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**THE COLUBRID SNAKE GENUS THAMNOPHIS:  
A REVISION OF THE SAURITUS GROUP**

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# THE COLUBRID SNAKE GENUS *THAMNOPHIS*: A REVISION OF THE SAURITUS GROUP

DOUGLAS A. ROSSMAN<sup>1</sup>

**SYNOPSIS:** The Sauritus group of the gartersnakes is composed of two polytypic species, *Thamnophis sauritus* (Linnaeus) and *Thamnophis proximus* (Say), commonly called the ribbonsnakes.

Both species vary geographically in number of ventrals, number of subcaudals, relative tail length, and several features of the color pattern. Supralabial number is subject to geographic variation in *T. sauritus* but not in *T. proximus*. Most of the geographic variation is discordant, transition zones in one character seldom corresponding with those of other characters. As color pattern fluctuates less locally than do the meristic characters, it is more reliable in defining geographic races.

Four subspecies of *T. sauritus* are recognized, two of them previously undescribed (*T. s. septentrionalis* of the Great Lakes region, northern New England, and Nova Scotia; *T. s. nitae* of northwestern peninsular Florida). Of six races of *T. proximus* four are new (*T. p. orarius* of coastal Louisiana, Texas, and northern Tamaulipas; *T. p. rubrilineatus* of the Edwards Plateau region of central Texas; *T. p. diabolicus* of New Mexico, trans-Pecos Texas, Coahuila, and Nuevo Leon; *T. p. alpinus* of the Chiapas Highlands in southern Mexico).

The evolutionary history of this species group and the trends within each species are discussed. Members of the group are highly specialized and occupy an advanced position within the genus.

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<sup>1</sup>The author, Instructor in Zoology at the University of North Carolina, Chapel Hill, completed this study while a graduate student at the University of Florida, Gainesville. An earlier version formed his doctoral dissertation, which was accepted by the Graduate School in August 1961. Manuscript submitted 18 January 1962.—Ed.

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## INTRODUCTION

More than half a century has elapsed since Ruthven (1908) produced his classic monograph of the gartersnake genus *Thamnophis*, a monumental work which has served as a model for most subsequent studies of geographic variation in ophidians. In that study he arranged the 12 species of *Thamnophis* then recognized into two primary phylogenetic divisions, each containing two species groups which he named for the "best known" species in each. Thus, his Division I comprised the *Radix* group and the *Sauritus* group, and his Division II the *Elegans* group and the *Sirtalis* group.

Ruthven based his revision on a study of approximately 3000 specimens. While impressive for that time, this sample was hardly adequate to show detailed variation when divided among the 12 species he recognized; moreover it apparently contained specimens of five or six additional species of *Thamnophis* then unrecognized. As additional material accumulated in American museums during the first half of the 20th century, more refined analyses of geographic variation became possible for many species (Fitch, 1940; Mittleman, 1949; A. G. Smith, 1949; and Milstead, 1953 for example). In the recent flurry of activity by students of gartersnake variation the *Sauritus* group has been overlooked except for a few brief and scattered notes buried in papers on other subjects. This general lack of interest in the ribbon-snakes is surprising when one considers their abundance and their extensive geographic range—Nova Scotia and the Great Plains to Costa Rica—and the large amount of material available for study—now more than 2400 specimens. The present investigation was undertaken to provide a more adequate definition of the *Sauritus* group as a possible basis for future comparative studies of all members of the genus *Thamnophis* (of which *T. sauritus* is the type species) by analyzing individual and geographic variation in the two species comprising it.

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Worthington, the curators of the institutions cited below, and the many helpful friends who cannot be mentioned individually because of space limitations. T. T. Allen prepared the drawings of the ribbon-snake heads, figure 1.

Special thanks for their constant encouragement and ready advice are due A. B. Grobman, under whose guidance this study was initiated, and A. F. Carr and W. J. Riemer, who supervised its completion.

#### MATERIALS AND METHODS

Although it was impossible to examine every specimen of *Thamnophis sauritus* and *T. proximus* in North American collections, the sample studied included more than 2400 specimens from all parts of the ranges of both species from the following institutional collections:

AMNH	American Museum of Natural History	NMC	National Museum of Canada
ANSP	Academy of Natural Sciences of Philadelphia	NSMS	Nova Scotia Museum of Science
CAS	Chicago Academy of Sciences	NYSM	New York State Museum
CM	Carnegie Museum	OSM	Ohio State Museum
CMNH	Cincinnati Museum of Natural History	TCWC	Texas Cooperative Wildlife Collection
CNHM	Chicago Natural History Museum	TNHC	University of Texas Natural History Collection
CUM	University of Colorado Museum	TTC	Texas Technological College
INHS	Illinois State Natural History Survey	TU	Tulane University
KU	University of Kansas Museum of Natural History	UADZ	University of Arkansas Department of Zoology
LSUMZ	Louisiana State University Museum of Zoology	UF	University of Florida Collections
MCZ	Museum of Comparative Zoology	UG	University of Georgia
MGFCM	Mississippi Game and Fish Commission Museum	UIMNH	University of Illinois Museum of Natural History
MPM	Milwaukee Public Museum	UK	University of Kentucky
MSC	Mississippi Southern College	UMMZ	University of Michigan Museum of Zoology
		USCM	University of South Carolina Museum
		USNM	United States National Museum
		UV	University of Vermont

In addition to preserved material, I have been fortunate in having available for examination live ribbonsnakes of all the subspecies rec-

ognized in this study from many parts of the United States and Mexico. These animals revealed several distinctive and diagnostic color-pattern characters not apparent in preserved specimens. A small series of articulated and disarticulated skeletons was prepared for comparative purposes, and the left maxilla was removed from a number of the preserved specimens for tooth counts. Sex was determined by dissection, except when males had the hemipenes everted.

The following measurements of cephalic scales were made: parietal length, frontal length and width, muzzle length, internasal-rostral suture length, and nasal-rostral suture length. Muzzle length, as used herein, is equivalent to the combined length of one prefrontal and the adjacent internasal when measured along the middorsal suture. These measurements are the basis of the following ratios: frontal length/parietal length; frontal width/frontal length; muzzle length/frontal length; internasal-rostral contact/nasal-rostral contact. Measurements of head length, body length (including the head), and tail length permitted calculation of head length/body length and tail length/total length ratios. Absence or distortion of the tail in many specimens reduced the number of tail length/total length values obtained. A few ratios (frontal length/parietal length and frontal width/frontal length) that showed no significant variation are not discussed further.

Standard counts were made of such meristic characters as number of supralabials and infralabials, preoculars and postoculars, temporals, intergenials, ventrals, and subcaudals, as well as of any anomalies occurring in these characters. The number of dorsal scale rows was determined at three points on the body: one head length behind the head, at midbody, and above the last ventral scute. The point of dorsal scale row reduction on the body was determined for a small number of specimens; caudodorsal reduction in a few individuals.

The number of teeth on each of the dentigerous bones was noted, empty sockets being included in the total count.

The state of certain elements of pattern that vary significantly in the *Sauritus* group was observed in each specimen: relative size and shape of the light-colored parietal spots, extent of the light spot on the postoculars, presence or absence of a black postorbital vitta, width of the vertebral stripe, presence or absence of a black paravertebral stripe, width of the light lateral stripe, degree of spotting between the vertebral and lateral stripes, and width of the dark ventrolateral stripe occupying the lateral margin of the ventral scutes on each side.

Color notes were made on living specimens, with consistent attention to the labials, vertebral and lateral stripes, the dorsum, and the venter. In most cases these evaluations were subjective, but, with only

two exceptions, at least one specimen of each geographic race was compared with a color atlas (Maerz and Paul, 1950). All color descriptions in this study are based on freshly killed, freshly shed specimens, unless otherwise stated.

### THE SAURITUS GROUP

As *Thamnophis proximus*, long thought to be a subspecies of *T. sauritus*, is a valid species (Rossman, 1962), the Sauritus group, long recognized as distinct from the other gartersnakes, is now known to be composed of two closely related species. Holbrook (1842) placed the species *sauritus* (including the unrecognized *proximus*) in *Leptophis*, a genus of slender, semiarboreal colubrids; the other gartersnake species were not thus allocated. Fitzinger (1843) erected the genus *Thamnophis*, in which later authors placed all gartersnakes, solely to accommodate the ribbonsnake. Even as late as 1893, Duméril and Bocourt included only *sauritus* in *Thamnophis*, allocating the other species to *Eutaenia*. While Ruthven (1908) placed *sauritus* in *Thamnophis*, he acknowledged its distinctive nature by designating a species group solely for that species.

### DEFINITION OF THE SAURITUS GROUP

These are snakes of the genus *Thamnophis* possessing a small hemipenis that extends to the 7th or 8th subcaudal in the inverted position. The teeth are numerous, usually 29 to 32 on each maxilla, 20 to 22 on each palatine, 33 to 36 on each pterygoid, and 36 to 38 on each dentary. The basal portion of the tongue is red; the forked tips are black. The tail is long, usually constituting 27 percent or more of the total length of adults. The maximum number of dorsal scale rows rarely exceeds 19. The ventrals range from 141 to 181 (both extremes in *T. proximus*); the subcaudals from 82 (*T. proximus*) to 136 (*T. sauritus*). In both species the males have a slightly greater number of scutes than the females. The lateral stripe is usually confined to dorsal scale rows 3 and 4. The supralabials always lack vertical black bars.

### MORPHOLOGY

FORM AND PROPORTIONS. Both species are relatively slender, long-tailed snakes in comparison with other members of the genus. *Thamnophis proximus* may exceed 1250 mm. in total length, equaled among the gartersnakes by *Thamnophis sirtalis* and surpassed only by *Thamnophis elegans gigas*. *T. sauritus* is smaller; the largest adult examined measured only slightly over one meter. The relatively narrow head



makes up 3.5 to 4.6 (mean 4.1) percent of the body length in adults. The muzzle is narrow, apparently reflecting the semiaquatic habits of these two species (Fitch, 1940), the internasal-rostral contact/nasal-rostral contact ratio exceeding 1.00 in only one of 29 adults examined for this character (mean 0.82). The tail is longer than in any other species of *Thamnophis* and constitutes 25.2 to 33.6 percent of the total length in adult *T. proximus*, and 28.8 to 38.8 percent in adult *T. sauritus*. Both species show sexual dimorphism in proportionate tail length.

**OSTEOLOGY.** Hypapophyses are present throughout the length of the vertebral column, a condition generally thought to be characteristic of natricine snakes (Malnate, 1961, however, has described a new genus apparently closely related to the natricine genus *Amphiesma* but lacking hypapophyses on the posterior trunk vertebrae). The skull is of the generalized colubrid type and similar to those of other species in the genus; although certain differences do exist, these must be analyzed by a comparative study of the skulls of all the species of *Thamnophis*, which is beyond the scope of the present investigation.

Members of the *Sauritus* group have more teeth on each of the dentigerous bones than any other species in the genus for which data are available. The number of maxillary teeth ranges from 27 to 34, palatine from 17 to 25, pterygoid from 26 to 38, and dentary from 31 to 40. The means for *T. proximus* and *T. sauritus* are presented in table 1. As no sexual dimorphism in tooth number is apparent, the counts for both sexes are combined. Maxillary counts were taken both

TABLE 1. Meristic dentitional variation in the *Sauritus* group  
(*N* = number of counts; *M* = mean; *R* = range)

	<i>T. proximus</i>			<i>T. sauritus</i>		
	<i>N</i>	<i>M</i>	<i>R</i>	<i>N</i>	<i>M</i>	<i>R</i>
Maxilla.....	37	30.0	27-34	49	30.4	27-34
Palatine.....	10	19.7	17-22	37	21.0	18-25
Pterygoid.....	11	32.7	26-37	38	34.3	28-38
Dentary.....	13	33.8	31-36	36	37.1	33-40

from preserved specimens (only the left maxilla examined) and from skeletons (both maxillae examined); all other counts were taken from skeletal material only. Because the dentigerous bones are paired the number of individual counts differs from the number of individual snakes examined. The number of teeth on the two bones of any given

pair often vary; the same number occurred on both maxillae in only 43.5 percent of the specimens examined, on both palatines in 39.1 percent, on both pterygoids in 30.4 percent, and on both dentaries in 28.6 percent. Differences in tooth count between the two members of a given pair range from 1 to 3 on the maxillae, 1 to 3 on the palatines, 1 to 7 on the pterygoids, and 1 to 2 on the dentaries.

Examination of the maxillae of western ribbonsnakes from Nicaragua, Chiapas, Veracruz, Tamaulipas, Texas, and Louisiana revealed no geographic variation in number of teeth. This may not prevail, however, when information on the more northern populations becomes available. Too few of the other dentigerous bones have been available to study geographic trends in their tooth counts. Southern *T. sauritus* do appear to have more maxillary teeth than their northern counterparts; 36 counts from a peninsular Florida series range from 28 to 34 (mean 31.1) while 13 counts from Pennsylvania ribbonsnakes range from 27 to 30 (mean 28.5). More data are needed to determine the exact nature and extent of this variation. The other toothed bones are represented by counts from Florida specimens only.

Maxillary teeth increase slightly in length posteriorly; the last three teeth are abruptly enlarged. Teeth on the other three pairs of bones decrease slightly in length posteriorly.

**HEMIPENIS.** The hemipenes of *T. proximus* and *T. sauritus* are virtually identical in all respects and are the smallest known for the genus (information is not available for many species). The inverted hemipenis usually extends to the level of the eighth subcaudal (see

TABLE 2. Hemipenis length in the *Sauritus* group

Species	Hemipenis extends to subcaudal	Species	Hemipenis extends to subcaudal
	6(11)*		6(2)
<i>T. proximus</i> . . . . .	7(15)	<i>T. sauritus</i> . . . . .	7
	8(16)		8(10)
	9		

\* Figures in parentheses in this and subsequent tables indicate the number of individuals when there is more than one.

table 2 for individual variation); the *m. retractor penis magnus* is undivided and inserts at the level of the 28th subcaudal. The everted organ is single and bears a simple straight *sulcus spermaticus* which terminates at the apex. Numerous rows of small spines occupy the distal half of the ornamented portion of the hemipenis, the margins

of the sulcus, and the extreme basal area. Those in the latter region are proximal to the two pairs of enlarged basal hooks (one pair on each side of the sulcus). Laterad to each pair of basal hooks is an unornamented area composed of nude patches separated from each other and from the many distal rows of small spines by several oblique rows of large spines which arise on the medial surface of the organ near the basal hooks and converge on the lateral surface. The most proximal of these spines are almost half as large as the basal hooks. The apical region of the hemipenis lacks ornamentation.

**SCUTELLATION.** The most distinctive feature in the scutellation of the *Sauritus* group is the unusually large number of subcaudals in both species. These range from a minimum of 82 in *T. proximus* to a maximum of 136 in *T. sauritus*, almost always exceeding 100 in *T. sauritus*, less frequently in *T. proximus*. Only rarely do other species in the genus have more than 100 subcaudals, and usually the number is much less. Other important scale characters include: a single preocular; 2 supralabials entering the orbit; a maximum of 19 dorsal scale rows in 98.6 percent of the *T. proximus* and 99.8 percent of the *T. sauritus* examined; all dorsal scales strongly keeled, those of the outermost row not greatly enlarged.

**COLORATION.** Both *T. proximus* and *T. sauritus* lack vertical black bars on the labials and black markings on the venter, though in all *T. sauritus* and in certain populations of *T. proximus* brown pigment extends onto the lateral margins of the ventral scutes to form a dark ventrolateral stripe. A light lateral stripe is always present on dorsal scale rows 3 and 4 (confined to row 3 posteriorly in one race of *T. proximus* and including row 2 anteriorly in northern populations of *T. sauritus*), but the vertebral stripe is frequently lacking in some geographic areas. The lateral stripe is usually a shade of yellow, white, or blue, the vertebral stripe a shade of yellow, orange, red, or brown. The color between the stripes ranges from olive-gray and light brown to black. On each preocular is a broad, vertical yellow bar.

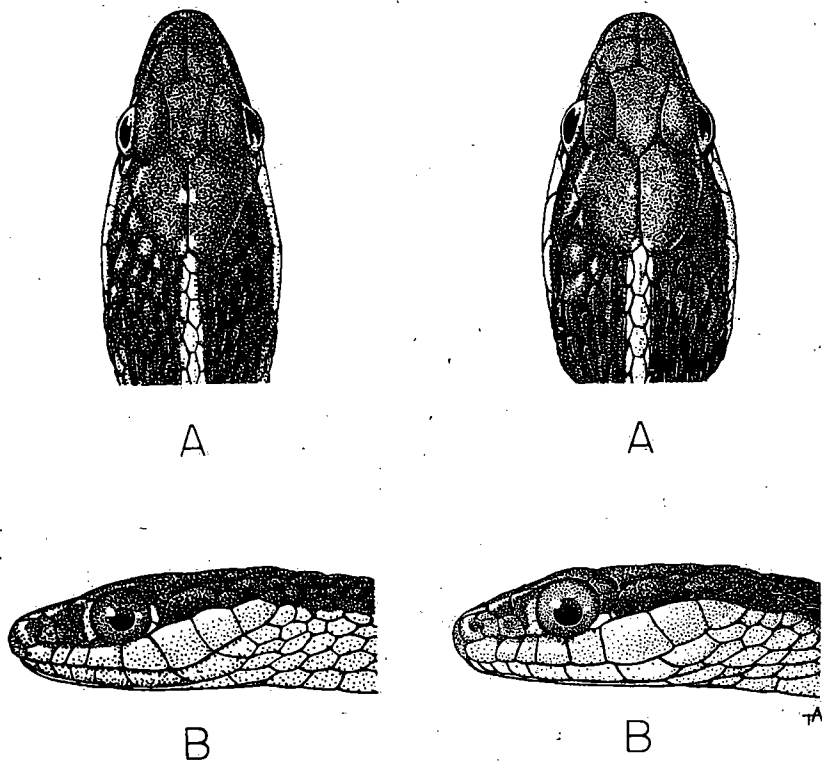
#### RELATIONSHIPS

*T. proximus* and *T. sauritus* form a closely knit species group which shows no particularly close affinities to the other species complexes in the genus. Though Ruthven (1908) suggested a relationship to the *Radix* group—more specifically to *Thamnophis eques*—this can be evaluated properly only by a comprehensive study of the interspecific relationships of the entire genus. For the present we can say that the relatively long tail, extreme reduction in spotting of the dorsum, and

transitional syncranterian maxillary dentition<sup>2</sup> indicate that members of the Sauritus group are highly specialized, and that the group itself occupies an advanced evolutionary position within the genus *Thamnophis*. The large number of teeth present in *T. sauritus* and *T. proximus* is interpreted here as a secondary modification rather than a primitive condition.

#### KEY TO THE SPECIES OF THE SAURITUS GROUP

Parietal spots almost always present, fused, bright, and usually fairly large (fig. 1A, left); brown pigment usually not extending onto the ventral scutes to form a dark ventrolateral stripe on each side or, if present, covering less



#### PROXIMUS

#### SAURITUS

FIGURE 1. Head patterns in the two species of the Sauritus group in dorsal view (A) and lateral view (B).

<sup>2</sup>Transitional syncranterian is equivalent to the "continuous-abrupt" arrangement characterized by Malnate (1960) and thought to represent an evolutionary transition between the more generalized syncranterian and the more specialized diacranterian conditions.

than 2/5 of the area of each scute (except in the Chiapas Highlands); mean muzzle length/frontal length for any given population usually greater than 0.700 \_\_\_\_\_ *T. proximus*

Parietal spots often lacking, when present small and rarely fused or bright (fig. 1A, right); brown pigment always extending onto ventral scutes and usually covering 2/5 or more of the area of each scute; mean muzzle length/frontal length usually less than 0.700 \_\_\_\_\_ *T. sauritus*

## THE WESTERN RIBBON SNAKE *THAMNOPHIS PROXIMUS* (SAY)

*Coluber proximus* Say, 1823:339

*Tropidonotus proximus*: Boie, 1827:535

*Eutainia Faireyi* Baird & Girard, 1853:25

*Eutainia proxima*: Baird & Girard, 1853:25

*Eutaenia proxima*: Baird, 1859:16

*Eutaenia faireyi*: Cooper, 1860:299

*Eutaenia rutiloris* Cope, 1885:388

*Thamnophis proxima*: S. Garman, 1892:105

*Thamnophis proximus*: Strecker, 1909:8

*Eutainia rutilorus*: Cochran, 1961:182

**HOLOTYPE.** According to Smith and Taylor (1945), the holotype is lost. It was probably deposited in the Academy of Natural Sciences of Philadelphia, though this is not a certainty (H. M. Smith, personal communication). The specimen was collected in Nebraska at a stone quarry on the west side of the Missouri River, 3 miles above the mouth of Boyer's River (Iowa) by Long's expedition to the Rocky Mountains in 1819 or 1820. The type locality lies approximately 3 miles ENE Fort Calhoun, Washington County, Nebraska.

**DEFINITION.** A large, long-tailed member of the genus *Thamnophis* characterized by: 19-19-17 dorsal scale rows; a single preocular; typically 8 supralabials, the 4th and 5th entering the orbit; 141 to 181 ventrals; 82 to 131 subcaudals; lateral stripe on dorsal scale rows 3 and 4, at least anteriorly; labials and ventrals without black markings; dark ventrolateral stripe absent or narrow in most populations; parietal spots fused, brightly colored, and usually large; hemipenis short, usually extending to the seventh or eighth subcaudal when inverted; teeth numerous, averaging about 30 to each maxilla, 34 to each dentary, 20 to each palatine, and 33 to each pterygoid.

**RANGE.** From southern Wisconsin, Indiana, and the Mississippi Valley west through the Great Plains to southeastern Colorado and eastern New Mexico, and south through eastern Mexico to central Costa

Rica (figs. 2 and 3). It occurs on the Pacific coast of Mexico near Acapulco, Guerrero, and on the Isthmus of Tehuantepec in Oaxaca (see *T. p. diabolicus* for discussion of an early published record for

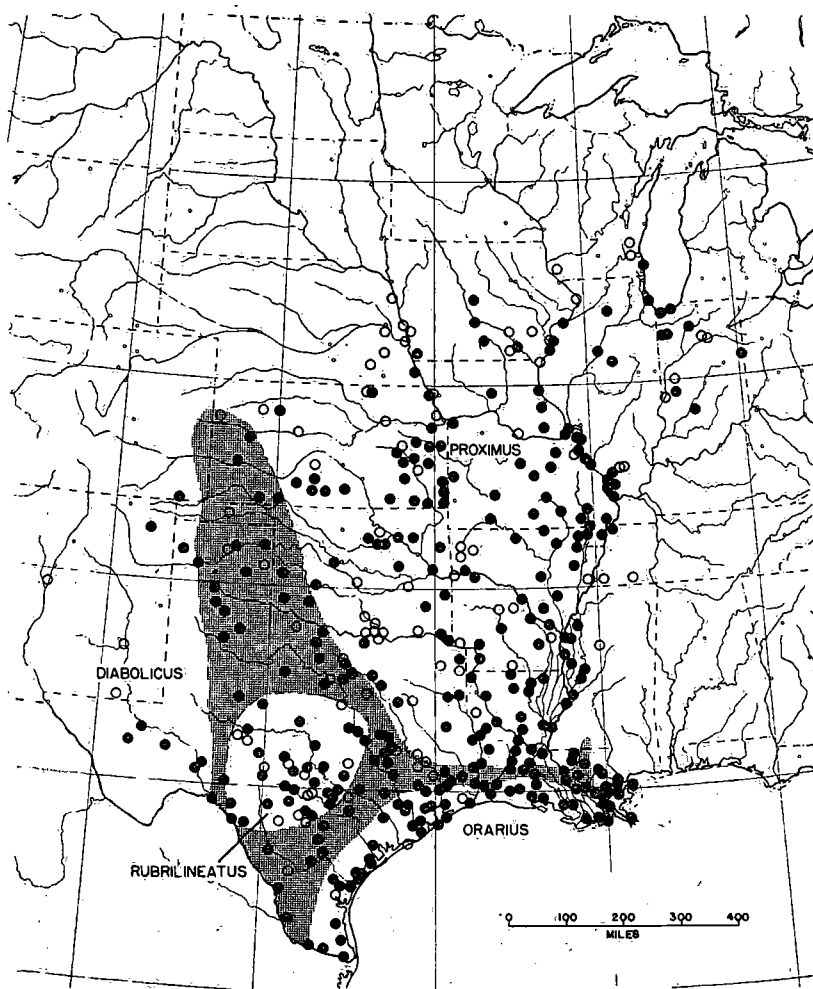


FIGURE 2. Distribution of *Thamnophis proximus* in the United States. Solid dots represent specimens examined; open circles are published records. Stippled areas represent the probable zones of intergradation between subspecies.

the Rio Grande Valley of western New Mexico). A western ribbon-snake (ANSP 6179) collected in the 1800's and labelled simply "Minnesota" requires authentication by further collecting. Another specimen (KU 21462), supposedly taken in Hamilton County, Ohio, is

probably incorrectly labelled. Wheeler (1947) recorded several specimens of *T. proximus* from north-central North Dakota; Thomas Uzzell examined these specimens (UMMZ 74337, 74339-342) at my request and reports they are actually *Thamnophis radix*. Apparently no valid record of *T. proximus* exists for the Great Plains north of Thurston County, Nebraska.

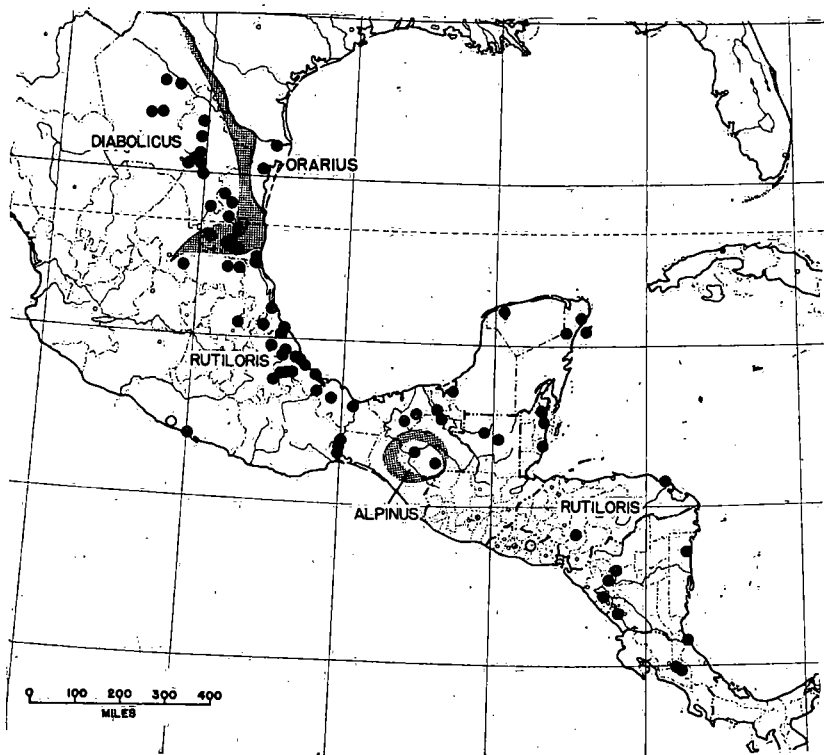


FIGURE 3. Distribution of *Thamnophis proximus* in Mexico and Central America. Solid dots represent specimens examined; open circles are published records. Stippled areas represent the probable zones of intergradation between subspecies.

#### VARIATION Sexual Dimorphism

Distinct sexual differences exist in number of ventrals, number of subcaudals, and relative tail length. The amount of dimorphism in each of these characters varies from one local population to the next with no apparent geographic correlation.

The difference in mean number of ventrals ranges from 0.3 of a scale in favor of the females in the sample from the Staked Plains of

western Texas (the only sample with at least five individuals of each sex in which females have more ventrals than males), to more than 5 in favor of the males. Those populations for which at least 15 adults of each sex are available are compared in table 3. This shows a marked

TABLE 3. Sexual dimorphism in ventrals of *Thamnophis proximus*

Population	Males		Differences		Females	
	N	M	DM	CD%	N	M
New Orleans area...	35	173.6 $\pm$ 0.50	3.2	1.86 $\pm$ 0.05	52	170.4 $\pm$ 0.39
East-central Texas...	18	168.9 $\pm$ 0.73	2.8	1.67 $\pm$ 0.09	18	166.1 $\pm$ 0.61
Edwards Plateau...	34	167.8 $\pm$ 0.46	3.9	2.35 $\pm$ 0.10	30	163.9 $\pm$ 0.74
Southern Texas...	46	166.6 $\pm$ 0.40	2.9	1.76 $\pm$ 0.04	49	163.7 $\pm$ 0.36
Chiapas Highlands...	15	161.7 $\pm$ 0.59	3.7	2.31 $\pm$ 0.08	22	158.0 $\pm$ 0.53

N = number of individuals; M = mean; DM = difference between means; CD% = coefficient of divergence expressed as a percent.

lack of geographic variation in degree of dimorphism as expressed by the coefficient of divergence, which is slight in members of the *Sauritus* group in comparison to most of the other forms for which comparable data exist (Klauber, 1943, table 3). *Thamnophis proximus* shows greater sexual dimorphism in number of ventrals than does *Thamnophis ordinoides*, less dimorphism than *T. radix* and *T. elegans*, and about the same amount as *Thamnophis brachystoma* and *T. sauritus* (table 4).

TABLE 4. Coefficients of sexual divergence in six species of *Thamnophis*

Species	Origin of Sample	Ventrals CD%	Subcaudals CD%
<i>T. brachystoma</i> <sup>1</sup>	Western Pennsylvania	2.00 $\pm$ ?	14.99 $\pm$ ?
<i>T. elegans</i> <sup>2</sup>	San Diego Co., Calif.	4.17 $\pm$ 0.20	10.94 $\pm$ 0.32
<i>T. ordinoides</i> <sup>2</sup>	Western Oregon	1.06 $\pm$ 0.35	12.48 $\pm$ 0.64
<i>T. proximus</i>	New Orleans area	1.86 $\pm$ 0.05	9.05 $\pm$ 0.24
	East-central Texas	1.67 $\pm$ 0.09	
	Edwards Plateau	2.35 $\pm$ 0.10	5.14 $\pm$ 0.18
	Southern Texas	1.76 $\pm$ 0.04	6.68 $\pm$ 0.26
	Chiapas Highlands	2.31 $\pm$ 0.08	
<i>T. radix</i> <sup>2</sup>	Cook Co., Ill.	4.01 $\pm$ 0.36	12.24 $\pm$ 0.71
<i>T. sauritus</i>	Southwestern Florida	3.33 $\pm$ 0.13	6.05 $\pm$ 0.39
	North-central Florida	2.31 $\pm$ 0.19	6.45 $\pm$ 0.39
	Southern Michigan	1.48 $\pm$ 0.09	5.02 $\pm$ 0.38

1. Data from Barton (1956).

2. Data from Klauber (1943).



Somewhat greater sexual differences exist in mean number of subcaudals. They range from 0.8 in favor of the females in the Galveston Bay, Texas, sample (the only one in which the males have fewer subcaudals than the females) to as much as 15.2 in favor of the males. Table 5 shows counts in those populations for which at least 15 adults

TABLE 5. Sexual dimorphism in subcaudals of *Thamnophis proximus*

Population	Males		Differences		Females	
	N	M	DM	CD%	N	M
New Orleans area . . . .	19	117.8 $\pm$ 1.04	10.2	9.05 $\pm$ 0.24	33	107.6 $\pm$ 0.91
Edwards Plateau . . . .	22	108.0 $\pm$ 0.82	5.9	5.14 $\pm$ 0.18	22	102.1 $\pm$ 0.87
Southern Texas . . . . .	16	108.3 $\pm$ 1.17	7.0	6.68 $\pm$ 0.26	18	101.3 $\pm$ 0.88

N = number of individuals; M = mean; DM = difference between means; CD% = coefficient of divergence expressed as a percent.

of each sex are available. The amount of sexual dimorphism in subcaudal numbers is not great either in this species or in *T. sauritus* compared to those of many other colubrid snakes (Klauber, 1943; Auffenberg, 1955; Duellman, 1958; Dowling, 1960; and others). The coefficients of sexual divergence are even less, in fact, than in other species of *Thamnophis* (table 4), which is in keeping with the hypothesis that sexual dimorphism in subcaudals tends to be greater in short-tailed than in long-tailed species (Klauber, 1943).

Females average longer than males but usually have a proportionally shorter tail. The largest female examined (USNM 761 from Cameron County, Texas) has a body length of 900 mm. plus a 332 mm. incomplete tail. The largest male (UF 12161.4 from St. Charles Parish, Louisiana) has a body length of 553 mm. and an incomplete tail. Wright and Wright (1957) reported animals with greater total lengths (1268 mm. female, 1119 mm. male), but gave no locality data. Adults of both sexes average well below these maxima.

The mean difference in adult tail length/total length ratios ranges from 0.004 in favor of the females (at Galveston Bay, Texas, the only area where the female ratio is higher than that for males) to 0.022 in favor of the males. Mean tail length/total length values for males range from 0.275 to 0.318, for females from 0.270 to 0.313. The muzzle length/frontal length ratio shows females apparently have slightly longer muzzles than do males.

Caudodorsal scale row reduction reflects sexual dimorphism, males having the more posterior reduction. This is almost surely a conse-

quence of the presence of the hemipenes and their retractor muscles in the proximal part of the tail. The reduction formulas for CAS 3091, an adult male from Comanche County, Oklahoma, and CAS 5099, an adult female from St. Charles County, Missouri, are presented below as examples. The formulas are slightly modified from the system proposed by Dowling (1951) in that the figures above the line represent the left side of the animal, those below the line the right.

$$\text{CAS 3091 } \begin{array}{c} \sigma^7 \\ 17 \frac{-2(2)}{-2(1)} \end{array} 15 \frac{-9(3)}{-2(1)} 14 \frac{2+3(4)}{-3(4)} 12 \frac{-3(7)}{-3(7)} 10 \frac{-4(17)}{-4(17)} 8 \frac{-3(36)}{-3(32)} \\ 6 \frac{-2(66)}{-2(64)} 4 \frac{-2(100)}{-2(102)} 2(113)$$

$$\text{CAS 5099 } \begin{array}{c} \text{♀} \\ 17 \frac{-1(1)}{-1(1)} \end{array} 15 \frac{-1(2)}{-1(2)} 13 \frac{-7(3)}{-2(4)} 12 \frac{-2(3)}{-2(4)} 10 \frac{-4(10)}{-4(10)} 8 \frac{-3(33)}{-3(33)} \\ 6 \frac{-2(66)}{-2(69)} 4 \frac{-2(96)}{-2(96)} 2(99)$$

### Ontogenetic Variation

Newly born *T. proximus* have proportionally shorter tails than adults (table 6), but differential growth must be rapid during the first year,

TABLE 6. Ontogenetic change of tail length/total length ratio in the *Sauritus* group

Species and Population	Males		Females		COD%	
	Juv.	Adult	Juv.	Adult	Male	Female
<i>T. proximus</i>						
New Orleans area . . . . .	.299	.317	.288	.302	5.84	4.75
<i>T. sauritus</i>						
Southern Florida . . . . .	.334	.347	.338	.340	3.82	0.59
Northwestern peninsular Florida . . . . .	.322	.343	.320	.340	6.32	6.06
Northern New Jersey . . . . .	.329	.353	.325	.341	7.04	4.80

COD% = coefficient of ontogenetic divergence expressed as a percent.

for subadults have essentially the same tail length/total length values as adults of the same population.

### Individual Variation

Characters that vary neither geographically, nor sexually, nor onto-

genetically are discussed below. Data on head scales refer to one side only. Individual variation in scutellation is summarized in table 7.

TABLE 7. Individual variation in scutellation of *Thamnophis proximus*

Pre-oculars	Post-oculars	Anterior temporals	Posterior temporals	Supra-labials	Infra-labials	Inter-genials
♂♂ 1 (653)*	2 (3)	1 (586)	1 (14)	6	8, 9	1 (22)
	2, 3 (8)	1, 2 (34)	1, 2 (9)	7 (12)	9 (14)	2 (543)
	3 (605)	2 (30)	2 (548)	7, 8 (35)	9, 10 (20)	3 (71)
	3, 4 (32)		2, 3 (55)	8 (600)	10 (579)	4 (2)
	4 (5)		3 (24)	8, 9 (8)	10, 11 (16)	5
					11 (14)	
♀♀ 1 (792)*	2 (8)	1 (671)	1 (10)	6	8 (2)	1 (29)
1, 2	2, 3 (5)	1, 2 (64)	1, 2 (15)	7 (15)	9 (11)	2 (590)
	3 (704)	2 (54)	2 (573)	7, 8 (20)	9, 10 (35)	3 (140)
	3, 4 (63)		2, 3 (127)	8 (746)	10 (693)	4 (11)
	4 (12)		3 (63)	8, 9 (13)	10, 11 (30)	5
	4, 5			9 (5)	11 (15)	6 (2)
					11, 12	8
♂♂	Dorsal scale rows					♀♀
17-18-17	17-19-17 (2)					
17-19-15	18-19-16					
17-19-17 (2)	19-19-17 (613)				18-19-17	19-19-17 (754)
18-19-17 (2)	19-19-18 (4)				19-17-17 (5)	19-19-18 (5)
19-17-16	19-19-19				19-18-17	19-21-17
19-17-17 (2)	19-21-17				19-19-15	19-21-19
19-18-17	20-19-17				19-19-16	20-19-17 (2)
19-19-15 (3)	21-19-17 (3)					21-19-17 (9)
19-19-16	21-19-19					21-21-17

\* Single numbers indicate that both sides of the head have the same count.

**OCULARS.** There is 1 preocular and usually 3 postoculars. The most frequent variation is the appearance of a 4th postocular on one or both sides. Only one individual of 1446 *T. proximus* has an extra preocular, and that on one side only. It is interesting to note the stability of this character in the *Sauritus* group in view of its extreme variability in other species of *Thamnophis* (Ruthven, 1908; Fitch, 1940).

**TEMPORALS.** One large anterior temporal and 2 slightly smaller posterior temporals is the usual condition, but this character shows greater individual variation than any other, most often an increase in number. Although the occurrence of 2 anterior temporals is common, only the lower is ever in contact with the postoculars. In addition to an increase in the number of scales, the anterior portion of the anterior temporal

is occasionally fragmented to form 1 or 2 small scales which are rarely much larger than the adjacent postocular scales. In the Chiapas Highlands 42 percent of the animals examined have this fragmentation of the anterior temporal on one or both sides of the head, a higher incidence of this variation than in any other area.

**SUPRALABIALS.** The usual number is 8, the 4th and 5th entering the orbit; 7 apparently occurs by loss of a preorbital supralabial, 9 by addition of a scale posterior to the orbit. Infrequently small scales may be wedged between two normal scales either at their upper or lower margins. Rarely an individual supralabial is partly divided by an incomplete suture.

Although marked geographic variation is not apparent, a number of populations in and east of the Mississippi Valley have a somewhat higher incidence of 7 supralabials than does the species as a whole.

**INFRALABIALS.** The usual number is 10, 9 and 11 being equally common as variations; 9 usually results from the elimination of the suture between the 3rd and 4th or the 8th and 9th infralabials, in that order of frequency; 11 usually results from a division of the 3rd infralabial. As in the supralabials, small anomalous scales are occasionally interposed between normal ones.

**INTERGENIALS.** Usually 2 small scales lie one behind the other between the genials, occasionally only 1 or as many as 8 are present. When several are present, some may be paired instead of in a linear series of single scales. In the Chiapas Highlands sample 50 percent of the individuals have more than two intergenials, an unusually high incidence. These animals also have a high frequency of anterior temporal fragmentation; over 76 percent of the series examined have one or both of these anomalies.

**ANAL PLATE.** In all but a few of the specimens examined the anal plate is undivided; it is completely divided in TCWC 865 (5 km. E Las Vigas, Veracruz) and CNHM 4441 (British Honduras), and partly divided in UIMNH 4499 (Crockett County, Texas). The anal plate is creased but not actually divided in CNHM 4228 (British Honduras).

**VENTRALS.** Anomalous divisions or partial duplications of ventral scutes, largely caused by partial duplication of vertebrae, occur in many groups of snakes (King, 1959), and the ribbonsnakes are no exception. All the types Peters (1960) illustrated in his study of the colubrid subfamily Dipsadinae occur in both *T. proximus* and *T. sauritus*, the commonest being that with one or more anomalous partial scutes

inserted between the terminal ventral and the anal plate, which occurs in 9.5 percent of the *T. proximus* examined. An additional 4.3 percent, including a few of the same animals, have partial scutes elsewhere on the venter. Barton (1956) reported that 19.5 percent of the specimens of *T. brachystoma* he examined showed ventral or subcaudal anomalies.

**SUBCAUDALS.** Of the individuals examined, 2.3 percent have one or more sets of fused subcaudals (with no longitudinal suture separating the adjacent members of a pair).

**DORSAL SCALE ROWS.** Only 4 percent of the snakes examined differ from the typical formula of 19-19-17. A large majority of the individuals having more than 19 rows at any point on the body are from the delta region of the Mississippi River, but these make up only a small part of that population. Of the specimens examined from Orizaba, Veraacruz, 31 percent have reductions in the dorsal scale row formula (i.e., 17-18-17, 18-19-16).

The normal posterior reduction in the number of dorsal scale rows is, in all but 4 of the 18 specimens checked for this character, the result of loss of row 4 on both sides of the body. In the four exceptions row 5 is lost on one or both sides.

Among males the reduction takes place opposite ventrals 83 through 105, mean 93.8, among females from ventral 78 through 107, mean 90.0. There appears to be a positive correlation between the total number of ventrals and the point of reduction, the greater the number the more posterior the reduction. Consequently the point of reduction varies geographically to some degree and also sexually, as males almost invariably have more ventrals than do females.

**PATTERN AND COLORATION.** Size of the parietal spots varies individually; some individuals have streaks of light pigment extending anteriorly from the parietal spots along the frontal-parietal suture and occasionally onto the frontal itself. Size and even presence of the light postocular spot and of the black postorbital vitta vary individually as well as geographically. Individual variation is also manifest in the relative darkness of the dorsal ground color and in the presence or absence of a row of spots above the lateral stripe or of a black margin along the vertebral stripe.

#### Geographic Variation

In an animal whose range extends about 3000 miles from southern Wisconsin to central Costa Rica, considerable geographic variation is not surprising. Because of the lack of concordance among most of



stitutes a subspecies. Meristic and proportional values discussed below are based on population samples large enough to represent fairly the population from which they were collected.

**VENTRALS.** The mean ventral counts are remarkably constant east of the Mississippi River from western Indiana to north of Lake Ponchartrain in Louisiana (fig. 4). The means for males fall between 170.4 and 171.8, for females between 166.9 and 169.0. South of Lake Ponchartrain in and adjacent to the Mississippi delta region the number of ventrals increases slightly, the means ranging from 171.9 to 174.1 in males, and from 168.9 to 171.4 in females. The highest means in both sexes occur near the mouth of the Mississippi River.

West and southwest, from the Mississippi Valley to the Rio Grande Valley, the mean number of ventrals decreases gradually and relatively uniformly, although with some interpopulational variation. A population in western Louisiana (fig. 4, B), however, shows more than the expected divergence in that the sample mean in females (only one male is available) is from 7 to 9 scales less than in females from populations less than 25 miles distant. It is perhaps of significance that all the localities for specimens of this population are relict prairie areas.

Southward from the Rio Grande Valley the mean ventral counts decrease only slightly in the Sierra Madre Oriental, but drop sharply in the coastal plain of Tamaulipas (fig. 5). Females from the lower Rio Grande Valley show a mean difference of almost 10 ventrals (males about 8) from those from southern Tamaulipas, little more than 200 miles distant. Essentially no change is manifest in the mean for females and only a slight decrease in that for males over the 200-mile stretch from southern Tamaulipas to central Veracruz, but within the next 50 to 75 miles southward along the coast to the vicinity of Ciudad Veracruz, the means for both sexes decrease by almost 4 scales.

The number of ventrals is lowest in the Tabasco-Campeche lowlands where the mean for males is 146.6, for females 144.9. This represents a decrease of almost 6½ scales in males and 4½ in females over the 300-mile distance from south-central Veracruz. Counts in a small series from isthmian Oaxaca indicate that ventral numbers in this region probably average somewhat higher than those in adjacent areas. From the Tabasco-Campeche region to the northern tip of the Yucatan Peninsula there is a slight increase in the mean number of ventrals, which then remains essentially constant along the 1000 miles of Caribbean coastland from Cozumel Island to Boca del Rio Colorado, Costa Rica.

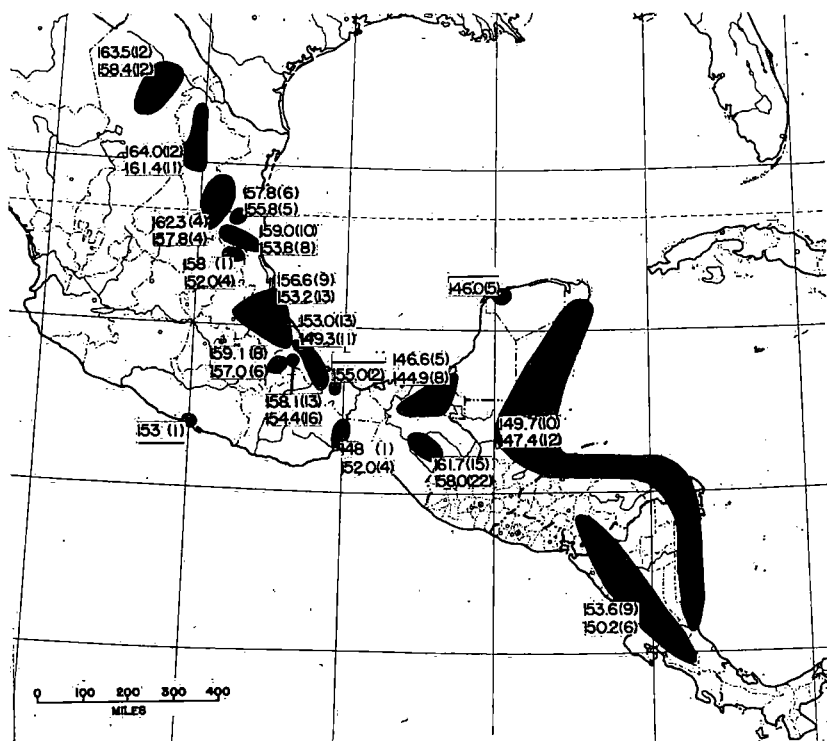


FIGURE 5. Geographic variation of ventral number in *Thamnophis proximus* in Mexico and Central America. Black blotches represent the areas from which samples were taken. The upper numbers associated with each blotch are the sample mean and sample size (in parentheses) for males; the lower numbers present the same data for females. When a line appears in place of either the upper or lower numbers, it signifies that no specimens of that sex were present in the sample.

The western ribbonsnake is not limited to the coastal plain in tropical America, but also occurs in the Sierra Madre Oriental at altitudes up to 8000 feet, in the Chiapas Highlands up to 7500 feet, and on the Pacific side of the Central American uplands up to 5000 feet. Most of these high-altitude populations have mean ventral numbers markedly different from those in the geographically adjacent lowlands. Rather than decreasing, as one might predict on the basis of temperature-scutellation studies on *T. elegans* (Fox, 1948; Fox, Gordon, and Fox, 1961), the number of ventrals increases. Furthermore, in certain areas the amount of increase seems roughly correlated with the amount of increase in altitude. Three populations in south-central Veracruz, only 85 airline miles apart, range in altitude



from sea level to 5500 feet. Near sea level in the vicinity of Ciudad Veracruz, males have 153.0 mean ventrals, females have 149.3. Near Cordoba (2000-3000 feet) the means are 5 scales greater in both sexes. In the sample from the Orizaba area (4000-5500 feet) the mean for males is only 1 scale more than at Cordoba; in females it is about  $2\frac{1}{2}$  scales more.

The population in the Chiapas Highlands has a greater mean ventral number (almost 8 higher in both sexes in the series examined) than the Central American upland population. As the two are widely separated geographically, factors other than altitude may be involved. On the other hand, the means for samples from the Central American upland population are 3 to 4 scales greater than means for the Caribbean lowland animals, and means for the Chiapas Highlands series are 13 to 15 scales more than for the Tabasco-Campeche lowlands population, 100 miles to the north and some 7000 feet lower in elevation. This relationship between high ventral count and high altitude does not appear to hold true north of the Orizaba-Cordoba area. A small series from the vicinity of Jalapa, Veracruz (3500-4500 feet), a juvenile female (CNHM 103445) from 6 miles S Zacualtipan, Hidalgo, and a subadult male (UIMNH 18919) from near Tezuítlan, Puebla (approximately 6500 feet), agree well with coastal specimens at the same latitudes. An adult male (TCWC 865) collected about 10 miles NW Jalapa at an altitude of 8000 feet further complicates the situation by having a much higher number of ventrals (166) than does any of the animals taken at lower altitudes.

Some other populations, unfortunately represented by only a few specimens, do not fit well into the variational pattern described above. Four females from eastern San Luis Potosí agree in mean number of ventrals with the south-central Veracruz females rather than with those in the intervening area. Two females (UMMZ 41555-556) from Cuatotolapam in southern Veracruz have a mean almost 6 scales higher than that of the population less than 50 miles to the northwest, and 10 scales greater than in the Tabasco-Campeche population barely 200 miles to the east.

**SUBCAUDALS.** Although the general pattern of reduction in subcaudal numbers is similar to that of the ventrals, many of the details are strikingly dissimilar. Whereas in ventrals the populations throughout the Mississippi Valley have essentially the same mean, and reduction in number occurs southwestward, in subcaudals the highest means are centered in southeastern Louisiana (both to the north and south of Lake Ponchartrain), and the number of subcaudals decreases fairly uniformly and rapidly northward east of the Mississippi River, north-

westward into the Great Plains, westward through central Texas, and along the Gulf Coast into Mexico (see figs. 6 and 7). The mean number of subcaudals in western Indiana is about 12 to 14 scales less than in southeastern Louisiana; means in central Kansas are 10 to 12 less; and the series representing the Edwards Plateau population has 8

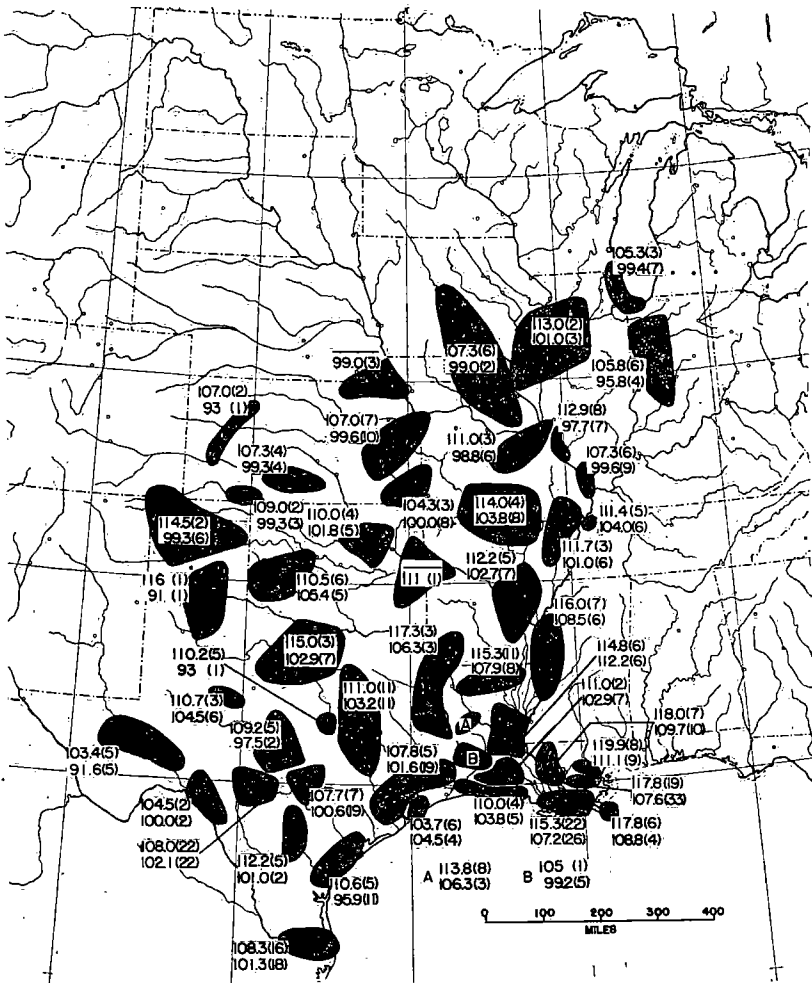


FIGURE 6. Geographic variation of subcaudal number in *Thamnophis proximus* in the United States. Black blotches represent the areas from which samples were taken. The upper numbers associated with each blotch are the sample mean and sample size (in parentheses) for males; the lower numbers present the same data for females. When a line appears in place of either the upper or lower numbers, it signifies that no specimens of that sex were present in the sample.

to 9 fewer mean subcaudals in females (10 to 12 in males), as does the sample from southern Texas.

West of the Pecos River the number of subcaudals decreases sharply, the mean for females being 10 scales less than on the Edwards Plateau less than 200 miles to the east. The Coahuilan desert ribbonsnakes

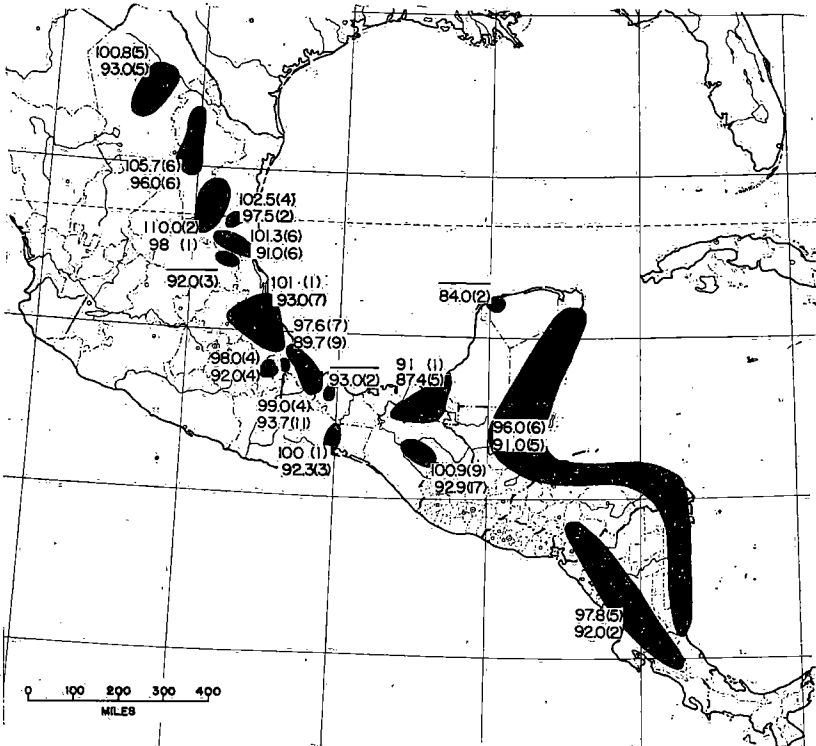


FIGURE 7. Geographic variation of subcaudal number in *Thamnophis proximus* in Mexico and Central America. Black blotches represent the areas from which samples were taken. The upper numbers associated with each blotch are the sample mean and sample size (in parentheses) for males; the lower numbers present the same data for females. When a line appears in place of either the upper or lower numbers, it signifies that no specimens of that sex were present in the sample.

are similar to the trans-Pecos population in subcaudal number, moreso in fact than to the geographically nearer Nuevo Leon population. Along the Gulf Coast of Texas, two populations show a rather anomalous variance from the pattern described above. The sample mean for Galveston Bay area females fits rather well into the previously mentioned sequence of reduction along the coast, but the mean for

males is almost 7 scales less than for the populations on either side of the Galveston Bay area; it is even less than the mean for females from the same population. Only 150 miles farther down the coast the situation is completely reversed; the males have the expected complement of subcaudals while the mean for females is from 5½ to 8½ scales less than in adjacent populations.

In south-central Tamaulipas the number of subcaudals drops sharply, the means decreasing by 8 or 9 scales within less than 100 miles. From thence southward and eastward to the Tabasco-Campeche area the decline in subcaudal number again appears to be fairly uniform and gradual (the drop in the mean for males may be fairly steep between south-central Veracruz and Tabasco-Campeche, but only one specimen with a complete tail is available from the latter population). The lowest mean subcaudal number in *T. proximus* apparently occurs in northern Yucatan. It increases markedly in the Caribbean lowlands, but more comparative material is needed from the Gulf side of the Yucatan Peninsula to determine the degree of increase.

Subcaudal number apparently is less well correlated with altitude than is the number of ventrals. The means of males from sea level show virtually no difference from those at an altitude of 5000 feet in south-central Veracruz, and those of the high-altitude females increase only by 2 to 4 scales. Females from the Caribbean lowlands, Central American uplands, and the Chiapas Highlands show no major differences although the high-altitude populations do have slightly higher means. The males from these populations may demonstrate altitudinal variation more clearly, although the Chiapas snakes are separated from the other two groups latitudinally as well as altitudinally. The fact that the isthmian Oaxaca series (all from less than 700 feet altitude) has means almost identical to those of the high-altitude Chiapas snakes emphasizes the need for caution in interpretation.

**PROPORTIONS.** Though many populations are represented by only a few specimens of either sex with complete tails, relative tail length (as expressed by the tail length/total length ratio) appears to be, with a few notable exceptions, fairly uniform over most of the range of *T. proximus*.

The snakes with the proportionally longest tails occur in the lower Mississippi Valley, where the means for males range from 0.312 to 0.318 and for females from 0.301 to 0.313 (except for those females from southwest of New Orleans and in the Atchafalaya delta region which have 0.296). Here the correlation between relative tail length and the number of subcaudals, weak or nonexistent in many parts of the range, is strong. East of the Mississippi River the means vary within

these extremes as far north as the Ohio River. Populations west of the Mississippi River having comparable means extend from the lower Mississippi Valley northward and westward through Arkansas and southern Missouri to the limits of the Ozark Plateau (the means for females, however, decrease in the Ozark region).

Beyond this circumscribed area the snakes have somewhat shorter tails, all but one of the means for males falling between 0.290 and 0.308 (the majority between 0.296 and 0.303). The one notable exception is the Chiapas Highlands population in which the nine males examined have a mean of 0.275. The lowest mean tail length/total length value for females, 0.270, also occurs in this population. Females from outside of the "long-tailed" region have means ranging from 0.279 to 0.298 (in most cases from 0.289 to 0.297), but in addition to the Chiapas females already mentioned, those from trans-Pecos Texas (also 0.270) have shorter tails than the adjacent populations.

Relative muzzle length as expressed by the muzzle length/frontal length ratio is apparently subject only to interpopulation variation throughout most of the range of *T. proximus*. The Chiapas Highlands population, however, in this as in so many other features, is different from all other populations, particularly those adjacent to it. Chiapas males have a mean of 0.681, females 0.694. Means for other populations with four or more adults of each sex range from 0.708 to 0.849 (mean 0.744) in males, from 0.711 to 0.838 (mean 0.759) in females.

**PATTERN.** The fused parietal spots attain their largest relative size in northern Mexico and adjacent Texas; in some individuals these occupy half the length of the interparietal suture, as in AMNH 67336 from Nuevo Leon. Snakes in this region also exhibit a high incidence of light areas or streaks extending forward from the parietal spots and forking out for varying distances along the frontal-parietal suture. In the Chiapas Highlands the parietal spots are incompletely fused and their anterior edges diverge at about a 30-degree angle from the interparietal suture, giving the entire arrangement the appearance of a thick chevron. This condition, which sporadically occurs in individuals elsewhere in the range of *T. proximus*, is present in 70 percent of the Chiapas specimens.

In most populations the light postocular spot occupies all of the lower and varying amounts of the middle postocular. In the southern part of the range from trans-Pecos Texas to Coahuila and Nuevo Leon, and in the coastal plain from the Tropic of Cancer to Central America, the postocular spot is frequently absent and when present is usually not brightly colored. The spot is also absent in an occasional individual from more northern populations.

The broad black postorbital vitta typical of *T. sauritus* is usually lacking in tropical American specimens of *T. proximus*. When present the stripe is usually narrow and does not extend onto the postocular scales. Throughout the rest of the range the presence and extent of the vitta vary individually.

In the lowlands of Mexico and Central America and along the coast to the lower Mississippi Valley, the vertebral stripe is usually broad and covers the entire vertebral and more than half, often all, of both paravertebral scale rows. INHS 9469 from near Ciudad Mante, Tamaulipas, has the vertebral stripe covering the entire vertebral-paravertebral series and a small portion of row 8 as well. Outside this region the stripe rarely includes more than half the width of each paravertebral row, and it is often somewhat narrower, particularly in the extreme northern part of the range.

Mexican and Central American specimens are also characterized by a narrow lateral stripe, which occupies less than half of 1 of the 2 scale rows bearing it and varying amounts of the other row, usually slightly more than half. The stripe becomes even narrower beyond the point of dorsal scale row reduction, where it is largely confined to the 3rd row and a small portion of row 4. The Chiapas Highlands population characteristically has the stripe involving only the 3rd row posteriorly. Only about half the snakes in the Nuevo Leon series have this reduction of the lateral stripe. North of the Rio Grande the lateral stripe almost invariably occupies more than half of both rows 3 and 4 and does not become noticeably reduced posterior to the loss of row 4.

The dark ventrolateral stripe, which is found in all specimens of *T. sauritus*, and is the most reliable single character for distinguishing between the two species in the areas of sympatry (Rossman, 1962), is well developed in certain populations of *T. proximus*. It is broadest in the Chiapas Highlands where the width of each stripe is 0.14 to 0.25 (usually 0.17 to 0.20) the width of a ventral scale. The stripe is slightly narrower in the Central American uplands, still narrower in the lowlands of Central America and Mexico, and usually disappears altogether north and east of central Texas.

**COLORATION.** Cope (1885) described a ribbonsnake from Cozumel Island, Quintana Roo, Mexico, as having reddish-orange labials. While I have not seen one of that particular color, the labials of living specimens from British Honduras, Chiapas, Veracruz, and eastern San Luis Potosí are yellow-orange instead of greenish white or greenish yellow as in individuals from Coahuila, Nuevo Leon, and the United States.

Because of the dearth of color descriptions in the literature or on

museum specimen labels, and of live captive snakes for study from the entire range of the species, the geographic variation in the colors of the dorsum and of the vertebral and lateral stripes can be discussed only generally and approximately. A more precise delineation of the geographical extent of each color variation awaits analysis from more adequate material.

Specimens from Coahuila, Nuevo Leon, and apparently trans-Pecos Texas (which were not seen in life) have an olive-gray dorsum. Throughout the rest of Mexico and Central America the dorsum is olive-brown. Chiapas Highlands examples are an exception; their dorsa are dark brown. The olive-brown of Central American snakes and several other shades of brown occur in southern and central Texas, along the Gulf coast of Texas and Louisiana, and apparently northward through the Texas panhandle to southeastern Colorado. The black-backed form ranges from central Kansas, central Oklahoma, and eastern Texas northward and eastward throughout the rest of the range.

The orange vertebral stripe has the most extensive geographical range, replaced by other colors only in tropical America, on the Edwards Plateau, and in coastal Texas and Louisiana. Ribbonsnakes on and about the Edwards Plateau have a bright red vertebral stripe. Where brown-backed populations occur along the Gulf Coast of Louisiana and Texas, the stripe is usually gold or greenish gold, but may have an orange cast. The stripe is also gold in the Chiapas Highlands. A fresh specimen (UF 12213) from near Acapulco, Guerrero, has a stripe that appears pale yellow, but may have been gold in life. Snakes from Central America and the southern and central Gulf Coast and adjoining uplands of Mexico have a grayish-tan vertebral stripe, sometimes with a metallic luster.

Throughout most of the range of *T. proximus*, the lateral stripe is usually some shade of light yellow, generally paler in lowland Mexico and Central America. Two specimens from Brazos County, Texas (UF 12193), are unique in having a lateral stripe that in life was bluish green on the neck and greenish white posteriorly. Whether this condition is characteristic of the entire population or merely an individual variant is not known. One of these two specimens also had a gold vertebral stripe; the other had the orange stripe typical of this area.

DISCUSSION. Obviously much of the geographic variation observed in *T. proximus* is of the discordant type. Almost all the characters I have discussed vary independently of each other; some are constant throughout a geographical range in which one or several other char-

acters undergo radical change. This discordant variation is to be expected, however, unless all these characters are genetically linked. If this were so, certain combinations could be selected as a single unit. Otherwise, as apparently in this case, each character must be subject to independent selection by the environment (Tilden, 1961).

In two areas marked changes do take place simultaneously in several characters—the Chiapas Highlands and southern Tamaulipas. In the Chiapas Highlands almost every character that varies geographically (except subcaudal number and labial color) differs from that in the adjoining populations. The high-altitude Chiapas population probably has been at least semi-isolated from the lowland populations for a long time. This isolation, whether partial or complete, coupled with adaptations to the rigors of life at high altitudes and perhaps furthered by genetic drift, has allowed these snakes to differ in many respects from adjoining populations. It is not understood why the high-altitude populations in the Sierra Madre Oriental do not differ from adjacent lowland populations to the same marked degree. The abrupt transition of characters in southern Tamaulipas coincides with the transition between the Neotropical and Nearctic faunal regions, long-recognized as a major faunal boundary (Darlington, 1957). Ventral number, subcaudal number, labial color, vertebral stripe color, and lateral stripe color and width all change markedly at this point.

In southern Louisiana lies a third and somewhat less important zone of concordance. Here dorsum color, and vertebral stripe width and color, change over a relatively narrow zone between the coast and the interior.

In studying geographic variation in these snakes, one is struck by the fact that the counts of ventrals and subcaudals are much more apt to fluctuate locally than are the elements of color pattern. The reason for this is not clear, but the relative instability of the meristic characters suggests they may be subject to less selective pressure than is color pattern.

#### TAXONOMY

Many arguments for and against the trinomen have been presented in recent years, most notably in the journal *Systematic Zoology*. In recognizing subspecies in this study I am not arguing for the "reality" of these or of any other geographic races as evolutionary units. With most geographic variation being of the discordant type, apparently it is the individual characters (or small groups thereof) that are undergoing evolutionary selection. The systematist is thus forced to select one or more characters to define each geographic population he recog-



nizes taxonomically. The subspecies is thus an arbitrary entity albeit, I believe, a useful one. It is a convenient tool which allows us to locate geographically and to denote the nature of distinctive intraspecific populations with a single word. This, to me, seems ample justification for its existence and continued usage.

The population samples discussed above group themselves into 6 fairly well defined major populations which occupy discrete geographic areas and appear to deserve taxonomic recognition. While some of these populations can be distinguished by differences in scale counts as well as in color pattern, I have placed more emphasis on color because it is usually less variable over wide geographic areas, a common phenomenon in the genus *Thamnophis* (Fitch, 1941, and others). Fox, Gordon, and Fox (1961) have shown that color patterns in individual *T. elegans* subjected to low temperatures during embryonic development do not differ from those of animals that developed at normal temperatures, while ventral and subcaudal numbers differ strikingly between the two groups.

Recent systematic work on the gartersnakes generally fits into one of two categories: recognition of intraspecific populations primarily on variations in color pattern, or mainly on differences in the number of ventral and subcaudal scales. This dichotomy of viewpoints is equally manifest in the work on most other snake genera that have received much taxonomic attention. A recent paper on *T. sirtalis parietalis* and its allies (Fitch and Maslin, 1961), which dismissed the number of ventrals and subcaudals with two brief sentences on their general clinal trends, and an earlier paper on *Thamnophis marcianus* (Mittleman, 1949), which recognized two subspecies solely on meristic differences, represent extremes of the two approaches. As variations in color pattern and in meristic characters are often discordant, the geographic races recognized by the two schools of interpretation are seldom equivalent. If the two schools were to study the same material, their respective delineation of range limits of the included subspecies would certainly differ even if both recognized the same number of races—which is unlikely.

The chaos inherent in such a situation provides opponents of the subspecies concept with an excellent argument for discontinuing the trinomial system of nomenclature. Neither interpretative approach can be said to be the only correct one, inasmuch as the characters emphasized in each case are merely different expressions of the same genetic system. However, if the subspecies is to play a meaningful role in ophidian systematics, a uniform basis for interpretation must be established. A compromise of sorts might be achieved by applying

subspecific names only to those populations that display concordance in both color pattern and meristic characters, but this apparently occurs so infrequently that many distinctive populations would go unrecognized. Consequently I suggest that geographic races in the gartersnakes be based on color pattern when variation is discordant. Application of this suggestion to other genera should await a careful evaluation of each individual genus. Meristic characters such as ventrals and subcaudals must not be ignored, however, but should be thoroughly and completely investigated, analyzed, and reported.

### Subspecies of *Thamnophis proximus*

The following key for distinguishing the subspecies of *T. proximus* is designed for use with living or freshly killed specimens. As preservatives alter certain colors quickly and drastically, emphasis should be placed on "geographic probability" when only preserved material is available.

1. Dorsum black; vertebral stripe orange and usually narrow; dark ventrolateral stripes lacking ..... *T. p. proximus*  
     Dorsum olive-gray or some shade of brown ..... 2
2. Dorsum dark brown; vertebral stripe gold, of medium width; dark ventrolateral stripe broad, usually 0.17 to 0.20 of a ventral scale wide; tail relatively short (mean tail length/total length in males 0.275, females 0.270); parietal spots usually chevron-shaped ..... *T. p. alpinus*  
     Dorsum olive-gray or brown (not dark); dark ventrolateral stripe relatively narrow or absent; tail relatively long (mean tail length/total length usually exceeding 0.290 in males, 0.280 in females); parietal spots rarely chevron-shaped ..... 3
3. Vertebral stripe bright red, of medium width; ventrolateral stripe narrow or lacking ..... *T. p. rubilineatus*  
     Vertebral stripe orange, grayish tan, or some shade of gold ..... 4
4. Vertebral stripe grayish tan, broad; labials yellow-orange; lateral stripe narrow anteriorly, further reduced posteriorly; mean number of ventrals not exceeding 160 in males or 157 in females ..... *T. p. rutiloris*  
     Vertebral stripe orange or some shade of gold; greenish-white or greenish-yellow labials; lateral stripe not narrow, at least anteriorly; mean number of ventrals exceeding 162 in males and 158 in females ..... 5
5. Vertebral stripe orange, of medium width; dorsum usually olive-gray; lateral stripe frequently reduced posteriorly; narrow ventrolateral stripe frequently present ..... *T. p. diabolicus*  
     Vertebral stripe usually some shade of gold, broad; dorsum usually olive-brown; lateral stripe rarely reduced; ventrolateral stripe usually absent ..... *T. p. orarius*

As geographic variation has already been discussed in detail, only those features pertinent to a formal description of the subspecies are presented below.

*Thamnophis proximus proximus* (Say), new combination

*Tropidonotus saurita* var. *Faireyi*: Duméril, Bibron, & Duméril, 1854:585 [by implication]

*Tropidonotus saurita* var. *proxima*: Jan, 1863:70

*Eutainia saurita* var. *faireyi*: H. Garman, 1892:264

*Eutainia saurita* var. *proxima*: H. Garman, 1892:264

*Thamnophis saurita* var. *proxima*: Duméril & Bocourt, 1893:757

*Thamnophis saurita* var. *faireyi*: Duméril & Bocourt, 1893:758

*Thamnophis sauritus proximus*: Ruthven, 1908:98

*Thamnophis proxima faireyi*: Hurter, 1911:159

*Thamnophis sirtalis proximus*: Klauber, 1948:9

**HOLOTYPE.** The information presented for the species applies here. Although the holotype is thought to be lost, a neotype has not been designated because the original description (Say, 1823) and the type locality are adequate to associate the name with a specific population.

**DEFINITION.** A subspecies of *Thamnophis proximus* characterized by a black dorsum, a narrow orange vertebral stripe, and lack of a dark ventrolateral stripe.

**RANGE.** From Indiana and southern Wisconsin south in the Mississippi Valley to, but not including, southern Louisiana, west through southern Iowa and extreme eastern Nebraska to central Kansas, central Oklahoma, and eastern Texas (exclusive of the coastal region).

**DESCRIPTION.** In the absence of the holotype, the following description is based on UF 12160.1, an adult male collected 6.5 miles S Saffordville, Chase County, Kansas, by William E. Duellman.

Scutellation: Oculars 1 + 3, temporals 1 + 2, supralabials 8, infralabials 10, intergenials 2, dorsal scale rows 19-19-17, ventrals 167, subcaudals 108. Body length is 392 mm., tail length 166, tail length/total length ratio 0.297.

The dorsum is black over most of the body, becoming dark brown posteriorly, and dark brown below the lateral stripe. The vertebral stripe is pale orange (Maerz & Paul 11L7), the lateral stripe light yellow. The venter is yellowish green with a pale orange tinge along the lateral margin of each scute, the dark ventrolateral stripe lacking entirely. The pale yellow postocular spot occupies all of the lower and the anterior half of the middle postocular; the fused parietal spots are moderately prominent and bright.

DISCUSSION: Counts and measurements of this subspecies may be summarized as: postoculars 2 to 4, temporals 1 + 1 to 2 + 3, supralabials 7 to 9, infralabials 8 to 11, intergenials 1 to 6, dorsal scale rows 17-19-15 to 21-19-17, male ventrals 151-178, female ventrals 154-176, male subcaudals 99-131, female subcaudals 90-120. Body length in males 122 to 522.5 mm., in females 128.5 to 680 mm. Total length in males 174 to 755 mm., in females 177.5 to 956 mm. Adult tail length/total length ratio in males 0.284 to 0.333, in females 0.267 to 0.336.

An adult female (KU 21462) supposedly collected in Hamilton County, Ohio, by R. Goodpaster was sent to the University of Kansas Museum of Natural History in a lot that included specimens from Reelfoot Lake, Tennessee, as well as from Hamilton County, Ohio (W. E. Duellman, personal communication). This snake agrees well in all respects with a series of females from the vicinity of Reelfoot Lake and, as no other western ribbonsnake has been taken within 80 miles of Hamilton County, I think this specimen was actually collected at Reelfoot Lake.

I have seen no intergrades between *T. p. proximus* and either *T. p. rubrilineatus* or *T. p. diabolicus* in life, but the few preserved specimens from regions where the ranges of the subspecies meet suggest that the black-backed *T. p. proximus* apparently intergrades with one brown race (*diabolicus*) over a broad zone in southwestern Kansas, western Oklahoma, and the eastern part of the Texas panhandle, with still another brown form (*rubrilineatus* × *diabolicus* intergrades) in north-central Texas, and finally with *T. p. rubrilineatus* in east-central Texas. Intergradation between *T. p. proximus* and *T. p. orarius* is discussed under the latter form.

The black dorsum of the nominate race and the narrowness of its light vertebral stripe may have adaptative value in increasing the absorption of solar radiation in the cooler, northern part of the species' range. The presence of the black-dorsum subspecies in the south-central United States where this adaptation would seem of little importance today may indicate that this race originally evolved in the South when the climate was much cooler, and has since extended its range northward.

#### *Thamnophis proximus orarius*, new subspecies

HOLOTYPE. TU 11764, an adult female from Waggaman, Jefferson Parish, Louisiana, collected 28 February 1950 by Horace Whitten.

DEFINITION. A subspecies of *Thamnophis proximus* characterized by an olive-brown dorsum, a broad gold vertebral stripe, and lack of a dark ventrolateral stripe.

RANGE. From Cat Island in Mississippi Sound, and southwestern Hancock County, Mississippi, through southern St. Tammany Parish, Louisiana, south and west along the Gulf Coast, probably as far as northern Tamaulipas.

DESCRIPTION OF HOLOTYPE. Scutellation: Oculars 1 + 3, temporals 1 + 2, supralabials 8, infralabials 10, intergenials 2, dorsal scale rows 19-19-17, ventrals 169, subcaudals 106. Body length is 463 mm., tail length 200 mm., tail length/total length ratio 0.302.

The following color description is based on UF 12165, an adult female collected 3 miles E Boutte, St. Charles Parish (approximately 7.5 miles W Waggaman), by H. A. Dundee. Dorsum olive-brown (Maerz & Paul 15H9), grayish brown below the lateral stripe (15E4); vertebral stripe gold (13K4), broad; lateral stripe yellow (10E1); venter pale green medially (18D3), lateral margins orange (11H6); dark ventrolateral stripe lacking entirely; chin shields white; supralabials pale yellowish green, anterior three tan. The pale yellow postocular spot occupies all of the lower and middle postoculars and the leading edge of the upper one; the fused parietal spots are moderately prominent and bright.

DISCUSSION. Counts and measurements of this subspecies may be summarized as: postoculars 2 to 4, temporals 1 + 1 to 2 + 3, supralabials 7 to 8, infralabials 8 to 11, intergenials 1 to 4, dorsal scale rows 17-19-17 to 21-21-17, male ventrals 161-181, female ventrals 158-177, male subcaudals 97-127, female subcaudals 87-124. Body length in males 139 to 553 mm., in females 170 to 900 mm. Total length in males 243 to 762 mm., in females 241.5 to 1232 + mm. Adult tail length/total length ratio in males 0.280 to 0.328, in females 0.273 to 0.329.

I have seen living *T. p. proximus* × *orarius* intergrades from Harris County and extreme southern Liberty County in Texas, and from St. James and northern St. Charles Parishes in Louisiana. All have vertebral stripes more or less typical of *orarius*. The St. Charles Parish specimens (UF 12161 from 1 mile N St. Rose) range from fairly typical brown-dorsum *orarius* to almost black. The keels of the dorsal scales are brown, but varying amounts of the remaining area of each scale are black. Specimens from Refugio, San Patricio, and Victoria Counties, Texas, also have varying amounts of black pigment on essentially brown scales. Most of the St. James Parish individuals are entirely black.

The situation in Harris County is not clear. Two adults (UF 12203) from Channelview at the head of Galveston Bay have entirely black dorsal and gold vertebral stripes, but a subadult from the same locality

appears typical of *T. p. orarius*, and I have seen five typical *orarius* from 9 miles W Tomball in northwestern Harris County, almost 40 miles inland from Channelview. Typical *T. p. proximus* have been found less than 70 miles northeastward in Liberty County.

Recognition of intergrades is complicated by the occasional appearance of vertebral stripes with a definite orange tinge as an individual variation in populations of *T. p. orarius* well removed from any possible contact either with *T. p. proximus* or with intergrades.

I have seen no live intergrades with other subspecies but I suspect that all of inland southern Texas is an area of intergradation between *T. p. orarius*, *T. p. rubrilineatus*, and *T. p. diabolicus*. Specimens from south-central Tamaulipas appear to be intergrades between *orarius* and *rutiloris*, *diabolicus* and *rutiloris*, or all three subspecies.

The subspecific name *orarius* (Latin, of the coast) refers to the fact that this race lives along the coast.

*Thamnophis proximus rubrilineatus*, new subspecies

HOLOTYPE. UF 12188.3, an adult male from the State Fish Hatchery, 8.2 miles NW Ingram, Kerr County, Texas, collected 26 June 1960 by M. J. Fouquette, Jr., and D. A. Rossman.

DEFINITION. A subspecies of *Thamnophis proximus* characterized by an olive-brown to olive-gray dorsum, a bright red vertebral stripe, and a narrow dark ventrolateral stripe or none at all.

RANGE. Throughout the Edwards Plateau region of central Texas and northward an undetermined distance, probably not far beyond San Angelo or Waco.

DESCRIPTION OF HOLOTYPE. Scutellation: Oculars 1 + 3, temporals 1 + 2, supralabials 8, infralabials 10, intergenials 2, dorsal scale rows 19-19-17, ventrals 170, subcaudals 107. Body length is 353 mm., tail length 141 mm., tail length/total length ratio 0.285.

The dorsum is olive-brown (Maerz & Paul 15J5), a lighter shade of brown below the lateral stripe (15L2). The vertebral stripe is red (4K12) on the posterior three-fourths of the body, orange (9I11) on the neck; the lateral stripe is light yellow (10F1). The venter is pale green (18F4), the posterior edge of each ventral scute cream yellow; the dark ventrolateral stripe is lacking. The chin shields are white, the supralabials pale greenish white. The pale yellow postocular spot occupies all the lower and leading edge of the middle postocular; the fused parietal spots are moderately prominent and bright.

DISCUSSION. Counts and measurements of this subspecies may be summarized as: postoculars 2 to 4, temporals 1 + 1 to 2 + 3, supralabials

7 to 9, infralabials 9 to 11, intergenials 1 to 4, dorsal scale rows 19-19-15 to 19-19-18, male ventrals 163-174, female ventrals 158-175, male subcaudals 98-119, female subcaudals 93-116. Body length in males 223 to 493 mm., in females 169 to 728 mm. Total length in males 319 to 711 mm., in females 234 to 994 mm. Adult tail length/total length ratio in males 0.260 to 0.322, in females 0.268 to 0.326.

In a series of 15 individuals from 8 miles S Oak Hill, Hays County, Texas, 14 have the usual bright red vertebral stripe; on the other specimen (UF 12204.1) the stripe is orange its entire length. A series of 5 snakes from Fern Bank Springs, Hays County, another 5 from a few miles NW Austin, Travis County, and 7 individuals from scattered localities in Blanco County all have the red stripe, as do 7 collected, and others seen but not collected, at the type locality in Kerr County. One of two specimens from the Devil's River in northern Val Verde County agrees well with them; in the other (UF 12189.2), the vertebral stripe is orange (Maerz & Paul 3B12) on the anterior half of the body, and bright red (3I12) thereafter.

In a series of 17 animals from 6.5 miles S Colorado City, Mitchell County, 14 have orange vertebral stripes, 1 has a reddish-orange stripe, and the remaining 2 have red stripes. This series apparently represents a population of *T. p. rubrilineatus* × *diabolicus* intergrades with a heavy genetic influence from *diabolicus*.

Stone (1903) reported a red-striped individual from the edge of the Balcones Escarpment at New Braunfels, Comal County, and Gloyd (1935) described another from near Floresville, Wilson County. As the latter locality is some distance from the Escarpment, the animals may be intergrades rather than typical *T. p. rubrilineatus*. Strecker (1908) indicated that the ribbonsnakes in McLennan County usually have a red vertebral stripe. Brown (1901) reported a red-striped snake from Pecos, Reeves County, more than 100 miles west of the westernmost verified localities for red-striped individuals. As all other records from trans-Pecos Texas are of animals with orange vertebral stripes, the locality or color data may be inaccurate.

The name *rubrilineatus* (Latin, red-lined) refers to the bright red vertebral stripe which characterizes this subspecies.

*Thamnophis proximus diabolicus*, new subspecies

HOLOTYPE. UF 12210, a large adult female from the Rio Nadadores, 3 miles W Nadadores, Coahuila, Mexico, collected 3 August 1960 by Roger Conant.

DEFINITION. A subspecies of *Thamnophis proximus* characterized by an olive-gray to olive-brown dorsum, an orange vertebral stripe, a

narrow dark ventrolateral stripe, and frequent reduction in the width of the lateral stripe on the posterior portion of the body in the southern part of the range.

**RANGE.** From west-central Tamaulipas, Nuevo Leon, and eastern Coahuila north-northwestward through the Pecos Valley of Texas and New Mexico and, possibly, the Staked Plains of western Texas and adjacent New Mexico to extreme southeastern Colorado (Baca County). Isolated populations may exist in the Rio Grande Valley in western New Mexico (see Discussion).

**DESCRIPTION OF HOLOTYPE.** Scutellation: Oculars 1 + 3, temporals 1 + 3, supralabials 8, infralabials 10, intergenials 2, dorsal scale rows 19-19-17, ventrals 160, subcaudals 99. Body length is 771 mm., tail length 309 mm., tail length/total length ratio 0.286.

Color pattern: Dorsum olive-gray; vertebral stripe of moderate width, yellowish orange immediately behind the head, a bright orange thereafter; lateral stripe reduced in width posteriorly; venter grayish white medially, pale orange marginally; dark ventrolateral stripe occupies 0.10 the width of a ventral scute on each side; chin shields white; supralabials pale greenish white. The light postocular spot is not bright and is confined to the lower postocular; the fused parietal spots are prominent, bright yellow, and broadly margined with black; a black postorbital vitta is lacking.

Because no color atlas was available when the above notes were made, the following supplementary notes are presented for a subadult female (UF 12217.1) collected in Huasteca Canyon, near Santa Catarina, Nuevo Leon, by M. J. Fouquette, Jr., and D. A. Rossman. Dorsum olive-brown (Maerz & Paul 15J7); vertebral stripe bright orange (10I10); lateral stripe bright yellow (10F1); venter pale yellow-green. (18E1).

**DISCUSSION.** Counts and measurements of this subspecies may be summarized as: postoculars 3 to 4, temporals 1 + 1 to 2 + 3, supralabials 8 to 9, infralabials 9 to 12, intergenials 1 to 4, dorsal scale rows 19-19-15 to 21-19-17, male ventrals 161-171½, female ventrals 154-169, male subcaudals 98-114, female subcaudals 87-102. Body length in males 185 to 415 mm., in females 179 to 771 mm. Total length in males 259 to 598 mm., in females 246 to 1080 mm. Adult tail length/total length ratio in males 0.285 to 0.307, in females 0.268 to 0.304.

The populations in Nuevo Leon, Coahuila, trans-Pecos Texas, and southern New Mexico are typical of the subspecies. A single specimen (USNM 86920) from Union County in extreme northeastern New Mexico also seems to belong with this group. KU 49585 from Hartley



County, Texas, and CUM 11669-673 from Baca County, Colorado, apparently represent populations of *T. p. diabolicus*, although the dorsum may be somewhat darker than usual. The northeastern New Mexico and Texas individuals were collected on tributaries of the Canadian River, the Colorado series from a tributary of the Cimarron River. Both these streams flow eastward, yet the snakes show much less affinity to the populations in the eastern parts of the Canadian and Cimarron drainages than they do to the animals of the Pecos River drainage. As ribbonsnakes in arid regions are generally restricted to the immediate vicinity of permanent springs and watercourses, these northern populations of *T. p. diabolicus* are probably effectively isolated from those in the Pecos drainage and may be relicts of an old population that was continuously distributed when conditions were more mesic.

A similar disjunct distribution in this region occurs in *Thamnophis sirtalis* (Fitch and Maslin, 1961) which has an isolated population in the Rio Grande Valley of New Mexico. Possibly *T. proximus* has one there too, but the several old records for the area are of questionable validity. Baird and Girard (1853) listed two *T. proximus* from Sabinal and Medina, New Mexico, and discuss in the text specimens from the Rio Grande Valley which, as they list no other specimens from anywhere near the Rio Grande, might be the "New Mexico" specimens. I cannot locate a Medina anywhere in New Mexico, but there is a Sabinal in northern Socorro County on the west side of the Rio Grande. F. R. Gehlbach, who is studying the herpetofauna of the state, suggests these snakes may actually have been collected in Texas at Sabinal, Uvalde County, and Medina, Bandera County. The specimens themselves apparently are no longer extant. Two *T. proximus* (UMMZ 68751) from "east of Albuquerque" are probably from the Pecos drainage in San Miguel County where their collector, an entomologist, took other material now also in the University of Michigan Museum of Zoology (F. R. Gehlbach, personal communication). Thus there is no conclusive evidence that the western ribbon-snake occurs in the Rio Grande Valley.

Specimens from the eastern edge of the Staked Plains appear to be intergrades between *T. p. diabolicus* and *proximus* in the north, *diabolicus* and *rubrilineatus* in the south. North-central Texas populations may be intermediate between all three races.

Intergradation between *T. p. diabolicus*, *rubrilineatus*, and *orarius*, apparently occurs in varying combinations throughout most of inland southern Texas. Individuals from the eastern foothills of the Sierra Madre Oriental in west-central Tamaulipas (as far south as Ciudad

Victoria) are here considered to represent the southernmost population of *diabolicus*, but living material may show them to be *diabolicus* × *orarius* intergrades. Possible intergrades between *diabolicus* and *rutiloris* are discussed under *T. p. rutiloris*.

The name *diabolicus* (Gr. *diabolikos*, devilish) alludes to a truly horned inhabitant of hot places. The ribbonsnake's "horns" are strictly imaginative, suggested by the forward-protruding forked arms of the parietal spots in many individuals of this inhabitant of arid regions.

*Thamnophis proximus rutiloris* (Cope), new combination

*Thamnophis sauritus rutiloris*: Smith, 1938:5

*Thamnophis sauritus chalcus*: Dunn, 1940:192

*Thamnophis sirtalis chalcus*: Klauber, 1948:9

HOLOTYPE. USNM 13906, an adult female from Cozumel Island, Quintana Roo, Mexico, collected 23-29 January 1885 by personnel of the U.S. Fish Commission vessel *Albatross* (Cochran, 1961).

DEFINITION. A subspecies of *Thamnophis proximus* characterized by an olive-brown dorsum, a broad grayish-tan vertebral stripe, yellow-orange labials, a narrow lateral stripe, and a moderately narrow ventrolateral stripe.

RANGE. From extreme southern Tamaulipas south along the coastal plain, eastern rim of the Sierra Madre Oriental, and Central American highlands to Cartago, Costa Rica. It occurs in the Pacific lowlands only at the Isthmus of Tehuantepec and in central Guerrero. There are no records for the highlands of Guatemala.

DESCRIPTION OF HOLOTYPE. Scutellation: Oculars 1 + 3, temporals 1 + 1, 2 (the left anterior temporal is fragmented anteriorly), supralabials 8, infralabials 10, intergenials 2, dorsal scale rows 19-19-17, ventrals 147, subcaudals 97 (tip damaged but apparently complete—in the original description Cope reported 92 subcaudals). Body length is 520 mm., tail length 215 mm., tail length/total length ratio 0.293. (Cope, in 1885, recorded a body length of 539 mm. and a tail length of 214 mm., the discrepancy doubtless resulting from shrinkage during 75 years storage in preservative.)

Cope (1885) described the holotype as having a brownish-olive dorsum, vertebral stripe existing only as a faint trace, lateral stripe pale olive, venter pale olive, supralabials, infralabials, and first 3 ventrals reddish orange or salmon, a pair of light parietal spots present. Whether or not this description was of the living animal is not clear, hence the following description of UF 12215, an adult female collected 13 miles WNW Veracruz, Veracruz, by M. J. Fouquette, Jr., and

D. A. Rossman. Dorsum olive-tan in life, somewhat lighter below the lateral stripe; vertebral stripe grayish tan, broad; lateral stripe pale yellow, narrow, and slightly reduced in width posteriorly; venter pale yellow at neck becoming pale green posteriorly; dark ventrolateral stripe narrow, occupying 0.10 the width of a ventral on each side; chin shields and lower margin of infralabials white; supralabials and upper margin of infralabials bright yellow (10 other live *T. p. rutiloris* have yellow-orange labials). The light postocular spot occupies the lower and leading edge of the middle postocular and is not brightly colored; the fused parietal spots are prominent, bright yellow, and broadly margined with black. The black postorbital vitta is narrow, irregular, and confined to the temporals.

Discussion. Counts and measurements of *T. p. rutiloris* may be summarized as: postoculars 2 to 5, temporals 1 + 1 to 2 + 3, supralabials 7 to 9, infralabials 8 to 11, intergenials 1 to 6, dorsal scale rows 17-18-17 to 21-19-17, male ventrals 142½-164, female ventrals 141-160, male subcaudals 91-104, female subcaudals 82-98. Body length in males 157.5 to 445 mm., in females 153 to 556 mm. Total length in males 222 to 625 mm., in females 210.5 to 776 mm. Adult tail length/total length ratio in males 0.286 to 0.307, in females 0.275 to 0.306.

Three specimens from between El Limon and Chamal in extreme southwestern Tamaulipas apparently represent intergrades between *T. p. rutiloris* and *diabolicus*. The two females (UMMZ 101222, 101908) have the broad vertebral stripe characteristic of *rutiloris*, but in life it almost surely was of some color other than tan (presumably orange). Their ventral counts (158, 160) are well within the normal range of variation for Mexican *diabolicus*. UMMZ 110815, a male, has 162 ventrals and a vertebral stripe which apparently was tan, the former characteristic of *diabolicus*, the latter of *rutiloris*.

A series of snakes (CNHM 114582-586, UMMZ 102893-894, UIMNH 18926-928, USNM 105305) from the Sierra de Tamaulipas on the Tropic of Cancer appears to combine the color pattern of *T. p. orarius* (or *orarius* × *diabolicus* intergrades) with ventral counts much closer to those of *rutiloris*. Snakes from the immediate vicinity of Ciudad Mante appear to have the color pattern of *rutiloris*, but the males have a rather high ventral count (the females have a ventral count comparable to those of female *rutiloris* 200 miles to the south). The populations in eastern San Luis Potosí and near Tampico are considered to be *rutiloris*.

The only available specimen of the possibly relict population in coastal Guerrero (UF 12213) has a moderately wide vertebral stripe that definitely was not tan in life, but rather seems to have been a

pale yellow. Furthermore, the lateral stripe is largely confined to row 3 as in *T. p. alpinus*. On the other hand, the specimen agrees with lowland *rutiloris* in scutellation, color of dorsum, width of ventrolateral stripe, and proportional muzzle length. Without additional material (particularly live specimens) to confirm the distinctiveness of this population, it is pointless to give it taxonomic recognition.

An adult male (TCWC 865) taken near Las Vigas, Veracruz, at an altitude of 8000 feet has been tentatively assigned to this subspecies largely on the basis of locality. The animal has 166 ventrals, 110 subcaudals, a tail length/total length value of 0.313, an unwidened vertebral stripe, and a large pair of fused parietal spots. Preservation has so darkened the specimen that nothing can be determined about its original color. The tail is longer than in any other specimen examined from south of the Rio Grande, and no other *rutiloris* possesses so high a ventral or subcaudal count or as large a pair of parietal spots. Whether this individual is aberrant or represents a distinctive high-altitude population remains to be determined.

A specimen (ANSP 20046) from the mountains of south-central San Luis Potosí near Zaragoza (km. 42, Potosí-Rio Verde Railroad) is rather far removed from the range of *T. p. rutiloris* as presently understood, and this record needs substantiation.

Found all the way from sea level to an altitude of 8000 feet, this neotropical subspecies of *T. proximus* appears to have an astounding range of temperature tolerance.

*Thamnophis proximus alpinus*, new subspecies

**HOLOTYPE.** UF 12216, an adult male from the trout hatchery at San Cristobal Las Casas, Chiapas, Mexico, collected 1 August 1960 by M. J. Fouquette, Jr., and D. A. Rossman.

**DEFINITION.** A subspecies of *Thamnophis proximus* characterized by a dark brown dorsum, a gold vertebral stripe, yellow-orange labials, a narrow lateral stripe, chevron-shaped parietal spots, a broad ventrolateral stripe, and a relatively short tail.

**RANGE.** Chiapas Highlands from San Cristobal Las Casas to Comitán at elevations above 5000 feet.

**DESCRIPTION OF HOLOTYPE.** Scutellation: Oculars 1 + 3, temporals 1 + 2 (the anterior temporal is fragmented anteriorly on both sides of the head), supralabials 8, infralabials 10, intergenials 2, dorsal scale rows 19-19-17, ventrals 163, subcaudal series and tail incomplete. Body length is 499 mm.

The dorsum is dark brown (Maerz & Paul 8L12), olive-brown below the lateral stripe (15J10). The vertebral stripe is gold (12K6) and only moderately wide; the lateral stripe is light yellow (10H1) overlaid with brown pigment, narrow, and present only on row 3 on the posterior part of the body. The venter is pale green (17E4), pale yellow at the neck; the dark ventrolateral stripe is broad, 0.25 the width of a ventral scute on each side (on the tail it covers the entire surface of the subcaudals). The chin shields are white, irregularly spotted with pale orange; the supralabials and infralabials are pale yellow-orange, but on the supralabials much brown pigment overlays the yellow-orange (the anterior 3 plates are completely overlaid and varying amounts are irregularly distributed on the posterior 5). The light postocular spot occupies all of the lower and the anterior part of the middle postocular, and is overlaid with brown pigment; the fused, chevron-shaped parietal spots are prominent and pale yellow overlaid with brown.

**DISCUSSION.** Counts and measurements of this subspecies may be summarized as: postoculars 2 to 4, temporals 1 + 1 to 2 + 3, supralabials 7 to 9, infralabials 9 to 11, intergenials 2 to 5, dorsal scale rows 19-19-17 to 20-19-17, male ventrals 157-165, female ventrals 153-163, male subcaudals 99-102, female subcaudals 86-99. Body length in males 175 to 499 mm., in females 141.5 to 528. Total length in males 241.5 to 642 mm., in females 194 to 722 mm. Adult tail length/total length ratio in males 0.268 to 0.280, in females 0.252 to 0.283.

I have seen no intergrades between *T. p. alpinus* and *rutiloris*, but they should occur at lower elevations on the northern and western slopes of the Chiapas Highlands. *T. p. alpinus* shows its relationship to the widespread *rutiloris* in supralabial color and lateral stripe width. Its darker dorsum, reduced width of vertebral stripe, and the dark pigment overlaying the lighter markings are apparently adaptations to increase absorption of solar radiation in an environment where low temperatures severely restrict the activity of ectotherms.

The frequency of such scutellation variations as three intergenials and fragmentation of the anterior temporal may result either from exposure of the mother to low temperatures during the gestation period (as demonstrated for *Thamnophis elegans* by Fox, 1948) or from the genetic intensification of a normally rare variation in an isolated population.

The subspecific name *alpinus* (Latin, of the Alps) refers to the high altitudes where this population lives.

## NATURAL HISTORY

This brief summary of the known ecology of *T. proximus* is by no means complete or exhaustive. Many aspects are treated in much greater detail elsewhere, particularly by Tinkle who has produced (1957) the most comprehensive study to date.

**HABITAT.** My personal experience has been that *T. proximus* is rather closely confined throughout its range to the vicinity of permanent or semipermanent bodies of water, either running or standing, which most literature accounts substantiate. Neill and Allen (1959), however, collected a large adult beneath a log in a high, dry savanna in British Honduras. The species seems to prefer open grassy situations, but I have also found it in wet woodlands, at a desert waterhole, and in rush-lined ponds. Ruthven (1908) reported ribbonsnakes from a brackish mangrove swamp at Progreso, Yucatan. Few authors have referred to the semiarboreal habits of this species. Specimens of *T. proximus* have been observed in bushes in British Honduras (Duméril and Bocourt, 1893), Kansas (Gloyd, 1926), and Nebraska (Hudson, 1942). I have collected individuals several feet above the water in rushes, one more than 6 feet up, in Chiapas and San Luis Potosí.

**FOOD.** The diet of the western ribbonsnake is chiefly confined to fishes and to amphibians and their larvae. Table 8 lists species *Thamnophis proximus* is known to have eaten in the wild. Taylor (1892) and Fouquette (1954) recorded insects in the diet, but these may have been secondary ingestions. Wright and Wright (1957) mentioned an account of *T. proximus* eating mice, which is probably based on Trowbridge's (1937) report of finding a *T. proximus* in a mouse nest in a log—the snake contained *Rana pipiens*, however, not mice. Endothermic vertebrates, lizards, earthworms and other invertebrates, all of which one or more species of gartersnake eat readily, are apparently not normal prey of *T. proximus*. Moreover, while captive ribbonsnakes readily accept newly transformed toads, they almost always refuse adult *Bufo*. Possibly members of the *Sauritus* group are not so tolerant as other gartersnakes to the toxic parotoid secretions of adult toads.

When food is plentiful, a ribbonsnake may continue eating as long as the supply lasts. Laughlin (1959) reported that a single *T. proximus* contained 64 metamorphosing toads of an unidentified species; and Klein (1949) observed that ribbonsnakes (and several species of watersnakes) feeding on aggregations of fish, tadpoles, and frogs in pools left by a drop in water level of the San Antonio River (Texas)

gorged themselves to the point that many of the snakes, especially the juveniles, died.

TABLE 8. Food of *Thamnophis proximus*

Species	Source
<b>Anurans</b>	
<i>Scaphiopus bombifrons</i>	Fouquette, 1954
<i>Bufo woodhousei</i>	Fouquette, 1954
<i>Acris crepitans</i>	Fouquette, 1954
<i>Acris gryllus</i>	Boyer and Heinze, 1934
<i>Hyla crucifer</i>	Fouquette, 1954
<i>Hyla versicolor</i>	Gloyd, 1926; Fouquette, 1954
<i>Smilisca baudini</i>	M. J. Fouquette, Jr., personal communication
<i>Pseudacris clarki</i>	Fouquette, 1954
<i>Pseudacris streckeri</i>	Fouquette, 1954
<i>Pseudacris triseriata</i>	Gloyd, 1926; Fouquette, 1954
<i>Rana catesbeiana</i>	Fouquette, 1954
<i>Rana clamitans</i>	Fouquette, 1954
<i>Rana pipiens</i>	Trowbridge, 1937; Clark, 1949; Fouquette, 1954
<i>Leptodactylus labialis</i>	personal observation
<i>Hypopachus cuneus</i>	Wright and Wright, 1957
<i>Microhyla carolinensis</i>	personal observation
<i>Microhyla olivacea</i> (larvae only)	Fouquette, 1954
<b>Salamanders</b>	
<i>Ambystoma texanum</i>	Fouquette, 1954
<i>Plethodon cinereus</i>	C. W. Myers, personal communication
<b>Fishes</b>	
<i>Salmo gairdneri</i>	Myers, 1957
<i>Gambusia affinis</i>	Fouquette, 1954
<i>Lepomis megalotis</i>	Fouquette, 1954
<i>Herichthys cyanoguttatus</i>	Fouquette, 1954

Ribbonsnakes are as active by night as by day where nocturnal temperatures permit, and apparently feed as readily at one time as the other. Near Ciudad Mante in Tamaulipas, M. J. Fouquette, Jr. (personal communication) watched a *T. proximus* stalk a calling *Smilisca baudini*. When the frog's vocal sacs moved, the snake moved closer, stopping each time the frog stopped calling.

REPRODUCTION. Tinkle (1957) found that ribbonsnakes in southeastern Louisiana reach sexual maturity in approximately 2 years and at minimum body lengths of 485 mm. in females and 410 mm. in males. Gloyd (1926) reported a Kansas female that bore young at 435 mm. body length, and Carpenter (1958) noted one from Oklahoma bearing

at 460 mm. Clark (1949) recorded a brood from a 20-inch female from northern Louisiana; if this is total length and the animal's tail was complete, its body length was probably between 350 and 360 mm. The smallest gravid females I have examined measured 355 (British Honduras), 385 (Veracruz), 390 (Veracruz), 442 (southeastern Texas), 450.5 (Veracruz), and 454 (San Luis Potosí) mm. These measurements suggest that ribbonsnakes achieve sexual maturity more rapidly and at smaller sizes in the tropics. Extrapolating from these and Tinkle's data, males in Mexico and Central America probably mature at body lengths of 300 to 350 mm.

Where ribbonsnakes are inactive in winter, mating apparently takes place soon after the spring emergence. Carpenter (1958), Neill and Allen (1959), and Tinkle (1957) all reported females gravid in April. The young are usually born in late July or early August, but dates range from 23 June (R. D. Worthington, personal communication) through 14 September (Carpenter, 1958). Brood size tends to increase with the size of the female, and ranges from 4 (Carpenter, 1958) to 27 (Klein, 1949), the mean for 34 broods being 12.8. Table 9 summarizes available data on body length of newly born *T. proximus*. Size of individuals at birth varies greatly between broods, but no

TABLE 9. Body length of newly born *Thamnophis proximus*

Locality	N	M	R
St. Charles Parish, La. <sup>1</sup> .....	22	202.6mm	187 -220mm
St. Charles Parish, La. <sup>2</sup> .....	5♂♂	201.7	188 -214
	3♀♀	198.0	190.5-206
	2♂♂	177.8	176.5-179
	2♀♀	173.3	170 -176.5
Alexander Co., Illinois <sup>3</sup> .....	8	157.3	151 -162
Southern Oklahoma <sup>4</sup> .....	5♂♂	206	192 -225
	7♀♀	201	199 -204
	4♂♂	170	165 -174
	7♂♂	159	156 -160
	2♀♀	152	148 -156
Eastern San Luis Potosí <sup>2</sup> .....	1♂	166	
	4♀♀	166	164 -168

N = number of individuals; M = mean; R = range

<sup>1</sup> Data from Tinkle, 1957

<sup>2</sup> Personal observation

<sup>3</sup> Data from N. J. Rossman, 1958

<sup>4</sup> Data from Carpenter, 1958



geographical correlation is readily apparent. Males, though smaller as adults, average larger than females at birth.

PARASITES. Harwood (1932) reported finding the helminths *Rhabdias vellardi* and *Kalicephalus agkistrodontis* in the lungs and stomach of *Thamnophis proximus*. On MCZ 53912, an adult female *proximus* taken near Merida, Yucatan, I found a small tick embedded between scales on the left side of the head. George Anastos identified it as a nymphal stage of the genus *Ixodes* (species undetermined).

### THE EASTERN RIBBONSNAKE *THAMNOPHIS SAURITUS* (LINNAEUS) —

- Coluber saurita* Linnaeus, 1766:385  
*Natrix saurita*: Merrem, 1820:122  
*Tropidonotus saurita*: Boie, 1827:535  
*Leptophis sauritus*: Holbrook, 1842:21  
*Thamnophis saurita*: Fitzinger, 1843:26 [by implication]  
*Eutainia saurita*: Baird & Girard, 1853:24  
*Eutaenia saurita*: Kennicott, 1859:98  
*Eutaenia sackenii* Kennicott, 1859:98  
*Prymnomiodon chalceus* Cope, 1860:558  
*Eutaenia sackeni*: Davis & Rice, 1883:39  
*Thamnophis sackenii*: Loennberg, 1894:329  
*Thamnophis sauritus*: Stone, 1906:164  
*Thamnophis sackeni*: Deckert, 1918:31  
*Thamnophis sirtalis*: Klauber, 1948:9

Klauber showed that Linnaeus's description of *Coluber sirtalis* does not fit the common gartersnake, and that the name probably should be applied to the eastern ribbonsnake. For several years some authors followed Klauber; others did not. The resulting confusion led to a request that the International Commission on Zoological Nomenclature conserve the pre-Klauber arrangement in the interest of nomenclatural stability. The Commission complied and neotypes were subsequently designated (Schmidt and Conant, 1956-57).

NEOTYPE. As the holotype (collected in "Carolina") is presumed lost, Schmidt and Conant (1956-57) designated as neotype an adult female, CNHM 73119, collected 15 miles NNE Charleston, Berkeley County, South Carolina, 20 July 1953, by John Quinby.

DEFINITION. A moderately large, long-tailed member of the genus *Thamnophis* characterized by: 19-19-17 dorsal scale rows; a single preocular; 7 or 8 supralabials, the 3rd and 4th or 4th and 5th, respectively, entering the orbit; 143 to 177 ventrals; 94 to 136 subcaudals; lateral stripe on dorsal scale rows 3 and 4 (row 2 is occasionally involved); labials and ventrals without black markings; dark ventrolateral stripe always present and broad; parietal spots frequently

lacking, when present they are small and rarely in contact or brightly colored; hemipenes short, extending to the 8th subcaudal when inverted; teeth numerous, averaging about 30 to each maxilla, 37 to each dentary, 21 to each palatine, and 34 to each pterygoid.

RANGE. From southern Ontario and southern Maine southward east of the Mississippi River to the Florida Keys and to the northern side of Lake Ponchartrain in Louisiana (fig. 8). A colony is isolated in

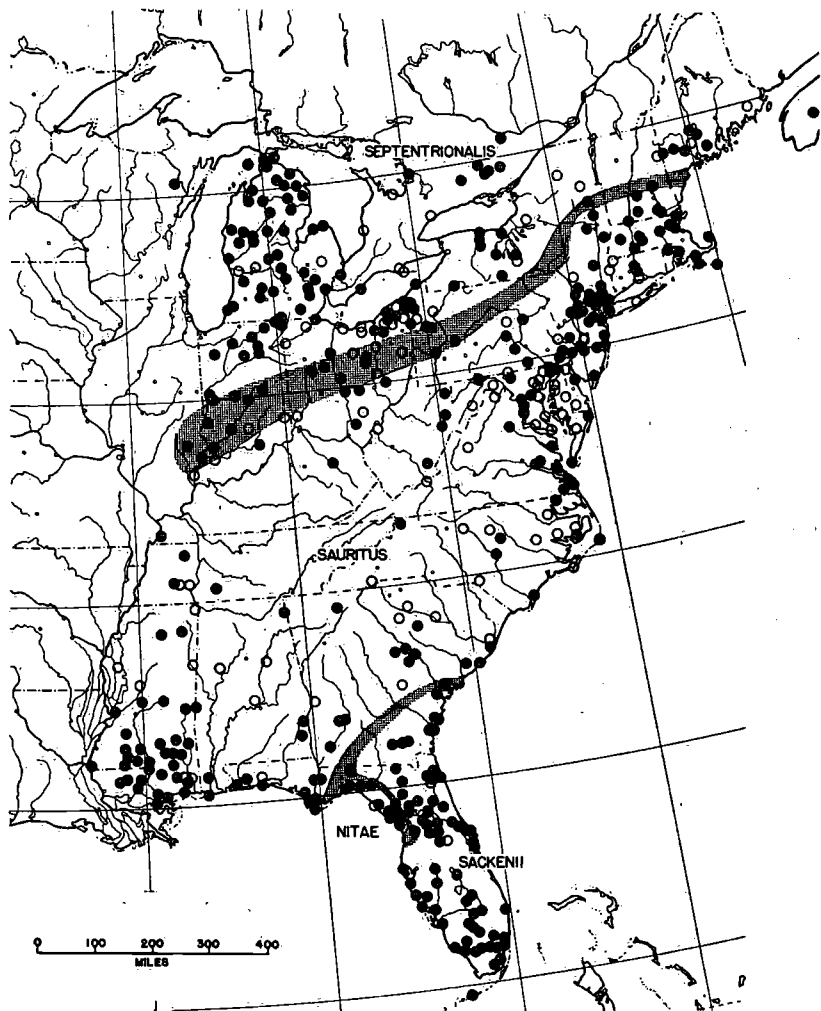


FIGURE 8. Distribution of *Thamnophis sauritus* in the United States and Canada. Solid dots represent specimens examined; open circles are literature records. Stippled areas represent probable zones of intergradation between subspecies.

central Nova Scotia, and perhaps another in northern Wisconsin. The species apparently is rare in much of the interior of the eastern United States.

### VARIATION Sexual Dimorphism

*Thamnophis sauritus* shows sexual dimorphism in the same characters as does *T. proximus*, and to about the same degree (see table 3). In populations for which at least five snakes of each sex are available, the differences in mean number of ventrals range from 0.8 scales in favor of the females (Charleston County, South Carolina) to 5.7 in favor of the males. While the greatest dimorphism occurs in western peninsular Florida, the degree of dimorphism does not appear to vary geographically. Populations represented by at least 15 adults of each sex are compared in table 10.

TABLE 10. Sexual dimorphism in ventrals of *Thamnophis sauritus*

Population	Males		Differences		Females	
	N	M	DM	CD%	N	M
Southwestern Florida.....	20	164.7±0.83	5.4	3.33±0.13	27	159.3±0.63
North-central Florida.....	15	157.8±0.99	3.6	2.31±0.19	29	154.2±0.74
Southern Michigan.....	16	163.1±0.58	2.4	1.48±0.09	25	160.7±0.60

N = number of individuals; M = mean; DM = difference between means; CD% = coefficient of divergence expressed as a percent.

Sexual dimorphism in subcaudal number also agrees well with that exhibited by *T. proximus* (table 5), but does not vary so widely. In no samples with at least five specimens of each sex do males average fewer subcaudals than the females. The mean differences range from 3.4 in south-central Mississippi to 10.2 in southeastern Pennsylvania. This character does not appear to vary geographically. Populations represented by at least 10 adults of each sex are compared in table 11.

TABLE 11. Sexual dimorphism in subcaudals of *Thamnophis sauritus*

Population	Males		Differences		Females	
	N	M	DM	CD%	N	M
Southwestern Florida.....	11	126.3±1.52	7.9	6.05±0.39	16	118.4±0.96
North-central Florida.....	12	123.3±1.23	7.7	6.45±0.39	18	115.6±1.26
Southern Michigan.....	10	108.3±1.16	5.3	5.02±0.38	16	103.0±1.29

N = number of individuals; M = mean; DM = difference between means; CD% = coefficient of divergence expressed as a percent.

Females average longer than the males but have proportionally shorter tails. The largest female examined (UF 12120 from Dade County, Florida) has a body length of 670 mm., a tail of 348 mm. The largest male (UMMZ 108313), also from Dade County, has a body 537 mm. long and a tail 283 mm. long. Wright and Wright (1957) cited a New Jersey male with a total length of 842 mm.

The mean differences in adult tail length/total length ratios ranges from 0.007 to 0.014. Males in all populations have proportionally longer tails than the females. Mean tail length/total length values range from 0.313 to 0.378 in males, 0.299 to 0.350 in females.

Although females have proportionally longer muzzles than the males in 5 of 7 populations in which muzzle length/frontal length values are available for at least 4 adults of each sex, the means for all populations measured are almost identical. In males they range from 0.628 to 0.715 (mean 0.666), in females from 0.607 to 0.707 (mean 0.669).

Caudodorsal scale row reduction occurs more posteriorly in males than in females. The reduction formulas for UF 12187.4, an adult male from Charleston County, South Carolina, and UF 12183, an adult female from Hyde County, North Carolina, are presented below.

$$\text{UF 12187.4 } \sigma^7 \quad 17 \frac{-2(1)}{-3(1)} \quad 15 \frac{-2?3(3)}{-2(3)} \quad 13 \frac{-7(4)}{-2?3(5)} \quad 12 \frac{-2?3(5)}{-2?3(5)} \quad 10 \frac{-4(18)}{-4(18)} \quad 8 \frac{-3(41)}{-3(42)} \\ 6 \frac{2+3(85)}{-3(85)} \quad 4 \frac{-2(112)}{-2(111)} \quad 2(117)$$

$$\text{UF 12183 } \phi \quad 14 \frac{-1(1)}{-1(2)} \quad 12 \frac{-2(2)}{-2?3(3)} \quad 10 \frac{-3(6)}{3+4(7)} \quad 8 \frac{-3(27)}{-3(30)} \quad 6 \frac{-3(70)}{-3(69)} \quad 4 \frac{-2(100)}{-2(100)} \\ 2(107)$$

### Ontogenetic Variation

Newly born *T. sauritus* have proportionally shorter tails than do adults (table 6). Coefficients of ontogenetic divergence are comparable with those obtained for one population of *T. proximus* except for southern Florida females which exhibit almost no change in proportional tail length from birth to adulthood (table 6). Females of two broods from southern Florida (Broward and Collier Counties) are unique in having proportionally longer tails than the males of the same brood; the situation is reversed in the adults.

All juveniles have a brown dorsum; there is a progressive darkening with age in those populations in which adults have either a black or dark brown dorsum.

## Individual Variation

Characters which vary neither geographically, nor sexually, nor ontogenetically are discussed below. Data on head scales refer to one side only. Individual variation in scutellation is summarized in table 12.

**OCULARS.** None of the 957 *T. sauritus* examined has more than one preocular. Postoculars are usually 3, with 4 the most frequent variation.

**TEMPORALS.** There are usually 1 anterior and 2 posterior temporals, but this character is highly variable. Unlike *T. proximus*, no population shows a high incidence of fragmentation of the anterior portion of the anterior temporal.

**SUPRALABIALS.** Though the number of supralabials varies geographically, the infrequent interposition of small scales between two of the normal supralabials does not.

TABLE 12. Individual variation in scutellation of *Thamnophis sauritus*

Pre-oculars	Post-oculars	Anterior temporals	Posterior temporals	Supra-labials	Infra-labials	Inter-genials
♂♂ 1*(363)	2,3 (2)	1 (325)	1 (5)	6,7 (2)	7,8	1 (21)
	3 (339)	1,2 (14)	1,2 (7)	7 (228)	8 (2)	2 (293)
	3,4 (17)	2 (21)	1,3	7,8 (37)	8,9 (3)	3 (28)
	3,5		2 (301)	8 (90)	8,10	4
	4 (4)		2,3 (33)	9	9 (11)	
			3 (11)		9,10(32)	
			3,4 (2)		9,11 (3)	
					10 (288)	
					10,11(14)	
♀ ♀ 1*(594)	2	1 (481)	1 (17)	6	8 (4)	0 (2)
	2,3 (10)	1,2 (56)	1,2 (13)	6,7 (3)	8,9 (6)	1 (34)
	3 (537)	2 (50)	1,3 (2)	7 (327)	8,10 (4)	2 (436)
	3,4 (32)		2 (402)	7,8 (51)	9 (34)	3 (68)
	4 (13)		2,3 (105)	8 (209)	9,10(56)	4 (2)
	4,5		3 (47)	8,9	9,11	
			3,4		10 (464)	
					10,11(11)	
					10,12	
					11	
♂♂	Dorsal scale rows				♀ ♀	
17-19-17. (3)					17-18-17	
19-17-17 (2)					18-19-17	
19-18-17					19-17-16	19-19-17 (536)
19-19-16 (3)	19-19-18			19-17-17 (19)	19-19-18	
19-19-17 (327)	19-19-19			19-19-16 (5)	19-19-19	
	19-21-18				21-19-17	

\*Single numbers indicate that both sides of the head have the same count.

**INFRALABIALS.** Ten is the usual number, 9 the most frequent variation. Infralabial number is more variable in *sauritus* than in *proximus*; 10 individual *sauritus* have two more infralabials on one side than on the other; no *proximus* shows so large a bilateral difference.

**INTERGENIALS.** Two is the usual condition, three the most frequent variation, but of low incidence in all populations.

**ANAL PLATE.** In no specimen examined is the anal plate divided.

**VENTRALS.** Anomalous scutes between the terminal ventral and the anal plate occur in 9.0 percent of the specimens examined; 4.6 percent, including a few of these, have partial scutes elsewhere on the venter.

**SUBCAUDALS.** Fusion of one or more pairs of subcaudals occurs in 2.2 percent of the material examined.

**DORSAL SCALE ROWS.** Almost all individuals examined have the typical 19-19-17 formula; only two animals have more than 19 rows. Reduction takes place by loss of row 4 on both sides of the body in 36 of the 58 specimens examined, and the 4th row is involved in the reduction on one side in all but 3 of the rest, which lost the 5th row on both sides. One snake dropped row 6 on one side of the body. The reduction occurs opposite ventrals 76 through 106 (mean 89.8) in males, 71 through 101 (mean 87.0) in females. Correlation between total number of ventrals and point of dorsal scale row reduction appears roughly positive, but not so strongly as in *T. proximus*.

**PATTERN AND COLORATION.** Presence or absence and size of parietal spots vary individually; so do the extent of the black postorbital vitta and the width of the black paravertebral stripes.

### Geographic Variation

Although *T. sauritus* has a less extensive range than *T. proximus*, it exhibits considerable geographic variation; some of its patterns of character distribution are even more complex than those in *proximus*. As in the discussion of the western ribbonsnake, all counts, measurements, and proportions are based on population samples.

**SUPRALABIALS.** Throughout peninsular Florida to the vicinity of Tallahassee in the west and the Okefenokee Swamp region in the north, and through coastal Georgia north to Jasper County, South Carolina, 91.8 percent of the snakes have 8 supralabials on both sides and an additional 5.5 percent have 8 on one side. Throughout the rest of the species' range, only 9.1 percent have 8 on both sides; another 10.8 percent have 8 on one side, 7 on the other. Almost all of the remaining

80.1 percent have 7 supralabials on both sides. The few that do not, have 6 on one or both sides, and all but one of these animals are from Michigan.

**VENTRALS.** Variation in number of ventrals is exceedingly complex and can be best visualized by reference to figure 9. In southeastern

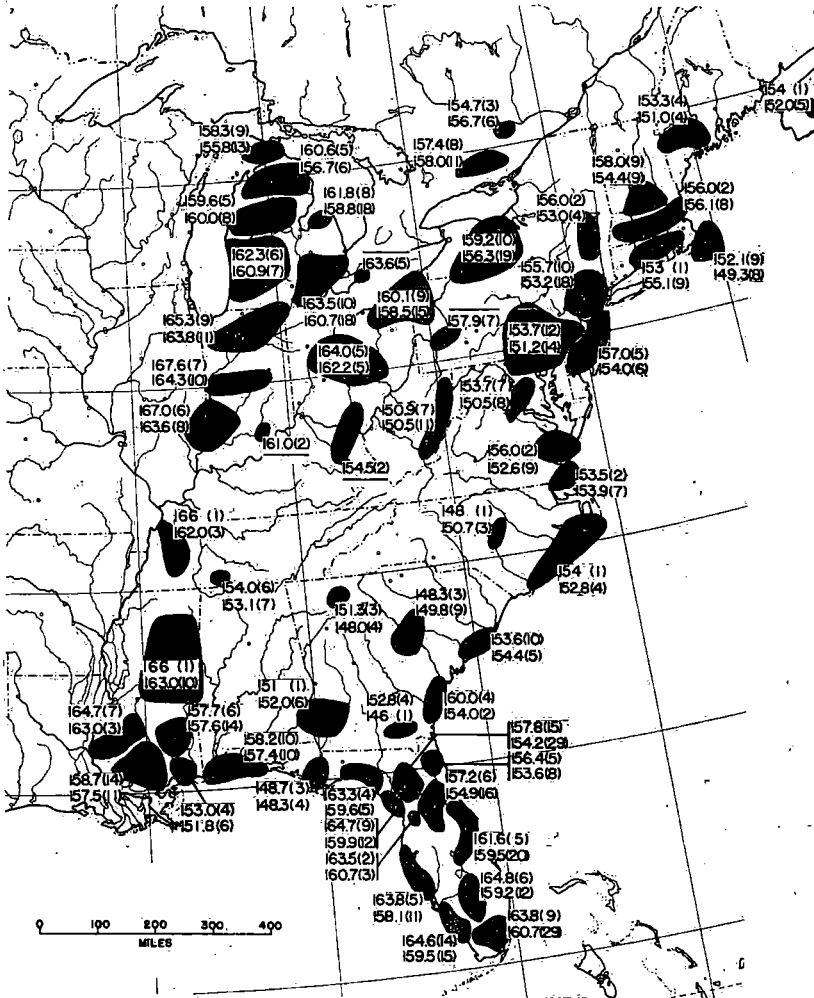


FIGURE 9. Geographic variation of ventral number in *Thamnophis sauritus*. Black blotches represent the areas from which samples were taken. The upper numbers associated with each blotch are the sample mean and sample size (in parentheses) for males; the lower numbers present the same data for females. When a line appears in place of either the upper or lower numbers, it signifies that no specimens of that sex were present in the sample.

Louisiana and adjacent Mississippi, males have a mean of 158.7 ventrals, females 157.5. Population samples from southeastern Mississippi (exclusive of the Biloxi area) and the Mobile Bay-Pensacola Bay area agree closely, but the snakes in southwestern Mississippi have a mean of 6 to 7 more ventrals in males,  $5\frac{1}{2}$  in females. From thence north-northeastward to northern Indiana (exclusive of central Tennessee) the mean number of ventrals in females is almost invariable. The mean for males increases slightly over this distance and reaches its peak (167.6) in central Indiana. In northern Indiana males the mean is about  $2\frac{1}{2}$  scales less, and it decreases gradually but steadily northward in Michigan to the Straits of Mackinac, the mean in extreme northern Michigan being another 7 scutes lower. The female mean ventral count drops by 3 scales between northern Indiana and southern Michigan; then lessens more gradually northward, being another 5 scales lower in extreme northern Michigan. A series of females (no males available) from extreme southern Ontario agrees well with the northern Indiana females, and those from central Ohio have only slightly lower means. Northeastward from these populations the mean number of ventrals in both sexes decreases abruptly, by about 4 scales in populations south of Lake Erie, and then tapers off gradually in western New York and eastern Ontario.

A series of 7 females (no males available) from the vicinity of Pittsburgh agrees closely with females from the northeastern Ohio-northwestern Pennsylvania area in mean ventral number. One hundred miles to the south in eastern West Virginia, the mean number of ventrals in both sexes decreases abruptly. A clinal reduction in ventral number is also apparent from central Ohio into West Virginia and eastern Kentucky. The reduction in this case is also abrupt, a decrease of  $11\frac{1}{2}$  (females) to 13 (males) taking place over a distance of less than 200 miles.

The snakes in central Tennessee have means at least 9 scales less than those of the populations to the west of the Tennessee River. A series from the vicinity of Biloxi, Mississippi, has a mean of 5 to 6 fewer ventrals than the populations surrounding it and no more than 50 miles distant. Snakes from southeastern Alabama and southern Georgia (exclusive of the coast) appear to be similar to the Biloxi animals in mean ventral count, but more specimens are needed to determine just how well they agree, and whether the two are connected by populations in southwestern Alabama north of Mobile Bay. In the Apalachicola River Valley, 150 miles east of the Mobile Bay-Pensacola Bay area the mean number of ventrals decreases by more than 9 scales. Populations just to the north in southern Georgia have



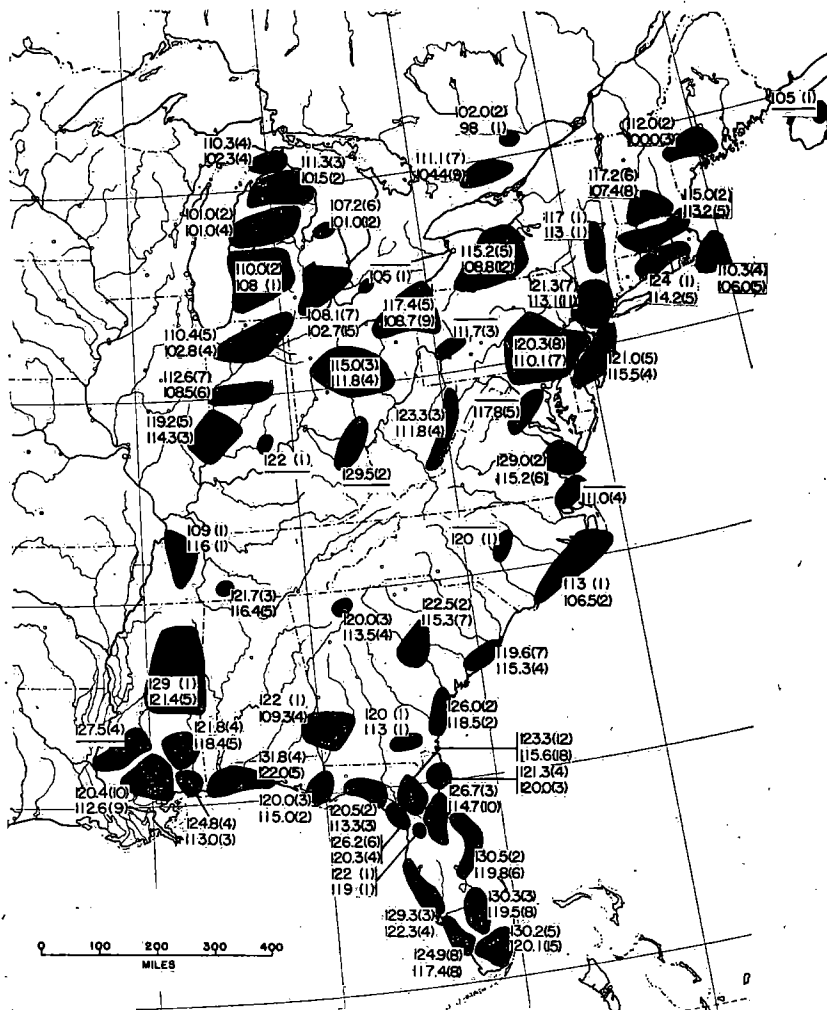
means less than 4 scales higher. A single adult female (UF 7385) from St. Vincent's Island off the mouth of the Apalachicola River has 161 ventrals, almost 13 more than the mean for the Apalachicola Valley series. From thence eastward and southward in the western coastal lowlands to southern Florida, and northward in the eastern coastal lowlands to about the latitude of Daytona Beach, the mean number of ventrals is remarkably constant, the majority ranging from 163.3 to 164.8 in males, 159.2 to 160.7 in females (females of the west-central Florida, and males of the east-central Florida, populations have means 1 to 2 scales less than those just mentioned).

In the central highlands of Florida and in the eastern coastal lowlands north of Daytona Beach, ventral counts decrease abruptly, the means ranging from 156.4 to 157.8 in males, 153.6 to 154.9 in females. Ventral number falls off sharply to the north in inland Georgia, but on the coast it varies from the mean range stated for northern Florida by less than 1 scute in females and less than 3 in males (larger series of males may somewhat alter this picture) from northeastern Florida to central New Jersey, thence inland up the west side of the Hudson River to the vicinity of Albany, New York. On and adjacent to the Piedmont from the Savannah River to southeastern Pennsylvania, mean ventral counts are 2 to 4 scales less than on the outer Atlantic Coastal Plain. In these inland populations the number of mean ventrals increases to the north, but by less than  $1\frac{1}{2}$  scales in females, somewhat more in males. These populations agree rather well in mean number of ventrals with those located in extreme northern Georgia and eastern West Virginia.

On Long Island and at scattered localities in New York east of the Hudson River as far north as Lake George, the ventral count in females rises abruptly to a mean of 158.0; there is virtually no change in males. As counts in New England females are somewhat lower, this change does not appear to be associated with any clinal trends. In central New England means for females range from 154.4 to 156.1; only the southern New Hampshire sample has a sufficient number of males to place any reliance on the resulting mean (i.e. 158.0). Thus, these populations show a slight increase in ventral number over the relatively stable Atlantic Coastal Plain series, but this trend is abruptly reversed in southeastern Massachusetts, Maine, and Nova Scotia, where the means fall between 152.1 and 154.0 in males, 149.3 and 152.0 in females.

**SUBCAUDALS.** Variation in subcaudal number appears to be almost chaotic when viewed in terms of local populations, and a meaningful evaluation is further hampered by having so few individuals with

complete tails in most series. A generalized pattern can be described, but see figure 10 for details. Mean subcaudal counts in males almost always exceed 120 in the area south of the Ohio River on the west, and as far north as southeastern Pennsylvania, northern New Jersey, and possibly Connecticut on the east. Within this area the means



exceed 125 in eastern Virginia, coastal Georgia, the southern 4/5 of peninsular Florida, the Mobile Bay-Pensacola Bay area (the highest mean, 131.8, occurs here), southwestern Mississippi, and northern Mississippi. The mean number decreases to the north, males from populations in northern Indiana, Michigan, Ontario, and Maine having not over 112. Females from this northern area have less than 105 mean ventrals. The mean number in females increases southward, rarely being less than 112 south of New Hampshire, southeastern New York, Pennsylvania, Ohio, and central Indiana. The mean exceeds 120 in females from northeastern Florida, southeastern Florida, west-central Florida (the highest mean, 122.3, occurs here), Levy County, Florida, the Mobile Bay-Pensacola Bay area, and northern Mississippi.

**PROPORTIONS.** Relative tail length is fairly constant in the area south of the Ohio River, and in southern Pennsylvania, New Jersey, and southeastern New York. Means of tail length/total length values in males usually fall between 0.345 and 0.355, in females between 0.335 and 0.345. Means are in excess of 0.360 in males from central Tennessee and the mid-Savannah River area, and as high as 0.378 for a small series from eastern West Virginia. In three New England series the mean for males is 0.343 as compared to 0.352 in New Jersey, in females the respective means are 0.330 and 0.342. The one male available from Nova Scotia (NSMS unnumbered) has a value of 0.310. Males from western New York, northwestern Pennsylvania, Ohio, and southern Indiana have means ranging from 0.327 to 0.336; means in females range from 0.317 to 0.319. In northern Indiana and Michigan means in males range from 0.310 to 0.315; in females from 0.299 to 0.308. In eastern Ontario the mean for females is 0.312.

**PATTERN.** The vertebral stripe is frequently poorly developed or lacking in the snakes inhabiting peninsular Florida and southeastern Georgia. As the stripe in this area is tan, often only a shade lighter than the dorsum, it tends to disappear with the loss of its narrow, black borders, though it is almost always at least faintly indicated for a short distance immediately behind the head. Throughout the rest of the species' range the vertebral stripe is always present and distinctly margined by the black paravertebral stripes, which may vary greatly in width. In the Great Lakes region, where the dorsum is usually black or nearly black, the stripe is often narrower, involving in addition to all of the vertebral row, somewhat less than half the width of each paravertebral row. The vertebral stripe in *T. proximus* is also often narrower in the northern part of the range.

In peninsular Florida and southeastern Georgia the lateral stripe is narrow, always occupying less than half of one of the two rows bearing it, and usually less than half of both rows. In the Great Lakes region frequently the lateral stripe slightly involves dorsal scale row 2 on the anterior part of the body in addition to the normal 3 and 4, thus paralleling the condition typical of *Thamnophis butleri*, which inhabits part of this same area. While the condition is not entirely characteristic of the eastern ribbonsnake in this region, it does occur here with much higher frequency than elsewhere in the species' range. Individuals with an anteriorly widened lateral stripe have also been observed in samples from central Tennessee, eastern West Virginia, and western Pennsylvania, where they are not associated with a black dorsum. CAS 15680 from West Virginia and NMC 3090.2 from Nova Scotia have rows 3, 4, and 5 incorporated in the lateral stripe.

**COLOR.** From western Levy County, Florida, northwestward along the Gulf Coast to a point almost due south of Tallahassee, the dorsum is usually dark brown to black. It is also black or dark brown in Nova Scotia, Maine, and the Great Lakes region. Throughout the rest of the range, except in peninsular Florida and coastal Georgia where it is tan or light brown, the dorsum is a reddish brown.

In ribbonsnakes from peninsular Florida and southeastern Georgia the vertebral stripe is usually some shade of tan, occasionally with a metallic luster, or it is lacking. Outside this area it is usually some shade of yellow, occasionally overlaid with dark pigment in the Great Lakes region.

The lateral stripe is yellow throughout most of the species' range; it is occasionally white at scattered localities on the Florida peninsula. In western Levy County and in the coastal lowlands to the northwest it is usually light blue or bluish white.

**DISCUSSION.** Geographic variation is, for the most part, of the discordant type discussed previously under *T. proximus*. Like that species, *T. sauritus* has two major zones of concordant character transition. An abrupt change in supralabial number, lateral stripe width, vertebral stripe color, and a slighter one in color of the dorsum takes place between the peninsular Florida-southeastern Georgia area and the region to the north and west. This transition may be related to the postulated isolation of much of peninsular Florida from the mainland in the form of islands during shifts in the level of Pleistocene seas (see Neill, 1957, for a detailed discussion of the effects of this isolation on vertebrate evolution).

The other transition zone appears associated to some degree with

the southern limits of Pleistocene glaciation. The animals occupying glaciated terrain have darker dorsa, relatively shorter tails, and fewer subcaudals than the populations south of the glacial boundary. This correlation breaks down in northern New Jersey, eastern New York, and southern New England where long-tailed snakes with brown dorsa and high subcaudal counts range well into glaciated territory. These may, however, represent a fairly recent invasion.

The elements of color pattern have less observable geographic variability in *T. sauritus* than do the numbers of ventrals or subcaudals.

### TAXONOMY

The population samples examined appear to represent four major populations which replace each other geographically. These are defined chiefly on the basis of differences in color pattern, to a lesser degree in scutellation and proportions. The salient features of these populations are discussed below within their formal descriptions as subspecies.

#### Subspecies of *Thamnophis sauritus*

The following key for distinguishing adults of the four races of *T. sauritus* was designed primarily for use with live material. If only preserved specimens are available, attention should be paid to the geographical source of the sample.

1. Supralabials 7, occasionally 8; vertebral stripe some shade of yellow; lateral stripe occupies  $\frac{1}{2}$  or more of both rows 3 and 4 ..... 2  
     Supralabials 8, rarely 7; vertebral stripe tan, or lacking; lateral stripe narrow, occupying less than  $\frac{1}{2}$  of either row 3 or 4, or both ..... 3
2. Dorsum reddish brown; lateral stripe rarely widened anteriorly; tail relatively long (mean tail length/total length usually exceeding 0.340 in males, 0.330 in females) ..... *T. s. sauritus*  
     Dorsum velvety black or dark brown; lateral stripe frequently widened anteriorly, involving row 2; tail relatively short (mean tail length/total length usually not exceeding 0.335 in males, 0.325 in females) ..... *T. s. septentrionalis*
3. Dorsum tan or brown, rarely dark; lateral stripe yellow, occasionally white ..... *T. s. sackenii*  
     Dorsum dark brown or black; lateral stripe bluish white or light blue, occasionally white ..... *T. s. nitae*

#### *Thamnophis sauritus sauritus* (Linnaeus)

*Thamnophis sauritus sauritus*: Ruthven, 1908:122 [by implication]

*Thamnophis sirtalis sirtalis*: Klauber, 1948:9

NEOTYPE. The data presented for the species apply here.

DEFINITION. A subspecies of *Thamnophis sauritus* characterized by 7

supralabials, a reddish-brown dorsum, a golden yellow vertebral stripe, and a relatively long tail.

**RANGE.** From southern New England, eastern New York, New Jersey, and eastern Pennsylvania, west-southwestward through southern Ohio and southern Indiana to the Mississippi River, south to the northern edge of Lake Ponchartrain on the west and to northwestern Florida and Georgia (exclusive of the southeastern third of the state) on the east.

**DESCRIPTION OF NEOTYPE.** Scutellation and proportions (from Schmidt and Conant, 1956-57): Oculars 1 + 3, temporals 1 + 3, supralabials 7, infralabials 10, dorsal scale rows 19-19-17, ventrals 156, subcaudals 113. Body length 388 mm., tail length 202 mm., tail length/total length ratio 0.342.

As Schmidt and Conant's (1956-57) description of the neotype is based on a preserved specimen, the following color notes are presented for UF 12187.1, an adult male collected 1.5 miles N Ravenel, Charleston County, South Carolina, by N. J. and D. A. Rossman. Dorsum reddish brown (Maerz and Paul 14B12), slightly lighter below the lateral stripe; vertebral stripe golden yellow (12J2); lateral stripe light yellow (10H1); venter cream (9F1); dark ventrolateral stripe broad, occupying 0.25 the width of a ventral scute on each side; chin shields and infralabials white, supralabials yellowish white. The light postocular spot is confined to the lower postocular; the black postorbital vitta is broad. The tiny parietal spots are separate and yellow, margined narrowly with black.

**DISCUSSION.** Counts and measurements of the nominate race may be summarized as: postoculars 2 to 4, temporals 1 + 1 to 2 + 3, supralabials 6 to 8, infralabials 8 to 11, intergenials 1 to 4, dorsal scale rows 17-18-17 to 19-19-17, male ventrals 145-166, female ventrals 143-169, male subcaudals 106-136, female subcaudals 96-130. Body length in males ranges from 124.5 to 451 mm., in females 129 to 636 mm. Total length in males 185 to 665 mm., in females 190 to 956 mm. Adult tail length/total length ratio in males 0.333 to 0.388, in females 0.317 to 0.388.

My concept of the color pattern in *T. s. sauritus* is based on living specimens from Cape May, Sussex, and Warren Counties, New Jersey; Hyde County, North Carolina; Charleston County, South Carolina; Barbour County, Alabama; and Forrest County, Mississippi, as well as on a colored slide of a snake from Burlington County, New Jersey, and color notes on one from Tolland County, Connecticut. Intergradation involving the nominate race is discussed later.

The subspecies *sauritus* is wide ranging and apparently thrives under a great many environmental conditions. It may have evolved on the mainland when the ancestral stock of the species (of which *T. s. sackenii* probably is closest to being the present-day representative) was isolated on one or more of the islands that constituted Florida at various times during the Pleistocene.

*Thamnophis sauritus septentrionalis*, new subspecies

**HOLOTYPE.** UF 12179.2, an adult female from Michigan Hollow, near Ithaca, Tompkins County, New York, collected 20 May 1959 by J. A. Bartley.

**DEFINITION.** A subspecies of *Thamnophis sauritus* characterized by 7 supralabials, a velvety black or dark brown dorsum, a yellow vertebral stripe often overlaid with brown pigment, and a relatively short tail.

**RANGE.** From Nova Scotia, Maine, and possibly central New Hampshire westward through southern Ontario and western New York to extreme northern Michigan and central Indiana. There may be an isolated colony in northeastern Wisconsin (see Discussion).

**DESCRIPTION OF HOLOTYPE.** Scutellation: Oculars 1 + 3, temporals 1 + 2, supralabials 7, infralabials 10, intergenials 2, dorsal scale rows 19-19-17, ventrals 156, subcaudals 108. Body length is 574 mm., tail length 271 mm., tail length/total length ratio 0.321.

The dorsum is velvety black on the anterior  $\frac{2}{3}$  of the body, dark brown posteriorly; below the lateral stripe the dorsum is dark brown (Maerz and Paul 7E12). The vertebral stripe is yellow, but so heavily overlaid with brown that it is impossible to determine the exact shade; the lateral stripe is light yellow (10J1). The venter is pale green suffused throughout with tan; the dark ventrolateral stripe is broad, occupying 0.20 the width of a ventral on each side. The chin shields and infralabials are white, the supralabials a pale greenish white. The head is black, hence no postorbital vitta is visible; the parietal spots are lacking.

**DISCUSSION.** Counts and measurements of this subspecies are: postoculars 2 to 5, temporals 1 + 1 to 2 + 3, supralabials 6 to 8, infralabials 7 to 11, intergenials 1 to 3, dorsal scale rows 18-19-17 to 19-21-18, male ventrals 152-177, female ventrals 148-169, male subcaudals 98-123, female subcaudals 94-114. Body length in males ranges from 125.5 to 438 mm., in females 128 to 574 mm. Total length in males 179 to 652 mm., in females 184 to 845 mm. Adult tail length/total length ratio in males 0.298 to 0.333, in females 0.288 to 0.335.

In defining *T. s. septentrionalis* and in attempting to delimit its range, I have had access to living ribbonsnakes from Monroe and Tompkins Counties, New York; Trumbull County, Ohio; Hillsdale and Washtenaw Counties, Michigan; and Marshall County, Indiana, as well as to colored slides of two live individuals from Honey Harbour, Ontario, and color notes on a series of specimens from Rondeau Provincial Park, Ontario. Each of these animals has the dorsum black or dark brown on at least the anterior half of the body and usually more.

Locating the zone of intergradation between *T. s. septentrionalis* and *sauritus* by examination of preserved specimens is hampered by the fading of what was a black dorsum in life to a brown one after several years in preservative, particularly if the animal was approaching ecdysis at the time of preservation. Nevertheless, a cautious evaluation of color in preserved specimens coupled with relative tail length values and the color data from live material permits an estimate of the subspecies' southern range limits. A more accurate delimitation awaits color notes on more live specimens from critical points.

The northern Indiana population clearly belongs to *T. s. septentrionalis*, the central Indiana snakes appear close to it (though they may possibly be intergrades), and the series from southwestern Indiana-southeastern Illinois represents either *sauritus*  $\times$  *septentrionalis* intergrades or *sauritus*. Two adult males (UMMZ 107916, 108092) from the Muscatatuck River in southeastern Indiana near the glacial boundary appear to be *T. s. sauritus*. The zone of intergradation probably extends through central Ohio. The color pattern of a live adult female from Licking County in south-central Ohio is typical of *T. s. sauritus*, but its tail is relatively short. OSM 758 from Jackson County in the southern part of the state is definitely *sauritus*. Northeastern Ohio ribbonsnakes are members of the northern race, and so presumably are the populations in adjacent Pennsylvania, although their exact status is not clear. Ribbonsnakes from the vicinity of Pittsburgh probably are intergrades. All the West Virginia animals examined appear to be typical *sauritus*, with the possible exception of CM 28127 from Preston County, which may have had a black dorsum in life, although it agrees with the nominate form in all other characters.

The eastern New York and southern and central New England ribbonsnakes all appear to be *T. s. sauritus*, but the southern New Hampshire sample may be representatives of an intergrade population. I have included the small series from Maine in *T. s. septentrionalis* because these animals appear to have had black dorsa in life, and at least one of them (MCZ 699) shows anterior widening of the lateral



stripe. This population seems to be disjunct from the main body of the range of *septentrionalis*, but the literature records for Essex and Franklin Counties, New York (Weber, 1928, and Evermann, 1918, respectively), probably are based on individuals of this race, and future collecting in central New Hampshire and central Vermont may well close the gap. Bleakney (1951) noted that the *T. sauritus* he collected in Nova Scotia were black with yellow stripes. The only specimen of that series with a complete tail (NSMS unnumbered) has the low tail length/total length value characteristic of *T. s. septentrionalis*. This population is unquestionably a relict; Bleakney (1958) has discussed the probable cause of the disjunction.

Dickinson (1950) reported that H. K. Suzuki observed a ribbon-snake at Bass Lake, Marinette County, Wisconsin, but that the specimen was not preserved. Nevertheless, a specimen in the Milwaukee Public Museum (MPM 1829) is listed as collected by Suzuki in Marinette County at Bass Lake. It agrees fairly closely with Michigan *T. s. septentrionalis* in details of scutellation, and dorsal scale row 2 is clearly involved anteriorly in the lateral stripe. Hence an isolated colony of *septentrionalis* quite possibly exists in northeastern Wisconsin and the upper peninsula of Michigan.

The black dorsum of *septentrionalis* and the frequent narrowing and darkening of its vertebral stripe probably are adaptations for absorption of solar radiation paralleling those in the northern race of *T. proximus*. As the brown young are almost identical in color to the young of *T. s. sauritus*, it seems fairly certain that *septentrionalis* represents a northern, more cold-tolerant derivative of the nominate race.

The subspecific name *septentrionalis* (Latin, of the north) refers to the northern distribution of this race in relation to the range of the species.

*Thamnophis sauritus sackenii* (Kennicott)

*Thamnophis saurita* var. *sackenii*: Duméril and Bocourt, 1893:759

*Thamnophis sauritus sackenii*: Ruthven, 1908:107

*Thamnophis sauritus sackenii*: Blanchard, 1925:18

*Thamnophis sirtalis sackenii*: Klauber, 1948:9

**HOLOTYPE.** The holotype was collected in "Florida" by Baron Osten Sacken and was originally deposited in the collection of Northwestern University, but Orlando Park informs me it is no longer there. As letters to a number of museums have failed to reveal it, we may presume it lost. A neotype has not been designated because the original description (Kennicott, 1859) and the type locality serve adequately

to associate the name with a specific population. Schmidt (1953) restricted the type locality to Gainesville, Alachua County, Florida.

**DEFINITION.** A subspecies of *Thamnophis sauritus* characterized by 8 supralabials, a tan to brown dorsum, a tan vertebral stripe often with a metallic luster, a narrow lateral stripe, and a relatively long tail.

**RANGE.** Throughout peninsular Florida (exclusive of western Levy County and the coastal area to the northwest of that county) west to the vicinity of Tallahassee, and north through the Okefenokee Swamp and coastal Georgia to Jasper County, South Carolina. Apparently a small colony is isolated on St. Vincent's Island just west of the mouth of the Apalachicola River. Contrary to virtually every recent statement of the western range limits of this subspecies, *T. s. sackenii* does not occur in Mississippi, Alabama, or in Florida west of the Apalachicola River.

**DESCRIPTION.** In the absence of the holotype, the following description is based on UF 12145.2, an adult female from 2.5 miles E Moss Bluff, Marion County, Florida, collected by W. T. Neill and S. R. Telford, Jr. Scutellation: Oculars 1 + 3, temporals 1 + 2, supralabials 8, infralabials 10, intergenials 2, dorsal scale rows 19-19-17, ventrals 151, subcaudals 114. Body length is 458 mm., tail length 223 mm., tail length/total length ratio 0.327.

The dorsum is brown. The vertebral stripe is metallic tan, the lateral stripe pale yellow and narrow, the stripe occupying slightly less than  $\frac{1}{2}$  the width of a scale on rows 3 and 4. The venter is pale greenish yellow, pale green on the tail; the dark ventrolateral stripe is broad, occupying slightly more than 0.25 the width of a ventral scute on each side. The chin shields and lower part of the infralabials are white, the supralabials and upper part of the infralabials pale yellow. Parietal spots are lacking.

**DISCUSSION.** Counts and measurements of this subspecies may be summarized as: postoculars 2 to 5, temporals 1 + 2 to 2 + 3, supralabials 7 to 9, infralabials 8 to 12, intergenials 0 to 3, dorsal scale rows 19-17-17 to 19-19-17, male ventrals 150-171 $\frac{1}{2}$ , female ventrals 146-166, male subcaudals 118-134, female subcaudals 105-131. Body length in males ranges from 144 to 537 mm., in females 137 to 670 mm. Total length in males 215 to 820 mm., in females 207 to 1018 mm. Adult tail length/total length ratio in males 0.328 to 0.382, in females 0.317 to 0.364.

I have seen living examples of this subspecies from Alachua, Brevard, Broward, Collier, Dade, Duval, Hendry, Lake, Levy, Manatee, Marion, Martin, and Palm Beach Counties, Florida, and from

Jasper County, South Carolina, as well as a colored slide of one from Charlton County, Georgia. The South Carolina specimen, from the Savannah National Wildlife Refuge, is typical of *T. s. sackenii* in every respect. A preserved specimen (UF 12186) from the same locality also appears assignable to the southern race. A living specimen (unfortunately no longer available) from Ridgeland, some 20 miles farther north in Jasper County, appeared to be either a *sackenii* or an intergrade. As individuals from less than 50 miles up the coast in Charleston County are characteristic of the nominate subspecies, intensive collecting in the intervening area should reveal intergrades.

Inland, a series from the Okefenokee Swamp I consider unquestionably *sackenii* despite a high incidence of 7 supralabials. Neill (1954) expressed the opinion that animals from as far inland as Emanuel County, Georgia, and Barnwell County, South Carolina, are closer to *sackenii* than to *T. s. sauritus*, and that *sauritus* does not occur below the Fall Line in eastern Georgia. I have not seen specimens from Emanuel County, but I find the sample from just below the Fall Line in eastern Georgia and adjacent South Carolina to be fairly typical of *sauritus*.

Two adult females (UMMZ 106234-235) from Lake Miccosukee, Jefferson County, Florida, are *T. s. sackenii*, although one of them has 7 supralabials on both sides of the head. They represent the westernmost locality for this race, except for UF 7385, an adult female from St. Vincent's Island, Franklin County, Florida. This specimen definitely appears to be *sackenii*, but all the specimens collected on the adjacent mainland are good examples of *sauritus*. Only further collecting can resolve the situation. All specimens available from southwestern Georgia appear to be *sauritus*. Intergrades between *sackenii* and *T. s. nitae* are discussed under *nitae*.

Cliburn (1961) recently demonstrated that *T. s. sackenii* is not found in southern Mississippi as had been generally accepted, but he stated that the genetic influence of *sackenii* was apparent in the slightly higher tail length/total length values in extreme southeastern Mississippi. This implies that *sackenii* has a relatively longer tail than *T. s. sauritus*, a contention not supported by my data. The southeastern Mississippi material I have examined is typical *sauritus*.

*Thamnophis sauritus nitae*, new subspecies

HOLOTYPE. UF 12150.2, an adult female from McDonald Slough, St. Marks National Wildlife Refuge, Wakulla County, Florida, collected 16 May 1959 by N. J. and D. A. Rossman.

**DEFINITION.** A subspecies of *Thamnophis sauritus* characterized by 8 supralabials, a dark brown or black dorsum on at least the anterior part of the body, the vertebral stripe obscure or absent, a bluish-white or light blue lateral stripe, and a relatively long tail.

**RANGE.** The coastal lowlands of northwestern peninsular Florida from the Withlacoochee River on the south to central Wakulla County on the west.

**DESCRIPTION OF HOLOTYPE.** Scutellation: Oculars 1 + 3, temporals 1 + 2, supralabials 8, infralabials 10, intergenials 3, dorsal scale rows 19-19-17, ventrals 160, subcaudal series and tail incomplete. Body length is 621 mm.

The dorsum is black for a short distance behind the head, becoming dark brown posteriorly (Maerz and Paul 15L12 at midbody) with much black pigment overlaying the brown. The vertebral stripe is lacking; the narrow lateral stripe is light blue (34G1). The venter is bluish white anteriorly, becoming pale tannish yellow thereafter (the posterior margin of each scute is light bluish green); the dark ventrolateral stripe is broad, occupying 0.20 the width of a ventral on each side. The chin shields are white, and supralabials light blue at least posteriorly. The head is black, hence no postorbital vitta is visible; the parietal spots are lacking.

**DISCUSSION.** Counts and measurements of this subspecies are: postoculars 3 to 4, temporals 1 + 2 to 2 + 2, supralabials 7 to 8, infralabials 9 to 11, intergenials 1 to 3, dorsal scale rows 17-19-17 to 19-19-17, male ventrals 161½-169, female ventrals 156-166, male subcaudals 119-131, female subcaudals 105-130. Body length in males ranges from 150 to 534 mm., in females 146.5 to 621 mm. Total length in males 220 to 756 mm., in females 216 to 701 mm. Adult tail length/total length ratio in males 0.335 to 0.358, in females 0.331 to 0.372.

I have examined living examples of this race from Jefferson, Levy, Taylor, and Wakulla Counties, and a freshly killed specimen from Dixie County, all in Florida. All those from localities northwest of the Suwannee River are fairly typical of this subspecies as defined above. The situation in Levy County is confusing: From about the vicinity of Bronson eastward, only *T. s. sackenii* occurs. Specimens fairly characteristic of *nitae* have been collected at or near Vista, Sumner, Otter Creek, Gulf Hammock, Lebanon Station, and Inglis; I have seen individuals intermediate in color pattern between *T. s. nitae* and *sackenii* from the vicinity of Lukens, Sumner, and Yankeetown. One subadult (UF 12141) from 4 miles WSW Sumner is assignable to

*sackenii* on its color pattern. Those ribbonsnakes from western Levy County have a higher mean number of ventrals than does a series from eastern Levy and adjacent Alachua Counties. This mean, however, does not differ from those of coastal lowland populations of *T. s. sackenii* which lie to the south. Insufficient fresh material is available to determine adequately, or perhaps even accurately, the status of the western Levy County snakes, but pending the acquisition of large series of live specimens from throughout this area, I am inclined to assign this population to *T. s. nitae*, as the majority of the specimens examined appear to be much closer to this form than to *sackenii*. The possibility that it is an intergrade population cannot be ruled out and should not be overlooked; if such is the case, it shows a heavier genetic influence from *nitae*. Several individuals from the vicinity of Lake Tsala Apopka in Citrus County are considered to be *sackenii*  $\times$  *nitae* intergrades.

I have seen a few unusually dark *T. s. sackenii* from the Everglades of southern Florida, but such individuals appear only rarely in the populations of that region and lack a continuous distribution.

If the present coloration of CM 12419, an adult female, at all closely approximates its colors in life, the animal is probably a *T. s. sackenii*  $\times$  *nitae* intergrade. The collecting data, however, show the snake was taken 40 miles W Tallahassee in Calhoun County, Florida. The mileage places the locality at Telogia Creek, which is in Liberty County, not Calhoun. If these data are accurate, then *sackenii*, or a derivative, penetrates the range of typical *T. s. sauritus* (which occurs 3 miles WNW Hosford, a locality less than 5 miles east of Telogia Creek) with no indication of intergradation. The specimen in question has 8 supralabials, 161 ventrals, and a tan vertebral stripe; the Hosford specimen (UF 9398, a male) has 7 supralabials, 148 ventrals, and agrees equally well with typical *sauritus* in all other respects. I believe the locality data are in error.

Within the range of *Thamnophis sauritus nitae*, the common gartersnake, *T. sirtalis*, exhibits a remarkable similarity to the ribbon-snake in color pattern (Neill, 1958). The adaptive significance of the dark dorsum and blue lateral stripe present in these gartersnakes is not readily apparent, if indeed there be any. To human eyes at least, *T. s. nitae* is much more conspicuous in each of the several habitats it occupies than would be the comparatively drab *T. s. sackenii*.

The subspecific name *nitae* is in honor of my wife Nita, who collected the first living example I saw of this strikingly beautiful race.

## NATURAL HISTORY

This summary of our knowledge of the ecology of *T. sauritus* is intentionally brief. For a detailed account of this species in the northern part of its range see Carpenter (1952a, 1952b, and 1953).

**HABITAT.** The eastern ribbonsnake occupies a great variety of habitats; the only basic requirement seems to be accessibility to permanent or semipermanent bodies of water. Its habitats include such diverse situations as sandy beach, salt marsh, roadside ditch, pine flatwoods, grassy stream bank, marshy meadow, rocky woodlands, sphagnum bog, and tamarack swamp. I have collected *T. sauritus* in most of these habitats; other records are from the literature and from field notes of colleagues.

Many authors have commented on the semiarboreal tendencies of this species (the generic name *Thamnophis*, which originally applied only to the species *sauritus*, means "bush snake"), which, with its relatively longer tail, is perhaps better adapted for climbing than is *T. proximus*. Carpenter (1952a) reported that 61 percent of the *T. sauritus* collected on his study area in southern Michigan during the summer were up in bushes. The night of 15 August 1961 I saw more than 30 *T. sauritus sackenii* along a sandy road running through a marshy "prairie" in north-central Florida; all were 2 to 4 feet above the ground in the vegetation bordering the road, not an unusual phenomenon in my experience.

**FOOD.** The diet of the eastern ribbonsnake consists chiefly of fishes and adult and larval amphibians. Table 13 lists species that *Thamnophis sauritus* definitely is known to eat in the wild. Several authors (Surface, 1906; Carpenter, 1952a; Hamilton and Pollack, 1956) have found invertebrates in the stomach contents of ribbonsnakes, and Fowler (1907) termed *sauritus* as largely insectivorous. On the basis of present knowledge, Fowler's statement does not seem justified, for the few instances in which invertebrates actually have been found in *sauritus* are probably cases of secondary or accidental ingestion. The eastern ribbonsnake does not seem any more prone than its western counterpart to eat invertebrates, lizards, or endothermic vertebrates voluntarily.

Nocturnal prowling and feeding is extremely common in the species, especially in the southern part of the range and during the warm months.

**REPRODUCTION.** Carpenter (1952b) found that female ribbonsnakes in southern Michigan attain sexual maturity at between 2 and 3 years, when they attain a minimum body length of 421 mm.; he did not

TABLE 13. Food of *Thamnophis sauritus*

Species	Source
<b>Anurans</b>	
<i>Bufo quercicus</i>	Duellman and Schwartz, 1958
<i>Bufo terrestris</i>	Duellman and Schwartz, 1958
<i>Acris gryllus</i>	personal observation
<i>Hyla cinerea</i>	Duellman and Schwartz, 1958
<i>Hyla crucifer</i>	Carpenter, 1952a
<i>Hyla ocularis</i>	Carr, 1940
<i>Hyla squirella</i>	Duellman and Schwartz, 1958
<i>Hyla versicolor</i>	Carpenter, 1952a
<i>Pseudacris nigrita</i>	Duellman and Schwartz, 1958
<i>Pseudacris triseriata</i>	Carpenter, 1952a
<i>Rana areolata</i> (larvae only) <sup>1</sup>	personal observation
<i>Rana clamitans</i>	Carpenter, 1952a
<i>Rana palustris</i>	Carpenter, 1952a
<i>Rana pipiens</i>	Carpenter, 1952a
<i>Rana sylvatica</i>	Carpenter, 1952a; Conant, 1951
<b>Salamanders</b>	
<i>Desmognathus ochrophaeus</i>	Carpenter, 1952a
<i>Desmognathus fuscescens</i>	Carpenter, 1952a
<i>Desmognathus maculatus</i>	Conant, 1951
<b>Fishes</b>	
<i>Umbra limi</i>	Carpenter, 1952a
<i>Gambusia affinis</i> <sup>1</sup>	personal observation
<i>Heterandria formosa</i> <sup>1</sup>	personal observation

<sup>1</sup> Identified by Sam R. Telford, Jr.

present corresponding data for males. McCauley (1945) reported a gravid female from Maryland 341 mm. in body length. The seven smallest gravid female *T. sauritus* I have measured had body lengths of 332. (Pennsylvania), 346 (Georgia), 350 (West Virginia), 365 (Nova Scotia), 371 (Georgia), 374 (West Virginia), and 410 mm. (Ohio) respectively. *Thamnophis sauritus* appears to mature at a smaller body size than does *T. proximus*.

Mating apparently occurs in April in the northern part of the range where spring emergence takes place in the latter part of March; in the extreme southern portion of the range where no true winter hibernation takes place, mating probably occurs earlier. The young are usually born in August in the north, July in the south, with considerable overlap. Dates range from 2 July through 4 October (personal observations). The latter date, surprisingly enough, is for a

female from northern Florida, and it might possibly have been her second brood of the year. Tinkle (1957) has indicated the possibility of a second brood in a female *T. proximus* from southeastern Louisiana, and Telford (1952) reported a female *T. sauritus sackenii* that gave birth to 12 normal young on 9 July and bore four more on 16 September which were malformed and born dead. Several female *sackenii* I collected in north-central Florida 15 August 1961 contained early embryos that almost certainly would not have been born until late September, and possibly represented second broods. This question certainly deserves more thorough investigation.

Brood size ranges from 3 (Ditmars, 1896) to 26 (Telford, 1952), the mean for 69 broods being 11 individuals. Geographic variation in brood size is pronounced. The mean number of individuals is 15.8 in 12 broods from Florida, 12.9 in 9 broods from southern Ontario, 10.7 in 7 broods from Maryland (McCauley, 1945), 10.0 in 5 broods from southern Michigan (Carpenter, 1952a), and 6.0 in 5 broods from northern Michigan (Burt, 1928). As the size of the brood tends to increase with the size of the female, these means may not be strictly comparable. Available data on body length of newly born *T. sauritus* are summarized in table 14. Males average markedly larger than females in the southern part of the range, slightly, if at all larger, in the North. Individuals of *T. sauritus* tend to average smaller at birth than *T. proximus*.

Burt (1928) observed twice as many embryos in the right oviduct than in the left one in 5 female *T. sauritus* she examined, and Tinkle (1957) found a similar ratio in 37 female *T. proximus*.

PARASITES. Langmann (1899) reported an eastern ribbonsnake infected with haemosporidia.

### CONCLUSIONS

*Thamnophis sauritus* is closely related to *T. proximus* and probably evolved from *proximus* or its prototype. Certainly *sauritus*, with its longer tail and reduced number of supralabials, appears the more specialized form. Speciation may have occurred, as in so many other species pairs (Blair, 1958), during division in Pleistocene time into eastern and western populations confined respectively to Floridian and Mexican refugia. In any case, to judge by present distribution of the two species, the Mississippi River, when it was wider than at present, apparently played an important role in the speciation process, possibly by delaying contact between the two populations as they expanded their ranges during glacial retreat. When the two popula-



TABLE 14. Body length of newly born *Thamnophis sauritus*

Locality	N	M	R
Alachua County, Florida.....	3♂♂ 6♀♀	170.7mm 155.7	144 -193 mm 137 -174
Broward County, Florida.....	6♂♂ 7♀♀	168.0 160.4	159.5-176 157 -164.5
Collier County, Florida.....	1♂ 5♀♀	181.0 172.6	170.5-175
Wakulla County, Florida.....	14♂♂ 11♀♀	158.9 153.3	150 -184.5 146.5-157.5
Sussex County, New Jersey.....	5♂♂ 4♀♀	135.0 140.6	124.5-147.5 134.5-144.5
Trumbull County, Ohio.....	13♂♂ 7♀♀	158.4 158.0	148 -169 150.5-165
Marshall County, Indiana.....	5♂♂ 5♀♀	141.0 140.4	125.5-146 131.5-149.5
Washtenaw County, Michigan.....	2♂♂ 4♀♀	149.8 141.8	142 -157.5 138 -145
Rondeau Provincial Park, Ontario*.....	12 11 9 21 9 13 9 11 15	159.2 164.0 149.8 149.3 141.1 154.4 165.3 152.2 163.7	150 -166 153 -170 144 -159 142 -156 130 -149 142 -163 160 -171 140 -160 149 -172

N = number of individuals; M = mean; R = range

\* Personal communication from B. McBride, all others from personal observation.

tions finally did meet, genetic isolation was either complete or nearly so. The great similarity between the two species in diet and habitat preference caused sufficient competition to prevent extensive sympatry. The overlap in ranges in Indiana may be the result of an eastward movement of *proximus* in the Prairie Peninsula during the postglacial Xerothermic period (Smith, 1957); the populations in Indiana, and perhaps those in eastern Illinois and southeastern Wisconsin, probably represent relicts of that earlier, more eastward, distribution.

Except for its long tail and small, separate, parietal spots, *T. sauritus sackenii* bears a striking resemblance to *T. proximus rutiloris* of Gulf and Caribbean Middle America. The similarity is so great that some taxonomic confusion has revolved about a specimen of *sackenii*

(ANSP 5826) which bears incorrect locality data (Rossman, 1961). Two alternative hypotheses present themselves: either *sackenii* and *rutiloris* evolved independently and their similarities are due to convergence, possibly in response to similar environmental conditions (a supposition which disregards the existence of the montane populations of *rutiloris*), or *sackenii* developed from *rutiloris* prior to the partition of the ribbonsnake into two species (*sackenii* in this case is considered to resemble most closely the prototype of the species *sauritus*, and *rutiloris* the prototype of *T. proximus*). The constancy with which the presumably ancestral supralabial number (8) is maintained in *sackenii* seems to indicate that it is the most primitive race of *T. sauritus*. If *sackenii* developed in this manner it explains how, other than through convergent evolution, the species *sauritus* acquired the dark ventrolateral stripe present in Mexican and Central American *T. proximus*, but lacking in those races now in contact with *T. sauritus*.

The ranges of *sackenii* and *rutiloris* are now separated by over 1000 miles and by the ranges of two other subspecies, *T. s. sauritus* and *T. p. orarius*, but roughly comparable disjunctions occur between the Mexican and eastern United States subspecies of *Drymarchon corais* and *Storeria occipitomaculata*. However, only in the latter species has an additional subspecies been interposed between the pair which became separated (assuming that, as certain elements of color pattern seem to indicate, *S. o. obscura* of Florida is more closely related to *S. o. hidalgoensis* of eastern Mexico than either are to the nominate race). The seemingly close relationship between *Storeria dekayi victa* of Florida and *Storeria tropica* (Anderson, 1961) presents an even closer parallel to the *sackenii-rutiloris* situation. This existence of close affinities between Floridian and Mexican forms seems to occur frequently among vertebrates (Neill, 1957; Neill and Allen, 1959).

The members of the *Sauritus* group are, ecologically speaking, both semiarboreal and semiaquatic. They have no peers within the genus in the former category, and in the latter must surely be considered the ecological equivalents in eastern Mexico and eastern United States of *Thamnophis angustirostris*, *T. eques*, and the aquatic group of *T. elegans* of western North America. Several studies (Carpenter, 1952a; Fouquette, 1954) have compared the diet and habitat preference of the ribbonsnakes with those of other species of *Thamnophis* with which they are sympatric, and have shown that of the sympatric species the common gartersnake, *T. sirtalis*, is most like the ribbonsnakes in habitat preference, although not in diet. These studies indicate that the ecological niches occupied by these sympatric species are different enough to prevent serious interspecific competition.

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