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SYSTEMATICS OF THE NEOTROPICAL POPULATIONS OF  
*THAMNOPHIS MARCIANUS* (SERPENTES: COLUBRIDAE)

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The existence of a garter snake other than *Thamnophis proximus* (Say) in the lowlands of tropical America has been known since 1892, when Bocourt described *Entaenia praeocularis* from Belize, British Honduras. The lowland garter snakes were ignored for nearly half a century, but during the period from 1937 through 1940 four additional "species" were described from adjacent areas: *Thamnophis arabdotus* from Catmis, Quintana Roo, México (Andrews, 1937); *T. ruthveni* from Tehuantepec, Oaxaca, México (Hartweg and Oliver, 1938); *T. bovallii* from Granada, Nicaragua (Dunn, 1940); and *T. rozellae* from Palenque, Chiapas, México (Smith, 1940). Of these taxa only *ruthveni* was based on an adequate sample. Hartweg and Oliver (1938) commented on its remarkable similarity to *T. marciannus* (Baird and Girard) in color and pattern, and they suggested that the two forms are parallel derivatives of an *eques*-like ancestor. Smith (1942) claimed that *marciannus* and *ruthveni* could be consistently distinguished by the width of the vertebral stripe, but Mittleman (1949) and Stebbins (1954) later showed that the only differences are in the mean ventral and subcaudal counts. McCoy and Van Horn (1962) were the first to formally treat *ruthveni* as a disjunct subspecies of *marciannus*.

In 1942 Smith resurrected the name *Thamnophis sumichrasti* (Cope) for the unstriped forms with 19 scale rows and their striped "derivatives." He included the then known specimens of *bovallii* and *rozellae*, USNM 25234

from "Guatemala" (now lost, so identity uncertain), and the syntypes of *sumichrasti* (incorrectly associated with the lowland group; see Rossman, 1965) under the name *T. s. sumichrasti*. He also recognized *T. s. praeocularis* (including *arabdotus*), *T. s. fulvus* (Duméril and Bocourt), and *T. s. cerebrosus* (which he described from Escuintla, Guatemala). The latter two taxa actually are highland races of *T. cyrtopsis* (Kennicott), with which species Smith considered his *sumichrasti* to be allied—the former supposedly having radiated in Mexico north of the Isthmus, the latter in Guatemala. Another Guatemalan race, *T. s. salvini*, was described some years later (Smith, Nixon, and Smith, 1950).

When Milstead (1953) revised *T. cyrtopsis*, he synonymized under the name *T. c. sumichrasti* all the forms included by Smith in his species *sumichrasti*. Correctly believing *cyrtopsis* to be a highland species (at least in the southern part of its range), Milstead rejected or ignored all lowland records of *T. sumichrasti* (*sensu* Smith), which was unfortunate since they did not apply to *cyrtopsis* at all.

As fresh material came to hand, several herpetologists became aware that a lowland species does exist. In 1958 Shreve and Gans resurrected *borallii* as a full species, and the following year Neill and Allen (1959) reestablished species status for *praeocularis*, although they did suggest that all the lowland forms might prove to be subspecifically related. In the preface of the reprint edition of their Mexican checklists, Smith and Taylor (1966) ignored the distinctness of the highland and lowland species complexes and lumped them in *T. praeocularis* (recognizing, in the process, all of the subspecies previously included by Smith in his concept of *T. sumichrasti*, even to the extent of resurrecting *T. rozellae* as a subspecies). There the matter has rested until the present study.

Having examined most of the existing specimens of lowland garter snakes from Tropical America, I am forced to conclude that all of them that are not referable to *Thamnophis proximus* belong to the wide-ranging North American species *T. marciannus* (Figure 1). These specimens have a number of basic features in common, the most significant of which is their unique head pattern (Figure 2), as was previously noted by Dunn (1940). Their dissimilarities reflect intraspecific clines as well as discontinuous geographic variation. The geographically variable meristic and mensural features are summarized in Table 1; along with color pattern, they are discussed below.

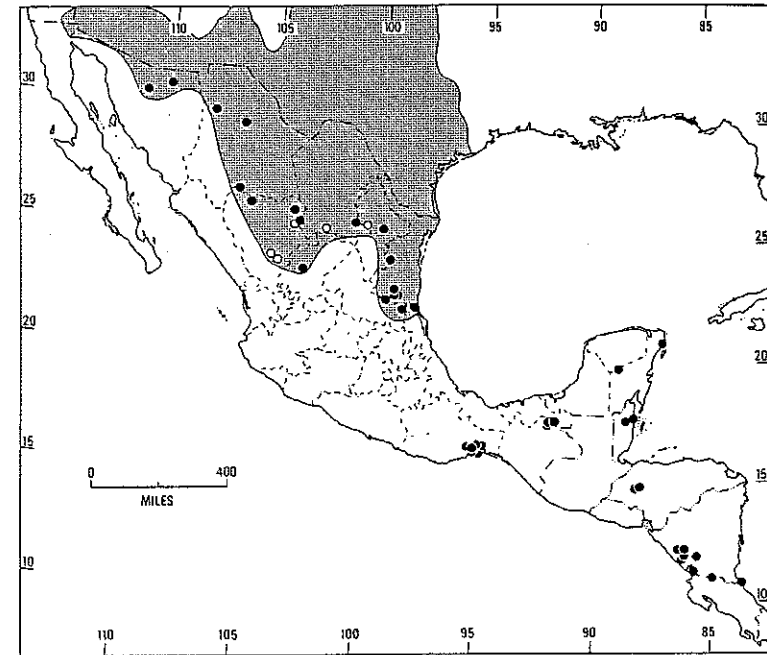


FIGURE 1. The distribution of *Thamnophis marciannus* in Mexico and Central America. Solid circles represent specimens examined, hollow circles represent literature records or museum specimens not examined by me. Within the main continuous range of the species (stippled area) only peripheral records are plotted, not all of the localities from which specimens were examined.

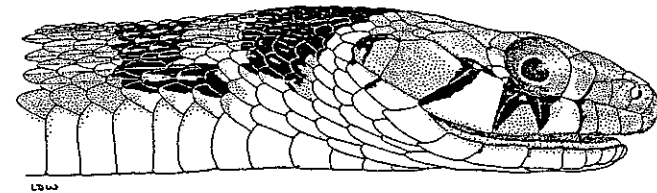


FIGURE 2. Head pattern typical of *Thamnophis marciannus*. Note especially the position of the light supralabials and the light crescent immediately posterior to the last supralabial.

TABLE 1. VARIATION OF SELECTED CHARACTERS IN *THAMNOPHIS* MARCIANUS FROM MEXICO AND CENTRAL AMERICA

| Character                 | Northeastern Mexico <sup>1</sup>                            | Northeastern Mexico <sup>2</sup>       | Northeastern Mexico <sup>3</sup>         |
|---------------------------|---|--|--|
| Maximum Dorsal Scale Rows | 21(96%) 24 <sup>4</sup><br>19(4%) 1                         | 21(100%) 22                            | 21(92%) 33<br>19(8%) 3                   |
| Preoculars                | 1(100%) 22  | 1(100%) 22                             | 1(97%) 29<br>>1(3%) 1                    |
| Ventrals                  | ♂ ♂ 160.6(156-165) 11 <sup>5</sup><br>♀ ♀ 153.5(149-159) 15 | 152.9(145-159) 14<br>147.5(141-155) 11 | 151.2(148-156) 21<br>145.0(139-155) 18   |
| Subcaudals                | ♂ ♂ 73.4(70-80) 7<br>♀ ♀ 65.0(62-68) 7                      | 74.1(68-81) 11<br>66.0(63-70) 6        | 73.6(67-80) 16<br>66.0(61-71) 11         |
| Tail as % of Total Length | ♂ ♂ 23.0(22.1-23.7) 4<br>♀ ♀ 21.2(20.4-22.0) 5              | 23.9(22.2-24.4) 7<br>22.3(22.0-23.0) 5 | 23.8(21.7-25.5) 14<br>22.8(21.7-23.7) 10 |
| Maxillary Teeth           | 24.0(23-25) 4   | 23.0(22-24) 4                          | 23.1(22-25) 14                           |

<sup>1</sup> Includes the states of Sonora, Chihuahua, Durango, and Zacatecas.

<sup>2</sup> Includes the states of Coahuila and western Nuevo Leon.

<sup>3</sup> Includes the states of Veracruz, San Luis Potosi, Tamaulipas, and eastern Nuevo Leon.

<sup>4</sup> Character state, percentage of total sample, and number of specimens.

<sup>5</sup> Mean, range of variation, and number of specimens.

TABLE 1. Continued

| Character                 | Isthmus of Tehuantepec                           | Chiapas-Tabasco                      | Upper Central America <sup>6</sup>     | Lower Central America <sup>7</sup>      |
|---------------------------|--|--------------------------------------|--|---|
| Maximum Dorsal Scale Rows | 21(100%) 28                                      | 19(100%) 4                           | 19(100%) 7                             | 19(100%) 20                             |
| Preoculars                | 1(100%) 28                                       | 1(100%) 4                            | 1(43%) 3<br>>1(57%) 4                  | 1(68%) 15<br>>1(32%) 7                  |
| Ventrals                  | ♂ ♂ 149.0(146-153) 16<br>♀ ♀ 142.5(138-146) 13   | 148.0(146-150) 2<br>138.5(138-139) 2 | 137.0(136-138) 2<br>136.0(134-138) 5   | 144.2(141-148) 13<br>141.4(138-145) 8   |
| Subcaudals                | ♂ ♂ 68.8(65-74) 11<br>♀ ♀ 59.5(56-65) 11         | .....<br>65.5(58-73) 2               | 72.5(69-76) 2<br>71.8(67-75) 4         | 76.5(74-79) 10<br>70.7(68-73) 7         |
| Tail as % of Total Length | ♂ ♂ 22.2(21.3-23.1) 10<br>♀ ♀ 20.4(18.9-21.5) 10 | .....<br>23.3(21.5-24.8) 2           | 25.8(24.7-26.8) 2<br>26.1(24.8-26.8) 4 | 25.7(25.1-26.5) 10<br>24.9(24.1-25.4) 6 |
| Maxillary Teeth           | 23.6(23-24) 5                                    | 23.3(22-25) 3                        | 29.2(27-31) 5                          | 27.1(26-28) 10                          |

<sup>6</sup> Includes Honduras, British Honduras, and the Mexican territory of Quintana Roo.

<sup>7</sup> Includes Nicaragua and Costa Rica.

## GEOGRAPHIC VARIATION

*Dorsal scale rows.*—A sharp break in this feature occurs at the Isthmus of Tehuantepec. At the Isthmus and in northern Mexico the maximum number of rows rarely is less than 21; east of the Isthmus and in Central America there are consistently 19 rows (two specimens from lower Central America have 21 rows at the neck but the number reduces to 19 anterior to the level of the 25th ventral).

*Preoculars.*—Only one of the 106 Mexican specimens examined has more than a single preocular on each side of the head. Roughly one-third of all Central American specimens have two or more preoculars, the incidence rising to 54 percent when we consider only those specimens from Nicaragua, Honduras, and British Honduras (the samples from Costa Rica and the eastern Yucatan Peninsula uniformly have a single preocular), and in many of those specimens recorded as having one preocular the scale is partially divided.

*Ventrals.*—Two clines of gradually increasing ventral numbers extend northwestward and southeastward from upper Central America, the center of low counts. The southeastward cline extends through the lower Central American populations, ventrals in males averaging 143.8 (141-146) in Nicaragua and 145.7 (143-148) in Costa Rica, females averaging 140.0 (138-142) in Nicaragua and 143.7 (142-145) in Costa Rica. From northeastern Mexico another increasing cline runs westward, there being a sizeable step between Coahuila and Chihuahua.

*Subcaudals.*—Instead of varying clinally, subcaudal number assumes a series of plateaus, although sample size in upper Central America and the Chiapas-Tabasco area is so small as to cast considerable doubt on the values obtained. Counts in northern Mexico are essentially uniform, the Isthmian population forms a pocket of low counts, and the highest values occur in Central America. Among the specimens from Chiapas-Tabasco only two have a complete tail. One female (USNM 46549 from Montecristo, Tabasco) has 73 subcaudals, and agrees well in this respect with Central American females, but the other (USNM 108597 from Palenque, Chiapas) has only 58 and thus aligns with the Tehuantepec females. This peculiar intrapopulation segregation is also reflected in the relative tail length of the two females. It is possible that the Palenque specimen has an incomplete tail with a regenerated tip, but careful examination of the animal (a subadult) does not clearly resolve this question one way or the other.

*Relative tail length.*—Tail/total length values exhibit essentially the same geographic pattern as subcaudal number, which is hardly surprising. Again the small sample size in upper Central America and Chiapas-Tabasco clouds the picture.

*Maxillary teeth.*—In terms of the number of teeth, all the Mexican populations agree closely with each other and with a sample of 13 specimens from Texas, Arizona, and California, which has a mean of 22.9 (22-24). In view of the uniformity of this feature over most of the range of the species, the markedly higher counts in Central America were not anticipated and serve to emphasize that tooth counts may be subject to as much geographic variation as any external character.

*Dorsal pattern.*—In northern Mexico the vertebral stripe is brightly colored and distinct from the brown dorsal ground color. The stripe may occupy the vertebral row alone or include the dorsal half of each paravertebral row; in a few cases the edge of the stripe may extend below the keels of the paravertebral scales. The lateral stripe is also distinct from the ground color and

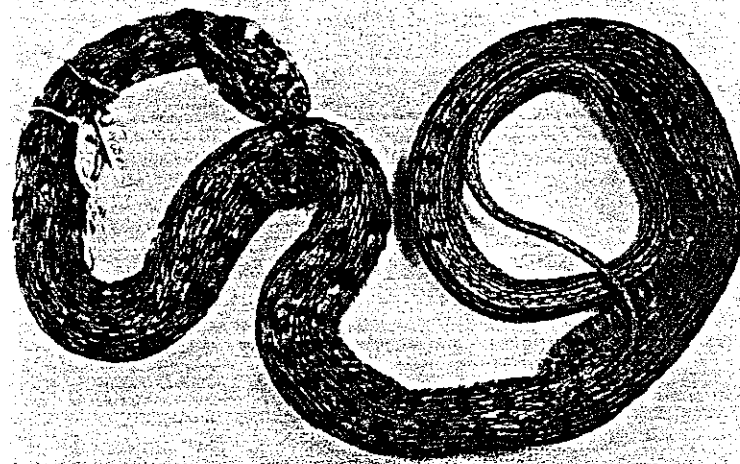


FIGURE 3. A female *Thamnophis m. marciannus* × *praeocularis* (USNM 46549) from Montecristo, Tabasco, México, which is atypical in apparently lacking stripes and having such extensive development of the dark blotches.

is rarely interrupted by ventral extensions of the black lateral body blotches (LSUMZ 11023 from northern Tamaulipas is an exception in having 12 to 15 anterior blotches interrupting the stripes).

In the Tehuantepec population the vertebral stripe is confined to the vertebral row and the color is usually light tan, which does not provide a great contrast to the light brown ground color. The lateral stripe also is less distinct than in the more northern populations. The small Chiapas sample agrees with the Tehuantepec animals, but USNM 46549 from Tabasco is peculiar in having no trace of stripes and extensive development of the lateral blotches (Figure 3).

In upper Central America, too, there is little contrast between the vertebral stripe and the ground color, but the stripe is consistently three full scales wide (Figure 4). The lateral stripe is weakly differentiated and is interrupted anteriorly by extensions of the first 4 to 8 lateral blotches, which also

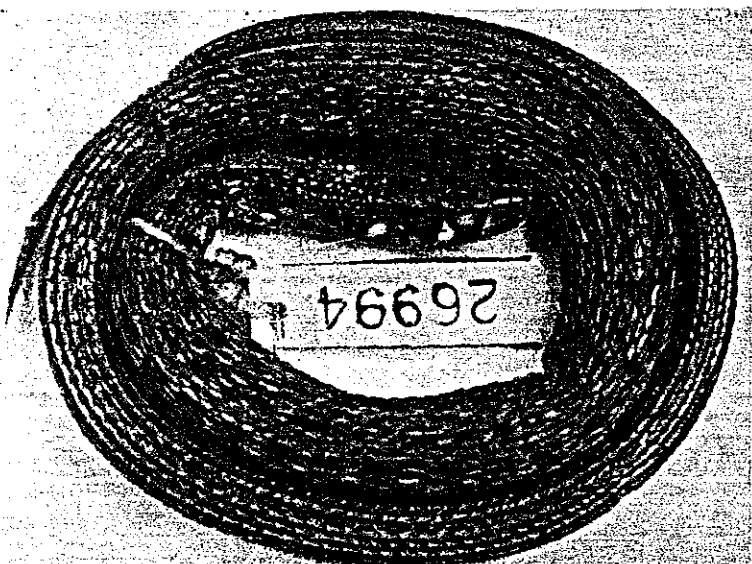


FIGURE 4. A male *Thamnophis marcianus praeocularis* (FMNH 26994; holotype of *T. aradotus*) from Catmis, Quintana Roo, México, which exhibits the broad vertebral stripe characteristic of the subspecies.

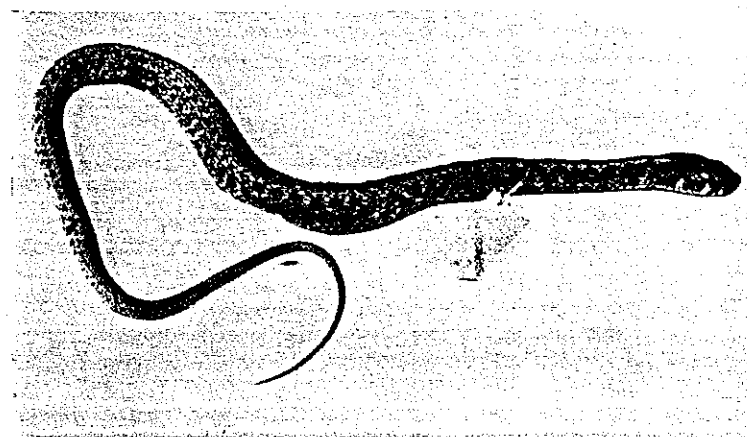


FIGURE 5. The female holotype of *Thamnophis marcianus praeocularis* (MHNP 1172) from Belize, British Honduras, which shows the manner in which the vertebral and lateral stripes are interrupted by expansion of the dark blotches.

encroach on the vertebral stripe in about half the specimens examined (Figure 5).

The vertebral stripe is nonexistent in all specimens from lower Central America except JV 161 and 934 from Nicaragua, in which there is a fairly broad stripe that is not clearly defined. As few as 3 and as many as 30 lateral blotches extend to the venter, interrupting the dull grey lateral stripe in the process. Although the dorsal ground color is brown, the skin between the scales may vary in life from a light orange (LSUMZ 12365 from Nicaragua) to a bright reddish orange (LSUMZ 12364 from Nicaragua). When agitated the latter individual would flatten out, presenting a very colorful sight. Such a display might well possess aposematic value in nature.

*Ventral pattern.*—With only a single exception (USNM 46549 from Tabasco), all specimens from northern Mexico, Tehuantepec, and the Chiapas-Tabasco lowlands have a virtually unspotted, cream-colored venter. In upper Central America the venter is consistently marked with two rows of small, rounded spots. In lower Central America (and in the aforementioned USNM 46549) the spots are larger and laterally expanded, becoming almost crescentic in shape (for a typical example see Shreve and Gans, 1958, Figure 1); in some individuals the spots are so expanded as to merge midventrally. The

field notes accompanying UCLA 14766 from Lake Nicaragua characterized its venter in life as being "vermillion with blue-black bars." The venter of the aforementioned LSUMZ 12364 was bright orange in life, whereas that of LSUMZ 12365 was cream-colored on the throat with a dull yellow median area, these light colors becoming progressively overlaid posteriorly by grey-brown pigment from the sides, which gave the venter a tannish cast anterior to the anal plate. The anal plate and the subcaudals had a light orange wash. Unfortunately the orange colors rapidly disappear in preservative, so that I cannot say if they are characteristic of the populations of lower Central America. Certainly they occur in no other region in the range of the species from which there are data.

*Summary and Taxonomic Conclusions.*—The Central American populations of *Thamnophis marciannus* are sharply set off from the more northern populations in almost all of the characters that vary geographically; only in ventral number do they appear to share a cline. In fact, were it not for the distinctive head pattern that they share and the intermediate nature of the Chiapas-Tabasco population, one would unhesitatingly declare these two groups of populations to be distinct species. The intermediacy of the Chiapas-Tabasco snakes is, however, almost classic. In number of dorsal scale rows and number of ventrals in females, they resemble the Central American populations; in number of ventrals in males, number of preoculars, and number of maxillary teeth, they are virtually indistinguishable from the population at the Isthmus of Tehuantepec. The latter is also true of the dorsal and ventral patterns of the three Chiapas specimens, whereas in these features USNM 46549 from Tabasco more nearly resembles snakes from lower Central America. This Tabasco female also has a subcaudal number and relative tail length comparable to those of Central American females. The lone Chiapas female agrees with Tehuantepec females in both respects. Fresh material from the Chiapas-Tabasco lowlands is much to be desired.

The distinctiveness of the two major geographic groups of *T. marciannus* implies a relatively long period of isolation and separate evolutionary histories, the Chiapas-Tabasco lowlands being the region of secondary contact. Within each group some differentiation of the component populations has occurred and the resulting phenotypes have been given nomenclatural recognition. *Thamnophis m. nigrolateris* Brown from southwestern United States and northwestern Mexico is distinguished solely by its high number of ventrals; this difference, while real, does not seem to me to be adequate grounds for subspecific recognition (see Rossman, 1963:129-130, for the rationale)

and *nigrolateris* is herewith relegated to the synonymy of *T. m. marciannus*. I am according the same treatment to *T. m. ruthveni*, a weakly differentiated form at best, which, although isolated from its northern relatives by a distributional gap of 450 miles, differs significantly from them only in having fewer subcaudals, a slightly shorter tail, and a more pallid vertebral stripe.

On the other hand, the populations in upper and lower Central America differ in both dorsal and ventral pattern, as well as in the numbers of maxillary teeth and ventrals. The snakes from upper Central America are characterized by a very broad vertebral stripe, two rows of small rounded spots on the ventrals, and the fewest ventrals and greatest number of maxillary teeth of any population of *T. marciannus*. This population should be referred to as *T. m. praeocularis*. In lower Central America there rarely is any vertebral stripe, the ventral spots are greatly expanded and may even be fused, and there are slightly more ventrals and slightly fewer maxillary teeth than in *praeocularis*. The population thus characterized should be known as *T. m. bovallii*. The Chiapas-Tabasco snakes are considered to represent *T. m. marciannus* × *praeocularis* intergrades.

The geographic races of *Thamnophis marciannus* that I consider valid are as follows:

- T. m. marciannus*—Southwestern United States and northern Mexico; an isolated population near Tehuantepec, Oaxaca.
- T. m. praeocularis*—Quintana Roo, México, coastal British Honduras, and Lake Yojoa, Honduras.<sup>1</sup>
- T. m. bovallii*—Lakes Managua and Nicaragua, Nicaragua, to northern Costa Rica.

*Problematical specimen.*—A specimen from British Honduras, which Neill and Allen (1959) reported, figured, and called *Thamnophis praeocularis*, defies easy allocation or explanation. Although they collected the specimen less than 27 airline miles southwest of Belize, the type locality of *praeocularis*, the animal agrees with the Tehuantepec population of *T. m. marciannus* in all diagnostic features. The specimen (NRU 2619; formerly ERA-WTN No. BH-201), a small adult male (erroneously identified as a female by Neill and Allen, 1959), has 143 ventrals, 68 subcaudals, a maximum of 21

<sup>1</sup> The Honduras specimens were mistakenly identified and reported as *Thamnophis cyrtopsis* by Neill and Allen (1961).

dorsal scale rows, the tail 22.6% of total length, 25 maxillary teeth, and a single preocular. The light vertebral stripe is distinct and confined to the vertebral scale row; there are no ventral spots comparable in position to those of either *T. m. praeocularis* or *T. m. bovallii* (the only spots present are more laterally situated and are concealed when the ventrals are in a normal position). The occurrence of this specimen in this particular locality defies explanation; obviously additional material is sorely needed.

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