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DESCRIPTION OF A NEW SUBSPECIES OF *RHABDOPHIS AURICULATA* IN THE PHILIPPINES, WITH COMMENTS ON THE ZOOGEOGRAPHY OF MINDANAO ISLAND

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During recent investigations on the snakes of the Philippine Islands, a study begun more than 15 years ago under the guidance of Professor George S. Myers, it became apparent that the island of Mindanao is inhabited by two clearly distinguishable populations of the diminutive natricine snake, *Rhabdophis auriculata*. That the two populations of this species occupy different but contiguous parts of Mindanao make this discovery the more interesting, inasmuch as it helps shed further light on the paleogeography of the island.

The type specimen of *Rhabdophis auriculata*, a species described by Günther in 1858, was collected by Hugh Cuming, its locality being given simply as "Philippine Islands." Miss Alice G. C. Grandison of the British Museum kindly examined Günther's type, compared it with the figure published by Boulenger (1893, pl. 17, fig. 1) [fig. 1], prepared a sketch [fig. 2] of the color pattern at the angle of the jaw, and responded that Boulenger's figure could well have been based on the type specimen. With Miss Grandison's sketch at hand, and after examining Boulenger's figure with care, I do not doubt that Günther's type is based on a specimen drawn from the eastern Mindanao population. I have seen specimens from Davao Province that closely approximate the Günther type, and

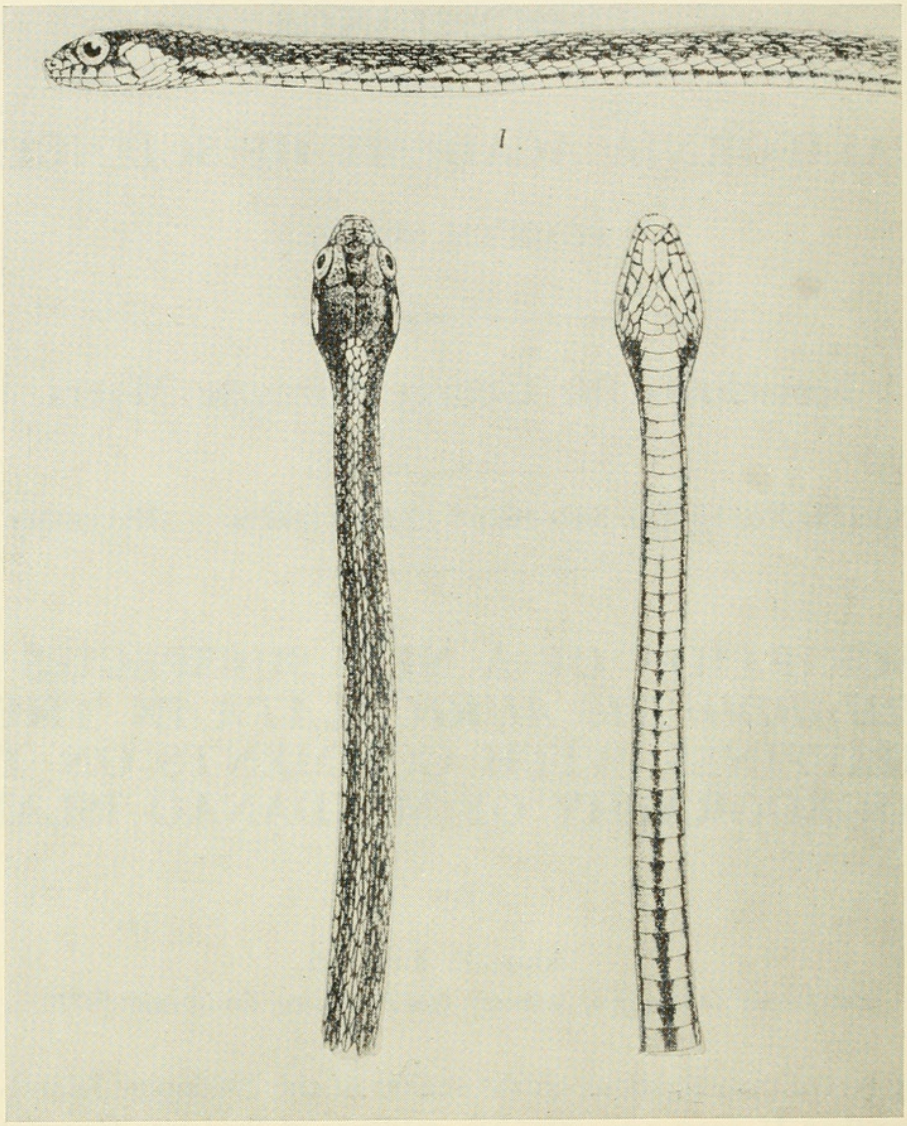

FIGURE 1. Figure of *Rhabdophis auriculata* published by Boulenger (1893).

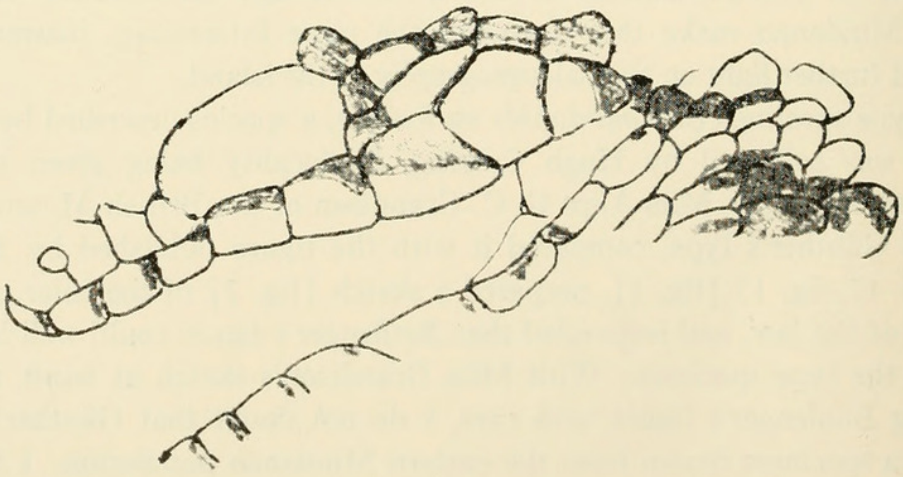

FIGURE 2. Sketch of scale and color pattern at angle of jaw on left side of holotype.

therefore, to insure stability of nomenclature, restrict the type locality of *Tropidonotus auriculatus* Günther to Mt. Apo, Davao Province, Mindanao Island.

Specimens of *Rhabdophis auriculata* from Zamboanga del Norte, Zamboanga del Sur, Misamis Occidental, and Bukidnon provinces of western Mindanao [fig. 3] differ from animals from the Davao-Agusan region in color pattern. These animals are referred to a new taxon, named in honor of Professor Myers, who has for many years concerned himself with the zoogeography of the Philippines, especially Mindanao Island:

Rhabdophis auriculata myersi Leviton, new subspecies.
(Figures 4–6.)

Tropidonotus auriculatus, BOULENGER, 1893, Cat. Snakes British Mus., vol. 1, p. 261 (part; Mindanao [Pasanaca, Zamboanga City]).

Natrix auriculata, TAYLOR, 1922, Philippine Jour. Sci., vol. 21, p. 294 (Basilan [Port Holland]); 1923, Philippine Jour. Sci., vol. 22, p. 542 (Basilan, Mindanao [Zamboanga City]).

DIAGNOSIS. Maxillary teeth 27–32, last 3 or 4 enlarged but not separated by diastemata from others; head short, distinct from neck; scales in 17 longitudinal rows on anterior third body, reducing to 15 at about level of 80th ventral plate; usually 3 labials bordering orbit; ventrals 143–162; subcaudals 80–93; hemipenes extending to end of 6th subcaudal plate, forked at end of 4th-mid 5th plate; sulcus forked; proximal portion opposite sulcus with longitudinal plicae, portion bordering sulcus spinose; 2 large basal spines present; distal forks uniformly spinose; ventrolateral black stripe extending forward to suture of 8th and 9th labials, continuing as diagonal stripe to corner of eye; lateral light stripe extending uninterrupted (rarely interrupted at angle of jaw by black spot on 8th upper labial) along side of body to anterior temporals. Measurements (of largest male and largest female, in mm.): ♂ s-v 342, tail 138; ♀ s-v 388, tail 165.

HOLOTYPE. CAS-SU 23391, an adult male, taken near Masawan, approximately 14 km. southeast of Buena Suerte, New Piñan, on west side of Dapitan Peak, Misamis Occidental Province, Mindanao Island, at an altitude of 4700 feet (1433 m.) on 13 April 1959 by Dr. Angel Alcala (figs. 4–5).

PARATYPES (61). MINDANAO: MISAMIS OCCIDENTAL PROVINCE: *West side of Dapitan Peak*: Masawan area, approximately 14 km. southeast of Buena Suerte, New Piñan, 26 March–20 April 1959 (CAS-SU 23372–23374, 23392–23394, 23397 [elev. 4400 ft. (1340 m.)]; 23375 [elev. 4400–4500 ft. (1340–1370 m.)]; 23376–23380, 23390 [elev. 4500 ft. (1370 m.)]; 23381–23382 [elev. 4700 ft. (1430 m.)]; 23383 [elev. 4300 ft. (1310 m.)]). Approximately 2 km. east of Masawan and 15 km. southeast of Buena Suerte, New Piñan, 5 April 1959 (CAS-SU 23384 [4700 ft. (130 m.)]). Approximately 12 km. east of Masawan, 6 April 1959 (CAS-SU 23387 [elev. 5500 ft. (1670 m.)]). Ap-

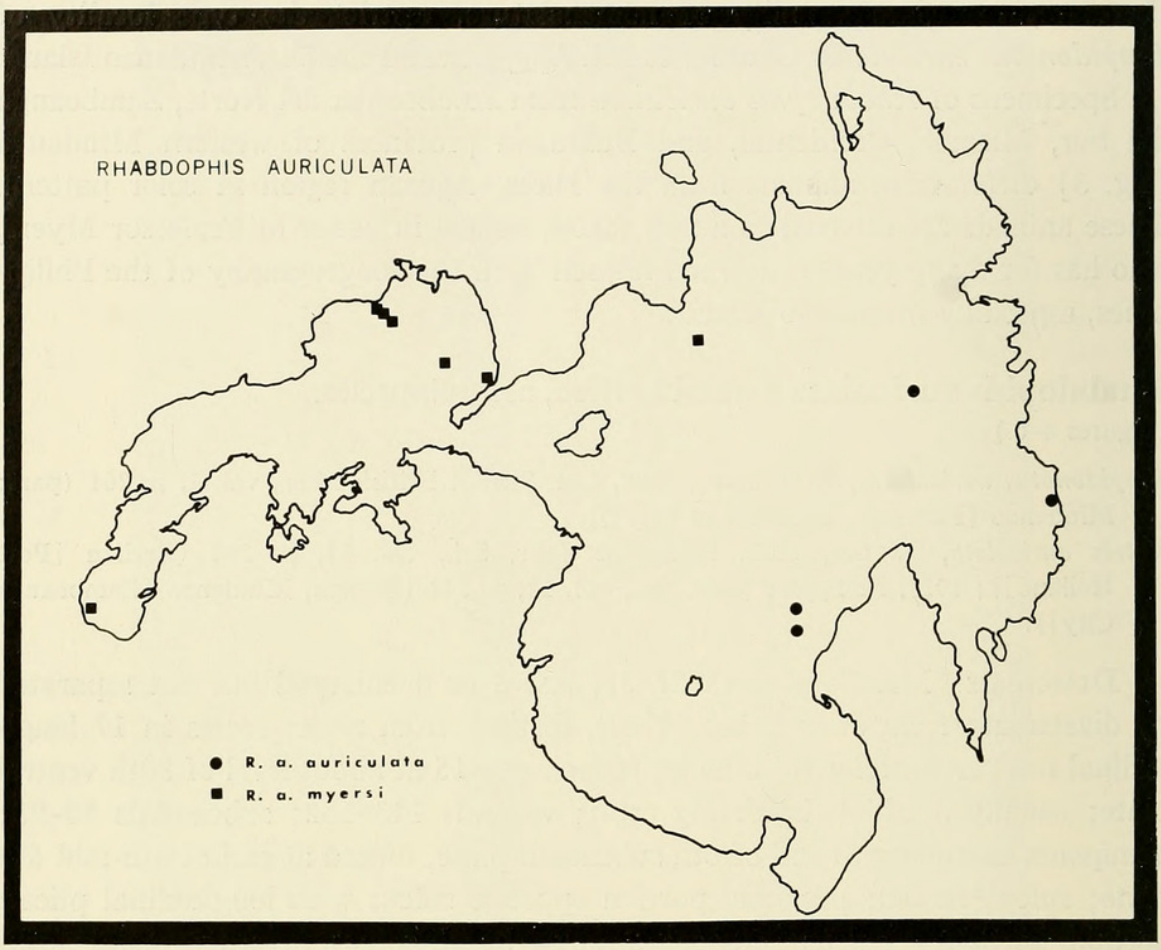

FIGURE 3. Known distribution of *Rhabdophis auriculata* on Mindanao Island.

proximately 2 km. southeast of Masawan and 16 km. southeast of Buena Suerte, New Piñan, 12 April 1959 (CAS-SU 23389 [elev. 4800 ft. (1460 m.)]). Approximately 2–3 km. southeast of Masawan, 19 April 1959 (CAS-SU 23395–23396 [elev. 5000–5200 ft. (1520–1580 m.)]). Ridge 11–12 km. southeast of Buena Suerte, New Piñan, 22 April 1959 (CAS-SU 23398 [elev. 4000 ft. (1220 m.)]). Bank of Dapitan River, 11–12 km. southeast of Buena Suerte, New Piñan, 23 April 1959 (CAS-SU 23399 [elev. 4000 ft. (1220 m.)]). Bank of Dapitan River, approximately 13 km. southeast of Buena Suerte, 25 April 1959 (CAS-SU 23400 [elev. 4200 ft. (1280 m.)]). ZAMBOANGA DEL NORTE PROVINCE: *West side of Dapitan Peak*: Gumay area, approximately 6 km. southeast of Buena Suerte, New Piñan, 28-29 April 1959 and 4–8 May 1959 (CAS-SU 23401, 23403–23404, 23419 [elev. 2500 ft. (760 m.)], 23402 [elev. 2400 ft. (730 m.)], 23426–23427 [elev. 2300 ft. (700 m.)]). Dapitan River area, approximately 1 km. southeast of Gumay and 7 km. southeast of Buena Suerte, New Piñan, 30 April–1 May 1959 (CAS-SU 23405–23413, 23415–23416 [elev. 2300 ft. (700 m.)], 23414 [elev. 2400 ft. (730 m.)]). Gumay Creek, approximately 6 km. southeast of Buena Suerte, 2–6 May 1959 (CAS-SU 23417, 23422

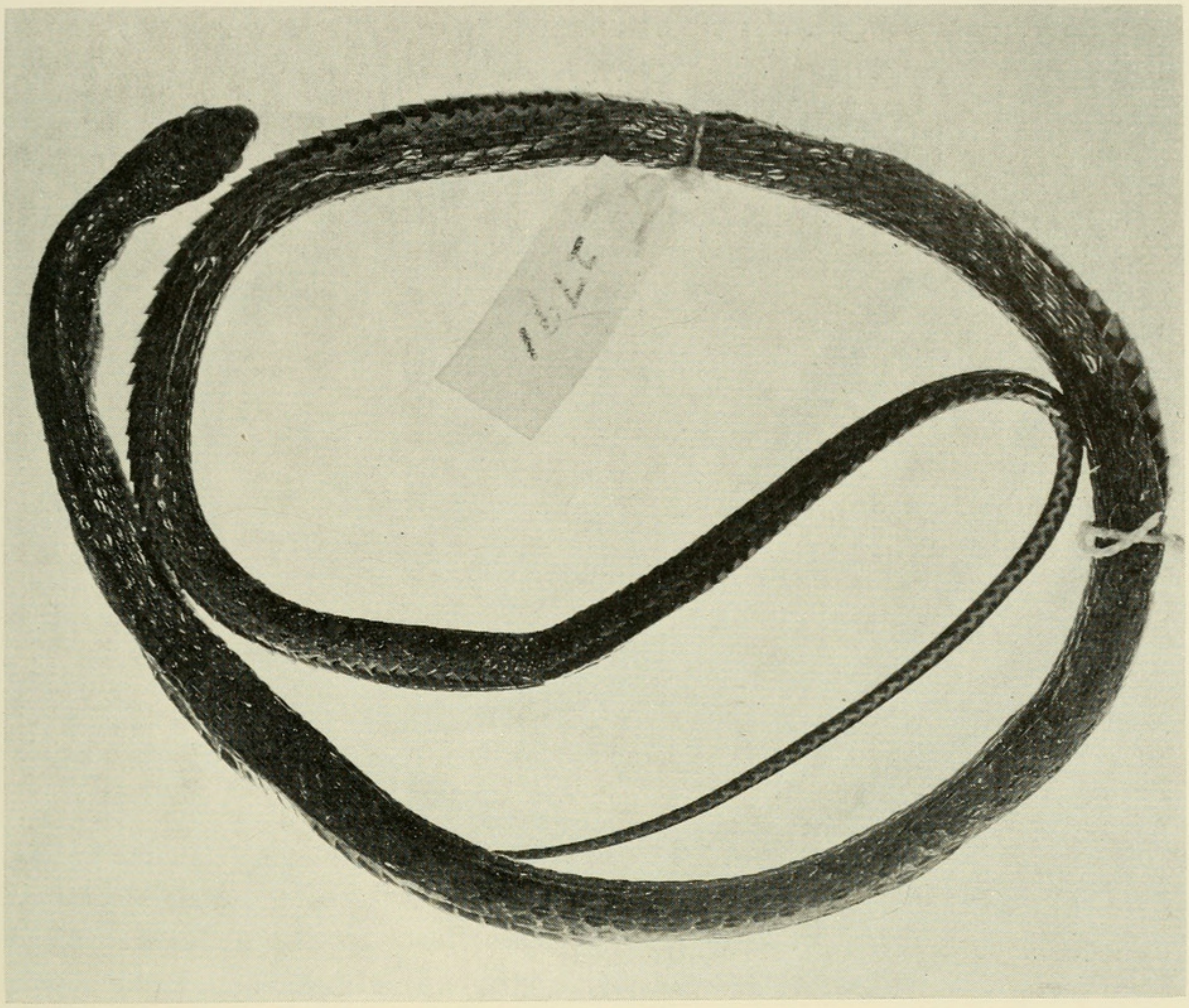

FIGURE 4. Holotype of *Rhabdophis auriculata myersi* Leviton (dorsal view).

[elev. 2300 ft. (700 m.)]). Bank of Dapitan River, approximately 2 km. southeast of Gumay and 8 km. southeast of Buena Suerte, New Piñan, 4 May 1959 (CAS-SU 23418 [elev. 2500 ft. (760 m.)]). Approximately 7 km. southeast of Buena Suerte, New Piñan, 5 May 1959 (CAS-SU 23420–23421 [elev. 2700–2800 ft. (820–850 m.)]). Approximately 10 km. southeast of Buena Suerte, New Piñan, 6 May 1959 (CAS-SU 23423–23425 [elev. 3500 ft. (1070 m.)]). Gumay, approximately 5–6 km. southeast of Buena Suerte, New Piñan, 26 March 1959 (CAS-SU 23371 [elev. 2500 ft. (760 m.)]). Gumay Creek, approximately 0.5 km. southwest of Gumay and 6 km. southeast of Buena Suerte, New Piñan, 8 May 1959 (CAS-SU 23428 [elev. 2400 ft. (730 m.)]). *Mt. Malindang*: Masawan, April-May 1956 (CAS-SU 19362–19364 [elev. 3500–4500 ft. (1067–1372 m.)]). Between Masawan and Gandawan, April 1956 (CAS-SU 19535). MISAMIS OCCIDENTAL AND ZAMBOANGA DEL NORTE PROVINCES BOUNDARY: *West side of Dapitan Peak*: Approximately 4 km. northwest of Masawan and 10 km. southeast of Buena Suerte, New Piñan, 9–11 April 1959 (CAS-SU 23385–23386 [elev. 3400 ft. (1040 m.)], 23388 [elev. 3500 ft. (1070 m.)]).

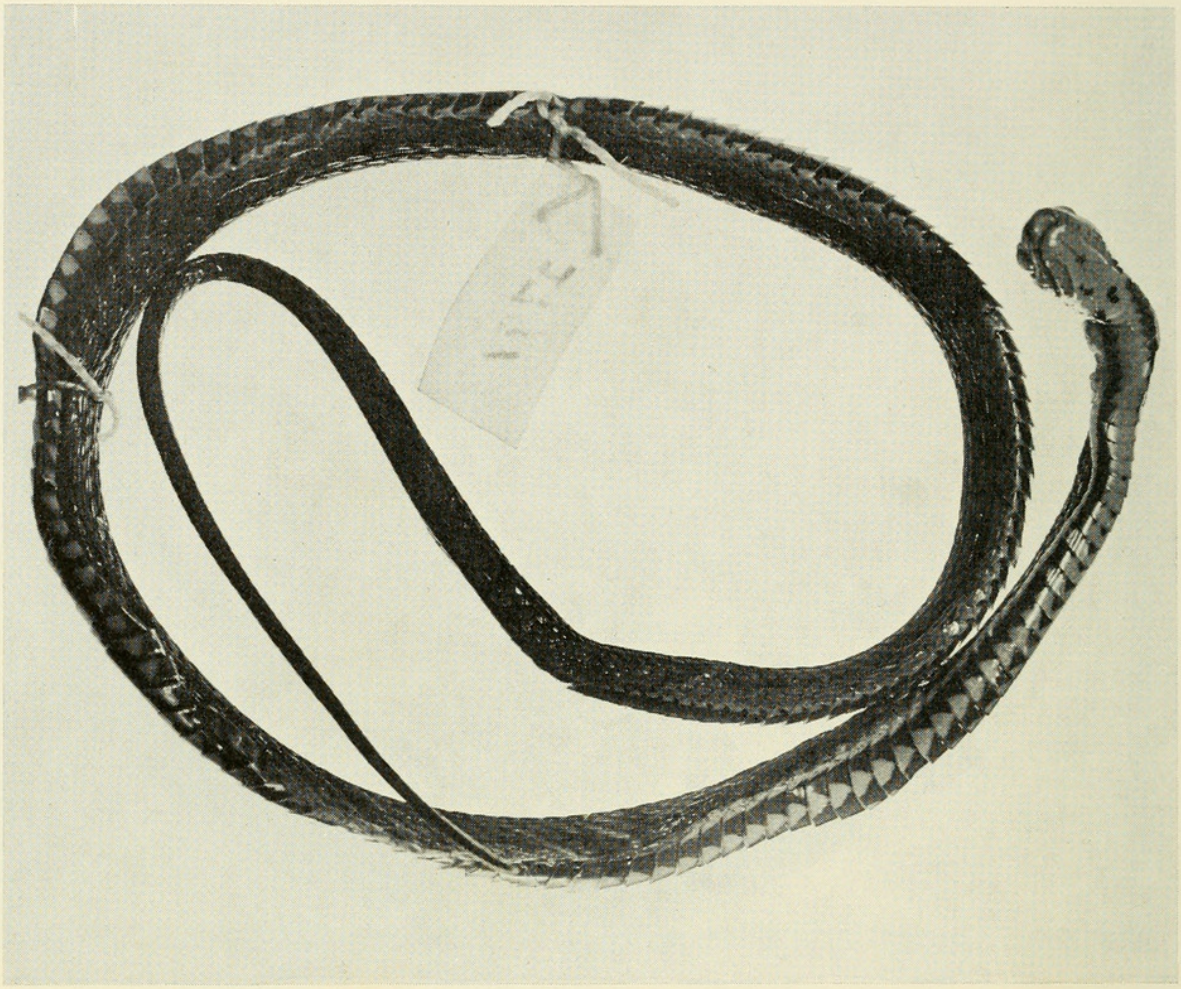

FIGURE 5. Holotype of *Rhabdophis auriculata myersi* Leviton (ventral view).

ADDITIONAL MATERIAL EXAMINED (30). BASILAN: Abung-Abung, 5–25 October 1921 (CAS 60332–60339). Port Holland, 5–25 October 1921 (CAS 60468). BOHOL: Cantaub Sitio, Sierra Bullones, 30 April 1955 (CAS-SU 18895). MINDANAO: BUKIDNON PROVINCE: Del Monte Plantation, 22 August 1940 (CAS-SU 12396). ZAMBOANGA DEL NORTE PROVINCE: Catagan, 15 May 1906 (USNM 37390). Katipunan, 30 km. up the Dicayo River (FMNH 68905–68906). Miatan, Katipunan (FMNH 68916–68917). ZAMBOANGA DEL SUR PROVINCE: San Ramon, 10 July 1929 (FMNH 14948). Zamboanga City, 23 September–6 October 1920 (CAS 62023–62029). PHILIPPINE ISLANDS: (FMNH 68909, USNM 37415–37418).

DESCRIPTION OF HOLOTYPE. Measurements (in mm.): snout-vent 318; tail 122; ventrals 157; subcaudals 82. Anal plate divided; 8 upper labials, 3–5 bordering orbit; nasal shield divided below nostril only; loreal 1; preocular 1; postoculars 3; temporals 2 + 3; dorsal scales reduce 17 (–4[89/91])15; hemipenes extend to end of 6th subcaudal plate, forked at middle of 5th plate; sulcus forked; forked portions spinose; half of proximal portion spinose on other

TABLE 1. *Comparison of ventral counts for samples of* Rhabdophis auriculata.

Locality	*Sex*	*Mean ± S.D. ± S.E.*	*Range*	*Number*
Mindanao				
Zamboanga del Norte[1]	♂	154.9 ± 2.6 ± 0.5	150–160	29
	♀	154.6 ± 2.5 ± 0.4	150–162	33
Zamboanga del Sur	♂	152.2 ± 2.3 ± 1.0	149–146	5
	♀	153.5	153–154	2
Bukidnon	♀	148	—	1
Davao	♂	150.9 ± 3.1 ± 0.6	143–155	28
	♀	152.7 ± 3.5 ± 0.7	146–160	28
Agusan	♂	150.5	149–153	4
	♀	150.5	147–154	4
Basilan	♂	146.7	143–150	3
	♀	152.2 ± 3.1 ± 1.3	147–157	6
Bohol	♂	148	—	1
Luzon	♀	145	—	1

[1] Based on a large sample from the Buena Suerta area, on Mt. Dapitan, along the boundary between Misamis Occidental and Zamboanga del Norte provinces.

side of sulcus; walls opposite sulcus with longitudinal plicae; 2 very large basal spines present on either side of sulcus. Color pattern as described in diagnosis; black ventrolateral stripe extending uninterrupted to meet lower postocular stripe; black midventral stripe originating on 24th ventral.

VARIATION. There is scarcely any variation in head and body scutellation beyond that already reported for ventral and subcaudal counts. Only two of

TABLE 2. *Comparison of subcaudal counts for samples of* Rhabdophis auriculata.

Locality	*Sex*	*Mean ± S.D. ± S.E.*	*Range*	*Number*
Mindanao				
Zamboanga del Norte[1]	♂	86.3 ± 3.1 ± 0.6	80–92	25
	♀	86.3 ± 2.8 ± 0.5	82–93	28
Zamboanga del Sur	♂	85.4 ± 2.4 ± 1.1	82–89	5
	♀	86.5	83–90	2
Davao	♂	79.7 ± 3.9 ± 0.8	71–86	22
	♀	80.5 ± 2.9 ± 0.6	73–87	26
Agusan	♂	82.3	81–85	4
	♀	81.7	73–87	3
Basilan	♂	83.7	80–86	3
	♀	83.4 ± 1.9 ± 0.8	80–86	5
Bohol	♂	84	—	1
Luzon	♀	78	—	1

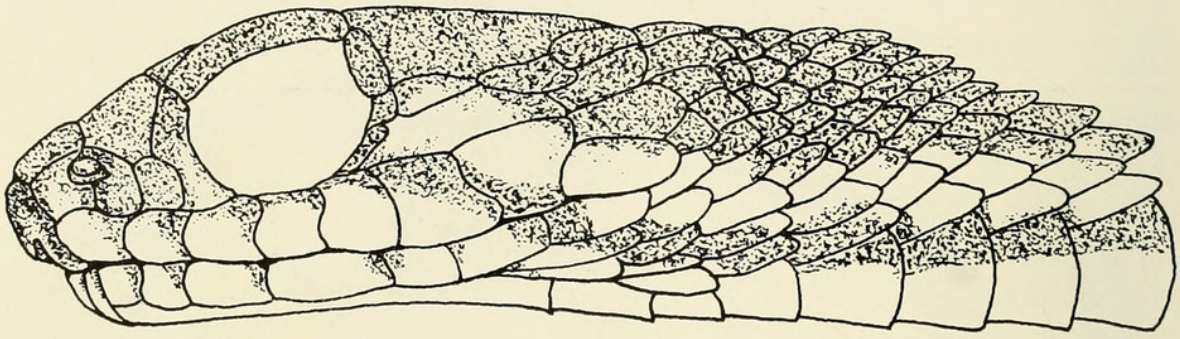

FIGURE 6. Side view of head of CAS-SU 19362, *Rhabdophis auriculata myersi* (drawn by Marilyn Kramer).

87 specimens had 9 upper labials on both sides, one had 7 on both sides, one had 7 on one side, 8 on the other, and one had 9 and 8 labials. In most specimens there were 2 anterior temporals; however, in more than ⅔ of the sample the upper anterior temporal is divided by a vertical suture; 3 posterior temporals are usually present, only eight specimens have 2, and three have 2 on one side, 3 on the other. No variation was observed in numbers of preoculars, postoculars, or loreals. The nasal shield was carefully scrutinized under high magnification of a binocular stereoscopic microscope, and in no instance was I able to detect a suture in the shield above the nostril; a vertical suture was always present, extending from below the nostril to the lower border of the shield. Therefore, the nasal is only partially divided.

The color pattern is remarkably stable, too. The dorsal ground color, in preserved specimens, is dark brown to black. There is a prominent middorsal light streak originating just behind the parietals and most distinct on the anterior fourth of the body. A lateral white stripe extends the length of the body along the outer edges of the ventrals to the neck, then angles forward onto the upper anterior temporals, ending just behind the postoculars [figure 6]. This stripe becomes narrower and less distinct posteriorly. It extends uninterrupted onto the side of the head, there being no squarish black spot on the neck behind the angle of the jaw as in the typical form [figure 7] connecting the dorsal ground color with the ventrolateral black stripe. This latter stripe, formed by black spots on the ventrals, extends forward, usually uninterrupted, onto the suture of the 8th and 9th lower labial and thence meets the lower postocular black bar which extends onto the 7th upper labial. Occasionally the stripe is interrupted for one scale width immediately behind the 8th lower labial. Otherwise it extends posteriorly along the sides of the ventrals, broadening and usually coalescing with the black middorsal stripe which originates on the 4th to 23rd ventral, extends posteriorly, becoming broad and joining the lateral black stripes. The

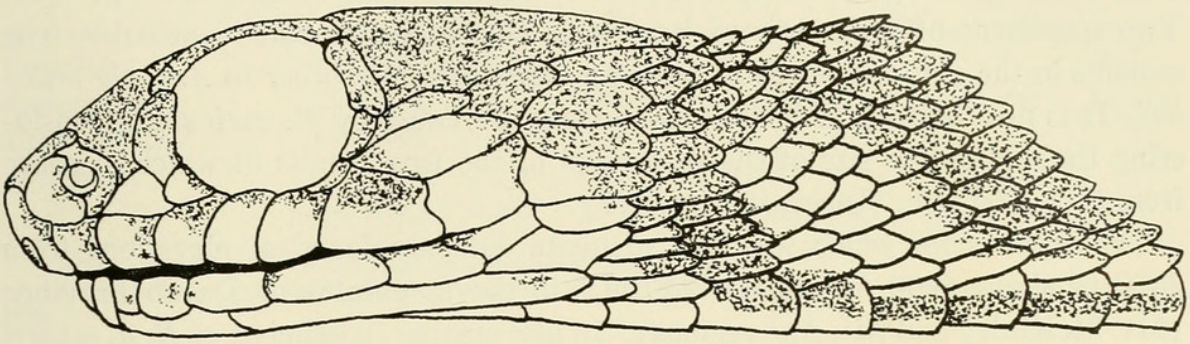

FIGURE 7. Side view of head of CM 2592, *Rhabdophis a. auriculata* (drawn by Marilyn Kramer).

venter is thus posteriorly almost entirely black except for a series of paramedial white spots, sometimes forming stripes.

ECOLOGICAL NOTES. The sample from Davao Province is large and is made up of both young and adult specimens. The smallest gravid female measured 299 mm. snout-vent length; young with umbilical scars still evident, though almost completely closed, measured up to 200 mm., although most animals above 150 mm. in snout-vent length showed no visible signs of the scar. The young, defined here arbitrarily as those with some evidence of an umbilical scar or less than 200 mm. in snout-vent length, were collected mostly during the months of October and November 1946 by members of the Hoogstraal Expedition to Mindanao. The fact that young animals measuring from 104 to 200 mm. were collected during this period suggests that some egg laying takes place almost year round. However, 11 of the 19 young measured between 104 and 125 mm., suggesting further that there is probably a peak reproductive period during late spring or early summer. Gravid females were collected in June and July as well as during the October-November period previously mentioned. At least two specimens of *R. a. myersi* from northern Zamboanga, collected in April, were also gravid. Since most of the animals from the Zamboanga Peninsula were collected during April and early May, and those from Basilan in late October, this would add weight to my argument, based on the survey of the Davao sample, that a peak in egg laying takes place in late spring, possibly late May or June. Six of the sample measured less than 150 mm. snout-vent length, the smallest being a young female, 121 mm. from snout to vent. The rest of the sample divides up as follows: 150–199 mm. snout-vent, 19 specimens; 200–249 mm., 8; 250–299 mm., 13; 300–349 mm., 6; 350–399 mm., 6; and 400 and over, 1.

Only amphibian remains were found in the gut, mostly frogs, though in two cases there were tadpoles, and in three, masses of gelatinous frog eggs. In three specimens of *R. a. auriculata* from Davao Province, the frogs were identified as *Oreophryne*, a small terrestrial species found in southern Mindanao living in

moss growing on logs or trees, under bark or in leaf axils (Inger, 1954, p. 447). Two specimens of *R. a. myersi* from near Buena Suerte had identifiable frog remains in the gut, one referable to *Rana magna* and the other to *Ansonia muelleri*. It is not too surprising that these frogs are eaten by *R. auriculata*, considering the diminutive size of the snake and of the frog, adults of which measure from 17.2–21.7 mm. (Inger, 1954, p. 447).

The snakes for which we have adequate data are found at elevations from 2800 to about 6400 feet (850–1950 m.) in the mountains of Davao Province (Mt. McKinley and Mt. Apo regions). In like manner, specimens of *R. a. myersi* from the northern part of the Zamboanga Peninsula were taken largely between 2300 feet and 4500 feet (700–1370 m.). The type and those of the paratypic series for which data are available were taken from beneath rocks in dry river beds, while others were collected in brush or among other vegetation, usually near water courses, even if dry at that time of year (late September through November). A Basilan series of *R. a. myersi* collected by Taylor at Abung-Abung appear to come from near sea level. Also Taylor obtained a series from Zamboanga City, at or near sea level. However, the hills immediately behind Abung-Abung may in fact have been the source of these specimens. The Bunawan, Agusan Province, series collected by Taylor in 1921 was taken in the Agusan River valley, in the vicinity of water, usually from beneath leaves or logs at the edge of a small swamp (Taylor, 1922, p. 90). This locality lies below 500 feet. Since Taylor's data seem quite reliable, the vertical distribution of *R. auriculata* is more than 600 feet, this being true for both nominal forms.

Rhabdophis auriculata auriculata (Günther).

Tropidonotus auriculatus GÜNTHER, 1858, Cat. Col. Snakes British Mus., p. 80 (type locality: Philippine Ids. [restricted here to Mt. Apo, Davao Province, Mindanao]; type in British Museum). PETERS, 1861, Monatsb. Akad. wiss. Berlin, 1861, p. 687 (Samar). MÜLLER, 1883, Verh. Naturf. Ges. Basel, vol. 7, p. 286. BOETTGER, 1886, Ber. Senckenberg Naturf. Ges., p. 108; 1898, Kat. Rept. Samml. Senckenberg Naturf. Gesell., Schlangen, p. 28 (Leyte). FISCHER, 1885, Jahrb. Hamburg wiss. Anst., vol. 2, p. 80 (Süd-Mindanao). BOULENGER, 1893, Cat. Snakes British Mus., vol. 1, p. 261, pl. 17, fig. 1 (part; "Philippines" [type specimen]).

Natrix auriculata, GRIFFIN, 1911, Philippine Jour. Sci., sec. D, vol. 6, p. 257 (part; distribution compiled). TAYLOR, 1922, Snakes Philippine Ids., p. 89, pl. 4, figs. 2–4 (Mindanao [Bunawan, Agusan], Samar).

DIAGNOSIS. See *Rhabdophis a. myersi* except as follows: ventrals 143–160; subcaudals 71–87; ventrolateral black stripe extends forward to side of neck, does not extend onto throat, does not meet dark lower postocular diagonal stripe; light lateral stripe usually interrupted on side of neck behind angle of jaw by squarish black spot joining black ventrolateral stripe to dark dorsal color. Measurements (of largest male and largest female, in mm.): ♂ s-v 352, tail 123; ♀ s-v 372, tail 140.

TABLE 3. *Variation in head scutellation in* Rhabdophis auriculata auriculata.

Preoculars	1 – 1[3](42) 2 – 2(3) 2 – 1(2) 1 – 2(3)
Postoculars	3 – 3(41) 3 – 2(2) 4 – 3(1) 4 – 4(1) 3 – 4(1) 2 – 3(1) 2 – 2(3)
Upper labials	8 – 8(46) 7 – 7(1)
Temporals	2 + 3[4](25) 2 + 2(12) 2 + 3/2 + 2(5) 2 + 2/2 + 3(4)
	1 + 3/2 + 3(1) 1 + 2(1) 2 + 1(1) 2 + 2 + 3(1)

[3] First number is count on right side, second number is for left side.
[4] 2 + 3 indicates anterior + posterior temporals for both sides; 2 + 3/2 + 2 are counts for right and left sides.

RANGE. *Leyte*[2]. *Mindanao*: Agusan Province (Bunawan); Cotabato Province (Burungkot); Davao Province (Mt. Apo [Baclayan, Todaya], Mt. McKinley). *Samar*[2]. *Luzon*[2].

MATERIAL EXAMINED (86). LUZON: (CAS 15231). MINDANAO. AGUSAN PROVINCE: Bunawan (CM 2590–2598). COTABATO PROVINCE: Burungkot (FMNH 53345 [elev. 1500 ft. (460 m.)]). DAVAO PROVINCE: Baganga River (USNM 34734–34735). Mt. Apo (FMNH 15016; 53322–53323 [elev. 2800 ft. (850 m.)]; 53326 [elev. 5500 ft. (1670 m.)]; USNM 34713 [2 July 1904; elev. 4000 ft. (1220 m.)]; 34719 [3 July 1904; elev. 5000 ft. (1520 m.)]; 34712, 34714–34718, 34720–34727, 34770–34771 [June-July 1904; elev. 6000 ft. (1829 m.)]; 34728–34734). Todaya, Mt. Apo, November 1946 (FMNH 53316–53321, 53324–53325, 53329–53344 [elev. 2800 ft. (850 m.)]). Baclayan, Mt. Apo, 11 November 1946 (FMNH 53327–53328 [elev. 6500 ft. (1980 m.)]). Mt. McKinley, 8 August–19 September 1946 (FMNH 53299–53314 [elev. 3000–6400 ft. (910–1950 m.)], 53315 [elev. 6300 ft. (1920 m.)], 53346 [elev. 3400 ft. (1040 m.)]).

VARIATION. Variation among the specimens examined is minimal. Ventral and subcaudal counts are summarized in tables 1 and 2. Variations in head scutellation are summarized in table 3.

In color pattern in the typical form, variation is limited also. The light mid-dorsal stripe is present in 76 percent of the sample. However, its presence or absence is not correlated with distribution, sex, or age group. The ventrolateral stripe is usually joined to the dorsal color by a vertical or almost vertical black bar on the neck behind the angle of the jaw in 83 percent of the sample. In 10 percent the vertical bar does not contact the dorsal pattern, being separated by about one-half of a scale width. In only four animals—one from Burungkot, Cotabato Province, one from Mt. McKinley, and two from Mt. Apo, Davao Prov-

[2] Specimens from Leyte and Samar were reported by Boettger (1898, p. 28) and Peters (1861, p. 687) respectively. The specimens on which these records were based are probably extant, Peters' at the Berlin Museum, Boettger's at Senckenberg, and should be examined. I have not done so.

The Luzon specimen is in the collection of the California Academy of Sciences, CAS 15231. Formerly it was in the Museo Santo Tomas and sent to the Academy around 1909 by Dr. J. C. Thompson, who said it probably came from Luzon. Indeed, the specimen may have originated on Luzon, but confirmation is needed. The specimen has an interrupted light lateral stripe and therefore is most similar to the eastern Mindanao population.

ince—is the bar absent. In most animals the ventrolateral stripe stops well short of the commissure of the mouth, being separated from the subpostocular blotch or stripe by at least 1 and usually 2 to 4 scales.

REMARKS. *Rhabdophis auriculata* is an unusually small natricine. I hesitate to venture an opinion on its relationships now, inasmuch as I haven't seen several Bornean forms such as *Rhabdophis sarawacensis* (Günther) with which, based on available descriptions, it seems to agree. Although *R. auriculata myersi* is readily separable from *R. a. auriculata* on the basis of color pattern alone, an examination of data for ventral and subcaudal counts is revealing (table 1). A comparison of the Zamboanga-Misamis sample with the eastern Mindanao samples does not indicate a statistically significant level of difference in these counts, yet inspection of the means and ranges, especially of subcaudal shields, suggests the populations do indeed differ, though there is a substantial overlap. Perhaps most interesting is the fact that in subcaudal counts both Basilan and Bohol samples agree with the western Mindanao population, and though this is not confirmed by similar close agreement of ventral counts, even here the counts are well within the range of the western Mindanao sample. Of course, in color pattern both Basilan and Bohol samples are readily referrable to the typical subspecies.

A further instructive comparison brings out the fact that the means and ranges of subcaudal counts for the Davao-Cotabato and Bunawan samples and the counts for the one specimen from Luzon are lower than for the typical form.

Mindanao has long been of considerable interest to biogeographers concerned with the Philippine fauna and flora. Unquestionably it has served as a principal route for faunal and floral movements to the northern islands. Also it has had a complex post-Miocene history, which is still not completely unraveled. To the extent that we must deal with the matter here, it is sufficient to note that a substantial body of evidence, particularly in the form of coral reefs and numerous terraces, indicate clearly that, during the early and mid-Pleistocene, and possibly during the Pliocene, too, the island was divided into at least five and possibly seven smaller islands (fig. 8). These islands have been detailed by Dickerson (1928, pp. 85–87, fig. 19). Inger (1954, p. 453), in a paleographic map portraying the probable land areas during the lower Miocene based on Umbgrove (1938), suggests that even at that date Mindanao was probably not a single island, but rather a series of at least four island masses. The distribution of certain elements of the flora and fauna (see Merrill, 1928, p. 290; Cook, 1928, p. 269; Dickerson, 1928, p. 295) suggests at least a division between the Zamboanga Peninsula and the rest of Mindanao. Further, these authors suggest a greater faunal and floral similarity between the Cotabato-Agusan-Surigao regions than between Cotabato and Zamboanga. This probably indicates that the Pleistocene islands depicted by Dickerson, i.e. Cotabato, Agusan, and Surigao, were connected by emerging

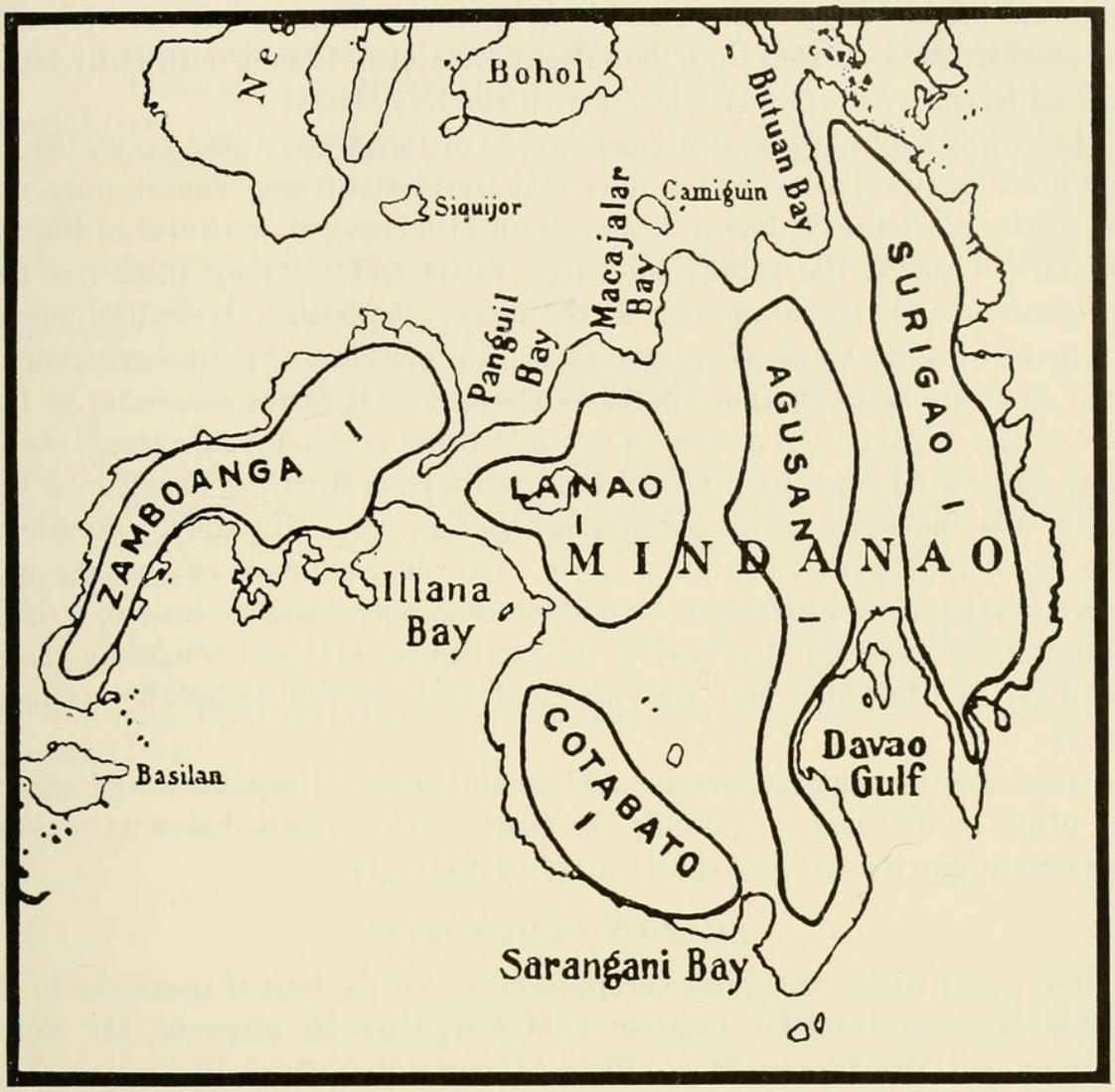

FIGURE 8. "Some probable Pleistocene islands in Mindanao," from Dickerson (1928, p. 86, fig. 19).

subaerial valleys before the Panguil-Illana Isthmus connecting the Zamboanga Peninsula with the Bukidnon-Lanao region emerged.

In an earlier paper I pointed out that the populations of *Cyclocorus nuchalis* from eastern and western Mindanao differed significantly from one another (Leviton, 1967). This was a clue that suggested that in all probability other species of snakes might show similar patterns which could be related to the Plio-Pleistocene paleogeographic history of Mindanao. A careful study of *Rhabdophis auriculata* on Mindanao would seem to confirm this supposition. Populations of this species from Cotabato and Davao are most similar to the Surigao-Agusan populations I have seen and quite distinct from animals from the Zamboanga Peninsula. Samples of *R. auriculata* from Bukidnon and Lanao provinces, on the other hand, are indistinguishable from those from the Zamboanga Peninsula and Basilan Island, raising the possibility that western Mindanao,

composed of the "Pleistocene islands" of Lano and Zamboanga, were joined to one another and separated from the eastern complex of islands until fairly late in the Pleistocene by a persistent Macajalar-Illana Bay seaway.

Indeed, it may have been the persistence of this seaway that prevented any significant eastward movement of the Lanao freshwater fishes. Significantly, only one species of *Puntius* is known from eastern Mindanao, *P. binotatus*, a Bornean species. Of course the seaway no longer exists and certainly there has been sufficient time for faunal movements throughout the island. Terrestrial animals can move with greater freedom than those that must wait for stream-capture in order to go from one drainage basin to another, so it is not surprising to find, for example, a paucity of species of cyprinid fishes in eastern Mindanao, though many forms are known from Lake Lanao and several from the Zamboanga Peninsula. On the other hand, many subspecies of frogs are widely distributed throughout Mindanao, Samar, and Leyte. This distribution is obviously a more recent development, probably a late Pleistocene phenomenon. Indeed, it is becoming more apparent that several faunal movements and radiations can be identified in Mindanao and are correlated with its post-Oligocene geological history.

Quite clearly, a more extensive and careful study of populations of animals and plants on Mindanao, especially the montane forms, should give us considerable insight into the late geological history of that region.

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The following abbreviations are used: CAS—California Academy of Sciences; CAS-SU—California Academy of Sciences-Stanford University (for specimens formerly housed at Stanford University and registered in the Stanford catalogues); CM—Carnegie Museum; FMNH—Field Museum of Natural History; USNM—United States National Museum.

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