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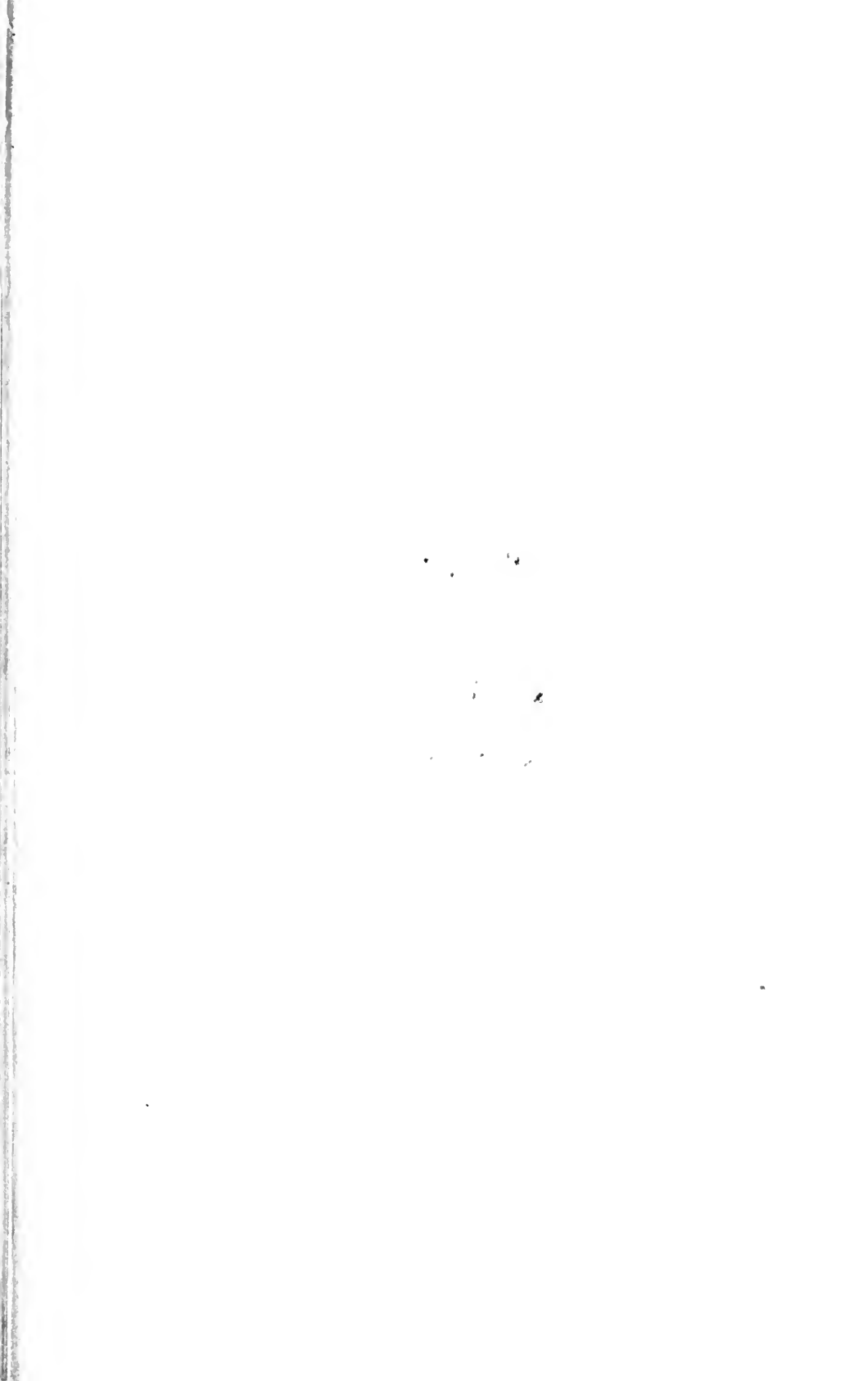
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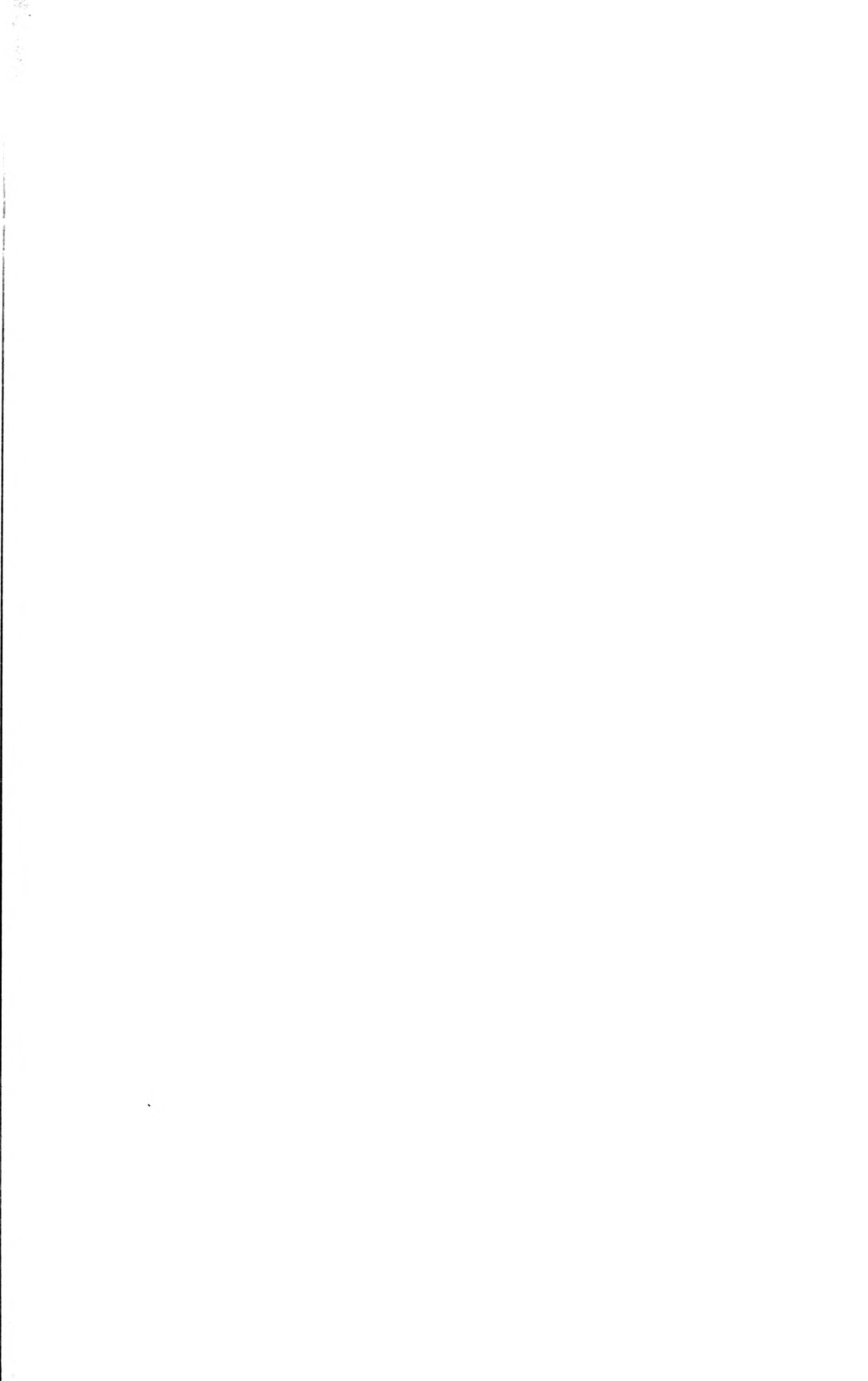
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GEOGRAPHIC VARIATION IN THE CENTRAL AMERICAN COLUBRINE SNAKE, NINIA SEBAE

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The small colubrine snake *Ninia sebae* is one of the characteristic species of Central America, confined to the region between southern Mexico and Panama. It is a terrestrial form, moderately secretive and hence commonly found in considerable numbers beneath trash, notably under the windrows of drying vegetation resulting from the clearing of the ground cover in coffee plantations. This habitat makes the name "coffee snake" appropriate for the snakes of the genus *Ninia*, and *Ninia sebae* may be referred to as Seba's coffee snake.

The very well-defined genus *Ninia* is characterized as follows: dorsal scales keeled and striate, without apical pits; an undivided anal plate; caudals divided; no preocular, the loreal more or less elongate and entering the eye; pupil vertically elliptic; and males with well-developed tubercles on the chin-shields. The genus, with five species, was competently reviewed by E. R. Dunn in 1935. He had examined 157 specimens of the species *Ninia sebae*, as many as of the other four species together. With much active collecting in upper Central America in the two decades since 1935, the material in American museums, or otherwise available, has grown to nearly 500 specimens. The collections made by the senior author in Guatemala in 1934 included an extremely distinct but evidently subspecifically related form, and the series obtained in Yucatan by E. Wyllys Andrews IV, in 1935, indicated the existence of a distinct

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subspecies at the northern end of the Yucatan Peninsula. The large collections made by L. C. Stuart in Alta Vera Paz complement the collections from the Pacific versant of Guatemala. The junior author had the opportunity to collect and observe *Ninia sebae* in the course of his participation in the Salvadorean Project of 1951. Thus a review of the single species *sebae* became a mutual interest, and we have examined the variation in scale counts and in coloration in the large material now available, amounting to nearly 500 specimens.

We are indebted to Dr. Norman Hartweg and George B. Rabb for the loan of the Mexican, Guatemalan, and Nicaraguan specimens in the Museum of Zoology of the University of Michigan. They have kindly included six fresh specimens collected in 1956 by Fred G. Thompson in the course of field collecting in Nicaragua, in the Department of Matagalpa. We are also indebted to Dr. Doris Cochran of the United States National Museum for the privilege of examining Nicaraguan material in her charge. Finally, we thank Dr. Joseph R. Slevin for examining for us the Guatemalan specimens collected by himself for the California Academy of Sciences.

Since undertaking our study another species of *Ninia*, *N. diademata*, has been examined from the taxonomic and ecological viewpoint by W. Leslie Burger and John E. Werler. Our examination of *sebae*, in which we are fortunate to have available a much larger number of specimens than had hitherto been examined, supplements the study of *diademata* by these authors.

Ninia sebae Duméril, Bibron, and Duméril

Streptophorus sebae Duméril, Bibron, and Duméril, 1854, *Erpét. Gén.*, 7: 515—Mexico (type locality restricted to Vera Cruz by Schmidt and Andrews, 1936).

Ninia sebae Dunn, 1935, *Proc. Nat. Acad. Sci.*, 21: 11.

Diagnosis.—Dorsal scales in 19 rows; upper labials 7 or 8; ventrals 131–156; caudals 40–74; red above, with or without black bars or spots on the sides; top of head black; a yellow collar and a broader black dorsal saddle; belly usually immaculate, never checkered.

Original description.¹—*Lepidosis*: The rostral, apparently triangular, has seven unequal sides, the longest emarginated for the passage of the tongue; two meet the anterior nasals; two shorter ones meet in an obtuse angle between the inter-

¹The original description is quoted in free translation as an example of the species descriptions of the *Erpétologie Générale*.

nasals; two, still shorter, meet the first upper labials. This rostral plate does not extend onto the upper surface of the snout, and it bears a semicircular excavation below.

The internasals are very small, subrectangular, with the most acute angle directed outward and backward.

The prefrontals are four times as large as the internasals, with three long subequal sides and three short ones touching the posterior nasal, the supraocular, and the eye.

The frontal is five-sided, with a curved side in front, two lateral somewhat convergent sides and two posterior ones that meet; each of the latter is a third shorter than the anterior side.

The oblong supraoculars are squarely truncate at each end, and are a little less narrow anteriorly than posteriorly.

The parietals, a third longer than their width, touch the supraocular with one edge, which extends to the upper postocular; they meet the temporal laterally, and the suture between them meets their outer borders; their posterior borders are sharply truncate.

The first nasal would be square if it were not for the emargination posteriorly by the opening for the nostril. The second nasal has five unequal sides; it is almost as high as the first but is shorter and a little concave.

The loreal is an oblong rectangle, extending to the eye, there being no pre-ocular scute. The single postocular on each side is narrow and vertically elongate.

On the temple there is a large elongate scute, which meets the postoculars. It precedes two other scutes, also oblong, and superposed; they are less developed and rest on the last upper labial. Behind these three scutes there are two vertical rows of three scales each, larger than those of the neck but not carinate like the body scales.

Among the seven upper labials, the third and fourth touch the eye; they become gradually higher from the first labial to the sixth, while the seventh is lower, though longer, than the one preceding.

The mental has three sides, the two posterior being shorter than the anterior.

There are eight pairs of lower labials, the first meeting behind the mental, forming a wide V, wedged between the anterior chin-shields. The chin-shields are nearly rectangular, truncate anteriorly, somewhat rounded posteriorly. The posterior pair of chin-shields, shorter than the anterior, are square-cut in front; posteriorly they have an acute angle, thus leaving a space between their tips occupied by the anterior end of a large pentagonal scale. The first of the ventral plates is immediately behind this scale.

The throat, on both right and left sides, has two or three oblique rows of scales, each almost square, but a little longer than wide.

Throughout the length of the body there are 17 scale rows on the back and 6 on the tail, 4 gular scutes, 131 to 138 ventrals, and 44 to 56 caudals.

Teeth 16 to 19 maxillary, 7 to 8 palatine, and 20 pterygoid.

Coloration.—The top and sides of the head and neck are a handsome black. Beginning at the labials and rising toward the occiput there is a whitish half-collar. All of the labial shields are more or less bordered by black. The upper parts of the body and sides, and the tail are flesh-colored or reddish brown. On the upper

part of the body and tail there is a double series of black markings, which are sometimes confluent over the back. The belly and the under side of the head and of the tail are yellowish white with scanty black spotting.

Dimensions.—The head is twice as long as its width at the temples. The diameter of the eye is a third of the space between the orbits. The body is 33 to 42 times as long as its diameter at mid-length. The tail is contained four or five times in the body length, which, in the largest specimen, is 318 mm.

Head 10 mm., body 247 mm., tail 61 mm.

Distribution.—The *Streptophorus* we are describing comes from Mexico. The collection of the museum contains several specimens with their coloration well preserved.

Observations.—This snake has not been described by any author, but there is a representation, or rather a figure recognizable in spite of the bad drawing, in the treasure of the famous pharmacist of Amsterdam. [End of original description.]

REGIONAL VARIATION IN VENTRALS AND CAUDALS: *Ninia sebae*

Number of specimens followed by a colon; averages in parentheses.

Region	Ventrals		Caudals					
	Males	Females	Males	Females				
<i>Ninia sebae sebae</i>								
Vera Cruz	47:132-146	(138)	44:137-149	(140)	45:48-62	(55)	43:40-59	(49)
British Honduras	20:133-142	(138)	21:136-147	(141)	18:51-71	(59)	20:42-60	(49)
Alta Verapaz	45:131-151	(140)	32:134-149	(143)	42:41-67	(56)	32:44-61	(50)
Northern Honduras	15:134-148	(138)	11:138-149	(144)	11:58-72	(62)	11:47-61	(53)
El Salvador	23:136-151	(143)	19:147-152	(150)	23:53-66	(60)	18:51-56	(53)
<i>Ninia sebae morleyi</i>								
Yucatan	33:140-151	(144)	45:142-156	(148)	32:41-56	(51)	42:37-49	(42)
Peten, Campeche, Quintana Roo	10:139-144	(142)	11:143-156	(148)	9:41-57	(51)	10:37-47	(42)
<i>Ninia sebae punctulata</i>								
Southwestern Guatemala	57:131-139	(134)	41:131-145	(138)	53:50-65	(58)	35:45-58	(50)
Chiapas	8:135-141	(138)	7:138-146	(142)	6:56-63	(60)	4:48-54	(51)
<i>Ninia sebae immaculata</i>								
Nicaragua	9:135-146	(140)	11:140-149	(145)	9:64-74	(69)	9:53-65	(60)
Costa Rica	2:131-132	(132)	2:138-140	(139)	2:65-66	(66)	1: 58	(58)

Only a few specimens are available from the area between Vera Cruz and British Honduras (*sebae sebae*) and Yucatan (*sebae morleyi*); twelve are from Peten, eight from Campeche, and one from Quintana

Roo. The variation in these twenty-one specimens is in the direction of *sebae sebae*, though only slightly. In scale counts they correspond most closely with *morleyi*.

Ninia sebae punctulata in southwestern Guatemala has much the lowest average number of ventrals of any series examined, though still broadly overlapping in range of variation. To the west and north the small series from Chiapas, mostly with the *punctulata* coloration, tends definitely toward *sebae sebae*, with higher averages of ventrals in both series. At the eastern end of the range of *punctulata* no intergradient population is known; there is a gap between the low average ventrals in female *punctulata* and the high average of the El Salvador series. The ranges of variation in males overlap somewhat.

In Nicaragua, there is little difference from *sebae sebae* in numbers of ventrals, but the caudals are distinctly more numerous in both sexes. The scale counts for the four Costa Rican specimens reported by Taylor are included in the table (Taylor, 1954, p. 695).

The series from El Salvador includes the scale counts of the eleven males and nine females reported by Mertens (1952, p. 68). Our series of twelve males and ten females agrees exactly with his in both extremes and averages in these characters. The ranges and averages of ventrals in both sexes are higher than in other populations of *sebae sebae* and compare with those of *morleyi* from Yucatan. The numbers of caudals, however, agree with those of *sebae sebae* and not at all with those of the Yucatan specimens. To the northwest of El Salvador *sebae punctulata* is sharply characterized by its coloration and is thus entirely distinct from the Salvadorean population. The same is true of the Nicaraguan subspecies to the southeast. Since the Salvadorean specimens agree in coloration with the Honduran and Guatemalan *sebae sebae*, they are thus best associated with that subspecies.

SYNOPSIS OF SUBSPECIES OF *Ninia sebae*

1. Dorsal markings of small spots rather than vertical bars, very numerous, never reduced in number or absent. *sebae punctulata*
Western part of Pacific versant of Guatemala, in Coffee Zone.
1. Black dorsal spots in the form of well-defined transverse bars, often reduced in both size and number or absent (nuchal black saddle invariable) 2
2. No dorsal crossbars; loreal usually narrowed posteriorly; caudals in males 64-74 (69), in females 53-65 (60) *sebae immaculata*
Nicaragua and Costa Rica.
2. Dorsal crossbars usually present, occasionally reduced or absent; loreal rectangular; caudals in males 41-72 (55), in females 37-61 (50) 3

3. Ventrals in males 139-151 (144), in females 142-156 (148); caudals in males 41-57 (51), in females 37-49 (42); about 50 per cent of specimens with much reduced body spots, or without spots. *sebae morleyi*
Northern half of Yucatan Peninsula.
3. Ventrals in males 131-151 (139), in females 134-152 (143); caudals in males 41-72 (58), in females 40-61 (50); majority of specimens boldly black-marked. *sebae sebae*
Vera Cruz, Tabasco, Oaxaca, Chiapas; Atlantic drainage of Guatemala; Honduras; El Salvador.

Ninia sebae sebae Duméril, Bibron, and Duméril

Streptophorus sebae Duméril, Bibron, and Duméril, 1854, *Erpét. Gén.*, 7: 515—Mexico (type locality restricted to Vera Cruz by Schmidt and Andrews, 1936; further restricted to Vera Cruz, Vera Cruz, by Smith and Taylor, 1950).

Ninia sebae sebae Schmidt and Andrews, 1936, *Field Mus. Nat. Hist., Zool. Ser.*, 20: 170.

Elapoides fasciatus Hallowell, 1855, *Jour. Acad. Nat. Sci. Phila.*, (2), 3: 35, pl. 4—Honduras.

Streptophorus sebae collaris Jan, 1862, *Arch. Zool. Anat. Fis.*, 2: 27—Mexico.

Streptophorus sebae dorsalis Bocourt, 1883, *Miss. Sci. Mex., Rept.*, p. 547—Belize.

Diagnosis.—Ventrals relatively few (131-151 in males, 134-152 in females) and caudals relatively numerous (41-72 in males, 40-61 in females); coloration very variable, usually with black dorsal crossbars, these often reduced in number, occasional specimens with only the black nuchal collar characteristic of the species.

Original description.—See above; the original description of the species applies to the typical subspecies only.

Synonymy.—The allocation of the three synonymic names listed above is made on geographic grounds. *Elapoides fasciatus*, described a year after the publication of the Duméril and Bibron volume, is from the southern portion of the range of *sebae sebae*. Its pattern agrees closely with the normal cross-banded type of southern Mexico. *Streptophorus sebae collaris* Jan is stated to be from Mexico, and though it is described as without dorsal spots, and thus might be *immaculata*, this coloration is sufficiently frequent as a variant in southern Mexico, the type locality of *sebae*, to make the allocation of *collaris* to the synonymy of *sebae sebae* entirely satisfactory. *Streptophorus sebae dorsalis*, finally, is from Belize. This variety is characterized by greatly reduced dorsal spotting, with only a median dorsal row of black spots on the anterior part of the body. This variant can be matched in a small proportion of the specimens from Belize and the base of the Yucatan Peninsula.

***Ninia sebae morleyi* Schmidt and Andrews**

Ninia sebae morleyi Schmidt and Andrews, 1936, Field Mus. Nat. Hist., Zool. Ser., 20: 169—Chichen Itzá, Yucatan.

Diagnosis.—"Closely allied to *Ninia sebae*, but distinguished by a higher number of ventral scales and a lower number of caudal scales." To this original diagnosis must be added: majority of specimens without dorsal black spots.

*Description of type.*¹—Body short; head only slightly distinct from neck; pupil round; rostral small, about as wide as high, little visible from above; internasal suture about one-third that of the prefrontal; frontal shield-shaped, nearly as wide as long; supraoculars small, narrower in front than behind; parietals large; nasal undivided, in contact with the first and second labials; loreal elongate, entering the eye; no preocular; large prefrontal entering the eye; two postoculars; temporals 1-2 on each side; upper labials seven, the third and fourth entering the eye on the left side, the fourth only on the right; lower labials eight, the first pair in contact behind the very small mental; anterior chin-shields much longer than the posterior; dorsal scales in nineteen rows, keeled; ventrals 149; anal entire; caudals 41.

General color (in alcoholic specimens) pale reddish brown above, lighter beneath; top of head to posterior border of parietals black; a black nuchal saddle, six scale rows in length and extending from the first scale row, separated from the parietals by a pale yellow space four scales wide, and with a narrow yellow border behind; black of head extending to the labials; chin with a black marking including the mental and first lower labials and extending backward on the sutures between labials and chin-shields; a single very small mid-dorsal spot. Ground color in life brilliant red.

Measurements.—Total length 202 mm., tail 44.

Remarks.—The thirty-eight specimens collected in Yucatan by Dr. E. Wyllys Andrews show that the tendency to reduction and loss of the dorsal black spotting is much more pronounced in *morleyi* than in any population of *sebae sebae*. In the Yucatan series, twenty specimens are without spots, ten have a very reduced number or only very small spots, and eight have the spots normally developed for the full length of the body, each several scale rows in width.

***Ninia sebae punctulata* Bocourt**

Streptophorus sebae var. *punctulata* Bocourt, 1883, Miss. Sci. Mexique, Rept., p. 547—Guatemala (here restricted to vicinity of Quezaltenango on the Pacific slope of southern Guatemala).

Diagnosis.—Differs sharply from *sebae sebae* in body pattern, in which the dark spots are small, numerous, in several rows, never with transverse bars, and never immaculate or with reduced spotting.

¹Original description of type, CNHM no. 20619.

*Original description.*¹—As with the preceding varieties [*dorsalis* Bocourt and *collaris* Jan], the head is black and its posterior part is ornamented by a yellow collar, bordered behind by a large dark blue spot; the sides and upper parts of the body exhibit brown maculations of angular form, disposed on each side in two or three series. These spots are bordered by yellow and are conspicuous on the grayish-rosy ground color. The lower parts are yellow, with faint grayish spots; the chin is spotted with brown.

There are 134 gasterosteges and 59 double urosteges.

Total length of a specimen.....	0.364 m.
Length from tip of snout to anus.....	0.279
Length of tail.....	0.085

This variety, common in Guatemala, reaches a relatively large size.

Remarks.—The original description of *punctulata* states that the top and sides of the body have brown spots, angular in shape, and arranged on each side in two or three series. This leaves no doubt that it applies to the present form, and there is no question as to the restriction of the type locality "Guatemala" to the western part of the Pacific slope of Guatemala; we have restricted it further to the vicinity of Quezaltenango because this area was reached by Bocourt.

The specimens available from western Guatemala are fairly uniform in pattern. None approach the type of spotting of *sebae sebae*. In the collections from Chiapas some specimens vary in the direction of *sebae sebae*, for ten of thirteen are less heavily spotted than the Guatemalan ones, and the remaining three have the number of spots still further reduced, as in Vera Cruz or Yucatan *sebae*. In their scale counts these Chiapas specimens likewise approach *sebae sebae*. The variation in scale counts by departments is as follows:

Locality	Ventrols		Caudals	
	Males	Females	Males	Females
Solola.....	21:132-139 (134)	13:134-141 (138)	21:50-62 (57)	11:46-52 (49)
Suchitepequez..	6:131-138 (133)	8:132-139 (136)	6:51-62 (57)	7:46-52 (49)
San Marcos...	30:132-139 (135)	20:131-145 (139)	26:53-65 (59)	17:45-58 (52)
Chimaltenango.	1:140 (140)	1:60 (60)

Intergrades toward *sebae sebae*

Chiapas.....	8:135-141 (138)	7:138-146 (142)	6:56-63 (60)	4:48-54 (51)
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Range.—Pacific versant of Guatemala, mainly between 500 and 2000 meters altitude (i.e., in the Coffee Zone), reaching contiguous Chiapas but not extending into El Salvador, where it is replaced by *sebae sebae*.

¹ Free translation.

Ninia sebae immaculata subsp. nov.

Type.—Chicago Natural History Museum no. 11584, adult female, Río Escondido (or Bluefields River), southeastern Nicaragua, received from W. F. H. Rosenberg.

Diagnosis.—A subspecies of *Ninia sebae* characterized by absence of dorsal spots other than the black collar, and a higher number of caudals than in other populations. There is no overlap in number of caudals in either sex with *Ninia sebae morleyi*, of Yucatan, which may have the unspotted pattern of *immaculata*.

Description of type.—Head somewhat pointed, slightly wider than neck; body stocky; rostral barely visible from above; internasals small, about one-third the length of the prefrontals; frontal little longer than wide; parietals once and a half as long as the frontal, their rear edge scalloped by the adjoining dorsals; nasal divided; loreal elongate, narrowed where it enters the eye; no preocular; two postoculars, temporals 1-2 on each side; upper labials 7; lower labials 7; posterior chin-shields shorter than anterior; dorsal scales 19 throughout; ventrals 147, anal entire, caudals 63.

Uniform brownish red above except for the dark brown top of the head, which color extends to the upper edge of the upper labials, and a broad nuchal crossband two scales behind the parietal and five or six scales long, extending to the second scale row on each side; ventral surface lighter than dorsum, yellowish brown.

Measurements.—Total length 348 mm., tail 78 mm.

Notes on paratypes.—The 25 paratypes, all from Nicaragua, are Univ. Mich. Mus. Zool. 79753-55, from 7 miles above Rama, Río Siquia, and 115021-26 from the Department of Matagalpa; and U. S. Nat. Mus. 15627-29, 15639, San Juan del Norte; 19564, 19571, 25319, Greytown; 79971-72, Managua; 15307, Cape Gracia; 19890, Escondido River; 118041-42, San Carlos; 15207-8, 25244, Nicaragua (no other data).

The series of paratypes shows, somewhat unexpectedly, that the Nicaraguan *immaculata* is found both in the humid forest region of the Mosquito Coast and in the semi-arid interior.

The ranges of variation and averages of ventrals and caudals (repeated from above) are as follows:

Sex	No. of specimens	Ventrals	
		Extremes	Average
♂	9	135-146	140
♀	11	140-149	145

	Caudals		
♂	9	64-74	69
♀	9	53-65	60

The longest male measures 326 mm., tail 91; the longest female 347 mm., tail 81. All are without dorsal bars except for the nuchal saddle, which is 2 to 3 scales behind the parietals and 4 to 5 scales in length. All except two specimens have the loreal distinctly more elongate than is normal in *sebae sebae*; in nos. 15207 and 15307 the loreal is like that of *sebae sebae*.

E. R. Dunn listed *Ninia sebae* from Costa Rica, and this occurrence is now substantiated by E. H. Taylor with fresh material from La Lola, Limón Province. The scale counts of his four specimens (included in the tabulation above, from Taylor, 1954) slightly extend the Nicaraguan variation ranges downward, and this may indicate a geographic cline within *immaculata*. The Costa Rican specimens agree satisfactorily with the Nicaraguan series in lacking dorsal spotting, and we have no hesitation in including them here. The specimen of *sebae* listed by Dunn as from Boquete, Panama, is a *Ninia maculata*.

DISCUSSION

The general geographical distribution of *Ninia sebae* points clearly to an origin, with that of the genus, during the Tertiary isolation of a Middle American island, cut off from the North and South American continents alike, and lying in parts of present-day Guatemala, Chiapas, El Salvador, and Honduras. The Americas were separated through most of the millions of years of the Tertiary, and on the great tropical island between them, whose population was derived mainly from the northern continent, there was opportunity for independent evolution. Re-connection of the Middle American island with Mexico and lower Central America and the emergence of the Yucatan Peninsula in its present form made possible the emigrations that populated Nicaragua to the south and Mexico and Yucatan to the north from the more ancient center. The development of the most sharply distinct of the subspecies of *sebae*, *punctulata*, seems to be correlated with the isolating palisade of the Guatemalan escarpment and to be much earlier than the spread of the much less well-distinguished *morleyi* and *immaculata*.

The ecological distribution is not yet fully clarified. The center of abundance, so far as existing collections are concerned, is in the

Coffee Zone, from 500 to 2,000 meters. It does not occur much above this altitude, but it does reach the low level coastal plains. From its abundance on the low-lying Yucatan Peninsula, it is by no means certain that the Coffee Zone is its optimum altitude zone.

It is of interest that the subspecies of *sebae* represent different ages of origin and different degrees of divergence and distinctness. The central and nominate form ranges from Vera Cruz and Oaxaca through northern Chiapas and Tabasco to all of Guatemala north of the volcanic escarpment, into the base of the Yucatan Peninsula, and throughout Honduras and El Salvador. *Ninia sebae sebae* is highly variable. With still further geographic analysis it seems evident that it would present a mosaic of only slightly differentiated populations, certainly not suitable for nomenclatorial designation. Of the three derived subspecies, *morleyi* of Yucatan and *immaculata* of Nicaragua are at the periphery of the broad range of *sebae sebae*, whereas the third, *punctulata*, though also peripheral on the southern slopes of the Guatemalan highland, is enclosed at both the northwest and the southeast by typical *sebae sebae*.

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