

CONTRIBUTIONS TO A REVIEW OF PHILIPPINE  
SNAKES, V

THE SNAKES OF THE GENUS *TRIMERESURUS*

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TWO TEXT FIGURES

The venomous pit vipers of the genus *Trimeresurus* are treated in this report. In 1922, Taylor recognized seven species, of which one, *T. wagleri*, he believed to be polytypic with three discernible subspecific populations. In the present work three species are recognized, and only *Trimeresurus flavomaculatus* is treated as polytypic, with three easily distinguishable subspecies.

The snakes of this genus are found on all the major islands of the Philippine Archipelago where they constitute one of the ever present health hazards. All members of the genus are easily recognized, however, by their chunky, broad triangular heads, deep pit between the nostril and the eye, and the vertically elliptic pupil.

TERMINOLOGY

Standard length: distance from tip of snout to anal opening. Data given under "Diagnosis" for largest male and largest female examined.

\*: following locality listed under "Range" indicates specimens were examined from that site by the author.

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## Genus TRIMERESURUS Lacépède

- Trimeresurus* LACÉPÈDE (1804) 209 [type species *Trimeresurus viridis* Lacépède, by subsequent selection by Stejneger (1907)].
- Megaera* WAGLER (1830) 174 (type species *Vipera trigonocephala* Daudin, by monotypy).
- Atropos* [not Oken (1815) Lepidoptera; LEACH (1815) Pscoptera; Rafinisque (1815) Reptilia] WAGLER (1830) 175 [type species *Trigonocephalus puniceus* Reinwardt in F. Boie (1827)].
- Tropidolaemus* WAGLER (1830) 175 [type species *Cophias wagneri* H. Boie in SCHLEGEL (1837) by monotypy].
- Trimesurus* GRAY (1842) 48 (erroneous subsequent spelling).
- Bothrophis* FITZINGER (1843) 28 (type species *Trigonocephalus viridis* Cuvier, by original designation).
- Pariasis* GRAY (1849) 11 [type species *Megaera flavomaculatus* Gray, by subsequent selection by Smith (1943)].
- Cryptelytrops* COPE (1859) 340 (type species *Trimesurus carinatus* Gray, by monotypy).
- Atropophus* PETERS (1871) 41 (substitute named for *Atropos* Wagler).

*Definition.*—Maxillary bone shortened, movable, with enlarged fang; palatine bone expanded, without a distinct dorsal apophysis; border of cavity of maxillary bone with a slight re-entering curve, forming two distinct curves; head distinct from neck, usually covered with small scales; deep loreal pit present between nostril and eye; pupil of eye vertical; scales smooth or keeled, in 17 to 31 longitudinal rows at midbody; body stout; tail short; ventrals rounded; subcaudals paired, rarely single; hypapophyses present throughout vertebral column; hemipenes forked, ornamentation variable.

*Remarks.*—Boulenger [(1896) 529-569] assigned a large number of South American and Asian pit vipers to the nominal genus *Lachesis*. Stejneger [(1907) 466] questioned this association stating, "It has not been demonstrated conclusively that they (snakes of the genus *Trimeresurus* of Asia) are generically identical with the numerous American pit-vipers of a similar head scutellation, and which are usually known as *Trigonocephalus* or *Bothrops*. The South American genus *Lachesis* is sufficiently characterized by the peculiar scutellation of the tail."

Mocquard (1915) clearly justified removing the South American snake, now known as *Lachesis muta*, from the association proposed by Boulenger. A large number of South American and Asian snakes were, however, retained in one genus, then known as *Trimeresurus*. Amaral [(1926) 35] and others ques-

tioned the association on zoogeographic grounds, and Maslin (1942) suggested that several morphological characters, especially the presence or absence of a minute nasal pore, would distinguish the New and Old World species. Smith (1942) point out that the morphological basis for distinguishing the New and Old World species proposed by Maslin was variable and could not be associated with the distribution of these snakes. In 1943, Smith stated "No morphological characters have yet been found to show that the South American species, called by some writers *Bothrops*, are generically distinct from the Asiatic ones." In commenting on his brief generic synonymy, Smith [(1943) 502] states, "The synonymies given above refer to the Asiatic members of the genus only." This clearly implies that the author believed that Asian and South American groups were congeneric. This view has not met with popular support in the United States where for many years the South American species have been placed in a distinct genus, *Bothrops*.

After a careful examination of the bones making up the palato-maxillary arch, Ruiz [(1952) 109-110] concluded that the genera of crotaline snakes could be distinguished as follows:

1. Osso transverso mais curto que a porção basal do pterigóide. *Agkistrodon*.
2. Osso transverso mais longo que a porção basal do pterigóide .... 2  
Osso palatino em forma de forquilha, apresentando uma apófise dorsal . . . Borda da cavidade maxilar (vista antero-lateral-externa) regular, formando uma curva simples sem semicírculo aberto .... *Bothrops*  
Osso palatino não bifurcado como anteriormente, a porção dorsal formando uma dilatação ampla, convexa ..... Borda da cavidade maxilar apresentando uma léve reentrância ou uma apófise pequena, formando duas curvaturas distintas ..... 3
3. Dentes pterigóides ultrapassando o nível da articulação transversopterigóide. Osso transverso muito forte com a parte distal ou anterior dilatada e de forma um tanto quadrangular .... *Trimeresurus*  
Dentes pterigóides não ultrapassando o nível da articulação transversopterigóide. Osso transverso mais delicado, não formando uma dilatação distal ..... 4  
Apófise da borda de cavidade maxilar lisa ..... *Crotalus* e *Sistrurus*  
Apófise da borda de cavidade maxilar apresentando uma cavidade bem diferenciada na parte externa ..... *Lachesis*.

Recognition of many species of *Trimeresurus* (*sensu stricto*) is made difficult because of the absence of stable characters in the scutellation and color pattern, because of convergence in scale characters in unrelated species and because of parallelism in adaptive characters among related and frequently sym-

patic species. Pope and Pope (1933) demonstrated that differences in the structure of the hemipenes frequently serve to distinguish species that are, on the basis of external characters, otherwise inseparable.

Taylor [(1922a) 283-284] listed seven nominal species in the Philippines. Of these, *T. gramineus* was regarded of doubtful occurrence and *Trimeresurus wagleri* was thought to be polytypic (Taylor recognized three subspecies). I have found it necessary to reduce the number of recognized species to three, of which one, *Trimeresurus flavomaculatus*, is polytypic.

*Trimeresurus halieus* Griffin and *T. mcgregori* Taylor are indistinguishable from *T. flavomaculatus* except for slight differences in color pattern and distribution. In scutellation and in the morphology of their copulatory organs they are identical. It is assumed that color pattern differences in the geographically distinct populations reflect differences in the genetic makeup of the respective populations; the populations are treated as subspecies.

The subspecies of *T. wagleri* recognized by Taylor could not be distinguished in the material at hand. Further, the characters used by Taylor to separate the subspecies were found to be more variable within a given population than he suspected.

*Trimeresurus philippensis* is tentatively regarded as a synonym of *T. wagleri*. There are no morphological characters by which to separate the two nominal species; and the differences in color pattern between the two that were cited by Taylor represent extremes of variation in *T. wagleri*.

*Trimeresurus schultzei* from the Palawan Archipelago appears to be a distinctive species. I have not been able to establish its probable affinities because of the lack of representatives of the western Indonesian species of *Trimeresurus* to which it should be compared.

*Key to the Philippine species and subspecies of Trimeresurus*

- 1a. Scales on head and chin smooth; second upper labial fused to shield forming anterior border of facial pit.
- 2a. No ventrolateral light stripe along outer scale row; dorsal color usually brown to purplish brown (Polillo Island) ... *T. f. halieus*
- 2b. A distinct light stripe, or at least a series of light spots, present along outer scale row; dorsal color variable, usually green, blue-green, dark blue gray, or light yellow (without any darker pigments present).

- 3a. Tail not distinctly differentiated from body by color; hemipenes without spines.
- 4a. Dorsal color lacks all dark pigments; yellow in life, white in alcohol (Batan Island) ..... *T. f. mcgregori*
- 4b. Dorsal color with dark pigments present usually blue green, green, or dark blue gray .... *T. f. flavomaculatus*
- 3b. Tail distinctly differentiated from body by color; hemipenes spinose ..... *T. schultzei*
- 1b. Scales on head and chin strongly keeled; second upper labial separated from shield forming anterior border of facial pit .... *T. wagleri*

**TRIMERESURUS FLAVOMACULATUS (Gray).**

*Megaera flavomaculata* GRAY (1842) 49.

*Taxonomic notes.*—In 1842, Gray described three species, *Megaera flavomaculata*, *M. ornata* and *M. variegata* from the Philippines. The type specimens of these nominal species are in the British Museum. Günther [(1879; 79] and Boulenger believed them to be conspecific.

Fischer, in 1885, described *Trimeresurus schadenbergi* from southern Mindanao, based upon three specimens collected by Dr. Schadenberg. The measurements, counts and color pattern of Fischer's specimens clearly indicate that *T. schadenbergi* and *T. flavomaculatus* are conspecific.

In 1910, Griffin described a new species of *Trimeresurus* from Polillo Island, based on ten specimens. The new species, *T. halieus*, was distinguished from *T. flavomaculatus* in lacking a ventrolateral yellowish-green stripe on the outer scale row. Taylor [(1922a) 287] stated *T. halieus* was close to *T. flavomaculatus*. I believe that the two nominal species are conspecific. There is general agreement between the two in scutellation, structure of the hemipenes and juvenile color pattern. Minor adult color pattern differences can, however, be correlated with geographic distribution, and consequently the Polillo population is recognized as a distinct subspecies.

In 1907, McGregor obtained a unique specimen of *Trimeresurus* from Batan Island, north of Luzon, in which all pigments except xanthophores were lacking. Taylor, in 1919, described *Trimeresurus mcgregori*, based upon this individual. According to Taylor [(1922a) 285], "It is differentiated from the other species [*T. flavomaculatus* and *T. halieus*], however, by the striking color with no dark markings, the larger number of scales on snout and supraocular region, and the larger unkeeled temporals; the supranasals are larger and more clearly differentiated."

The type specimen of *T. mcgregori* was formerly in the collection of the Bureau of Science, Manila, but was destroyed during World War II. A second specimen, from the type locality, is in the collection of the California Academy of Sciences and was examined and compared with specimens of *T. flavomaculatus*. Except for the color, the other characters cited by Taylor as diagnostic were found to vary between Taylor's description of the type and the available specimen; further, the characters (other than color) were found to fall well within the range of variation of *T. flavomaculatus*. The remarkable color of the two Batan specimens suggests that a xanthic population had become established on that isolated island. Assuming that the Batan population characteristically lacks melanin pigment, and in view of the geographic isolation of the population, it is accorded subspecific status under *T. flavomaculatus*.

*Trimeresurus flavomaculatus* is known only from the Philippines where it has been recorded from most of the larger islands with the exception of Palawan and the central Visayan group. It is related to the *T. gramineus* section of the genus and is most similar to *T. popeorum* from Borneo and the Malay Peninsula.

*Diagnosis*.—Hemipenes long and slender, deeply forked; spines absent; distal sections calyculate, proximal section with series of thick longitudinal ridges; second upper labial fused with loreal (shield bordering anterior side of pit); scales on dorsum of head and gular scales smooth; dorsal scales in 21 (rarely 19) longitudinal rows at midbody; tail colored as dorsum. Standard length: (♂) 614 mm, (♀) 929 mm; tail length: (♂) 151 mm, (♀) 163 mm.

*Descriptive notes*.—Snout 2.0 to 2.7 times as long as horizontal diameter of eye (young specimens tend to have larger eyes in proportion to snout length so that the length of the snout may be as little as 1.5 times greater than the horizontal diameter of the eye); rostral about twice as broad at base as at tip and 1 to 1.5 times more broad at base than deep; internasals distinct, separated by two scales which are only slightly smaller than themselves; supraoculars small, distinct, three to four times as large as surrounding scales, separated from each other by 9 to 14 small, imbricate, smooth scales, and separated from internasals by 3 to 4 scales; upper head scales small, imbricate, smooth; nasal not constricted in middle but tapers

posteriorly, undivided, completely separated from first labial by a suture; second upper labial fused with loreal and forms anterior border of pit, in contact with nasal; three preoculars, the lower most elongate and forming ventral border of pit; one or two suboculars, when two the posterior shield longest, posterior most portion of subocular forming part of posterior border of orbit; third upper labial in contact with subocular; fourth upper labial usually separated from preocular by one or two scales; 2 or 3 small postoculars; 9 to 11 upper labials, third largest; temporal scales smooth, larger than scales on dorsum of head; 10 to 13 lower labials, the first pair largest and the contact at midline; mental large, triangular, separated from large anterior chin shields; scales of gular region all smooth; scales of dorsum in 21, occasionally 19, longitudinal rows at midbody, keeled; ventrals 171 to 184 (Table 1); subcaudals 58 to 71 (see Table 2); anal plate single.

Color (in alcohol) variable, light yellow, light green, bluish green, blue-gray, brown, or purplish brown, somewhat lighter below; a series of irregular brown blotches or crossbars are present on dorsum; light ventrolateral stripe of yellowish green blotches frequently present along outer scale row.

*Inter-island variation.*—The most prominent differences among island populations are in color pattern. As indicated in the taxonomic discussion (see above) the Batan and Polillo populations may be distinguished by color pattern differences from *T. flavomaculatus* from elsewhere. In addition to the absence of dark pigments or lack of a ventrolateral stripe, other less pronounced color pattern variations can be discerned within the species. However, these variations, e.g., lack of distinct crossbars, cannot be correlated with distribution but appear to represent random individual differences.

As indicated by the data for ventral and subcaudal count and proportional measurements, summarized by island units in Tables 1 and 2, those characters do not appear to vary very greatly geographically.

Three subspecies of *T. flavomaculatus* are recognized: *T. flavomaculatus flavomaculatus*, *T. flavomaculatus habieus*, *T. flavomaculatus mcgregori*.

**TRIMERESURUS FLAVOMACULATUS FLAVOMACULATUS (Gray).**

*Megaera flavomaculata* GRAY (1842) 49 (type loc: "Philippine Islands"; types in British Museum; original description).

*Parias flavomaculata* GRAY (1849) 11 (color pattern).

- Trimeresurus flavomaculatus* GÜNTHER (1879) 79 (Mindanao [Pia-  
cer]; color pattern; *M. ornata* and *M. variegata* regarded as  
synonyms); TAYLOR (1922a) 288, text-fig. 32 (Bohol, Jolo, Luzon,  
Mindanao; synonymy, description, variation); (1922c) 139 (Luzon  
[Mt. Makiling]; listed); MASLIN (1942) 23 (listed in key).  
*Lachesis flavomaculatus* BOULENGER (1896) 556, pl. 25, fig. 3  
(synonymy, description); BOETTGER (1898) 140 (Luzon [Majay-  
jay]; listed).  
*Trimerisurus flavomaculatus* GRIFFIN (1911) 267 (in part; listed  
in key distribution compiled).  
*Trimeresurus flavomaculatus flavomaculatus* LEVITON (1961) 105  
(Camiguin, Jolo, Luzon, Mindanao).  
*Megaera ornata* GRAY (1842) 49 (type loc: "Philippine Islands";  
type in British Museum; original description).  
*Parias ornata* GRAY (1849) 11 (color pattern).  
*Megaera variegata* GRAY (1842) 50 (type loc: "Philippine Islands";  
type in British Museum; original description).  
*Parias variegata* GRAY (1849) 11 (color pattern).  
*Trimeresurus gramineus* (nec Shaw) MÜLLER (1883) 290 (Min-  
danao; listed); FISCHER (1885) 81 (south Mindanao; listed);  
GRIFFIN (1911) 267 (in part; listed in key).  
*Trimeresurus schadenbergi* FISCHER (1885) 116 (type loc: "Sud-  
Mindanao"; types in Dresden Museum; original description).

TABLE 1.—Summary of the variation in the number of ventral shields in  
*Trimeresurus flavomaculatus*.

Island	Male			Female		
	N	Mean	Range	N	Mean	Range
Batan.....				1	177.0	
Camiguin.....				1	175.0	
Leyte.....	1	174.0				
Luzon.....	3	173.3	171-175	4	179.3	177-184
Mindanao.....	4	175.5	174-178	3	181.0	178-183
Mindoro.....	2	171.5	170-173			
Polillo.....				9	177.9	175-182
Jolo.....	1	175.0		1	182.0	

TABLE 2.—Summary of the variation in the number of subcaudal shields  
in *Trimeresurus flavomaculatus*.

Island	Male			Female		
	N	Mean	Range	N	Mean	Range
Batan.....				1	59.0	
Camiguin.....				1	56.0	
Leyte.....	1	65.0				
Luzon.....	3	66.6	62-69	3	60.3	59-63
Mindanao.....	4	69.0	68-71	2	53.5	58-59
Mindoro.....	2	62.5	62-63			
Polillo.....				9	57.7	56-59
Jolo.....	1	68.0		1	59.0	



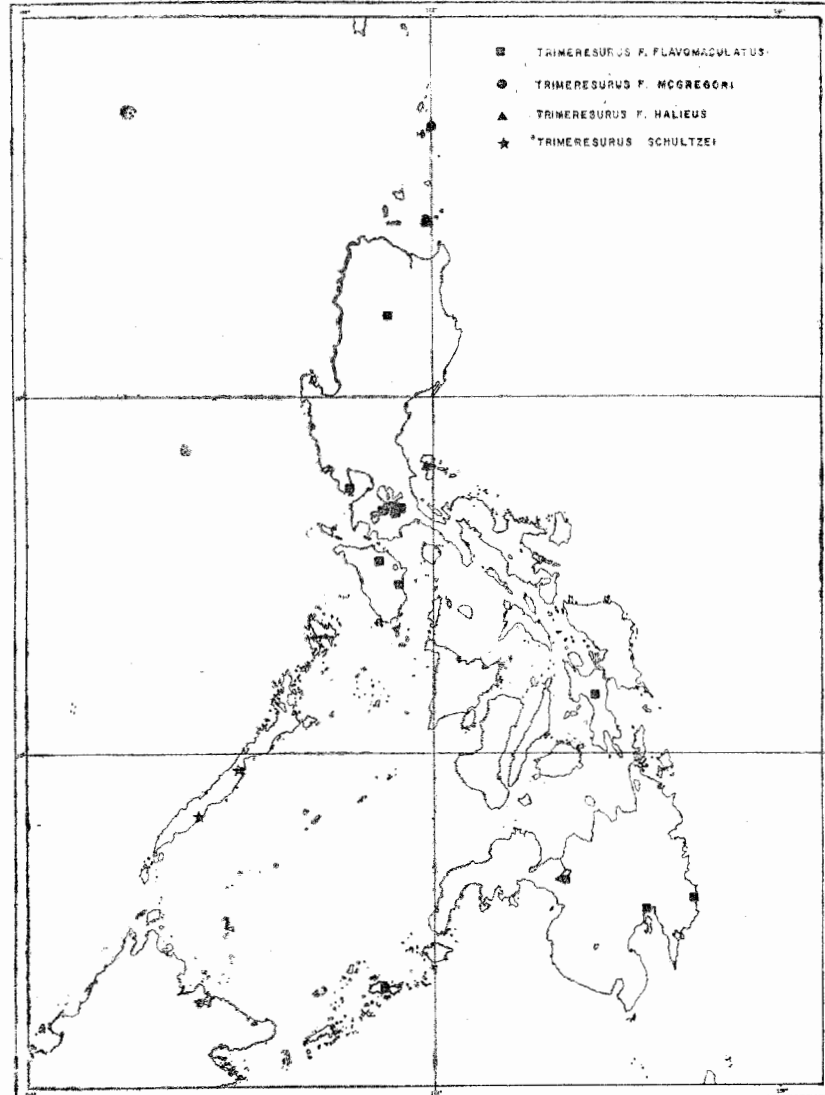


FIG. 1. Distribution of *Trimeresurus schultzei* and *Trimeresurus flavomaculatus* in the Philippines. See key for identification of symbols.

*Range (Figure 1).*—CAMIGUIN \*. Jolo: without exact locality \*. LEYTE: Mt. Lobi, Dagami, Bo. Patok \*. LUZON: Bataan Province (Lamao \*); Kalinga Subprovince (Balbalan\*); Laguna Province (Mt. Banahao\*; Los Baños\*; Mt. Makiling\*; Majayjay). MINDANAO: Davao Province (Tagum\*); Lanao Province (Lake Lanao\*). MINDORO: Mt. Halcon, Alag River\*; Balete\*.

Material examined (18).—CAMIGUIN: (CAS 15352). JOLO: without exact locality (CNHM 41123 and 41124). LEYTE: Bo. Patok, Dagami, Mt. Lobi (AMNH 88158). LUZON: Bataan Province: Lamao (CNHM 15040); Kalinga Subprovince: Balbalan (CAS 61545, 62661); Laguna Province: Mt. Banahao (CNHM 15044); Los Baños (CAS 61155, USNM 56014); Mt. Makiling (MCZ 25853). MINDANAO: Davao Province: Tagum (CNHM 53562 and 53563). Lanao Province: Lake Lanao (CAS 15353 to 15357). MINDORO: Balete (USNM 36111); Mt. Halcon, Alag River (USNM 37872 to 37873). PALAWAN:<sup>1</sup> Victoria Peak (USNM 37871). PHILIPPINES: without exact locality (CAS 15383; MCZ 46973).

62551

15358

*Taxonomic notes.*—The type specimens of *T. flavomaculatus flavomaculatus* were collected in the Philippines (exact locality unknown). Recognition of several subspecies necessitates selection and restriction of type localities of each of the nominate forms to provide a stable base for nomenclature. Gray's description [(1849) 11] of *T. flavomaculatus* is very brief and the characters cited fit samples of this subspecies from several islands. The ventral and subcaudal counts of the types have been given by Boulenger [(1896) 557], but they are inconclusive. The same comments apply to the type specimens of Gray's nominal species *Megaera ornata* and *M. variegata*. Examination of the available samples suggests the Luzon population is typical. Therefore, I hereby restrict the type locality of *T. flavomaculatus* to Luzon Island. Further, I believe it advisable to restrict the type localities of *Megaera ornata* and *M. variegatus*, both synonyms of *T. flavomaculatus*. The type locality of both is hereby restricted to Luzon Island, too.

*Diagnosis.*—Melanin and other dark pigments present in dorsal color, usually green, bluish green, or dark blue-gray; a distinct yellow or yellowish-green series of spots, sometimes continuous and forming a stripe, along outer scale row.

*Descriptive notes.*—The most striking differences noted among the available samples of this subspecies are in the juvenile color patterns. Young specimens from Mindanao are boldly marked, especially on the sides of the head. A white or yellow streak passes forward from the angle of the jaw along

<sup>1</sup> This Palawan record is doubted; I believe the locality datum is in error.

the upper labials to beneath the eye: a short vertical bar is present just beneath and at the posterior corner of the eye, and another bar is present below and just in front of the eye. The Mindanao young also are slightly darker in color, tending toward a dark blue-gray. Young specimens from Luzon lacked the bold head markings and tend to be somewhat lighter, usually green or greenish brown.

*Sexual dimorphism.*—There is a slight difference in ventral counts between sexes, and though the samples are small, there is no overlap in counts, if island samples are treated separately. Males tend to have fewer ventrals than females. Dimorphism in subcaudal counts seems to be more marked, males having the higher number of shields. It is not necessary to treat samples from each of the islands separately for there is no overlap in counts between sexes from different islands as in the case of ventrals. Data for ventral and subcaudal counts are summarized in Tables 1 and 2.

There is considerable range of overlap in the tail length/standard length ratio between sexes. However, the means are quite distinct and the difference is probably significant (see Table 3).

*Ecological notes.*—Two females from Kalinga Subprovince, Luzon Island, collected April 28, 1920, contained large eggs in the oviducts. One specimen had 11 eggs in the right oviduct, 9 in the left; the second specimen had 13 eggs in one oviduct.

Adult frogs and tadpoles and the remains of geckos were found in the stomachs of several individuals.

**TRIMERESURUS FLAVOMACULATUS MCGREGORI** Taylor.

*Trimeresurus flavomaculatus* GRIFFIN (1911) 267 (in part; Batan Islands; listed in key).

*Trimeresurus mcgregori* TAYLOR (1919) 110, text-fig. 1 (type loc: Batan Island, Batanes Group; type formerly in Bureau of Science, Manila, destroyed during World War II; original description; records incident of snake bite); (1922a) 284, text-figs. 31a-c (redescription of type specimen); (MASLIN (1942) 23 (listed in key).

*Trimeresurus flavomaculatus mcgregori* LEVITON (1961) 105 (Batan Ids.).

*Range.*—(Figure 1.) Bataan Island\*.

*Material examined (1).*—BATAN: (CAS 60525, neotype).

*Taxonomic notes.*—The holotype specimen of this subspecies was destroyed when the Bureau of Science building, in Manila,

TABLE 3.—Summary of the variation between sexes in the ratio of tail length/standard length in *Trimeresurus f. flavomaculatus*.

Sex	N	Mean	Range
Male	7	0.209	0.172-0.233
Female	7	0.176	0.158-0.207

itself was destroyed during the early days of the second World War. Some years earlier a second specimen had been deposited in the collections of the California Academy of Sciences. This specimen, itself a topotype, is herein designated as neotype to stand in place of the lost holotype. The description of this specimen follows the diagnosis.

*Diagnosis.*—Melanin pigments absent in the color; guanophores predominate; no dark marking of any kind present.

*Description of neotype.*—(CAS 60525) Female, differing from destroyed holotype [see original description, Taylor (1919) 110] as follows: internasals (or supranasals) separated by 3 scales, and separated from narrow supraocular by 4 to 5 scales; on right side supraocular very narrow and elongate, on left side shield broken up into two small scales not much larger than adjoining head scales; two narrow scales between nasal and upper preocular forming canthus rostralis; 4/3 postoculars; 10/11 upper labials; 12/11 lower labials; 30 scales from angles of mouth across occiput; ventral 177 [179 according to Taylor (1919) 111]; subcaudals 59.

Color (in alcohol) dull white above and below; tip of tail has some faint crossbands of darker pigments; eyes very pale, suggesting albinism.

#### TRIMERESURUS FLAVOMACULATUS HALIEUS Griffin.

*Trimeresurus halieus* GRIFFIN (1910) 214 (type loc: Polillo Island; lectoholotype, California Academy of Sciences 62576 [formerly number Griffin 767]; original description).

*Trimeresurus halieus* GRIFFIN (1911) 268 (listed in key); TAYLOR (1922a) 286 (Polillo, Pantnanongan; description of syntypic material; suggests relationship to *T. flavomaculatus*); MASLIN (1942) 23 (listed in key).

*Trimeresurus flavomaculatus halieus* LEVITON (1960) 105 (Polillo).

*Range.*—(Figure 1.) POLILLO: without exact locality.

*Material examined* (9).—POLILLO: without exact locality (CAS 62576, lectoholotype, 62407 to 62413; MCZ 25854).

*Taxonomic notes.*—Griffin [(1910) 214] and before him 10 specimens from Polillo Island. He did not select any single

specimen as type. Therefore, the series must stand as syntypes. The syntypic series has been broken up and specimens distributed among several museums. As a consequence it seems desirable to select one of the syntypes to stand as the lectoholotype. A single specimen in the collection of the California Academy of Sciences, Number 62576 (formerly R 41 and Cesario Cononizado 767) was part of the syntypic series. The specimen is a female in an excellent state of preservation. I hereby select this specimen to stand as lectoholotype of *Trimerisurus* (= *Trimeresurus*) *halieus* Griffin.

*Diagnosis.*—Melanin and other dark pigments present in dorsal color, usually greenish-brown, medium brown, or darker purplish brown; there is no green or yellowish-green series of spots or a stripe present along outer scale row although a discontinuous series of greenish spots may be present in young individuals.

*Sexual dimorphism.*—The specimens examined here were all females. Griffin [(1910) 215] records the counts for a single male as 170 ventrals, 58 subcaudals. The range of ventrals and of subcaudals for the nine female specimens are: ventrals 177 to 182; subcaudals 56 to 59. Two females listed by Griffin have 54 to 55 subcaudals. It would seem, then, that the number of subcaudals is not subject to sexual dimorphism; however, the male does have fewer ventrals than the females.

*Ecological notes.*—According to Griffin [(1910) 215] the specimens listed by him were collected along the banks of streams or in damp localities. Their food seems to consist of frogs, fish and perhaps mammals.

**TRIMERESURUS SCHULTZEI** Griffin.

*Trimeresurus formosanus* BOULENGER (1894) 85 (in part; Palawan).

*Trimeresurus schultzei* GRIFFIN (1909) 601 type loc: Iwahig, Palawan; type destroyed, formerly in Bureau of Science, Manila; original description; (1911) 267 (listed in key); TAYLOR (1922a) 292, pl. 36 (Palawan [Iwahig], Balabac; description, variation, counts and measurements of material examined, comparison with *T. sumatranus*); MASLIN (1942) 23 (listed in key); LEVITON (1961) 105 (Balabac, Palawan).

*Trimeresurus gramineus* GRIFFIN (1909) 600 (Palawan [Iwahig]; color pattern); (1911) 267 (in part; listed in key).

*Trimeresurus sumatranus* GRIFFIN (1909) 601 (Palawan [after Boulenger, 1894]); (1911) 367 (after Boulenger, 1894; listed in key).

*Range*.—(Figure 1.) BALABAC: without exact locality. PALAWAN: Iwahig; Brooke's Point\*.

*Material examined* (3).—PALAWAN: Tiglopan River, Brooke's Point (CNHM 53560 and 53561); without exact locality (CAS 62563).

*Taxonomic notes*.—Taylor [(1922a) 294] suggests this distinctive species of Philippine *Trimeresurus* has its closest affinities with *T. sumatranus* from western Indonesia. That conclusion was based on the superficial similarities in color pattern and scutellation between the two species. However, Pope and Pope [(1933) 1-3] have shown that among species of *Trimeresurus* convergence in external characters has led to a confusing taxonomic situation in which distantly related or unrelated species have been grouped together. Should the hemipenes of *T. sumatranus* be found to be similar to those in *T. schultzei*, then Taylor's suggestion would seem reasonable. However, at the present state of our knowledge no such conclusion is justified.

*Trimeresurus schultzei* has been distinguished from *T. gramineus* on the basis of rather trivial and frequently variable characters [Griffins (1909) 601]. The two species, however, are very distinct as indicated by the differences in the structure of their hemipenes. *Trimeresurus schultzei* cannot be immediately related to any known Philippine species, although it looks remarkably similar to *T. flavomaculatus*.

In so far as is known, this species is confined to the Palawan Archipelago.

*Diagnosis*.—Hemipenes forked, spinose distally, smooth-walled proximally; first upper labial entirely separated from nasal by distinct suture; second upper labial fused with loreal (shield bordering anterior side of pit); scales on dorsum of head and gular scales smooth; dorsal scales in 21 (rarely 23) longitudinal rows at midbody; tail uniformly light colored and distinct from dorsum. Standard length: (♂) 706 mm, (♀) 478 mm; tail length: (♂) 162 mm, (♀) 83 mm.

*Descriptive notes*.—First upper labial in contact with but not fused to nasal; second upper labial fused with loreal (shield forming anterior border of pit); third upper labial in contact with subocular; scales of head smooth; 9 to 11 small scales between moderate, but narrow, supraoculars; 9 to 11 (usually 10) upper labials; 10 to 14 lower labials; 3 pre- and 2 (rarely

1) postoculars; scales in 21 longitudinal rows at midbody; ventrals 185 to 203; subcaudals 66 to 78; anal plate single.

Hemipenes forked; distal portion (forked sections) spinose; proximal half smooth, without ridges; sulcus spermaticus deeply forked.

Color (in alcohol) above yellowish-green, greenish-brown to dark purple-brown or black; the dorsum crossed by from 50 to 62 indistinct black crossbars or zig-zag lines, each 2 to 3 scale rows wide, as wide as interspaces; a distinct yellow line along outer scale row; tail uniformly light, flesh or red; below variously colored yellowish-green, greenish-brown, to light purple-brown or black; upper part of head with reticulum of black lines; a yellow line which passes from behind eye to angle of jaw may be present.

*Sexual dimorphism.*—There is no clear evidence of sexual dimorphism among characters normally subject to that variation. The sample is, of course, too small for adequate analysis. Of the three specimens examined, two were males and one a female. Two specimens sexed by Taylor [(1922a) 294] were females. Sexual differences are in evidence in the number of black crossbands on the dorsum and in the tail length/standard length ratio. The data for these characters and for the ventral and subcaudal counts are summarized in Table 4.

TABLE 4.—Summary of variation between sexes in *Trimeresurus schultzei*.

Character	Male			Female		
	N	Mean	Range	N	Mean	Range
Ventrals.....	2	194.5	185-194	3*	195.3	192-198
Subcaudals.....	2	71.5	67-76	3	69.0	66-75
Black crossbands.....	2	52.0	50-54	3	61.0	60-62
Tail length/standard length	2	0.214	0.182-0.245	3	0.185	0.166-0.196

\* Includes records by Taylor [(1922a) 294].

**TRIMERESURUS WAGLERI (H. Boie).**

*Cophias wagleri* H. BOIE (1826) 239 (*nomen nudum*); in F. BOIE (1827) column 561 (*nomen nudum*).

*Trigonocephalus wagleri* H. Boie in SCHLEGEL (1837) 542, pl. 19, figs. 16-18 (type loc: Sumatra; type in Leiden Museum; original description).

*Tropidolaemus wagleri* DUMÉRIL, BIBRON, and DUMÉRIL (1854) 1524 (Malaya to Malacca; description); MÜLLER (1883) 290 (Mindanao; color pattern).

- Trimeresurus wagleri* GÜNTHER (1864) 388 (description; Gray's specimens of *T. maculatus* are young of *T. wagleri*; *T. formosus* Gray is *T. wagleri*); (1879) 78 (Butuan; listed), STEINDACHNER (1891) 296 (Sulu Islands; listed); GRIFFIN (1909) 601 (Luzon [Albay], Mindanao, Palawan [Iwahig]; color pattern); (1911) 267 (distribution compiled; listed in key); TAYLOR (1822a) 296 (synonymy, systematic notes, key to subspecies); LEVITON (1961) 106 (Balabac, Basilan, Jolo, Leyte, Luzon, Mindanao, Negros, Palawan, Samar).
- Bothrops wagleri* MÜLLER (1880) 155 (Sumatra; listed); VAN LIDH DE JEUDE (1886) 44 (not seen); MASLIN (1942) 19-20 (transfers *T. wagleri* to *Bothrops*).
- Lachesis wagleri* BOULENGER (1896) 562 (Palawan [Puerto Princesa], LUZON [Albay], *et alli*; description, counts of material examined); BOETTGER (1898) 141 (Luzon, Leyte, Mindanao [Philippine localities only]; listed).
- Trimeresurus wagleri wagleri* TAYLOR (1922a) 298, pl. 37, fig. 4 (restricted to Palawan in the Philippines; color pattern); (1922b) 302 (Balabac; measurements and counts of material examined); HAAS (1950) 611 (synonymy, distribution compiled).
- Trimeresurus philippensis* GRAY (1842) 48 (type loc: Philippine Islands; type in British Museum; original description); (1849) 10 (color pattern).
- Trimeresurus wagleri philippensis* GRAY (1853) 23, pl. 2, fig. 2 (not seen).
- Tropidolaemus philippensis* PETERS (1861) 691 (Samar [Calbigan]; listed).
- Trimeresurus philippensis* TAYLOR (1922a) 295 (synonymy, description).
- Bothrops philippinensis* MASLIN (1942) 19-20 (erroneous spelling, transfers *T. philippensis* to *Bothrops*).
- Trimeresurus maculatus* GRAY (1842) 48 (type loc: Philippine Islands; type in British Museum; original description); (1849) 8 (Singapore, Borneo; color pattern).
- Trimeresurus subannulatus* GRAY (1842) 48 (type loc: Philippine Islands; type in British Museum; original description); (1849) 8 (color pattern).
- Tropidolaemus subannulatus* PETERS (1861) 691 (Luzon [Albay, Daraga]; listed).
- Trimeresurus wagleri subannulatus* TAYLOR (1922a) 300, pl. 37, fig. 3 (Mindanao; description, color in life).
- Trimeresurus sumatranus* (*nec* Raffles) GRAY (1842) 48 (= *T. wagleri*, *fide* ZOULENGER (1896) 562); GRAY (1849) 10 (Malaya [Singapore, Penang]; description).
- Trigonocephalus sumatranus* CANTOR (1847) 121, pl. 40, fig. 9 [= *T. wagleri*, *fide* Boulenger (1896) 562].
- Trigonocephalus wagleri sumatrensis* GRAY (1849) 9 (Sumatra; color pattern).
- Trigonocephalus wagleri celebensis* GRAY (1842) 9 type loc: Celebes; type in Leiden Museum; original description).



- Tropidolæmus subannulatus celebensis* PETERS (1872a) 584 (Sangi-Islands; listed).
- Trimeresurus formosus* (*nec* Schlegel) GRAY (1849) 10 [= *T. wagleri*, *fide* BOULENGER (1896) 562; Borneo; description].
- Tropidolæmus hombroni* Guichenot in DUMONT d'ORVILLE (1848) 23, pl. 2 [1853], fig. 2 (not seen; type loc: western Mindanao; type in Paris Mus.; original description); DUMÉRIL, BIBRON, and DUMÉRIL (1854) 1527 (Mindanao [Zamboanga]; description); PETERS (1867) 29 (listed).
- Trimeresurus subannulatus immaculatus* PETERS (1872b) 42 (type loc: Sarawak, Borneo; type in Genova Museum; original description).
- Trimeresurus wagleri alboviridis* TAYLOR (1917) 366 (type loc: Isabela, Negros Occidental Province, Negros Islands; type in Carnegie Museum; original description); (1922a) 299, pl. 37, fig. 2 (redescription of type).

*Range*.—(Philippine localities only, figure 2.) BALABAC: without exact locality. BASILAN: Port Holland \*; Isabela \*. JOLO: without exact locality\*. LEYTE: without exact locality. LUZON: Albay Province (Daraga). MINDANAO: Agusan Province (Bunawan \*); Bukidnon Province (Del Monte Plantation \*); Cotobato Province (Saub \*); Davao Province (Davao \*; Tagum \*); Zamboanga Province (Katipunan \*; San Ramon \*). Negros Occidental Province (Cauayan Town \*; Bagtik River Valley \*; Isabela \*); Negros Oriental Province (Camp Lookout \*; Pagyabunan \*). PALAWAN: Brooke's Point \*; Iwahig; Puerto Princesa \*; Thumb Peak \*, SAMAR: Calbigan. Tumindo \*.

*Material examined* (45).—BASILAN: Port Holland (CAS 60469); Isabela (USNM 37408). JOLO: without exact locality (CAS 60803; CNHM 41122; SU 8685). MINDANAO: Locality unknown; EHT 138 (50), USNM 38893; Agusan Province: Bunawan (CNHM 15046, 22580; MCZ 20082 to 20083). Bukidnon Province: Del Monte Plantation (SU 8686 to 8687); Cotobato Province: Saub (25855); Davao Province: Davao (SU 7265); Tagum (CNHM 53564 to 53568); Zamboanga Province: Katipunan (CNHM 68902); San Ramon (SU 8679); without exact locality (CAS 44141; CNHM 15017). Negros: Locality unknown; AMNH 2419; Negros Occidental Province: Bagtik River Valley (SU 21049); Cauayan Town (SU 21038); Isabela (CM 2433, holotype of *T. wagleri alboviridis*). Negros Oriental Province: Camp Lookout area (SU 18462; CNHM 77893); Pagyabunan (CNHM 61626). PALAWAN: Brooke's Point (MCZ 25851); Iwahig (CNHM 53569, 15047); Puerto Princesa (CAS 15815 and 15816); Thumb Peak

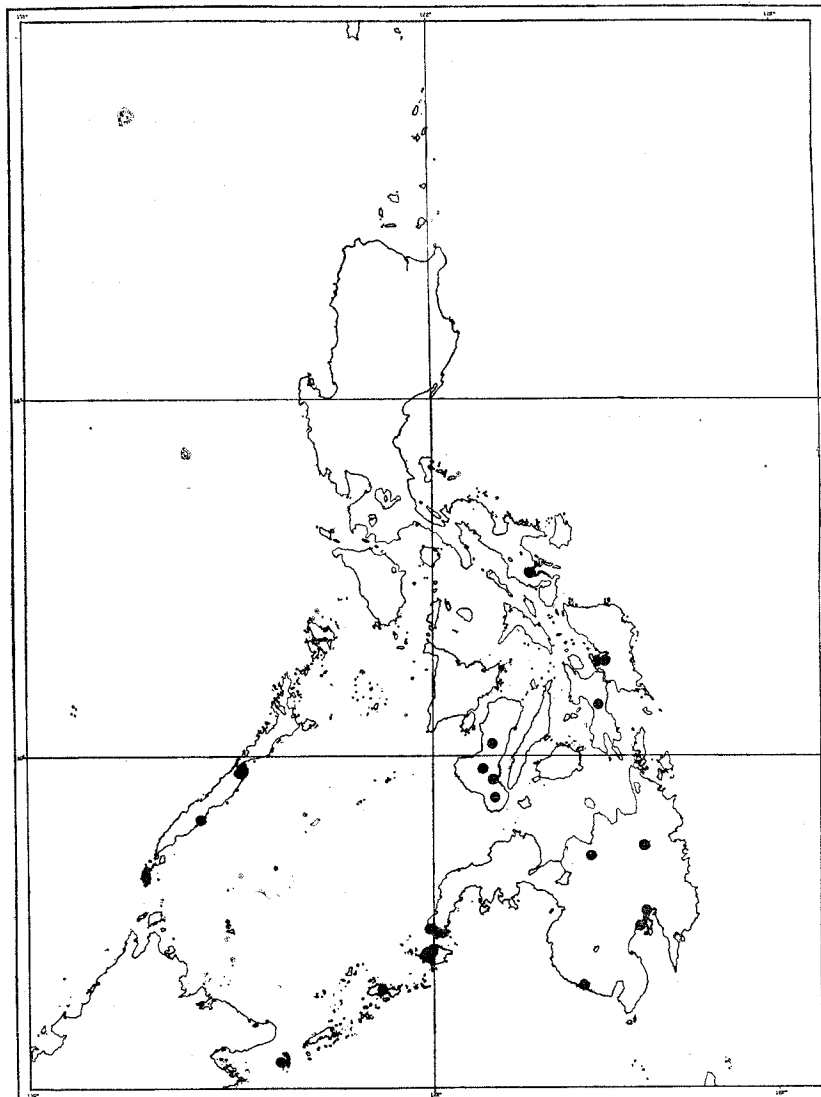


FIG. 2. Distribution of *Trimeresurus wagleri* in the Philippines.

(MCZ 25852); without exact locality (CAS 62149 and 62150; MCZ 25850). TUMINDO ID: USNM 37870. PHILIPPINES: without exact locality (CAS 15359). INDONESIA: Sumatra: 60 km south of Kota Penang (CAS 80925). MALAYA: Singapore (CAS 16781 and 16782).

*Taxonomic notes.*—Variation in color pattern is very great in this species; it has not been possible to correlate differences in pattern with geographic populations or with morphological

differences. Taylor recognized three subspecies of *T. wagleri*, based in part on color pattern differences. One of these, *T. wagleri alboviridis*, described from a single specimen from Negros Island, was further distinguished by a higher ventral count. Examination of additional material from Negros suggests Taylor's specimen was abnormal in this character, or at least represented the extreme count of ventral shields for the Negros population.

*Trimeresurus philippensis*, recognized by Taylor as a distinct species, appears to be a color pattern variant of *T. wagleri*. There are no scutellations or other morphological differences by which to distinguish the two nominal species. I have seen at least one specimen which Taylor assigned to this species [Taylor (1922a) pl. 36] and several other specimens which were intermediate between typical *T. wagleri* and the *T. philippensis* pattern shown by Taylor. The exact status of the nominal species and subspecies I have placed into the synonymy of *T. wagleri* cannot be settled until the type specimens and additional material from scattered localities can be examined.

Within the Philippines the most varied pattern differences were found within the sample from Mindanao Island. The most homogeneous and distinct sample was from Jolo Island; the color pattern of this sample, alternating brown and black crossbands of equal width dorsally and laterally, was distinct from all others seen and was not duplicated within any other sample. The Jolo Island sample could be readily distinguished from *T. wagleri* from elsewhere and future study may show that population on Jolo should be given taxonomic recognition.

*Diagnosis*.—Hemipenes long and slender, deeply forked, small spines present; first upper labial entirely separated from nasal by a distinct suture; second upper labial separated from loreal (shield bordering anterior side of pit); scales on dorsum of head and gular scales strongly keeled; dorsal scales in 19 to 25 longitudinal rows at midbody; tail banded. Standard length: (♂) 679 mm, (♀) 679 mm; tail length: (♂) 133 mm, (♀) 121 mm.

*Descriptive notes*.—First upper labial in contact with but not fused to nasal; second upper labial separated by a suture from the loreal (the shield forming the anterior border of the facial pit); third and fourth upper labials separated from the subocular by small scales; lower preocular small, separated from scale forming base of facial pit; scales of head and chin

strongly keeled; 7 to 15 small scales between narrow supraoculars; 8 to 10 upper labials; 8 to 12 lower labials; 2 to 3 pre- and 2 to 3 postoculars; scales in 19 to 25 longitudinal rows at midbody; ventrals 123 to 146 [168, *vide* Taylor (1922a) 299]; subcaudals 42 to 54; anal plate single.

Hemipenes elongate, extends to fifteenth subcaudal plate, forked at end of sixth subcaudal plate; sulcus spermaticus deeply forked; basal end without spines but with fine longitudinal ridges; remainder of organ with small subequal spines.

Color (in alcohol) varied; usually blue-green with a series of narrow white, yellowish or yellowish green or brownish, usually black bordered narrow crossbars; the crossbars may be without borders or may be entirely black, and may number from 19 to 40; the crossbars may be narrow, occupying not more than one scale row, and separated by interspaces of 5 to 10 scales, or they may be as broad as the interspaces, occupying three or four scales width; the color of the dorsum may vary from light blue-green to dark blue-black and be without any visible crossbands. The venter is usually light yellowish green; frequently well-defined black spots with borders are present.

*Individual variation.*—Intrapopulation variation is striking. Data showing the extent of variation are summarized in Table 5.

*Inter-island variation.*—Clearly definable inter-island variation is limited to meristic characters. Variation in color pattern, such as there may be, cannot be correlated with geographic populations. Indeed, intra-island variation in color pattern, on the island of Mindanao, is more extensive than the known range of color pattern variation among all the other islands of the Philippines, excluding Jolo Island, combined. Furthermore, an examination of several specimens from extra-Philippine localities suggests that there is a considerable variation in color pattern throughout the entire range of the species.

Basic to Taylor's subdivision of *T. wagleri* were presumed differences in the number of crossbars on the dorsum. On Mindanao, several specimens lacked crossbars entirely and were uniform blue-green, and several had rather irregular crossbars, frequently black, or at least formed of a series of four or five longitudinal rows of black-edged green scales

TABLE 5.—Summary of variation in some scale characters in *Trimeresurus wagleri*.

Upper labials	7(1)	8(8)	9(19)	10(4)	9/10(1)	10/9(1)	8/9(2)	9/8(3)	10/12(1)
Preocular	-----	2(9)	3(27)	3/2(1)	2/3(2)	-----	-----	-----	-----
Postocular	-----	1(2)	2(26)	3(1)	3/2(6)	-----	1/2(2)	2/1(2)	-----
Scales between eyes	-----	8(3)	9-10(14)	11-12(7)	13-14(5)	-----	15-16(2)	-----	-----
Scale rows, midbody	-----	19(5)	21(17)	23(9)	25(3)	-----	-----	-----	-----

separated by a series of scales lacking the black bordering. Among the specimens having well-defined, narrow, yellowish to green crossbars, the number of these bars of the body varied from 19 to 25. Seven specimens from Palawan having similar crossbars ranged from 20 to 29. On Negros one specimen lacked all traces of barring; four specimens ranged from 21 to 29. Specimens from outside the Philippines ranged from 29 to 30 crossbars. On two islands, Jolo and Basilan, the crossbars on the dorsum were broad, black, and about as wide as the interspaces, though the black was predominant on the edges in the Basilan specimens of the scales and thus did not differ greatly from Mindanao animals.

TABLE 6.—Summary of the variation in the number of ventral shields in *Trimeresurus wagleri*.

Island	Male				Female	
	N	Mean	Range	N	Mean	Range
Basilan				2	134.5	132-137
Jolo				3	139.7	137-143
Mindanao	5	129.8	123-134	1	130.5	126-134
Negros	3	140.3	137-143	3	137.5	135-140 (168)*
Palawan	4	141.8	137-146	5	135.4	134-137

\* Holotype of *T. w. albovidis*; count not included in determination of mean.

TABLE 7.—Summary of the variation in the number of subcaudal shields in *Trimeresurus wagleri*.

Island	Male			Female		
	N	Mean	Range	N	Mean	Range
Basilan				2	46.5	45-48
Jolo				2	47.0	47
Mindanao	5	44.8	41-46	10	45.7	42-48
Negros	3	48.0	47-49	3	49.0	48-50
Palawan	4	52.0	48-54	5	49.5	47-52

TABLE 8.—Summary of the variation between sexes in the ratio of tail length/standard length in *Trimeresurus wagleri*.

Sex	N	Mean	Range
Male	12	0.196	0.177-0.213
Female	22	0.185	0.171-0.210

There do not appear to be significant differences in ventral or subcaudal counts among island populations. Taylor [(1917) 366] described a new subspecies from Negros Island partly on the basis of a higher ventral count (168 shields). Examination of recent material from Negros indicate a lower ventral count, 135 to 141 for both males and females. I have seen Taylor's type and in characters other than ventral count it is normal; it seems probable that this specimen has an abnormally high number of ventral shields. The Mindanao sample averages a few ventrals than the samples from elsewhere, but the differences are slight, and because of the small sample size, I doubt that any significance can be attached to the difference at this time. A summary of the ventral and subcaudal counts is given in Tables 6 and 7.

The number of scale rows at midbody varies from 19 to 25. Specimens from Mindanao were found to vary between 19 to 23; those from Negros from 21 to 25; specimens from elsewhere varied from 21 to 23.

*Sexual dimorphism.*—Comparison of the data summarized in Tables 6 and 7, for ventral and subcaudal counts suggests that these characters are not subject to sexual dimorphism. There is no evidence of dimorphism in the number of crossbars on the body, nor does one sex seem to be subject to greater individual variation in scutellation than the other. Most surprising, however, is the apparent absence of any differences in the tail length/standard length ratio between sexes (see Table 8).

*Ecological notes.*—According to Taylor [(1922a) 300, 301] this species has been found in bushes and in small trees. Tweedie [(1953) 117] states that the species is mainly arboreal and is common in the low jungle, including mangrove areas, throughout the Malay Peninsula.

Stomach contents of several specimens examined here included skinks (*Sphenomorphus fasciatus* and *Mabuya* sp.) and some snake scales.

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