SNAKES OF SULAWESI: CHECKLIST, KEY AND ADDITIONAL BIOGEOGRAPHICAL REMARKS

by

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Bosch, H. A. J. in den: Snakes of Sulawesi: checklist, key and additional biogeographical remarks.

Zool. Verh. Leiden 217, 27-ii-1985: 1-50, figs. 1-2, tables 1-2. — ISSN 0024-1652.

Key words: Snakes; checklist; key; species; Sulawesi; Indopacific region; biogeography.

A checklist with concise synonymy and a key to the snakes of Sulawesi is presented, comprising 63 species in 38 genera; 3 subspecies and 15 species, of which one constitutes a monotypic genus, are considered endemic. There is a strong Indo-Malayan relationship. Sea-snakes and *Candoia carinata* excluded, no Philippine, Papuan or Australian affinities were found. Geological and ecological barriers, together with a low immigration pressure from the south and east, are considered causal factors. Although Sulawesi has been an instable island region at least since the Late Cretaceous as compared with most surrounding islands, which were parts of Sundaland or Sahulland and as such were formed relatively recently, the species richness in Wallacea is of the same order as in the neighbouring islands and more dependent of the Asian relationships of the snakes and the present day distance from landmasses.

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INTRODUCTION

Sulawesi, formerly named Celebes, is one of the island provinces of the Republic of Indonesia with a territory of 189,036 square kilometers straddling the equator. The island is composed of four peninsulas and apart from the narrow coastal plains is mountainous, covered with tropical rain forest (or, what remains of it after intensive human exploitation during several hundreds of years) on a mainly lateritic soil, and influenced by the monsoon, though in some parts of the South and West savannah conditions prevail.

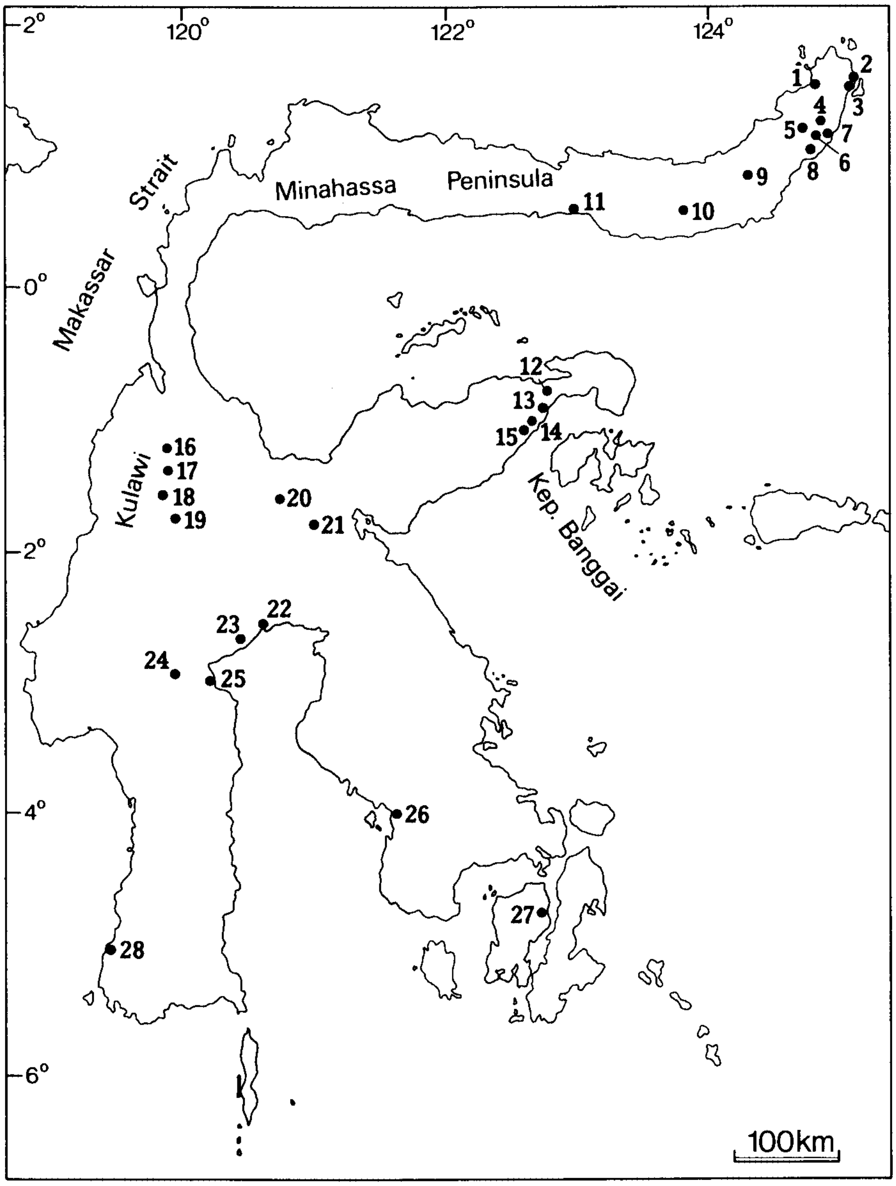

Fig. 1. Map of Sulawesi and adjacent islands with localities mentioned in the text, arranged from West to East and from North to South. 1: Manado, 2: Nature reserve Tongkoko-Batuangus, 3: Bitung, 4: Lake Darau, 5: Amurang, 6: Modajag, 7: Motongkad, 8: Gurupahi, 9: Kotamobagu, 10: Dumoga, 11: Gorontalo, 12: Kamumu, 13: Biak, 14: Pinapuan, 15: Luwuk, 16: Kalawara; 17: Lemo, 18: Kantewu, 19: Peana, 20: Kuku, 21: Taripa, 22: Bonebone, 23: Ba Ebunta, 24: Makale, 25: Palopo, 26: Kolaka, 27: Raha, 28: Makassar.

Herpetological collecting has been done mainly in the nineteenth century and in the beginning of the twentieth century. Several species of Sulawesi snakes were named in honour of these naturalists. Mention should be made of C.G.C. Reinwardt (1821); S. Müller (1828); E. A. Forsten (1840-1842); A. R. Wallace (1856, 1857, 1859), who demarcated the zoogeographic line of division in the Indo-Australian transitional zone, mainly based on butterflies, birds and mammals (Wallace, 1860); C.B.H. von Rosenberg (1863-1864), many of whose specimens are in the unnumbered collection of the Rijksmuseum van Natuurlijke Historie (RMNH), Leiden; J.G.F. Riedel (1865) and D.S. Hoedt (1865): a few snakes in the unnumbered RMNH collection; A.B. Meyer (1870-1873), whose locality data unfortunately are unreliable (e.g. Van Steenis-Kruseman, 1950); L.M. d'Albertis, O. Beccari and A.A. Bruijn (1873-1874); M.W.C. Weber (1888); A.H. Everett (1895) and P. Sarasin & F. Sarasin (1893-1896) (Müller, 1895a, 1895b; Boettger 1901; Sarasin & Sarasin, 1905).

These collections allowed the publication of a catalogue of reptiles and amphibians of Sulawesi (Boulenger, 1897) in which also data from older literature are taken into account. To the list of authors provided by Boulenger can be added Bleeker (1858, 1860), and Boettger (1892). P. Sarasin and F. Sarasin visited the island again from 1901 to 1903. Roux (1904) reported on the herpetological material gathered during this stay. T. Barbour collected in Sulawesi in 1907 (Barbour, 1912). De Rooij (1917) published a summary of the species of snakes in the Indo-Australian archipelago. The Swedish ethnologist/zoologist W.A. Kaudern visited Sulawesi from 1917 to 1920 (Kaudern, 1921, 1925). His specimens were deposited in the Naturhistoriska Museet Gøteborg, Sweden. Further collections were made by M. A. Smith in 1924 (Smith, 1927) and by the ornithologist G. Heinrich from 1930 to 1932 (Ahl, 1933). Kopstein (1936) reported on the collection made by M. Mansjour. Recently the Rijksmuseum van Natuurlijke Historie acquired some snakes collected by W. F. Rodenburg (1980-1982). A rather uncritical list of landsnakes of Sulawesi, based solely on part of the literature, recently appeared in Cranbrook (1981).

CHECKLIST

I here follow the classification as proposed by Rieppel (1979), superimposed on the more detailed systematic arrangement of Dowling & Duellman (1978). The subfamily Cylindrophinae is included in the Uropeltidae (fide McDowell, 1975). As far as the Colubridae is concerned, I did not accept the views of Smith et al. (1977) in changing the tribes of Dowling & Duellman

(1978) into subfamilies, even though the former may imply too detailed a knowledge of the colubrid relationships. In concordance with Rage (1978), McDowell (1979) and Rieppel (1979), *Acrochordus* is placed in a superfamily of its own to indicate that is has no close affinities to any living snake, as recently also concluded by Schwaner & Dessauer (1982) in a comparative immunological study. In the Booidea the Corallini are recognised (fide McDowell, 1979).

Records of sea snakes are included when these animals were found near or on the coast.

The synonymy is concise: reference is made only to the original description, the works of De Rooij (1917) and De Haas (1950) and the most significant papers (including all recent taxonomic publications) dealing with Sulawesi snakes. New locality data from the collections of Kaudern and Rodenburg and specimens in the RMNH concerning Sulawesi are to be found under „new material". Localities in Sulawesi are indicated in fig. 1 (partly after Kaudern, 1921, 1925). Numbers in brackets in the checklist indicate the number of specimens from one locality when no museum registering number was affixed (which is always the case in Kaudern's collection). Rodenburg's field numbers are mentioned. Species dealt with in the section „Taxonomic notes" are indicated with an asterisk.

Infraordo Scolecophidia

Family Typhlopidae

* **Rhamphotyphlops braminus** (Daudin, 1803)

Eryx braminus Daudin, 1803: 279.
Typhlops braminus – De Rooij, 1917: 5; De Haas, 1950: 514.
Typhlina bramina – Hahn, 1980: 39.
Rhamphotyphlops braminus – Melville, 1982: 106.

Range. — Widely distributed in Asia, Indonesia, Philippines, Australia, Madagaskar, Africa, Mexico.

New material. — Gorontalo: RMNH 6339.

Typhlops ater Schlegel, 1839

Typhlops ater Schlegel, 1839: 39; De Rooij, 1917: 13; Hahn, 1980: 51.
Typhlops ater ater – De Haas, 1950: 513.

Range. — Sulawesi; Java; Ternate; Halmahera; Waigeu; Salawati; Andai in West New Guinea. Negros Islands, Philippines, if conspecific with *Typhlops hedraeus.*

* **Typhlops conradi** Peters, 1874

Typhlops Conradi Peters, 1874: 162.
Typhlops conradi – De Rooij, 1917: 10; De Haas, 1950: 514; Hahn, 1980: 54.

Range. — Sulawesi (Minahassa).

Infraordo Alethinophidia
Parvordo Henophidia
Suprafamily Anilioidea
Family Uropeltidae
Subfamily Cylindrophinae

Cylindrophis melanotus Wagler, 1830

Cylindrophis melanotus, Wagler, 1830: 195; McDowell, 1975: 25.
Tortrix rufa var. *Celebica* Schlegel, 1844: 111.
Cylindrophis rufus (partim) – De Rooij, 1917: 36.
Cylindrophis celebensis – Smith, 1927: 220.
Cylindrophis heinrichi Ahl, 1935: 578.

Range. — Sulawesi; Batjan; Halmahera; Kepulauan Sangihe; Kepulauan Sula.

New material. — Modajag (5); Kulawi (2); without exact locality (1). All leg. W. A. Kaudern.

Cylindrophis rufus rufus (Laurenti, 1768)

Anguis rufa Laurenti, 1768: 71.
Cylindrophis rufus (partim) – De Rooij, 1917: 36.
Cylindrophis rufus rufus De Haas, 1950: 527.

Range. — Sulawesi; southeast Asia; Sumatra; Java; Borneo; Kepulauan Sangihe, Kepulauan Sula.

Suprafamily Booidea
Family Boidae
Subfamily Boinae
Tribus Corallini

Candoia carinata (Schneider, 1801)

Boa carinata Schneider, 1801: 261.
Enygrus carinatus – De Rooij, 1917: 31; De Haas, 1950: 525.
Candoia carinata carinata – Stimson, 1969: 7.
Candoia carinata – McDowell, 1979: 27.

Range. — From Sulawesi (Minahassa), Kepulauan Sangihe and Kepulauan Talaud eastwards through the Moluccas and New Guinea to the Solomon Islands.

Subfamily Pythoninae

Python molurus bivittatus Kuhl, 1820

Python bivittatus Kuhl, 1820: 94; — De Rooij, 1917: 22.
Python molurus bivittatus — De Haas, 1950: 523; Stimson, 1969: 30.

Range. — Sulawesi; southeast Asia; Hainan; Borneo; Java; Sumbawa.

Python reticulatus (Schneider, 1801)

Boa reticulata Schneider, 1801: 264.
Python reticulatus — De Rooij, 1917: 20; De Haas, 1950: 523; Stimson, 1969: 30.

Range. — Southeast Asia, eastwards to the Philippines and through Indonesia to Kepulauan Tanimbar.

New material. — Lemo (1); Luwuk (1); without exact locality (1). All leg. W. A. Kaudern.

Mentioned from Bonebone by Foekema & Verhaart (1977).

Subfamily Xenopeltinae

Xenopeltis unicolor Reinwardt, 1827

Xenopeltis unicolor Reinwardt, 1827: 564 (in: Boie, 1827); De Rooij, 1917: 39, De Haas, 1950: 527.

Range. — Sulawesi; southeast Asia; Philippines; Sumatra; Borneo; Java.

New material. — Gurupahi (2); Modajag (1); Kalawara (3); Luwuk (1); without exact locality (1). All leg. W. A. Kaudern.

Dumoga (near river Kuaik, near Matayangan) (1) field no. 918, leg. W. F. Rodenburg. RMNH unnumbered: northern Sulawesi (1).

Parvordo Caenophidia
Suprafamily Acrochordoidea
Family Acrochordidae

Acrochordus granulatus (Schneider, 1799)

Hydrus granulatus Schneider, 1799: 243.
Chersydrus granulatus — De Rooij, 1917: 43.
Acrochordus granulatus granulatus — De Haas, 1950: 529.
Acrochordus granulatus — McDowell, 1979: 79.

Range. — India; Sri Lanka; southeast Asia; eastwards to the Philippines, through Indonesia to the Solomon Islands.

Suprafamily Colubroidea
Family Colubridae
Subfamily Lycodontinae
Tribus Geodipsadini

Psammodynastes pulverulentus (Boie, 1827)

Psammophis pulverulenta Boie, 1827: 547.
Psammodynastes pulverulentus – De Rooij, 1917: 202; De Haas, 1950: 584.

Range. — Malaya; Indo-China; Hainan; Taiwan; Philippines; Kepulauan Bunguran; Borneo to Kepulauan Sula; from Sumatra eastwards to Flores.

New material. — Gurupahi (3); Modajag (1); Kulawi (4); Pinapuan (2); between Biak and Kamumu (1). All leg. W. A. Kaudern.

Tribus Lycodontini

Lycodon aulicus capucinus Boie, 1827

Lycodon capucinus Boie, 1827: 551.
Lycodon aulicus – De Rooij, 1917: 111.
Lycodon aulicus capucinus – De Haas, 1950: 550.

Range. — Sulawesi; southeast Asia; from Sumatra eastwards to Baber; Philippines.

* **Lycodon stormi** Boettger, 1892

Lycodon stormi Boettger, 1892: 48; De Rooij, 1917: 110; De Haas, 1950: 551.

Range. — Sulawesi.

New material. — Gurupahi (1); „Central Celebes" (2); without exact locality (1). All leg. W. A. Kaudern.

Tribus Oligodontini

Oligodon octolineatus (Schneider, 1801)

Elaps octolineatus Schneider, 1801: 229.
Simotes octolineatus – De Rooij, 1917: 123.
Oligodon octolineatus – De Haas, 1950: 556.

Range. — Sulawesi; Malaya peninsula; Sumatra; Borneo; Java.

Oligodon waandersi (Bleeker, 1860)

Rhabdion Waandersi Bleeker, 1860: 83.
Oligodon waandersi – De Rooij, 1917: 133; De Haas, 1950: 558.

Range. — Sulawesi; Kepulauan Sula; Buton.

New material. — Gurupahi (1); „Mongondow" (3); Kantewu (3); Lemo (1); Peana (4). All leg. W. A. Kaudern.

Nature reserve Tongkoko-Batuangus (1), field no. 913, leg. W. F. Rodenburg.

Subfamily Colubrinae
Tribus Colubrini

Elaphe erythrura celebensis (Jan, 1863)

Elaphis melanurum var. *celebensis* Jan, 1863: 61; Jan & Sordelli, 1867: pl. V, fig. 2.
Coluber erythrurus (partim) – De Rooij, 1917: 102.
Elaphe erythrura (partim) – De Haas, 1950: 547.
Elaphe erythrura celebensis – Leviton, 1977: 115.

Range. — Sulawesi.

New material. — Modajag (11); Kantewu (6); Lemo (3); Luwuk (1); Pinapuan (1); without exact locality (2). All leg. W. A. Kaudern.

Three km south of Manado (1), field no. 815; Modoinding (between Kotamobagu and Amurang) (1), field no. 816; near Amurang (1), field no. 842; Kepulauan Banggai (Bonepuso) (1), field no. 900. All leg. W. F. Rodenburg.

RMNH unnumbered: northern Sulawesi (Manado) (1).

Mentioned by Foekema & Verhaart (1977) from Bonebone.

Elaphe flavolineata (Schlegel, 1837)

Coluber flavolineata Schlegel, 1826: 237 (nomen nudum); Schlegel, 1837: 141.
Coluber melanurus Boie, 1827: 536; Schlegel, 1837: 141; De Rooij, 1917: 99.
Elaphe flavolineata – De Haas, 1950, 548.

Range. — Sulawesi; Malayan peninsula; Sumatra; Borneo; Java.

* **Elaphe jansenii** (Bleeker, 1858)

Gonyosoma Jansenii Bleeker, 1858: 242; Müller, 1895a: 829.
„2 Variété brune et noire *Gonyosoma oxycephalum*" Duméril, Bibron & Duméril, 1854: 217.
Coluber janseni – De Rooij, 1917: 102.
Elaphe jansenii – De Haas, 1950: 548.

Range. — Central and northern Sulawesi.

New material. — Modajag (7); Kantewu (2); Lemo (5); without exact locality (1). All leg. W.A. Kaudern.

Three km south of Manado (Winangur) (1), field no. 882, leg. W. F. Rodenburg.

Manado: RMNH 678.

Gonyosoma oxycephalum (Boie, 1827)

Coluber oxycephalus Boie, 1827: 537; De Rooij, 1917: 104.
Elaphe oxycephala – De Haas, 1950: 548; Hemming, 1957: 182.
Gonyosoma oxycephalum – Dowling, 1958: 38.

Range. — Southeast Asia; east- and southwards to the Philippines, Sulawesi and Lombok.

New material. — „North Celebes" (2), leg. W. A. Kaudern.

RMNH unnumbered: northern Sulawesi (2).

Ptyas dipsas (Schlegel, 1837)

Herpetodryas dipsas Schlegel, 1837: 197.
Zamensis dipsas – De Rooij, 1917: 96.
Ptyas dipsas – De Haas, 1950: 546.

Range. — Sulawesi; Halmahera.

New material. — Kulawi (1); Kantewu (2); Lemo (1). All leg. W. A. Kaudern.

Dumoga (slopes Kabila range) (1), field no. 857, leg. W. F. Rodenburg.

Tribus Philothamnini

Chrysopelea paradisi celebensis Mertens, 1968

Chrysopelea paradisi Boie, 1827: 547.
Chrysopelea rhodopleuron – Müller, 1895a: 832.
Chrysopelea ornata – De Rooij, 1917: 212.
Chrysopelea paradisi – De Haas, 1950: 586.
Chrysopelea paradisi celebensis – Mertens, 1968: 206.

Range. — Sulawesi.

New material. — Gurapahi (1); Modajag (3); Kulawi (2). All leg. W. A. Kaudern.

Five km south of Manado (1), field no. 801, leg. W. F. Rodenburg.

RMNH unnumbered: northern Sulawesi (2).

Dendrelaphis caudolineatus terrificus (Peters, 1872)

Dendrophis terrificus Peters, 1872: 583.
Dendrelaphis terrificus — De Rooij, 1917: 69.
Dendrophis caudolineatus terrificus — Meise & Hennig, 1932: 280.
Ahaetulla caudolineata terrifica — De Haas, 1950: 535.
Dendrelaphis caudolineatus terrificus — Hemming, 1958: 263.

Range. — Northern Sulawesi; southern Philippines.

New material. — Nature Reserve Tangkoko-Batuangus (1), field no. 802, leg. W. F. Rodenburg.

RMNH unnumbered: northern Sulawesi (6).

* **Dendrelaphis pictus pictus** (Gmelin, 1789)

Coluber pictus Gmelin, 1789: 1116.
Dendrophis pictus — De Rooij, 1917: 58.
Dendrophis pictus pictus — Meise & Hennig, 1932: 289.
Ahaetulla picta picta — De Haas, 1950: 536.
Dendrelaphis pictus pictus — Hemming, 1958: 279.

Range. — From India through southeast Asia, east- and southwards to the Philippines, the Moluccas and Lombok.

New material. — Kulawi (19) Kantewu (6); Lemo (18); Gurupahi (2); Modajag (1); Montongkad (1); Luwuk (1). All leg. W. A. Kaudern.

Dumoga (Siniung) (1), field no. 930; Dumoga (near Kosinggolan) (1), field no. 942. Both leg. W. F. Rodenburg.

Makassar, RMNH 848. RMNH unnumbered: Manado (4) and northern Sulawesi (19).

Mentioned from Bonebone by Foekema & Verhaart (1977).

Tribus Boigini

Ahaetulla prasina prasina (Boie, 1827)

Dryophis prasinus Boie, 1827: 545; De Rooij, 1917: 206.
Dryophis prasinus prasinus — De Haas, 1950: 585.
Ahaetulla prasina prasina — Hemming, 1958: 263; Leviton, 1967: 81.

Range. — Southeast Asia; from Borneo to the Philippines; from Sumatra eastwards to Sulawesi, Kepulauan Sangihe and Sula, and Sumbawa.

New material. — Gurupahi (2); Modajag (5); Kuku (1); without exact locality (1). All leg. W. A. Kaudern.

Nature Reserve Tangkoko-Batuangus (1), field no. 909, leg. W. F. Rodenburg.

* **Boiga dendrophila gemmicincta** (Duméril, Bibron & Duméril, 1854)

Triglyphodon gemmi-cinctum (partim) Duméril, Bibron & Duméril, 1854: 1091.
Dipsadomorphus dendrophilus – De Rooij, 1917: 197.
Naja celebensis Ahl, 1933: 580.
Boiga dendrophila gemmicincta – Brongersma, 1934: 219.
Boiga dendrophila atra – Kopstein, 1936: 257.
Boiga dendrophila gemmicincta – De Haas, 1950: 581.

Range. — Sulawesi.

New material. — Gurupahi (2); Modajag (2); Kulawi (1); Lemo (1). All leg. W. A. Kaudern.

Makale: RMNH 8381.

Mentioned from Bonebone by Foekema & Verhaart (1977).

* **Boiga irregularis irregularis** (Merrem, 1802)

Coluber irregularis Merrem in Bechstein, 1802: 239.
Triglyphodon flavescens Duméril & Bibron, 1854: 1080.
Dipsadomorphus irregularis – De Rooij, 1917: 201.
Dipsadomorphus flavescens – De Rooij, 1917: 202.
Boiga flavescens – De Haas, 1950: 582.
Boiga irregularis irregularis – De Haas, 1950: 582.

Range. — From Sulawesi eastwards to the Solomon Islands.

New material. — Gurupahi (5); „extreme tip of Minahassa" (1); Modajag (6): Kantewu (1); Lemo (1); Luwuk (1); without exact locality (1). All leg. W.A. Kaudern.

RMNH unnumbered: northern Sulawesi (7).

Boiga multimaculata multimaculata (Boie, 1827)

Dipsas multimaculata Boie, 1827: 549.
Dipsadomorphus multimaculata – De Rooij, 1917: 195.
Boiga multimaculata multimaculata – De Haas, 1950: 583.

Range. — Sulawesi; southeast Asia; Sumatra; Borneo; Java.

Tribus Calamariini

Calamaria acutirostris Boulenger, 1896

Calamaria acutirostris Boulenger, 1896b: 394; De Rooij, 1917: 160; De Haas, 1950: 563; Inger & Marx, 1965: 73.

Range. — Southwestern Sulawesi.

Calamaria apraeocularis Smith, 1927

Calamaria apraeocularis Smith, 1927: 224; Inger & Marx, 1965: 237.

Range. — Southwestern Sulawesi.

Calamaria boesemani Inger & Marx, 1965

Calamaria boesemani Inger & Marx, 1965: 171.

Range. — Extreme eastern Sulawesi (near Luwuk and Biak).

Calamaria brongersmai Inger & Marx, 1965

Calamaria brongersmai Inger & Marx, 1965: 118.

Range. — Central and eastern Sulawesi.

Calamaria curta Boulenger, 1896

Calamaria curta Boulenger, 1896a: 62; De Rooij, 1917: 160; De Haas, 1950: 566; Inger & Marx, 1965: 71.

Range. — Southwestern Sulawesi.

Calamaria muelleri Boulenger, 1896

Calamaria Muelleri Boulenger, 1896b: 394.
Calamaria mulleri – De Rooij, 1917: 161.
Calamaria muelleri – De Haas, 1950: 572; Inger & Marx, 1965: 99.

Range. — Central and southwestern Sulawesi.

Calamaria nuchalis Boulenger, 1896

Calamaria nuchalis Boulenger, 1896a: 62; De Rooij, 1917: 157; De Haas, 1950: 572; Inger & Marx, 1965: 170.

Range. — Central and southwestern Sulawesi.
New material. — Lemo (4), leg W. A. Kaudern.

Calamaria virgulata Boie, 1827

Calamaria virgulata Boie, 1827: 540; De Haas, 1950: 575; Inger & Marx, 1965: 186.
Calamaria gracilis Boulenger, 1896a: 63; De Rooij, 1917: 159; De Haas, 1950: 567.
Calamaria collaris Boulenger, 1897: 225; De Rooij, 1917: 167; De Haas, 1950: 565.

Range. — Sulawesi; Sumatra; Borneo; Java; southern Philippines.

Calamorhabdium acuticeps Ahl, 1933

Calamorhabdium acuticeps Ahl, 1933: 579; De Haas, 1950: 563.

Range. — Northern Sulawesi.

Pseudorabdion longiceps (Cantor, 1847)

Calamaria longiceps Cantor, 1847: 910.
Pseudorhabdium longiceps – De Rooij, 1917: 146.
Pseudorhabdion longiceps – De Haas, 1950: 562.
Pseudorabdion longiceps – Leviton & Brown, 1959: 481.

Range. — Sulawesi; Thailand; Malayan peninsula; Sumatra; Borneo.

Pseudorabdion sarasinorum (Müller, 1895)

Agrophis sarasinorum Müller, 1895a: 827; De Rooij, 1917: 143; De Haas, 1950: 561.
Pseudorabdion sarasinorum – Leviton & Brown, 1959: 474.

Range. — Northern Sulawesi.

New material. — Dumoga (slopes Kabila range) (1), field no. 872, leg. W. F. Rodenburg.

Rabdion forsteni Duméril, Bibron & Duméril, 1854

Rabdion Forsteni Duméril, Bibron & Duméril, 1854: 115.
Rhabdophidium forsteni – De Rooij, 1917: 145; De Haas, 1950: 562.
Rabdion forsteni – Leviton, 1958: 47.

Range. — Central and northern Sulawesi.

New material. — Gurupahi (1); Modajag (3); Kantewu (1); Pinapuan (1). All leg. W. A. Kaudern.

Makobang (D.O.R. from Kotamobagu to Amurang (1), field no. 818, leg. W. F. Rodenburg.

RMNH unnumbered: Manado (5).

Subfamily Natricinae

Tribus Natricini

Amphiesma celebica (Peters & Doria, 1878)

Styporynchus celebicus Peters & Doria, 1878: 386.
Tropidonotus celebicus – De Rooij, 1917: 78.
Natrix celebica – De Haas, 1950: 538.
Amphiesma celebica – Malnate, 1960: 50.

Range. — Sulawesi; Kepulauan Sula.

New material. — Dumoga (southern slopes Mt. Ali) (1), field no. 924, leg. W. F. Rodenburg.

Amphiesma sarasinora (Boulenger, 1896)

Tropidonotus Sarasinorum Boulenger, 1896b: 393.
Tropidonotus sarasinorum – De Rooij, 1917: 79.
Natrix sarasinorum – De Haas, 1950: 543.
Amphiesma sarasinora – Malnate, 1960: 51.

Range. — Sulawesi.

Rhabdophis chrysarga (Schlegel, 1837)

Tropidonotus chrysargos Schlegel, 1837: 312
Tropidonotus chrysargus – De Rooij, 1917: 89.
Rhabdophis chrysargus chrysargus – Bourret, 1936: 100.
Natrix chrysarga chrysarga – De Haas, 1950: 538.
Natrix chrysarga – Leviton, 1959: 396.
Rhabdophis chrysarga – Malnate, 1960: 49.

Range. — Southeast Asia; from Sumatra eastwards to Sulawesi and Flores.

Rhabdophis chrysargoides (Duméril, Bibron & Duméril, 1854)

Amphiesma chrysargum Duméril, Bibron & Duméril, 1854: 739.
Tropidonotus chrysargoides – De Rooij, 1917: 86.
Natrix chrysargoides – De Haas, 1950: 539.
Rhabdophis chrysargoides – Malnate, 1960: 49.

Range. — Sulawesi; Java; Kepulauan Sangihe.

New material. — Lake Darau (1); Gurupahi (2); Modajag (9); Kantewu (2); without exact locality (4). All leg. W. A. Kaudern.

Dumoga valley: Werdhi Agung (1), field no. 811; slopes Kabila range (2) field numbers 845, 941; Nature Reserve Tangkoko-Batuangus (1), field no. 911. All leg. W. F. Rodenburg.

RMNH unnumbered: northern Sulawesi (4).

Sinonatrix trianguligera (Boie, 1827)

Tropidonotus trianguligerus Boie, 1827: 535: De Rooij, 1917: 84.
Natrix trianguligera – De Haas, 1950: 544; Malnate, 1960: 50.
Sinonatrix trianguligera – Rossman & Eberle, 1977: 42.

Range. — Southeast Asia; from Sumatra to Java and Sulawesi.

New material. — Kantewu (1); Lemo (5); Taripa (1). All leg. W.A. Kaudern.

* **Xenochrophis piscator melanzostus** (Gravenhorst, 1807)

Coluber melanzostus Gravenhorst, 1807: 402.
Tropidonotus melanzostus – H. Boie, 1826: 206.
Tropidonotus melanorostis Schlegel, 1826: 236.
Tropidonotus Melanozostus F. Boie, 1827: 535.
Tropidonotus piscator – De Rooij, 1917: 75.
Natrix piscator melanzostus – De Haas, 1950: 542.
Fowlea piscator – Malnate, 1960: 48.
Xenochrophis piscator – Malnate & Minton, 1965: 22.

Range. — Sulawesi (?); Sumatra; Java; Borneo (?).

Tribus Homalopsinii

Cerberus rynchops rynchops (Schneider, 1799)

Hydrus rynchops (partim) Schneider, 1799: 246.
Cerberus rynchops – De Rooij, 1917: 187.
Cerberus rynchops rynchops – De Haas, 1950: 577; Gyi, 1970: 160.

Range. — From India, via Malaysia, Indonesia and the Philippines to the Palau Islands.

New material. — Kepulauan Banggai (Luksagu) (1), field no. 884, leg. W. F. Rodenburg.

RMNH unnumbered: northern Sulawesi (1).

Enhydris enhydris (Schneider, 1799)

Hydrus enhydris Schneider, 1799: 245.
Hypsirhina enhydris – De Rooij, 1917: 181.
Enhydris enhydris enhydris – Bourret, 1936: 281; De Haas, 1950: 576.
Enhydris enhydris – Gyi, 1970: 90.

Range. — Sulawesi; southeast Asia; Sumatra; Java; Borneo.

Enhydris matannensis (Boulenger, 1897)

Hypsirhina matannensis Boulenger, 1897: 225; De Rooij, 1917: 182.
Enhydris matannensis – De Haas, 1950: 576; Gyi, 1970: 112.

Range and new material. — Type locality: Lake Matanna, Central Sulawesi. Second known specimen mentioned in Iskander (1979), from fish pond in Raha, Muna Island, southeast of Sulawesi.

Enhydris plumbea (Boie, 1827)

Homalopsis plumbea Boie, 1827: 560.
Hypsirhina plumbea – De Rooij, 1917: 181.
Enhydris plumbea – De Haas, 1950: 576; Gyi, 1970: 82.

Range. — Southeast Asia; Hainan; Taiwan; Borneo; Sumatra to Bali and Sulawesi.

New material. — RMNH unnumbered: Sulawesi (4).

Mentioned from Bonebone by Foekema & Verhaart (1977).

Homalopsis buccata (Linnaeus, 1758)

Coluber buccata Linnaeus, 1758: 217.
Homalopsis buccata – De Rooij, 1917: 186; De Haas, 1950: 577; Gyi, 1970: 136.

Range. — From India, via southeast Asia to Borneo, Sumatra, Java and Sulawesi.

Family Elapidae
Subfamily Elapinae

Bungarus candidus (Linnaeus, 1758)

Coluber candidus Linnaeus, 1758: 223.
Bungarus candidus – De Rooij, 1917: 244; De Haas, 1950: 597.

Range. — From southeast Asia to Bali and Sulawesi.

Maticora intestinalis nigrotaeniata (Peters, 1871)

Adeniophis nigrotaeniatus Peters, 1871: 578.
Doliophis intestinalis – De Rooij, 1917: 253.
Maticora intestinalis intestinalis – De Haas, 1950: 601.
Maticora intestinalis nigroteaniata – Leviton, 1963b: 529.

Range. — Sulawesi; Borneo.

New material. — RMNH 1439: Makassar (1).

Ophiophagus hannah (Cantor, 1836)

Hamadryas hannah Cantor, 1836: 187.
Naja bungarus De Rooij, 1917: 249.
Naja hannah – De Haas, 1950: 598.
Ophiophagus hannah – Mertens, 1962: 190; China, 1964: 211.

Range. — India, via southeast Asia to Borneo, Philippines, Java, Sumatra, Bali and Sulawesi.

New material. — Kepulauan Banggai (1), leg. W. A. Kaudern.

Naja naja sputatrix (Boie, 1827)

Naja sputatrix Boie, 1827: 557.
Naja tripudians sputatrix – De Rooij, 1917: 248.
Naja naja sputatrix – De Haas, 1950: 599.

Range. — Southeast Asia; from Sumatra to Komodo, Sulawesi and Borneo.

Subfamily Laticaudinae

Laticauda colubrina (Schneider, 1799)

Hydrus colubrinus Schneider, 1799: 238.
Platurus colubrinus – De Rooij, 1917: 217.
Laticauda colubrina – De Haas, 1950: 587.

Range. — From India via Indonesia to New Guinea and the Pacific Islands.

Laticauda laticaudata (Linneaus, 1758)

Coluber laticaudatus Linneaus, 1758: 222 (partim).
Platurus laticaudatus – De Rooij, 1917: 217.
Laticauda laticaudata – De Haas, 1950: 587.

Range. — From the Bay of Bengal to the Riu Kius, Tonga Island and from China via Indonesia to New Guinea, Australia and Tasmania (according to unpublished manuscript of Mr. J. C. Enderman in the RMNH).

New material. — RMNH 6274: Manado (2).

Subfamily Hydrophiinae

* **Aipysurus fuscus** (Tschudi, 1837)

Stephanohydra fusca Tschudi, 1837: 335.
Aipysurus fuscus – Smith, 1926: 16.
Aepysurus fuscus – De Haas, 1950: 589.

Range. — Sulawesi; Ashmore Reef, northwest of Western Australia; Banda Sea (?).

Hydrophis fasciatus atriceps Günther, 1864

Hydrophis atriceps Günther, 1864: 371.
Hydrophis fasciatus – De Rooij, 1917: 230.
Hydrophis fasciatus atriceps Smith, 1926: 97; De Haas, 1950: 592.

Range. — Southeast Asia; Indonesia; Philippines.

Hydrophis melanosoma Günther, 1864

Hydrophis melanosoma Günther, 1864: 367: Smith, 1926: 51; De Haas, 1950: 593.
Hydrophis floweri De Rooij, 1917: 229.

Range. — Sulawesi; Malaysia; Sumatra; Borneo.

Hydrophis spiralis (Shaw, 1802)

Hydrus Spiralis Shaw, 1802: 564.
Hydrophis spiralis – De Rooij, 1917: 234; Smith, 1926: 48; De Haas, 1950: 594.

Range. — From Persian Gulf via Java, Borneo and Sulawesi to the Philippines and Taiwan.

Lapemis hardwickii Gray, 1834

Lapemis Hardwickii Gray, 1834: pl. LXXXVII, fig. 2 (not seen); ibid, 1842: 60.
Enhydris hardwickei – De Rooij, 1917: 240.
Lapemis hardwickii – Smith, 1926: 108; De Haas, 1950: 595.

Range. — From India, via Indonesia, Philippines and Taiwan to south Japan.

Pelamis platurus (Linnaeus, 1766)

Anguis platura Linnaeus, 1766: 391.
Hydrus platurus – De Rooij, 1917: 224.
Pelamis platurus – Smith, 1926: 116; De Haas, 1950: 596.

Range. — Widely distributed: from the east coast of Africa to the west coast of America.

Family Viperidae
Subfamily Crotalinae

Trimeresurus wagleri (Schlegel, 1837)

Trigonocephalus Wagleri Schlegel, 1837: 542.
Lachesis wagleri – De Rooij, 1917: 286.
Trimeresurus wagleri wagleri – De Haas, 1950: 611.
Trimeresurus wagleri – Leviton, 1964b: 265.

Range. — Sulawesi; southeast Asia; Sumatra; Borneo; Philippines; Kepulauan Sangihe.

New material. — Gurupahi (2); Modajag (9). All leg. W. A. Kaudern.

Dumoga valley: Kinomaligan (1), field no. 812; near Matayangan (1), field no. 917. Both leg. W. F. Rodenburg.

TAXONOMIC NOTES

In some instances changes might not be clear at first glance from the synonymy. These are accounted for in this section. For several species general remarks are added. Also species incorrectly reported for Sulawesi are mentioned here.

Rhamphotyphlops braminus (Daudin)

The genus name *Typhlina* was recently rejected in favour of *Rhamphotyphlops* in Opinion 1207: Melville (1982).

Typhlops conradi Peters

Ever since Boulenger (1897: 217) the possibility has been put forward that the single specimen is identical with a *T. ater* in which the division of the preocular is overlooked. According to McDowell (1974) the suggestion of synonymy seems unlikely, since the tail is very short and broad, the preocular overlaps the upper end of the second supralabial and the fourth labial is conspicuously larger than the third.

Liasis boa (Schlegel)

In De Jong (1930: 118) reference is made to a specimen of *Nordoa boa* (err. typogr.) in the Museum at Buitenzorg with locality "Manado, Selebes", and the author allready expressed doubt as to the correctness of this record, and I concur with him.

Acrochordus javanicus Hornstedt

This species can be expected to occur on Sulawesi, though no locality data are available: its range overlaps with that of *A. granulatus*; northwards to south-eastern Asia and southwards to northern Australia (Cogger, 1979).

A. javanicus can be distinguished from *A. granulatus* by the number of midbody scale rows (>110) and the absence of a mid-ventral fold.

Lycodon stormi Boettger

In the literature available no mention is made of the juvenile colouration and the transition into the adult pattern. In the four available specimens of, respectively, 25, 48, 62 and 71 cm long, the white annuli on a brown coloured snake (in preservative) tend to disappear with increasing length and thus apparently with age, commencing dorsally. Only the smallest specimen has a ring around the neck, it has 20 rings on the body and ten on the tail. The 48 cm specimen has seven rings on the anterior dorsum and segments of 21 on the ventral surface, ten vague ones around the tail. In the 62 cm specimen the anterior dorsal rings have decreased to five and these are disintegrating, ventrally there are 22 rings and on the mutilated tail seven; in the longest *L. stormi* the rings dorsally are no longer distinguishable and the 20 bands across the ventral part of the body and especially the seven on the tail are hardly distinct. This last condition represents the situation as in the 72 + 13,5 cm specimen reported on by Boulenger (1897): "slate-colour or dark brown, with whitish annuli speckled with black, the white most marked on the lower surface; 23 annuli on the body."

Elaphe jansenii Bleeker (including remarks on *E. enganensis* Vinciguerra)

Dowling (1958) without any explanation included this species and *Elaphe enganensis* (Vinciguerra, 1892) in *Gonyosoma oxycephalum*. Though an overall resemblance exists, comparison of literature data (Boulenger, 1894: 56, 63), De Rooij (1917), the original descriptions and study of the type material of *E. enganensis* and *E. jansenii*, RMNH material and specimens in the Kaudern collection, showed consistent differences between the three species.

The conspicuously projecting elongate muzzle of *G. oxycephalum* is nearly absent in *E. jansenii* where it is obtuse and rather shorter. *E. jansenii* has an olive or yellowish colour of the anterior third part of the body, then black cross bars appear on the lateral and dorsal surfaces, and the pattern gradually merges into a uniform black posteriorly. Sometimes a broad black lateral band is present. Tail completely black. This pattern is recognisable in preserved as well as live specimens, though the latter are brighter yellow and violet black. Bleeker (1858) states that the anterior third part of the body is of an orange-green. *G. oxycephalum*, instead, has a bright green or blue-green colouration, sometimes with a brown tail, very few being brown throughout. Separating characters in pholidosis are mainly the fifth, sixth and seventh supralabial entering the eye in *E. jansenii*, instead of the fifth and sixth or sixth and seventh in *G. oxycephalum* and 23 (25) scale rows compared to 23-27. A fine plate of *E. jansenii* can be found in Boulenger (1894: pl. I fig. 2) and additional descriptive details in Müller (1895a).

Brongersma (1934) was in favour of a subspecific status of *Elaphe enganensis* Vinciguerra (*Elaphe subradiata enganensis*), to which Kopstein (1937) was opposed because of a striking difference in pattern and colouration of juvenile *E. enganensis* and *E. subradiata*. After examination of the two syntypes I have reached the tentative conclusion that *enganensis* is not a subspecies of *E. subradiata* (Schlegel), a.o. because of the absence of a subocular scale (characteristically present in *subradiata*) in those types. Kopstein's (1937) observations reinforce my conclusion. Therefore, for the time being *enganensis* is still considered a valid species. Synonymisation with *G. oxycephalum* or with *E. jansenii*, however, is completely unjustified.

Duméril et al. (1854: 217) mentioned a brown and black variety at the end of their description of *Gonyosoma oxycephalum*. This was known to Bleeker (1858: 242) when he reported on his new species *Gonyosoma Jansenii*. He dismissed their description of this variety as not applicable to his specimen. I am not of the same opinion and surmise that their brown and black specimens, only collected in Sulawesi, in fact belong to *E. jansenii*, though I have not yet been able to verify this.

The doubtful status of the subspecies described by Werner (1926) as *Coluber janseni elegans* from Thailand ("Siam"), which he regarded as a colour morph, has not been taken into consideration.

Dendrelaphis p. pictus (Gmelin)

The Kaudern collection contains a completely black (in ethanol) specimen: "Central Celebes, IX-1918, W. Kaudern". It is not clear whether this is an artifact of preservation or a genuine case of melanism.

Boiga dendrophila gemmicincta (Duméril, Bibron & Duméril, 1854)

Until further collecting has been done, it does not seem advisable to recognise the subspecies *B. d. atra*, differing from *B. d. gemmicincta* by being completely black dorsally. Moreover, as Mertens (1961) has pointed out, *B. d. celebensis* would have priority here, since *Naja celebensis* (from the Mekongga mountains) proved to be a black specimen of *B. dendrophila*.

In Foekema & Verhaart (1977) two black snakes found near Bonebone are depicted in fig. 30 and fig. 33, the captions and text – in which a third is mentioned – suggesting these to be *B. dendrophila*. In the immediate surroundings a normally coloured specimen was observed. The terra typica of Kopstein's (1936) *B. d. atra* is situated nearby (Ba Ebunta, Laowu). Two other localities mentioned by him are Palapo to the southwest, and Kolaka southeast of the Mekongga range.

Boiga flavescens (Duméril & Bibron, 1854)

B. flavescens is here synonymized with *B. i. irregularis* (Merrem, 1802). The characters used thusfar to separate *B. flavescens* from *B. i. irregularis* are, apart from the colour, the former species having preoculars not extending to the upper surface of the head and the possesion of three instead of two postoculars: Duméril, Bibron & Duméril (1854: 1081), later repeated in e.g. Boulenger (1897: 226) and De Rooij (1917: 202). These last conditions are also met with in *B. i. irregularis*. Examination of the type specimen (MNHP 3021, "Macassar, Celebes") and the only other known specimen (MNHP 3020) said to have been collected in "Australie" by "J. Verriaux" (or J. Verreaux: J. Lescure, in litt.) did not reveal other distinctive characters. Since the skull of the type has been removed and could not be traced, the relative position of the preocular cannot be definitively confirmed, but in the second specimen it does reach the upper surface of the head. The type has three postoculars on both sides of the head. The lower one on the left, however, being much smaller and wedged in between the fifth an sixth supralabial. All other data prove to fall well within the range of *B. irregularis*. Therefore it is assumed that *B. flavescens* is identical with *B. irregularis*. Even in the original description of *flavescens* a close resemblance is already mentioned and the three postoculars are suspected to be an individual aberration and reference is made to Schlegel's (1837: 273) remark in his description of *Dipsas irregularis* of a uniform brown yellow coloured specimen, almost certainly the same one, collected by Lesson, on which Duméril, Bibron & Duméril based their *Triglyphodon flavescens*. At present the type is brownish yellow with extremely faint traces of transverse bands or angular spots, has 19 scale rows with somewhat enlarged vertebrals, 259 ventrals, 116 subcaudals in two rows and one terminal scale, anal entire, eight left supralabials (third to fifth entering the eye), eight (or nine?: damaged) right supralabials (third to sixth entering the eye) and 11 infralabials (first five touching anterior chinshields) on both sides. The snout-vent length is ca. 880 mm, the tail ca. 230 mm. The conditions in MNHP 3820 are similar. It has 19 scale rows with somewhat enlarged vertebrals, 229 ventrals, 103 subcaudals, and one terminal scale, anal entire, eight supralabials (fourth and fifth entering the eye) on both sides and 11 infralabials (first four touching anterior chinshields) on both sides. Snout-vent length is ca. 330 mm, tail ca. 80 mm. Its colouration is beige, yellowish brown, with much clearer markings of dark transverse bands or angular spots on the dorsal part of the body and tail and a dark streak behind the eye. Supralabials dark edged. It is unmistakenly a *B. i. irregularis*.

There are no indications that *flavescens* could be considered a subspecies of *irregularis*, because there are not sufficient morphological characters distinguishing it from this species. Moreover, the locality data do not permit such a conclusion. Therefore *flavescens* is judged a simple colour morph, occuring throughout Sulawesi, of *B. irregularis*.

Xenochropis piscator melanzostus (Gravenhorst)

De Haas (1950: 542) considered the name *melanzostus* in Gravenhorst (1807: 420 [err. typogr. viz. on p. 402]) a nomen nudum. This is clearly not the case, since a pertinent description of this snake covering more than half a page is given. The subsequent alterations of the spelling into *melanorostis* Schlegel (1826) and *Melanozostus* Boie (1827) are unjustified emendations. The incorrect mentioning of nomen nudem behind Gravenhorst's citation in De Haas (1950: 542) is probably a lapse.

De Haas (1950) included both Sulawesi and Borneo in its range "on authority of De Rooij". Only one specimen in the RMNH, collected by Peitsch, is from Sulawesi (RMNH 1036: "Makassar"). Removal from the list seems as yet unjustified.

Aipysurus fuscus (Tschudi)

There seems to exist some doubt as to the correctness of the type-locality being Sulawesi (e.g. Cogger, 1979: (414). Its range is frequently cited as Ashmore Reef. Tschudi (1837: 331) specifically cited "Celebes" and later on (l.c.: 335) "Asia". Dunson (1975: 80) concluded that the type-specimen is from Sulawesi, but all the other records are from the Ashmore Reef complex and he considered its occurence in the Banda Sea as doubtful.¹)

DOUBTFUL RECORDS

The occurrence of the following species is rather doubtful and these are therefore not included in the checklist.

Boiga drapiezii (Boie)

Mentioned from Manado by Bleeker (1857: 232) as "*Triglyphodon Drapiezii* DB", but this record was never confirmed.

Calamaria linnaei Boie

The specimen from Sulawesi was collected by A.B. Meyer. Inger & Marx (1965: 207) regarded the locality Manado of this common Javanese snake as very doubtful. Meyer's "Manado" collection also included three other common Javanese snakers no one else has encountered in Sulawesi: *Calamaria modesta* Duméril & Bibron, *"Natrix" subminiata* (Schlegel) and *"Natrix" vittata* (Linneaus).

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¹) The same conclusion was reached by Mr. J. C. Enderman (1968) in his unpublished manuscript on sea-snakes.

Calamaria lumbricoidea Boie

The species' range includes Sulawesi in Boulenger (1894: 333), De Rooij (1917: 153) and De Haas (1950: 570), but not in Inger & Marx (1965). Bleeker (1857: 232) recorded the species from Manado. However, "many of his localities of reptiles need further investigation" (De Haas, 1950: 544) (see also under *B. drapiezii*). It is unknown which specimen De Rooij (1917) referred to, though RMNH 40 is labeled "*Calamaria lumbricoidea* Boie, Celebes, Menado", and so most probably is the one she has seen. R. F. Inger identified and relabeled this specimen as *C. virgulata* and I agree with his identification. The species *C. lumbricoidea* is therefore omitted.

Calamaria modesta Duméril & Bibron

See under *C. linnaei*

Macropistodon rhodomelas (Boie)

According to De Rooij (1917: 92) there should be a specimen in the Raffles Museum, Singapore, purportedly collected in Sulawesi. This was never confirmed, nor were additional specimens reported.

Rhabdophis subminiata subminiata (Schlegel)

De Haas (1950: 544) already stated that the records from Ternate and Sulawesi are old and had never been confirmed.

Xenochrophis vittata (Linneaus)

The specimens in the British Museum referred to by Boulenger (1897: 196) and De Rooij (1917: 89) are most probably those De Haas (1950: 544) mentioned as having been collected by A. B. Meyer (see under *Calamaria linnaei*): a Javanese origin is assumed.

KEY TO THE SPECIES

The key proposed here employs external characters only. Scales or scale rows are dorsal scales, counted at midbody, unless stated otherwise. The key provided for *Calamaria* by Inger & Marx (1965) was found to be most satisfactory and therefore has been incorporated in an only slightly adapted form. Terminology conform to Peters (1964).

1. Eye concealed beneath head shields that do not conform to the outlines of the eye, not transparent; mandible toothless 2

— Scute covering the eye conforming closely to the outline of the eye, transparent; mandible toothed 4

2. One or two suboculars; preocular not in contact with labials .... *Typhlops ater*

— Suboculars absent; preocular in contact with labials 3

3. 20 scales around the body; preocular nearly as large as ocular .... *Rhamphotyphlops braminus*

— 18 scales around the body; preocular much larger than the ocular .... *Typhlops conradi*

4. Top of head covered with small, strongly keeled scales; loreal pit present .... *Trimeresurus wagleri*

— Top of head covered with shields (or with non-keeled granular scales); loreal pit absent 5

5. A pair of spur-like protrusions flanking the cloaca 6

— Spur-like protrusions flanking the cloaca absent 10

6. Deep (sensory) pits in the labials; 60 or more subcaudals 7

— No deep pits in labials; subcaudals 50 or less 8

7. First four upper labials pitted; seventh or eighth labial entering the eye .... *Python reticulatus*

— First two upper labials pitted; labials separated from the eye by suboculars .... *Python molurus bivittatus*

8. Anal entire; scales strongly keeled .... *Candoia carinata*

— Anal divided; scales smooth 9

9. Ventrals 224-254, subcaudals 8-10 (anal region blackish); maxillary teeth 10 .... *Cylindrophis melanotus*

— Ventrals 215 or less, subcaudals 5-7 (anal region red, white in preservative); maxillary teeth 11-13 .... *Cylindrophis r. rufus*

10. Large azygous occipital shield in contact with the frontal; premaxillary toothed .... *Xenopeltis unicolor*

— No such occipital; premaxillary toothless 11

11. Maxillary teeth subequal (or posterior ones enlarged); loreal absent or present 12

— Anterior maxillary teeth grooved or perforated, enlarged; loreal absent (sometimes present in *Lapemis hardwicki*) 53

12. Posterior maxillary teeth normal or enlarged, not grooved 13

— Posterior maxillary teeth enlarged and grooved 43

13. Small granular juxtaposed scales in 100 or more rows .... *Acrochordus granulatus*

— Scales imbricate, less than 27 rows 14
14. Loreal present (rarely absent in *Oligodon waandersi*); internasals distinct 15
— Loreal absent; internasals and prefrontals fused 34
15. Head distinct from neck 16
— Head not distinct from neck 30
16. Pupil vertically elliptic; anterior maxillary diastema (posterior to 3-6 anterior teeth) 17
— Pupil round; maxillary teeth continuous or with posterior diastema (anterior to 3-2 posterior teeth) 18
17. Scales in 19 rows; subcaudals single .... *Lycodon stormi*
— Scales in 17 rows; subcaudals double .... *Lycodon aulicus capucinus*
18. Scales oblique, at least anteriorly; anal divided 19
— Scales in longitudinal series; anal divided or entire 20
19. Scales in 13 rows, subequal .... *Dendrelaphis caudolineatus terrificus*
— Scales in 15 rows, vertebrals and outer row enlarged .... *Dendrelaphis p. pictus*
20. Anterior mandibular teeth largest; maxillary teeth subequal 21
— Mandibular teeth subequal; maxillary teeth enlarged posteriorly 24
21. Scales with elongate apical pits; two labials entering the eye .... *Gonyosoma oxycephalum*
— Scales with faint rounded apical pits; three labials entering the eye ... 22
22. Scales in 23-25 rows; anal divided .... *Elaphe jansenii*
— Scales in 19-21 rows; anal entire 23
23. Scales at midbody in 21 rows, 23 on the neck; black chevron-shaped on the neck. .... *Elaphe erythrura celebensis*
— Scales at midbody in 19 rows, 21 on the neck; without black chevron-shaped marking on the neck .... *Elaphe flavolineata*
24. Scales smooth, in 13 rows; anal entire .... *Ptyas dipsas*
— Scales keeled, in 15 or more rows; anal divided 25
25. Scales in 15 rows 26
— Scales in 19 or 21 rows 27
26. Maxillary teeth 20; anterior scale rows smooth or feebly keeled; internasals shorter than the prefrontals .... *Amphiesma celebica*
— Maxillary teeth 25; scale rows strongly keeled; internasals as long as the prefrontals .... *Amphiesma sarasinora*
27. Scales in 21 rows .... *Rhabdophis chrysargoides*
— Scales in 19 rows 28
28. Last two maxillary teeth strongly enlarged, preceded by a diastema; nostrils lateral .... *Rhabdophis chrysarga*

— Maxillary teeth in continuous series, teeth gradually enlarged posteriorly; nostrils dorsolateral 29
29. Scales strongly keeled, outer row feebly or smooth, internasals trapezoid (broadly truncate in front) .... *Sinonatrix trianguligera*
— Scales keeled, outer two or three rows smooth; internasals narrowed in front .... *Xenochrophis piscator melanzostus*
30. Posterior maxillary teeth enlarged, scales in 15 or 17 rows 31
— Maxillary teeth subequal; scales in 15 rows 32
31. Scales in 17 rows; anal entire .... *Oligodon octolineatus*
— Scales in 15 rows; anal divided .... *Oligodon waandersi*
32. Nostril in between anterior and posterior nasal .... *Pseudorabdion sarasinorum*
— Nostril in a single nasal 33
33. Preocular large, reaching or nearly reaching the nasal .. *Rabdion forsteni*
— Preocular small or absent .... *Pseudorabdion longiceps*
34. Nostril in between anterior and posterior nasal; scales in 15 rows .... *Calamorhabdium acuticeps*
— Nostril in a single nasal; scales in 13 rows 35
35. Preocular absent .... *Calamaria apraeocularis*
— Preocular present 36
36. Mental not touching anterior chin shields 37
— Mental touching anterior chin shields 39
37. Paraparietal surrounded by five scales and shields .... *Calamaria brongersmai*
— Paraparietal surrounded by six scales and shields 38
38. Eye almost 1.5 times eye-mouth distance .... *Calamaria boesemani*
— Eye, at its largest, slightly greater than eye-mouth distance .... *Calamaria virgulata*
39. First gular touching anterior chin shields .... *Calamaria acutirostris*
— First gular not touching anterior chin shields 40
40. Paraparietal surrounded by five scales and shields .. *Calamaria muelleri*
— Paraparietal surrounded by six scales and shields 41
41. Tail thick, tapering abruptly at end .... *Calamaria virgulata*
— Tail tapering gradually from base 42
42. Ventrals yellow, immaculate except for dark lateral tips .... *Calamaria nuchalis*
— Ventrals dark, yellowish on posterior edges only .... *Calamaria curta*
43. Nostrils superior, valvular; aquatic species 44
— Nostrils lateral; terrestrial or arboreal species 48
44. Scales keeled; parietals entire or fragmented 45

— Scales smooth; parietals entire 46

45. Scales in 37-47 rows; parietals well developed .... *Homalopsis buccata*

— Scales in 23 or 25 (27) rows; parietals broken up into scales .... *Cerberus r. rynchops*

46. Scales in 19 rows .... *Enhydris plumbea*

— Scales in 21 (19-23) rows 47

47. Loreal in contact with the internasal; anterior chin shields smaller than or same size as posterior ones, and in contact with the first three or four lower labials .... *Enhydris e. enhydris*

— Loreal not in contact with the internasal; anterior chin shields larger than posterior ones, and in contact with the first four or five lower labials .... *Enhydris matannensis*

48. Pupil horizontal; scales in 15 rows .... *Ahaetulla p. prasina*

— Pupil round, vertical or vertically elliptic; scales in 17-23 rows 49

49. Pupil round; scales in 17 (rarely 15) rows .... *Chrysopelea paradisi celebensis*

— Pupil vertical or vertically elliptical; scales in 17-23 rows 50

50. Body round in cross section; vertebrals not enlarged; apical pits absent .... *Psammodynastes pulverulentus*

— Body compressed in cross section; vertebral scales enlarged; scales with apical pits 51

51. Anterior palatine teeth strongly enlarged; a dark streak behind the eye .... *Boiga i. irregularis*

— Anterior palatine teeth not or hardly enlarged; no dark streak behind the eye 52

52. Scales in 19 (sometimes 17) rows .... *Boiga m. multimaculata*

— Scales in 21 (sometimes 23) rows .... *Boiga dendrophila gemmicincta*

53. Tail strongly compressed laterally; marine species 54

— Tail round in cross section; terrestrial species 61

54. Ventrals large, one third to over half the body width 55

— Ventrals small, not more than one quarter of the body width 57

55. Nostrils superior; nasals in contact .... *Aipysurus fuscus*

— Nostrils lateral; nasals separated by internasals 56

56. Scales in 21-25 rows; upper lip yellow .... *Laticauda colubrina*

— Scales in 19 rows; upper lip brown .... *Laticauda laticaudata*

57. Scales juxtaposed 58

— Scales imbricate, at least on the anterior part of the body 59

58. Scales in 45-47 rows, of subequal size .... *Pelamis platurus*

— Scales in 25-43 rows, outer three or four rows enlarged .... *Lapemis hardwickii*

59. Scales in 33-35 rows ..... *Hydrophis spiralis*
— Scales in 37-48 rows 60
60. Scales in 37 rows (27 anteriorly); 298-321 ventrals ..... *Hydrophis melanosoma*
— Scales in 40-48 rows (25-31 anteriorly); 345-500 ventrals ..... *Hydrophis fasciatus atriceps*
61. Vertebrals much enlarged ..... *Bungarus candidus*
— Vertebrals not enlarged 62
62. Scales in 13 rows; internasal not bordering the nostril; six upper labials ..... *Maticora intestinalis nigrotaeniata*
— Scales in 15-25 rows; internasal bordering the nostril; seven upper labials 63
63. Scales in 15 rows, 19-21 anteriorly; subcaudals 80-120; a pair of large occipital shields present ..... *Ophiophagus hannah*
— Scales in 19-21 rows, 25 anteriorly; subcaudals 42-75; a pair of large occipital shields absent ..... *Naja naja sputatrix*

BIOGEOGRAPHY

Sulawesi occupies an intermediate position in many respects, which is biogeographically reflected in the various zoogeographical boundary lines around this area, often referred to as Wallacea (e.g. Rensch, 1936; Müller, 1974), and largely coinciding with the 200 m isobath boundaries of the Sunda and Sahul shelf. Wallacea stretches from the Lesser Sunda Islands, Sulawesi and Lombok to the Moluccas and the Kai and Aru Islands, and sometimes even the Philippines are included. A recent assessment of these boundaries can be found in Simpson (1977).

Geological history of the Indo-Australian region – as recently summarized in Whitmore (1981), and here sketched using some additional information from Sarasin & Sarasin (1901), though omitting most of their landbridges, and Umbgrove (1949) – indicates that Sulawesi is situated in an area that has been unstable ever since the connections with the surrounding landmasses thought to have existed in the Late Cretaceous, broke up. A major orogenic phase occurred between the Late Cretaceous and the end of the Eocene. In the Miocene renewed subduction must have taken place further north to accommodate continuing drift; orogenesis occurred with the emergence of land in the Philippines (where some volcanoes may have been above sea level since Late Jura (Audley-Charles, 1981)), Sulawesi (Minahassa and in the south) as well as in northern Borneo and parts of New Guinea, the Bismarck Islands and possibly in the Solomons. An extensive line of islands may have come into existence in Middle Miocene, joining Asia through Sulawesi and New Guinea to Australia and thereby forming a first possibility of exchange between the Gondwanian and Laurasian parts of the Indo-Australian archipelago. In the Late Miocene the two Banda arcs emerged, the outer one (Andamans, Nias, Sumba, Timor, Tanimbar, Kai, South Moluccas) rose as a result of buoyancy of parts of the continental margin of the underthrusted Australian crust in the collision zone. This was preceded in the Early Miocene by volcanic processes giving rise to the inner Banda arc (Sumatra, Java, northern Lesser Sunda Islands, via Flores and Wetar to the Banda Islands), which at that time consisted of no more than a chain of small islands. Terrestrial sediments and volcanic rocks are known from western Sulawesi at least from the Late Miocene onward. The outer and inner chain were further uplifted in the Pliocene/Pleistocene, resulting roughly in the present form of the Sunda shelf. The geomorphology of the Philippines and Sulawesi has not changed significantly since then either. A potential migration pathway was thus created from the Early Pliocene between Laurasia and Gondwanaland, and by the Middle Pliocene there was dry land from Java to Timor. In an updated geological history of eastern Indonesia, studying plate tectonics, Audley-Charles et al. (1972) considered the eastern and southeastern peninsulas of Sulawesi including Butung as part of the outer Banda arc (marking the margin of the Australian continent at least from the early Permian till the early Cretaceous) and the northern and southwestern arms as part of Southeast Asia. This implies that eastern Sulawesi has since been detached from Australia and has undergone a 90° anticlockwise rotation resulting from westward pressure from the Pacific plate during the Neogene, and a remarkable northward movement of the northwestern part. A Pliocene junction of the Gondwanian and Laurasian arms of Sulawesi is postulated by orogenesis. However, this view is not yet generally accepted.

The first land-connection between Australia and southeast Asia was provided by the Middle Miocene collision of the "Sula Peninsula" (parts are Banggai, Sula islands, Obi, Misool), this in fact being a detached slice of Australia/New Guinea (Audley-Charles, 1981). According to the same author, the earliest migration route for land animals between Sulawesi and eastern Australia could have been established by latest Miocene or early Pliocene. By Late Pliocene it was "almost as well established as at present", though then the available area above sea must have been considerably less, and biological evidence in favour of this connection is not exactly abundant.

The Pleistocene glaciations resulted in drastic sea level fluctuations from 100 m above to 200 m below the present level. However, during this time, Sulawesi probably was not connected above sea level to the Sunda shelf and never to the Sahul shelf (on which New Guinea and the Aru Islands are connected with Australia), and remained an island, surrounded locally by sea depths down to 2000 m and by open stretches of sea of 250 km wide. Nevertheless some Sundaic land connections are mentioned in the literature. Audley-Charles (1981) suggested that western Sulawesi may have been intermittently linked with Borneo by land during the Cenozoic and particularly during part of the Quarternary, although he is contradicted by Cranbrook (1981), especially with regard to freshwater fishes. Groves (1976) tentatively discussed a brief land bridge in the Late Tertiairy between Java and Sulawesi, invoking Van Bemmelen's (1949) "Pulau Laut Centre of Diastrophism". This route was already mentioned in Sarasin & Sarasin (1901) as the Java bridge via the Kangean Islands, later advocated by e.g. Mertens (1930) as a mode of entry for large mammals. The land bridge – if it ever existed as such – could of course have been a route for other animals as well.

The cause of most geological events in Wallacea is assumed to be a northwards drift of Australia starting in the Palaeocene (McElhinny, 1970; Audley-Charles et al., 1981), resulting in plate collisions and subsequent orogenesis and a series of northward dipping subduction zones. Relative and absolute distances between the various areas thus changed considerably (Smith & Hallam, 1970).

The much warmer tropical climate of the Early Tertiairy, with tropical zones extending far to the North, is most commonly believed to have changed gradually and the cooling to have culminated in periods of glaciation in the Pleistocene (Frakes, 1979). These glacial periods, aside from the geological changes, shaped and at the same time levelled barriers, according to the ecotype of the organism. Whitmore (1981) assumed that there is enough evidence to accept a continuously fluctuating climate. The drop in sea level in the glacial periods resulted in a drier and more seasonal climate than today, with greater circadian differences. Sulawesi appears to be one of the areas that was most affected by these climatic fluctuations (Whitmore, 1981).

GEOGRAPHICAL RELATIONSHIPS OF THE SNAKE FAUNA

In table 1 the occurrence of species common to Sulawesi and the surrounding landmasses is summarized, using Haile (1958) and Smith (1931) for Borneo, Leviton (1959, 1962, 1963a, 1963b, 1963c, 1964a, 1964b, 1965, 1967, 1968a, 1968b, 1977), Leviton & Brown (1959) and Taylor (1922) for the Philippines, De Haas (1950) for Sumatra, Java and New Guinea, and Tweedie (1953) for the Malay peninsula, and Smith (1943) and Taylor (1965) for adjacent southeast Asia, supplemented by Hahn (1980), Inger & Marx (1965),

Species	E	M	J	B	P	NG
Rhamphotyphlops braminus		1, 2	1, 2	1, 2	1, 2	1, 2
Typhlops ater		1	1, 2	1	1, 2	1, 2
T. conradi	×	1	1	1	1	1
Cylindrophis melanotus		1	1	1		
C. r. rufus		1	1, 2	1, 2		
Candoia carinata						1, 2
Python molurus bivittatus		1, 2, 3	1, 2, 3	1, 2, 3	1	
P. reticulatus		1, 2	1, 2	1, 2	1, 2	
Xenopeltis unicolor		1, 2	1, 2	1, 2	1, 2	
Acrochordus granulatus		1, 2	1, 2	1, 2	1, 2	1, 2
Psammodynastes pulverulentus		1, 2	1, 2	1, 2	1, 2	
Lycodon aulicus capucinus		1, 2	1, 2, 3	1	1, 2, 3	
L. stormi	×	1	1	1	1	
Oligodon octolineatus		1, 2	1, 2	1, 2	1	
O. waandersi		1	1	1	1	
Elaphe erythrura celebensis	×	1	1	1	1, 2	
E. flavolineata		1, 2	1, 2	1, 2	1	
E. jansenii	×	1	1	1	1	
Gonyosoma oxycephalum		1, 2	1, 2	1, 2	1, 2	
Ptyas dipsas		1	1			
Chrysopelea paradisi celebensis	×	1, 2	1, 2	1, 2	1, 2	
Dendrelaphis caudolineatus terrificus		1, 2	1	1, 2	1, 2, 3	1
D. p. pictus		1, 2, 3	1, 2, 3	1, 2, 3	1, 2, 3	1
Ahaetulla p. prasina		1, 2, 3	1, 2, 3	1, 2, 3	1, 2, 3	
Boiga dendrophila gemmicincta	×	1, 2	1, 2	1, 2	1, 2	1, 2
B. i. irregularis		1	1	1	1	1, 2
B. m. multimaculata		1, 2, 3	1, 2, 3	1, 2, 3	1	1
Calamaria acutirostris	×	1	1	1	1	
C. apraeocularis	×	1	1	1	1	
C. boesemani	×	1	1	1	1	
C. brongersmai	×	1	1	1	1	
C. curta	×	1	1	1	1	
C. muelleri	×	1	1	1	1	
C. nuchalis	×	1	1	1	1	
C. virgulata		1	1, 2	1, 2	1, 2	
Calamorhabdium acuticeps	×					

Species	E	M	J	B	P	NG
Pseudorabdion longiceps		1, 2		1, 2	1	
P. sarasinorum	×	1		1	1	
Rabdion forsteni	×					
Amphiesma celebica		1		1		1
A. sarasinora	×	1		1		1
Rhabdophis chrysarga		1, 2	1, 2	1, 2	1, 2	
R. chrysargoides		1	1, 2	1	1	
Sinonatrix trianguligera		1, 2	1, 2	1, 2		
Xenochrophis piscator melanzostus		1, 2	1, 2, 3	1, 2, 3		
Cerberus r. rynchops		1, 2, 3	1, 2, 3	1, 2, 3	1, 2, 3	1, 2
Enhydris enhydris		1, 2	1, 2	1, 2		1, 2*
E. matannensis	×	1	1	1		1
E. plumbea		1	1, 2	1, 2		1
Homalopsis buccata		1, 2	1, 2	1, 2		
Bungarus candidus		1, 2	1, 2	1		
Maticora intestinalis nigrotaeniata		1, 2	1, 2	1, 2, 3	1, 2	
Ophiophagus hannah		1, 2	1, 2	1, 2	1, 2	
Naja n. sputatrix		1, 2, 3	1, 2, 3	1, 2, 3	1	
Laticauda colubrina		1, 2	1, 2	1, 2	1, 2	1, 2
L. laticaudata		1, 2	1, 2	1, 2	1, 2	1, 2
Aipysurus fuscus		1	1	1	1	1
Hydrophis fasciatus atriceps		1, 2, 3	1, 2, 3	1, 2, 3	1, 2, 3	1, 2, 3
H. melanosoma		1, 2	1	1, 2	1	1
H. spiralis		1, 2	1, 2	1, 2	1, 2	1
Lapemis hardwickii		1, 2	1, 2	1, 2	1, 2	1, 2
Pelamis platurus		1, 2	1, 2	1, 2	1, 2	1, 2
Trimeresurus wagleri		1, 2	1	1, 2	1, 2	

* According to De Rooij (1917: 182): Lorentz River. Species not mentioned from New Guinea by Gyi (1970).

Table 1. Occurence of Sulawesian snakes on neighbouring major landmasses. 1: snake present on genus level; 1, 2: snake present on species level; 1, 2, 3: snake present on subspecies level; X: endemic on Sulawesi; blank space: absent. B = Borneo; J = Java; M = Malay peninsula and adjacent southeast Asia; NG = New Guinea; P = Philippines; E = Endemic.

McDowell (1974, 1975, 1979), Mertens (1957, 1968) and Stimson (1969).

Few of the 63 species of Sulawesian snakes are closely related to any in the Australo-Papuan realm (with the obvious exception of sea- or sea-going snakes: *Acrochordus granulatus, Cerberus r. rynchops, Enhydris e. enhydris,* *Laticauda colubrina, L. laticaudata, Lapemis hardwickii, Pelamis platurus*) viz. *Typhlops ater, Rhamphotyphlops braminus, Candoia carinata* and *Boiga i. irregularis*. All others are members of groups with a clearly continental southeast Asian or Indo-Malayan distribution. Some, like *Calamaria*, are near their southern or eastern limit in Sulawesi. Even the 18 endemics, including the only endemic genus *Rabdion*, have phylogenetical Oriental relationships. And as Leviton (1963a) remarked, there are no genera or species of Philippine snakes which show affinities with strictly Sulawesian ones; nor are there species of Papuan or Taiwanese origin in the Philippines. He assumed therefore a western Indonesian-Malayan origin of Philippine snakes, mainly via Borneo, explained for the most part by geological events.

The only species deviating from the rule of Oriental ancestry in Sulawesi are *Candoia carinata* and *Boiga i. irregularis*, with a distribution pattern that covers the Moluccas, New Guinea and Polynesia, *Candoia* even reaching its western limit on Minahassa.

The distribution of the Pythoninae suggests a derivation from the Xenopeltinae in Asia, with later dispersal to Africa and Australasia (Underwood, 1976). The same author is in favour of a "Kon-Tiki" dispersal of *Candoia*, from tropical America westwards across the Pacific. McDowell (1979) also spoke of South American affinities. This situation is not that uncommon. Numerous families, from flies to snails on South Pacific islands, have in fact been used to justify the establishment of an independent realm lying south of the Palaeotropical and Neotropical ones, essentially corresponding to the plant realms of Antarctica (Müller, 1974: 62). Nur & Ben-Avraham (1977) even invoked a completely lost continent, Pacifica, initially (Trias) situated close to the east of present day Australia, later breaking up in fragments, remnants of which are to be looked for on the shore lines of Asia and the America's. However, their concept is irrelevant to the snake fauna of Sulawesi, because most of the supposed drifting had occurred by the time the first snakes made their appearance in the Cretaceous.

Rasmussen (1979) assumed that boigine snakes originated in Africa and that the boigine invasion of Asia may have taken place in the Late Oligocene. *Boiga* presumably entered the Indo-Australian region in the Pleistocene, during which it ultimately reached Australia (Storr, 1964). Thus, the genus *Boiga* undoubtedly has western affinities.

Typhlops ater barely reaches New Guinea (according to Hahn (1980): Waigeo, Sulawati and Andai) and apart from Sulawesi is also known from Halmahera, Ternate and Java. The present (circumtropical) dispersal pattern of *Rhamphotyphlops braminus* is mainly due to human activity. *Lycodon aulicus capucinus* according to Leviton (1965) also fits this explanation. He

	Species in common							
FRF	M	Sum	J	B	Sul	P	Min	NG
Malay peninsula/ southeast Asia	**135**	78	55	76	26	21	12	3
Sumatra	0.63	**114**	59	75	26	26	15	3
Java	0.52	0.62	**76**	57	28	23	15	4
Borneo	0.59	0.64	0.58	**121**	27	26	17	4
Sulawesi	0.28	0.31	0.43	0.31	**53**	19	15	6
Philippines	0.20	0.28	0.31	0.27	0.31	**71**	34	3
Mindanao	0.14	0.20	0.27	0.22	0.34	0.65	**34**	3
New Guinea	0.03	0.04	0.06	0.05	0.11	0.05	0.07	**52**

Table 2. Comparison of terrestrial snake faunas of different regions in the Indo-Malayan archipelago. The total number of terrestrial species in each locality (bold face) is on the diagonal from upper left to lower right. The number of species common to each combination of regions is to the right and above the diagonal with the totals. To the left and below the diagonal are the faunal resemblance factors. For abbreviations see table 1. Sum = Sumatra, Sul = Sulawesi, Min = Mindanao.

accounted for its occurrence outside the southeast Asian mainland in this way. Leviton (1959: 827) suspected introduction into Sulawesi "by natives in the course of their local activities" of *Dendrelaphis caudolineatus terrificus* because of the absence on Sulawesi of any other Philippine (Mindanao) snake on subspecific level.

The same references (mentioned on p. 33 and 35) used in compiling data for table 1, were used in a limited comparison of resemblance in terrestrial snake faunas between Sulawesi and different regions in the Indonesian archipelago and adjacent southeast Asia. This was done using the Faunal Resemblance Factor (FRF) formula (Duellman, 1966: Hoogmoed, 1979) $FRF = \frac{2C}{N_1+N_2}$ where N_1 and N_2 are the numbers of species occurring in any two given regions and C is the number of species common to the two regions compared, resulting in table 2.

The Philippinian islands form a diverse and disjunct area. Therefore, one of the largest islands (Mindanao) close to Sulawesi, also was taken into consideration as an entity if its own. The data are to be treated with some reserve as to the correctness of the records, considering the fact that no comparable recent work has been done in that area.

The same general picture as before emerges. The resemblance of any of the regions considered with New Guinea is almost nonexistent. The highest resemblance is found between the Malay peninsula/southeast Asia, Sumatra, Java and Borneo; parts of the former Sundaland. A slight negative correlation as to the distance from the continent can be observed. The resemblance between the Philippines and one of its islands (Mindanao) was of course to be expected. A special status of Mindanao is not warranted. The faunal resemblance factors of all non-Sundaland regions are distinctly lower.

The resemblance between Sulawesi and the Philippines is of the same order as that between Sulawesi and the different parts of Sundaland. Resemblance between Sulawesi and Borneo, Sumatra and mainland Southeast Asia is slightly lower than that with Java, and this figure might suggest that immigration into Sulawesi from Sundaland probably occurred mainly via dispersal from Java over the Java and Flores Seas, rather than from Borneo over Street Makassar. It also might reflect our better knowledge of Javanese snakes as compared to that of the snake faunas of Sumatra and Borneo.

In general, factors influencing the distribution of animal species range from geological and biological circumstances to climate and chance dispersal, such as rafting in the case of islands. The geological events as outlined above no doubt play a role in the present distribution, notably the postulated land connections to Sundaland from the Middle Miocene onward or at least the greatly diminished sea distances which permitted rafting more easily. Both past and present ecological barriers, especially the transition from tropical rainforest to savannah and vice versa, may form an even greater obstacle to dispersal than sea depths. This could be concluded from the fact that the migration route from Sulawesi to Australia/New Guinea, presumed to have been available from at least latest Miocene (Audley-Charles, 1981) does not seem to have been used intensively and certainly not so in the east-west direction.

The recent snake fauna hardly reflects the much drier climatic conditions of the Pliocene. There are, apart perhaps from the Elapinae, no xerophilic snakes in Sulawesi. Unfortunately, the fossil record of snakes is much too scanty (more or less summarized in Dowling & Duellman, 1978) to infer pertinent conclusions as to their distribution and dispersal in geological times. But it does not contradict the history thusfar deducted from plate tectonics with respect to Sulawesi. *Python* as a genus theoretically is the only group that could have reached Sulawesi via the northern (from mainland Southeast Asia) as well as the southern (from Australia) route. For all other snakes – including the two pythons present on Sulawesi, *P. molurus bivittatus* and *P. reticulatus* – only the northern one seems probable. More detailed historical remarks are impossible, as I am not aware of any fossil snake remains having been described from Sulawesi.

Compared to the 12 endemic amphibians (57.1% of a total of 21 authenticated species: Inger in Cranbrook, 1981), 84 endemic birds (38,2% of a total of 220 species (Stresemann, 1941) and 71 endemic mammals of the 100 species (71%) listed in Groves (1976), the 23.3% (15 out of 63 species) for snakes are not unexpected and even rather low. The figures are nevertheless quite high in comparison with e.g. Java: about 10% endemic snake species (uncorrected data De Haas, 1950) and 4.8% endemic bird species (Stresemann, 1941) and seem to indicate a long isolation.

Three amphibian species show Sahulland affinities; two of these may have originated in Sulawesi (Cranbrook, 1981). As far as the mammals are concerned the figures are strongly biased by bats for a number of reasons. When excluding these, and introduced animals, there are no species in common with New Guinea, three with Sundaland and one with the Philippines; the same picture holds for the traceable relationships of endemics (Groves, 1976). The same author favoured a relationship almost entirely with Sundaland, with no trace of a major Philippine element to suggest a southerly dispersal to Sulawesi. In contrast, Stresemann (1939) concluded that many birds are immigrants from the Philippines, some from or via the Moluccas, and a few from Timor and Borneo. These differences in origin are not readily explained, but might be related to a fairly recent arrival of modern snakes and mammals in Australia: a secondary centre of dispersal for these groups has not yet developed there.

Sulawesi itself cannot be considered a centre of snake radiation of major importance. Even in *Calamaria* with seven out of eight (87.5%) Sulawesian species being endemic, Inger & Marx (1965) assumed the centres of evolution and dispersal of the genus to be on Sundaland, where the number of species is much higher. Especially on Borneo, where 52.4% of the *Calamaria* are endemic, and on Sumatra (with 50% endemics). Nevertheless they justly considered Sulawesi a site for minor radiation in *Calamaria*. The other endemics, ranging from generic to subspecific level, reflect colonization by chance from ancient to more recent arrival over a long period, lasting at least from the Miocene onward, till the present day.

One could treat Kepulauan Banggai as faunistically not belonging to Sulawesi. One of the early indications is found in Van Vuuren (1920), who assumed a zoogeographic boundary line formed by the Strait of Peleng, based on the absence in Banggai of monkeys, deer, *Babyrousa babyrussa* (Linnaeus) (Suidae, Mammalia) and on a different colouration in *Phalanger celebensis* (Gray) (Phalangeridae, Mammalia); moreover he made a general remark on the existence of a different avifauna. *B. babyrussa*, however, is present east and west of the supposed boundary on Sulawesi, Buru, Togian and Sula Islands (Thenius, 1970). In the case of *P. celebensis* there is probably no sharp distinction (Tate, 1945). These facts undermine the line for these species at least. The distribution of birds in this region is far more complex than was known then. According to Musters (1983), one could state that based on the lizard genus *Draco*, Banggai is zoogeographically more related to the Sula Archipelago than to Sulawesi. Kopstein (1927) regarded the Sula islands to possess a reptilian fauna resembling that of Sulawesi but with fewer species, and with the addition of some elements from Halmahera. A geological similarity between the Banggai and Sula islands is mentioned in Audley-Charles (1981). Exclusion of the ophidian fauna of Banggai would not affect the number of snake species present on Sulawesi as here defined, as no species was exclusively found on Banggai.

Mertens (1934) considered the peninsulas of Sulawesi faunistically different, though he did not specify his reasons. Audley-Charles et al. (1972) adhere to the same opinion. Snakes, however, do not seem to justify this, though admittedly they have been collected haphazardly and only are present in the available collections in relatively low numbers, whereas herpetogeographic fieldwork is completely lacking. Because of the last two reasons mentioned, no elaborate attempt is made to discuss the possible differences per peninsula or the altitudinal distribution. But, since geographical and meteorological conditions are not uniform, a somewhat differentiated pattern can be expected. Van der Vecht (1953) for example, recognised geographic variation in carpenter bees (*Xylocopa* spec.) in Sulawesi.

The well sampled Minahassa seems to harbour forms not found elsewhere on the island (viz. *Typhlops conradi, Candoia carinata, Calamorhabdium acuticeps, Pseudorabdion sarasinorum* and *Rabdion forsteni*), not altogether unexpectedly, since it probably was the earliest mainland (Miocene or even Eocene). The *Calamaria* species, which are endemic with the exception of *C. virgulata*, on the other hand are distributed over the remainder of the island, with emphasis on the southwestern part. Minahassa, as well as the southwestern peninsula form the western arm of Sulawesi and geologically speaking, these have been connected with Indo-Asian elements from the Cretaceous onward, and a greater influx from these areas is more likely than from Australia. The recent (Pliocene) junction of the two arms (the eastern and south eastern peninsulas linked to Minahassa and western Sulawesi) could possibly be perceptible in more detailed faunistic analyses.

SPECIES RICHNESS

A comparison of the terrestrial species-area relations (e.g. Diamond & May, in: May, 1981) in the Indonesian archipelago is made, to see whether or not the complex geological history is reflected in the species richness of snakes. This is done by using the papers referred to in the "Geographical relationships of the snake fauna" as well as those by Forcart (1953) and Mertens

(1930). However, in doing so, one introduces an error, since we are confronted with areas which have not all been sampled to the same degree. However, this is not expected to affect the general trend. Doubtful occurrences are omitted. "Sea-snakes" are excluded since they do not contribute to the terrestrial fauna. Areas were obtained mainly from the Times Atlas (1980), Paulus (1917), De Graaf & Stibbe (1918) and Stibbe (1919, 1921).

A presupposition in using the species-area equation is that habitat heterogenity does not vary appreciably among islands (MacArthur & Wilson, 1967). This condition is not completely met, as is seldom the case in nature.

Sulawesi has few snake species in common with New Guinea (see table 1) and of these most are sea-snakes. New Guinea is faunistically more related to Australia than to the rest of the Indo-Australian archipelago, though, according to e.g. Storr (1964), the Australian reptiles are ultimately derived from southeast Asia, most now are adapted to the widespread savannah conditions prevailing in Australia, preventing exchange by ecological barriers. Therefore continental Australia is not included in the comparison.

The empirical relation between number of species (S) and area (A) is usually presented in the form of $S = c. A^z$, in which c is a proportionality constant and z the slope of the regression line on a log S versus log A plot. A critical review of the correlation, the parameters involved and its use and interpretations is found in Conner & McCoy (1979).

Fig. 2 illustrates the species-area relations for 20 Indonesian islands and one Philippinian island for snakes. The points above the regression line could be considered an indication of supersaturation, the ones below as undersaturation of the corresponding areas, as is frequently done (e.g. Gorman, 1982; Wilcox, 1978). The first impression of the plot is that there are no clear cases of undersaturation or supersaturation. Despite the fact that Sulawesi has been an instable island region for a long time and is composed of several smaller islands of geologically different origins and ages (Umbgrove, 1949; Audley-Charles et al., 1972), Sulawesi does not appear to be in an aberrant position and in fact fits the regression line calculated for the other twenty islands (1000 km^2 intercept 3.06, $r = 0.932$, $z = 0.572$) rather nicely. Incorporation of Sulawesi makes $z = 0.567$, 1000 km^2 intercept 3.09 and $r = 0.938$. As far as snakes are concerned there is no reason to speak of an impoverished situation on Sulawesi compared to Sumatra, Borneo and Java, as suggested by Guibé (1953) for its herpetofauna in general. The last three islands have a maximum sea-depth of about 60 m between them and are parts of the Sunda shelf, recently (10,000 years in the case of Borneo (May 1981)) fragmented by sea level rising.

Since possible supersaturation or undersaturation influences the slope of

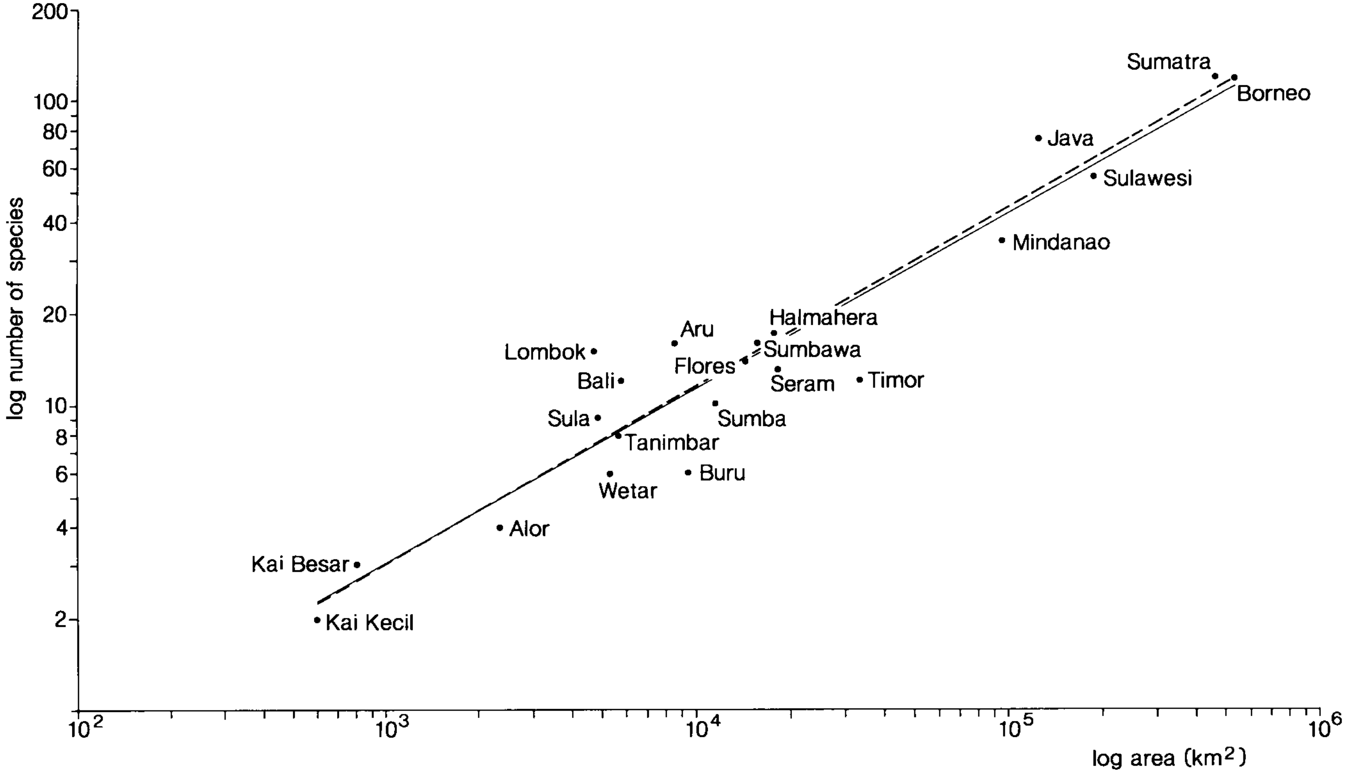

Fig. 2. Relation of species number of snakes on islands in the Indonesian archipelago, plotted as a function of island area on a double logarithmic scale. The dashed line ($z = 0.572$) was fitted by least mean squares, Sulawesi not taken into consideration; incorporation resultated in the solid line ($z = 0.567$).

the regression line, fig. 2 suggests to omit Buru, Java, Lombok and Timor. As expected this produces a high correlation: $r = 0.984$ ($z = 0.573$, 1000 km^2 intercept 3.05). Calculation of the number of species per island having a probality of less than 5% of being inside the range of the numbers found, using the residual mean square (Steel & Torrie, 1980), will not allow further remodeling of the plot ($t\ s_{y_{res}} = \pm\ 0.244$). This renders the concepts of supersaturation and undersaturation less appropriate, since each island still has a wide confidence interval. Since a logarithmic scale is used, even small confidence intervals can greatly influence the absolute number of species.

So, the quite complex and different history of many islands in the Indo-Australian archipelago is not reflected in their species richness of snakes, due to the different time scales involved. Wilcox (1978) pointed out a quantitative relationship for the expectation that the loss of species (of lizards) on continental islands will be faster on small ($<$1,000 km^2) islands and that a new dynamic steady state is reached within several thousand years. This implicates that even on larger areas, these processes only take tens of thousands of years.

The "undersaturated" as well as the "supersaturated" islands in fig. 2 are separable as groups not so much on their geological history, area or ecological diversity, but more so on their present day distance from landmasses. Sumatra, Java and Borneo can be considered as a recently fragmented continental area, Sulawesi is in "equilibrium" and south and eastward increasingly "undersaturation" is encountered, keeping in mind the mainly Asian affinities. In Halmahera an additional influence of New Guinean species is seen, and on Aru — the only one in this comparison on the Sahul shelf — the nearness of Australia is felt.

A commonly cited herpetological example of species-area relations is Darlington (1957: 483) (e.g. Cody & Diamond, 1975), though based on only four islands in the Caribbean. A $z = 0.426$ can be deduced for snakes ($r = 0.986$). Using all of Leviton's (1959) data, with the addition of the Typhlopidae from Hahn (1980), a value of $z = 0.370$ is obtained for 28 islands in the Philippines (10 km^2 intercept 1.11, $r = 0.723$). However, as closer analysis will show, the history of and the conditions on the islands, are diverse and they are not always well explored (Leviton, 1959), e.g. in the case of Panay (11,510 km^2) with nine species as compared to Palawan (11,785 km^2) or Negros (12,704 km^2) with 29 and 26 species respectively. Deleting such islands that would negatively influence the fitting of a linear regression line (Catanduanes, Dinagat, Masbate, Tawi-Tawi, Ticao and Panay), leaves 22 islands: $z = 0.378$, 10 km^2 intercept 1.51, $r = 0.892$.

For the 22 Philippinian islands the linear model does not seem to hold. The regression line through the islands smaller than 1,000 km^2 has a higher slope than the one through the larger islands. Subsequently, to obtain considerable overlap in area and thereby a more realistic comparison of z-values in the Philippinian and Indonesian archipelago, all islands of less than 1,000 km^2 were dropped. This leaves ten Philippinian islands: $z = 0.260$, 1,000 km^2 intercept 10.5, $r = 0.827$. The linear model for the ten islands does not fit the total of the Philippine data and illustrates the necessity of caution about extrapolating from a regression equation beyond the area limits.

In comparing regression coefficients ($= z$) of snakes (0.43 in the Caribbean, 0.26 in the Philippines and 0.57 in the Indonesian archipelago) these prove in this case to be devoid of general predictive value, and use as such is advised against. The y-intercepts (number of species) at 1,000 km^2 differ considerably: Indonesian 3.5; Philippinian 10.5 (for 22 islands 7.5); Caribbean 2.3. These, just as the z and r values, cannot be explained by latitudinal diversity gradients. Since small areas were not considered in the comparison of the three regions and extension of the regression lines is judged unjustified, Heatwole's (1975) hypothesis of a minimal area necessary to support a breeding population of a taxon, about which the x-intercept could give an indication, cannot be tested. Moreover, interpretation of the intercepts is fraught with analytical problems, and as yet I concur with Connor & McCoy (1979), who see the parameters simply as fitted constants.

ACKNOWLEDGEMENTS

For the loan of specimens in their care I thank E. N. Arnold, British Museum (Natural History), (London), L. Capocaccia, Museo civico di Storia naturele "G. Doria", (Genova), and J. Lescure, Museum National d'Histoire Naturelle, (Paris). M.S. Hoogmoed read and constructively criticised the manuscript in its different stages. Discussions on statistics with R. G. Bout are highly appreciated. L. M. Brittijn prepared the figures.

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