examined material; φ : 0.39, Taylor (1922b)); nostril completely directed upward; supralabials 11-15 (Stejneger, 1908; Taylor, 1922b), smooth; three median teeth in upper jaw; head scales small, subequal, faintly keeled; an indistinct Λ -shaped figure on snout; no thornlike scale on the supraciliary edge; tubercle at the end of the supraciliary edge low, rounded; tympanum covered with slightly enlarged or small scales; no enlarged scales between the tympanum and the eye; only a slightly enlarged, keeled scale above and one behind the tympanum; no nuchal crest or fold; gular pouch without enlarged scales, 0.82-1.21 times the head length in males ($\bar{x} = 1.01$, $sd = 0.16$, $N = 4$, based on Stejneger (1908), Taylor (1922b) and examined material), 0.47 times in females (Taylor, 1922b)); lateral pouch without enlarged scales; dorsals 202-224 ($N = 2$), subequal, faintly keeled, with a few indistinctly enlarged scales on the border between the body and the patagium; ventrals 107-125 ($N = 2$), keeled, larger than dorsals; five ribs in patagium; 23-26 ($N = 2$) faintly keeled subdigital lamellae under the fourth finger, 27-31 ($N = 2$) under the fourth toe; hindlimbs 0.57-0.61 times the snout-vent length (σ : $\bar{x} = 0.59$, $sd = 0.02$, $N = 4$, based on Stejneger (1908), Taylor (1922b), and examined material; φ : 0.59, Taylor (1922b)) and 0.98-1.06 ($N = 2$) times the distance between the limbs; posterior edge of thigh with fringelike scales; maximum tail length 178 mm (Taylor, 1922b), 1.90-2.05 times the snout-vent length (σ : $\bar{x} = 1.91$, $sd = 0.01$, $N = 3$, based on Stejneger (1908), and examined material; φ : 2.05, Taylor (1922b)); no caudal crest.

Colour in preservative (males). — Above brown with some darker and lighter, bandlike markings; supraorbital region bluish grey; a bluish grey or light-dark, chequered line on the place of the nuchal crest; patagium dark brown with small, light spots and rests of lines; chest and belly light yellowish brown; chin with lighter spots; ventral parts of patagium grey brown or yellowish; gular pouch light yellowish grey with dark brown base or with dark lines; lateral parts of head with light spots.

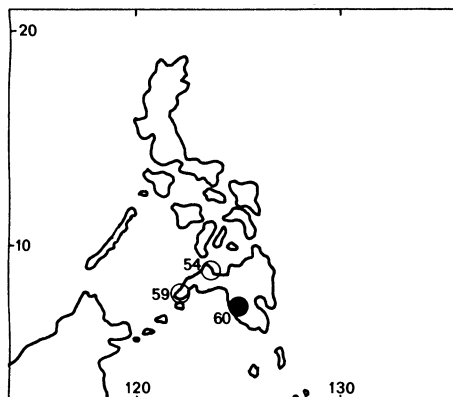


Fig. 14. Distribution of *Draco mindanensis*. Open symbols are localities from the literature.

In life the colour of the patagium is red and that of the gular pouch is vivid, orange yellow (Taylor, 1922b). In females the patagia are blackish with numerous narrow lines and small spots, the tip of the gular pouch is cream yellow (Taylor, 1922b).

Distribution. — This species occurs on the Philippines (fig. 14). The type was found on 350 m above sealevel. Taylor (1922b) also found two specimens at an altitude of 300 m.

Remark. — This species certainly is not related to *D. fimbriatus* as Hennig (1936a) thought. Possibly it is closely related to *D. maximus* or *D. haematopogon/melanopogon*.

Draco obscurus Boulenger

Diagnosis. — Species of moderate to large size (maximum snout-vent length 101 mm); nostril directed upward; a row of keeled scales on the snout; usually two median teeth in upper jaw; supralabials 8-12, keeled; no thornlike scale on supraciliary edge; tympanum at least partly covered with smooth skin; gular pouch and lateral pouches in males and females with enlarged scales; nuchal fold in males; dorsals 146-204, smooth, subequal; five ribs in patagium; males with caudal crest; patagium grey brown, with dark spots or thin bands.

KEY TO THE SUBSPECIES

1. Gular pouch males strongly widened distally; West Malaysia *D. obscurus formosus* (p. 67)
Gular pouch only slightly widened in males; not from West Malaysia 2
2. From Sumatra, Natuna Islands or Borneo *D. obscurus obscurus* (p. 65)
From Kepulauan Mentawai *D. obscurus laetepictus* (p. 69)

Since *D. obscurus* was described in 1887 and *D. formosus* in 1900 (both by Boulenger) the species name should be *D. obscurus* and not *D. formosus* as Hennig (1936a) named this taxon.

I could not find distinct differences between the material of *D. o. obscurus* examined by me and *D. o. laetepictus* as described by Hennig (1936a).

Draco obscurus obscurus Boulenger

Draco obscurus Boulenger, 1887a: 95 (terra typica: Mount Kina Baloo, Borneo); Mocquard, 1890: 128; De Rooy, 1915: 85; Lloyd et al., 1968: 499; Voris, 1977: 377.

Draco formosus: Werner, 1910: 12; Boulenger, 1912: 61 (partim); De Rooy, 1915: 83; Smith, 1925a: 24; Smedley, 1931: 47.

Draco affinis Baumann, 1913: 261, fig. a (non *Draco affinis* Bartlett, 1894) (terra typica: Battak Mnts., W. Sumatra).

Draco formosus obscurus: Hennig, 1936a: 218, fig. 11k, l, map 14; Wermuth, 1967: 48.

Material examined. — MALAYSIA. SARAWAK. Kina Balu: 1 ♀, BM 95.11.7.6, leg. A. Everett. Kiau, Kina Balu, 3000 ft.: 1 ♂, BM 1929.12.22.91, iv.1929, Raffles Mus. INDONESIA. SUMATRA. 1 ♂, RMNH 4761, 1903, leg. E. Fruhstorfer. Deli: 1 ♂, 1 ♀, ZMA 15227-28, 1908/09, leg. L. P. le Cosquino de Bussy. Lebong Tandai, Benkodin?: 1 ♂, BM 1920.1.16.9, leg. C. J. Brooks.

Diagnosis. — Gular pouch in males only slightly widened distally; dorsals 146-174; hindlimbs 0.92-1.08 times the distance between the limbs; tail length 1.83-2.00 times the snout-vent length; chin with large light yellowish spots, making a reticulated impression.

Description. — Maximum snout-vent length in males 100 mm ($\bar{x} = 90.5$, $sd = 7.9$, $N = 4$), in females 94 mm ($\bar{x} = 90.0$, $N = 2$); maximum head length 18.9 mm, 0.19-0.21 times the snout-vent length (σ : $\bar{x} = 0.19$, $sd = 0.01$, $N = 4$; φ : 0.19-0.21, $N = 2$); head width 0.63-0.66 times the head length (σ : $\bar{x} = 0.65$, $sd = 0.02$, $N = 4$; φ : 0.63-0.66, $N = 2$); head depth 0.49-0.53 times the head length (σ : $\bar{x} = 0.52$, $sd = 0.02$, $N = 4$; φ : 0.52-0.53, $N = 2$); snout 0.29-0.33 times the head length (σ : $\bar{x} = 0.31$, $sd = 0.02$, $N = 4$; φ : 0.32, $N = 2$); nostril directed upward; supralabials 9-12 (Hennig, 1936a), keeled; usually two median teeth in the upper jaw (two teeth: 83.3 %, three teeth: 16.7 %); head scales subequal, more or less keeled, smaller in the supraocular region, enlarged, keeled in the preocular region; a row of enlarged, keeled scales on the snout; no thornlike scale on the supraciliary edge; tubercle at the end of the supraciliary edge very low, indistinct; tympanum completely (58.3 %) or partly covered with smooth skin; one enlarged scale between the eye and the tympanum; a spinelike tubercle above the tympanum; a longitudinal nuchal fold instead of a crest in males, no such fold in females; gular pouch in males with enlarged scales, only slightly widened distally, 1.16-1.86 times the head length ($\bar{x} = 1.54$, $sd = 0.32$, $N = 4$), in females with enlarged scales at the tip, 0.63-0.77 ($N = 2$) times the head length; lateral pouches with enlarged scales; dorsals 146-174 (σ : $\bar{x} = 165.0$, $sd = 13.0$, $N = 4$; φ : 152-173, $N = 2$), subequal, smooth or very faintly keeled; a few enlarged, keeled scales on the border between body and patagium; ventrals 98-109 (σ : $\bar{x} = 103.5$, $sd = 5.8$, $N = 4$; φ : 99-105, $N = 2$), subequal, keeled, slightly larger than dorsals; five ribs in patagium; 19-24 (σ : $\bar{x} = 20.6$, $sd = 1.3$, $N = 4$; φ : 23-24, $N = 2$) keeled subdigital lamellae under the fourth finger, 23-27 (σ : $\bar{x} = 24.6$, $sd = 1.5$, $N = 4$; φ : 25-27, $N = 2$) under the fourth toe; hindlimbs 0.53-0.59 times the snout-vent length (σ : $\bar{x} = 0.55$, $sd = 0.02$, $N = 4$; φ : 0.58-0.59, $N = 2$) and 0.92-1.08 times the distance between the limbs (σ : $\bar{x} = 0.97$, $sd = 0.04$, $N = 4$; φ : 0.96-1.08, $N = 2$); base of tail and posterior edge of thigh with fringelike scales; maximum tail length 186 mm, 1.83-2.00 times the snout-vent length (σ : $\bar{x} = 1.86$, $sd = 0.03$, $N = 4$; φ : 2.0, $N = 1$); males with a caudal crest of strongly keeled scales.

Colour in preservative. — Males dark brown above, with several blackish markings: interorbital spot, four nuchal bands and distinct spots on the body; females brown with a dark head, black interorbital spot present, body with indistinct, darker spots; patagium dark brown with longitudinal lighter lines and with or without darker, indistinct bands or irregular spots (rests of bands); ventral parts of body and patagium orangish or yellowish light brown, in some specimens with some transverse bands on the lateral parts of the chest or with fine, dark spots; chin with large light spots, giving it a reticulated impression; gular pouch in males yellowish to grey, blackish near base, ventral parts of

lateral pouches orangish or yellowish light brown; in females gular pouch dark grey, basal parts orange brown; ventral parts of lateral pouches yellowish grey.

Ecological notes. — One female (ZMA 15227) had three eggs in the oviducts, the other (BM 95.11.7.6) had five.

Distribution. — This subspecies is known to occur on Sumatra, the Natuna Islands and Borneo (fig. 15). It was found to an altitude of 1000 m (Baumann, 1913).

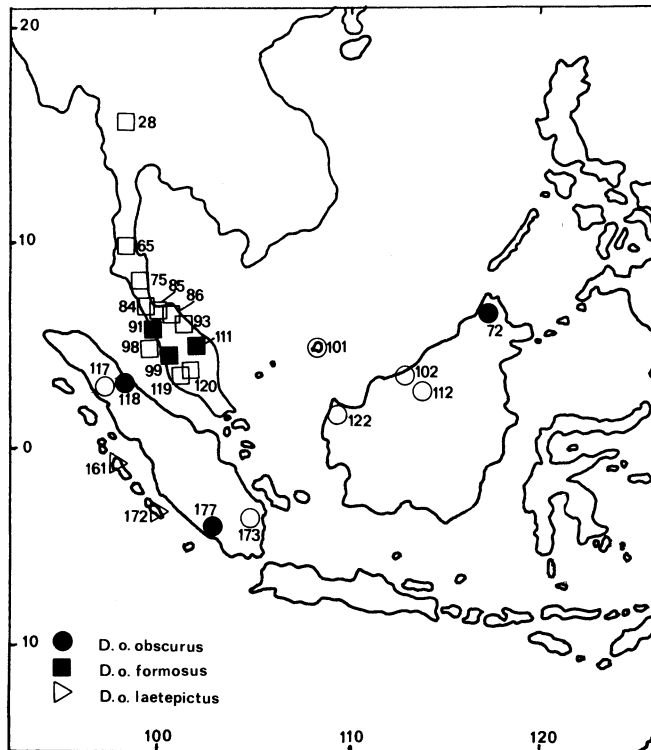


Fig. 15. Distribution of *Draco obscurus*. Open symbols are localities from the literature.

Draco obscurus formosus Boulenger

Draco formosus Boulenger, 1900: 190 (terra typica: Larut Hills, Perak) (partim); Laidlaw, 1901: 306; Boulenger, 1903: 152 (partim); Boulenger, 1908: 65; 1912: 61; Smith, 1916a: 53; 1916b: 153; 1922: 268; 1930: 22; 1937: 75, pl. 8 fig. 2; Taylor & Elbel, 1958: 1042; Dring, 1979: 232.

Draco formosus formosus: Hennig, 1936a: 216, fig. 11m, map 14; Bourret, 1943: 13; Taylor, 1963: 858, fig. 45; Wermuth, 1967: 47; Grandison, 1972: 77.

Material examined. — MALAYSIA. WEST MALAYSIA. Bukit Balang, Kedah: 1♂, RMNH 19739, iv.1935, leg. G. H. Swarder. Perak: 1♂, ZFMK 20901, 1913, leg. W. Schlüter. Larut Hills, Perak, 3000 ft.: 1♂, BM 1946.8.13.43 (1900.6.14.3) (lectotype), leg. A. L. Butler. Gunong Benon, C. Pahang, 600-2500 ft.: 1♂, 3♀, BM 1967.2808,2816,2817,2819,2821, 18-24.ii.1967, BM/Univ. Malaya Exp. 1967.

Diagnosis. — Gular pouch in males strongly widened distally; dorsals 147-204; hindlimbs 0.85-1.00 times the distance between the limbs; tail length 1.76-2.01 times the snout-vent length; chin yellowish with indistinct darker spots forming a reticulated pattern.

Description. — Maximum snout-vent length in males 101 mm ($\bar{x} = 98.3$, $sd = 3.0$, $N = 4$), in females 89 mm ($\bar{x} = 82.0$, $sd = 7.0$, $N = 4$); maximum head length in males 18.8 mm, in females 17.2 mm, 0.18-0.20 times the snout-vent length (σ : $\bar{x} = 0.19$, $sd = 0.0$, $N = 4$; φ : $\bar{x} = 0.20$, $sd = 0.0$, $N = 4$); head depth 0.50-0.57 times the head length (σ : $\bar{x} = 0.54$, $sd = 0.03$, $N = 4$; φ : $\bar{x} = 0.51$, $sd = 0.01$, $N = 4$); head width 0.62-0.68 times the head length (σ : $\bar{x} = 0.65$, $sd = 0.01$, $N = 4$; φ : $\bar{x} = 0.65$, $sd = 0.03$, $N = 4$); snout length 0.28-0.35 times the head length (σ : $\bar{x} = 0.32$, $sd = 0.03$, $N = 4$; φ : $\bar{x} = 0.29$, $sd = 0.01$, $N = 4$); nostrils directed upward; supralabials 8-12, keeled; usually two median teeth in upper jaw (two teeth: 83.3 %, three teeth: 16.7 %); head scales variably keeled, subequal, slightly smaller in the supraocular region; a short row of strongly keeled, enlarged scales on the snout; no thornlike scale on the supraciliary edge; a low, rounded tubercle at the end of the supraciliary edge; tympana usually covered with smooth skin (one specimen had them partly covered with small scales), one indistinct, enlarged scale between the eye and the tympanum; a thornlike tubercle above the tympanum; a longitudinal nuchal fold, instead of a nuchal crest in males; gular pouch in males with enlarged scales, widened to an almost circular, rounded flap, 1.03-1.56 times the head length ($\bar{x} = 1.27$, $sd = 0.22$, $N = 4$); in females with enlarged scales at the tip, 0.63-0.85 times the head length ($\bar{x} = 0.75$, $sd = 0.09$, $N = 4$); dorsals 147-204 (σ : $\bar{x} = 184.5$, $sd = 13.3$, $N = 4$; φ : $\bar{x} = 157.5$, $sd = 9.5$, $N = 4$); subequal, smooth or faintly keeled; a few enlarged, keeled scales on the border between the body and the patagium; ventrals 98-140 (σ : $\bar{x} = 118.8$, $sd = 14.7$, $N = 4$; φ : $\bar{x} = 102.3$, $sd = 4.7$, $N = 4$), subequal, keeled, slightly larger than the dorsals; five ribs in the patagium; 18-25 (σ : $\bar{x} = 22.4$, $sd = 1.7$, $N = 4$; φ : $\bar{x} = 20.8$, $sd = 2.3$, $N = 4$), keeled subdigital lamellae under the fourth finger, 21-28 (σ : $\bar{x} = 25.4$, $sd = 1.9$, $N = 4$; φ : $\bar{x} = 23.0$, $sd = 2.1$, $N = 4$) under the fourth toe; hindlimbs 0.47-0.57 times the snout-vent length (σ : $\bar{x} = 0.50$, $sd = 0.02$, $N = 4$; φ : $\bar{x} = 0.55$, $sd = 0.03$, $N = 4$) and 0.85-1.00 times the distance between the limbs (σ : $\bar{x} = 0.89$, $sd = 0.04$, $N = 4$; φ : $\bar{x} = 0.95$, $sd = 0.05$, $N = 4$); base of tail and posterior edge of thigh with fringelike scales; maximum tail length 190 mm, 1.76-2.01 times the snout-vent length (σ : $\bar{x} = 1.86$, $sd = 0.12$, $N = 4$; φ : $\bar{x} = 1.87$ -1.99, $N = 2$); males with a low caudal crest of strongly keeled scales.

Colour in preservative. — Above bluish or brownish grey, sometimes with indistinct dark spots; an interorbital and a nuchal spot present; patagium dark-brown, with 4-5 irregular dark bands in females and with irregular dark spots, sometimes forming bands, in males; posterior edge of the patagium orangish red; chest and belly yellowish grey brown; ventral parts of patagium yellowish grey without any markings; chin yellowish with indistinct, darker spots forming a reticulated pattern; gular pouch in males yellowish at the distal tip, towards the

base changing into dark grey, base orangish brown; in females yellowish or greyish brown; the ventral parts of the lateral pouches orangish brown.

In life the patagium is olive grey above, the distal parts maroon; a large maroon spot at the base of the gular pouch and the ventral parts of the lateral pouches; the rest of the gular pouch is smoky grey, the edge is whitish (after Taylor (1963) and Grandison (1972)).

Ecological note. — Three of the four females carried eggs in the oviducts. Two (BM 1967.2816, 2819) had four eggs and one (BM 1967.2821) had three eggs. They were all collected in February.

Distribution. — This subspecies occurs in Southern Thailand and in West Malaysia (fig. 15). It is found to an altitude of 900 m. According to Boulenger (1908) above that altitude it is replaced by *D. blanfordii*.

Remark. — Of the two syntypes of this taxon, one, viz. the female (BM 1946.8.26.80) belongs to *D. b. blanfordii*. Therefore the male (BM 1946.8.13.43) is here selected as lectotype. Description: male; snout-vent length: 99 mm; tail length: 174 mm; head length: 18.6 mm; head depth: 9.8 mm; head width: 12.4 mm; snout length: 6.6 mm; gular pouch length: 19.1 mm; hindlimb length: 47/51 mm; distance limbs: 51/54 mm; two median upper teeth; tympanum covered with smooth skin; supralabials: 8/9; dorsals: 174; ventrals: 110; subdigital lamellae fourth finger: 25/24; ditto fourth toe: 25/27; indistinct nuchal fold; ribs patagium: 5/5; nostril directed upward; gular pouch and lateral pouches with enlarged scales; low caudal crest; grey brown above; interorbital spot indistinct; nuchal spot distinct; paired nuchal spots; patagium dark brown; with light, grey lines and indistinct dark spots near the body; ventral parts yellowish white; those of the patagium yellowish without spots; chin light, greyish brown with indistinct, light spots; gular pouch dark grey, orangish brown near the base; ventral parts of the lateral pouches light, orangish brown.

***Draco obscurus laetepictus* Hennig**

Draco formosus: Smith, 1926: 78.

Draco formosus laetepictus Hennig, 1936a: 217, fig. 11i, map 14 (terra typica: Siberut); Wermuth, 1967: 48.

No material examined.

Diagnosis. — Gular pouch in males with enlarged scales, slightly widened distally; number of dorsals unknown; hindlimbs probably as long as the distance between the limbs, 1.4-1.7 times the distance between the elbow and the hindlimb (when the arm is pressed to the body); tail length 1.6-1.8 times the snout-vent length; chin with distinct large yellow spots, giving it a reticulated impression (after Hennig, 1936a).

Distribution. — This subspecies occurs on the Kepulauan Mentawai (fig. 15).

Remark. — Since no material was examined, I suggest to recognise this subspecies till further investigations, although no distinct differences could be found between this subspecies according to Hennig (1936a) and the examined material of *D. o. obscurus*.

Draco quinquefasciatus Hardwicke & Gray

Draco quinquefasciatus Hardwicke & Gray, 1827: 219 (terra typica: Penang, Malaya); Gray, 1831: 59; Duméril & Bibron, 1837: 455; Günther, 1864: 126; Stoliczka, 1873: 118; Boulenger, 1885: 268; Mocquard, 1890: 128; Boulenger, 1891b: 288; Bartlett, 1894: 82; Flower, 1896: 870; Flower, 1899: 636; Lampe & Lindholm, 1901: 202; Boulenger, 1912: 63; De Rooy, 1915: 81; Smith, 1916a: 53; Smith, 1916b: 154; Smith, 1930: 23; Tanner, 1953: 4; Inger & Greenberg, 1966: 1014; Lloyd et al., 1968: 499; Dring, 1979: 232.

Dracunculus quinquefasciatus: Gray, 1845: 235.

Draco quinquefasciatus quinquefasciatus: Hennig, 1936a: 192, map 6; Bourret, 1943: 12; Taylor, 1963: 844; fig. 41; Wermuth, 1967: 52; Grandison, 1972: 78.

Draco quinquefasciatus longibarba Hennig, 1936a: 193, fig. 10h, map 6 (terra typica: Baram, Sarawak); Wermuth, 1967: 53 (new synonym).

Material examined. — MALAYSIA. WEST MALAYSIA. 1 ♂, BM 1956.1.12.1, leg. J. D. Romer. Penang: 1 ♂, BM 1946.8.27.4 (23.6a) (holotype), leg. T. Hardwicke. Kg. Kuala Menora, Perak, 200 ft.: 1 ♂, BM 1974.3817, 18.ii.1969, leg. P. Y. Berry. W. Kuala Langhit, Selangor: 1 ♂, BM 1904.7.19.8, Selangor Mus. INDONESIA. SUMATRA. Southern Sumatra: 1 juv., ZMA 14682 A, 1930/34, leg. J. van Tuyn. Deli: 1 ♂, RMNH 4996 (paratype of *D. q. longibarba* Hennig). BILLITON. 1 ♂, RMNH 19734, leg. A. G. Vorderman. KALIMANTAN. Samarinda: 1 ♂, 1 ♀, ZMA 11022-23 (paratypes of *D. q. longibarba* Hennig), 24.v.1909, leg. H. A. Lorentz. Bloecoe: 1 ♂, 1 ♀, RMNH 4997, ii.1897, leg. A. W. Nieuwenhuis. S. foot of the G. Kenepai: 1 ♂, RMNH 19737, 27.xii.1893; 1 ♀, RMNH 19735, 30.xii.1893; 1 ♂, RMNH 19736, 8.i.1894, all leg. J. Büttikofer.

Diagnosis. — Large or moderately sized species (maximum snout-vent length 106 mm); nostril directed upward; no **A**-shaped figure on the snout; usually two median teeth in upper jaw; supralabials 11-15, keeled; no thornlike scale on supraciliary edge; tympanum covered with small scales; gular pouch in males with slightly enlarged scales; lateral pouches with enlarged scales; nuchal fold in males; dorsals 178-213, smooth, subequal; usually six ribs in patagium; hindlimbs shorter than the distance between the limbs; no caudal crest.

Description. — Maximum snout-vent length in males 105 mm (\bar{x} = 95.3, sd = 5.1, N = 6) and in females 106 mm (\bar{x} = 90.5, sd = 11.8, N = 4) (juv.: 53 mm, N = 1); maximum head length 20.1 mm in males and 21.7 mm in females, 0.17-0.20 times the snout-vent length (♂: \bar{x} = 0.18, sd = 0.01, N = 6; ♀: \bar{x} = 0.20, sd = 0.01, N = 4; juv.: 0.20); head width 0.61-0.69 times the head length (♂: \bar{x} = 0.66, sd = 0.03, N = 6; ♀: \bar{x} = 0.63, sd = 0.01, N = 4; juv.: 0.63); head depth 0.49-0.54 times the head length (♂: \bar{x} = 0.53, sd = 0.01, N = 6; ♀: \bar{x} = 0.51, sd = 0.02, N = 4; juv.: 0.54); snout length 0.27-0.36 times the head length (♂: \bar{x} = 0.31, sd = 0.03, N = 6; ♀: \bar{x} = 0.31, sd = 0.02, N = 4; juv.: 0.27); nostril directed upward; supralabials 11-15, keeled; usually two median teeth in the upper jaw (two teeth: 91.7 %, three teeth: 8.3 %); head scales small, subequal, keeled; a more or less distinct row of slightly enlarged scales on the snout; no thornlike scale on the supraciliary edge; no tubercle at the end of the supraciliary edge; tympanum completely covered with small scales; no enlarged scales between the eye and the tympanum; sometimes with several, slightly enlarged scales in the lateral parts of the nuchal region; no nuchal crest, a low nuchal fold in males; gular pouch in males with slightly enlarged scales at the tip, 1.71-2.44 times the head length in specimens from the Sunda Islands (\bar{x} = 2.08,

sd = 0.29, N = 6), 1.53-2.01 times the head length in specimens from Malaya (\bar{x} = 1.74, sd = 0.20, N = 4), in females without enlarged scales, 0.69-1.03 times the head length (\bar{x} = 0.83, sd = 0.02, N = 4) (juv.: 1.14); lateral pouches with slightly enlarged scales; dorsals 178-213 (σ : \bar{x} = 194.0, sd = 11.8, N = 6; φ : \bar{x} = 190.8, sd = 5.9, N = 4; juv.: 190), subequal, smooth or faintly keeled; a row of slightly enlarged, distinctly keeled scales on the border between body and patagium; ventrals 119-135 (σ : \bar{x} = 126.4, sd = 5.3, N = 6; φ : \bar{x} = 124.3, sd = 5.1, N = 4; juv.: 135), keeled, about as large as or a little larger than the dorsals; usually six ribs in the patagium (six ribs: 91.7 %, five ribs: 8.3 %); subdigital lamellae under the fourth finger 17-22 (σ : \bar{x} = 19.4, sd = 1.5, N = 6; φ : \bar{x} = 19.5, sd = 0.9, N = 4; juv.: 19.5), only the most distal ones faintly keeled, those under the fourth toe 17-23 (σ : \bar{x} = 21.7, sd = 1.0, N = 6; φ : \bar{x} = 20.9, sd = 2.6, N = 4; juv.: 22.5), only the most distal ones faintly keeled; hindlimbs 0.46-0.53 times the snout-vent length (σ : \bar{x} = 0.48, sd = 0.02, N = 6; φ : \bar{x} = 0.51, sd = 0.02, N = 4; juv.: 0.49), 0.75-0.87 times the distance between the limbs (σ : \bar{x} = 0.78, sd = 0.04, N = 6; φ : \bar{x} = 0.82, sd = 0.03, N = 4; juv.: 0.81); posterior edge of thigh and base of tail with fringelike scales; maximum tail length 174 mm, 1.55-1.74 times the snout-vent length (σ : \bar{x} = 1.65, sd = 0.07, N = 6; φ : \bar{x} = 1.65, sd = 0.06, N = 4; juv.: 1.62); no caudal crest.

Colour in preservative. — Above light to dark brown, with small, dark brown spots, sometimes bands are recognizable; patagium light to dark brown, with four or five distinct, dark, transverse bands; dark spots present between the bands, which may be covered with light parts of lines or with light spots; chest and belly light brown to yellowish; chin with small dark spots; ventral parts of patagium yellowish or light brown, with dark bands; gular pouch in males light grey with darker lines and anterior edge in females dark grey or brown; a dark band behind the gular pouch, across the shoulders.

For colour in life see Grandison (1972).

Ecological notes. — Of the four females, one (RMNH 4997 A) had four eggs in the oviducts and another (RMNH 19735) had two eggs. The former was collected in February, the latter in December. See for further notes on the reproduction cyclus Inger & Greenberg (1966).

Distribution. — This species is known to occur on Sumatra, Singkep, Billiton, Borneo, in West Malaysia and Southern Thailand (fig. 16).

Remarks. — Although there is a difference in relative gular pouch length between the specimens from Malaya and those from the Sunda Islands, the overlap is very large. Since this relative gular pouch length is the only difference between *D. q. quinquefasciatus* and *D. q. longibarba*, these two taxa are here regarded as synonyms. Hennig (1936a) found that the gular pouch length in his material from Malaya was only 1.1-1.4 times the head length. Since all the material examined by him, was collected in Perak, this could be due to the fact that the Perak-population is different. But since BM 1974.3817 had a relative gular pouch of 1.76 this probably is not true. More material should be examined to solve this problem completely.

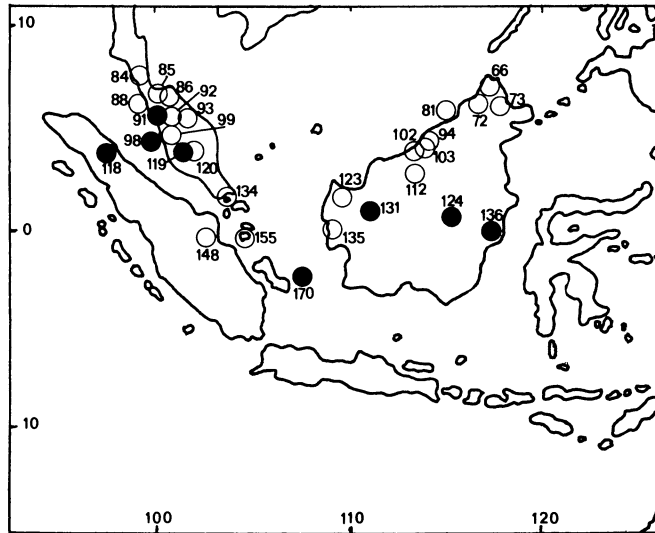


Fig. 16. Distribution of *Draco quinquefasciatus*. Open symbols are localities from the literature.

Draco spilopterus (Wiegmann)

Dracunculus spilopterus Wiegmann, 1834b: 216, 218, pl. 15 (terra typica: Manila, Luzon); Gray, 1845: 236.

Draco spilopterus: Duméril & Bibron, 1837: 461; Schlegel, 1844: 92; Günther, 1864: 124; Günther, 1873: 167; Boulenger, 1885: 260; Boettger, 1886: 98; Boettger, 1893a: 41; Wandolleck, 1900: 11, fig. 4, 13; Taylor, 1917: 371; Taylor, 1922a: 119, pl. 6 fig. 4; Bourret, 1943: 12.

Dracunculus ornatus Gray, 1845: 235 (terra typica: Philippine Islands).

Draco ornatus: Günther, 1864: 124; Günther, 1873: 167; Boulenger, 1885: 260; Boettger, 1886: 97; Boettger, 1893a: 41; Taylor, 1917: 370; Taylor, 1922a: 117, pl. 6 fig. 1.

Draco rostratus Günther, 1864: 127 (terra typica: ? Borneo); Boulenger, 1885: 261, pl. 20 fig. 5; Bartlett, 1894: 81; De Rooy, 1915: 87.

Draco quadrasi Boettger, 1893a: 41 (terra typica: Sibuyan, Philippines); Taylor, 1922a: 123, pl. 8 fig. 1, 2.

Draco spilopterus spilopterus: Hennig, 1936a: 185, fig. 10g, map 3; Hennig, 1936b: fig. 2; Wermuth, 1967: 53.

Material examined. — PHILIPPINES. 1 ♀, BM 1946.8.27.30 (lectotype of *D. ornatus* Gray), 1 ♀, 1 juv., BM 1946.8.27.29, 31 (paralectotypes of *D. ornatus* Gray), all leg. H. Cuming. 2 ♂, 2 ♀, RMNH 2955 A, B, C, D, 1847, Frank. SIBUYAN: 1 ♂, BM 1946.8.26.84 (93.11.1) (paralectotype of *D. quadrasi* Boettger), Senckenberg Mus.; 1 ♀, 2 juv., BM 1946.8.26.83,85,86 (93.11.1) (paralectotypes of *D. quadrasi* Boettger), Senckenberg Mus.; 1 ♂, ZMA 12044, 1923, leg. E. H. Taylor. LUZON. Pollillo, Manilla: 1 ♂, 1 ♀, ZMA 12047, 1923, leg. E. H. Taylor. Salajala: 1 ♂, IG 9422 reg. 819, leg. Déchange. PANAY: 1 ♀, ZFMK 26392, 1911, leg. G. Semper. NEGROS, E. Slope Cuernos de Negros, 1000 ft.: 1 ♂, 1 juv., BM 1964.671,672, leg. W. C. Brown. '? BORNEO'. 1 ♂, BM 1946.8.27.25 (47.3.4.23) (holotype of *D. rostratus* Günther), leg. E. Belcher. 'JAVA'. 1 ♂, BM 56.11.17.18, leg. J. Bowring. '? CHINA. Canton': 1 ♂, RMNH 2953, leg. Eidoux. LOC. UNKNOWN: 1 ♂, IG 9422 reg. 819b.

Diagnosis. — Small or moderately sized species (maximum snout-vent length 96 mm); nostril directed outward; usually two median teeth in the upper jaw; a series of keeled scales, forming a row or a Λ -shaped figure; supralabials 9-11, smooth; thornlike scale on supraciliary edge very low or absent; tympanum usually covered with small scales; gular pouch in males with slightly enlarged scales; lateral pouches in males and females with slightly enlarged scales; nuchal crest present; dorsals 101-142, unequal, keeled; usually six ribs in patagium; hindlimbs about as long as the distance between the legs; no caudal crest.

Description. — Maximum snout-vent length in males 88 mm (Hennig, 1936a), 80 mm in material examined (\bar{x} = 75.3, sd = 3.5, N = 9), in females 96 mm (Hennig, 1936a), 91 mm in material examined (\bar{x} = 76.7, sd = 10.5, N = 7) (juv.: \bar{x} = 41.7, sd = 6.4, N = 3, max.: 50 mm); maximum head length 16.5 mm in males, 19 mm in females (Hennig, 1936a), 0.18-0.24 times the snout-vent length (σ : \bar{x} = 0.19, sd = 0.01, N = 9; φ : \bar{x} = 0.21, sd = 0.01, N = 7; juv.: \bar{x} = 0.22, sd = 0.02, N = 3); head width 0.58-0.71 times the head length (σ : \bar{x} = 0.62, sd = 0.05, N = 9; φ : \bar{x} = 0.64, sd = 0.03, N = 7; juv.: \bar{x} = 0.71, sd = 0.00, N = 3); head depth 0.48-0.62 times the head length (σ : \bar{x} = 0.54, sd = 0.04, N = 9; φ : \bar{x} = 0.53, sd = 0.02, N = 7; juv.: \bar{x} = 0.61, sd = 0.01, N = 3); snout length 0.26-0.35 times the head length (σ : \bar{x} = 0.32, sd = 0.02, N = 9; φ : \bar{x} = 0.30, sd = 0.03, N = 7; juv.: \bar{x} = 0.29, sd = 0.03, N = 3); nostril directed outward; supralabials 9-11, smooth; usually two median teeth in the upper jaw (two teeth: 70.6 %, three teeth: 29.4 %); head scales, subequal, keeled, enlarged in the supraocular region; a series of enlarged scales on the snout forming a row or a Λ -shaped figure; thornlike scales on supraciliary edge absent (52.6 %) or very low (to 0.02 times the head length); a low rounded tubercle at the end of the supraciliary edge; tympanum usually covered with small scales (89.5 %), in one specimen it was completely, in another one partly, covered with smooth skin; three or four enlarged scales between the tympanum and the eye; a conical tubercle above the tympanum and one behind it; a longitudinal row of triangular tubercles between the nuchal fold and the lateral pouches; nuchal crest on a longitudinal fold in males, consisting of 20-33 (\bar{x} = 27.6, sd = 3.8, N = 9) slightly enlarged, compressed or strongly keeled scales; in females with 6-20 (\bar{x} = 12.9, sd = 6.2, N = 7) slightly enlarged, compressed or keeled scales (juv.: \bar{x} = 20.7, sd = 7.5, N = 3); gular pouch with slightly enlarged scales in males, 1.38-2.16 times the head length (\bar{x} = 1.66, sd = 0.28, N = 9); in females without enlarged scales, 0.38-0.60 (\bar{x} = 0.49, sd = 0.08, N = 7) times the head length (juv.: \bar{x} = 0.60, sd = 0.11, N = 3); lateral pouches in males and females with enlarged scales; dorsals 101-142 (σ : \bar{x} = 118.8, sd = 13.5, N = 9; φ : \bar{x} = 125.7, sd = 11.2, N = 7; juv.: \bar{x} = 111.7, sd = 9.6, N = 3), unequal, enlarged in the vertebral region, keeled; enlarged, keeled scales on the border between body and patagium; ventrals 80-104 (σ : \bar{x} = 95.1, sd = 7.8, N = 9; φ : \bar{x} = 95.7, sd = 4.9, N = 7; juv.: \bar{x} = 88.7, sd = 3.2, N = 3), keeled, about as large as the dorsals; usually six ribs in patagium (six ribs: 89.5 %, seven ribs: 5.3 %, five ribs: 5.3 %); 20-26 (σ : \bar{x} = 23.1, sd = 1.9, N = 9; φ : \bar{x} = 23.6, sd = 1.4, N = 7; juv.:

\bar{x} = 21.8, sd = 1.3, N = 3) keeled subdigital lamellae under the fourth finger, 23-31 (σ : \bar{x} = 25.5, sd = 2.0, N = 9; φ : \bar{x} = 25.6, sd = 1.6, N = 7; juv.: \bar{x} = 26.7, sd = 2.4, N = 3) under the fourth toe; hindlimbs 0.47-0.60 times the snout-vent length (σ : \bar{x} = 0.53, sd = 0.04, N = 9; φ : \bar{x} = 0.53, sd = 0.04, N = 7; juv.: \bar{x} = 0.54, sd = 0.02, N = 3) and 0.84-1.06 times the distance between the limbs (σ : \bar{x} = 0.94, sd = 0.07, N = 9; φ : \bar{x} = 0.91, sd = 0.06, N = 7; juv.: \bar{x} = 1.0, sd = 0.02, N = 3); small fringelike scales on posterior edge of thigh; maximum tail length 166 mm (Hennig, 1936a), 1.57-1.91 times the snout-vent length (σ : \bar{x} = 1.79, sd = 0.08, N = 9; φ : \bar{x} = 1.77, sd = 0.13, N = 7; juv.: \bar{x} = 1.72, sd = 0.09, N = 3); no caudal crest.

Colour in preservative. — Above brown to bluish grey with interorbital spot; females with nuchal spot; body without any distinct markings; patagium in males light brown, with or without dark brown spots and more or less distinct rests of dark bands at the most distal parts; patagium in females dark brown with more or less distinct, light spots and longitudinal lines connecting them; chest and belly light bluish or brownish grey; chin with fine, dark spots, forming a more or less distinct, reticulated pattern; ventral parts of patagium light orangish brown in males; light bluish grey in females with dark spots or rests of bands; gular pouch in males bluish, brownish or yellowish light grey with very fine dark spots near the base, distal part lighter than other parts, in females light grey, bluish or brown with larger spots than in males over its entire surface.

For colour in life see Taylor (1922a).

Ecological note. — Five of the seven available females had eggs in the oviducts: one (BM 1946.8.27.30) with two eggs, three (RMNH 2955 A, B, BM 1946.8.26.83) with three eggs and one (BM 1946.8.27.29) with four eggs. No collecting dates are available.

Distribution. — The species occurs on the Philippines (fig. 17).

Remarks. — Since Gray (1845) did not specify the type material of *D. ornatus*, BM 1946.8.27.30 is selected as lectotype. Description: female; snout-vent length: 80 mm; tail length: 149 mm; head length: 17.9 mm; head depth: 9.3 mm; head width: 10.8 mm; snout length: 5.2 mm; gular pouch length: 10.7 mm; thorn length: 0.0/0.16 mm; thorn width: 0.0/0.47 mm; hindlimb length: 41/42 mm; distance limbs: 46/47 mm; two median upper teeth; tympanum covered with small scales; supralabials: 9/11; dorsals: 134; ventrals: 99; subdigital lamellae fourth finger: 24/25; ditto fourth toe: ?/26; nuchal crest scales: 19; ribs patagium: 6/6; nostril directed outward; gular pouch without, lateral pouches with enlarged scales; no caudal crest; probably two eggs; bluish grey above; dark brown interorbital band; body with irregular, small, brown spots; patagium dark brown with large, light spots, forming a reticulated pattern; ventral parts yellowish and bluish white with fine, brown spots; those of the patagium yellowish with a brown spot; chin yellowish blue with fine brown spots and indistinct, lighter spots; gular pouch blue with brown spots, ventral parts of the lateral pouches similar.

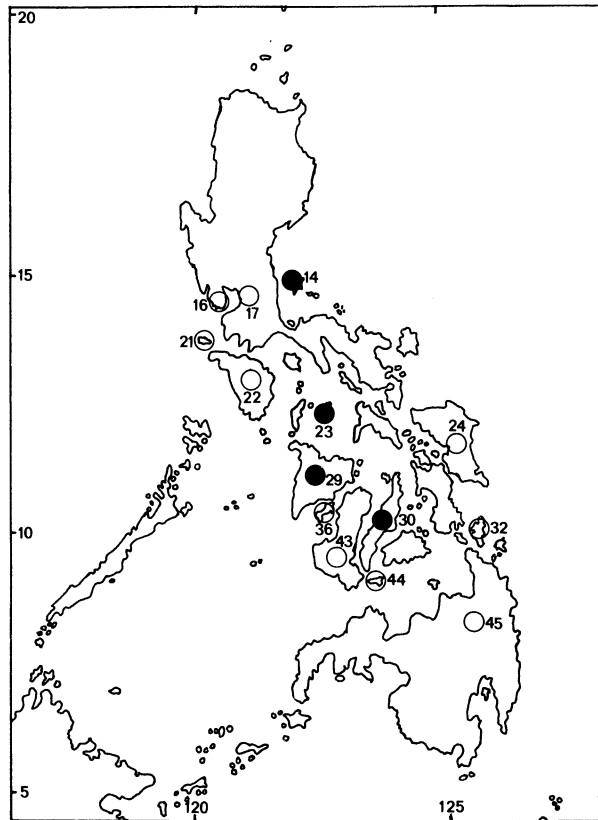


Fig. 17. Distribution of *Draco spilopterus*. Open symbols are localities from the literature.

Of the two syntypes of *D. quadrasi*, of which the measurements were given by Boettger (1893a), the male is BM 1946.8.26.84.

All the types of *D. ornatus* are females and they do not differ from the females of *D. spilopterus*. The name *ornatus* therefore can be considered a name for the females of this taxon.

The male of *D. quadrasi* differs from other males of *D. spilopterus* in having no spots on the dorsal surfaces of the patagia. One other specimen of the examined material had the same colour: ZMA 12044. Both the types and this specimen were collected on Sibuyan. Taylor (1922a) also found most specimens of the *quadrasi* form on Sibuyan, although he did find one specimen on Mindoro. As he also found *spilopterus* on this latter island, *quadrasi* is not considered a subspecies of *spilopterus* here. It was not possible to detect any other difference between *spilopterus* and the types of *quadrasi*. Further study of more extensive material with exact locality data, could reveal that *quadrasi* is a good subspecies.

The snout of the type of *D. rostratus* Günther is not longer than that of the specimens of *spilopterus* (viz.: 0.30 times the head length), as Günther stated. Nor does it differ from this taxon in any other characters or markings. Therefore *D. rostratus* is undoubtedly synonymous with *D. spilopterus*.

The localities 'Canton (China)', 'Borneo' and 'Java' are here regarded incorrect.

***Draco taeniopterus* Günther**

Draco taeniopterus Günther, 1861: 187 (terra typica: Chartaboum, coast of Siam); Günther, 1864: 126, pl. 13 fig. e; Blanford, 1878: 126; Boulenger, 1885: 269; Boulenger, 1887 c: 429; Boulenger, 1890a: 113; Bartlett, 1894: 81; Flower, 1899: 637; Wandolleck, 1900: 15; De Rooy, 1915: 85; Smith & Kloss, 1915: 239; Smith, 1916a: 53; Smith, 1930: 22; Smith, 1935: 140; Smith, 1937: 75, pl. 8 fig. 1.

Draco taeniopterus taeniopterus: Hennig, 1936a: 209, fig. 11h, map 11; Hennig, 1936b: fig. 3; Taylor, 1963: 852, fig. 43; Wermuth, 1967: 54.

Material examined. — BURMA. Mergui: 1 ♀, BM 88.7.19.1, leg. Anderson. Tavoy, Tenasserin: 1 ♀, BM 81.1.14.1, leg. A. J. Blanford. Tazan: 2 ♂, BM 1921.4.1.93.8, leg. M. A. Smith. THAILAND. Chartaboum: 1 ♂, BM 1946.8.26.75 (61.4.12) (holotype), leg. M. Mouhot. Nakon Sri Tamarat: 1 ♀, BM 1921.4.1.93.8, leg. M. A. Smith. Phra Phutabat: 1 ♂, ZFMK 13170, 1972, leg. H. Meier. Trang: 1 ♀, ZFMK 16631, 29.vii.1975, leg. G. Nikolaus.

Diagnosis. — Species of small to moderate size (maximum snout-vent length 78 mm); nostril directed upward; row of keeled scales on snout; usually two median teeth in the upper jaw; supralabials 6-10, keeled; no thornlike scale on supraciliary edge; tympanum covered with smooth skin; gular pouch in males with enlarged scales; lateral pouches with enlarged scales in both sexes; males with low nuchal fold; dorsals 138-173, feebly keeled, subequal; usually five ribs in patagium; hindlimbs as long as the distance between the limbs; no caudal crest; patagium with distinct, light-margined, dark bands.

Description. — Maximum snout-vent length in females 78 mm ($\bar{x} = 70.5$, $sd = 8.6$, $N = 4$), in males 77 mm ($\bar{x} = 72.8$, $sd = 3.8$, $N = 4$); maximum head length 15.3 mm, 0.19-0.21 times the snout-vent length (♂: $\bar{x} = 0.19$, $sd = 0.01$, $N = 4$; ♀: $\bar{x} = 0.20$, $sd = 0.01$, $N = 4$); head width 0.66-0.69 times the head length (♂: $\bar{x} = 0.67$, $sd = 0.01$, $N = 4$; ♀: $\bar{x} = 0.67$, $sd = 0.02$, $N = 4$); head depth 0.49-0.55 times the head length (♂: $\bar{x} = 0.54$, $sd = 0.01$, $N = 4$; ♀: $\bar{x} = 0.52$, $sd = 0.03$, $N = 4$); snout length 0.28-0.31 times the head length (♂: $\bar{x} = 0.30$, $sd = 0.01$, $N = 4$; ♀: $\bar{x} = 0.29$, $sd = 0.01$, $N = 4$); nostril directed upward; supralabials 6-10, keeled; usually two median teeth in the upper jaw (two teeth: 71.4 %, three teeth: 28.6 %); head scales unequal, keeled; a row of enlarged scales on the snout; no thornlike scale on supraciliary edge; low tubercle at the end of the supraciliary edge; tympanum covered with smooth skin; one to three enlarged scales between eye and tympanum; one pyramidal tubercle above the tympanum; males with a low nuchal fold; gular pouch in males with enlarged scales, 1.30-1.72 times the head length ($\bar{x} = 1.59$, $sd = 0.20$, $N = 4$); gular pouch in females without enlarged scales, 0.42-0.66 times the head length ($\bar{x} = 0.54$, $sd = 0.11$, $N = 4$); lateral pouch with enlarged scales; dorsals 138-173 (♂:

\bar{x} = 157.0, sd = 13.4, N = 4; ♀: \bar{x} = 150.0, sd = 10.1, N = 4), subequal, smooth or faintly keeled; enlarged, strongly keeled scales on the border between body and patagium; ventrals 95-112 (♂: \bar{x} = 104.0, sd = 7.5, N = 4; ♀: \bar{x} = 102.0, sd = 6.2, N = 4), keeled, larger than dorsals; usually five ribs in patagium (five ribs: 87.5 %, six ribs: 12.5 %); 20-26 (♂: \bar{x} = 23.3, sd = 2.2, N = 4; ♀: \bar{x} = 21.8, sd = 1.2, N = 4) keeled subdigital lamellae under the fourth finger, 21-27 (♂: \bar{x} = 26.0, sd = 1.4, N = 4; ♀: \bar{x} = 23.9, sd = 2.1, N = 4) under the fourth toe; hindlimbs 0.52-0.60 times the snout-vent length (♂: \bar{x} = 0.60, sd = 0.0, N = 4; ♀: \bar{x} = 0.60, sd = 0.05, N = 4), 0.91-1.18 times the distance between the legs (♂: \bar{x} = 1.02, sd = 0.09, N = 4; ♀: \bar{x} = 1.05, sd = 0.11, N = 4); fringelike scales on posterior edge of thigh and base of tail; maximum tail length 157 mm, 1.77-2.07 times the snout-vent length (♂: \bar{x} = 1.91, sd = 0.11, N = 4; ♀: \bar{x} = 2.01, sd = 0.05, N = 4); no caudal crest.

Colour in preservative. — Above brown grey, interorbital spot present, nuchal band may be present; males sometimes with recognizable bands or spots on the body; patagium brown with four or five irregular, distinct, usually light-margined, dark bands with lighter spots in the middle in both sexes; chest and belly light brown; chin yellowish, sometimes spotted; ventral parts of patagium yellowish, no spots; gular pouch in males yellowish brown with orange base and posterior parts; gular pouch in females orangish yellow; ventral parts of lateral pouches orangish yellow.

For colour in life see Taylor (1963).

Ecological notes. — One female (ZFMK 16631), collected in July, carried four eggs, another female (BM 81.1.14.1) had two eggs in the oviducts. Taylor (1963) stated that the species lays four eggs.

Distribution. — This species occurs in Thailand and Burma (fig. 18). Bartlett (1894) mentioned a locality on Borneo (Matang, 800-900 ft., Sarawak), but it was probably based on a wrong identification (Hennig, 1936a).

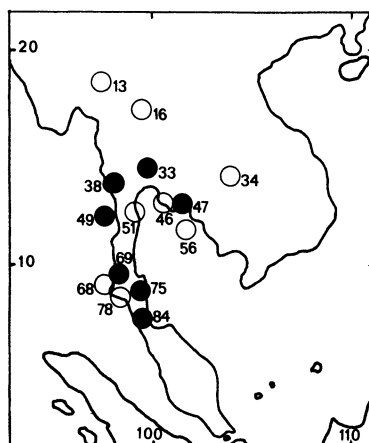


Fig. 18. Distribution of *Draco taeniopterus*. Open symbols are localities from the literature.

Draco volans Linnaeus

Diagnosis. — Small to moderately sized species (maximum snout-vent length 96 mm); nostril directed outward; series of scales on the snout, forming a Λ -shaped figure; usually three median teeth in the upper jaw; supralabials 6-12, smooth; a more or less distinct, thornlike scale on the supraciliary edge; tympanum usually covered with smooth skin; gular pouch with slightly enlarged scales; lateral pouches with enlarged scales; nuchal crest present; dorsals 84-166, feebly or strongly keeled, unequal; usually six ribs in patagium; hindlimbs usually not as long as the distance between the limbs; no caudal crest.

KEY TO THE SUBSPECIES

1. A row of strongly enlarged, keeled scales on each side of the vertebral line; Timor, Roti, Semau, Alor and Wetar *D. volans timoriensis* (p. 91)
Not such distinctly enlarged scales along the vertebral line; not from Timor and surrounding islands 2
2. Lateral parts of head in males with dark spots forming a reticulated pattern 3
Lateral parts of head in males without a reticulated pattern 4
3. Thornlike scale on supraciliary edge usually larger than 0.03 times the head length; males with more than 22 nuchal crest scales; Philippines *D. volans reticulatus* (p. 85)
Thornlike scale on supraciliary edge usually smaller than 0.03 times the head length; males with less than 22 nuchal crest scales; Lesser Sunda Islands (except Timor and surroundings) or Sulawesi *D. volans boschmai* (p. 83)
4. Thornlike scale distinct to large; patagium in males with distinct bands in outer parts, in females reticulated in outer parts; Java and Bali *D. volans volans* (p. 78)
Thornlike scale small; patagium in males and females dark brown with lighter spots in outer parts; West Malaysia, Sumatra, Borneo and surrounding islands *D. volans sumatranus* (p. 87)

The name *sumatranus* is reestablished here because the differences in colouration coincide with constant differences in morphometric characters between the populations from Java and Bali and those from the rest of 'Sundaland'. One could state, however, that the difference between *volans* and *sumatranus* is of another level than that between, for example *D. v. boschmai* and *D. v. timoriensis*, which could be described as different species. This is not done, because of the allopatry and the obvious relationship of the taxa.

Draco volans volans Linnaeus

(pl. 3 figs. a, b)

Draco volans Linnaeus, 1758: 199 (terra typica: Java); Linnaeus, 1766: 358; Wiegmann, 1834a: 14; Gray, 1845: 233 (partim); Günther, 1864: 124 (partim); Boulenger, 1885: 256 (partim); Boulenger, 1887c: 492; Weber, 1890: 166 (partim); Boettger, 1892: 116; Boettger, 1893a: 40 (partim); Wandolleck, 1900: 10; Laidlaw, 1901: 307; Lampe & Lindholm, 1901: 202 (partim); Barbour, 1912: 85; De Rooy, 1915: 70, fig. 43 (partim); Dunn, 1927: 3; Mertens, 1929a: 168; Mertens, 1929b: 27; Kopstein, 1930: 304; Lederer, 1932: 185; Saint-Girons & Saint-Girons, 1956: 137; Pfeffer, 1962: 417 (partim).

Draco praeopus Linnaeus, 1766: 358 (terra typica: "America").

Draco major Laurenti, 1768: 50 (terra typica: "America").

- Draco minor* Laurenti, 1768: 51 (terra typica: "America").
Draco viridis Daudin, 1802: 301, pl. 41 (terra typica: Java); Kuhl, 1820: 102; Hardwicke & Gray, 1827: 219; Fitzinger, 1843: 50; Bleeker, 1859: 207; Fitzinger, 1864: fig. 6.
Draco fuscus Daudin, 1802: 307 (terra typica: unknown); Kuhl, 1820: 102; Bleeker, 1859: 207.
Draco daudinii Duméril & Bibron, 1837: 451 (terra typica: Java).
Draco viridis var. *javanica* Schlegel, 1844: 91, pl. 24 fig. 1 (terra typica: Java).
Draco volans volans: Mertens, 1930a: 248 (partim); Hennig, 1936a: 176, fig. 10a, map 2 (partim); Wermuth, 1967: 54 (partim).

Material examined. — INDONESIA. JAVA. 1♂, RMNH 19832; 1♂, 2♀, RMNH 19893-95; 1♂, 1♀, RMNH 18761, leg. E. Dubois; 2♂, 1♀, ZFMK 20891-93, 1846/53; 4♂, 1♀, RMNH 19901, 19906-08, 19911, leg. W. C. van Heurn; 1♂, 2♀, RMNH 18763, leg. P. Buitendijk; 4♂, 1♀, RMNH 7178, leg. dr. H. Brummund; 3♂, RMNH 2928 (paralectotypes *D. viridis* var. *javanica*), leg. C. G. C. Reinwardt; 1♂, RMNH 2934 A (lectotype *D. viridis* var. *javanica* Schlegel), 4♂, 1♀, RMNH 2934 B-F (paralectotypes *D. viridis* var. *javanica*), all leg. H. C. Macklot; 3♀, RMNH 2932 (paralectotypes *D. viridis* var. *javanica*), leg. C. G. C. Reinwardt; 2♂, 4♀, RMNH 20004-09, leg. A. G. Vorderman; 1♀, ZMA 15270, leg. W. Docters van Leeuwen; 4♂, 5♀, ZMA 10303, leg. A. C. Oudemans; 2♂, 7♀, ZMA 15254, 1879-87, leg. J. Kruizinga a.o.; 1♀, ZMA 15249, 1887, leg. kpt. Mollinger. W. Java: 7 juv., RMNH 19840-46, 1930/32, W. C. van Heurn; 1♀, ZMA 15278, 1899, leg. M. E. G. Bartels. Garut: 1♀, RMNH 19824, 1928, 1♀, RMNH 19825, xi/xii.1928, 1♀, RMNH 19830, 1930, 1 juv., RMNH 19847, 1929, 1♂, RMNH 19852, 17.xii.1930, 1♂, RMNH 19851, 3.xii.1930, 15♂, 5♀, RMNH 19853-72, 4.x.1929, 1♂, 2♀, RMNH 19882-84, 1930; 2♂, RMNH 19890-91, 25.xii.1929, 1♂, 1♀, RMNH 19909-10, 1928; 1♀, RMNH 19915, 1929, 700-1500 m, all leg. W. C. van Heurn; 1♀, RMNH 19904, 4.ii.1931, 700 m; 2 juv., RMNH 9013, viii.1930, 800 m, all leg. F. Kopstein. Bogor: 1♀, RMNH 19826; 1♂, RMNH 19829, 24.xi.1926; 2♀, RMNH 19827, 1926, all leg. W. C. van Heurn; 1♀, SMF 23159, 1927, leg. R. Mertens; 1♀, ZFMK 26391, 1884, leg. Count Solms; 1♂, RMNH 5334, 25.vi.1921, leg. W. C. van Heurn; 2♂, 3♀, RMNH 20010-14, ii.1929, leg. P. Buitendijk; 5♂, 2♀, RMNH 5352, leg. H. v. d. Weele; 1♀, ZMA 15261, 3♀, ZMA 15250, 1888, all leg. M. Weber. Tjimahi: 1♂, 2♀, 5 juv., RMNH 19848-50, 19835-39, leg. J. K. van Hoessel. Djakarta: 5♂, 4♀, RMNH 19873-81, leg. P. Buitendijk; 1♂, ZMA 15257, leg. P. N. van Kampen; 1♀, ZMA 15258, leg. J. J. Vingerkoets. Poentjak Gedeh Mnts: 1♀, RMNH 19892, x.1891, leg. J. D. Pasteur. Djokjokarta: 2♂, RMNH 19898-99, leg. F. A. van Velsen. Tjikadjang: 1♂, RMNH 19912, v.1935, 900 m, leg. C. P. J. de Haas; 1♀, RMNH 19918, iv.1939, 900 m, leg. C. P. J. de Haas. Gambir: 1♀, RMNH 19919, leg. P. Buitendijk; 1♂, 1♀, ZMA 15273, v.1914, leg. P. Buitendijk. Poentjak-pass: 1♀, RMNH 19920, 18.vi.1932, 1000 m, leg. W. C. van Heurn. Djoeja and Bogor: 3♂, 4♀, ZMA 15271, 1924, leg. G. J. Terwiel. Preanger: 1♀, ZMA 15266, xi.1911, leg. P. Buitendijk. M. Java. Semarang: 1♂, 2♀, RMNH 19905, 19833-34, 1945/48, leg. C. H. Munnig Schmidt; 1♂, RMNH 8059, 1896, leg. E. Jacobson; 1♂, ZMA 15274, leg. E. Jacobson; 1♀, ZMA 15276, leg. P. H. van Doesburgh. Salatiga: 1♂, 1♀, RMNH 2948, leg. S. C. J. W. van Musschenbroek; 1♂, ZMA 15281, vii.1915, leg. P. Buitendijk. Parang: 3♂, 12♀, RMNH 2931, paralectotypes *D. viridis* var. *javanica*, leg. H. Boie & H. C. Macklot. Tjilatjap: 1♂, ZMA 15260, leg. H. v. d. Horst. Tulungagung: 2♀, ZMA 15287, 8.xii.1931; 1♀, ZMA 15285, 30.xi.1931; 1♀, ZMA 15286, 5.xii.1931; 1♀, ZMA 15288, 26.v.1931, all leg. C. J. Louwerens. South slope of Merapi: 3♀, ZMA 14680, 1920, leg. Th. H. MacGillarry. E. Java: 1♂, RMNH 6930, leg. P. Buitendijk. Malang: 1♀, RMNH 19889, leg. Fr. M. Vianney; 4♀, RMNH 5738, 2, 4, 5, 10, leg. A. Koller. Soerabaja: 1 juv., RMNH 19839, 1933/34; 1♀, RMNH 19885, 24.xi.1936, leg. W. C. van Heurn; 2♂, RMNH 19902-03, iii.1935, leg. W. C. van Heurn; 1♂, RMNH 19916, 1933, leg. W. C. van Heurn. Kendeng ridge, Idjen hills: 3♀, RMNH 19886-88, xi.1936, leg. W. C. van Heurn. Slopes of the Ardjoeno: 1♀, RMNH 19896, 27.vi.1906, leg. P. Buitendijk. Nongkodjadar: 1♀, 1 juv., RMNH 9018, 1934, 1200 m, leg. F. Kopstein; 1♀, RMNH 19900, 1934, 1200 m, leg. F. Kopstein; 1♀, RMNH 19921, 1934, 1200 m, leg. F. Kopstein; 1♀, ZMA 15275, leg. E. Jacobson. Bezoeki: 2♂, RMNH 5738 B, C, leg. J. Semmelink. Bremlang Mnts: 1♀, RMNH 7863, 19.vi.1939, 1000 m, leg. W. C. van Heurn. Slope Smeroe: 2♂, RMNH 19913-14, vi.1914, leg. P. Buitendijk. Poed-

jon: 1 ♀, RMNH 19917, vii.1938, 1000 m, leg. W. C. van Heurn. Soember Doeren, near Malang: 1 ♀, ZMA 15269, leg. mrs. R. Hojel-Berg. Bajolali: 1 ♂, RMNH 19823, xii.1914, leg. A. G. Horst. Bandung: 1 ♀, RMNH 5738, leg. A. P. Neervoort v. d. Poll, C. Kannegieter. BALI. Gitgit: 1 ♂, SMF 23160, 1927, leg. R. Mertens. Tjandikoesoema: 1 ♀, IG 9796 reg. 634, 25/26.iv.1932, leg. S. R. R. la Prince Léopold. 'AMBOINE, MOLUQUES': 5 ♂, 3 ♀, IG 3737 reg. 1120, 814, don. Suyckerbuyk. 'BATCHIAN, MOLUQUES': 2 ♀, IG 4313 reg. 814b, don. Vermersch.

Diagnosis. — A subspecies reaching a snout-vent length of 96 mm; gular pouch with slightly enlarged scales in males; thornlike scale usually distinct, or even large (to 0.06 times the head length); dorsals 90-137; patagium in males with distinct, dark bands near the outer edge; in females these bands are less distinct, broken up into a reticulated pattern.

Description. — Maximum snout-vent length in males 82 mm (\bar{x} = 71.1, sd = 6.5, N = 51) and in females 96 mm (\bar{x} = 76.8, sd = 7.7, N = 55) (juv.: \bar{x} = 29.9, sd = 8.4, N = 14, max. = 55 mm, min. = 21 mm); maximum head length in males 15.5 mm, in females 18.5 mm, 0.17-0.29 times the snout-vent length (♂: \bar{x} = 0.19, sd = 0.01, N = 51, ♀: \bar{x} = 0.20, sd = 0.01, N = 55; juv.: \bar{x} = 0.25, sd = 0.02, N = 14); head width 0.57-0.76 times the head length (♂: \bar{x} = 0.68, sd = 0.03, N = 51, ♀: \bar{x} = 0.68, sd = 0.03, N = 55; juv.: \bar{x} = 0.68, sd = 0.05, N = 14); head depth 0.47-0.72 times the head length (♂: \bar{x} = 0.58, sd = 0.04, N = 51; ♀: \bar{x} = 0.57, sd = 0.04, N = 55; juv.: \bar{x} = 0.62, sd = 0.04, N = 14); snout length 0.22-0.38 times the head length (♂: \bar{x} = 0.31, sd = 0.03, N = 51; ♀: \bar{x} = 0.31, sd = 0.02, N = 55; juv.: \bar{x} = 0.26, sd = 0.02, N = 14); nostril directed outward; supralabials 6-12, smooth; usually three median teeth in the upper jaw (three teeth: 67.8 %, two teeth: 18.6 %, one tooth: 10.2 %, no teeth: 3.4 %); head scales large, subequal, keeled; a series of strongly keeled scales, forming a Λ -shaped figure on the snout; thornlike scale on the supraciliary edge, usually distinct or large (to 0.06 times the head length; ♂: \bar{x} = 0.029, sd = 0.013, N = 51; ♀: \bar{x} = 0.029, sd = 0.010, N = 55; juv.: \bar{x} = 0.024, sd = 0.007, N = 14); tubercle at the end of the supraciliary edge distinct; tympanum covered with smooth skin; 2-4 strongly keeled, enlarged scales between the eye and the tympanum; one to three large spinelike tubercles above the tympanum and one or two behind it; a longitudinal row of compressed tubercles between the nuchal crest and the lateral pouch; nuchal crest consisting of 7-17 triangular, compressed scales in males (\bar{x} = 12.1, sd = 2.7, N = 51) and of 2-14 such scales in females (\bar{x} = 8.5, sd = 3.3, N = 55) (juv.: \bar{x} = 6.6, sd = 3.4, N = 14); gular pouch in males with slightly enlarged scales, 0.96-1.75 times the head length (\bar{x} = 1.24, sd = 0.17, N = 51), in females 0.47-1.38 times the head length (\bar{x} = 0.66, sd = 0.15, N = 55) (juv.: \bar{x} = 0.52, sd = 0.13, N = 14); lateral pouches with enlarged scales; dorsals 90-137 (♂: \bar{x} = 113.1, sd = 9.3, N = 51; ♀: \bar{x} = 113.0, sd = 8.7, N = 55; juv.: \bar{x} = 105.9, sd = 9.4, N = 14), unequal, smooth or keeled; a row of enlarged, strongly keeled scales on the border between body and patagium; ventrals 82-117 (♂: \bar{x} = 100.0, sd = 7.9, N = 51; ♀: \bar{x} = 101.2, sd = 6.6, N = 55; juv.: \bar{x} = 94.8, sd = 7.2, N = 14), keeled, smaller than dorsals; usually six ribs in patagium (six ribs: 90.3 %, seven ribs: 7.6 %, five ribs:

2.1 %); 17-27 (σ : \bar{x} = 22.9, sd = 2.0, N = 51; φ : \bar{x} = 23.1, sd = 1.9, N = 55; juv.: \bar{x} = 23.3, sd = 1.9, N = 14) keeled subdigital lamellae under the fourth finger, 21-30 (σ : \bar{x} = 25.4, sd = 2.0, N = 51; φ : \bar{x} = 26.0, sd = 1.7, N = 55; juv.: \bar{x} = 25.2, sd = 1.9, N = 14) under the fourth toe; hindlimbs 0.37-0.54 times the snout-vent length (σ : \bar{x} = 0.45, sd = 0.03, N = 51; φ : \bar{x} = 0.45, sd = 0.03, N = 55; juv.: \bar{x} = 0.48, sd = 0.02, N = 14), 0.63-1.00 times the distance between the limbs (σ : \bar{x} = 0.78, sd = 0.07, N = 51; φ : \bar{x} = 0.77, sd = 0.07, N = 55; juv.: \bar{x} = 0.90, sd = 0.07, N = 14); small, fringelike scales on posterior edge of thigh; maximum tail length 128 mm, 1.19-1.81 times the snout-vent length (σ : \bar{x} = 1.46, sd = 0.12, N = 51; φ : \bar{x} = 1.46, sd = 0.10, N = 55; juv.: \bar{x} = 1.59, sd = 0.10, N = 14); no caudal crest.

Colour in preservative. — Above dark to pale brown, sometimes bluish; interorbital spot present, females with nuchal spot too; body without distinct markings, sometimes with vague, darker and lighter spots; usually short, indistinct, radial lines around the eyes; patagium brownish, about the same colour as the body or lighter, with more or less distinct lighter spots near the body edge; in males with 3-5 distinct, dark bands on the distal parts; in females the bands are less distinct, being broken up by lighter spots, which give it a reticulated impression (between the first and second rib, two bands are recognizable); chest and belly brownish, yellowish or bluish light grey, sometimes the lateral parts with fine, dark spots; chin with fine spots, sometimes forming bands; ventral parts of patagium bluish grey, usually with dark spots, varying very much in size and density, sometimes forming bands; gular pouch in males yellowish or orangish, at the base with small dark spots; in females light to dark bluish grey, with black spots, usually in high density.

Ecological notes. — 58.1 % of the females had eggs in the oviducts. Of these 59.4 % had four eggs, 21.9 % had three, 9.5 % had five, 6.2 % had two and 3.1 % had six eggs. Females with eggs were collected in February, June, October, November and December. In one case, the juveniles hatched after 29 days (Kopstein, 1930). For further data on behaviour and ecology see Pfeffer (1962).

Distribution. — This subspecies is known to occur on Java and Bali (fig. 19). It is found to an altitude of 1500 m (Boulenger, 1887c).

Remarks. — On plate 15 fig. 1, 2 (pl. 3 fig. a, b) of the manuscript of the 'Erpétologie de Java' of H. Boie, two lizards are depicted under the name *D. viridis*, which clearly belong to *D. v. volans*. In the text *D. viridis* is described as follows:

“*Draco viridis*.

Draco- naribus lateraliter apertis; occipite tuberculato tuberculis post superciliaribus duobus conicis prominentibus; paleari lato triquetro apice angusto, producto, in mari citrino in femina cijaneo nigro punctato; squamis dorsalibus carinatis, serie squamarum majorum interrupta in utroque latere dorsi; alis in mare supra fuscis facis quinque marginalibus nigris, infra albicantibus fasciis quatuor nigris ad basin; in femina supra ex aurantiaco nigroque varies, infra albicantibus maculis nigris non nullis sparsis”.

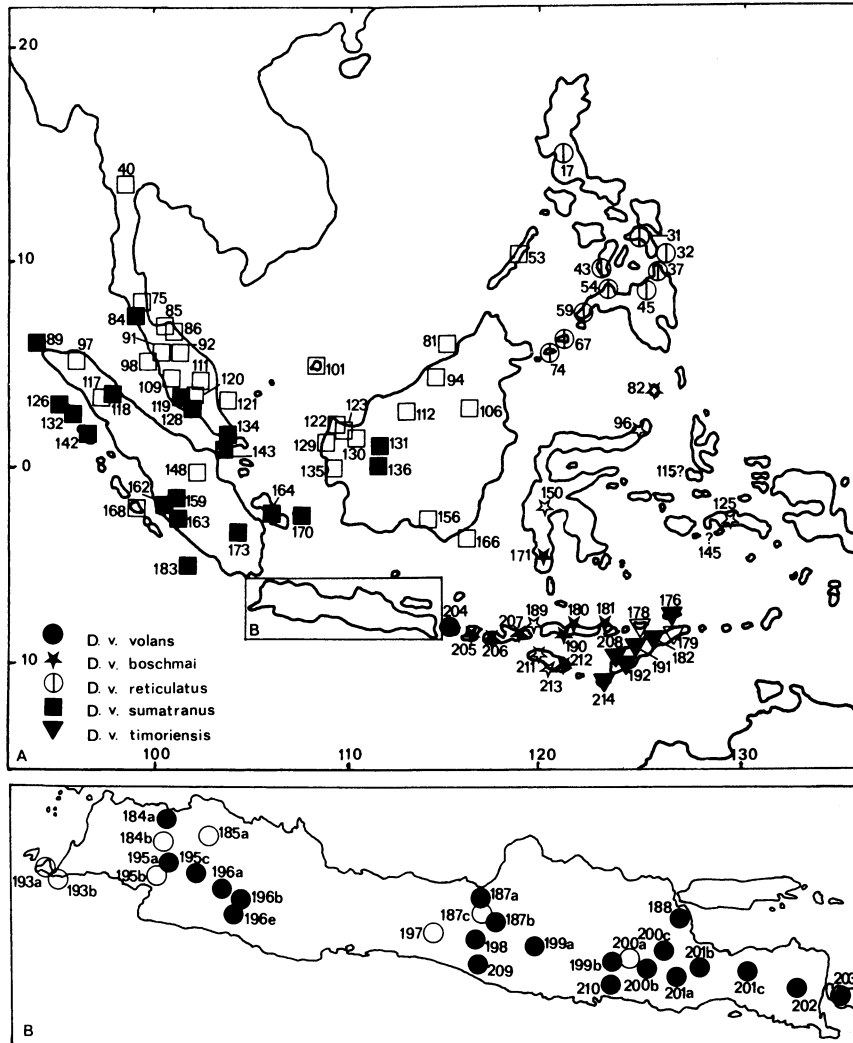


Fig. 19. Distribution of *Draco volans*. Open symbols are localities from the literature.

The female RMNH 2934 A resembles best the picture that Schlegel (1844: pl. 24 fig. 1) gave of *D. viridis* var. *javanica*, both in markings and in dimensions. Therefore this female is selected here as lectotype of *D. viridis* var. *javanica*. All the other specimens Schlegel could have examined are regarded as paralectotypes.

Description of the lectotype: female; snout-vent length: 85 mm; tail length: 114 mm; head length: 15.8 mm; head depth: 8.9 mm; head width: 11.0 mm; snout length: 5.5 mm; gular pouch length: 9.5 mm; thornlike scale length:

0.56/0.56 mm; thornlike scale width: 0.98/0.98 mm; hindlimb length: 39/39 mm; distance limbs: 51/49 mm; two median upper teeth; tympanum covered with smooth skin; supralabials: 10/8; dorsals: 114; ventrals: 119; subdigital lamellae fourth finger: 24/26; ditto fourth toe: 29/30; nuchal crest scales: 9; ribs patagium: 7/7; no eggs; interorbital spot present; dorsal parts pale, bluish white; patagium light brown with fine dark spots on the central parts and large spots on the margins, ventrally with fine spots too; gular pouch light bluish grey with large, black spots.

The specimens from 'Amboina' (= Ambon) (IG 3737 reg. 1120, 814) and those from 'Batchian' (= Bacan) (IG 4313 reg. 814) agree very much with *D. v. volans*: dorsals unequal, faintly keeled; short hindlimbs (0.74-0.80 times the distance between the legs) and short tail (1.35-1.53 times the snout-vent length); low number of nuchal crest scales (4-15), but the most remarkable character is the colour, which is exactly like that of *D. v. volans*: interorbital spot present; females with nuchal spot; patagium in males with distinct, dark bands near the outer edge; in females the dark parts give a reticulated impression. I strongly doubt the alleged origin of these specimens (they were donations of Suyckerbuyk (Amboina) and Vermersch (Batchian) and arrived in Brussels in resp. 1876 and 1879). Another reason to justify this doubt is that two other specimens from 'Batchian' (IG 4313 reg. 815, p. 91) do not agree at all with the preceding ones. They very much resemble *D. v. timoriensis*, having two rows of enlarged, keeled scales on the back along the vertebral line and many spinelike tubercles in the lateral parts of the nuchal region. The male is too discoloured to say anything about the colourpattern, the female has brown patagia without any blue. Thus the localities of IG 3737 reg. 1120, 814 and IG 4313 reg. 814, 815 are here regarded as being wrong.

Draco volans boschmai Hennig

Draco reticulatus: Peters & Doria, 1878: 374 (?); Boulenger, 1885: 257 (partim); Boulenger, 1897a: 504 (partim); Weber, 1890: 166; Sarasin & Sarasin, 1901: 70, 75; De Rooy, 1915: 72 (partim); Dunn, 1927: 3; Pfeffer, 1962: 417.

Draco volans: Roux, 1911: 496; Boulenger, 1912: 57 (partim); De Rooy, 1915: 70 (partim).

Draco timoriensis: De Rooy, 1915, 74 (partim).

Draco volans reticulatus: Mertens, 1930a: 248; Forcart, 1953: 369; Darevsky, 1964: 568; Auffenberg, 1980: 94, fig. 25.

Draco volans boschmai Hennig, 1936a: 180, fig. 10b, map 2 (terra: typica: Maumeri, E. Flores); Wermuth, 1967: 55.

Material examined. — INDONESIA. LOMBOK. 1 ♀, ZMA 14679, leg. J. P. Kleiweg de Zwaan. Narmada: 2 ♂, 2 ♀, SMF 23161-64, 1927, leg. R. Mertens. SUMBAWA. Dompoe: 1 ♂, SMF 23169, 1927, leg. R. Mertens. Semonkat-Atos: 2 ♂, SMF 23167-68, 1927, leg. R. Mertens. Sumbawa Besar: 1 ♂, 1 ♀, SMF 23165-66, 1927, leg. R. Mertens. SUMBA. Kambera: 1 ♀, ZMA 15248, iii.1925, leg. Dammernan. FLORES. 1 ♂, RMNH 2943 (paratype), 1863, leg. E. W. A. Ludeking. Maumeri: 1 ♂, ZMA 11025 (holotype), 1888, leg. M. Weber; 1 ♀, ZMA 11026 (paratype), 1888, leg. M. Weber. Sikka: 2 ♂, 1 ♀, RMNH 4990 (paratypes), 1891, leg. H. ten Kate; 1 ♂, 1 ♀, ZMA 11030-31 (paratypes), 1888, leg. M. Weber. Larantuka: 1 ♂, 1 ♀, ZMA 11027-28 (paratypes), iv.1908, leg. G. A. J. v. d. Sande. Endeh: 1 ♀, ZMA 11029 (paratype), 1888, leg. M. Weber; 1 ♂,

SMF 23173, 1927, leg. R. Mertens. Kottling: 1 ♂, ZMA 15255, 1908, leg. G. A. J. v. d. Sande. Wolo Waroe: 1 ♀, SMF 23174, 1927, leg. R. Mertens. Komba Ndaroe: 1 ♀, SMF 23172, 1927, leg. R. Mertens. Sita: 1 juv., SMF 23171, 1927, leg. R. Mertens. Kempoh: 1 ♂, SMF 23170, 1927, leg. R. Mertens. ANDUNARA. 1 ♂, RMNH 4991 (paratype), leg. H. ten Kate. SULAWESI. Macassar: 1 ♀, IG 1156 reg. 818b, 24.vi.1849, leg. Castillon du Portail.

Diagnosis. — A subspecies reaching a snout-vent length of 89 mm; gular pouch without enlarged scales; dorsals 97-139, unequal, keeled; thornlike scale on supraciliary edge smaller than 0.035 times the head length; nuchal crest in males consisting of 13-22 scales; lateral parts of head and nuchal region in males usually light with dark spots, forming a more or less distinct, reticulated pattern, females without such markings; patagium dark brown, never clear blue.

Description. — Maximum snout-vent length 80 mm in males (\bar{x} = 68.9, sd = 7.5, N = 16), 89 mm in females (\bar{x} = 75.9, sd = 8.5, N = 13) (juv.: 31 mm, N = 1); maximum length in males 16.2 mm, in females 18.7 mm, 0.18-0.26 times the snout-vent length (♂: \bar{x} = 0.20, sd = 0.01, N = 16; ♀: \bar{x} = 0.21, sd = 0.01, N = 13; juv.: 0.26); head width 0.58-0.67 times the head length (♂: \bar{x} = 0.64, sd = 0.04, N = 16; ♀: \bar{x} = 0.64, sd = 0.02, N = 13; juv.: 0.64); head depth 0.42-0.63 times the head length (♂: \bar{x} = 0.54, sd = 0.05, N = 16; ♀: \bar{x} = 0.54, sd = 0.02, N = 13; juv.: 0.53); snout length 0.25-0.37 times the head length (♂: \bar{x} = 0.31, sd = 0.02, N = 16; ♀: \bar{x} = 0.32, sd = 0.03, N = 13; juv.: 0.25); nostril directed outward; supralabials 7-12, smooth; usually three median teeth in upper jaw (three teeth: 90.0 %, one teeth: 6.7 %, two teeth: 3.3 %); head scales unequal, keeled; a series of enlarged, strongly keeled scales, forming a Λ -shaped figure on the snout; low thornlike scale on the supraciliary edge (up to 0.035 times the head length; ♂: \bar{x} = 0.018, sd = 0.007, N = 16; ♀: \bar{x} = 0.020, sd = 0.007, N = 13; juv.: 0.027); a rather low, keeled tubercle at the end of the supraciliary edge; tympanum usually covered with smooth skin (96.6 %, in the available specimen from Sulawesi the tympanum is completely covered with small scales); two or three enlarged scales between the eye and the tympanum; one or two spinelike tubercles above the tympanum and two groups of one to three spinelike tubercles behind it; nuchal crest consisting of 13-22 compressed, triangular scales in males (\bar{x} = 16.9, sd = 2.7, N = 16) and 3-15 compressed or strongly keeled scales in females (\bar{x} = 8.5, sd = 3.8, N = 13) (juv.: 15); gular pouch without enlarged scales, 0.62-1.51 times the head length in males (\bar{x} = 1.19, sd = 0.23, N = 16), 0.45-0.78 times the head length in females (\bar{x} = 0.59, sd = 0.09, N = 13) (juv.: 0.47); lateral pouches with enlarged scales; dorsals 97-139 (♂: \bar{x} = 119.1, sd = 10.1, N = 16; ♀: \bar{x} = 118.2, sd = 12.4, N = 13; juv.: 104), unequal, more or less enlarged near the vertebral line, keeled; a row of enlarged scales on the border between body and patagium; ventrals 80-117 (♂: \bar{x} = 99.5, sd = 8.1, N = 16; ♀: \bar{x} = 98.2, sd = 6.6, N = 13; juv.: 80), keeled, smaller than dorsals; usually six ribs in patagium (six ribs: 93.3 %, five ribs: 3.3 %, seven ribs: 3.3 %); 20-26 (♂: \bar{x} = 23.0, sd = 1.4, N = 16; ♀: \bar{x} = 22.6, sd = 1.5, N = 13; juv.: 22.5) keeled subdigital lamellae under the fourth finger, 22-31 (♂: \bar{x} = 26.9, sd = 2.5, N = 16; ♀: \bar{x} = 26.6, sd = 1.9, N = 13; juv.: 25.5)

under the fourth toe; hindlimbs 0.42-0.54 times the snout-vent length (σ : $\bar{x} = 0.49$, $sd = 0.03$, $N = 16$; φ : $\bar{x} = 0.48$, $sd = 0.03$, $N = 13$; juv.: 0.53), 0.74-1.03 times the distance between the limbs (σ : $\bar{x} = 0.84$, $sd = 0.05$, $N = 16$; φ : $\bar{x} = 0.85$, $sd = 0.05$, $N = 13$; juv.: 1.03); small fringelike scales on posterior edge of thigh; maximum tail length 155 mm in females, 142 mm in males, 1.45-2.06 times the snout-vent length (σ : $\bar{x} = 1.79$, $sd = 0.15$, $N = 16$; φ : $\bar{x} = 1.74$, $sd = 0.12$, $N = 13$; juv.: 1.58); no caudal crest.

Colour in preservative. — Above brown; specimens from Flores and Sumba sometimes with indistinct, darker or lighter spots, only a fine interorbital band; usually no nuchal spot; specimens from Lombok and Sumbawa with more or less distinct, light and dark spots, with distinct, interorbital spot, in females and in some of the males a nuchal spot; lateral parts of head in males usually light, with dark spots, forming a more or less distinct, reticulated pattern; females without such markings; eye sometimes surrounded by radial lines; patagium in males dark brown, usually with indistinct, lighter lines and spots, especially near the body edge, sometimes the spots are more distinct and the bands are recognizable; in females the patagium is dark brown, usually with distinct, light spots, sometimes giving it a reticulated impression; chest and belly usually yellowish white, sometimes bluish with small, brown spots; chin in males yellowish white with distinct, dark spots, usually forming a reticulated pattern; chin in females yellowish with sparsely scattered brown spots; ventral parts of patagium yellowish with small to large brown spots, sometimes even completely dark brown; gular pouch in males yellowish white at the base, sometimes bluish, with dark spots; in females usually bluish, sometimes bleached to yellowish, with dark spots.

Ecological notes. — Only four females (= 30.6 %) had eggs in the oviduct, two of them (IG 1156 reg. 818b, ZMA 14679) four, the other two (ZMA 11027, 11029) three. Two of these females were respectively collected in April (ZMA 11027) and June (IG 1156 reg. 818b). More ecological and ethological data are provided by Pfeffer (1962).

Distribution. — This subspecies is known to occur on Lombok, Sumbawa, Komodo, Rintja, Sumba, Adunara, Flores, Sulawesi and perhaps on the Kepulauan Sangihe (fig. 19). The occurrence on Seram (Hennig, 1936a) seems questionable to me. The museum of Brussels possesses several specimens, said to come from Ambon and Bacan. See for the discussion about these specimens page 83. The subspecies has been found to an altitude of 1000 m (De Rooy, 1915).

Remark. — When series are examined (see the description of 'Colour in preservative') differences between specimens from Flores and Sumba on the one hand and those from Lombok and Sumbawa on the other hand are evident. As intermediate forms do occur splitting of this subspecies does not seem justified.

***Draco volans reticulatus* Günther**

Draco volans: Gray, 1845: 233 (partim); Hairston, 1957: 262; Alcalá, 1967: 335; Reyes, 1968: 353.
Draco timorensis: Gray, 1845: 233 (partim).

- Draco reticulatus* Günther, 1864: 125 (terra typica: Philippine Islands); Boulenger, 1885: 257, pl. 20 fig. 1 (partim); De Rooy, 1915: 72 (partim); Taylor, 1922a: 110 (partim).
Draco reticulatus var. *cyanopterus* Peters, 1867: 15 (terra typica: Mindanao); Boettger, 1886: 97.
Draco guentheri Boulenger, 1885: 257, pl. 20 fig. 2 (terra typica: Philippines); Boettger, 1886: 97; Boettger, 1893a: 41; Werner, 1910: 9; Taylor, 1922a: 111.
Draco everetti Boulenger, 1885: 258, pl. 20 fig. 3 (terra typica: Isl. Mindanao); Boettger, 1886: 97; Boettger, 1893a: 41; Wandolleck, 1900: 10, fig. 2, 15; Taylor, 1922a: 112, pl. 6 fig. 2.
Draco rizali Wandolleck, 1900: 15, fig. 6, 7 (terra typica: Dapitan, Mindanao); Taylor, 1918: 245, pl. 2 fig. 3, 4; Taylor, 1922a: 115, pl. 7 fig. 3, 4.
Draco volans reticulatus: Hennig, 1936a: 179, map 2; Wermuth, 1967: 55.

Material examined. — PHILIPPINES. 1 ♂, BM 1946.8.27.28 (23.2b) (holotype of *D. reticulatus* Günther); 1 ♀, BM 79.4.16.4 (holotype of *D. guentheri* Boulenger) leg. A. Everett; 1 ♂, ZFMK 20900, 1871, leg. G. Semper. MINDANAO. Placer, N.E. Mindanao: 1 ♀, BM 77.12.13.16 (lectotype of *D. everetti* Boulenger), leg. Higgins. DINAGAT ISL. : 1 ♀, BM 77.10.9.13 (paralectotype of *D. everetti* Boulenger), leg. A. Everett.

Diagnosis. — A subspecies reaching a snout-vent length of 84 mm; thornlike scale on supraciliary edge larger than 0.028 times the head length; males with more than 22 nuchal crest scales; patagium in males sometimes with clear blue area; a dark ring around the eye; lateral parts of nuchal region with light spots; chin white with a distinct, reticulated pattern, formed by small, dark spots.

Description. — Maximum snout-vent length 84 mm in males (84-78, N = 2), 81 mm in females (\bar{x} = 76.3, sd = 5.0, N = 3); maximum head length 18 mm in females (Taylor, 1922a), 16.7 mm in males, 0.19-0.21 times the snout-vent length (♂: 0.20, N = 2; ♀: \bar{x} = 0.21, sd = 0.01, N = 3); head width 0.63-0.65 times the head length (♂: 0.63-0.64, N = 2; ♀: \bar{x} = 0.64, sd = 0.01, N = 3); head depth 0.49-0.55 times the head length (♂: 0.55-0.56, N = 2; ♀: \bar{x} = 0.52, sd = 0.03, N = 3); snout length 0.30-0.35 times the head length (♂: 0.31-0.32, N = 2; ♀: \bar{x} = 0.32, sd = 0.03, N = 3); nostrils directed outward; supralabials 9-12, smooth; usually three median teeth in the upper jaw (three teeth: 66.7 %, two teeth: 33.3 %); head scales unequal, faintly keeled; a series of enlarged, keeled scales, forming a Λ -shaped figure on the snout; a rather large thornlike scale, 0.028-0.073 times the head length (♂: 0.028-0.056, N = 2; ♀: \bar{x} = 0.052, sd = 0.09, N = 3), on the supraciliary edge; conical tubercle at the end of the supraciliary edge; tympanum covered with smooth skin; two enlarged scales between the tympanum and the eye; a low tubercle above and a pyramidal tubercle behind the tympanum; a longitudinal row of compressed, triangular scales between the nuchal crest and the lateral pouches; nuchal crest consisting of 22-26 compressed, triangular scales placed on a fold in males (N = 2), 9-21 such scales in females (\bar{x} = 16.3, sd = 6.4, N = 3); gular pouch with slightly enlarged scales, 1.14-1.44 times the head length in males (N = 2) and 0.45-0.53 times the head length in females (\bar{x} = 0.48, sd = 0.04, N = 3); lateral pouches with enlarged scales; dorsals 100-131 (♂: 110-122, N = 2; ♀: \bar{x} = 115.7, sd = 15.5, N = 3), keeled, unequal; a row of enlarged, keeled scales on the border between body and patagium; ventrals 99-106 (♂: 99-104, N = 2; ♀: \bar{x} = 102.7, sd = 2.9, N = 3), keeled, smaller than dorsals; six ribs in patagium; 22-26 (♂: 24-26,

N = 2; ♀: \bar{x} = 23.3, sd = 1.4, N = 3), keeled subdigital lamellae under the fourth finger, 24-29 (♂: 26-29, N = 2; ♀: \bar{x} = 25.8, sd = 1.3, N = 3) under the fourth toe; hindlimbs 0.45-0.51 times the snout-vent length (♂: 0.46-0.51, N = 2; ♀: \bar{x} = 0.46, sd = 0.02, N = 3) and 0.78-0.86 times the distance between the legs (♂: 0.78-0.86, N = 2; ♀: \bar{x} = 0.81, sd = 0.03, N = 3); fringelike scales on posterior edge of the thigh; maximum tail length 139 mm, 1.45-1.73 times the snout-vent length (♂: 1.64-1.65, N = 2; ♀: \bar{x} = 1.57, sd = 0.15, N = 3); no caudal crest.

Colour in preservative. — Above greenish or bluish grey, head darker; interorbital spot usually and nuchal spot sometimes present; no markings on the body; patagium brownish with indistinct, light spots near the body edge with a clear blue central area or without such blue, in the latter case the patagium is dark brown with distinct, light spots, giving it a reticulated impression; a dark and a light line around the eye with radial lines around them; light spots on the lateral parts of the nuchal region; chest and belly yellowish or bluish white; chin white with a more or less distinct, reticulated pattern, formed by small, dark spots; ventral parts of patagium yellowish white with indistinct, dark brown spots in the outer parts; gular pouch dark brown with light spots and a yellow, distal tip in males and greyish, with a lighter tip and indistinct lighter spots in females.

For colour in life see Taylor (1922a).

Ecological note. — The three females examined had respectively one (BM 79.4.16.4), two (BM 77.10.9.13) and three eggs (BM 77.12.13.16) in the oviducts. For ethological data see Hairston (1957). Reyes (1968) published data on food and Alcalá (1967) on the population dynamics of this subspecies.

Distribution. — This subspecies occurs on the Philippines (fig. 19).

Remarks. — BM 77.12.13.16 is selected here as lectotype of *D. everetti*, because the measurements of this specimen were given by Boulenger (1885).

Three specimens of the material examined (the types and ZFMK 20900) belong to the *everetti*-form. They differ from the other two specimens examined in the blue colour of the patagium. Apart from that they have a lower number of dorsals (100-110) and a larger thornlike scale (0.047-0.073 times the head length).

No distinct differences could be found between the types of *D. guentheri* and *D. reticulatus*.

Again (as in *D. spilopterus*), a study of variation within this subspecies might reveal, that names here considered synonyms, belong to distinct taxa.

***Draco volans sumatranus* Schlegel**

Draco viridis var. *sumatrana* Schlegel, 1844: 91 (terra typica: Sumatra).

Draco viridis: Bleeker, 1859: 200.

Draco volans: Gray, 1845: 233 (partim); Cantor, 1847: 643; Günther, 1864: 124; Boulenger, 1885: 256 (partim); Mocquard, 1890: 128; Weber, 1890: 166 (partim); Boettger, 1893a: 40 (partim); Boulenger, 1894: 613; Bartlett, 1894: 79; Günther, 1895: 499; Flower, 1896: 868; Flower, 1899: 636; Laidlaw, 1901: 307; Lampe & Lindholm, 1901: 202 (partim); Volz, 1903: 424; Boulenger,

1912: 57; Baumann, 1913: 259; De Rooy, 1915: 70, fig. 43 (partim); Smith, 1916a: 52; Smith, 1916b: 152; Smith, 1922: 268; Taylor, 1922a: 109, pl. 6 fig. 3; Löhnberg & Rendahl, 1925: 3; Smith, 1925b: 24; Mertens, 1930b: 64; Chasen & Smedley, 1927: 352; Smith, 1930: 21; Smedley, 1931b: 104; Brongersma, 1933: 22; Pfeffer, 1962: 417 (partim); Lloyd et al., 1968: 499.
Draco volans volans: Hennig, 1936a: 176, fig. 10a, map 2 (partim); Bourret, 1943: 12; Taylor, 1963: 834, fig. 38; Wermuth, 1967: 54 (partim); Grandison, 1972: 79.

Material examined. — THAILAND. Trang Waterfall: 1♂, 1♀, IG 10688 reg. 1120e, 19/26.vii.1935, leg. Layang Gaddi. MALAYSIA. WEST MALAYSIA. Port Dickson: 2♂, RMNH 8314, iii.1946, leg. J. J. Parmentier. Kepong, near Kuala Lumpur: 1♀, ZFMK 25492, 1978, leg. E. Rupp. Singapore: 1♀, RMNH 19929, 14.viii.1902, leg. G. H. Sworder; 8♂, 3♀, RMNH 19928, 19930-39, xii.1958, leg. J. R. Hendrickson. INDONESIA. RIAU ARCH. Riau: 1♀, RMNH 18762, xii.1886, leg. A. G. H. Blokzijl. Karimon: 1♂, RMNH 19944, 1895, leg. A. W. M. v. Hasselt. SUMATRA. 1♂, RMNH 2933 F (lectotype); 4♂, 2♀, RMNH 2933 A-E, G (paralectotypes), leg. S. Müller; 1♂, RMNH 5737, 1865, leg. G. F. Wienecke; 2♂, RMNH 19922-23; 2♂, 2♀, IG 3919 reg. 1120b, don. Suyckerbuyk. Moeara Laboe: 1♂, RMNH 3938, 1878, Sumatra exp.; Dehli: 1♀, RMNH 19924, xi.1882, leg. B. Hagen; 9♂, 8♀, ZMA 10373, don. Tropeninstituut; 17♂, 8♀, 1 juv., ZMA 15264, 15253 A-P, R-Z, 4♂, 3♀, ZMA 15252, 1920, 1♂, 1♀, ZMA 15283, 2♀, ZMA 15277, 1908/09, all leg. L. P. le Cosquino de Bussy. N.E. Sumatra: 2♀, RMNH 19925-26, v.1882, leg. B. Hagen. Medan: 1♀, ZMA 15265, 1920, leg. W. C. van Heurn; 1♂, 1♀, ZMA 15279, leg. J. B. Caporaal; 1♂, 1♀, ZMA 15282, leg. L. P. le Cosquino de Bussy; 1♂, RMNH 7164, 1922/24, leg. W. F. van Hell. Medan, Dolok Merangir: 1♂, 2♀, ZFMK 13369-70, 13746, 1972, leg. U. Rösler & P. Küppers. Gambir: 1♂, 1♀, ZMA 15280, leg. L. P. le Cosquino de Bussy. Palembang: 1♂, 3♀, ZMA 15284. Platjoe: 1♂, RMNH 19927, leg. M. D. Horst. Talook: 4♂, ZMA 15259, 1907, leg. J. P. Kleiweg de Zwaan. Singkarak: 2♀, ZMA 15256, 1889, leg. Rofs. Siboe Langit: 1♀, ZMA 14429 A, 25.v.1916, leg. L. P. le Cosquino de Bussy. Kahoetanam: 2♂, 1♀, ZMA 15251, 1888, leg. M. Weber; 1♂, RMNH 7218, 25.vii, 1893, leg. Mrs. H. A. ter Meulen. PULU WEH: 2♀, RMNH 19945-46, leg. P. Buitendijk. SIMEULUE. Pulu Babi: 1♀, RMNH 5143, iv.1913, leg. E. Jacobson. Sigule: 1♀, RMNH 5484, vii.1913, leg. E. Jacobson. Laboean Badjan: 1♀, ZMA 15262, vi. 1913, leg. E. Jacobson. Sinabang: 1♀, RMNH 5144, vii.1913, leg. E. Jacobson. NIAS. Gunung Sitoli: 1♂, ZMA 15272, 1910, leg. L. P. Kleiweg de Zwaan. S. Nias: 5♂, ZMA 15263, 1910, leg. L. P. Kleiweg de Zwaan. ENGGANO. 1♀, RMNH 19822, vi.1936, leg. J. K. de Jong. BANGKA. 1♀, RMNH 19940, 1877. BILLITON: 3♀, RMNH 19941-43, leg. A. G. Vorderman. KALIMANTAN. Sintang: 1♂, RMNH 19950, 1893, leg. G. Leignes Goedhuis. S. foot Gunung Kenipai: 3♂, 3♀, RMNH 19955, 9.i.1894; RMNH 19958, 27.xii.1893; RMNH 19961-63, 7/9.i.1894; RMNH 19965, 7.i.1894, leg. J. Büttikofer exp. BORNEO. 8♂, 4♀, RMNH 19957, 19947-49, 19951-54, 19956, 19959-60, 19964, 1891?, leg. Prakke; 1♂, 2♀, ZFMK 20895-97, 1849, Frank; 1♂, 1♀, BM 64.12.30.3, leg. Stevens; 1♀, BM 24.1e, leg. E. Belcher; 1♂, 1♀, 1 juv., BM 47.12.30.49, leg. Lowe.

Diagnosis. — A subspecies reaching a snout-vent length of 85 mm; gular pouch with or without slightly enlarged scales in males; thornlike scale usually small, to 0.03 times the head length; dorsals 103-166, more or less subequal; outer parts of patagium in males and females dark brown with lighter spots, bands usually not well recognizable.

Description (table 3). — Maximum snout-vent length in males 79 mm, in females 85 mm (juv.: 36, N = 1); maximum head length in males 14.8 mm, in females 17.0 mm, 0.17-0.22 times the snout-vent length (juv.: 0.19); head width 0.53-0.72 times the head length (juv.: 0.71); head depth 0.41-0.69 times the head length (juv.: 0.64); snout length 0.22-0.35 times the head length (juv.: 0.32); nostril directed outward; supralabials 6-12, smooth; usually three median

TABLE 3
Morphometric data of *Draco volans sumatranus*

	A Males N=56	A Females N=46	B Males N=13	B Females N=9	C Males N=10	C Females N=4
1	69.6 ± 5.9	73.8 ± 8.0	64.6 ± 10.7	73.2 ± 5.5	71.1 ± 3.6	71.0 ± 3.4
2	108.6 ± 9.6	114.4 ± 12.8	98.9 ± 12.7	109.3 ± 10.2	107.0 ± 6.2	109.3 ± 4.4
3	12.89 ± 1.00	13.88 ± 1.37	11.94 ± 1.68	13.80 ± 0.85	12.91 ± 0.72	13.15 ± 0.49
4	8.9 ± 0.8	9.0 ± 0.8	8.4 ± 1.0	8.2 ± 1.1	9.5 ± 0.4	8.5 ± 0.7
5	125.5 ± 9.2	126.0 ± 10.5	122.5 ± 7.7	117.1 ± 8.6	118.3 ± 6.0	121.5 ± 7.4
6	103.2 ± 8.2	101.4 ± 7.8	94.9 ± 7.4	96.3 ± 6.7	102.0 ± 4.6	99.3 ± 15.0
7	20.5 ± 1.5	21.1 ± 1.4	20.7 ± 1.6	20.5 ± 1.7	21.0 ± 0.8	21.2 ± 1.0
8	23.4 ± 1.6	23.6 ± 1.5	23.0 ± 1.5	23.4 ± 1.4	23.8 ± 1.0	24.3 ± 0.8
9	15.8 ± 2.6	5.9 ± 3.0	11.1 ± 3.1	6.6 ± 3.2	16.4 ± 2.2	6.3 ± 0.5
10	1.56 ± 0.09	1.55 ± 0.08	1.54 ± 0.10	1.49 ± 0.07	1.51 ± 0.08	1.54 ± 0.04
11	0.19 ± 0.01	0.19 ± 0.01	0.19 ± 0.01	0.19 ± 0.01	0.18 ± 0.01	0.19 ± 0.01
12	0.57 ± 0.03	0.55 ± 0.03	0.55 ± 0.05	0.51 ± 0.04	0.57 ± 0.03	0.56 ± 0.01
13	0.65 ± 0.02	0.65 ± 0.02	0.64 ± 0.04	0.65 ± 0.04	0.67 ± 0.03	0.64 ± 0.04
14	0.29 ± 0.02	0.31 ± 0.02	0.27 ± 0.03	0.32 ± 0.02	0.27 ± 0.02	0.30 ± 0.02
15	1.37 ± 0.22	0.67 ± 0.10	1.37 ± 0.21	0.74 ± 0.07	1.38 ± 0.30	0.67 ± 0.12
16	0.018 ± 0.006	0.017 ± 0.006	0.011 ± 0.006	0.011 ± 0.003	0.021 ± 0.004	0.018 ± 0.003
17	0.45 ± 0.02	0.45 ± 0.03	0.44 ± 0.02	0.45 ± 0.02	0.45 ± 0.03	0.46 ± 0.02
18	0.77 ± 0.04	0.77 ± 0.05	0.77 ± 0.04	0.79 ± 0.06	0.76 ± 0.07	0.73 ± 0.05

Means and standard deviations. A: specimens from Sumatra; B: specimens from Borneo; C: specimens from West Malaysia; 1 = snout-vent length (mm); 2 = tail length (mm); 3 = head length (mm); 4 = mean number of supralabials; 5 = number of dorsals; 6 = number of ventrals; 7 = mean number of subdigital lamellae of the fourth finger; 8 = mean number of the subdigital lamellae of the fourth toe; 9 = number of nuchal crest scales; 10 = tail length/snout-vent length; 11 = head length/snout-vent length; 12 = head depth/head length; 13 = head width/head length; 14 = snout length/head length; 15 = gular pouch length/head length; 16 = thorn length/head length; 17 = hindlimbs length/snout-vent length; 18 = hindlimbs length/distance limbs.

teeth in the upper jaw (three teeth: 73.2 %, two teeth: 22.5 %, one tooth: 4,3 %; specimens from Borneo more often have two median teeth: 50 %, 31.8 % has three teeth and 18.2 % has one tooth); head scales subequal, large, keeled; a series of enlarged, strongly keeled scales, forming a Λ -shaped figure on the snout; thornlike scale on the supraciliary edge, usually low (to 0.03 times the head length), in specimens from Borneo even lower (to 0.02 times the head length); tubercle at the end of the supraciliary edge distinct; tympanum usually covered with smooth skin (84.1 %, 5.1 % has a tympanum covered with small scales only, the rest has a tympanum partly covered with small scales); two to four enlarged, keeled scales between the tympanum and the eye; one spinelike tubercle above and one behind the tympanum; a longitudinal row of compressed scales between the nuchal crest and lateral pouches; nuchal crest consisting of 6-20 compressed, triangular or strongly keeled scales in males and of 0-14 such scales in females; gular pouch in males with or without slightly enlarged scales,

0.54-1.84 times the head length, in females 0.44-0.88 times the head length (juv.: 0.70); lateral pouches with enlarged scales; dorsals 103-166 (juv.: 121), more or less subequal, keeled; a row of enlarged, keeled scales on the border between body and patagium; ventrals 83-124 (juv.: 99), keeled, about as large as the dorsals; usually six ribs in patagium (six ribs: 93.8 %, five ribs: 4.3 %, seven ribs: 1.8 %); 17-25 (juv.: 23) keeled subdigital lamellae under the fourth finger, 20-27 (juv.: 24.5) under the fourth toe; hindlimbs 0.37-0.51 times the snout-vent length (juv.: 0.43), 0.63-0.92 times the distance between the limbs (juv.: 0.77); small fringelike scales on posterior edge of thigh; maximum length 145 mm, 1.33-1.76 times the snout-vent length (juv.: 1.58); no caudal crest.

Colour in preservative. — Above brown, sometimes bluish grey; interorbital spot present; females with distinct, nuchal spot; males usually without nuchal spot; females usually with paired, dark spots on body; males without distinct markings; short radial lines around the eye; patagium in males and females brownish with more or less distinct, light spots near the body edge, marginal areas dark brown with lighter spots, bands usually not recognizable, except between the first and second rib; chest and belly bluish (median) and yellowish (lateral), sometimes with dark spots on lateral parts; chin with fine, dark spots, sometimes forming bands; ventral parts of patagium bluish grey with smaller or larger, dark brown spots, sometimes forming bands; gular pouch in males yellowish or orangish white with small, dark spots at the base; in females bluish grey with dark spots.

In life the lighter parts of the patagium are orange red in males and yellowish in females (Flower, 1896). See also Grandison (1972) for colour in life.

Ecological notes. — 54.3 % of the females had eggs in the oviducts. Of these females 44.8 % had four eggs, 28.0 % had three, 20.1 % had two and 7.9 % had one egg(s). Females with eggs were collected in May, June, July, August, November and December. For data on ethology and ecology see Pfeffer (1962).

Distribution. — This subspecies is known to occur in Southern Thailand, in West Malaysia, on Sumatra, Simeulue, Sipora, Nias, Enggano, Kepulauan Riau, Bangka, Belitung, Natuna Islands, Borneo, Pulau Laut and Palawan (fig. 19). It is found to an altitude of 900 m (De Rooy, 1915).

Remarks. — Schlegel (1844) probably based the name *D. v. sumatranus* on seven specimens collected on Sumatra by Müller (RMNH 2934). From these the best preserved male was selected as lectotype: RMNH 2934 F. Description of this lectotype: male; snout-vent length: 74 mm; tail length: 108 mm; head length: 13.3 mm; head depth: 7.3 mm; head width: 8.6 mm; snout length: 3.7 mm; gular pouch length: 21.0 mm; thornlike scale length: 0.14/0.14 mm; thornlike scale width: 0.7/0.98 mm; hindlimb length: 34/36 mm; distance limbs: 46/45 mm; two median upper teeth; tympanum covered with smooth skin; supralabials: 9/9; dorsals: 134; ventrals: 96; subdigital lamellae under the fourth finger: 22/21; ditto fourth toe: 22/23; nuchal crest scales: 19; ribs patagium: 6/6; interorbital spot present; dorsally pale bluish; patagium with dark brown remains of markings; ventrally pale spotted; chin and gular pouch with small spots.

Three specimens, all bought from Frank in 1849 (ZFMK 20895-97) from Borneo, do resemble *D. v. volans*, and incorrectness of the locality seems possible.

There are some differences between specimens from Borneo and those from Sumatra and Malaya (tab. 3: the length of the thornlike scale and the number of median teeth, see 'Description'), but since these differences are not clear-cut and since they do not coincide with differences in colour, it does not seem sage to describe the populations as different subspecies.

The material examined from the continent and from the islands around Borneo and Sumatra is not differentiated from that of the latter two big islands.

***Draco volans timoriensis* Kuhl**

Draco timoriensis Kuhl, 1820: 103 (terra typica: Timor); Gray, 1831: 59; Duméril & Bibron, 1837: 454.

Draco viridis var. *timoriensis*: Schlegel, 1844: 91.

Draco viridis var. *samaoensis* Schlegel, 1844: 92 (terra typica: Samoa).

Draco timorensis: Gray, 1845: 233 (partim); Boulenger, 1885: 261; Lidth de Jeude, 1895: 122; Wandolleck, 1900: 11, fig. 8, 11; Werner, 1910: 9; Barbour, 1912: 29; De Rooy, 1915: 74 (partim); Dunn, 1927: 3; Manaças, 1956: 271, pl.

Draco volans timoriensis: Hennig, 1936a: 182, map 2; Wermuth, 1967: 55.

Material examined. — INDONESIA. TIMOR. 1 ♂, RMNH 2927, leg. S. Müller; 4 ♂, 7 ♀, RMNH 2935, leg. S. Müller & H. Macklot; 1 ♂, RMNH 4989, 1881, leg. J. W. v. Langsberghe; 1 ♂, RMNH 7216, leg. H. ten Kate; 1 ♀, ZMA 12048, R. H. no. 13; 1 ♂, ZFMK 21295, 1846, Frank. Atapupu: 4 ♀, RMNH 2940, 1862, leg. J. C. B. Bernelot Moens. Noil Toka: 1 ♀, RMNH 7031, 1937, leg. P. F. van West. Kaslioe and Menas, near Mutis Mnts: 2 ♂, RMNH 7029, ix/x.1937, leg. W. P. de Röver. WETAR. 2 ♀, RMNH 4992, 1898, leg. K. Schädler. SEMAU. 1 ♀, RMNH 2903 (holotype of *D. viridis* var. *samaoensis* Schlegel), leg. S. Müller & H. Macklot. ROTI. 2 ♂, 3 ♀, RMNH 2950, 1863, leg. G. F. Wienecke. E. Roti: 1 ♂, RMNH 19966, 1891, leg. H. ten Kate. 'BATCHIAN. MOLUQUES': 1 ♂, 1 ♀, IG 4313 reg. 815, don. Vermersch.

Diagnosis. — A subspecies reaching a snout-vent length of 93 mm; large spinelike tubercles in nuchal region; dorsals 84-129, unequal, keeled, with a row of enlarged, keeled scales along each side of the vertebral line; chin in males light with more or less dense, dark spots, in females light, sometimes with few spots.

Description. — Maximum snout-vent length in males 78 mm ($\bar{x} = 70.3$, $sd = 4.7$, $N = 11$), in females 93 mm ($\bar{x} = 80.9$, $sd = 8.0$, $N = 16$); maximum head length in males 14.9 mm, in females 19.4 mm, 0.19-0.23 times the snout-vent length (♂: $\bar{x} = 0.20$, $sd = 0.01$, $N = 11$; ♀: $\bar{x} = 0.20$, $sd = 0.01$, $N = 16$); head width 0.61-0.70 times the head length (♂: $\bar{x} = 0.64$, $sd = 0.03$, $N = 11$; ♀: $\bar{x} = 0.64$, $sd = 0.02$, $N = 16$); head depth 0.50-0.80 times the head length (♂: $\bar{x} = 0.54$, $sd = 0.02$, $N = 11$; ♀: $\bar{x} = 0.53$, $sd = 0.03$, $N = 16$); snout length 0.28-0.35 times the head length (♂: $\bar{x} = 0.30$, $sd = 0.02$, $N = 11$; ♀: $\bar{x} = 0.33$, $sd = 0.02$, $N = 16$); nostril directed outward; supralabials 7-11, smooth; usually three median teeth in upper jaw (three teeth: 88.5 %, two teeth: 3.8 %, one tooth: 7.6 %); head scales subequal, large, keeled; a series of strongly keeled scales, forming a **Λ**-shaped figure on the snout; thornlike scale on supraciliary edge, usually not very high (to 0.04 times the head length; ♂: $\bar{x} = 0.024$,

sd = 0.007, N = 11; ♀: \bar{x} = 0.018, sd = 0.006, N = 16); distinct, triangular or pyramidal tubercle at the end of the supraciliary edge; tympanum usually covered with smooth skin (98.2 %), in one specimen partly covered with small scales on one side; a concentration of enlarged, keeled scales between the eye and the tympanum and above the tympanum; large, spinelike tubercles above and behind the tympanum, usually arranged in rows of at least two such tubercles; nuchal crest consisting of 10-18 triangular, compressed or enlarged, keeled scales in both sexes (♂: \bar{x} = 13.4, sd = 1.9, N = 11; ♀: \bar{x} = 13.5, sd = 2.5, N = 16); gular pouch without enlarged scales, in males 1.00-1.39 times the head length (\bar{x} = 1.20, sd = 0.12, N = 11), in females 0.46-0.67 times the head length (\bar{x} = 0.58, sd = 0.06, N = 16); lateral pouches with enlarged scales; dorsals 84-129 (♂: \bar{x} = 98.6, sd = 13.3, N = 11; ♀: \bar{x} = 94.9, sd = 7.1, N = 16), unequal, smooth or keeled; a row of enlarged, keeled scales on each side along the vertebral line and a row of enlarged, keeled scales on the border between body and patagium; ventrals 75-106 (♂: \bar{x} = 86.2, sd = 7.6, N = 11; ♀: \bar{x} = 85.4, sd = 5.4, N = 16), keeled, about as large as the smaller dorsals; usually six ribs in patagium (90.8 %, five ribs: 9.2 %); 19-25 (♂: \bar{x} = 21.6, sd = 1.6, N = 11; ♀: \bar{x} = 22.6, sd = 0.9, N = 16) keeled subdigital lamellae under the fourth finger, 23-30 (♂: \bar{x} = 25.6, sd = 1.8, N = 11; ♀: \bar{x} = 26.5, sd = 1.6, N = 16) under the fourth toe; hindlimbs 0.44-0.55 times the snout-vent length (♂: \bar{x} = 0.51, sd = 0.02, N = 11; ♀: \bar{x} = 0.50, sd = 0.02, N = 16) and 0.75-1.01 times the distance between the limbs (♂: \bar{x} = 0.87, sd = 0.06, N = 11; ♀: \bar{x} = 0.85, sd = 0.05, N = 16); fringelike scales on posterior edge of thigh; maximum tail length 157 mm, 1.19-1.78 times the snout-vent length (♂: \bar{x} = 1.53, sd = 0.23, N = 11; ♀: \bar{x} = 1.67, sd = 0.07, N = 16); no caudal crest.

Colour in preservative. — Above pale brown to brown, sometimes bluish; neither interorbital, nor nuchal spot; body without distinct markings; lateral parts of the head in males without reticulated spots; patagium in males dark brown with light spots, forming more or less distinct, light bands, light lines usually are present; patagium in females dark brown with light lines and spots, rarely forming bands (in the two females from Wetar the light spots are so large, that the dark pattern elements form a very fine, reticulated pattern); chest and belly yellowish or brownish white, sometimes with small spots (mainly on the lateral parts); chin in males light with dark spots, more or less dense; in females light, sometimes with few spots; ventral parts of patagium light yellowish with dark brown spots of variable size, sometimes even completely dark; gular pouch in males yellowish, at the base with dark spots, in females whitish, sometimes with small dark spots (not bluish).

Ecological notes. — 68.9 % of the females had eggs in the oviducts, of which 9.1 % had five, 63.6 % had four, 9.1 % had three and 18.1 % had one egg(s). No further data are available.

Distribution. — This subspecies is known to occur on Timor, Roti, Alor, Semau and Wetar (fig. 19).

Remarks. — Being the only specimen in the RMNH and already available when Schlegel was working there, RMNH 2903 is considered here as the holotype of *D. viridis* var. *samaoensis* Schlegel.

Two females from Wetar (RMNH 4992) may belong to a distinct subspecies. They differ from the specimens from Timor in the colour of the patagium (see above). However, in all other characters they resemble those from Timor (large, spinelike tubercle in the nuchal region; a double row of enlarged, keeled scales along the vertebral line). Because of lack of sufficient material I refrain from describing these specimens as a new taxon.

Because of the unlikelihood, the locality Ceram, mentioned by Werner (1910), is here regarded as due to incorrect labelling.

See for the discussion of the specimens from 'Batchian' p. 83.

5. RESULTS B. THE CHARACTERS

To investigate the relationships between the (sub) species and the importance of the different characters, two multivariate analyses were made with the help of a computer: dendrograms were drawn and principal component analyses in R-mode were made. These analyses are described, followed by a discussion of the more important characters.

5.1. MULTIVARIATE ANALYSES

5.1.1. PROCEDURES AND RESULTS

At first a group of 109 specimens was selected, composed of at the most five randomly selected specimens of each subspecies as described by Hennig (1936a). As variables the states of the following characters were used: sex; snout-vent length; tail length; head length; head depth; head width; snout length; gular pouch length; thorn length; thorn width; length of both hindlimbs; distance between fore- and hindlimbs; number of median teeth in upper jaw; differentiation of the skin covering the tympanum; number of supralabials; number of dorsals; number of ventrals; number of subdigital lamellae under the fourth fingers and toes; number of nuchal crest scales; number of ribs supporting the patagium; direction of the nostril; presence of a caudal crest; number of eggs in the oviducts of females.

After standardization of these character states, a similarity matrix of the mean square distance between the specimens was calculated. This was used to cluster them with the Ward average ("Incremental sum of Squares") to get the most distinct clusters (Clifford & Stephenson, 1975) and a dendrogram was drawn. The result was a dendrogram with clusters consisting of specimens that clearly belonged to different species. Two main clusters could be recognized: one, containing three specimens of *D. maximus*, and the other consisting of two subclusters: one containing specimens of *D. maximus*, *D. mindanensis*, *D. quinquefasciatus*, *D. taeniopterus*, *D. melanopogon*, *D. dussumieri*, *D. obscurus*, *D. blanfordii*

and *D. fimbriatus*, the other containing all the specimens of *D. volans*, *D. lineatus*, *D. cornutus*, *D. maculatus*, *D. spilopterus* and one or two specimens each of *D. quinquefasciatus*, *D. fimbriatus* and *D. melanopogon*. After this another dendrogram was drawn, based on a similarity matrix of the correlation coefficients between the specimens. It is known that this is a better similarity coefficient for taxonomical use, because the influence of the absolute size is minimized (Clifford & Stephenson, 1975: 64). The dendrogram shows two distinct clusters: one containing all the specimens of *D. quinquefasciatus*, *D. taeniopterus*, *D. haematopogon*, *D. melanopogon*, *D. dussumieri*, *D. fimbriatus*, *D. maximus*, *D. mindanensis*, *D. blanfordii* and *D. obscurus*, the other containing all the specimens of *D. maculatus*, *D. lineatus*, *D. spilopterus*, *D. volans* and *D. cornutus*. However, although in the first cluster the specimens of *D. dussumieri* and, in the second one, those of *D. maculatus*, *D. l. bimaculatus*, *D. l. modiglianii* and *D. cornutus* occur in distinct subclusters, the specimens of all the other (sub)species are mixed up within the clusters. In most cases males and females belonged to different subclusters. A principal component analysis was done on the character states of the 109 specimens. The three first components were calculated (explaining 60% of the total variation). The factor loads of the first principal component indicate that this is as usual a "size vector" (Blackith & Reyment, 1971). The main characters attributing to this component were: snout-vent length, head length, head width, head depth, snout length, length of the hindlimbs, distance between the legs. Less important characters were: length of the gular pouch, width of the thorn, number of supralabials, dorsals, ventrals and direction of the nostril. The main characters attributing to the second component were: number of median teeth, number of subdigital lamellae and nuchal crest scales. The earcovering was less important. Number of supralabials and direction of the nostril had high, negative values (indicating a negative correlation between these characters and the preceding ones). The third component was almost completely based on the length of the thorn; the number of ribs and eggs only contributed slightly. The specimens were plotted along the component axes. Along the first component axis *D. maximus* showed very high values. Also high values, but always less than *D. maximus*, were shown by: *D. blanfordii*, *D. obscurus*, *D. mindanensis* and *D. fimbriatus*. High negative values were shown by *D. l. modiglianii*, *D. l. bimaculatus* and *D. cornutus*. It is clear that this is mainly based on the size of the animals. Along the second axis high values were shown by the following (sub)species: *D. l. bourouniensis* and *D. l. spilonotus*; low values by *D. dussumieri*, *D. quinquefasciatus*, *D. melanopogon*, *D. haematopogon* and *D. taeniopterus*. Along the third axis only *D. cornutus*, *D. v. reticulatus* and two specimens of *D. v. volans* are remarkable in having a high value.

To eliminate the great influence of the size of the animals, the data set was changed so that not the characters, but ratios, together with numerable characters were used. This gave rise to the next 25 variables: relative tail length (tail length/snout-vent length), rel. head length (head length/snout-vent length), rel. head depth (head depth/head length), rel. head width (head width/head

length), rel. snout length (snout length/head length), snout length/head width, rel. gular pouch length (pouch length/head length), head depth/head width, rel. mean thorn length (mean thorn length/head length), rel. mean thorn width (mean thorn width/head length), rel. mean hindlimb length (mean hindlimb length/snout-vent length), mean hindlimb length/mean distance limbs, rel. mean distance limbs (mean distance limbs/snout-vent length), number of median teeth in the upper jaw, mean earcovering, mean number of supralabials, number of dorsals, number of ventrals, mean number of subdigital lamellae under fourth finger, mean number of subdigital lamellae under fourth toe, number of nuchal crest scales, mean number of ribs, direction of nostrils, presence of caudal crest, number of eggs. Again, after standardization, a similarity matrix of the mean square distance was calculated and the specimens were clustered according to Ward. The dendrogram resulting from this, was very much more satisfactory, since it showed more distinct clusters and since specimens of distinct species were put together. The complete set is divided into two main clusters. The first of these consists of a distinct subcluster containing the specimens of *D. maximus* and *D. mindanensis* and a subcluster containing *D. taeniopterus*, *D. haematopogon*, *D. melanopogon* and strangely enough the males of *D. l. bimaculatus*. Further there is a subcluster with *D. quinquefasciatus* only and a subcluster with *D. dussumieri*, *D. obscurus*, *D. blanfordii* and *D. fimbriatus*. The other main cluster consists of a subcluster containing the remaining specimens of *D. lineatus* and a subcluster containing *D. volans*, *D. cornutus*, *D. spilopterus* and *D. maculatus*. In this subcluster, three (sub)clusters can be recognized: one containing *D. cornutus* and *D. v. volans* (sensu Hennig, 1936a), one containing the other subspecies of *D. volans* and one containing *D. maculatus* and *D. spilopterus*.

A principal component analysis (in R-mode) was made on the new data set. The three first components explained only 50% of the variation now. These components are much more difficult to interpret than those of the unmodified data. From the factor loads it appeared that the main variables attributing to the first component are: relative head length, snout length/head width, number of median teeth and number of nuchal crest scales. Relative snout length and the number of subdigital lamellae under finger and toe are less important. High negative values are shown by the direction of the nostril, the number of supralabials, dorsals and ventrals and, less important, the relative head width and the relative pouch length. Thus, this component is composed of a few ratios together with the second component of the unmodified data. The variables that attribute to the second component are the relative hindlimb length and the hindlimb length/distance limbs and, less important, the relative tail length. Relative thorn length and, less important, number of ribs showed high negative values. The third component is made up by the relative length of the snout again (rel. length and length/head width). The relative head depth in this case is highly negative.

When plotted, *D. lineatus* (except *D. l. bimaculatus*), *D. v. boschmai* and *D. v. reticulatus* showed high values along the first axis. Low values were shown by *D.*

melanopogon, *D. dussumieri*, *D. haematopogon* and *D. quinquefasciatus*. Along the second axis *D. cornutus* and *D. v. volans* showed low values, whereas there were no (sub)species with extremely high values. Along the third axis *D. maximus*, *D. mindanensis*, *D. blanfordii*, *D. quinquefasciatus* and *D. o. formosus* had high values, whereas *D. l. bimaculatus*, *D. l. modiglianii*, *D. melanopogon* and *D. l. bourouniensis* had low values.

To eliminate the influence of sex and to investigate the influence of localities, two new data sets were made. One containing at the most five males of each (sub)species or important locality (for example from *D. v. volans* (sensu Hennig, 1936a) five specimens each from Borneo, from Sumatra, from Java etc. were used), the other containing at the most five females of each (sub)species or important locality. Again the ratios were used as variables, the mean square distance was used as similarity coefficient and clustering was done following Ward.

For the males (135 specimens) this gives a dendrogram (fig. 20) that consists of two main clusters. One containing a subcluster with all, except one, specimens of *D. fimbriatus*, a subcluster with *D. quinquefasciatus* and a subcluster containing *D. haematopogon*, *D. melanopogon*, *D. taeniopterus*, *D. dussumieri*, *D. obscurus*, *D. blanfordii* and the remaining specimen of *D. fimbriatus* (from Padang, Sumatra, see p. 27), more or less mixed up with each other. The other main cluster consists of two distinct subclusters: one containing the specimens of *D. lineatus*, *D. spilopterus* and *D. maculatus* (and two specimens of *D. volans*) and the other the specimens of *D. volans* and *D. cornutus* (and one *D. lineatus*). Within these two clusters *D. maculatus*, *D. spilopterus*, *D. l. bimaculatus*, *D. l. modiglianii* and *D. cornutus* form distinct units, whereas the locality of *D. v. volans* (sensu Hennig, 1936a) does not seem to play any role.

The dendrogram of the females (121 specimens, fig. 21) again shows two main clusters. The first consists of four small subclusters, containing resp. *D. quinquefasciatus* together with *D. dussumieri*, *D. maximus*, *D. haematopogon* together with *D. melanopogon* and *D. taeniopterus*, and *D. fimbriatus*. The second consists of two main clusters, one containing *D. lineatus* and one specimen each of *D. volans*, *D. spilopterus*, and *D. o. obscurus*, the other containing the rest of *D. volans* and *D. spilopterus*, and *D. cornutus*. Units within these two main subclusters are much less distinct than in the dendrogram of the males. The occurrence of *D. o. obscurus* in one cluster together with *D. lineatus* is probably due to the fact that only one female of *D. o. obscurus* was available.

A principal component analysis was done on the two data sets (in R-mode). The three first components were calculated. In males the variables that mainly contribute to the first component are the number of subdigital lamellae under the fourth toe and the relative tail length. High negative values are shown by the mean number of supralabials, relative gular pouch length and the direction of the nostril. The main variables of the second component are the relative length of the hindlimb, the hindlimb/distance limbs and the number of dorsals. The mean number of ribs shows a high negative value. The third component is based

STANDARDIZED DATA MEAN SQUARE DISTANCES IN Q-MODE WARD'S AVERAGING

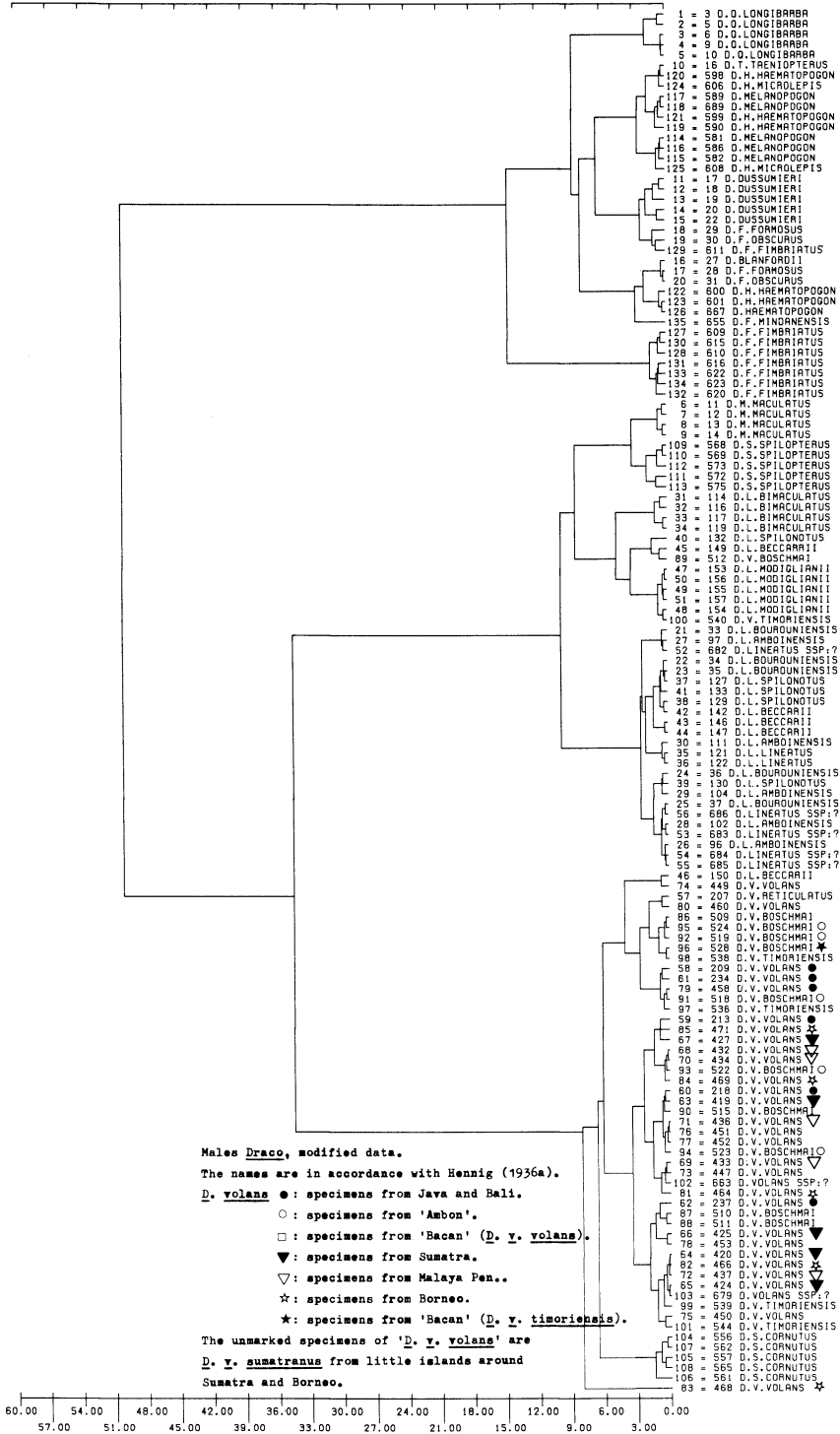


Fig. 20. Dendrogram of the males of *Draco*, modified data.

STANDARDIZED DATA MEAN SQUARE DISTANCES IN Q-MODE WARD'S AVERAGING

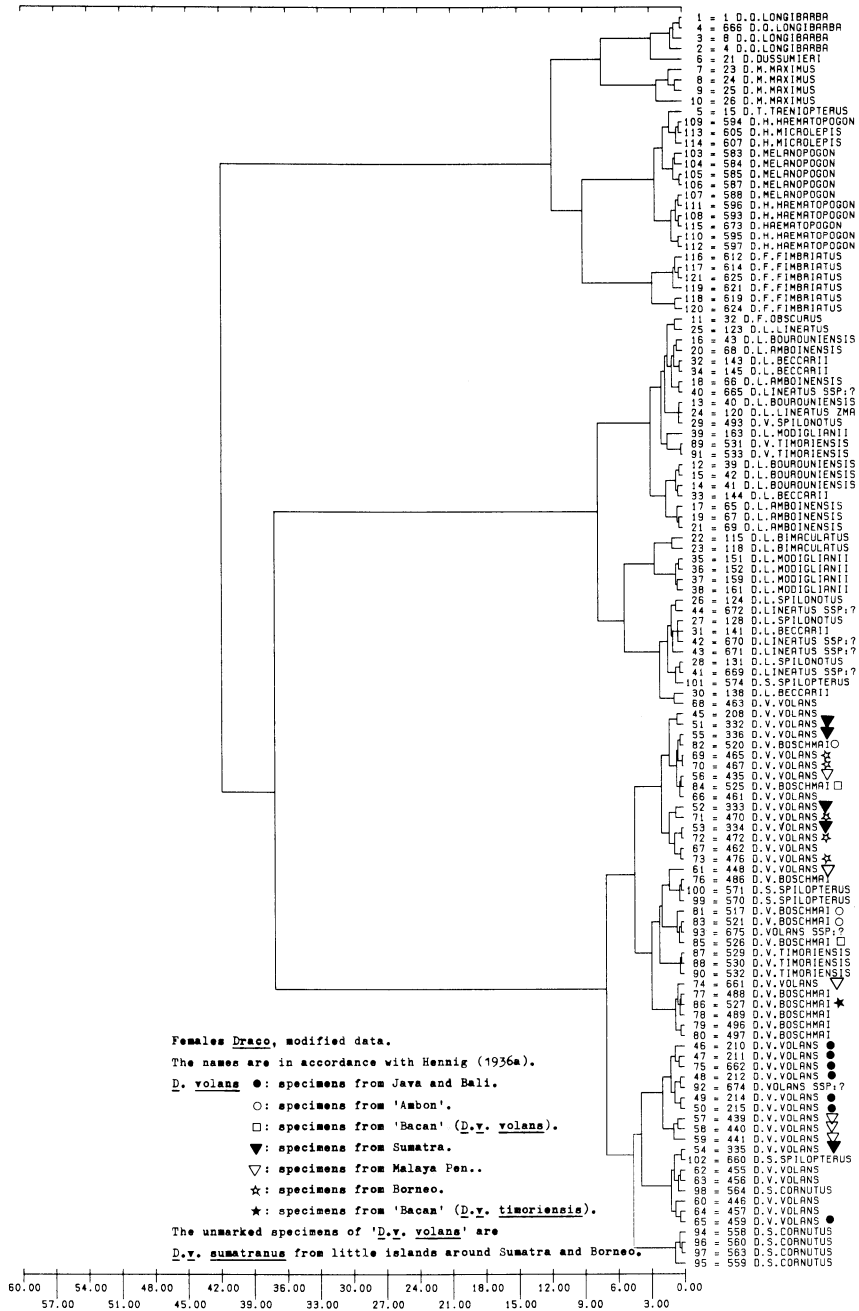
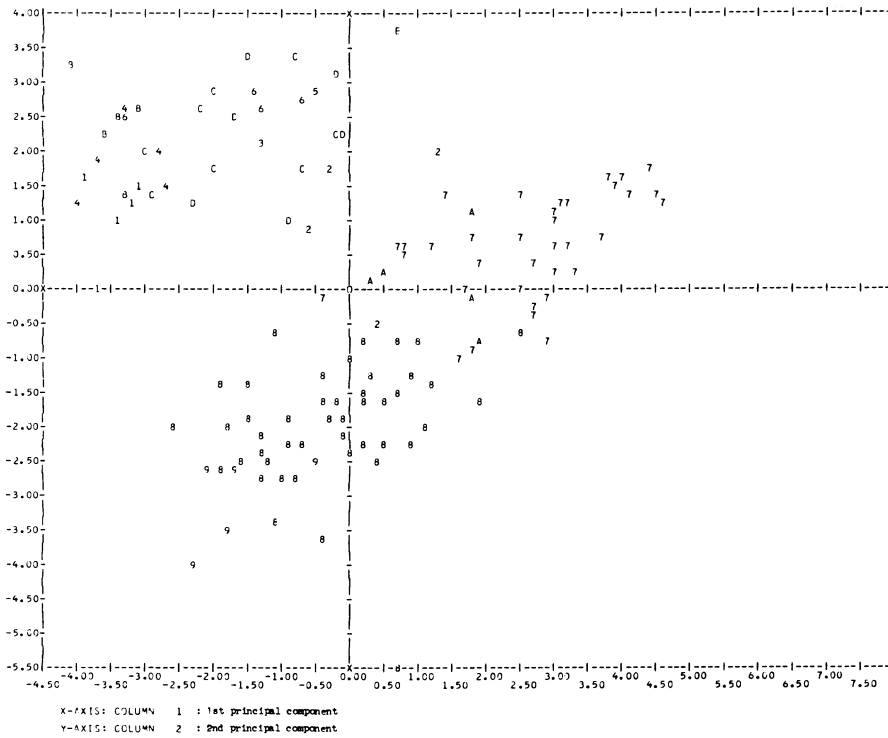


Fig. 21. Dendrogram of the females of *Draco*, modified data.

on the relative snout length, the snout length/head width and, to a much lesser degree, on the length of the thornlike scale. In females the main variables attributing to the first component are the relative tail length, relative hindlimb length and hindlimb length/ distance limbs. The mean number of ribs is highly negative. The second component is based on the mean number of supralabials, the number of dorsals and, less important, the number of ventrals. The head depth/head width, number of median teeth and number of nuchal crest scales show high, negative values. The main variables attributing to the third component are again the relative snout length and snout length/head width. The plotting of the specimens with the first and second component as axes shows two cluster for the males (fig. 22). One cluster containing the specimens of *D. quinquefasciatus*, *D. taeniopterus*, *D. dussumieri*, *D. blanfordii*, *D. obscurus*, *D. melanopogon*, *D. haematopogon*, *D. fimbriatus* and *D. mindanensis*, has low values along the first and high values along the second axis. The other cluster is elliptic and runs from the neg.-neg., over the pos.-neg. to the pos.-pos. field. It contains the specimens of *D. cornutus* (very low values along both axes), *D. volans* (low values along the second axis) and *D. lineatus* (positive values along the first axis). *D. spilopterus* seems to be intermediate between *D. volans* and *D. lineatus*. *D. maculatus* occurs in between the two main clusters. The third component does not seem very useful to discriminate between the species.

The females were plotted too, using the first and second component as axes (fig. 23) for the graph. Here three clusters can be recognized. The first, with high values along the second axis contains *D. maximus*, *D. melanopogon*, *D. haematopogon*, *D. quinquefasciatus*, *D. fimbriatus* and *D. dussumieri*. The second, with low values along the first as well as second axis contains *D. volans* and *D. cornutus*. The third, with high values along the first and low values along the second axis, contains *D. lineatus*. Again *D. spilopterus* seems to be intermediate between *D. volans* and *D. lineatus*, together with *D. taeniopterus* and *D. o. obscurus*. For the third component it is remarkable that all the specimens of both *D. haematopogon* and *D. melanopogon* have low values.

Apart from the preceding cluster analyses the following analyses were done also: a cluster analysis (group average) of the centroids of each species of the 135 males and those of the 121 females, using the modified data. The dendrograms showed a very different picture from the dendrogram of the specimens (fig. 24). This is probably due to the fact, that of some species there was only one specimen available and that the influence of intermediate specimens is minimized (this explains the extraordinary position of *D. cornutus*). To test the influence of the modification of the data set, the 135 males were clustered the same way with unmodified data as they were with modified data. The correlation coefficient between the two similarity matrices was calculated. The same was done for the females. The result was a correlation of only 0.59 for the males and 0.71 for the females. This indicates that the use of ratios has a great influence on the clustering.



***** PLOTAR PART OF BIOPAT *****

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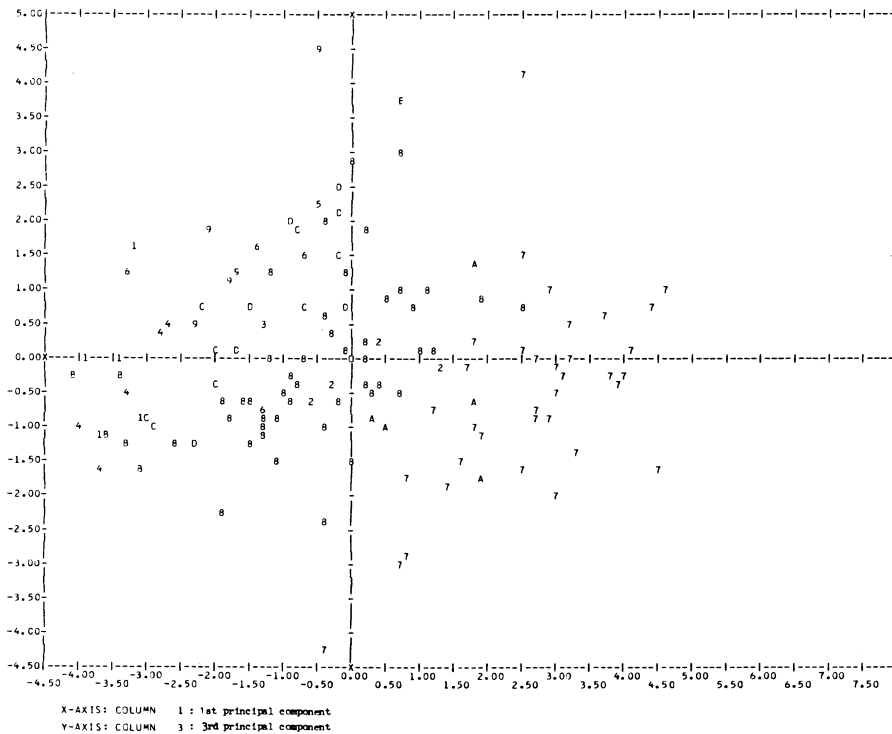
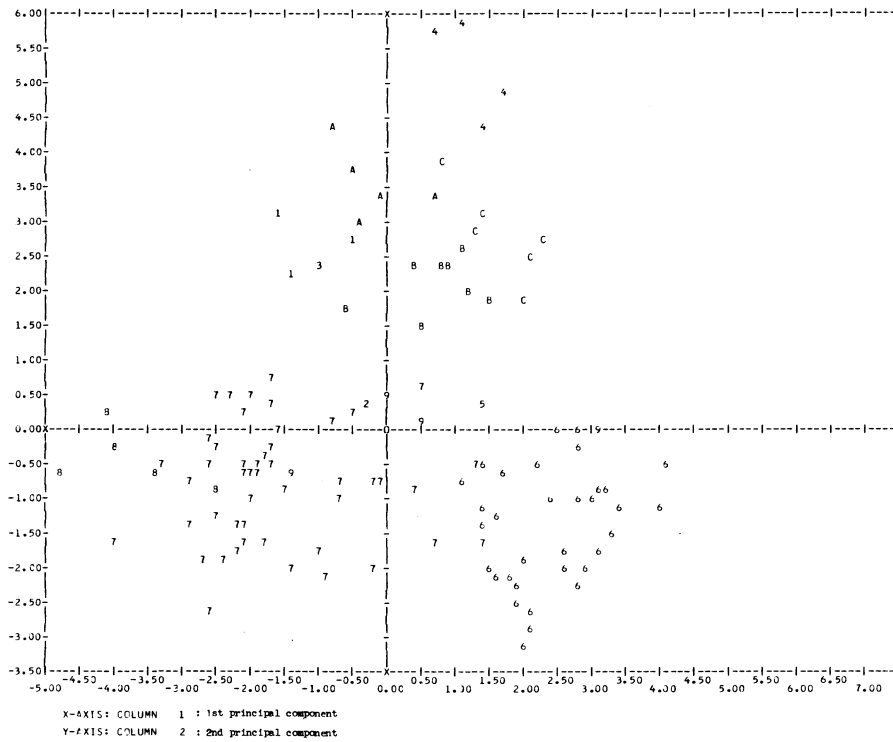


Fig. 22. Plots of the principal component analysis of the males of *Draco*, modified data, 1 = *D. quinquefasciatus*; 2 = *D. maculatus*; 3 = *D. taeniopterus*; 4 = *D. dussumieri*; 5 = *D. blanfordii*; 6 = *D. obscurus*; 7 = *D. lineatus*; 8 = *D. volans*; 9 = *D. cornutus*; A = *D. spilopterus*; B = *D. melanopogon*; C = *D. haematopogon*; D = *D. fimbriatus*; E = *D. mindanensis*.



***** PLOTAS PART OF BIOPAT *****

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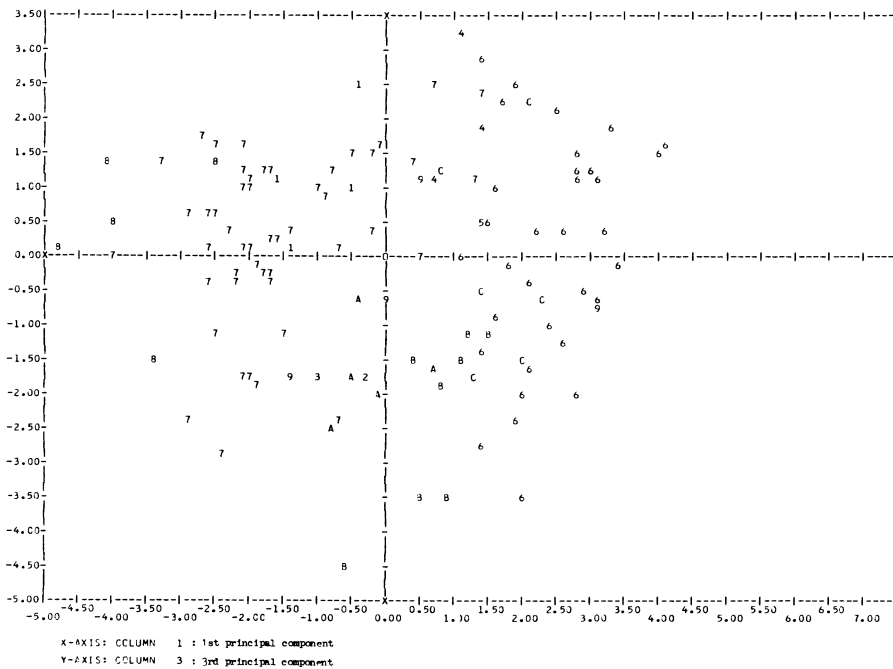


Fig. 23. Plots of the principal component analysis of the females of *Draco*, modified data. 1 = *D. quinquefasciatus*; 2 = *D. taeniopterus*; 3 = *D. dussumieri*; 4 = *D. maximus*; 5 = *D. obscurus*; 6 = *D. lineatus*; 7 = *D. volans*; 8 = *D. cornutus*; 9 = *D. spilopterus*; A = *D. melanopogon*; B = *D. haematopogon*; C = *D. fimbriatus*.

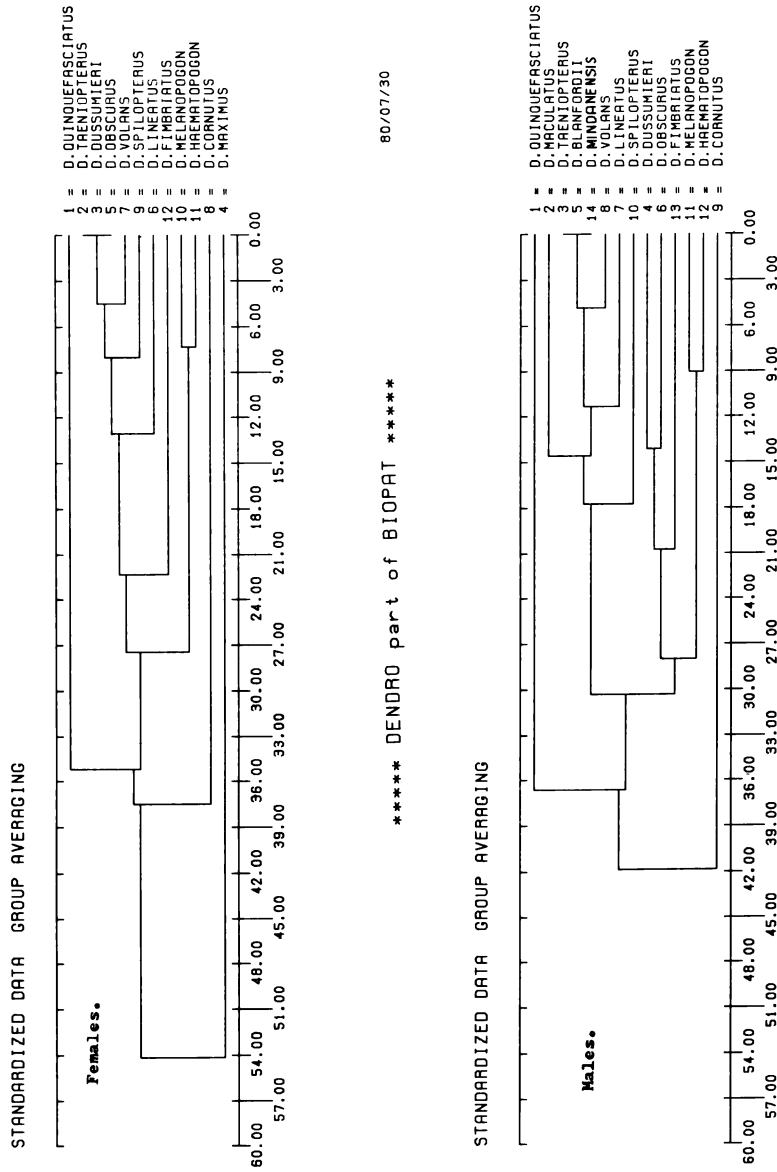


Fig. 24. Dendrograms of the centroids of the species of *Draco*, modified data.

5.1.2. CONCLUSIONS

From the preceding cluster analyses, the following conclusions could be drawn:

— The genus can be divided into two main clusters: one containing *D. maximus*, *D. mindanensis*, *D. quinquefasciatus*, *D. dussumieri*, *D. melanopogon*, *D. haematopogon*, *D. blanfordii*, *D. obscurus*, *D. taeniopterus* and *D. fimbriatus*. Within this cluster *D. maximus* and *D. quinquefasciatus* usually form distinct units. The second main cluster contains two large subclusters: one with *D. lineatus*, *D. spilopterus* and *D. maculatus* and the other with *D. volans* and *D. cornutus*. Within *D. lineatus*, *D. l. modiglianii* and *D. l. bimaculatus* are distinct units.

— The use of ratios instead of measurements as data, results in a clustering that is much more in accordance with what presently are regarded to be distinct species.

From the principal component analysis a group of characters and ratios can be chosen, which are most useful in discriminating between the (sub)species. They are: relative tail length, relative head length, relative snout length, relative gular pouch length, relative hindlimb length, number of supralabials, number of dorsals, number of subdigital lamellae, number of nuchal crest scales, number of ribs, direction of nostril. For this reason, these characters are discussed in chap. 5.2. As the plots of the specimens along the principal axes are multidimensional, they contain more information than the dendrograms. In the plots, based on the modified data set, three clusters are recognizable: one with *D. lineatus*, one with *D. volans* and *D. cornutus* and one with *D. maximus*, *D. mindanensis*, *D. quinquefasciatus*, *D. melanopogon*, *D. haematopogon*, *D. dussumieri*, *D. blanfordii* and *D. fimbriatus*. *D. spilopterus* is intermediate between *D. volans* and *D. lineatus*; *D. maculatus* (and perhaps *D. obscurus* and *D. taeniopterus*) is (are) intermediate between the three clusters. In the third cluster *D. maximus* and *D. quinquefasciatus* are usually distinct units. Of the subspecies of *D. lineatus*, *D. l. modiglianii* and *D. l. bimaculatus* are usually distinct.

5.2 THE MORE IMPORTANT DISTINGUISHING CHARACTERS

It was tested whether the character states were distributed equally among the (sub)species with the Kurskal-Wallis or the chi-square test for all the taxa of which more than three specimens were available (Siegel, 1956). All the character states and ratios, except the thorn width and the relative thorn width, turned out to be distributed unequally at a significance level of 0.1%. Although this is true, most character states within a (sub)species overlap with that of other (sub)species.

The more important characters are discussed below. Of nine of them comparisons of the states within the genus are given in figs. 25-28. The species are arranged in such a way that those species that are probably closely related (see chap. 7) are next to each other.

The distribution of the snout-vent length within the (sub)species shows (fig. 25A) that in most cases females are larger than males.

The relative tail length is shown in fig. 25B. It shows that there are many intermediate forms between species with a long tail (*D. lineatus*) and those with a short one (*D. volans*). Note that *D. v. boschmai* has a longer tail than the other subspecies of *D. volans*.

Of the head dimensions only the relative head length and the relative snout length are important. The head length in most species is 0.19 or 0.20 times the snout-vent length. *D. fimbriatus* and *D. l. modiglianii* have a long head (0.22 times the snout-vent length), *D. melanopogon* has a shorter one (0.17 times the snout-vent length).

The relative snout length is shown in fig. 26A as an example of a character that, although it may play a role in a multivariate analysis, is not usable as a character to distinguish between the species (The fact that the snout length/head width always occurs together with the relative snout length in the principal component analyses, means that they are highly correlated. Therefore only the relative snout length is shown here).

The relative gular pouch length in males is shown in fig. 26B. It shows that *D. dussumieri* and *D. quinquefasciatus* have long gular pouches, whereas *D. mindanensis*, *D. lineatus* and *D. cornutus* have short ones. In females too the relative gular pouch length varies between species. Again *D. lineatus* has a short one (about 0.5 times the head length), but now *D. maximus* and *D. dussumieir* have long ones (about 1.1 times the head length).

The relative thorn length is of special interest for the difference between *D. volans* and *D. cornutus* (fig. 27A). It is remarkable that *D. v. reticulatus* has a large thorn and that *D. v. sumatranus* from Borneo has a smaller thorn than *D. v. sumatranus* from the other localities. Other species with a small thornlike scale are *D. fimbriatus*, *D. maculatus* and *D. spilopterus*.

The data on hindlimb length/distance limbs is shown in fig. 27B. It shows that *D. cornutus*, *D. volans* and *D. quinquefasciatus* have short legs. *D. v. timoriensis* and *D. v. boschmai* have longer legs than the other subspecies of *D. volans*.

Fig. 28A shows the mean number of supralabials. This number is low in *D. lineatus*, but varies slightly between the subspecies. *D. maximus* has a high number, only overlapping with *D. quinquefasciatus* and *D. mindanensis*.

The number of dorsals is shown in fig. 28B. The differences between the subspecies of *D. fimbriatus*, those of *D. obscurus* and those of *D. blanfordii* are remarkable.

All the (sub)species have about 25 subdigital lamellae under the fourth toe, except *D. maximus* with 28-32 and *D. quinquefasciatus* with 17-23 subdigital lamellae.

The number of nuchal crest scales is shown in fig. 27C. Males of *D. spilopterus* have high numbers of these scales. Apparently, the distinct sexual dimorphism in this character usually exhibited by species in this genus, is absent in *D. cornutus*, *D. v. timoriensis* and *D. l. bourouniensis*.

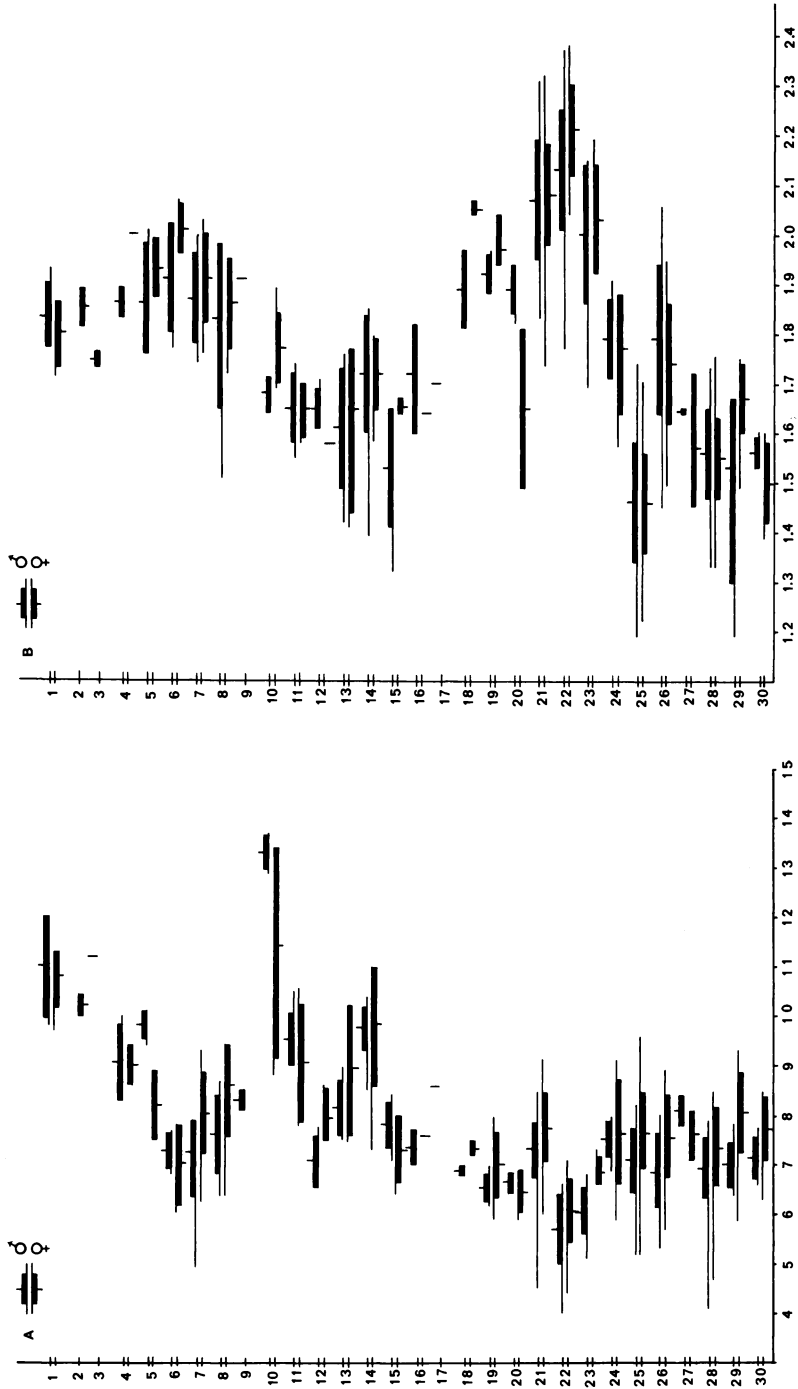


Fig. 25. Comparison of the character states within *Draco*. A: snout-vent length. 1 = *D. b. blanfordii*; 2 = *D. b. dochlorinensis*; 3 = *D. b. norvillii*; 4 = *D. o. obscurus*; 5 = *D. o. formosus*; 6 = *D. taeniopogon*; 7 = *D. melanopogon*; 8 = *D. haematopogon*; 9 = *D. mindanensis*; 10 = *D. maximus*; 11 = *D. quinquefasciatus*; 12 = *D. dussumieri*; 13 = *D. f. fimbriatus*; 14 = *D. f. hennigi*; 15 = *D. m. maculatus*; 16 = *D. m. haasei*; 17 = *D. m. whiteheadi*; 18 = *D. l. lineatus*; 19 = *D. l. beccarii*; 20 = *D. l. bimaculatus*; 21 = *D. l. bourountensis*; 22 = *D. l. modiglianii*; 23 = *D. l. splanotus*; 24 = *D. splanotus*; 25 = *D. v. volans*; 26 = *D. v. boschmai*; 27 = *D. v. reticulatus*; 28 = *D. v. sumatranus*, a: Sumatra, b: West Malaysia, c: Borneo; 29 = *D. v. timoriensis*; 30 = *D. cornutus*.

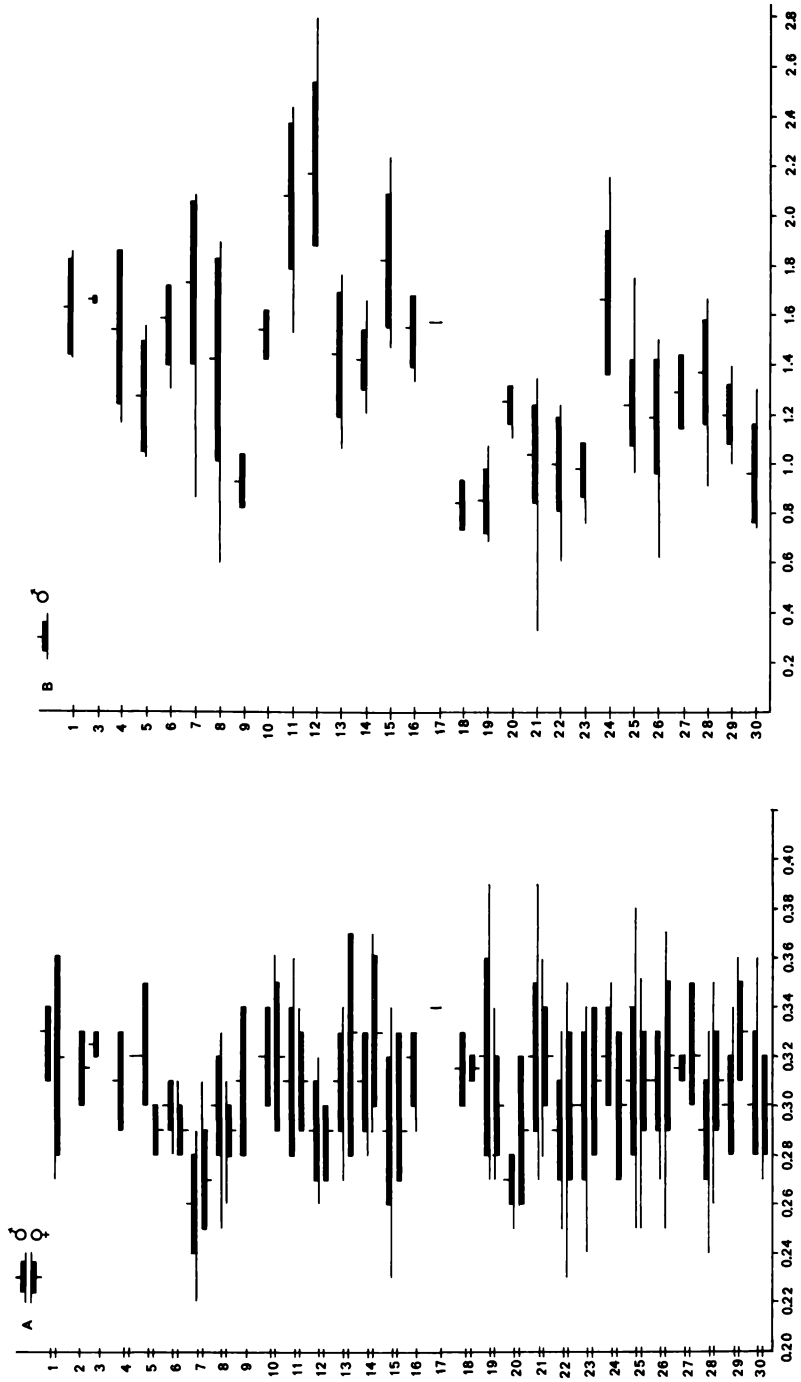


Fig. 26. Comparison of the character states within *Draco*. A: snout length/head length; B: gular pouch length/head length in males. For explanation of numbers see fig. 25.

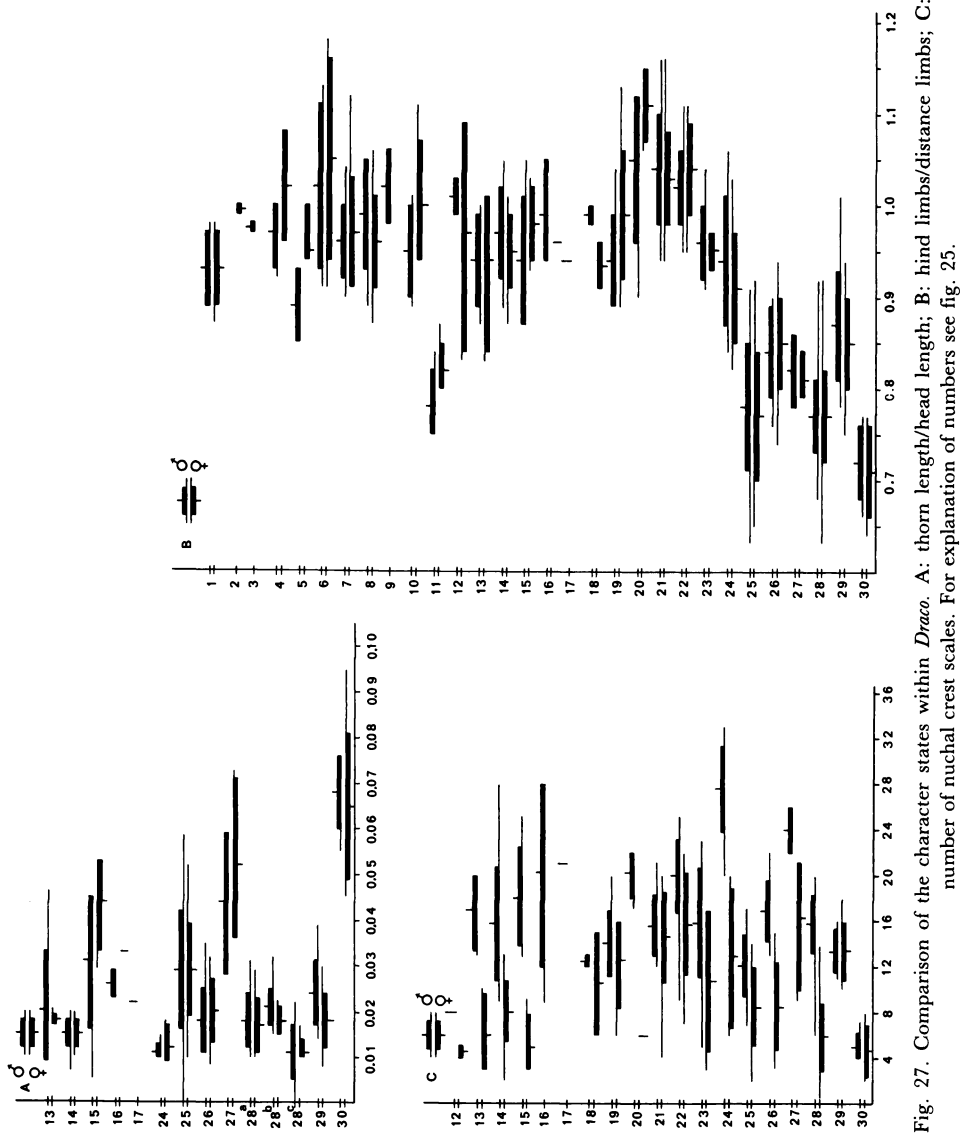


Fig. 27. Comparison of the character states within *Draco*. A: thorn length/head length; B: hind limbs/distance limbs; C: number of nuchal crest scales. For explanation of numbers see fig. 25.

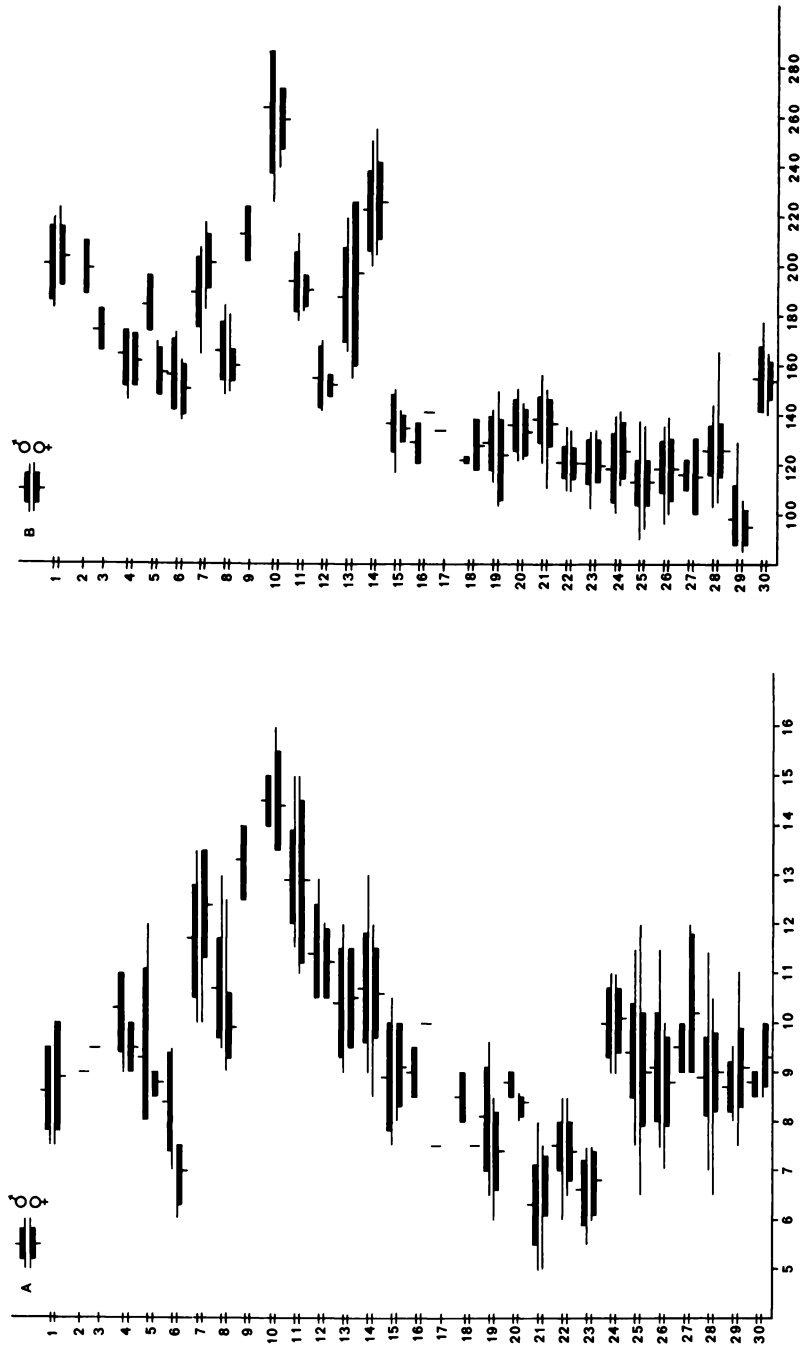


Fig. 28. Comparison of the character states within *Draco*. A: number of labials; B: number of dorsals. For explanation of numbers see fig. 25.

The number of ribs in the patagium seems to be a character that may be used to divide the genus into artificial groups just for convenience. But one should be careful, since 7.4% of the examined specimens have a number that differs at least at one side of the body from the usual number of the (sub)species they belong to. In (sub)species, usually having six ribs, this could either be five or seven, in (sub)species, usually having five ribs, this could be four or six. In any case this character does not divide the genus into two natural groups as Hennig (1936a) thought: *D. l. modiglianii*, which clearly belongs to *D. lineatus*, usually has six ribs, while all the other subspecies usually have five ribs. For this reason, the argument of Hennig (1936a) that *D. cornutus* and *D. spilopterus* are subspecies of the same species, because they both usually have six ribs, is invalid.

The direction of the nostril is usually distinctly upward or outward. The species with the nostril directed outward are *D. volans*, *D. lineatus*, *D. cornutus*, *D. spilopterus*, *D. fimbriatus* and *D. maculatus*. All the other species have it directed upward.

6. ZOOGEOGRAPHY

The distribution of the genus *Draco* is shown in fig. 3. The numerals indicate the number of species found on each island or in mainland areas. There is a striking discontinuity in the distribution: one species is found in Southern India, all the others in South-East Asia and in the Malayan Archipelago. A good explanation for this possibly could be found in the strong climatological changes that have taken place during the Pleistocene. During a certain (interglacial) period a species must have been distributed all over India and South-East Asia. During the following glaciation the rain forest in the northern part of this area disappeared. This could have been caused by the climate getting colder or drier. The species was split into two populations, one in Southern India, the other on the Malayan Peninsula, which both evolved independently. During new interglacial periods *D. dussumieri* was cut off (in India) from the other species (in SE. Asia) by an ecological barrier (N., M. and E. India are covered with non-forested habitats). If this took place only recently, a closely related species should be present on the Malayan Peninsula. As this is not the case, we must assume that it has been long ago. The population of the Malayan Peninsula probably was split into several other species.

The highest numbers of species are found in S. Thailand, Malaya, Borneo and Sumatra. This area is undoubtedly the centre of the recent speciation. This too can be explained by the climatological changes that took place during the Pleistocene. During glacial periods the sealevel may have been 200 m below the sealevel of today (Holloway & Jardine, 1968). The entire continental Sundashelf was land during these periods. The species evolved on the several islands could spread over the entire Sunda region. During interglacial periods the sealevel may have been 100 m higher than it is today. S. Thailand and Malaya may even have been separated by a sea arm. In these periods the species were split into

island populations under different circumstances. This might have caused differentiation. During the next glacial period, members of the different populations would meet again and sometimes would turn out to be different species, which now could spread all over Sundaland. The reason that only five species occur on Java might have been the presence of an ecological barrier between Java and S. Borneo and the rest of Sundaland during glacial periods. It is assumed (Darlington, 1957), that two river systems existed in Sundaland: one in the northern part, running from Northern Borneo, Sumatra and the Malay Peninsula to the Yellow Sea, the other from Southern Borneo and Java to the Flores Sea. The lowlands, surrounding these river systems, probably were covered with rain forest, but the land in between could have been dry and have formed a barrier for most species.

The three species occurring in N. Thailand, Burma, Assam, Cambodia, Vietnam and Hainan, also occur in S. Thailand. The afore mentioned northern area probably was invaded from the south, although there may have been some isolation of populations during the last glacial period, that could explain the subspecies of *D. maculatus* and *D. blanfordii*, which are found here.

East of Bali, Borneo and south of the Philippines (the Wallace-line) only two species are found: *D. lineatus* and *D. volans*, which reach the Kei Islands, Seram and Misoöl. New Guinea is mentioned in the literature (Boulenger, 1885; De Jong, 1926) as locality of *Draco*, but Brongersma (in Hennig, 1936a) doubts whether this is correct. The present distribution of these species could be explained by assuming that the ancestors of *D. lineatus* colonized the area along the outer Banda-arc, during the early Miocene (Holloway & Jardine, 1968). It explains why *D. lineatus* occurs on Enggano and Java, but not on Sumatra and Borneo. From this arc it must have been able to invade Celebes and the Philippines. Later *D. volans* invaded the same area along the inner Banda-arc. That is why *D. volans* does occur on the greater Sunda Islands as well as on the lesser Sunda Islands. The details concerning the migration in the area, east of the Wallace-line are not very clear.

The Philippines are the last area to be discussed here. Four species are found on Mindanao. Two of them probably invaded it from Borneo (*D. volans*, and *D. mindanensis*, as a descendant from a species, that gave rise to *D. melanopogon* and *D. haematopogon* in Sundaland, see chap. 7). *D. lineatus* probably invaded it from Celebes (unless one assumes that there has existed or still exists an unknown form of *D. lineatus* on Borneo). Although this is unusual, it does not seem impossible (Inger, 1954). *D. spilopterus* can be regarded as a relict of a species that lived in the area during the Miocene and gave rise to *D. lineatus* on the outer Banda-arc, to *D. volans* on Sundaland and later on the inner Banda-arc and to *D. maculatus* in Thailand (chap. 7).

7. PHYLOGENY

In the literature no data could be found on the phylogeny within the family Agamidae. Since I am not very familiar with the other genera of this family, I

cannot say anything about the place of *Draco* within it. It is, however, clear that the occurrence of the patagium must be regarded as a derived feature. And in view of the difficulties to distinguish the species, *Draco* must be regarded as a holophyletic taxon. Because the sister-group is not known, it is not possible to determine which state of the characters, used to distinguish the species, is the derived one. Apart from this, most of the characters must be given low weight, due to the high intraspecific variation (Arnold, 1981: 24). Therefore the overall resemblance is taken here as a base for the phylogenetic analysis.

From the analyses in chap. 5 it is clear that two groups of species can be distinguished. One of them consists of *D. maculatus*, *D. volans*, *D. lineatus*, *D. cornutus* and *D. spilopterus*. From the distribution of these species it is clear that the centres of distribution of these species are quite different. It is assumed that the common ancestor of these species was distributed all over SE. Asia during the Miocene and gave rise to *D. maculatus* in Thailand, to *D. volans* in Sundaland, to *D. lineatus* on the outer Banda-arc and to *D. spilopterus* in the Philippines. Later, during an interglacial, *D. cornutus* was split from *D. volans* in Borneo.

The other group is much more difficult to interpret. Except *D. dussumieri*, all the species originate from Sundaland or Thailand. *D. fimbriatus* has several characters in common with the preceding group: irregular head scales, thornlike scale, direction of the nostril, nuchal crest. Therefore it is regarded here as an early side-branch of the first group, originating in Sundaland. All the other species have the nostril directed upward, a rather high number of dorsals (= small dorsals) and no distinct nuchal crest. These remaining species can be divided into three groups: one with a nuchal fold, a gular pouch with enlarged scales in males and five ribs in the patagia (*D. blanfordii*, *D. taeniopterus* and *D. obscurus*), another one with a nuchal fold, no enlarged scales on the gular pouch and six ribs in the patagia (*D. dussumieri*, *D. quinquefasciatus* and *D. maximus*) and a group without a nuchal fold, without enlarged scales on the gular pouch and five ribs in the patagia (*D. mindanensis*, *D. haematopogon* and *D. melanopogon*). Apart from this, the species within these three groups resemble each other in markings and colour. *D. blanfordii*, *D. obscurus* and *D. taeniopterus* have grey or brown patagia with more or less distinct, dark markings and yellowish or orangish ventral parts of the lateral pouches (in preservative); *D. mindanensis*, *D. haematopogon* and *D. melanopogon* have dark brown patagia with light spots and *D. dussumieri*, *D. quinquefasciatus* and *D. maximus* have a dark band ventrally in front of the shoulders. When we consider the *volans-cornutus-lineatus-maculatus-spilopterus-fimbriatus*-group as the sister-group, the enlarged gular pouch scales and the absence of a nuchal crest or fold can be regarded as derived characters. One can imagine the phylogeny of this group as follows: the ancestor lived in continental SE. Asia and India. It had six ribs, a nuchal crest or fold and a dark band in front of the shoulders. During a glacial period *D. dussumieri* was split from the rest of the population and remained isolated. Later the population of Southern Thailand was split off from that of Sundaland and gave rise to the ancestor of *D. blanfordii*, *D. obscurus* and *D. taeniopterus*. It evolved enlarged gular

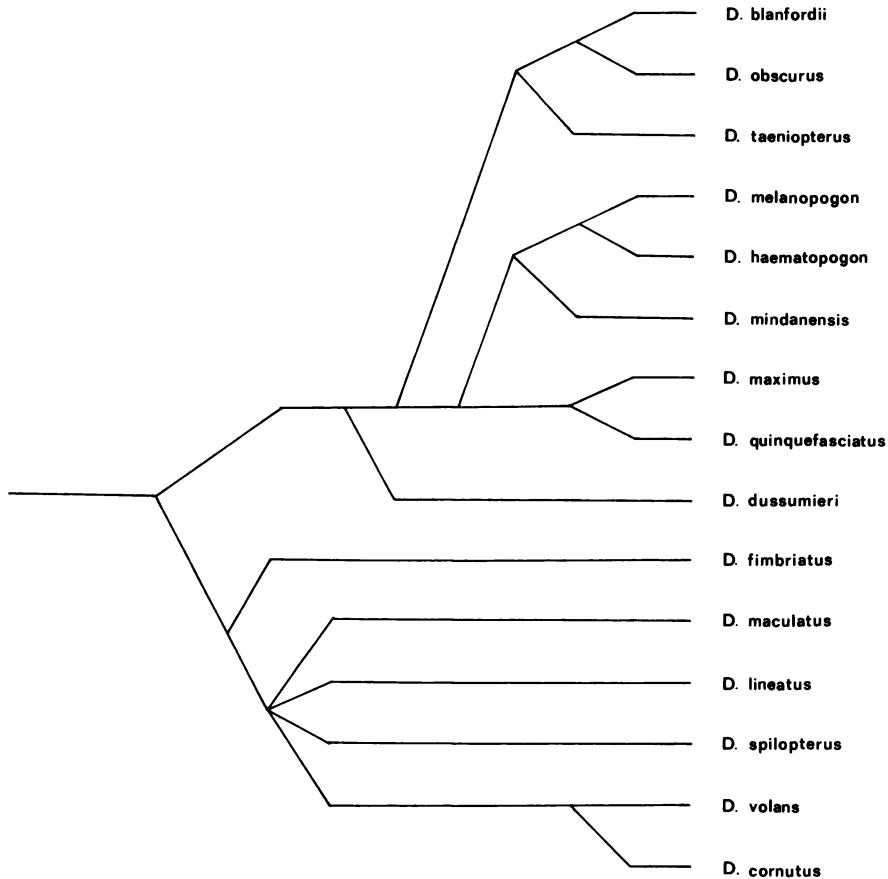


Fig. 29. Phylogenetic tree of the genus *Draco*.

pouch scales and five ribs in the patagium. The dark shoulder band either changed into the dark base of the gular pouch in *D. obscurus* or into the dark band at the base of the gular pouch in *D. blanfordii*. Later the remaining population of Sundaland split into one species with the ancestral features and one which again evolved five ribs in the patagium and lost the nuchal crest or fold. This was the ancestor of *D. mindanensis*, *D. melanopogon* and *D. haematopogon*. In this group too there are dark or black markings at the base of the gular pouch. The 'ancestral' species later split into *D. quinquefasciatus* and *D. maximus*.

If the phylogeny as described is correct, at least three periods of isolation (interglacials) must have taken place: *dussumieri* was split off from the ancestral species during a glacial; the ancestor of the *taeniopterus*-group during the next interglacial; the ancestor of the *haematopogon*-group during the second one and *haematopogon* from *melanopogon* during the third (*mindanensis* can not have reached the Philippines by land, therefore no interglacial is needed to explain its isola-

TABLE 4
Synopsis of the names used for *Draco* and taxa within this genus

Name	Autor(s)	Original allocation	Current status
<i>abbreviata</i>	Hardwicke & Gray, 1827	<i>D. abbreviata</i>	<i>D. fimbriatus fimbriatus</i>
<i>affinis</i>	Bartlett, 1894	<i>D. affinis</i>	<i>D. affinis</i>
<i>affinis</i>	Baumann, 1913	<i>D. affinis</i>	<i>D. obscurus obscurus</i>
<i>amboinensis</i>	Lesson, 1834	<i>D. amboinensis</i>	<i>D. lineatus amboinensis</i>
<i>beccarii</i>	Peters & Doria, 1878	<i>D. beccarii</i>	<i>D. lineatus beccarii</i>
<i>bimaculatus</i>	Günther, 1864	<i>D. bimaculatus</i>	<i>D. lineatus bimaculatus</i>
<i>blanfordii</i>	Boulenger, 1885	<i>D. blanfordii</i>	<i>D. blanfordii blanfordii</i>
<i>boschmai</i>	Hennig, 1936	<i>D. volans boschmai</i>	<i>D. volans boschmai</i>
<i>bouroumiensis</i>	Lesson, 1834	<i>D. bouroumiensis</i>	<i>D. lineatus bouroumiensis</i>
<i>buruensis</i>	De Jong, 1926	<i>D. buruensis</i>	<i>D. lineatus bouroumiensis</i>
<i>cornutus</i>	Günther, 1864	<i>D. cornutus</i>	<i>D. cornutus</i>
<i>crystalinus</i>	Günther, 1872	<i>D. crystalinus</i>	<i>D. fimbriatus fimbriatus</i>
<i>cryptotis</i>	Despax, 1912	<i>D. cryptotis</i>	<i>D. maximus</i>
<i>cyanoaemus</i>	Boulenger, 1900	<i>D. cyanoaemus</i>	<i>D. blanfordii blanfordii</i>
<i>cyanopterus</i>	Peters, 1867	<i>D. reticulatus</i> var. <i>cyanopterus</i>	<i>D. volans reticulatus</i>
<i>daudini</i>	Duméril & Bibron, 1837	<i>D. daudini</i>	<i>D. volans volans</i>
<i>divergens</i>	Taylor, 1934	<i>D. divergens</i>	<i>D. maculatus divergens</i>
<i>Draco</i>	Linnaeus, 1758	Reptilia	<i>Draco</i>
<i>Dracoella</i>	Gray, 1845	Agamidae	<i>Draco</i>
<i>Dracontoides</i>	Fitzinger, 1843	Dracones	<i>Draco</i>
<i>Draconus</i>	Rafinesque, 1815	Chondronia	<i>Draco</i>
<i>Draconculus</i>	Wiegmann, 1834	Dendrobatae	<i>Draco</i>
<i>dussumieri</i>	Duméril & Bibron, 1837	<i>D. dussumieri</i>	<i>D. dussumieri</i>
<i>Duvaucelii</i>	Fitzinger, 1843	<i>D. Duvaucelii</i>	<i>D. dussumieri</i>
<i>everetti</i>	Boulenger, 1885	<i>D. everetti</i>	<i>D. volans reticulatus</i>
<i>fimbriatus</i>	Kuhl, 1820	<i>D. fimbriatus</i>	<i>D. fimbriatus fimbriatus</i>
<i>formosus</i>	Boulenger, 1900	<i>D. formosus</i>	<i>D. obscurus formosus</i>
<i>fuscus</i>	Daudin, 1802	<i>D. fuscus</i>	<i>D. volans volans</i>
<i>gracilis</i>	Barbour, 1903	<i>D. gracilis</i>	<i>D. cornutus</i>
<i>grandis</i>	Bartlett, 1894	<i>D. grandis</i>	<i>D. fimbriatus fimbriatus</i>
<i>guentheri</i>	Boulenger, 1885	<i>D. guentheri</i>	<i>D. volans reticulatus</i>
<i>haasei</i>	Boettger, 1893	<i>D. haasei</i>	<i>D. maculatus haasei</i>
<i>haematopogon</i>	Gray, 1931	<i>D. haematopogon</i>	<i>D. haematopogon</i>
<i>hemigi</i>	nov. subsp.		<i>D. fimbriatus hemigi</i>
<i>indochinensis</i>	Smith, 1928	<i>D. indochinensis</i>	<i>D. blanfordii indochinensis</i>
<i>intermedius</i>	Werner, 1910	<i>D. intermedius</i>	<i>D. maximus</i>
<i>javanica</i>	Schlegel, 1844	<i>D. viridis</i> var. <i>javanica</i>	<i>D. volans volans</i>
<i>laetepictus</i>	Hennig, 1936	<i>D. formosus laetepictus</i>	<i>D. obscurus laetepictus</i>
<i>lineatus</i>	Daudin, 1802	<i>D. lineatus</i>	<i>D. lineatus lineatus</i>
<i>longibarba</i>	Hennig, 1936	<i>D. quinquefasciatus longibarba</i>	<i>D. quinquefasciatus</i>
<i>maculatus</i>	Gray, 1845	<i>Draconculus maculatus</i>	<i>D. maculatus maculatus</i>
<i>major</i>	Blanford, 1878	<i>D. major</i>	<i>D. blanfordii blanfordii</i>
<i>major</i>	Laurenti, 1768	<i>D. major</i>	<i>D. volans volans</i>
<i>maximus</i>	Boulenger, 1893	<i>D. maximus</i>	<i>D. maximus</i>
<i>melanopogon</i>	Boulenger, 1887	<i>D. melanopogon</i>	<i>D. melanopogon</i>
<i>microlepis</i>	Boulenger, 1893	<i>D. microlepis</i>	<i>D. haematopogon</i>
<i>mindanensis</i>	Stejneger, 1908	<i>D. mindanensis</i>	<i>D. mindanensis</i>
<i>minor</i>	Laurenti, 1768	<i>D. minor</i>	<i>D. volans volans</i>
<i>modiglianii</i>	Vinciguerra, 1892	<i>D. modiglianii</i>	<i>D. lineatus modiglianii</i>
<i>nigriappendiculatus</i>	Bartlett, 1894	<i>D. nigriappendiculatus</i>	<i>D. melanopogon</i>
<i>norvillii</i>	Alcock, 1895	<i>D. norvillii</i>	<i>D. blanfordii norvillii</i>
<i>obscurus</i>	Boulenger, 1887	<i>D. obscurus</i>	<i>D. obscurus obscurus</i>
<i>ochropterus</i>	Werner, 1910	<i>D. ochropterus</i>	<i>D. lineatus ochropterus</i>
<i>ornatus</i>	Gray, 1864	<i>Draconculus ornatus</i>	<i>D. spilopterus</i>
<i>personatus</i>	Wiegmann, 1834	<i>Draconculus personatus</i>	<i>D. lineatus lineatus</i>
<i>Pleuropterus</i>	Fitzinger, 1843	<i>Draco</i>	<i>Draco</i>
<i>praepos</i>	Linnaeus, 1766	<i>D. praepos</i>	<i>D. volans volans</i>
<i>Pterosaurus</i>	Fitzinger, 1843	<i>Draco</i>	<i>Draco</i>
<i>punctatus</i>	Boulenger, 1900	<i>D. punctatus</i>	<i>D. fimbriatus fimbriatus</i>
<i>quadrasi</i>	Boettger, 1893	<i>D. quadrasi</i>	<i>D. spilopterus</i>
<i>quinquefasciatus</i>	Hardwicke & Gray, 1827	<i>D. quinquefasciatus</i>	<i>D. quinquefasciatus</i>
<i>Reinwardtii</i>	Fitzinger, 1843	<i>D. Reinwardtii</i>	<i>D. lineatus lineatus</i>
<i>reticulatus</i>	Günther, 1864	<i>D. reticulatus</i>	<i>D. volans reticulatus</i>
<i>Rhacodracon</i>	Fitzinger, 1843	<i>Draco</i>	<i>Draco</i>
<i>rizali</i>	Wandolleck, 1900	<i>D. rizali</i>	<i>D. volans reticulatus</i>
<i>rostratus</i>	Günther, 1864	<i>D. rostratus</i>	<i>D. spilopterus</i>
<i>samaoensis</i>	Schlegel, 1844	<i>D. viridis</i> var. <i>samaoensis</i>	<i>D. volans timoriensis</i>
<i>spilonotus</i>	Günther, 1872	<i>D. spilonotus</i>	<i>D. lineatus spilonotus</i>
<i>spilopterus</i>	Günther, 1872	<i>D. spilopterus</i>	<i>D. lineatus spilonotus</i>
<i>spilopterus</i>	Wiegmann, 1834	<i>Draconculus spilopterus</i>	<i>D. spilopterus</i>
<i>sumatrana</i>	Schlegel, 1844	<i>D. viridis</i> var. <i>sumatrana</i>	<i>D. volans sumatranus</i>
<i>taeniopterus</i>	Günther, 1861	<i>D. taeniopterus</i>	<i>D. taeniopterus</i>
<i>timoriensis</i>	Kuhl, 1820	<i>D. timoriensis</i>	<i>D. volans timoriensis</i>
<i>toxopei</i>	De Jong, 1926	<i>D. toxopei</i>	<i>D. lineatus bouroumiensis</i>
<i>viridis</i>	Daudin, 1802	<i>D. viridis</i>	<i>D. volans volans</i>
<i>volans</i>	Linnaeus, 1758	<i>D. volans</i>	<i>D. volans volans</i>
<i>walkeri</i>	Boulenger, 1891	<i>D. walkeri</i>	<i>D. lineatus beccarii</i>
<i>whiteheadi</i>	Boulenger, 1899	<i>D. whiteheadi</i>	<i>D. maculatus whiteheadi</i>

tion). In this case we would now be living in the fourth interglacial during which the subspecies of *blanfordii* and *obscurus* have originated.

Since nothing is known about the differences in niches of the several species, it is not possible to relate the phylogeny with the ecology of the species. It is, for example, possible that the resemblance between *D. volans*, *D. maculatus*, *D. lineatus* and *D. spilopterus* is due to similar niches and not to common ancestors.

The phylogeny, as described, and the tree as given in fig. 29, are of course quite speculative, but it might serve as a starting point for further investigations.

8. SUMMARY

The variation within and the differences between species of the genus *Draco* L. (Agamidae, Reptilia) were studied. The state of 22 characters, together with data on colour of about 900 specimens were examined. The results are given in the description of the taxa examined and in the keys to the species and subspecies.

Two new subspecies are described (*D. fimbriatus hennigi* and *D. lineatus rhytisma*), the name *sumatranus* Schlegel is reestablished for a subspecies of *D. volans*, one species (*D. spilopterus*) is split into two (*D. spilopterus* and *D. cornutus*), some names are regarded as synonyms (*D. punctatus* and *D. cristatellus* synonyms of *D. f. fimbriatus*; *D. haematopogon microlepis* synonym of *D. haematopogon*; *D. lineatus amboinensis* synonym of *D. lineatus bourouniensis*; *D. maximus cryptotis* synonym of *D. maximus*; *D. quinquefasciatus longibarba* synonym of *D. quinquefasciatus*) and other nomenclatural changes are proposed (*D. formosus* becomes *D. obscurus*; *D. fimbriatus mindanensis* becomes *D. mindanensis*; *D. taeniopterus indochinensis* becomes *D. blanfordii indochinensis*; *D. norvillii* becomes *D. blanfordii norvillii*). For several taxa lectotypes were selected. A summary of the current nomenclature is given in table 4.

Of the taxa that occurred in the unpublished 'Erpétologie de Java' of H. Boie the descriptions of Boie are cited and the plates are here reproduced. Synonyms, references, diagnoses and distributions are given for all the known taxa. A more extensive description of the character states and the colour in preservative is given for all the taxa examined.

A cluster analysis and a principal component analysis were executed on a part of the specimens. This resulted in dendrograms that are given and in the selection of 11 characters that are discussed separately.

The zoogeography is discussed and explained with the climatological changes and changes of the sealevel that took place in the past.

The conclusions of the cluster analyses and zoogeography result in a short discussion of the phylogeny within the genus. A phylogenetic tree is given.

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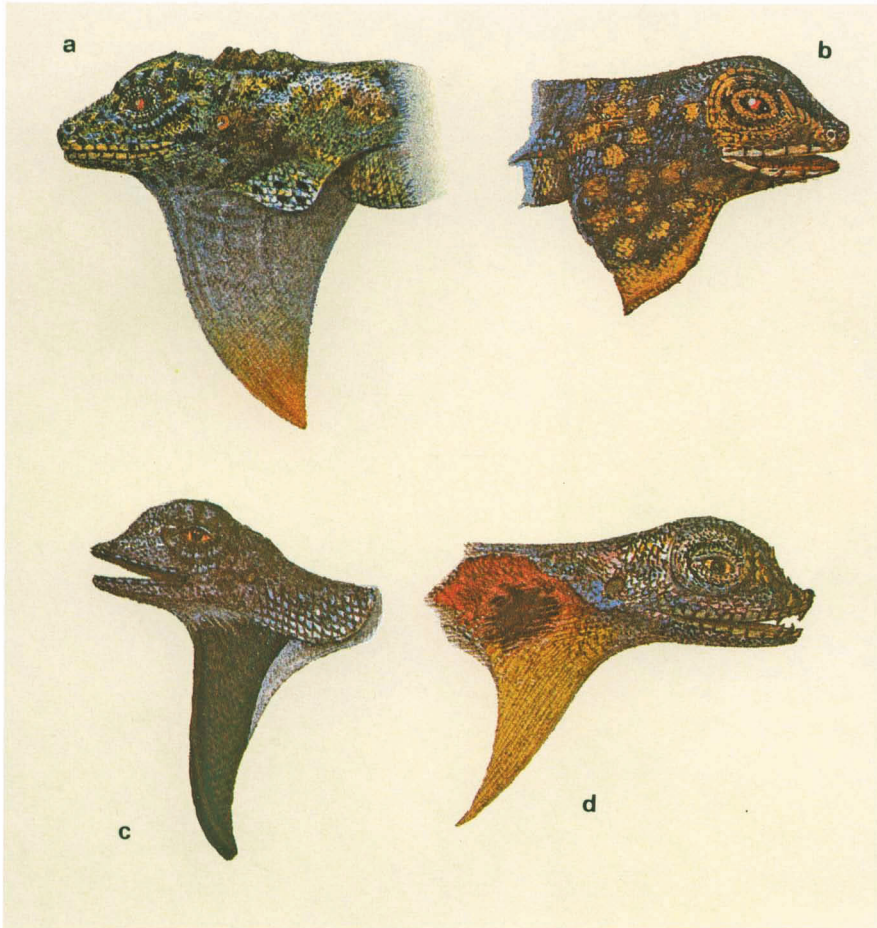
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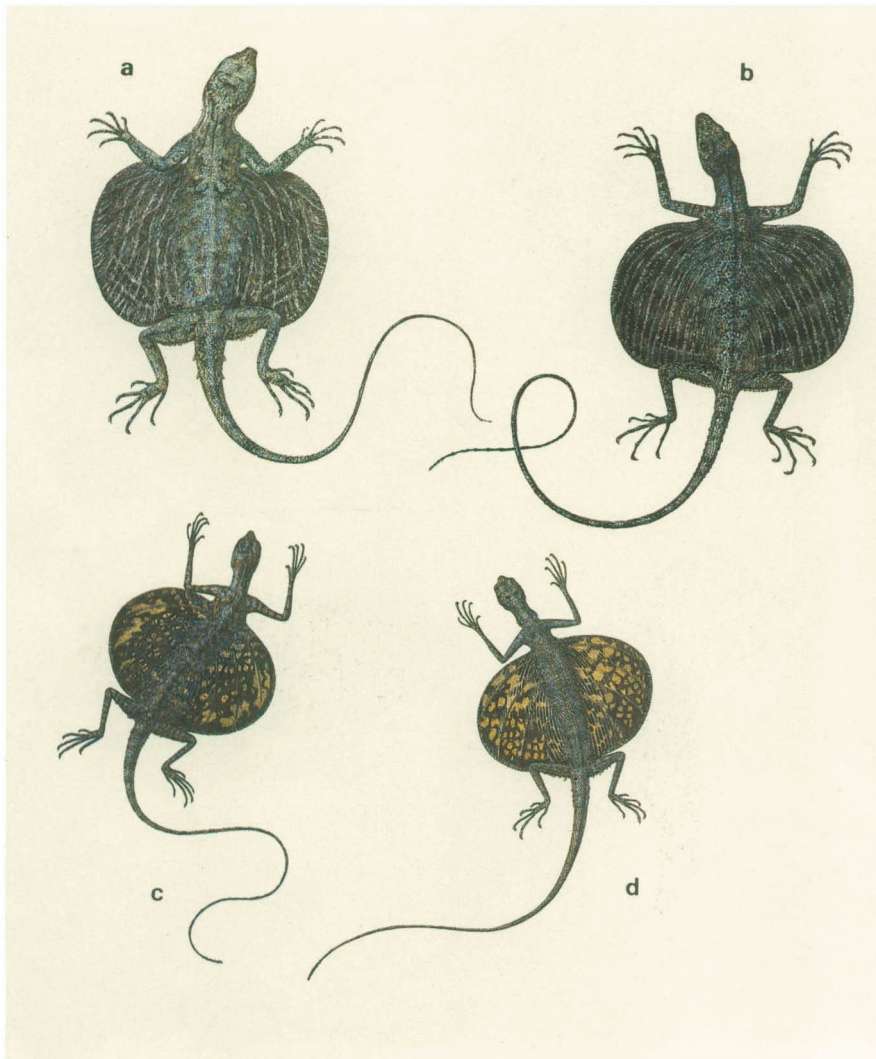
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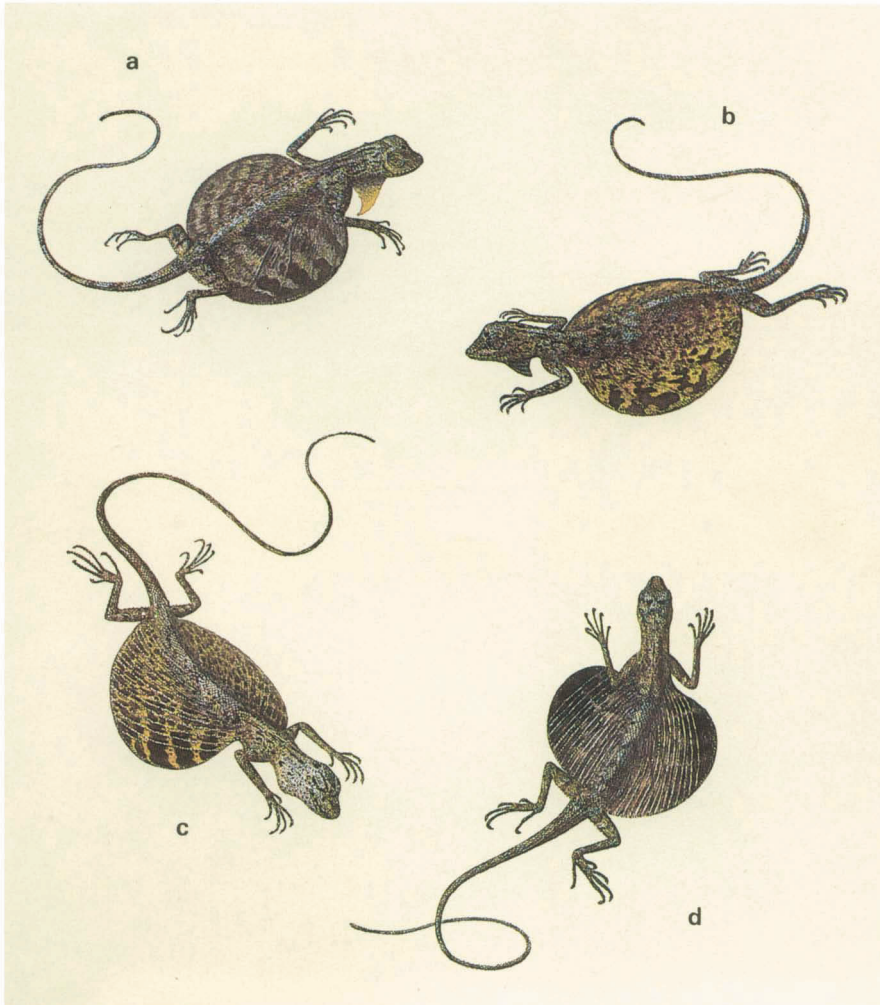
PLATES



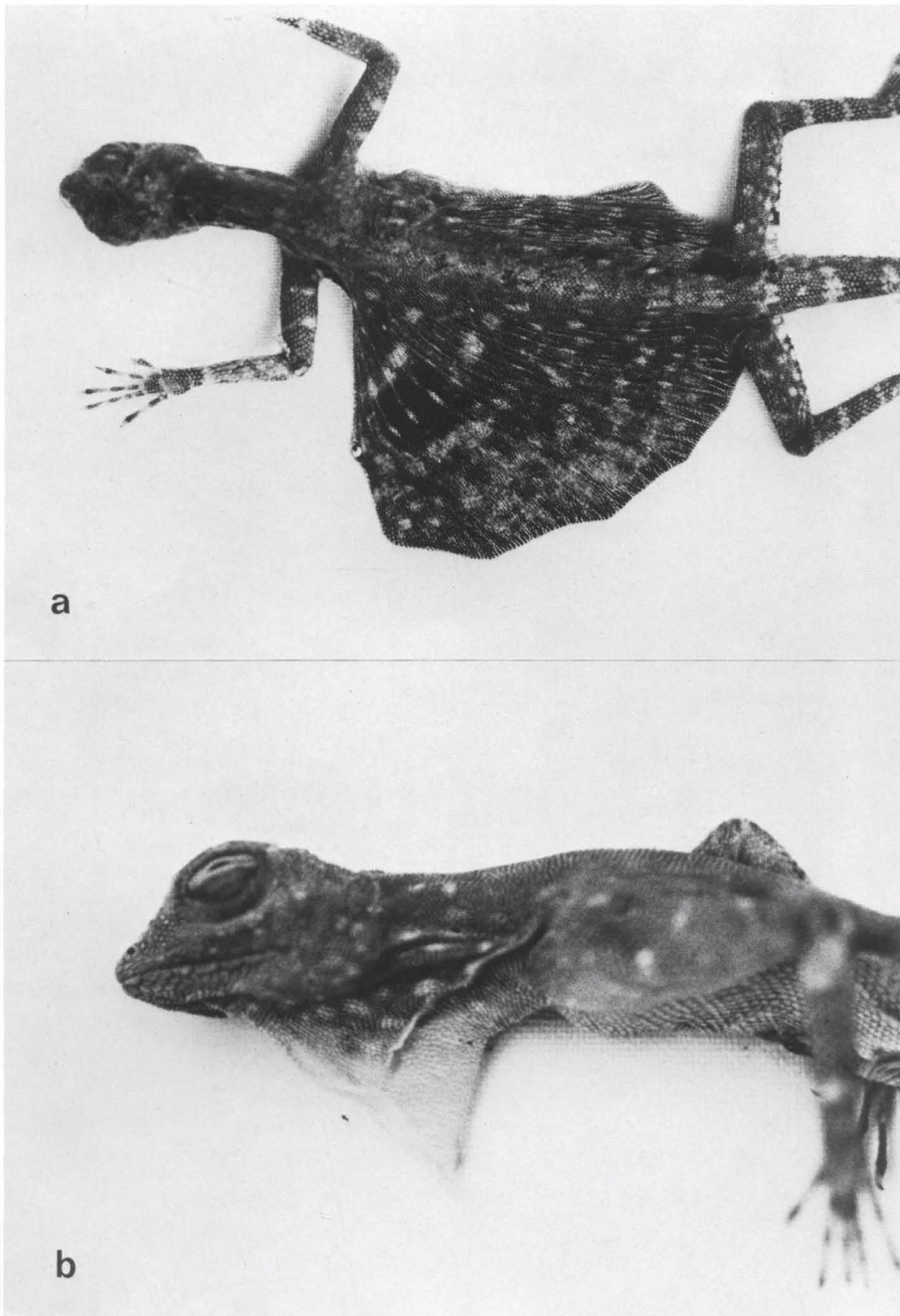
Drawings of the heads of males, meant for the unpublished 'Erpétologie de Java' by H. Boie. Del. P. van Oort. Fig. a. *Draco fimbriatus hennigi* (after RMNH 2924 A). Fig. b. *D. lineatus bourouniensis*. Fig. c. *D. melanopogon*. Fig. d. *D. haematopogon*.



Drawings of males, meant for the unpublished 'Erpétologie de Java' by H. Boie. Del. P. van Oort.
 Fig. a. *Draco fimbriatus hennigi* (after RMNH 2924 A). Fig. b. *D. lineatus bourouniensis*. Fig. c. *D. melanopogon*. Fig. d. *D. haematopogon*.



Drawings of *Draco*, meant for the unpublished 'Erpétologie de Java' by H. Boie. Del. P. van Oort.
Fig. a. *D. v. volans* ♂. Fig. b. *D. v. volans* ♀. Fig. c. *D. l. lineatus* ♀. Fig. d. *D. l. lineatus* ♂.



Holotype of *D. lineatus rhytisma*. Fig. a. Dorsal view. Fig. b. Lateral view of head. (Photographs after colour slides by W. F. Rodenburg).

