Systemics of the neotropical populations of *Thamnophis marcianus* (Serpentes: Colubridae)

Douglas A. Rossman
SYSTEMATICS OF THE NEOTROPICAL POPULATIONS OF THAMNOPHIS MARCIANUS (SERPENTES: COLUMBRIDAE)

By DOUGLAS A. ROSSMAN

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 praecocularis 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 arbadotus from Catmis, Quintana Roo, México (Andrews, 1957); 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 simiebrasti (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 *sunichrasti* (incorrectly associated with the lowland group; see Rossman, 1965) under the name *T. s. sunichrasti*. He also recognized *T. s. praeocularis* (including *arubatina*), *T. s. falvus* (DuMéril and Bocourt), and *T. s. cerebrosum* (which he described from Escuintla, Guatemala). The latter two taxa actually are lowland races of *T. cyrtopis* (Kennicott), with which species Smith considered his *sunichrasti* to be allied—the former supposedly having radiated in Mexico north of the Isthmus, the latter in Guatemala. Another Guatemalan race, *T. s. salvinii*, was described some years later (Smith, Nixon, and Smith, 1930).

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

As fresh material came to hand, several herpetologists became aware that a lowland species does exist. In 1938 Shreve and Gans resurrected *bavillii* 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. sunichrasti*, even to the extent of resurrecting *T. rotellae* 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. marcianus* (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.
Table 1. Variation of Selected Characters in *Thamnophis marcellinus* from Mexico and Central America

<table>
<thead>
<tr>
<th>Character</th>
<th>Northwestern Mexico¹</th>
<th>Northcentral Mexico²</th>
<th>Northeastern Mexico³</th>
</tr>
</thead>
<tbody>
<tr>
<td>Maximum Dorsal Scale Rows</td>
<td>21(96%) 24⁴</td>
<td>21(100%) 22</td>
<td>21(97%) 22</td>
</tr>
<tr>
<td>Precuneals</td>
<td>1(100%) 22</td>
<td>1(100%) 22</td>
<td>1(97%) 22</td>
</tr>
<tr>
<td>Ventrals</td>
<td>8 8</td>
<td>160.6(154-168) 11⁵</td>
<td>152.9(143-159) 14</td>
</tr>
<tr>
<td></td>
<td>9 9</td>
<td>153.5(149-159) 15</td>
<td>147.5(141-155) 11</td>
</tr>
<tr>
<td>Subcaudals</td>
<td>9 8</td>
<td>73.4(70-80) 7</td>
<td>74.1(68-81) 11</td>
</tr>
<tr>
<td>Total length</td>
<td>8 9</td>
<td>61.0(62-68) 7</td>
<td>66.0(60-70) 6</td>
</tr>
<tr>
<td>Tail as % of Total length</td>
<td>8 8</td>
<td>23.0(22.1-23.7) 4</td>
<td>23.9(22.2-24.7) 4</td>
</tr>
<tr>
<td>Maxillary Teeth</td>
<td>8 9</td>
<td>21.2(20.4-22.0) 5</td>
<td>22.3(21.2-23.0) 5</td>
</tr>
<tr>
<td></td>
<td></td>
<td>24.0(23-25) 4</td>
<td>23.0(22-24) 4</td>
</tr>
</tbody>
</table>

¹ Includes the states of Sinaloa, Chihuahua, Durango, and Zacatecas.
² Includes the states of Coahuila and western Nuevo Leon.
³ Includes the states of Veracruz, San Luis Potosí, Tamaulipas, and eastern Nuevo Leon.
⁴ Character state, percentage of total sample, and number of specimens.
⁵ Mean, range of variation, and number of specimens.

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Table 1. Continued

<table>
<thead>
<tr>
<th>Character</th>
<th>Lithuan of Tequesquite</th>
<th>Chiquito-Tehuacán</th>
<th>Upper Central America⁶</th>
<th>Lower Central America⁷</th>
</tr>
</thead>
<tbody>
<tr>
<td>Maximum Dorsal Scale Rows</td>
<td>21(100%) 28</td>
<td>19(100%) 22</td>
<td>19(100%) 7</td>
<td>19(100%) 22</td>
</tr>
<tr>
<td>Precuneals</td>
<td>1(100%) 28</td>
<td>1(100%) 1</td>
<td>1(100%) 3</td>
<td>1(100%) 4</td>
</tr>
<tr>
<td>Ventrals</td>
<td>8 8</td>
<td>149.0(146-153) 16</td>
<td>148.0(146-150) 2</td>
<td>137.0(136-138) 2</td>
</tr>
<tr>
<td></td>
<td>9 9</td>
<td>142.5(138-146) 13</td>
<td>138.5(138-139) 2</td>
<td>136.0(134-138) 5</td>
</tr>
<tr>
<td>Subcaudals</td>
<td>9 8</td>
<td>68.8(65-74) 11</td>
<td>72.5(69-76) 2</td>
<td>76.5(74-79) 10</td>
</tr>
<tr>
<td>Total length</td>
<td>8 9</td>
<td>59.5(56-65) 11</td>
<td>65.5(58-73) 2</td>
<td>71.8(67-75) 1</td>
</tr>
<tr>
<td>Tail as % of Total Length</td>
<td>8 8</td>
<td>22.8(21.3-23.1) 10</td>
<td>23.8(24.7-26.8) 2</td>
<td>25.0(24.7-26.8) 2</td>
</tr>
<tr>
<td>Maxillary Teeth</td>
<td>8 9</td>
<td>20.4(19.0-21.5) 10</td>
<td>23.2(21.3-24.3) 2</td>
<td>26.1(24.8-26.8) 4</td>
</tr>
<tr>
<td></td>
<td>25.6(23-24) 5</td>
<td>23.3(22-25) 3</td>
<td>29.2(27-31) 5</td>
<td>27.1(26-28) 10</td>
</tr>
</tbody>
</table>

⁶ Includes Honduras, British Honduras, and the Mexican territory of Quintana Roo.
⁷ Includes Nicaragua and Costa Rica.
Geographic Variation

Dorsal scale row.—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 29th ventral).

Preocular.—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 preoculi, 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 northwestern and southeastern from upper Central America, the center of low counts. The southeastern 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.

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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. marcianus × priscusculus (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 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 12367 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
tis venter in life as being "vermillon with blue-black bars." The venter of
the aforementioned LSUMZ 12364 was bright vermillon 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 popula-
tions of Thamnophis marcianus 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 Chiap-
as-Tabasco snakes is, however, almost classic. In number of dorsal scale
crowns and number of ventrals in females, they resemble the Central American
populations; in number of ventrals in males, number of preoculals, and
number of maxillary teeth, they are virtually indistinguishable from the popu-
lation 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. marcianus
implies a relatively long period of isolation and separate evolutionary his-
tories, 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 recog-
nition. Thamnophis m. nigrolateris Brown from southwestern United States
and northwestern Mexico is distinguished solely by its high number of ven-
trals; this difference, while real, does not seem to me to be adequate grounds
for subspecific recognition (see Rossman, 1963:129-130, for the rationale).

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and nigrolateris is herewith relegated to the synonymy of T. m. marcianus.
I am accordingly the same treatment to T. m. ruthveni, a weakly differen-
tiated form at best, which, although isolated from its northern relatives by a dis-
tributary 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 maxil-
lar teeth and ventrals. The snakes from upper Central America are charac-
terized 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. marcianus. This population should be referred to
as T. m. praecocularis. 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
praecocularis. The population thus characterized should be known as T. m.
bovalii. The Chiapas-Tabasco snakes are considered to represent T. m.
marcianus X praecocularis intergrades.

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

T. m. marcianus—Southwestern United States and northern Mexico; an
isolated population near Tehuantepec, Oaxaca.

T. m. praecocularis—Quintana Roo, Mexico, coastal British Honduras, and
Lake Yojos, Honduras.

T. m. bovalii—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 praecocularis,
defies easy allocation or explanation. Although they collected the specimen
less than 27 airline miles southwest of Belize, the type locality of praecocularis,
the animal agrees with the Tehuantepec population of T. m. marcianus in
all diagnostic features. The specimen (NRM 2619; formerly ERA-WTN
No. 99201), a small adult male (erroneously identified as a female by
Neill and Allen, 1959), has 143 ventrals, 68 subcaudals, a maximum of 21

1 The Honduras specimen was mistakenly identified and reported as Thamnophis
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. procerus or T. m. boralli (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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