# THE SPECIES OF STEGONOTUS (SERPENTES, COLUBRIDAE) IN PAPUA NEW GUINEA

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#### Introduction

Currently, New Guinea Stegonotus with 17 scales at midbody and divided subcaudals are identified as S. modestus. But this will not account for the disparity in dentition within "S. modestus", nor the colour differences even at one locality, nor that in East and West Sepik Districts there are three quite distinct "S. modestus": (1) a large form with high ventral count and high tooth count; (2) a small form with low ventral count but high tooth count; and (3) a medium-sized form with high ventral count but low tooth count (fig. 1). The material in the British Museum and American Museum of Natural History indicates that scale count does not correctly identify the species, and that such features as dentition, form of the palatine bone, scale pits, size, and coloration are more reliable.

# GENERAL FEATURES OF NEW GUINEA STEGONOTUS

New Guinea Stegonotus are very closely related to the Oriental genus Dinodon; the supposed dental differences between these genera do not hold and the maxillary dentition of (for example) Stegonotus diehli more closely resembles that of Dinodon orientale than it does that of Stegonotus cucullatus. I find only one character that will separate New Guinea Stegonotus from Dinodon: in Dinodon, the membranous dorsal wall of the trachea is expanded as a large and simple sac continuous with the lung 1); but in all New Guinea Stegonotus, dorsal tracheal perforations lead into a series of separate membranous sacs, as described by Brongersma (1957).

Stegonotus and Dinodon show a general similarity in form and a sexual dimorphism in ventral count with males exceeding females (the reverse of the usual dimorphism). The pattern of the head of juvenile S. diehli

<sup>1)</sup> Examined: Dinodon refozonatum, AMNH 28331, 28333; D. flavozonatum, AMNH 34372; D. orientale, AMNH 97549; D. semicarinatum, AMNH 82384.

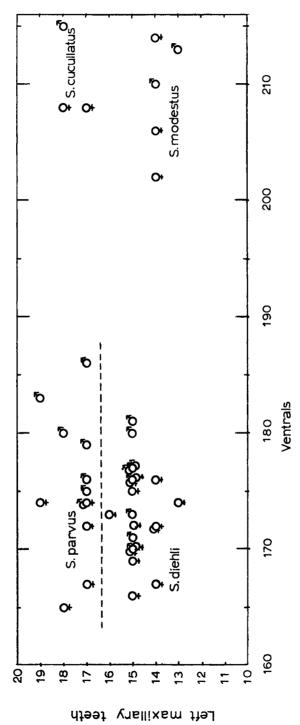


Fig. 1. Stegonotus from West Sepik, East Sepik, and Madang Districts, ventrals (X axis) against left maxillary teeth (Y axis). S. diehli is here characterised by 15 scales at midbody (17 in the others, which are currently all identified as S. "modestus").

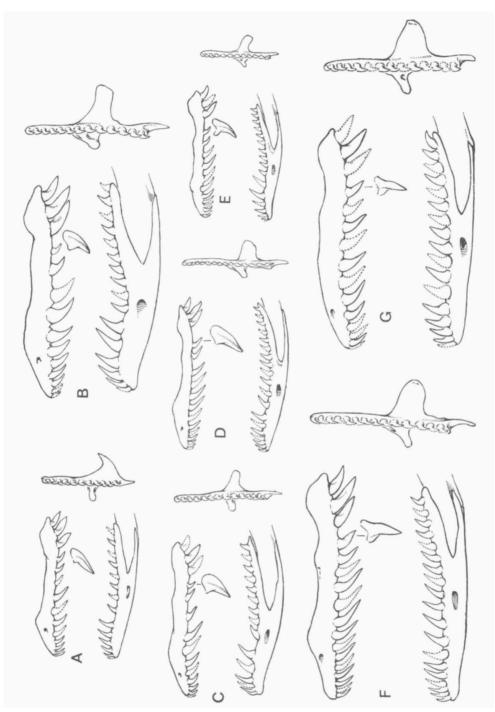


Fig. 2. Left maxilla, enlarged posteromedial view of fourth maxillary tooth from rear, left dentary, and right palatine of Stegonotus: A, S. diehli (AMNH 10043, Mt. Nibo, maxilla and dentary; AMNH 75000, Wewak, palatine); B, S. modestus (AMNH 75026, Wewak); C, S. heterurus (AMNH 107181, Rabaul, palatine reversed from left); D, S. parvus (AMNH 85723, Lae, maxilla and dentary reversed from right); E, S. spec. cf. parvus (AMNH 82316, Iambon, partly reversed from right); F, S. cucullatus (AMNH 75358, Wewak, partly reversed from right); G, S. guentheri (AMNH 42379, Goodenough I.). × 4.

closely resembles that of adult *Dinodon*. In both genera, the maxillary teeth (fig. 2) just behind the maxillo-prefrontal articulation are longer and stouter than those anterior and posterior to them, and the last three maxillary teeth are enlarged and compressed with a knife-like posterior edge (serving to slit open squamatan eggs, the most frequent item in the stomach of New Guinea *Stegonotus*). A striking resemblance between the two genera is the form of the sphenoid (first noted in *Dinodon* by Underwood, 1967); the rostrum is expanded beneath the trabecular cartilages, with its lateral edges meeting the supratrabecular ridges of the frontals, enclosing the trabeculae in bony canals.

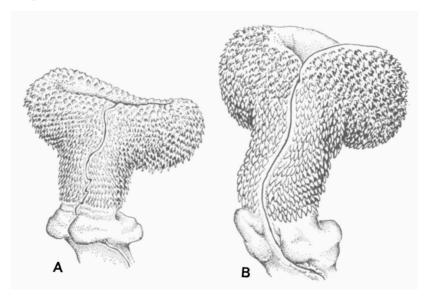


Fig. 3. Right hemipenis (posterior view) of: A, Stegonotus modestus (YPM Field No. 122, Bostrem Bay); B, S. cucullatus (AMNH 107180, Garaina). × 3.

The hemipenis (fig. 3) differs only in details among the New Guinea species of *Stegonotus*, and that of *Dinodon* appears to be similar (but I have not seen everted preparations of the latter). The everted organ shows an abrupt expansion of its terminal portion (when inverted, the tissue allowing this expansion is tucked into a pair of "longitudinal folds" flanking the sulcus). At the tip of the everted organ there is a terminal concavity directed distad, into which the simple sulcus opens by a divided orifice (this terminal concavity is indicated on the inverted organ by a bare area at the tip opposite the sulcus). The armature of the expanded region consists of numerous small spines, seen in *S. cucullatus* to represent the spinose borders

of many small calyces, but the central depressions of the calyces are not conspicuous and there is a very gradual transition between these spines and the somewhat larger spines of the cylindrical base. Near the base of the organ, a pair of swellings flank the sulcus and a third swelling lies opposite the sulcus (appearing as welts on the inverted organ).

# Distinguishing characters of New Guinea species

- Ia. Medial (choanal) process of palatine tapering rapidly from a broad base on the rear half of the bone into a pointed tip that is hooked forward toward the vomer; nearly every scale of the body and anterior tail with two well-developed apical pits; juvenile with bold head markings that involve: a dark blotch from orbit to orbit across the frontal, a dark snout patch (sometimes broken up), a dark posterior temporal blotch, and a pair of dark blotches on the parietals (separate from each other but smoothly confluent with temporal blotches in West Irian, more or less distinct from temporal blotches but partly confluent with each other in Papua New Guinea).
  Stegonotus diehli Lindholm
- Ib. Medial (choanal) process of palatine strap-shaped, with broadly rounded or truncated tip extending straight mediad or even curved slightly backward, away from the vomer; scales without pits or a few scattered scales with tiny vestigial pits; head without blotches at any age.
  - 2a. Fourth maxillary tooth from rear (immediately preceding the conspicuous diastema) similar to the teeth in front and triangular in cross-section, with a posterolateral and a posteromedial keel; an abrupt diminution of the teeth behind the enlarged teeth at the middle of the maxilla; distal half of hemipenis with numerous small spines that may suggest transverse flounces, but not calyces except at margin of terminal concavity; rarely reaching I m in length and scales 17 or more at midbody.
    - 3a. Maxillary teeth 13 or 14, the enlarged middle teeth equalling or exceeding the enlarged rear teeth, the small teeth following the enlarged middle teeth so reduced that dentition suggests *Dinodon*; adult with sagittal crest formed partly by parietal.
      - 4a. Subcaudals divided; ventrals 208-216 (males), 195-214 (females).

        Stegonotus modestus (Schlegel)
      - 4b. Subcaudals all or most entire; ventrals 193 (male), 178-185 (females).

        Stegonotus heterurus Boulenger
    - 3b. Maxillary teeth 15-19, the enlarged middle teeth shorter than the rear teeth, only moderately larger than the small teeth behind them; adult with sagittal crest confined to supraoccipital.
      - 4a. Dark colour of crown not covering upper lip, which is whitish or light tan; inverted hemipenis extending to subcaudal 8-15; ventrals 174-196 (males), 165-192 (females). Stegonotus parvus (Meyer)
      - 4b. Dark colour of crown covering upper lip to reach edge of mouth; inverted hemipenis (one male seen) extending to subcaudal 18; ventrals 209-218 (males), 184-196 (females) Stegonotus spec. cf. parvus

- 2b. Fourth maxillary tooth from rear similar in shape (though smaller in size) to the rear three teeth, compressed and with a single posterior cutting edge (the diastema between this tooth and third from rear short, sometimes absent); a gradual diminution of the teeth behind the enlarged middle maxillary teeth; distal half of hemipenis with the spines forming borders of inconspicuous, but discernible, calyces; adult with sagittal crest formed about equally by parietal and supraoccipital; except in some S. guentheri (which has scales 15 at midbody), adults (males with calcified hemipenial spines, females with large eggs) rarely less than 1 m long.
  - 3a. Scales 17, 18 or 19 at midbody; colour showing great geographic variation, but in d'Entrecasteaux Islands, pale greyish with conspicuous dark margins of scales. Stegonotus cucullatus (Duméril, Bibron & Duméril)
  - 3b. Scales 15 at midbody; brown, with white margins of scales on lower sides; d'Entrecasteaux and Kiriwina (= Trobriand) Islands.

Stegonotus guentheri Boulenger

## Stegonotus diehli Lindholm

Stegonotus diehli Lindholm, 1905: 236 (original description; Bogadjim); Andersson, 1913: 75 (Bogadjim); Lampe, 1913: 84 (Bogadjim); De Rooij, 1917: 118 (Kaiserin-Augusta R., Bégowre R., Lorentz R.); De Jong, 1927: 302 (Pionierbivak, Mamberamo R.; Sermowari [sic] R.); Ewers, 1968: 173 (Maprik, East Sepik Dist.; haemogregarine infection).

Stegonotus modestus (part); Boulenger, 1893: 366 (Mansinam); De Rooij, 1917: 115 (Utakwa R., Haveri, Mt. Victoria, Madew).

Stegonotus modestus (part, not of Schlegel); Boulenger, 1897: 704 (Haveri); Boulenger, 1914: 264 (Utakwa R.).

Stegonotus guentheri (not of Boulenger); Lidth de Jeude, 1906: 525 (Humboldt Bay); Loveridge, 1948: 383 (Fak-Fak).

Material examined: 48 specimens:

WEST IRIAN: — Fak-Fak: MCZ 7313a, b (males); — Mansinam: BM 78.2.11.13 (female); — Toem: MCZ 49475, 49484 (females); — Lake Sentani: BM 1938.6.9.41 (male); — "Dutch New Guinea" (near Hollandia?): BM 1938.6.9.42-43 (male, female); — Utakwa River, 2500 ft: BM 1913.11.1.105 (male).

Papua New Guinea: West Sepik District: — Nuku (800 ft): AMNH 100036 (male); — Miliom (1500 ft): AMNH 100038 (female); — Lumi (1750 ft): AMNH 100039-40 (males), 100041 (female). East Sepik District: — Wewak: AMNH 75000 (male). Madang District: — Ramu River delta: BM 1926.5.31.15-16 (females); — Bostrem Bay: YPM [Field Nos.] 101, 105, 116 (males), 115, 117 (females), AMNH 107184-7 (females), 107188 (male); — Alexishafen: AMNH 107182-3 (females); — Saidor: MCZ 49491 (female). Morobe District: — Munum Waters (12 mi. W of Lae): AMNH 103672 (male); — Lae: AMNH 95155 (male); — "Huon Gulf": BM 1922.11.24. 40-41 (male, female); — Garaina: AMNH 95620 (male). Chimbu District: — Karimui (3600 ft): AMNH 98870 (male). Northern District: — Mt. Victoria: BM 1896.10.31.21 (male). Western District: — 5 mi. below Palmer Junction: AMNH 57530 (male). Gulf District: — Purari River: BM 1936.7.7.30 (male). Central District: — Kubuna (100 m): AMNH 59087 (male); — Port Moresby: AMNH 82522 (male); — Haveri: BM 97.12.10.119 (female). Milne Bay District: — Menapi, Cape Vogel: AMNH 73951 (male), 73956 (female).

Description. — Supralabials 7 (8 unilaterally in one), third and fourth entering eye; infralabials usually 8 (sometimes 9); preocular 1, rarely 2; postoculars I or 2; anterior temporals 2 (I unilaterally in two), the lower usually excluded from postoculars; scales show geographic variation, 17-17-15 or 15-15-15 (irregularly 15 and 16 at midbody in one, irregularly 15, 16, and 17 in another); ventrals show sexual dimorphism and geographic variation, 170-208 (males), 159-196 (females); subcaudals show sexual dimorphism and geographic variation, 74-104 (males), 65-94 (females). Maxillary teeth 13-16, the last three set off by a diastema, the enlarged middle front teeth followed by 3 (rarely 4 or 2) teeth that are abruptly shorter; palatine teeth 11-16; pterygoid teeth 15-20 (varying geographically); dentary teeth 13-18. Hemipenis to subcaudal 10-16, the distal region with numerous small spines suggesting chevron-like flounces but not calvees. Colour of head, see Distinguishing characters (p. 10); body brown in adults, almost black vertebrally, but with at least slightly paler margins to lateral scales (these margins much broader and paler in juveniles); colour of belly and subcaudals varying geographically.

Geographic variation. — This is most conspicuous in scale count and specimens with 17 rows have previously been identified as *S. modestus*. In general, specimens from north of the central watershed (the Mansinam specimen is an exception) eastward, in Astrolabe Bay, have 15 scales, whereas those from Morobe District, the central range and southern New Guinea have 17 rows at midbody; in Papua New Guinea, specimens with 17 scale rows have 21-29 pterygoid teeth and usually 181-208 (males) or 180-196 (females) ventrals, whereas specimens with 15 rows have 15-22 pterygoid teeth and 170-181 (males) or 166-176 (females) ventrals. These differences hold for two specimens collected at "Huon Gulf" by Potter, where BM 1922.11.24.40 (male) with 17 scales has about 185 ventrals (specimen broken) and 27 pterygoid teeth, while BM 1922.11.24.41 (female) has 175 ventrals and 15 pterygoid teeth. If "Huon Gulf" represents a single locality, these specimens suggest that the 17-scaled and 15-scaled forms occur together as if distinct species.

But to the west these distinctions break down. AMNH 57530, a male from the upper Fly River, combines 17 scale rows with 174 ventrals and 21 pterygoid teeth. Nor is the geographical pattern without exception, since BM 1936.7.7.30, a male from the Purari River in Papua, has 15 scale rows, 177 ventrals, and 20 pterygoid teeth, counts more in keeping with the Sepik region well to the north.

The Purari River specimen is also anomalous in its low subcaudal count of 74, for specimens from most of West Irian, Papua, and Morobe and

Northern Districts have high subcaudal counts (90-104 in males, 78-94 in females), whereas specimens from the region of former Hollandia, and from East and West Sepik, and Madang Districts have 75-88 (males) or 65-84 (females) subcaudals. 1)

The ventrals are strongly pigmented above the angulation and usually along the anterior border medially, as well, in Central and Northern Districts, but the venter is almost or quite immaculate in the others; except in the Fak-Fak specimens, the underside of the tail is at least moderately pigmented and darker than the belly, and in specimens with 17 scale rows the pigmentation of the subcaudals forms conspicuous spots.

Distribution. — Probably most of New Guinea mainland, and Mansinam Island, but not other islands near New Guinea.

# Stegonotus modestus (Schlegel)

Lycodon modestus (part) Schlegel, 1837: 119, pl. 4 (original description, fig.; Amboyna and New Guinea).

Lycodon modestum; Duméril, Bibron & Duméril, 1854: 379 (description, restriction of type to Amboyna specimen [RMNH 324]).

(?) Lycodon lividum Duméril, Bibron & Duméril, 1854: 381 (original description; Samao I. [RMNH 325, 2 specimens, are syntypes]).

Coronella rosenbergii Bleeker, 1860a: 37 (original description; lectotype, now BM 1946.1.13.88, from Ceram). 2)

Ablabes greineri Bleeker, 1860b: 43 (original description; holotype, now BM 1946.1.13.74, from Ceram).

Coluber holochrous Günther, 1863: 59 (original description, fig.; holotype, BM 1946.1.11.40, from north Ceram; type of section Lielaphis).

(?) Lycodon aruensis Doria, 1875: 352, pl. 12 (original description, fig.; Wokan, Aru Is.).

Stegonotus modestus (part); Boulenger, 1893: 366 [not fig. on p. 364] (synonymy, description; Ceram, Amboyna. Mysol); Lidth de Jeude, 1896: 254 (Astrolabe Bay: S. cucullatus synonymized; re-examination of types of Lycodon modestus and L. lividum); Méhely, 1898: 171 (Stephansort [female with 212 ventrals only; the males with 176-181 ventrals probably S. parvus]); Lidth de Jeude, 1906: 525 (Lake Sen-

<sup>1)</sup> This is not the only case of a reptile typical of the northern watershed appearing on the southern watershed in the Purari River region; McDowell (1969: 482) has noted that a *Toxicocalamus preussi* from this region appeared similar to northern specimens. Van Deusen & George (1969) find the probable explanation for this is the "Baiyer Gap", northeast of Mt. Hagen, where the Purari and Sepik drainages are approximated at the (comparatively) low elevation of 1675 metres.

<sup>2)</sup> Bleeker based his description on two specimens, now BM 1946.1.13.88 (with incomplete tail) and RMNH 4066 (tail complete), without specifically designating either as the holotype. Necessarily, it was the Leiden (RMNH) specimen that allowed giving the proportion of tail to body and served as the "type" of Bleeker's concept. But Boulenger (1893: 367) listed the London specimen as "Type of C. rosenbergii", which probably constitutes a restrictive designation of a lectotype. I am most grateful to Mr. M. S. Hoogmoed for information on the Leiden type specimens of Coronella rosenbergii, Lycodon modestus, and L. lividum.

tani, ventrals 213, 211); De Rooij, 1917: 115 [not fig. which is S. cucullatus]; Werner, 1929: 60 (diagnosis in key).

Stegonotus modestus; Kopstein, 1926: 106 (Ceram, Buru, Amboyna, Nusalaut); Hediger, 1933: 19 (Lou I. and Iringou, Manus I.).

Lielaphis modestus (part); Günther, 1877: 129 (general account, synonymy, [erroneous] record from Duke of York).

Material examined: 12 specimens:

MOLUCCAS: — Amboyna: BM 1946.1.13.74 (female, holotype of Ablabes greineri); — Ceram: BM 1946.1.13.88 (female, lectotype of Coronclla rosenbergii); — north Ceram: BM 1946.1.11.40 (male, holotype of Coluber holochrous); — Misol: [18]70.8.3.147 (female). WEST IRIAN: — Sabron, Cyclops Range: BM 1938.6.9.45 (male); — Hollandia: AMNH 62038 (male).

PAPUA NEW GUINEA: West Sepik District: — Miliom (1500 ft): AMNH 100037 (female). East Sepik District: — Wewak: AMNH 75026 (male). Madang District: — Alexishafen: AMNH 107190-1 (females); — Bostrem Bay: YPM [Field No.] 122 (male). Manus District: — Manus I.: AMNH 107189 (male).

Description. — Supralabials normally 7, third and fourth entering eye (8, at least on one side, in Manus specimen, fourth and fifth entering eye); infralabials 8-10; preoculars 1 or (usually) 2; postoculars 2; anterior temporals 2, both touching postoculars in most, but lower excluded from postoculars in the Misol and Ceram specimens; scales usually 17-15, sometimes 18 at midbody (18 or 19 at midbody in Manus specimens). Ventrals 208-216 (males), 195-214 (females); subcaudals 85-91 (males), 86-88 (females), all divided. Maxillary teeth 9 + 2 + 3, 8 + 3 + 3, 8 + 2 + 3, or 7 + 3 + 3; palatine teeth 12-16; pterygoid teeth 21-25 (Moluccan specimens), 25-27 (New Guinea and Manus specimens); dentary teeth 14-19. Hemipenis to subcaudal 11-14, similar in structure to that of S. diehli. Brown above, almost black vertebrally, fading to pale tan on the first scale row and the ventrals above the angulation and on the upper lip (or upper lip may be nearly white); the edges of the lateral scales slightly paler than the centres; subcaudals tan with white angulation and posterior edge; ventrals white between angulations anteriorly, but showing tan anterior edges posteriorly in most specimens. In my Misol and Amboyna specimens, the white of the belly extends upward on the side of the neck behind the jaw articulation, suggesting an incomplete collar; in all my Moluccan specimens the first scale row and ventrals are pure white, at least on the anterior half of the body.

Remarks. — Although amply distinct from S. diehli, this species is in many respects (e.g. maxillary dentition and low supralabial count) so similar to S. diehli that it seems derived from that species. The greatest resemblance is to Papua and Morobe District S. diehli, which have similar scale, ventral,

and pterygoid tooth counts, and it is worth noting that S. modestus is not known from any region where S. diehli with 17 scale rows occur.

Probably S. modestus was originally a northern race of S. diehli and occupied the arc of islands that now form mountain ranges on the north coast as far east as the Adelberts; and a S. diehli similar to that now living in the Port Moresby region inhabited the more southern arc that now forms the central mountain spine of New Guinea; with development of reproductive isolation between the northern and southern forms, and with development of land continuity between the two island arcs, the new lowlands were invaded by S. diehli, but with some "character displacement" to adapt to the presence of S. modestus. In Papua New Guinea, the S. diehli that occupy regions where S. modestus occurs (East and West Sepik and Madang Districts) are reduced forms with low ventral and subcaudal counts, shortened pterygoid tooth rows, and only 15 scale rows; to the east of the range of S. modestus (Morobe and Northern Districts) and in the highlands south of the range of S. modestus, the S. diehli are quite similar to S. modestus in these respects.

Unfortunately, the characters that identify true S. modestus are almost never noted in published accounts. I suspect that most published records are erroneous, since in Papua New Guinea it is the least common species in American Museum of Natural History collections (the British Museum has no specimens from Papua New Guinea).

Distribution. — Amboyna, Ceram, and Misol, Buru(?), Aru Islands(?), Samao(?), northern New Guinea as far east as Astrolabe Bay; Manus, but not New Britain.

#### Stegonotus heterurus Boulenger

Stegonotus heterurus Boulenger, 1893: 365 (key), 367, pl. 25 (two syntypes from Duke of York Island [now BM 1946.1.15.10 and 1946.1.14.95, females] and a syntype from New Britain [now BM 1946.1.14.91, female]); Werner, 1899: 374 (largest specimen, Berlin Museum, 840 mm long, the tail 120 mm); Werner, 1900: 87 (review, fig.); Wandolleck, 1911: 14 (Namatanai and Muliama, New Ireland).

Material examined: four specimens:

New Britain District: — New Britain (no other data): BM 1946.1.14.91 (female, syntype); — Rabaul, New Britain Island: AMNH 107181 (male); — Duke of York Island: BM 1946.1.14.95, 1946.1.15.10 (females, syntypes).

Description. — Supralabials 7 (third and fourth entering eye); infralabials 8-10; preoculars 2; postoculars 1 (2 in one); anterior temporals 2, lower excluded from postoculars; scales 17-17-15 (17-17-16 in one); ventrals 193 (New Britain male), 185 (New Britain female), 178-181 (two Duke of York females); subcaudals 87 (male), 76-82 (females), all entire in New Britain specimens, but 8, 18 divided in the two Duke of York specimens. Maxillary teeth 9 (or 8) + 2 + 3; palatine teeth 13 or 14; pterygoid teeth 20-26; dentary teeth 15 or 16. Hemipenis (inverted) of AMNH 107181 extending to subcaudal 13, with spinulose armature beginning at subcaudal 5, the spines diminishing in length distally, most conspicuously at subcaudal 9; a bare area at tip opposite sulcus, bordered by numerous small and spineless calyces. Sooty vertebrally, lightening to brown on sides and under-surface (but BM 1946.1.14.91 showing only faint pigmentation on ventrals and Werner's [1899] Berlin Museum specimen uniformly yellowish white); lateral two scale rows, ventrals, and subcaudals with whitish edges; upper lip dirty white at light brown, paler than crown.

Remarks. — So closely does this form resemble S. modestus that I suspect it is only a geographic variation of that species.

Distribution. — New Britain, Duke of York, and New Ireland.

# Stegonotus parvus (Meyer)

Lycodon parvus Meyer, 1875: 137 (original description; "Neu-Guinea, Johi"). Stegonotus modestus (part); Boulenger, 1893: 366 [and fig. 25 on p. 364?] (Murray I., Torres Straits); De Rooij, 1917: 115 (general account).

- (?) Stegonotus modestus (part); Lidth de Jeude, 1896: 254 (15 specimens from Astrolabe Bay, "agreeing with Boulenger's description of S. reticulatus"; [since S. cucullatus has not been taken near Astrolabe Bay, but S. parrus is not uncommon there, it is likely at least some of these specimens are S. parrus]); Lidth de Jeude, 1906: 525 (Manokwari, ventrals 181); Méhelÿ, 1898: 171 (Stephansort, 3 males with 176-181 ventrals [female with 212 ventrals is probably S. modestus]).
- (?) Stegonotus modestus (not of Schlegel); Lidth de Jeude, 1911: 272 (Lorentz R.: Bivak I., Lorentz R. [these may be S. diehli with 17 scale rows]); Andersson, 1913: 74 (Bogadjim, with 170 ventrals, 90 subcaudals); Lampe, 1913: 84 (Bogadjim); De Jong, 1927: 302 (Digoel R., Pionierbivak on Mamberamo R., with 178-188 ventrals, 94-101 subcaudals).

Material examined: 40 specimens:

West Irian: — Sabron, Cyclops Range: BM 1938.6.9.44 (female).

AUSTRALIA: — Murray Island, Torres Straits: BM 83.4.14.25-26 (male and female), 85.6.30.65-66 (male and female).

"New Guinea" (collected by MacFarlane and probably from lower Fly River): BM 78.10.16.17 (male).

Papua New Guinea: Western District: — Lake Daviumbo: AMNH 59891 (female). West Sepik District: — Miliom (1500 ft): AMNH 100044 (male); — Lumi (1700 ft): AMNH 100045 (female). East Sepik District: — Wewak: AMNH 75023-4 (females), 75025 (male). Western Highlands District: — Tigi Plantation (Sepik drainage): AMNH 103668, 103671 (males), 103669-70 (females) Madang District: — Manam I.: YPM [Field No.] 139 (male); — Ramu River delta: BM 1926.5.31.17 (male); — Bostrem Bay: AMNH 107193, YPM [Field No.] 123 (females); — Errima: BM 1922.11.24.36-7 (males). Morobe District: — Kassam (Upper Markham valley): AMNH 85724; —

Gurakor: AMNH 85716 (female); — 12 mi. west of Lae: AMNH 95156 (male); — Lae: BM 1922.11.24.38 (female), 1967.595 (male), AMNH 66750, 66752, 85721, 85723 (females), 85722, 95154 (males); — Butibum River 7 mi. north of Lae: AMNH 95577 (male); — Pindiu (Rawlinson Range, Huon Peninsula, 3000 ft): AMNH 95571, 95573 (males), 95572, 95574 (females); — Kotyen (Rawlinson Range): AMNH 95576 (male).

Description. — Supralabials 7 (third and fourth entering eye) or 8 (fourth and fifth entering eye), rarely 9 with fourth and fifth entering eye (7 usual in Morobe District, 8 usual in Sepik and Madang Districts); infralabials 8-10; preoculars 2, occasionally 1; postoculars 2, occasionally 1; anterior temporals 2 (rarely 1), the lower in contact or not with the postoculars; scales 17-17-15; ventrals subject to geographic variation and sexual dimorphism, 174-196 (males), 165-192 (females); subcaudals subject to sexual dimorphism: 88-99 (males), 82-94 (females) in north, 73 (male), 68-77 (females) in Fly River and Murray Island specimens. Maxillary teeth 15-19; palatine teeth 12-18; pterygoid teeth 23-33; dentary teeth 16-18 (Fly River and Murray Island), 17-21 (Northern). All tooth counts subject to geographic variation. Hemipenis as in S. diehli and S. modestus, to subcaudal 8-15 (18 specimens). Colour as in S. modestus, but upper lip paler (nearly or quite the same tone as the lower lip and throat) and venter and underside of anterior half (or more) of tail of an immaculate pale colour between the angulations. Usually the venter, underside of tail, and edges of more lateral scales yellowish white, but pinkish tan in Huon Peninsula (Pindiu, Kotyen) specimens.

Geographic variation. — Ventral count is highest in Huon Peninsula specimens: 190-196 (three males), 187-192 (two females). The lowest ventral counts are found in Sepik and Madang Districts: 174-186 (seven males), 165-174 (five females). East and West Sepik District specimens (five) have 17-19 maxillary teeth, against 15-17 in the others examined. Other variations noted in Description.

Remarks. — The low ventral count (177) combined with the 17 scales "Ohne Endgruben" and two preoculars make it virtually certain that the Lycodon parvus of Meyer (1875) is this species, which has been confounded with Stegonotus modestus by all subsequent workers. In the Districts where S. parvus is sympatric with S. modestus (East and West Sepik, Madang) the two are distinguished by the seven supralabials and ventrals in excess of 200 of S. modestus against eight supralabials and ventrals fewer than 190 in S. parvus. But east of the range of S. modestus, in Morobe District, S. parvus usually has seven supralabials and Huon Peninsula specimens have 187-196 ventrals.

S. parvus probably originated as an eastern variation of S. modestus,

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perhaps in the Huon Peninsula at a time when the Saruwaged-Rawlinson-Finisterre Range formed an island. After development of reproductive isolation, S. parvus invaded the lowlands and extended westward into the range of S. modestus (and also, S. diehli). In this westward invasion, selection favoured those S. parvus least like S. modestus, and hence the "character displacement" in supralabial, ventral, and dental counts. The four Western Highlands District specimens of S. parvus have rather high ventral counts (189-190); one has only seven supralabials and another has seven (right) and eight (left). Although western, they are from south of the range of S. modestus and are not under selective pressure to maintain a "character displacement" relative to S. modestus.

I refer to this species some specimens from the Fly River drainage in Western District and Murray Island in Torres Straits, because of their similarity in colour, dentition, and ventral counts to the Western Highlands specimens; but the subcaudal counts of Fly River-Murray Island specimens are conspicuously lower (see Description) and further material may show that this is a distinct form.

Distribution. — Range in West Irian uncertain, but including Jobi Island, Pionierbivak on Mamberamo River (De Jong, 1927: 302, as S. modestus, but ventrals given as 183-187); the Lorentz and Digoel Rivers? (these perhaps S. diehli with 17 scales); the Cyclops Range; northern Papua New Guinea in Torricelli and Prince Alexander ranges, the Sepik slope of the Bismarck range, the Adelberts, the Markham Valley (the most abundant Stegonotus at Lae), and the Huon Peninsula; Manam Island; the Fly River, and Murray Island, Torres Straits(?).

#### Stegonotus spec. cf. parvus

Stegonotus modestus (part); Boulenger, 1893: 366 (Duke of York I.); Werner, 1900: 85 (Ralum, northeast coast of New Britain).

Material examined: three specimens:

New Britain District: New Britain Island: — Iambon (1500 ft), Whiteman Range: AMNH 82316 (female); — Gazelle Peninsula: BM 98.3.3.23 (male). Duke of York Island: BM 77.2.24.20 (female).

Description. — Supralabials 8 (fourth and fifth entering eye); infralabials 8-10; preoculars 2; postoculars 2 (1 in a specimen recorded by Werner, 1900: 87); anterior temporals 2, both reaching postoculars except in AMNH 82316, where lower excluded; scales 17-17-15; ventrals showing wide variation, but material available does not permit discriminating geographic variation from sex dimorphism: three males from eastern end of New Britain (including counts from Werner, 1900) 209-218, female from western part of New Britain 184, female from Duke of York Island 196; subcaudals for three males from eastern end of New Britain (including Werner's counts) 80-90, for female from western part of New Britain 73, for female from Duke of York Island 87. Maxillary teeth 12 + 3 to 14 + 3; palatine teeth 14-16; pterygoid teeth 24-31; dentary teeth 17-19. Hemipenis of BM 98.3.3.23 (inverted) to subcaudal 18, with smooth area at tip (presumably representing terminal concavity of everted organ), covered with small spines from subcaudal 4 distad, without indication of calyces. Dark brown above, including whole of upper lip, the scales less pigmented marginally than basally, those of first and second row with whitish margins. In specimen from western New Britain, all ventrals and subcaudals brownish grey with pale posterior borders; in specimens from eastern New Britain, throat and ventrals of anterior and middle part of body white (posterior ventrals and subcaudals as above); in specimen from Duke of York Island, all ventrals and subcaudals white.

Remarks. — I suspect that this is a distinct species, but further material from western New Britain may prove it only a geographic variation of *S. parvus*, with which it agrees in dentition and in having the scales more deeply pigmented basally than marginally. The western New Britain specimen agrees with *S. parvus* in ventral count, but specimens from eastern New Britain and Duke of York have high counts suggestive of *S. cucullatus* and *S. modestus*. But it is only the Duke of York specimen that agrees with *S. parvus* in unpigmented venter and subcaudals. The single male seen has a longer hemipenis than in all other *Stegonotus* examined, and since the spinulose armature begins unusually proximally (at subcaudal 4), the spinulose region is particularly long. Unfortunately, no male from western New Britain is available.

Distribution. — New Britain and Duke of York Islands.

## Stegonotus cucullatus (Duméril, Bibron & Duméril)

Lycodon cucullatum Duméril, Bibron & Duméril, 1854: 376 (original description; New Guinea); Sauvage, 1877: 19 (redescription of holotype).

Stegonotus cucullatus; Boulenger, 1893: 365 (synonymy; Fly R., Murray I., Cape York); Boulenger, 1914: 264 (Mimika R.).

Zamenophis australis Günther, 1872: 21 (original description; holotype, now BM 1946.1.14.93, from Cape York); Günther, 1877: 130 (referred to Lielaphis; Lycodon keyensis Doria a synonym).

Lycodon keyensis Doria, 1875: 31, pl. 12 (original description; Kei Is.; fig.).

Lycodon magnus Meyer, 1875: 136 (original description; New Guinea, Mysore

[= Biak] I.).

Stegonotus magnus; Lidth de Jeude, 1911: 273 (Bivak I., Lorentz R.); De Rooij, 1917: 114 (Lorentz R., Mysore [= Biak] I.); Werner, 1929: 20 (key); Forcart, 1953: 62 (Vogelkop near Sorong); Brongersma, 1957: 310 (trachea).

Lycodon darleyensis Macleay, 1878: 38 (original description; Darnley I., Torres Straits).

Herbertophis plumbeus Macleay, 1883: 432 (original description; Herbert R., Queensland).

Stegonotus plumbeus; Boulenger, 1893: 368 (copied description); Boulenger, 1914: 264 (Launch Camp, Setekwa R.; distinctness from S. modestus doubtful); De Rooij, 1917: 117 (Setekwa R.).

Stegonotus reticulatus Boulenger, 1895: 31 (original description; syntypes, now BM 1946.1.14.87-8, from Fergusson I.); Boulenger, 1896: 619 (Fergusson I. and New Guinea).

Stegonotus modestus (not of Schlegel); Boettger, 1894: 120 (southeast New Guinea [first description of reticulatus pattern]); Roux, 1910: 242 (Kei Is.); Burt & Burt, 1932: 567 (Bougainville I.); Parker, 1936: 90 (Mafulu; Kokoda).

Stegonotus modestus (part); Lidth de Jeude, 1896: 254 (S. cucullatus, S. reticulatus synonyms of S. modestus); De Rooij, 1917: 115 (fig.); Werner, 1929: 60 (key).

Stegonotus modestus (part, neither of Schlegel); Boulenger, 1897: 704 (Bara-Bara; S. reticulatus a variety of S. modestus); Boulenger, 1914: 264 (Launch Camp, Setekwa R.); Loveridge, 1948: 382 (Finschhafen, Toem).

# Material examined: 92 specimens:

West Irian: — Fak-Fak: BM 1908.6.30.12 (female), MCZ 7312a, b (males); — Mimika River: BM 1913.10.31.198-9 (males); — Launch Camp, Setekwa River: BM 1913.11.1.106-7 (males); — Hollandia: AMNH 62037 (male).

"New Guinea" (probably lower Fly River): BM 80.9.23.5 (male). Papua New Guinea Western District: - "Fly River": BM 85.6.30.32-3 (females); - 5 mi. below Palmer Junction: AMNH 57504 (male), 57526 (skin, sex?), 57529 (female); -Daru I.: AMNH 106279 (female). Gulf District: — Purari River: BM 1936.7.7.31 (male); — Middletown: MCZ 59051 (male). Central District: — Mafulu (4000 ft): BM 1935.5.10.160 (female), AMNH 59065 (male). — Karema: AMNH 103673 (male); — Port Moresby: AMNH 82523 (female); — Ower's Corner: AMNH 82524 (male). Milne Bay District: -- Baiwa, Moi-Biri Bay: AMNH 73967 (female); --Menapi, Cape Vogel: AMNH 73971 (male); — Samarai I.: AMNH 73957 (male); — Bara Bara, Normanby I.: BM 97.12.10.120 (male); - Waikaiuna, Normanby I.: AMNH 76718 (male); — Fergusson I.: BM 1946.1.14.87-8 (female and male, syntypes of Stegonotus reticulatus); — Woodlark I.: BM 96.7.8.5-6 (males); — Kulumadau, Woodlark I.: AMNH 76622-4 (males), 76614 (female); — Abaleti, Rossel I.: AMNH 76677 (female), 76678 (male). East Sepik District: — Wewak: AMNH 75249 (male), 75258-9 (females). Western Highlands District: — Nondugl: AMNH 82525 (male). Chimbu District: — Kup: AMNH 72783, 72785-6 (males), 72784 (female); — Bomai: AMNH 98865 (male); - Karimui: AMNH 98866-7, 98871-2 (males, last head only), 08868-9 (females). Eastern Highlands District: — Oruge: AMNH 08492 (male); — Aiyura: AMNH 95643 (male); — Arau: AMNH 85720 (male); — Gono: AMNH 85717-8 (females); — Purosa, near Okapa: AMNH 85719 (male). Morobe District: - Umi River: AMNH 85713-4 (males); - Gurakor: AMNH 85715 (female); -- 13 mi. NW of Lae: AMNH 95157 (male); -- Munum, near Lae: BM 1922.11.24.39 (male); - Pindiu (Rawlinson Range, Huon Peninsula): AMNH 95575 (male); — Garaina, 2300 ft: AMNH 95619, 95621-2, 101086, 101093, 101095, 107180 (males), 95623, 101094, 101096-8, 103666-7, 104082-3 (females). Northern District: — Kokoda: BM 1935.5.10.159; — Mt. Victoria: BM 96.10.31.22. Bougainville District: — "Bougainville I.": AMNH 42402.

AUSTRALIA: — Murray I., Torres Straits: BM 78.10.16.26-7 (males), 78.10.16.28 (female). Queensland: — "Cape York": BM 1946.1.14.93 (female, holotype of Zamenophis australis); — Mossiman River Gorge, 300 ft: AMNH 69262 (female); — Lake

Eadman, 2400 ft: AMNH 69264 (male); — Atherton: AMNH 82227 (male). Northern Territory: — King River: BM 1926.2.25.95 (skin, sex?); — Katherine: BM 1926.2.25.94 (female).

Description. — Supralabials 8 or 9 (third and fourth, rarely third to fifth, entering eye); infralabials 8-11, usually 10; preoculars usually 2, occasionally 1; postoculars 2 (rarely 1 or 3); anterior temporals 2, usually both meeting postoculars except in southern Morobe, Northern, and Milne Bay (mainland and islands) Districts, where lower usually excluded; scales 17-17-15 (most common), 17-19-15, 19-19-15, 18-19-15, or 19-19-17; ventrals showing geographic variation and sex dimorphism, 187-228 (males), 189-222 (females); subcaudals showing geographic variation and sex dimorphism, 75-101 (males), 69-91 (females). Maxillary teeth 15-20; palatine teeth 12-18; pterygoid teeth 21-33; dentary teeth 16-23; all tooth counts showing geographic variation. Hemipenis to subcaudal 8-17 (49 specimens), with spinose calyces on distal half; specimens from Woodlark and Rossel Islands (inverted organ examined) with a much smaller bare terminal area than in other Stegonotus, perhaps indicating a smaller terminal concavity of the everted organ.

Colour and geographic variation. — In West Irian, brown, this extending conspicuously onto lateral ends of ventrals, with pale borders on lower lateral scales, but with darker brown borders of more dorsal scales, on nape, and on head scutes; upper lip light tan; yellowish white or tan below, usually with brown on anterior edge of each subcaudal; Australian, lower Fly River (Daru Island), and Murray Island specimens similar in colour, except AMNH 82227 (Atherton, Queensland) which is plumbous grey with a conspicuous dark spot on each subcaudal (the pattern of "Herbertophis plumbeus" but not associated here with any other peculiarity). Rossel Island, Woodlark Island, and Bougainville specimens agree in colour with Australian and West Irian specimens; so does a Kratke Mountains specimen (AMNH 85720), except that the scales show (under magnification) very narrow black borders and the tan belly is almost as dark as the sides.

In Central District and the upper Fly River (Palmer Junction) of Western District, the mainland of Milne Bay District, Samarai, Fergusson, and Normanby Islands, Western Highlands and Chimbu Districts, at Wewak (East Sepik District) and Gono (Eastern Highlands District) the ground colour pale grey, with very conspicuous dark borders of the scales (the "Stegonotus reticulatus" pattern). This pattern can be derived from that of the Kratke Mountains snake by broadening of the dark edging of the scales and elimination of the reddish and brownish tone to make the ground colour pale grey. AMNH 85719 (Purosa, Eastern Highlands District) seems intermediate,

since the dark scale margins are conspicuous, but the ground colour is pinkish tan. In Morobe District and at Kokoda the colour is dark sooty grey or dark greyish brown, this colour extending conspicuously onto the ventrals, with inconspicuously darker margins of the scales (sometimes visible only when the specimen is immersed). This "sooty" pattern can be derived from the reticulatus pattern by darkening of the ground colour, with or without some lightening of the scale borders, and some intermediate specimens occur. AMNH 98492 (Oruge, Eastern Highlands District) is light sooty with rather easily visible darker sooty borders of the scales. In AMNH 98865-9, 98871-2, a series from Bomai and Karimui, Chimbu District, most are of the reticulatus pattern, but 98866 is dark brownish grey above, fading to light smokey grey on the sides and lateral ends of the ventrals, but with the edges of the scales slightly darker to show a faint reticulatus pattern; in 98871 this reticulatus pattern is more conspicuous than in 98866, but less so than in the others.

AMNH 57529 (Palmer Junction, Fly River) and MCZ 59051 (Middletown, Gulf District) show a possibly mimic pattern, suggestive of *Micropechis ikaheka*. Head brown and scales behind head mottled with brown, but most of anterior half of body creamy white above and beneath; from midbody backward, more and more scales showing brown tips or borders until posteriorly and on tail each scale brown with a light basal spot; a few ventrals with dark lateral spots, but otherwise whitish; subcaudals edged with light greyish brown.

Remarks. — Duméril, Bibron & Duméril (1854) and Boulenger (1893) chose a worthless character (shape of the rostral shield) to diagnose this species, and when this character failed, most workers jumped to the conclusion that this quite distinct species is a synonym of *S. modestus*. *S. cucullatus* differs from *S. modestus* in many respects, but most strikingly in being much larger, sexually mature specimens rarely measuring less than a metre, whereas the other New Guinea *Stegonotus* (except Fergusson Island *S. guentheri*) are rarely more than a metre long.

Stegonotus cucullatus appears to be the New Guinea and Australian representative of the Moluccan S. batjanensis, but differs in having the lower preocular not fused to the third supralabial, and so there are two preoculars (unless fused with each other) and usually only two supralabials enter the eye; further, a strong minority of the scales of S. batjanensis show tiny scale pits, absent in S. cucullatus; and juvenile S. batjanensis show transverse pale cross bands, absent at all ages in S. cucullatus. None the less, these large (adults between 1 and 2 m) snakes may prove to be conspecific, the Moluccan form seeming the more primitive in having vestiges of scale

pits. The equally large S. muelleri of the Philippines seems also to be closely related; indeed, nothing in Inger's (1967) account of that form will exclude all New Guinea specimens of S. cucullatus.

Stegonotus magnus (Meyer, 1875), supposedly characterized by having 19 scales at midbody, is a synonym of this species. Of three specimens collected at Fak-Fak by Pratt and homogeneous in most features, one (BM 1908.6.30.12) has the scales 17-17-15, another (MCZ 7312a) has 18-19-15, and the third (MCZ 7312b) has 17-19-15. Five of six Australian specimens have the scales 17-17-15, but BM 1926.2.25.94 (Katherine, Northern Territory) has 19-19-17 without showing other differences. Among six seemingly alike specimens from Woodlark Island, BM 96.7.8.5 has the scales 19-19-15, the others having 17-17-15. AMNH 57529 (Palmer Junction, Western District, scales 17-17-15) and MCZ 59051 (Middletown, Gulf District, scales 17-19-15) agree in a peculiar Micropechis-like colour pattern. There is no indication that presence of 19 scale rows is correlated with any other difference.

This species seems more omnivorous than the other New Guinea forms. Among 18 stomachs with identifiable food, 6 contained squamatan eggs, 2 contained frogs, 9 contained lizard remains, 2 contained orthopterans, and 4 contained mice. This contrasts with: S. guentheri (four stomachs with identifiable food), only squamatan eggs; S. parvus (8 stomachs with identifiable contents), 5 with squamatan eggs, and 4 with lizard remains; S. diehli (10 stomachs with identifiable contents), 6 with squamatan eggs and 5 with lizard remains. The large size of S. cucullatus permits such omnivorous habits.

Distribution. — New Guinea, including Biak Island; Kei Islands; Fergusson and Normanby Islands; and Woodlark and Rossel Islands; if data correct for AMNH 42402, Bougainville Island in the Solomons, although Parker did not take it there; Queensland and Northern Territory, Australia and Torres Straits islands.

## Stegonotus guentheri Boulenger

Stegonotus guentheri Boulenger, 1895: 31 (original description; syntypes, now BM 1946.1.11.37-9, from Fergusson I.); Boulenger, 1896: 619 (repeat of above).

Stegonotus guentheri (part); De Rooij, 1917: 118 (Fergusson I.; Bongu [Astrolabe Bay region; probably S. diehli]); Burt & Burt, 1932: 657 (Goodenough I. [one is an Aspidomorphus lineaticollis]; Kitava, Kiriwina Group).

Stegonotus modestus (not of Schlegel); Boulenger, 1896: 619 (Trobriand Is.).

Material examined: 16 specimens:

MILNE BAY DISTRICT: Fergusson Island: BM 1946.1.11.37 (male, syntype), 1946.1.11.38-9 (females, syntypes). Goodenough Island: AMNH 42375, 43278-9, 42381,

73964, 73985 (males), 42374, 42377, 42380 (females). Normanby Island: — Waikaiuna: AMNH 76702, 76704, 76715 (males), 76712 (female). Kiriwina (= Trobriand) Islands: — no other data: BM 95.10.17.47 (male); — Kitava: AMNH 42389 (male).

Description. — Supralabials usually 8 (fourth and fifth entering eye), but 7 (third and fourth entering eye) in Kiriwina specimens and unilaterally in a Goodenough and a Normanby specimen (in addition, AMNH 76702, Normanby, has 7 [left], 6 [right], third and fourth entering eye); infralabials 8-10; preocular 1 (2 in AMNH 76712); postoculars 2; anterior temporals 1 or 2 (when 2, the lower usually not meeting postoculars); scales 15-15-15, ventrals sexually dimorphic (no significant geographic difference), 188-195 (males), 176-190 (females); subcaudals 71-76 (five males), 64-78 (four females). Maxillary teeth 12 + 3 (11 + 3 in two), the diastema short and the tooth preceding it compressed and with a single posterior cutting edge; palatine teeth 12-14; pterygoid teeth 20-23; dentary teeth 15-18, with gradual transition from long anterior to short posterior teeth. Hemipenis as in S. cucullatus, to subcaudal 9-15 (12 specimens); brown, the lower scales with white edges, those of first row almost entirely white; ventral surface and upper lip yellowish white, the lateral ends of the ventrals with small brown spots in Fergusson Island specimens.

Remarks. — Although dental and hemipenial characters show this species is closely allied to S. cucullatus, the 15 scale rows of S. guentheri have led to its confusion with S. diehli (e.g. Loveridge (1948: 383) referred two S. diehli from Fak-Fak to this species). On Fergusson and Normanby Islands this species is sympatric with S. cucullatus, which there shows the reticulatus pattern, this sympatry proving specific distinction. However, S. guentheri is rather similar in colour to the brown Australian and lower Fly River S. cucullatus, still more so to Woodlark and Rossel Island S. cucullatus. Probably the brown S. guentheri retains the primitive colour of S. cucullatus, from which it was derived as an insular race, and Normanby and Fergusson Islands have been re-invaded by reticulated S. cucullatus, subsequent to development of reproductive isolation.

Distribution. — Fergusson, Goodenough, Normanby, and Kiriwana (= Trobriand) Islands.

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