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Results of the Archbold Expeditions. No. 112. The Snakes of the Huon Peninsula, Papua New Guinea

S. B. MCDOWELL¹

ABSTRACT

The snakes known from the Huon Peninsula (from the longitude of Lae eastward) are listed and discussed, mainly on the basis of specimens collected by the Seventh Archbold Expedition but using other collections as well. The taxonomy of the genus *Dendrelaphis* in the Australian region is discussed and the following species are recognized: *D. punctulatus* (including *D. lineolatus*); *D. calligastra*, *D. salomonis*, *D. lorentzi*, *D. papuensis* (these four have usually been regarded as conspecific); and *D. gastrostictus* (including *D. meeki*); hemipenial morphology, dentition, and braincase

form are used for discriminating the species. A misidentification of *Typhlops inornatus* as *Ramphotyphlops flaviventer* is corrected. The snake fauna, like the frog and lizard faunas previously discussed by Zweifel, is most easily explained as the result of dispersal to a Pliocene island that became joined (probably in the Pleistocene) to the New Guinea mainland, with a lowland fauna occupying this zone of juncture. Little, if any, endemism is indicated for the Huon snake fauna and there is no special resemblance to the snake fauna of nearby New Britain and Umboi.

INTRODUCTION

This represents a long-delayed report on the snakes collected by the Seventh Archbold Expedition to the Huon Peninsula with particular attention to the region of Mt. Rawlinson. Zweifel (1980) has already reported on the frogs and lizards from there.

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¹ Professor of Zoology, Department of Zoology and Physiology, Rutgers University, Newark, New Jersey 07102.

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THE GEOGRAPHIC SETTING

"Huon Peninsula" is here used in the same sense as used by Zweifel (1980), to include the portion of mainland New Guinea projecting east of the longitude of Lae, between the Vitiaz Strait and the Huon Gulf. Lae is included in the "Huon Peninsula," even though much of the fauna of Lae is from the Markham Valley; Saidor is *not* included in the "Huon Peninsula," since Saidor is west of Lae, even though Saidor is on the north coast of the Finisterre-Saruwaket region and might be expected to have a fauna similar to

that of the eastern end of the Finisterre-Saruwaket elevation (the exclusion of the western end of this elevation has the practical advantage of concealing a colossal ignorance of the fauna of a part of Papua New Guinea that has been insufficiently collected). "Lae" in the literature has had various meanings, including mountains to the west or south of Lae and separated from the Huon Peninsula by the Markham River Valley, and the inclusion of Lae as part of the Huon Peninsula introduces some problems of ambiguous locality references.

The localities of the Huon Peninsula, as here defined, are given in Van Deusen (1977) and Zweifel (1980). These papers also give a summary of previous work on the Huon Peninsula fauna, to which should be added two small collections: Potter collected some specimens, now in the British Museum (Natural History) from "Huon Gulf" which may have come from the northern shore of the Gulf (i.e., the Huon Peninsula); M. C. Kurtz collected some specimens, now in the American Museum of Natural History, from Lae and from Gusiko.

Unless otherwise noted, specimen numbers given below are American Museum of Natural History numbers (AMNH).

SYSTEMATIC ACCOUNTS

TYPHLOPIDAE

Typhlops inornatus Boulenger

ZMB 24345 Sattelberg

Vogt (1911) and Sternfeld (1913) listed "*Typhlops flaviventer*" from Sattelberg, on the basis of this specimen, which is a female *Typhlops inornatus*, similar in most respects to the Bulolo specimen described and figured by McDowell (1974). ZMB 24345 has: scales 22-22-22, with 359 + 15 along the back between rostral and terminal caudal spine; nasal cleft almost complete, from very near rostral to supralabial II, horizontal in its anterodorsal portion; supralabial II overlapping lower end of preocular; supralabial III overlapping lower end of a subocular cut off from the ocular; preocular undivided, larger than ocular; nasals separated by rostral-prefrontal contact; nasals, preoculars, and rostral dense-

ly studded with glands, centrally as well as along scale margins; no distinct rectal caecum. This re-identification removes *Ramphotyphlops flaviventer* from the list of Huon Peninsula records and that species would have a range from Ternate and Halmahera, Morotai, Batjan, Batanta, Salawati, the Vogelkop and Onin Peninsula of western New Guinea, Manus, New Britain and Duke of York Is., Nissan Atoll, the Solomons, and Vuna Pi in Fiji.

Typhlops depressiceps Sternfeld

66739 Lae

This specimen has already been used in the description given by McDowell (1974); since then, it has been discovered that this species ranges to the Trobriand (Kiriwina) Islands, where Heatwole (1975) recorded it (I have

seen a Trobriand specimen and agree with this identification); it is not unlikely that this seemingly rare species has a fairly extensive distribution in New Guinea. The Lae specimen was discovered about a foot under sod and was, unfortunately, cut in half by the spade; attempts to recover the rear half were unsuccessful.

Ramphotyphlops erycinus (Werner)

66737, 95513 Lae

In addition to these Lae records, Loveridge (1948) has recorded this species from Finschhafen. The species has a fairly extensive distribution in northern New Guinea, extending westward to the Mamberamo River in Irian Jaya.

Ramphotyphlops braminus (Daudin)

66738, 66740, 95130, 95512, 126580–85 Lae

It is certain that this species is now established at Lae; whether or not it occurred there before World War II is uncertain. As an all-female species, presumably able to propagate itself in a new locality from a single individual (see McDowell, 1974), and a commensal of man, this form is readily introduced by man and has a very extensive distribution; just where it is autochthonous is unknown.

BOIDAE

Liasis papuanus Peters and Doria

66761 Lae

This species is found almost throughout mainland New Guinea, as well as on Mysol, Biak, and Fergusson Islands. According to M. C. Kurtz's field notes, the Lae specimen was taken in the morning in a field of Kunai and cane grass.

Liasis albertisii Peters and Doria

95532 Finschhafen at about 500 ft.; 95533 same, but sea level. Also, from Lae and vicinity: 66746, 66756, 95531, 95535, 103869, 107148

Widespread throughout New Guinea (also Salawati, Biak, Normanby, and Mussau) at from sea level to 4000 ft. and one of the more common species. McDowell (1975) suggests that this species and *L. boa* (Bismarck Archipelago other than Mussau; also Umboi Is.

and Nissan Atoll) make up a superspecies and it is interesting that one of the two Finschhafen specimens (95532, juvenile female) shows faint traces of light and dark rings on the body, an approach to *L. boa*. This feature cannot be attributed entirely to juvenility, since Brongersma (1953) did not find crossbands even in late embryos from Fak-Fak. However, no trace of dark crossbars can be found in the other Finschhafen specimen (95533, adult male). This latter specimen was found dead on the road, but 95532 was found crawling on the tunnel ceiling about 200 ft. inside Seborgisung Cave and had a ball of hair in the intestine.

Python amethistinus (Schneider)

95530 Mt. Rawlinson at south ridge above Gang Creek, about 5200 ft.; 95531 Masba Creek, about 2000 ft.; 95141–42 Lae

The first of these two specimens represents the highest altitude record for the species, which elsewhere in its extensive distribution through the Moluccas, New Guinea and adjacent islands, and Queensland is not known from above 4800 ft. (AMNH 82327, Mt. Vale, western New Britain) and most records are from between sea level and 1000 m. The total length of 95530 was 3.47 m. (body length 2.94 m.); 95531 had a total length of 121 in. (3.07 m.) (collectors' measurements; both specimens are skinned out, except for head and tail; both are females, without note of any stomach contents). Zweifel (field notes) records that 95530 had been in a hole 90 ft. above ground level in the trunk of a tree of the genus *Syzygium*.

Another species of *Python*, *P. boeleni*, has been recorded from "Lae" by Worrell (1958; as *Liasis taronga*). No other specimens have been taken from Lae, although the species is known from the Eastern Highlands west of Lae and from Wau, southwest of Lae, and as noted by Brongersma (1969), this "Lae" record probably refers to the mountains behind Lae, rather than to Lae itself.

Chondropython viridis (Schlegel)

95131–33 Lae; 95521 Butibum R., 7 mi. n of Lae; 95522–23 Kabwum, about 4500 ft.; 95524–25 Pindiu, 3000 ft.; 95526 Masba Creek; 95527 Numbut; 95528 Kotkin, Mt. Rawlinson; 95529 "Huon Peninsula." Also

recorded from Sattelberg by Lönnberg (1900), Vogt (1911), and Sternfeld (1913)

Both 95527 and 95528 had hair in the stomach; the stomach was empty in the others, aside from nematode parasites found in all except 95526. All show the northern color pattern for their species, with the white scales scattered randomly rather than organized into a vertebral stripe (as it is in specimens from southern New Guinea).

This is a widespread and fairly common New Guinea species (also Mysol, Salawati, the Arus, and Geelvink Bay islands) but is unknown from Umboi or the Bismarck Archipelago.

Candoia carinata (Schneider)

95516 near Pependangu, about 3200 ft.; 95517 near Pindiu, about 3000 ft.; 95519–20 Finschhafen; 66747, 85665, 95138–30, 95518, 103635 Lae

As discussed by McDowell (1979), most populations of this wide-ranging (from Sulawesi to the Santa Cruz Is.) species fall clearly into two classes: *long-tails*, with all individuals having more subcaudals than predicted by the regression line describing the closely related species *C. bibroni* (expected subcaudals = $1.13 + 0.238$ ventrals); and *short-tails*, with all individuals having fewer subcaudals than predicted by the regression line for *C. bibroni*. These two classes, defined by subcaudal count relative to ventral count, fit well—but not exactly—with the occurrence of certain color patterns, frequency of pelvic spurs in females, length of separation between furcation of the hemipenis and of sulcus spermaticus, and shape of the post-orbital bone.

The four specimens from the eastern Huon Peninsula (95516–17, 95519–20) are typical short-tails, not much different from specimens from the eastern Papuan Peninsula and d'Entrecasteaux Is. Lae, on the other hand, is anomalous and of the six Lae specimens seen by me, three (66747, 95138–39) are typical long-tails (similar to Irian Jaya, north coast of Papua New Guinea, and Bismarck Archipelago specimens) but the other three (85665, 95518, 103635) are typical short-tails. The sample is too small to permit conclusions as to whether short-tails and long-tails are

behaving as one species or as two in the Lae region, and it is hoped that those with ready access to *Candoia carinata* in the Lae region will settle the question.

It may be noted that Umboi specimens (see McDowell, 1979) are short-tails, but differ from Huon Peninsula specimens in color, having one pair of longitudinal stripes or none on the neck, rather than the two pairs of longitudinal stripes seen in Huon Peninsula specimens. New Britain specimens are long-tails.

Candoia aspera (Günther)

95515 Masba Creek, 2000 ft.; 66741–44, 95137, 95514 Lae; BPBM 3727, 5507–08 Busu R., nw of Lae, about 100 ft. Also recorded from Sattelberg by Vogt (1911), and from Finschhafen by Loveridge (1948)

The Masba Creek specimen had an empty stomach, but BPBM 5507 (Busu R.) regurgitated a partly digested frog and lizard when chloroformed (F. J. Radovsky's notes on label) and 66741 (Lae) contained skink fragments and a beetle, the latter probably secondarily ingested. This species is found throughout New Guinea (except the Oriomo Plateau and the higher elevations of the central mountainous spine) and the Bismarck Archipelago, Manus Group, Geelvink Bay islands, Waigoe, Batanta, Salawati, and Mysol.

COLUBRIDAE

GENUS *DENDRELAPHIS* BOULENGER

All New Guinea–Solomons–Australian members of this genus (except for the Sunda–Malayan *D. pictus*, known also from Mysol) seem closely related; they have but 13 scale rows, lack longitudinal black stripes on most or all of their body, and have a medium or short hemipenis (not extending past the fifteenth subcaudal). Previous taxonomy of Australasian *Dendrelaphis* has not taken hemipenial structure into account, and when the hemipenis is considered, "*D. calligastra*" appears to represent at least three quite distinct species (*D. lorentzi*, *D. papuensis*, and *D. calligastra*) with the last of these probably closely related to, but distinct from, the Solomon Island form, *D. salomonis*, that has usually been considered conspecific with it.

Since my re-interpretation of *Dendrelaphis* considerably affects my identification of Huon Peninsula material, it is necessary to give a brief summary of my conclusions.

On the basis of hemipenial structure, Australasian *Dendrelaphis* fall into three groups: the *D. lorentzi* Group, the *D. punctulatus* Group, and the *D. papuensis* Group. The *D. punctulatus* Group contains four species, but the other two groups are monotypic. These groups and species differ as follows:

I. *Dendrelaphis lorentzi* Group. The organ is moderately long (ending opposite subcaudal 12 to 15), with the major retractor muscle attaching almost, but not quite, at its tip, so that there is a short uninverted terminal awn formed by the narrowed extreme tip of the organ lying distal to the attachment of the major retractor; the distal part of the organ has numerous closely packed calyces, but each calyx has numerous small spines along its border, so that the general texture of the distal end of the organ is spinose, with inconspicuous longitudinal folds between the bases of the spinules; proximal to this spinose-calyculate region there is a region of numerous spines not mounted on calyces, but each spine much less than a subcaudal in length; this spinose zone is distinctly, but not conspicuously, set off from the spinose-calyculate zone.

Only one New Guinea species, *D. lorentzi* (van Lidth de Jeude), but the Lesser Sunda *D. inornatus* Boulenger has a similar hemipenis (although having 15 scale rows). *D. lorentzi* is known to occur sympatrically with New Guinea members of Group II.

II. *Dendrelaphis punctulatus* Group. The organ is short (not past subcaudal 10) and has a subterminal attachment of the major retractor muscles, so that (as in Group I) there is a narrow and uninverted terminal awn, which may be short (*D. gastrostictus*, *D. salomonis*) or several caudals long (*D. punctulatus*, at least some *D. calligastra*); distally, the organ has large and longitudinally drawn-out calyces that are almost or quite without spinules, so that the general texture of the inverted distal end of the organ is one of closely packed longitudinal soft folds; the proximal edge of this calyculate zone forms a diagonal free fold partially hiding the more proximal spinose zone; this proximal spinose zone has numerous small spines, much as in

Group I, but is better defined by the diagonal fold of the calyculate zone.

Represented on the New Guinea mainland by three species, *D. gastrostictus* (Boulenger), *D. punctulatus* (Gray), and *D. calligastra* (Günther), all occurring sympatrically in some parts of their ranges and also occurring sympatrically with Group I and Group III; *D. punctulatus* and *D. calligastra* also occur in eastern Australia. In addition, a fourth species (?), *D. salomonis* (Günther) occurs allopatrically to the others throughout the Solomons, from Bougainville to the Santa Cruz Is., and seems about equally similar to the three New Guinea species; it may be conspecific with one of the New Guinea species, but I am unable to guess which one, and recognize it as distinct in part out of expediency (Misima I. *Dendrelaphis* are peculiar in being melanistic, but similar in dentition, hemipenis, and counts to Solomon Is. specimens and are here referred to *D. salomonis*).

IIA. *Dendrelaphis gastrostictus* (Boulenger) [including *D. meeki* (Boulenger) and *D. nouhuysi* (van Lidth de Jeude)]. Specially characterized by the short and wide braincase, an index of which is the shape of the part of the supraoccipital bone exposed between the jaw adductor muscles, covering its lateral edges, and anterior to the axial muscles that cover the rear portion of the bone; the exposed supraoccipital is much broader than long (easily ascertained by slitting the skin just behind the parietal scutes).

Maxillary teeth very numerous, 30–41, last 3–5 longest (this count diagnostically greater than for *D. lorentzi*, *D. calligastra*, *D. papuensis*, but with slight overlap with *D. salomonis*, considerable overlap with *D. punctulatus*).

Ventrals few, 160–180 (this count diagnostically lower than for *D. punctulatus*, slightly overlapping lowest variations of *D. salomonis* and *D. papuensis*, broadly overlapping *D. calligastra*, not distinguishing from *D. lorentzi*).

Hemipenis short (ending opposite subcaudal 6–9) with short (usually less than two caudals long) terminal awn that bears small spinules and a continuation of the sulcus.

A blackish stripe on temporal region defining pale lip from dark crown (this stripe may or may not continue forward onto snout).

Known from New Guinea mainland, including the elevated interior, from Manokwari, and from Normanby Is. and Fergusson Is.

IIB. *D. calligastra* (Günther). Specially characterized among Group II forms by having maxillary teeth beneath prefrontal-maxillary articulation at least as long as—usually longer than—the posterior maxillary teeth (seen also in *D. papuensis*) and by low number of maxillary teeth, 19–25 (diagnostically lower than *D. gastrostictus*, overlapped by *D. salomonis* and *D. punctulatus*, not distinguishing from *D. lorentzi* and *D. papuensis*).

Ventral count moderate, 169–199 (overlapping counts for all other Australasian species).

Exposed supraoccipital longer than wide.

Terminal awn of hemipenis long to very long (at least two subcaudals) without continuation of the sulcus, smooth or with a few minute spinules; calyculate region proximal to the awn with few or no spinules; hemipenis of moderate length (6–11, usually 8 caudals).

A blackish stripe on temporal region isolating the pale upper lip from the dark crown, continued forward on snout to the rostral.

With an extensive distribution from the Moluccas to the Bismarck Archipelago, perhaps including Normanby Is. but not the other islands of Milne Bay Province, and to Queensland; but except on the eastern edge of the Eastern Highlands, not penetrating the elevated interior of New Guinea, although extensively distributed around the rim of the island.

IIC. *D. punctulatus* (Gray) [including *D. lineolatus* (C. Duméril); *D. macrops* (Günther); *D. elegans* (Ogilby)]. Specially characterized by large size (all Australasian *Dendrelaphis* with a snout-vent length of a meter or more belong to this species) and differs from all other Australasian *Dendrelaphis* except some specimens of *D. salomonis* in: (1) lacking a distinct black band along the temporal region isolating the dark crown from the pale upper lip, the dark crown usually fading into the pale upper lip or extending raggedly onto the supralabials; and (2) having numerous large scale pits (slightly larger than those of body scales) on the loreal, ocular, anterior temporal, and anterior supralabial regions.

Exposed supraoccipital longer than broad.

Maxillary teeth longest posteriorly, 20 to 33 in number (slightly overlapping *D. gastrostictus* counts and broadly overlapping counts for *D. calligastra*, *D. lorentzi*, *D. salomonis*, and *D. papuensis*; however, lower counts for *D. punctulatus* come from Australian material, outside the range of other species of the genus with the possible exception of *D. calligastra*, and in New Guinea and the Bismarck Archipelago, maxillary tooth counts for *D. punctulatus* are 25–33, diagnostically higher than for *D. lorentzi* and *D. calligastra* and all but eastern Louisiade Is. specimens of *D. papuensis*; there is broad overlap with *D. salomonis* in this character).

Ventrals numerous, 185–219 (diagnostically higher than for *D. gastrostictus* and, probably, for *D. lorentzi*; overlap of this count with that for *D. calligastra*, *D. papuensis*, and *D. salomonis* is too extensive to allow identification of an individual specimen, although in all regions where *D. punctulatus* and *D. calligastra* occur together and sample is adequate, the mean ventral count for *D. punctulatus* is higher than that for *D. calligastra*); highest ventral counts for *D. punctulatus*—that is, those most different from counts for *D. calligastra*—come from Australian material, where maxillary count is least efficient in separating *D. punctulatus* from *D. calligastra*.

Hemipenis as in *D. calligastra*, with similarly long awn, but sulcus extending along awn nearly or quite to the tip; inverted organ ending opposite subcaudal 6–10, modally subcaudal 8.

Palau Is., Mysol, Waigoe, Aru Is., New Guinea, d'Entrecasteaux Archipelago, Bismarck Archipelago, Torres Strait Is. and eastern Australia.

IID. *D. salomonis* (Günther). With a confusing combination of the characters of *D. punctulatus* and *D. calligastra* (allopatric to both and quite possibly conspecific with one or the other). The types (BM 1946.1.5.97 and 1946.1.6.11, "Salomon Is.") have a low maxillary tooth count (21 in each, left maxilla) and a sharply defined dark temporal streak on the dorsal ends of the supralabials, as in *D. calligastra*, combined with numerous large sensory pits on the preocular, loreal, supralabials, and temporals and a high ventral count (190, 191, respectively) as in *D. punc-*

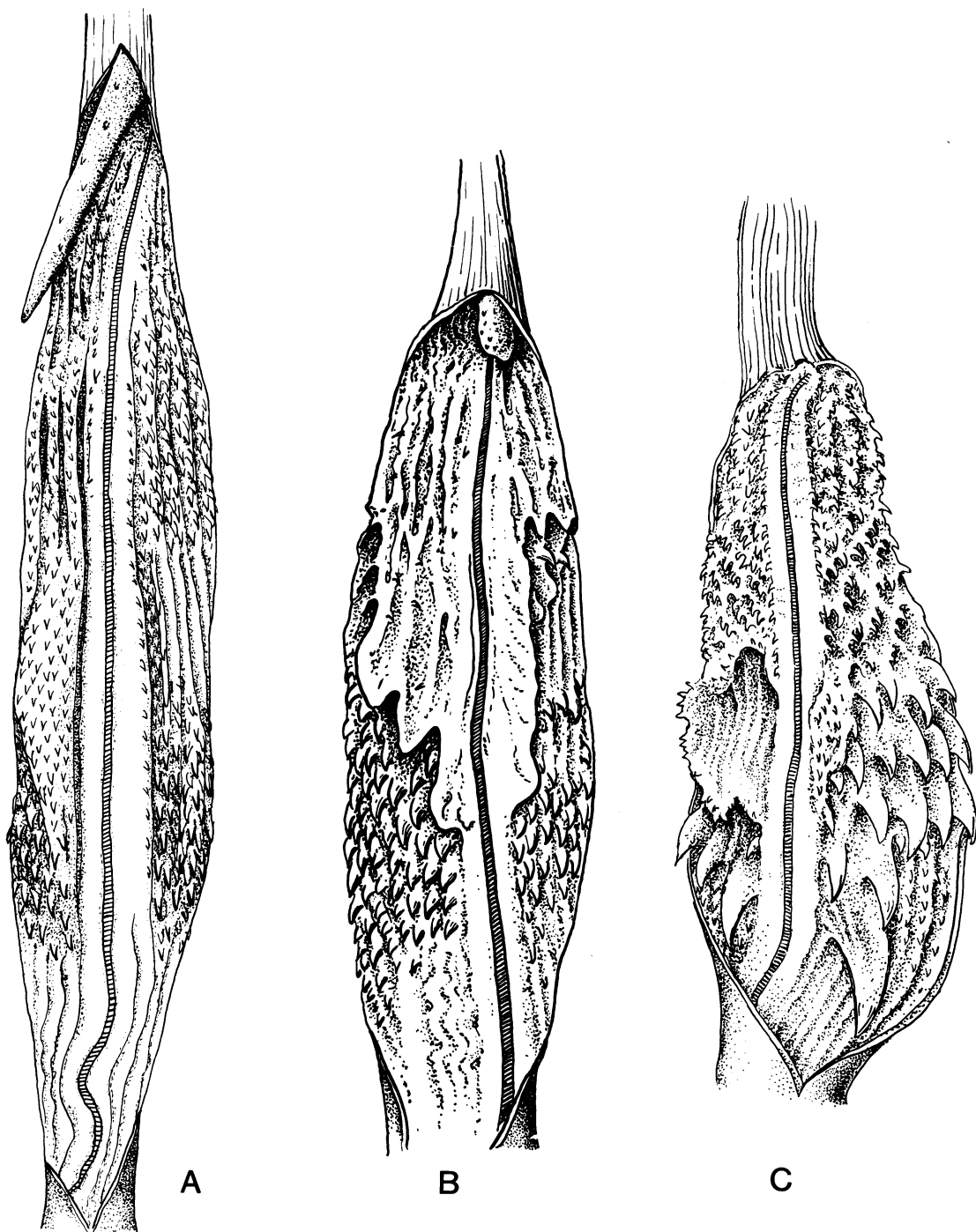


FIG. 1. Left hemipenis (inverted, opened by medial incision) of: A. *Dendrelaphis lorentzi* (MCZ 54329, Papua New Guinea: Western Province: Aramia R.), showing Group I organ; B. *D. salomonis* (MCZ 72053, Papua New Guinea; Bougainville Is.: Kunua), showing Group II organ; C. *D. papuensis* (AMNH 76648, Papua New Guinea: Sudest [=Tagula] Is.), showing Group III organ.

tulatus. However, most specimens have the reverse combination: a high maxillary count (25–31 teeth) as in *D. punctulatus*, combined with a rather low ventral count (173–189 for Buka, Bougainville, Fauro, Rubiana [=New Georgia], Kolombangara, Choiseul, Ysabel, Malaita, and Guadalcanal, but 190–195 for Vella Lavella and Gizo, and 195 for single Bio Is. specimen seen) suggesting *D. calligastra*.

Posterior maxillary teeth always longest.

Exposed supraoccipital longer than wide (but only slightly so in the type BM 1946.1.5.97, in which the exposed supraoccipital is broader than usual for either *D. calligastra* or *D. punctulatus*, thus making an approach to *D. gastrostictus*).

Hemipenis most like that of *D. gastrostictus*, with short terminal awn (less than two subcaudals long, usually less than one) that bears a well-defined continuation of the sulcus spermaticus, but organ usually longer (ending opposite sixth to tenth, usually eighth to tenth, subcaudal).

Although a blackish temporal streak may be present, even extending to the rostral (it does so in BPBM 3437, but not in BPBM 3705, both female, February 1964, Pepele, Kolombangara Is.), most often there is no concentration of pigment along the temporal-supralabial juncture but the dark pigment of the crown stops abruptly and evenly on the dorsal ends of the supralabials as if defined by a temporal streak.

Except for the types, conspicuous sensory pits absent from side of head in material seen by me.

Several hypotheses, between which I cannot choose at present, might explain the Solomon Islands *Dendrelaphis*: (1) they are a relict of a stage when the characters that now distinguish reproductively isolated New Guinea species were individually variable within populations; (2) the Solomons *Dendrelaphis* is of hybrid origin, derived from multiple invasions, perhaps before the present reproductive isolation of New Guinea *Dendrelaphis* had been achieved; (3) the characters that mark off the species of New Guinea *Dendrelaphis* (but are not in themselves the basis for reproductive isolation or ecological distinctiveness) are maintained in New Guinea by selective pressure arising from

competition between the species, but in the Solomons, where only one species is present and this competition is absent, random variation is permitted in characters that are under strong selective restraint in New Guinea. Quite possibly, protein electrophoretic study of New Guinea and Solomon *Dendrelaphis* would resolve the problem and might well yield important insights into the general problem of species formation. All the Solomon Is., from Buka and Bougainville to the Santa Cruz Group.

In addition, the melanistic *Dendrelaphis* of Misima Is. (76691, 76693 [males], 76692, 76694 [females] examined) seems to fit best with this species, having a similar hemipenis, maxillary teeth 28–29 and longest posteriorly, ventrals 178–179 (males) or 189–191 (females).

III. *Dendrelaphis papuensis* Group. The organ is of moderate length (ending at subcaudal 8–13; opposite subcaudal 8–12 in five Woodlark Is. males), with a strictly terminal attachment of the retractor longus, so that there is no suggestion of a terminal awn; distally, the organ has numerous shallow calyces with many small spines on their borders; proximally there are one to five transverse whorls of large spines, some of which are at least equal to one subcaudal in length. Specimens from the New Guinea mainland, Ferguson, Trobriand, Sudest, and Rossel Is. have a distinct transverse fold between the calyculate and spinose zones, the obvious homologue of the fold between the (smooth) calyces and small proximal spines of Group II *Dendrelaphis*, but no such fold is evident in Woodlark Is. specimens or in AMNH 42400 (Whitney South Sea Expedition, "Bougainville"; but very extensive collecting on Bougainville by Fred Parker failed to confirm the presence of *D. papuensis* on that island).

Probably one species, *Dendrelaphis papuensis* Boulenger.

Dendrelaphis papuensis occurs on the eastern Papuan peninsula, extending at least as far westward as Konedobu and Kila Kila, Central Province (MCZ specimens) and (fide Fred Parker) probably into Western Province, and at least as far northward as Garaina, Morobe Province (AMNH specimens), as well as Popondetta and Sangara, Northern Prov-

ince (BPBM 3802, 3814), the Cape Vogel region of Milne Bay Province mainland (AMNH specimens) and Fife Bay, Milne Bay mainland (BM 1946.1.6.7, a decapitated male, cotype of *Dendrelaphis schlenkeri* Ogilby; another cotype of *D. schlenkeri* from Fife Bay, BM 1946.1.6.9, is a male *D. calligastra*).

On the eastern Papuan peninsula, *D. papuensis* is sympatric with *D. punctulatus*, *D. gastrostictus*, and *D. calligastra* of Group II, but in this region of overlap, *D. papuensis* is characterized by the color of the interstitial skin of the neck (exposed by the inflation of the neck in members of this genus and probably analogous to the dewlap display of *Anolis* lizards); *D. papuensis* has black interstitial skin with a longitudinal white stripe between the first and second scale rows, but the Group II species show either alternating vertical white and dark bars on the interstitial skin or a spangled pattern of uniformly dark interstitial skin with a concealed white spot at the base of each scale.

Outside this region of sympatry, interstitial skin pattern is not diagnostic. For example, BM 1946.1.6.57, male from the type series of *D. papuensis*, from the Trobriand Is. (where this is probably the only species of the genus) has black interstitial skin on the neck with a concealed white spot at the base of each scale; this spangled pattern is found in some *D. calligastra* from northern and northeastern New Guinea. Conversely, north of the range of *D. papuensis*, *D. calligastra* may show a longitudinal white stripe between the first and second rows, usually in conjunction with alternating black and white bars on the interstitial skin at level of rows 5 and 6 (seen in some Wewak, Jayapura and Manokwari specimens of *D. calligastra* and also in a Lae *D. punctulatus*, AMNH 95143).

In the region of sympatry with Group II species, as well as in the Trobriand Is., *D. papuensis* has a maxillary dentition similar to that of *D. calligastra*, with the teeth beneath the prefrontal articulation longest and tooth count 19–23; but for 11 Rossel Is. specimens the count is 22–27; four Sudest Is. specimens have 26 maxillary teeth; and five Woodlark Is. specimens have 26–27 teeth.

The observed range in ventrals for *D. papuensis* from the eastern Papuan peninsula is

178–193, overlapping the observed range of *D. calligastra* from the same region (173–186) but the difference between the means (186.44 for 16 *D. papuensis* and 181.31 for 13 *D. calligastra*) is significant at the 1 percent level ($F_{1,27} = 12.47$); Fergusson Is., Trobriand Is., Sudest Is., and Woodlark Is. specimens of *D. papuensis* approximate the range for eastern Papuan peninsula specimens, but for 11 specimens from Rossel Is. the observed range is 183–203 (two lowest counts 183, 184 are two females, therefore not certainly identifiable to this species and differing from remainder of series in having one scale pit, rather than two, and the lowest maxillary tooth counts, 22 and 23, of the series; omitting these two specimens, the observed range in ventrals for Rossel Is. is 189–203). A color pattern feature seen in many—but not all—*D. papuensis* but unknown in the Group II species is the presence of a pale vertebral stripe.

Of the six Australasian species of *Dendrelaphis* recognized here, all but *D. papuensis* and *D. salomonis* are known from the Huon Peninsula.

Dendrelaphis lorentzi
(van Lidth de Jeude)

USNM 119505 Gusiko

The above specimen, previously reported by Loveridge (1948) as *Ahaetulla calligaster schlenkeri*, is a male with the hemipenis extending to subcaudal 13, with longitudinal rows of small spines (each about one-sixth of a subcaudal long), the rows of spines nearly to the tip and well distal to the rightward angulation of the sulcus at subcaudal 9; an apical awn, about three subcaudals long and with numerous tiny spinules; no crossfold on organ, but lips of sulcus raised as a pair of prominent folds. The 23 (left) maxillary teeth slightly (and equally) enlarged beneath the prefrontal and at the rear of the series. Scales 13–13–11; ventrals 181; anal divided; subcaudals 134 + spine. Nasal scute entire above nostril, a narrow strip of cornification extending between nostril and internasal; supralabials 9 (fifth and sixth entering eye); one preocular; two postoculars; temporals 2+2+2; infralabials 10 (first six touching genials). Color (as preserved) light bronze-tan above with pale bluish gray crossbands, this pattern

extending throughout the body; dorsal surface of head with conspicuous black spotting; a longitudinal black stripe on side of neck extending along dorsal ends of postorbital supralabials as a postocular streak, represented on snout by row of black spots reaching rostral; interstitial skin of neck with bold vertical black and pale bars extending to the vertebral region. Nuchal line of attachment of axial muscles at anterior edge of supraoccipital, so that there is no exposed supraoccipital bone.

Except for this Huon Peninsula specimen, the species is known only from southern New Guinea, at least as far west as Sabang on the Lorentz River, Irian Jaya (type locality) and as far east as the Aramia River, Western Province, Papua New Guinea (MCZ specimens), extending at least as far inland in Western Province as Tabubil, 2000 ft. (MCZ 135006). The Huon Peninsula specimen thus represents a notable disjunction of distribution (the only such case among Huon Peninsula snakes). At least the specimen "resembling var. *D.* in Boulenger's 'Catalogue of Snakes'" recorded from Simbang (near Finschhafen) by Lönnberg (1900) as *Dendrophis calligaster* may be this species.

Although the structure of the hemipenis, the black spotting on the top of the head (like calligraphic penciling) and the continuous cornification of the nasal scute above the nostril all indicate that this specimen is referable to *D. lorentzi*, the Gusiko specimen differs in several particulars from southern New Guinea specimens. The apical awn of the hemipenis is longer (only 1–2 subcaudals long in southern New Guinea specimens; five males, including type of *Dendrophis lorentzi*, examined). The ventral count of the Gusiko specimen is higher than for southern New Guinea specimens, which show a range of 156–173 (both sexes; for males, 156–170). Even when all southern New Guinea *D. lorentzi* are grouped together without distinguishing between sexes or localities (which, by ignoring possible sex dimorphism and local differentiation, may overestimate variance within the sample and, thus, overestimate the standard error of the mean), the difference between ventral count of southern New Guinea ($N = 12$) and Gusiko ($N = 1$) is significant at the 1 percent level ($F_{1,11} = 11.44$). Additionally, all southern New

Guinea *D. lorentzi* have eight supralabials except for the Tabubil specimen with nine on the left side; the occurrence of nine supralabials bilaterally in the Gusiko specimen suggests a difference in frequency for this count between southern New Guinea and the Huon Peninsula. The Gusiko specimen is also the only *Dendrelaphis* I have seen with the entire supraoccipital covered by the axial musculature.

Considering the disjunction in distribution, these differences are not surprising. I do not believe these differences are more than intra-specific, but I wish to call attention to them because the Gusiko isolate of *D. lorentzi* seems to be the nearest approach to an endemic species among the Huon Peninsula snakes.

Dendrelaphis gastrostictus (Boulenger)

95569 Kabwum, about 4500 ft.; 95570 Masba Creek, 2100 ft.; 66669 Gusiko

The Kabwum specimen is a juvenile with 37 left maxillary teeth, 164 ventrals; the Masba Creek specimen is a male with 36 left maxillary teeth, 170 ventrals; the Gusiko specimen is a juvenile male with 34 left maxillary teeth, 170 ventrals. In general, this species is characterized by having the highest maxillary counts and lowest ventral counts (except for southern New Guinea *D. lorentzi*) and these characters seem to be accentuated in the Huon Peninsula specimens. The interstitial skin of the neck is black in the Masba Creek and Gusiko specimens.

Except for the extension of *D. calligaster* into the Eastern Highlands, *D. gastrostictus* seems to be the only species of the genus to extend into the elevated interior of the island, but it is not confined to high altitudes and extends to the lowlands of Western Province (e.g., 59897, Lake Daviumbo, and MCZ 54226–27, Aramia River). Nonetheless, there are no specimens in the American Museum of Natural History from Lae or the lower Markham River Valley, in spite of considerable collecting there, and the species may be excluded from low elevations in northeastern New Guinea, apart from the Gusiko record (on the east coast of the Huon Peninsula).

The Huon Peninsula specimens differ from

11 Eastern Highlands–Chimbu–Western Highlands specimens and from a Mt. Missim specimen (MCZ 44170) in having dark interstitial skin on the neck, without vertical white bars, thus resembling two Normanby Is. specimens. The Huon Peninsula specimens have significantly (at 5% level) more maxillary teeth (34–37, mean = 35.667) than do the 11 Eastern Highlands–Chimbu–Western Highlands specimens (30–36, mean = 32.636). The Mt. Missim specimen has 30 left maxillary teeth. The Huon Peninsula population thus seems sufficiently differentiated to suggest it has been isolated for some considerable time.

Dendrelaphis calligastra (Günther)

USNM 119190, 119504 Gusiko; BPBM 3922 Finschhafen; BPBM 5136 Busu River near Lae; 66749, 66751, 66755 Lae; 95566 10 mi. w of Lae

Although this is a common species at Lae and has been taken on the eastern coast of the Huon Peninsula, the failure of the Seventh Archbold Expedition to collect it in the Mt. Rawlinson region suggests this species is confined to the coastal lowlands. I find no significant differences (at 5% level) in maxillary count (22–23 for Gusiko and Finschhafen, 23–24 for Lae region) or ventral count (173–179 for Gusiko and Finschhafen; 173–189 for Lae region but 173–178 omitting specimen from west of Lae), but there may be a difference between the Lae region and Finschhafen–Gusiko region in the color pattern of the interstitial skin. In both regions, the interstitial skin of the neck shows alternating vertical black and white bars, but for Lae region specimens, the color of the cornified scales is not in register with the pattern of the interstitial skin, so that white bases of scales contrast with dark interstitial bars (Busu River specimen) or dark edging on the scales stands out against the white interstitial bars; in the Finschhafen–Gusiko specimens, the concealed bases of the scales agree with the color of the interstitial skin, so that the interstitial pattern of vertical bars is not disrupted by any coarse stippling provided by the cornified scales.

Kurtz's field notes give the color in life for 66749 (juvenile female, Lae) as "abdomen,

yellowish. Inside of mouth red. Bluish cast to some dorsal scales"; for 66751 (adult female, Lae): "Inside of mouth pink. Under-side anteriorly white, becomes rust brown gradually to tip of tail, increasing in intensity toward tail. Supralabials whitish." During his stay at Lae, Kurtz did observe a *Dendrelaphis* in a banana tree, but did not take the specimen, so that its specific identity is uncertain. His other field notes on Lae *D. calligastra* do not suggest the species is particularly arboreal at Lae: for 66749, "collected swimming in rain pool from which tadpoles were taken"; for 66751, "marshy field, midday, in grass"; for 66755 (an adult male), on the ground in the campsite. This last specimen contains a skink tail in its stomach and BPBM 5136 (Busu River) contains a skink and two skink eggs (probably secondarily ingested with the skink); Stickel's field tag indicates USNM 119504 (adult female, Gusiko) was caught eating a frog.

Dendrelaphis punctulatus (Gray)

95568 Finschhafen; USNM 711482 Gusiko; 85673, 95143 Lae; 95567 10 mi. w of Lae

These specimens, all females, are typical *D. punctulatus* with conspicuous large scale pits clustered on the loreal, postoculars, anterior temporals, and dorsal ends of the supralabials; they lack a temporal streak; they also show a characteristic of *D. punctulatus* that is probably diagnostic, at least on New Guinea: the internasal enters the dorsal rim of the nostril. In 95567, the interstitial skin shows a pattern of alternating gray and white vertical bars (in the preserved specimen), with the uniformly dark cornified scales standing out as dark spots against this pale pattern; in 85673, the pattern of the interstitial neck skin is similar, except that the white bars are joined together by a longitudinal white stripe between the first and second scale rows; in 95143, there is a similar white stripe between the first and second rows, but the gray bars fuse dorsal to it, to isolate white interstitial spots at the level of the fifth and sixth rows from the white interstitial stripe. In the adult Finschhafen specimen, 95568 (the juvenile Gusiko specimen, USNM 711482, seems similar), the interstitial skin shows black and white vertical bars, with the cornified scales

in the black bars uniformly dark but the cornified scales in the white bars bearing a white basal spot (but with the dark dorsal edges of these scales standing out as blackish spots against the white interstitial background).

I present these notes on interstitial neck pattern in the hope it will stimulate collectors to record the color in life of this region. As noted in the outline of taxonomy of the genus, this interstitial pattern is known to be exhibited by neck inflation among species of *Dendrelaphis* and probably has a function analogous to the dewlap of *Anolis* lizards. My own observations, based on preserved specimens and thus confined to melanin distribution, suggest that the interstitial neck pattern distinguishes the species within a small geographic region, as usual for *Anolis*, but shows considerable geographic variation within the species, so that the rules change from place to place as to how the species differ in this display pattern—again, as in *Anolis*. In this case, the pattern of the neck of *D. punctulatus* from the east coast of the Huon Peninsula seems similar to that of Lae *D. calligastra*; however, around Lae, *D. punctulatus* has a pale interstitial pattern against which the dark scales stand out as conspicuous spots as the most conspicuous element of the pattern, whereas on the east coast of the Huon Peninsula, *D. calligastra* shows a concordance of scale and interstitial skin color to make the inflated neck pattern one of vertical black and white barring without dark spots on the white bars. I have no information about any differences in movements of the inflated neck by live *Dendrelaphis* or any precise observations on the degree of neck-inflation of which the various species are capable.

As with *D. calligastra*, *D. punctulatus* appears to be confined to low coastal localities on the Huon Peninsula and shows little differentiation between Lae and the extreme eastern end of the peninsula. Of the four Huon Peninsula *Dendrelaphis*, *D. lorentzi* and *D. gastrostictus* would appear to be “old inhabitants” and *D. calligastra* and *D. punctulatus* seem to be “recent invaders.”

Stegonotus diehli Lindholm

Form with 17 scale rows: 95155 Lae; 103672 Munim Waters (12 mi. w of Lae); (pertinence

doubtful) BM 1922.11.24.40 (Potter Field No. 47) “Huon Gulf.”

Form with 15 scale rows: (pertinence doubtful) BM 1922.11.24.41 (Potter collector) “Huon Gulf.”

McDowell (1972) has given reasons to believe this species contains both populations with 15 scale rows, mainly from northern New Guinea, and populations with 17 scale rows, mainly from southern New Guinea. The species is characterized by: (1) having two well-developed scale pits on each scale, including those of the base of the tail (some Manus specimens of *S. modestus* are similar in this respect, but other *Stegonotus* either lack scale pits entirely or have a few scattered scales with a tiny pit); (2) pointed and anteriorly directed choanal process of palatine (diagnostic); (3) a juvenile head pattern (masked by a general darkening of the head in adults, but usually still distinguishable through close inspection) involving a dark orbital blotch, dark posterior temporal blotch, a dark bar across the top of the head between the orbits, and dark parietal blotches that join the interorbital bar. The Lae and Munim Waters specimen and one of Potter’s “Huon Gulf” specimens have 17 scale rows and are generally similar to southern New Guinea specimens (such as those of Garaina in Morobe Province, and of Northern, Central, Chimbu, and Milne Bay Provinces) with a large number of palatopterygoid teeth (39 in 95155, 43 in 103672 and BM 1922.11.24.40). This last-mentioned specimen agrees with specimens from farther south in having a dark spot on the lateral end of each ventral, as well as in each subcaudal being brown anteriorly (this specimen may have come from the Huon Gulf region well south of Lae); in 103672 (adult male), many of the ventrals, particularly anteriorly, lack a lateral brown spot and thus approach the northern (15 scale rows) form that has immaculate ventrals; in 95155 (juvenile male) there is a further approach to more northern specimens in that the ventrals are immaculate and the subcaudals have brown pigment confined to their anteromedial edges (forming a narrow median zigzag subcaudal stripe). These specimens would suggest that the Lae region is part of an intergrade zone between the southern and northern forms of the species.

However, BM 1926.5.31.16, labeled as "Huon Gulf," Potter collector, is a typical northern specimen, indistinguishable from Astrolabe Bay (Madang Province) material, with but 28 palatopterygoid teeth, 15 scale rows, immaculate ventrals, and a median dark zigzag on the pale gray subcaudals. If this specimen really came from the same locality as Potter's "Huon Gulf" specimen with 17 scale rows, then it would indicate that the 15 and 17-scaled forms are probably good species, occurring sympatrically without evident introgression. But there are two other possibilities.

One possibility is that the 15-scaled specimen came from the *northern* coast of the Huon Gulf—that is, the Huon Peninsula. Although neither the Seventh Archbold Expedition nor any other collector known to me has taken this species on the peninsula east of Lae, the typical northern form is known from Saidor (MCZ 49491), near the same mountain range that forms the central elevation of the Huon Peninsula; it would not be implausible for any snake occurring at Saidor to extend eastward onto the Huon Peninsula (as here, somewhat arbitrarily, defined).

Another possibility is that, somehow, data on Potter's specimens got transposed. The 17-scaled "Huon Gulf" specimen bears Potter's field number 47. But the snake bearing Potter's field number 48 is a 15-scaled *Stegonotus diehli* from the "Ramu River delta" (BM 1926.5.31.16) suggesting that Potter went to the Astrolabe Bay coast from the Huon Gulf region just after collecting the 17-scaled *S. diehli*. The 15-scaled specimen may, then, have been collected on the Astrolabe Bay coast and somehow been mingled with the Huon Gulf collection.

Stegonotus parvus (A. B. Mayer)

95571–74 Pindiu, about 3000 ft.; 95576 Mt. Rawlinson; BPBM 5439, BPBM 5441 Kalolo; 95577 Butibum River near Lae; 66750, 66752, 85721–23, 95154, BM 1922.11.24.38, BM 1967.595 Lae; 95156 12 mi. w, 4 mi. n of Lae

There is a significant (at 1% level) difference in ventral count between specimens from Pindiu and Mt. Rawlinson on the one hand and specimens from the Lae region on the

other, as well as a significant (at 1% level) sex dimorphism for both populations, with males expected to average 4.72 more ventrals than do females for the same locality. For Pindiu and Mt. Rawlinson, ventrals average 193.00 for three males, 189.50 for two females; for the Lae region, ventrals average 181.50 for four males, 176.17 for six females. In addition, all nine Lae region specimens for which the head scutes are countable show (bilaterally) only one anterior temporal meeting the postoculars. Of the five Pindiu and Mt. Rawlinson specimens, only the left side is countable in 95573 and shows two anterior temporals meeting the postoculars; of the other four, 95574 shows two temporals meeting the postoculars bilaterally and the remaining three show two temporals meeting the postoculars on the left side and one (the more dorsal) anterior temporal meeting the postocular on the right side. There is a slight, but significant (at the 5% level) difference in number of maxillary teeth: for the Lae region, observed range 15–16, mean = 15.78, $s = 0.441$, $s_x = 0.147$ ($N = 9$); for Pindiu and Mt. Rawlinson, observed range 16–17, mean = 16.40, $s = 0.548$, $s_x = 0.245$ ($N = 5$). There is a similarly slight, but significant (at the 5% level), difference in the number of dentary teeth: for the Lae region, observed range 18–21, mean = 18.78, $s = 0.667$, $s_x = 0.222$ ($N = 9$) for Pindiu and Mt. Rawlinson, observed range 19–21, mean = 19.80, $s = 0.837$, $s_x = 0.374$ ($N = 5$). There is no significant difference in palatine (observed range 14–16, mean = 15.28, $s = 0.726$, $s_x = 0.194$, $N = 14$) or pterygoid (observed range 23–31, mean = 26.14, $s = 2.070$, $s_x = 0.553$, $N = 14$) tooth counts, in head scute counts, or in coloration. I can find no differences between two Kalolo specimens and the Lae region series.

McDowell (1972) suggested that this species may have originated as an eastern variation of *S. modestus* on the Huon Peninsula, at a time when the Huon Peninsula formed an island. *Stegonotus modestus* is not known from east of Astrolabe Bay on the New Guinea mainland, but *S. parvus* extends westward into Madang, East and West Sepik Provinces and northern Irian Jaya to be sympatric with *S. modestus*. Where sympatric with *S. modestus*, *S. parvus* has eight supralabial scutes, a ventral count below 190, and 17–19 max-

illary teeth, thus contrasting strongly with *S. modestus* from the same region, which there has seven supralabials, 200 or more ventrals, and 13 or 14 maxillary teeth. East of the range of *S. modestus*, in the Markham Valley, Kalolo, around Lae, and in the Wau region, *S. parvus* has seven (occasionally eight, but rarely bilaterally) supralabials, 173–187 ventrals, and 14–17 (modally, 16) maxillary teeth; farther east, in the central Huon Peninsula there are seven supralabials and 16 or 17 maxillary teeth, but ventral count rises to 187–196 (overlapping the ventral count for Moluccan specimens of *S. modestus*). Although McDowell (1972) states that the hemipenis of *S. parvus* is similar to that of *S. diehli* and *S. modestus*, there seems to be a hemipenial difference separating *S. modestus* from other *Stegonotus* (except for *S. heterurus*): the distal one or two transverse tiers of calyces have smooth edges and are readily identified as calyces; in the others, the distal calyces have spinulose rims and the entire texture of the organ appears spinose, with only a slight basal webbing of the more distal spines indicating the existence of a calyculate zone.

Stegonotus parvus seems to be the most common species of its genus on the Huon Peninsula, lower Markham Valley and southward to the Wau–Bulolo region (of 11 BPBM specimens from the Wau region, 10 are *S. parvus* and one is *S. cucullatus*). Farther south, at Garaina, the species must be rare if not absent (17 AMNH *Stegonotus* from Garaina comprise 16 *S. cucullatus* and one *S. diehli*). In the Astrolabe Bay region (24 specimens), *S. parvus* (six) seems more abundant than *S. modestus* (three), but less common than *S. diehli* (15) and this relative abundance probably holds for the northern edge of New Guinea from Toem, Irian Jaya, to Wewak (of 27 *Stegonotus* from this region, 13 are *S. diehli*, six are *S. parvus*, and four each are *S. modestus* and *S. cucullatus*). In the highlands of northeastern New Guinea other than the Huon Peninsula—that is, Eastern Highlands, Western Highlands, and Chimbu Provinces and Morobe Province west of the Ramu–Markham Valley—the most common *Stegonotus* is *S. cucullatus* (19 of 26 specimens), with *S. parvus* (six) and *S. diehli* (one) conspicuously less abundant. It would appear,

then, that the Pindiu–Mt. Rawlinson region (five *S. parvus*, one *S. cucullatus*), in spite of its elevation, is more like the Markham Valley than like the northeastern highlands in the relative abundance of the species of *Stegonotus*.

All the Huon Peninsula specimens of *S. parvus* have the usual coloration for this species (and *S. modestus*); dark brown ventrally, fading through a warm brown dorsolaterally to a warm tan ventrolaterally (the ventrolateral scales distinctly paler on their edges than on their centers), with clear whitish ventral surface, including the lower side of the tail, and upper lip. Most stomachs examined from the Huon Peninsula series were empty, but 95154 (Lae) contained a skink and two squamatan eggs; 95156 (west of Lae) contained two squamatan eggs; 95573 (Pindiu) also contained squamatan eggs but 95574 contained a few scincid scales and an unidentifiable material.

Stegonotus cucullatus
(Duméril, Bibron, and Duméril)

95575 Pindiu, 3000 ft.; 95157 13 mi. nw of Lae; BM 1922.11.24.39 “Munum, 17 mi. from mouth of Markham River” [=Munim Waters?]

Of the localities listed above, only Pindiu conforms strictly to the definition of “Huon Peninsula” used here; the specimens from northwest of Lae and from “Munum” are both males, with ventrals 194 and 191, respectively; these are unusually low counts for this species, but matched by 85715, a female from Gurakor (farther up the Markham Valley) with 191, and by BPBM 4160, a juvenile male from Wau, also with 191 ventrals. The Pindiu specimen is an adult male with 200 ventrals, also low for this species but in fair agreement with 85713–14, two males from Umi River, upper Markham Valley, with 198 and 197 ventrals, respectively. Although these counts are low for *S. cucullatus*, they are higher than those for *S. parvus* from the corresponding geographic region and it is a rule to which I do not know any exception that where *S. cucullatus* and *S. parvus* occur together, the former has a higher ventral count, although the geographic variation in each

species produces an overlap in ventral counts for the two species when locality is not considered.

The color of these specimens is as for other Morobe Province (and also Kokoda and Eastern Highlands) specimens seen by me: cool dark smoky gray with distinct dark edging to the scales dorsal to the second row, the subcaudals with distinct dark edging, the ventrals with dark smudges above the angulation, the supralabials light gray with darker gray borders. As with other Morobe specimens, the darker edging of the dorsal scales is more conspicuous after long preservation in alcohol (the dark edging is now quite evident when the Pindiu specimen is immersed in alcohol, but it was not at all evident when the specimen was unpacked more than 15 years previously).

The sagittal crest on the parietal of the Pindiu specimen is equal to the sagittal crest on the supraoccipital, as usual for adult *S. cucullatus*; in *S. parvus* the sagittal crest is confined to the supraoccipital and the parietal has a flat shield-shaped dorsal exposure between the jaw adductor muscles. The Pindiu *S. cucullatus* is also a considerably larger snake (snout-vent 1200 mm.) than *S. parvus* (95571, Pindiu, the largest specimen of *S. parvus* known to me, has a snout-vent length of 800 mm.); the Pindiu *S. cucullatus* would be only a "medium size" specimen for this species, which, along with *Boiga irregularis* and *Dendrelaphis punctulatus*, comprises the "large colubrid" fauna of New Guinea. The tooth counts (left side) for the Pindiu *S. cucullatus* are: maxillary 14 + 3; palatine 17; pterygoid 26; dentary 19 (gradual transitions in length for dentary teeth and pre-diastemal maxillary teeth); these counts are all within the observed range of Eastern Highlands and western Morobe Province specimens. The supralabial count of nine (fourth and fifth entering eye) of the Pindiu specimen is modal for Eastern Highlands-western Morobe. Nothing, indeed, about the Pindiu *S. cucullatus* suggests even an endemic race and the species may well be a recent immigrant to the Huon Peninsula, most probably from the eastern highlands region by way of the upper Markham Valley.

The Pindiu specimen was caught in grass

by a dog. The stomach contains the thoroughly digested remains of a murid rodent.

GENUS *STYPORHYNCHUS* PETERS

Malnate (1975) has given a preliminary paper referring the Moluccan and New Guinea (and some Philippine) species of "*Amphiesma*" to a separate genus *Styporhynchus*, characterized, in part, by presence of scale pits on the subcaudals. Malnate and Underwood are now engaged in a revision of this difficult genus and the following discussion of the Huon Peninsula forms is quite tentative; more definitive statements about New Guinea *Styporhynchus* must await Malnate and Underwood's revision.

The Huon Peninsula *Styporhynchus* belong to a complex within that genus containing *S. montanus*, *S. multiscutellatus*, and *S. mairi*; the last two are usually considered conspecific, but *S. mairi* appears to co-exist with *S. multiscutellatus* in the Oriomo Plateau (essentially, Merauke to Fly River region) and Port Moresby region of New Guinea without indications of introgression. Although *S. mairi* frequently has two preoculars in Australia (where it is the only species of the genus), New Guinea *S. mairi* are characterized by a single preocular. It may be added that there is no evidence to indicate that *S. mairi* is more closely related to *S. multiscutellatus* than it is to *S. montanus*.

Over most of New Guinea, except the elevated interior, there are two members of the *S. mairi* complex: a form with a lower ventral count and preferring lower elevations (*S. multiscutellatus*); and a form with higher ventral count, preferring higher elevations and also occurring in the elevated interior of the island (*S. montanus*). Discriminating between these species is not always easy, because both show geographic variation and the critical value of ventral count distinguishing the two taxa varies from place to place; furthermore, the identification characteristics additional to ventral count also change from place to place (e.g., the feebleness of keeling on the first scale row that distinguishes *S. montanus* in Irian Jaya is useless as a criterion in Papua New Guinea). The following is my own attempt to determine the best cri-

teria for identifying material from the general region of the Huon Peninsula.

To the west of the Ramu–Markham Valley, in the Goroka region of Eastern Highlands Province, there appears to be but one species, *S. montanus*, represented in the 22 specimens available to me; ventrals show a significant (5% level) sex dimorphism and are: for males, observed range 160–171, mean = 164.571, $s = 3.345$, $s_x = 0.894$, $N = 14$; for females, observed range 156–165, mean = 160.623, $s = 3.114$, $s_x = 1.101$, $N = 8$; subcaudals show no significant sex dimorphism, with observed range 75–89, mean = 81.526, $s = 4.575$, $s_x = 1.050$, $N = 19$; left maxillary teeth show an observed range of 31–36, mean = 34.143, $s = 1.711$, $s_x = 0.373$, $N = 21$. There is no significant correlation between subcaudals and ventrals, either within each sex or when data for the sexes are combined.

When 30 specimens from farther east, on the western–southern shoulder of the Ramu–Markham Valley (more precisely, 12 from the Aiyura–Kainantu region, eight from the Kratke Mts., and 10 from the Bulolo–Wau region) are considered, it is evident that this sample (and each of the three component subsamples) shows a marked bimodality in ventral count, with the two clusters of each subsample separated by a gap of nine or more ventrals for which there are no observed counts. The clusters with higher ventral count in each subsample are not significantly (at the 5% level) different from one another or from the Goroka sample and are evidently *Styphorhynchus montanus*; when ventral counts for Goroka, Aiyura–Kainantu, Kratke Mts., and Bulolo–Wau are combined, parameter estimates are: for males, observed range 160–171, mean = 164.769, $s = 3.037$, $s_x = 0.596$, $N = 26$; for females, observed range 156–165, mean = 161.462, $s = 2.847$, $s_x = 0.789$, $N = 13$.

The clusters with lower ventral count would seem to represent *S. multiscutellatus*. There is no significant (at 5% level) geographic difference or sexual difference in ventral counts for these clusters and the parameter estimates for the combined samples are: observed range 145–151, mean = 148.923, $s = 1.977$, $s_x = 0.548$, $N = 13$.

The two species differ in subcaudal count, but the difference is not uniform throughout the range from Aiyura to the Wau region. Neither species shows significant (at the 5% level) sexual dimorphism, but in both species the geographic variation is significant (at the 5% level in the case of *S. montanus*, at the 1% level in the case of *S. multiscutellatus*) and the geographic trend is opposite in the two species; in *S. montanus* the subcaudal count is highest in the Aiyura–Kainantu region (where not significantly different, at the 5% level, from the Goroka region sample) and declines in the Kratke Mts., to decline still further in the Wau–Bulolo region; but *S. multiscutellatus* shows highest counts in the Wau–Bulolo region, with a decline in the Kratke Mts. and lowest counts in Aiyura–Kainantu region, where the mean for *S. multiscutellatus* is below that for *S. montanus*, although *S. multiscutellatus* has conspicuously higher subcaudal counts than does *S. montanus* in the Wau–Bulolo region. Table 1 gives the parameter estimates.

No significant (at the 5% level) correlation between ventral and subcaudal count is demonstrable in *S. multiscutellatus* in a sample of nine from Aiyura–Kainantu, the Kratke Mts., and the Bulolo–Wau region; but for 14 *S. montanus* from these regions, $r = -0.5985$ (significant at the 5% level), yielding the regression equation: estimated subcaudals = $262.9 - 1.123$ ventrals. That the slope of the regression line approximates -1.0 suggests that total somites (about equal to ventrals + subcaudals) approximate a constant and that decrease in the number of subcaudals leads to a corresponding increase in the number of ventrals (but note that while the number of subcaudals for Bulolo–Wau *S. montanus* is significantly lower than the mean for Goroka, there is no significant difference in ventral count; perhaps this can be ascribed to the rather high variance for ventrals in the Goroka sample). The above regression line does not differ significantly from: estimated subcaudals = $242.643 - 1.000$ ventrals (based on the mean = 242.643 for sum of ventrals and subcaudals in this sample). In the Wau–Bulolo region, the total of ventrals and subcaudals for *S. multiscutellatus* is not diagnostically different from that for *S. monta-*

TABLE 1
Subcaudal counts for *Styporhynchus montanus* and *Styporhynchus multiscutellatus* West and South of the Markham Valley

	<i>Styporhynchus montanus</i>	<i>Styporhynchus multiscutellatus</i>
Aiyura-Kainantu region	(Sample of six not distinguishable from 19 Goroka region specimens; combined estimates given) Observed range 75–89 Mean = 81.440 $s = 4.263$; $s_x = 0.853$; $N = 25$	Observed range 75–80 Mean = 76.667 $s = 2.887$; $s_x = 1.667$; $N = 3$
Kratke Mts.	Observed range 72–82 Mean = 77.000 $s = 4.041$; $s_x = 2.021$; $N = 4$	Observed range 84–86 Mean = 85.000 $s = 1.414$; $s_x = 1.000$; $N = 2$
Bulolo-Wau region	Observed range 67–80 Mean = 74.000 $s = 5.477$; $s_x = 2.739$; $N = 4$	Observed range 88–96 Mean = 91.800 $s = 2.950$; $s_x = 1.319$; $N = 5$

nus, but the two species differ conspicuously in subcaudal count; farther to the northwest, in the Aiyura–Kainantu region, subcaudal count is no longer diagnostic, but total of ventrals and subcaudals probably does distinguish the species (observed range 221–230 for three *S. multiscutellatus*, 239–249 for six *S. montanus*).

There is no significant difference between *S. montanus* and *S. multiscutellatus* in the Aiyura–Wau region in the mean for left maxillary teeth (33.353 for 17 *S. montanus*; 33.545 for 11 *S. multiscutellatus*), but there is a significant (at the 1% level) difference in variance (for *S. montanus*, $s = 0.931$, observed range 32–35; for *S. multiscutellatus*, $s = 2.162$, observed range 31–37). In the region under discussion, the two species are most easily distinguished in the juvenile stage, which has a pale collar, bordered anteriorly and posteriorly with black, in *S. multiscutellatus* but is without any collar in *S. montanus*. Even before sexual maturity, this collar darkens to the same brown tint as the back and crown in *S. multiscutellatus*, but the dark marks that formed anterior and posterior borders for the collar remain, and usually can be made out in fully adult specimens, at least when they are wet, showing as a posterior expansion of the black postorbital stripe on the temporal region (a remnant of the anterior border of the collar) and as a black mark

behind the angle of the jaw (a remnant of the posterior border of the collar). In *S. montanus* no such marks appear, and the postocular stripe, if not altogether obscured, fades out posteriorly on the last supralabial. This character is not completely clearcut, however, because *S. montanus* frequently has a checkerboard pattern of black spots and the more anterior of such spots may lie in the general position of the posterior collar-borders of *S. multiscutellatus*.

In the Markham Valley and Huon Peninsula, ventral counts are bimodal, but the higher-count cluster shows lower values than seen in the higher count cluster for the western and southern shoulders of the Markham Valley. The Huon Peninsula higher-count cluster (it does not appear to occur in the Markham Valley) has an observed range of 153–160, with mean = 156.250, $s = 1.765$, $s_x = 0.509$, $N = 12$. In most respects, it does not seem to differ from *Styporhynchus montanus* from west of the Markham Valley, but has a reduced somite number, reflected in both the reduced ventral count and in a reduced subcaudal count (observed range 70–78, mean = 74.375, $s = 2.825$, $s_x = 0.999$, $N = 8$) and, consequently, with a conspicuously lower sum of ventrals plus subcaudals (observed range 227–233, mean = 229.875, $s = 2.642$, $s_x = 0.934$, $N = 8$; for the Aiyura–Kainantu region, Kratke Mts., and Bulolo–

Wau region, observed range is 236–249, mean = 242.643, $s = 4.031$, $s_x = 1.077$, $N = 14$). Because of this reduction, ventral counts for Huon Peninsula *S. montanus* fall mainly in the region of the gap between the lower ventral count cluster (*S. multiscutellatus*) and higher ventral count cluster (*S. montanus*) for samples from west and south of the Markham Valley. Nonetheless, the ventral count cluster for *S. montanus* is well defined for the Huon Peninsula–Markham Valley sample, because the lower-count cluster is also displaced towards lower values (143–149).

This lower-count cluster, which seems to correspond to the *S. multiscutellatus* cluster of the Aiyura–Kratke–Wau sample, contains two quite different forms in the Huon Peninsula–Markham Valley sample. One of them, from low elevations around Lae and also Gusiko on the eastern coast of the Huon Peninsula, has a high subcaudal count (86–90, mean = 87.250, $s = 1.893$, $s_x = 0.946$, $N = 4$) and a distinct pale collar in the juvenile that leaves traces of its black borders in the adult; these snakes do not appear distinguishable from *S. multiscutellatus* from the Bulolo–Wau region and probably represent a recent invasion of the lower Markham Valley and coast of the Huon Peninsula from the south.

The other *S. multiscutellatus*, represented by specimens from the Rawlinson Range, at elevations of 1340 to 1580 m., has far fewer subcaudals (67–73, mean = 69.333, $s = 3.215$, $s_x = 1.856$, $N = 3$) and I can see no trace of a former collar on the four specimens available. As noted above, there is a decrease in subcaudal count going from the Wau region northwestward to Aiyura. The Rawlinson Range *S. multiscutellatus* has still lower subcaudal counts than does the Aiyura–Kainantu sample, but seems to be a continuation of this trend. I interpret these Rawlinson Range specimens as representing an earlier invasion of the Huon Peninsula, probably from the west, now showing some differentiation in the form of reduced subcaudal count and also reduced ventral count (143–146, mean = 144.500, $s = 1.291$, $s_x = 0.645$, $N = 4$), and in obliteration of the collar—at least, in the adult.

Although there are conspicuous differences between Lae region and Rawlinson Range *S.*

multiscutellatus, there is no evidence of reproductive isolation and I know of one specimen that appears to be intermediate: BPBM 3398, an adult female from Tewep, in the Sarawaket Range at 1350 m., shows distinct, but inconspicuous, black spots that appear to be the remnants of the borders of a pale juvenile collar and has 81 subcaudals.

Judging from a sample of 12 *S. montanus* and 10 *S. multiscutellatus* from the Huon Peninsula (including the Lae region), the zone of 150–152 ventrals lies above mean + 2s for *S. multiscutellatus* and below mean – 2s for *S. montanus*. In addition, all but one of 12 *S. montanus* from this region have a single anterior temporal, whereas all 10 *S. multiscutellatus* have two anterior temporals, at least on one side of the head. In the Wau–Bulolo region, this difference in anterior temporals appears also to be diagnostic, but the Goroka sample, apparently representing only *S. montanus*, is variable in anterior temporal number and the character will not correctly identify specimens from the Aiyura–Kainantu region. It should be noted that the diagnostic gap (150–152) in ventral count for the Huon Peninsula nearly corresponds to the peak of the distribution for *S. multiscutellatus* from west and south of the Markham Valley. For the western and southern shoulder of the Markham Valley, the diagnostic gap in ventral count (between mean + 2s for *S. multiscutellatus* and mean – 2s for female *S. montanus*) is 154–155 ventrals.

Styporhynchus montanus
(van Lidth de Jeude)

95535, 95539–43, 95545 Gang Creek, Mt. Rawlinson, 4400–5200 ft.; 95546 Gumun; BPBM [Field No.] NG-28337 Kabwum, 7500 ft.; BPBM [Field No.] NG-52763 Kilolo, 6900 ft.; 95006 Gevak; BPBM 3734 Sarawaket Range, 1920 m. [probably in general region of Tewep]

Of these specimens, 95541, 95546, 93006, and BPBM 3734 contained microhylid frogs and 95540 contained a papery material perhaps representing much digested frog skin; BPBM 3734 also contained two beetle larvae. Since microhylids are most likely to be encountered on the ground, this supports Zweifel's (personal commun.) impression that

Styporhynchus is not particularly aquatic on the Huon Peninsula.

Zweifel's notes on the color in life of 95536 are: "dark olive dorsal color, no pattern, skin between scales yellowish; dorsal color extends onto tips of ventrals, ventrals otherwise yellowish; iris yellow-brown." To judge from preserved material, this absence of dorsal pattern would hold true for another Gang Creek specimen (95545) and the Gumun specimen, but the remaining specimens show more or less conspicuous small black spots, separated from one another but in an alternating checkerboard arrangement. All the *S. montanus* from the Rawlinson Range show a cream-colored (in preservative) oral border for the entire supralabial series, in contrast to the *S. multiscutellatus* from the same region, which have the last two supralabials brownish gray, like the temporal region; however, this difference will not hold outside the Rawlinson Range and BPBM 3734, a *S. montanus* from the Sarawaket Range, has considerable gray suffusion of the last two supralabials, while BPBM 3398, a *S. multiscutellatus* from Tewep, has the entire upper lip cream with dark borders to the supralabials.

Styporhynchus multiscutellatus
(Brongersma)

66670 Gusiko; 95537–38, 95544 Gang Creek, Mt. Rawlinson, 5000–5200 ft.; 95150 Tumnang, 4400 ft.; BPBM 3398 Tewep, 1350 m.; 66753, 103640 Lae; 85712, 95547 Oomsis Creek, 500 ft., 17 mi. sw of Lae

The specimens from Tewep and Oomsis Creek are from slightly west of the Huon Peninsula as defined for this report, but are listed because they were used in analysis of the Huon sample. The Gusiko specimen is a juvenile male, with conspicuous black neck marks representing the borders of a former collar, and with 149 ventrals and 90 subcaudals. It is quite unlike the Tumnang and Gang Creek specimens (subcaudals 67–73, no trace of collar) and similar to Lae region specimens.

Zweifel made notes on the color in life of several Rawlinson Range specimens of *S. multiscutellatus*: 95150 (Tumnang, female), "The ground color is a dark greenish gray overlain with a pattern of black spots; on the

tail the spots coalesce to form a vertebral line but this is not present on the body; the skin between the scales shows as a rather greenish yellow when the body is stretched; the under-surfaces are a dark cloudy gray." For 95537 (Gang Creek, female), "Rich brown dorsal color, no pattern except thin black stripe on tail, skin between scales yellowish; pink tint to labials and chin, fading gradually to tan under tail; ventrals speckled gray; dorsal color extends onto ventrals." For 95538 (Gang Creek, male), "Dark gray-brown dorsally with darker spots less than one scale in area, dark central line on tail; skin between scales grayish; ventral surfaces gray with a slight pinkish tint; chin and lower labials white, upper labials lighter brown than rest of head." The Gang Creek specimens (95537–38) were collected by local residents, who found them during preparation of gardens; the Tumnang specimen (95150) was found among leaves beside a trail in heavy forest.

Boiga irregularis (Merrem)

BPBM 5438, BPBM 5444–45, BPBM 5447 Kalolo, 750 m.; 66671–72 Gusiko; 66992, 95565, BPBM 3920, BPBM 3931 Finschhafen; 95548–53 Pindiu 2900–3000 ft.; 95554 Masba Creek, 2500 ft.; 95555–58 Numbut, 4500 ft.; 95559, 95561 Maran, 4000 ft.; 95560 Zangaren, 4000 ft.; 95151 Tumnang; BPBM 3278, BPBM 3658 Singaua River (6°40'S, 147°09'E, 50 m.); 66745, 77648, 66762–64, 85731–34, 95153, 95562–63 Lae; 95152 Oomsis; 95574 10 mi. w of Lae

Also recorded from Simbang by Lönnberg (1900) and from "Lialun" [=Sialum] by Vogt (1911).

This is probably the most abundant snake in the lowlands of New Guinea and the Seventh Archbold Expedition collection would indicate that it is the commonest snake in the Rawlinson Range up to 1220 m.; at higher elevations, *Styporhynchus montanus* seems to be the most abundant snake. The habitat of *Boiga irregularis* seems varied: it was taken within the town limits of Lae (95562), in a tree (95554), crawling on open ground (66764), on the roof of a grass house (95560), in kunai grass (BPBM 3278), in primary forest (BPBM 3658). Of specimens with recognizable stomach contents, rats or rat hair is

the most frequent element (66762, 95549–51, 95556, 95560), with 95556 containing an adult *Rattus exulans* (G. Musser determination) but 95560 and 66762 containing nestling murids; 66763 contains a much-digested skink and fin spines of a fish; 85731 contains a gecko tail and 95553 contains bird eggs.

Dividing the Huon Peninsula sample into four subsamples (Kalolo, Finschhafen–Gusiko, Rawlinson Range–Pindiu–Tumnang, and Lae region), no significant (at 5% level) difference in ventral count or subcaudal count is apparent either between geographic regions or between sexes (parameters are: ventrals 240–255, mean = 246.81, $s = 3.429$, $s_x = 0.572$, $N = 36$; subcaudals 104–120, mean = 110.13, $s = 3.882$, $s_x = 0.792$, $N = 24$).

FAMILY HYDROPHIIDAE

I follow Smith, Smith, and Sawin (1977) in referring all Australasian proteroglyphs except *Laticauda* and *Parapistocalamus* to the Hydrophiidae, which thus includes all the “palatine draggers” of McDowell (1970). Although a “typical” sea snake is different in many anatomical features from a “typical” terrestrial Australasian proteroglyph, transitional genera exist; but it is at present impossible to ally the terrestrial Australasian proteroglyphs to any known Asiatic, African, or American genus or even generic group.

Acanthophis antarcticus (Shaw)

66757–60 Lae; 85740–41 “few miles west of Lae”

In addition to these Lae records, *Acanthophis* is known from Gusiko (Loveridge, 1948). I do not know of any records from the elevated interior of the Huon Peninsula.

Of the Lae specimens examined, 66757 and 66760 contain hair in the stomach, similar to *Rattus* hair; 66758 contains digested fragments of *Rattus exulans* and 66759 contains a *Rattus exulans* skull (G. Musser determination). Kurtz’s field notes state that he removed juvenile bandicoots of the genus *Echimypera* from 66757–59; probably Kurtz misidentified these much-digested and fragmentary stomach contents in the field, since 66757 was taken “near nest of bandicoot—

Echimypera sp.” and the resident people told him that bandicoots were the principal food of *Acanthophis*.

Kurtz’s field notes further state that 66757–58 were taken together in kunai grass in a low, moist spot; 66759–60 were taken in the U.S. Army campsite area at Lae, described by Kurtz as “swampy grassland, flat terrain.”

Acanthophis antarcticus shows considerable geographic variation in New Guinea in ventral count, in color pattern, and in whether the temporolabial scute (=supralabial 6 of a series of seven supralabials) is excluded from the mouth as a “lower temporal” by contact of supralabial 5 with supralabial 7 (giving a supralabial count of six) (see van Lidth de Jeude, 1911, for discussion of this variation in Irian Jaya *Acanthophis*). Lae region *Acanthophis* have the temporolabial excluded from the mouth as a temporal (66759 has the temporolabial excluded from the mouth by horizontal division, so that there are seven supralabials, but the others have six supralabials, with the original seventh in contact with the fifth); in this respect, as in all others noted by me, Lae specimens agree with those from the Markham Valley, Kratke Mountains, and Bulolo region. Ventral count for specimens from the Markham Valley (including Lae), Kratkes, and Bulolo region are: males 119–122, mean = 120.33, $s = 1.033$, $s_x = 0.422$, $N = 6$; females 119–126, mean = 122.33, $s = 2.733$, $s_x = 1.116$, $N = 6$. In all, each infralabial and supralabial (and the temporolabial) bears a large black blotch and all the scales of the first row (and, on the neck, the second row) have black centers and the pale ground color of the ventrals is much less extensive than the black ventral spotting. Specimens from Eastern Highlands Province (exclusive of the Kratke Mountains) have much lower ventral counts (109 in single male seen; for females, 111–116, mean = 112.60, $s = 1.949$, $s_x = 0.872$, $N = 5$) and have the temporolabial broadly entering the edge of the mouth; the single male seen (Univ. Colorado 51625, Kamaliki, 8 mi. e of Goroka, 5000 ft.) has black spotting on all the labial scutes and scales of the first row, but 98494 (Nivi) and 101146–49 (Dunantine River, 5000 ft.) have black spots restricted to the anterior infralabials and to the sixth [=tem-

porolabial] and seventh supralabials, with pale ground color predominating over dark spots on the ventrals and the first scale row with few or no black spots.

The geographic pattern in New Guinea is not a simple one. Baiyer River (Western Highlands Province) specimens are similar to Markham Valley specimens, as are Sepik lowlands specimens. But specimens from Central and Western Provinces are most like Eastern Highlands specimens, as are most from Irian Jaya (except for those from near former Hollandia and, *fide* van Lidth de Jeude [1911], from Merauke). The nature of the temporolabial (whether a supralabial or a temporal) is variable within some populations (e.g., Kubuna, Central Province; Wipim, Western Province; Bernhard Camp, Idenburg River, Irian Jaya) and when the entire series of New Guinea *Acanthophis* available to me (20 males, 42 females) is plotted for ventral count it does not fall into two discrete clusters; nor is there a complete correlation of color pattern with ventral count or with condition of the temporolabial. There does not seem to be any real evidence that more than a single species is involved, but the geographic variation within this species does not form a simple cline or easily mapped pattern. Perhaps certain geographic variations are better adapted than others to higher altitudes and most lowland localities in eastern New Guinea, including Lae, have been occupied by a form that is closely similar to eastern Queensland *Acanthophis*, but higher elevations have been occupied by a form with reduced ventral count, reduced black pigmentation, and with the temporolabial entering the mouth. This latter form has also succeeded in entering lowland localities in Western Province, as well as in parts of Irian Jaya, producing a situation unknown to me for any other snake known from both New Guinea and Australia: Oriomo Plateau (southern Western Province) specimens are less similar to Queensland specimens than are those from northeastern New Guinea.

Storr (1981) has revised the *Acanthophis* of Western Australia, where the problem seems closely comparable to that in New Guinea: sympatry without introgression cannot be demonstrated anywhere to prove spe-

ciation has occurred, but changes are so abrupt where strongly differentiated forms approach one another geographically that some sort of reproductive isolation is suggested, but without the ecological differentiation that would permit two species to occur together without direct competition (that is, the pattern suggests biological species constituting a super-species). Storr assigned the Western Australian death adders to three distinct species: *Acanthophis pyrrhus* Boulenger (a wholly Australian form), *A. antarcticus* (Shaw) (at least strongly analogous to the "highland" New Guinea form), and *A. praelongus* Ramsay (at least strongly analogous to the "lowland" New Guinea form). Although the analogy with New Guinea is suggestive and it is tempting to identify the Huon Peninsula region death adders as *A. praelongus*, the analogy is not exact. For example, in Western Australia, *A. praelongus* shows a greater tendency than does *A. antarcticus* to raise the supraocular scute into a horn; but in New Guinea, it is the *antarcticus*-like form that usually has a supraocular horn and the supraocular is flat in the *praelongus*-like form.

For the present, it seems best to call New Guinea death adders *A. antarcticus* but to note a real problem as to how many species exist in New Guinea and which ones (if any) are represented in Australia.

Micropechis ikaheka (Lesson)

BPBM 5548 Kalolo, 750 m.; 95585 Pindiu, 2800 ft.; 95586 Kotkin, Mt. Rawlinson; 95587 Butibum R., 7 mi. n of Lae; 66754, 95588 Lae; 85746 3 mi. nw of Lae; 85757 Oomis Creek, w of Lae

Also recorded from Sattelberg by Vogt (1911), and from Gusiko by Loveridge (1948).

Of the specimens examined by me, 95588 contains an intact *Sphenomorphus jobiensis* (R. G. Zweifel determination) and 85746 and 95585 each contain a scincid tail. Although 85746 was taken in a clearing in rain forest and 85757 was taken in secondary rain forest, 95588 was taken in tall grass within the town limits of Lae and 95586 was taken in a garden.

The Pindiu, Mt. Rawlinson, and Lae region specimens show the pattern usual for

this species in Morobe Province: head dark above and laterally, with the tan anterior neck showing large black spots anteriorly, but these spots breaking up more posteriorly into scattered dark scales and the body essentially patternless tan one-third of the way back from the head; posterior body with 12 to 24 black-edged russet crossbands, these bands becoming darker posteriorly and the tail with eight to 12 black rings. The Kalolo specimen shows a pattern more like that of Sepik Provinces specimens: every scale with tan edge and dark center anteriorly, but slight variations in the width of the pale edging from scale to scale give a faint suggestion of spots on the anterior neck, becoming a speckling of scattered dark scales against a tan ground in the midbody region; posteriorly, the scales mostly dark, with a hint of about 20 crossbands (very poorly set off from the intervening spaces) and the tail with 10 black rings.

The Pindiu specimen is unusual in having four (rather than three) solid maxillary teeth on each side.

Toxicocalamus (Apistocalamus) loriae
(Boulenger)

BM 1946.1.17.57 [cotype of *Pseudapistocalamus nymani* Lönnberg] probably Sattelberg; MCZ 76627–28 Sattelberg; 95579–80 Masba Creek 2300–2500 ft.; 95578, 95582 Pindiu, 2600 ft.; 95581 Mt. Rawlinson, 4400 ft.

Also recorded from “Lialun” [=Sialum] by Vogt (1911).

Except for 95578, with a plant rootlet and unidentifiable matter, the stomach is empty in my specimens. McDowell (1969) has presented the evidence for considering the Huon Peninsula population (“*Pseudapistocalamus nymani*”) conspecific with *Toxicocalamus loriae*, but it should be noted that the Huon Peninsula population is distinguishable by a lower mean number of ventrals, although the observed range overlaps that of other eastern New Guinea populations. Ventrals of the Huon Peninsula sample are: males, 178–186, mean = 181.75, $s = 4.35$, $s_x = 2.17$, $N = 4$; females, 190–201, mean = 194.75, $s = 5.62$, $s_x = 3.25$, $N = 4$. The largest specimen in the Huon sample (95579) has a snout-vent length of 393 mm., tail 81 mm.

Aspidomorphus lineaticollis (Werner)

BPBM 5446 Kalolo, 750 m.; 95584 Masba Creek; 95583 Busu River, 12 mi. n of Lae.

This species has frequently been confused with *A. muelleri* (see McDowell, 1967) and probably Vogt's (1911) record of “*Pseudelaps muelleri*” from Sattelberg was based on *A. lineaticollis*. This is probably the only species of its genus in the Huon Peninsula region.

The stomach of 95583 contains a skink tail and that of 95584 contains the head and other fragments of a *Sphenomorphus* (R. G. Zweifel determination).

[MARINE HYDROPHIIDAE]

I have not found any records of sea snakes from the coast of the Huon Peninsula; almost certainly, this reflects the failure of herpetologists to collect in the sea, rather than the absence of sea snakes from the Huon coast.

BIOGEOGRAPHY

The geological history of the Huon Peninsula and the faunal relationships of its lizards and frogs have been summarized by Zweifel (1980). Analysis of the snake fauna of the Huon Peninsula gives results similar to those of Zweifel's analysis of the lizards. Table 2 lists the 24 snakes known for the peninsula, dividing the records into those for the low coastal region at the eastern end, those for the low region around Lae, and those from the higher elevations of the interior of the Huon Peninsula.

This list is almost a list of the common snakes of New Guinea. There is a striking lack of endemism at the specific level and only one case, *Dendrelaphis lorentzi*, represents a disjunction in distribution of considerable magnitude.

Some of the species occurring in the “elevated interior” of the Huon Peninsula show some incipient differentiation: *Stegonotus parvus* from the interior of the peninsula differs from other populations of the species, including the Lae population, in having a higher ventral count; *Styporhynchus montanus* and *S. multiscutellatus* from the interior of the peninsula both differ from the nearest populations of their respective species in lower ventral count (interior Huon Pen-

TABLE 2
Snakes Recorded from the Huon Peninsula^a

	Eastern Lowlands	Lae	Elevated Interior
TYPHLOPIDAE			
<i>Typhlops inornatus</i> Boulenger	—	—	X
<i>Typhlops depressiceps</i> Sternfeld	—	X	—
<i>Ramphotyphlops erycinus</i> (Werner)	X	X	—
<i>Ramphotyphlops braminus</i> (Daudin)	—	X	—
BOIDAE			
<i>Liasis papuanus</i> Peters and Doria	—	X	—
<i>Liasis albertisii</i> Peters and Doria	X	X	—
<i>Python amethistinus</i> (Schneider)	—	X	X
<i>Chondropython viridis</i> (Schlegel)	—	X	X
<i>Candoia carinata</i> (Schneider)	X	X	X
<i>Candoia aspera</i> (Günther)	X	X	X
COLUBRIDAE			
<i>Dendrelaphis lorentzi</i> (van Lidth de Jeude)	X	—	—
<i>Dendrelaphis gastrostictus</i> Boulenger	X	—	—
<i>Dendrelaphis calligastra</i> (Günther)	X	X	—
<i>Dendrelaphis punctulatus</i> (Gray)	X	X	—
<i>Stegonotus diehli</i> Lindholm	—	X	—
<i>Stegonotus parvus</i> (A. B. Meyer)	—	X	X
<i>Stegonotus cucullatus</i> (Duméril, Bibron, and Duméril)	—	X	X
<i>Styporhynchus montanus</i> (van Lidth de Jeude)	—	—	X
<i>Styporhynchus multiscutellatus</i> (Brongersma)	X	X	X
<i>Boiga irregularis</i> (Merrem)	X	X	X
HYDROPHIIDAE			
<i>Acanthophis antarcticus</i> (Shaw)	X	X	—
<i>Micropechis ikaheka</i> (Lesson)	X	X	X
<i>Toxicocalamus loriae</i> (Boulenger)	X	—	X
<i>Aspidomorphus lineaticollis</i> (Werner)	—	X	X

^a Authority for records given in the Systematic Accounts. "Eastern Lowlands" refers to coastal records from the eastern end of the peninsula, mainly Gusiko and Finschhafen; "Lae" refers to the low elevations at or near Lae; "Elevated Interior" includes records from the Rawlinson range, Sattelberg, Kalolo, and various other localities at over 1000 ft.

insula *S. multiscutellatus* appears to differ further from adjacent populations in lacking the juvenile pale collar); *Toxicocalamus loriae* from the interior of the Huon Peninsula has an unusually low ventral count; *Dendrelaphis gastrostictus* from the interior of the Huon Peninsula appears to be more like d'Entrecasteaux Archipelago specimens than like Eastern Highlands forms in coloration of the interstitial skin of the neck. One species, *Python amethistinus*, known from 5200 ft. on Mt. Rawlinson, is a lowland form over most of its range in New Guinea and Australia (but there are montane records for New

Britain; see McDowell, 1975); perhaps the absence of *P. boeleni*, which is a high altitude species in eastern New Guinea and (at least) the Wissel Lakes region of Irian Jaya, permits *P. amethistinus* to occupy the montane region of the Huon Peninsula, but it is not so easy to explain why there are no records for the low coastal region of the Huon Peninsula, except at Lae, since *P. amethistinus* is one of the commonest lowland snakes elsewhere in New Guinea.

Although there are no species of snake endemic to the Huon Peninsula (revision of *Styporhynchus* by Malnate and Underwood

may change this), study of the list of "elevated interior" forms shows that this list contains two main components: (1) the ubiquitous forms (*Candoia carinata*, *C. aspera*, *Boiga irregularis*) that can be expected in any New Guinea region collection of snakes; and (2) characteristic endemic (or nearly endemic) snakes of New Guinea (*Typhlops inornatus*, *Chondropython viridis*, *Stegonotus parvus*, *Dendrelaphis gastrostictus*, *Styporhynchus montanus*, *S. multiscutellatus*, *Micropechis ikaheka*, *Toxicocalamus loriae*, *Aspidomorphus lineaticollis*). I suspect that this assemblage represents the "old" New Guinea snake fauna, probably the early invaders of the Huon Peninsula when it was an island. As noted in the systematic accounts of *Styporhynchus multiscutellatus* and *Stegonotus parvus*, the elevated interior form is differentiated (but not, it would appear, at the species level) from the lowland form of the Lae region; in these cases, we are perhaps dealing with "old invaders" of the Huon Peninsula, when it was an island, that have come into contact with conspecific mainland populations when the Huon Peninsula became joined to northeastern New Guinea by the emergence of the Markham Valley lowlands. *Python amethistinus* might also belong to this "old snake fauna" of the Huon Peninsula.

The "new snake fauna" would probably include *Typhlops depressiceps*, *Ramphotyphlops erycinus* (and *R. braminus*, if that species is not too recent to warrant consideration), *Liasis papuanus* and *L. albertisii*, *Dendrelaphis calligastra* and *D. punctulatus*, and *Acanthophis antarcticus*. These species appear not to have penetrated the interior but are confined to the most newly formed land, along the coastal lowlands. One apparently coastal form, *Dendrelaphis lorentzi*, is so far isolated from other populations of its species, and so much differentiated, that it seems likely that it is a member of the "old fauna" rather than the "new fauna." It is impossible to guess whether *Boiga irregularis*, *Candoia carinata*, and *C. aspera* are very successful members of the "new fauna" that have succeeded in penetrating the interior or are "old fauna" elements.

The snake fauna of the Huon Peninsula is strikingly unlike the fauna of the Bismarck

Archipelago—or even the fauna of Rooke or Umboi Island, lying between New Britain and the Huon Peninsula. Zweifel (1980) found few special resemblances between New Britain and the Huon Peninsula in the frog and lizard faunas, and I cannot find any snake species at all showing a Huon Peninsula–Bismarck Archipelago distribution pattern. The differences between my findings with snakes and Zweifel's findings with lizards and frogs probably represents a difference in sample size: Zweifel listed 90 species of lizards and frogs for the Huon Peninsula (as here defined), whereas I list only 24 snakes. Thus Zweifel could note that although there were no shared highland forms of frogs and lizards, two lowland species of *Litoria* (abundant and widespread in the New Guinea region) and perhaps a *Rana* (taxonomy uncertain because of sibling species) were shared, along with many lowland species of lizards (mostly widespread) but no highland forms. With the snakes, there is remarkably little resemblance even when ubiquitous lowland forms are included. *Python amethistinus*, *Candoia aspera*, *C. carinata*, *Dendrelaphis calligastra*, *D. punctulata*, and *Boiga irregularis* are shared (on New Britain and the Huon Peninsula, *P. amethistinus* is a highland form, but elsewhere, over a broad range, it is a lowland species). Even this list may be too long, for the *Candoia carinata* of the Huon Peninsula is a "short-tail" (sense of McDowell, 1979), except in the Lae region, where both "long-tails" and "short-tails" occur, but New Britain *C. carinata* are "long-tails." At present, evidence is insufficient to prove that "long-tails" and "short-tails" are reproductively isolated and for general taxonomic purposes, the burden of proof is on those who would assert a reproductive isolation exists; but for the zoogeographic argument, it must be remembered that the "long-tails" of New Britain may not be conspecific with the "short-tails" of the Huon Peninsula.

More striking are the differences between the Huon Peninsula and New Britain that would not be expected by any hypothesis of either over-water dispersal or former land connection. Thus, the *Aspidomorphus* of New Britain (there, the only terrestrial hydrophiid) is *A. muelleri*, a widespread species occurring

in the Moluccas as well as over most of New Guinea *except* for the Huon Peninsula, where the genus is represented by *A. lineaticollis*; this latter is also the only species of the genus on the islands (other than the Bismarck Archipelago) east of New Guinea and occurs sympatrically with *A. muelleri* on the Papuan peninsula. Perhaps the resources of the Huon Peninsula will not support two species of *Aspidomorphus* and *A. lineaticollis* has excluded (or exterminated, through competition) *A. muelleri*, but I see no easy explanation for the presence on New Britain of the species of *Aspidomorphus* missing from the nearest mainland and islands. It may be noted that the major pattern Zweifel found among New Britain frogs, special affinity with those of the Solomon Islands, does not appear among the snakes except for one typhlopoid (*Ramphotyphlops subocularis*), also known from the tip of the Papuan peninsula (MCZ R-145955, Alotau, Milne Bay Province); among terrestrial proteroglyphs, there is no suggestion of this pattern, since the Solomons genera (*Parapistocalamus*, *Salomonelaps*, *Loveridge-laps*) do not occur outside the Solomons and *Aspidomorphus* does not extend to the Solomons.

Liasis albertisii of the Huon Peninsula (and most of New Guinea) is represented on New Britain (and Umboi and New Ireland) by the closely related, but quite distinct, *L. boa*; however, *L. albertisii*, rather than *L. boa*, represents this superspecies complex on Mussau I., the part of the Bismarck Archipelago farthest from the New Guinea mainland. *Stegonotus* is represented in the Bismarck Archipelago by two species: *S. heterurus* (perhaps only a geographic variation of *S. modestus* of the Moluccas, Manus, and northern New Guinea, but not recorded from the Huon Peninsula); and an unnamed endemic with dark upper lip, perhaps related to *S. parvus* of the Huon Peninsula and other regions of New Guinea. The *Styporhynchus* of New Britain and Umboi is *S. hypomelas* (and, if it is distinct, *S. dahlí*), an endemic species (or endemic complex of two closely related species), sharply distinguished from Huon Peninsula *Styporhynchus* but perhaps related to an unnamed form from more western New Guinea (a 15-scale-rowed species,

but with the attenuate form of *S. hypomelas* and probably the basis for Sternfeld's [1913] erroneous record of the latter from New Guinea).

The snake fauna of Umboi Island might be expected to be a mixture of New Britain and Huon Peninsula elements, favoring the latter (because of the larger species pool); it is not; it is almost purely a New Britain fauna, but with a "short-tail" *Candoia carinata* (as for the Huon Peninsula) rather than a "long-tail" (as for New Britain). Combining my own identifications of Umboi material with Hediger's (1934), the snakes known from Umboi Island are: *Ramphotyphlops subocularis* (New Britain also), *Liasis boa* (New Britain also), *Python amethistinus* (species common to both New Britain and the Huon Peninsula, but Umboi population highly peculiar in head pattern and representing endemic geographic variation), *Candoia carinata* (more like Huon Peninsula than like New Britain in being "short-tail"), *C. aspera* (common to both New Britain and Huon Peninsula), *Styporhynchus hypomelas* (New Britain also), *Boiga irregularis* (common to both New Britain and Huon Peninsula).

Although Zweifel's observations on the frogs and lizards and my own on snakes are in close agreement so far as the lack of similarity between the Huon Peninsula and New Britain are concerned, Koopman (1979 and personal commun.) found no such striking dissimilarity in the distribution of mammals (mostly bats) and his (1979) analysis of the small islands northeast of New Guinea shows a similarity between Umboi and mainland New Guinea in mammalian fauna that is not apparent among snakes.

However, the similarity between New Britain and New Guinea in the mammals makes it difficult to assign the Umboi species to one or the other source; nearly all the Umboi species are common to both sources. Furthermore, Koopman (personal commun.) finds that although there is no striking dissimilarity between New Britain and the Huon Peninsula fauna, this represents a general similarity between New Guinea and New Britain and there is no indication of a special resemblance between the Huon Peninsula and the Bismarck Archipelago fauna. From the

literature and the (not yet completely identified) Seventh Archbold Expedition collections, Koopman finds 53 species of mammals on the Huon Peninsula (17 Chiroptera, 36 non-flying); of these, none is endemic to the Huon Peninsula and none is found on the Huon Peninsula and Bismarck Archipelago and not elsewhere in New Guinea; 20 (13 flying, seven non-flying) species are found on Huon and the Bismarck Archipelago and also in other New Guinea localities; 33 (four flying, 29 non-flying) are found on the Huon Peninsula and other New Guinea mainland localities but are unknown from the Bismarck Archipelago. It is worth noting that although bats make up only one-third of the mammals recorded from the Huon Peninsula, they make up two-thirds of the species shared with the Bismarck Archipelago.

By Koopman's (personal commun.) listing of mammal species for the New Guinea-Solomons region, for non-flying mammals the pattern is one of progressive loss of species (or species groups) reading from west (New Guinea) to east (the Solomons) through the Bismarck Archipelago. This is also the most common pattern for bats, but among Pteropodidae and Emballonuridae there are a few cases of progressive loss of species reading from east to west or of shared Bismarck Archipelago-Solomons endemism: the Tribe Notopterini (also in Oceania and New Caledonia) of the Pteropodidae, *Pteropus admiralitatum*, *Nyctimene vizcaccia*, and *Emballonura diana*. These bats would fit the pattern of frogs (but not lizards) noted by Zweifel (1980), of special affinity between the Bismarck Archipelago and Solomons; but even among Chiroptera, this is not the predominant pattern.

For Umboi, it is impossible to guess whether the differences between the mammalian pattern (mostly a flying mammal pattern) and the snake pattern result from: (1) differences in means of dispersal; or (2) from sampling error in collection (more precisely, a different bias between herpetological sampling and bat sampling in which species of the true fauna will be missed); or (3) from differences in rate of faunal turnover. Because of the obvious impossibility of sampling the entire faunal diversity in any single expedition, I—and others—assume zero faunal

turnover and accept nineteenth-century records of snakes as members of the present fauna unless the record seems to have been erroneous at the time it was made. I believe—but have no evidence to prove—that this method gives a better estimate of the true fauna than would acceptance of only those records made in the last decade as the true present fauna, but undoubtedly some turnover must exist; in point of fact, the snake fauna of Umboi Island as given by Hediger (1934) is entirely different from the fauna of Umboi seen by me in the Bernice P. Bishop Museum and American Museum collections made after World War II, and I cannot from my own data disprove a total turnover of the snake fauna of Umboi around the time of World War II, even though I doubt any such thing happened.

Zweifel (1980) reviewed the geology of the Huon Peninsula, which indicates a Pliocene origin as an island (in the biologist's sense of "island," an area capable of supporting a terrestrial fauna and flora and isolated by a water barrier). Zweifel documents this relatively recent insular origin of the Huon Peninsula with distribution patterns of highland lizards and frogs showing disjunct distributions, in the interior of the Huon Peninsula and, most often, on the central spine of New Guinea, but sometimes on the isolated mountain ranges of the north coast or the islands east of New Guinea. The distributions of snakes fit fairly well with this pattern based on lizards and frogs, but there are some differences, largely exaggerations of the peculiarities noted by Zweifel. Zweifel noted that "a curious aspect of the (frog and lizard) fauna is the scarcity of endemic species" but could cite three poorly known frogs; I cannot cite any positively known endemic snake, but the most conspicuous disjunction, *Dendrelaphis lorentzi*, may represent a distinct species, since the Huon specimen is distinguishable by hemipenial details and ventral count from specimens from the southern coast of New Guinea (and it must be remembered that Malnate and Underwood's revision of *Styporhynchus* may add an endemic). The expectation would be that such endemism as there is should be among forms in the interior, presumably the forms that have been isolated for the longest time. But neither the

frogs nor the *Dendrelaphis* support this—the very limited “endemism” in the herpetofauna is from coastal localities.

Zweifel noted the absence of high montane frogs of more central New Guinea from the high interior of the Huon Peninsula, even though a distinct highland fauna of Huon can be distinguished. This “highland fauna” of Huon is made up of medium-elevation or even lowland forms of more central New Guinea. This is particularly evident in the snakes, as well. The “highland fauna” of Huon contains *Python amethystinus*, rather than *P. boeleni*, and *Toxicocalamus loriae*, rather than *T. stanleyanus*.

All of this is in keeping with the Huon Peninsula herpetofauna being a young fauna, derived from the most likely New Guinea species to colonize an island—the coastal forms.

So far as resemblance of the New Britain fauna to that of the Huon Peninsula is concerned, the pattern seems to depend on the taxonomic group considered. The surprising lack of resemblance seen in the herpetofauna is not conspicuous in the bats. The special resemblance between the frog fauna of New Britain and that of the Solomons is not apparent in the snakes or the lizards. This is consistent with settlement by dispersal across water barriers, but with the differences in major means of dispersal between taxonomic groups resulting in somewhat different patterns. Aside from the Typhlopidae (which I would discount for zoogeographic discussion because the difficulty of collection makes the true ranges of the species very uncertain), snakes must be among the last groups to colonize an island, because they are high-order predators and their survival depends on the existence of prey fauna. Because most New Guinea snakes feed on lizards or frogs (but no lizard or frog is primarily a snake-eater), the colonization by snakes might be expected to lag behind the colonization by lizards and frogs.

It may be noted that Hamilton's (1979) analysis of the plate tectonics of this region, unavailable to Zweifel at the time he was preparing his report, do not change his geological assumptions and do not give any support to any previous connection of the Huon Peninsula with New Britain; New Britain and

the Huon Peninsula are converging, rather than diverging.

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