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VARIATION IN THE MEXICAN GARTER SNAKE *THAMNOPHIS*  
*SCALARIS* COPE AND THE TAXONOMIC STATUS OF *T. SCALIGER* (JAN)

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The last revision of the *Thamnophis scalaris* complex (Smith, 1942) recognized three subspecies: the nominate form, thought to range from west-central Veracruz across the Transverse Volcanic Axis to Morelos; *T. scalaris scaliger*, known from the southeastern Mesa Central just north of the range of *T. s. scalaris* (with an apparently isolated record from north-central Michoacán); and *T. scalaris godmani*, ranging from the Puebla-Veracruz state line above Acultzingo southward to central Oaxaca and westward to central Guerrero. A subsequent paper (Smith *et al.*, 1950) reported a second Michoacán locality for *T. scalaris scaliger* as well as one in the mountains of western Jalisco.

*Thamnophis godmani* has long been recognized as a species distinct from the members of the *T. scalaris* complex (Rossman, in Varkey, 1979), but only recently has any evidence been presented (de Queiroz and Lawson, 1994; Rossman, *et al.*, 1996). Molecular data link *T. godmani* with *T. errans*--not *T. scalaris* and *T. scaliger*--and we need not consider it further in this paper.

Smith *et al.* (1950) distinguished between *T. s. scalaris* and *T. scalaris scaliger* primarily on the basis of the number of dorsal scale rows (*scalaris* predominantly having 17 DSR anteriorly, fewer than 17 rows posteriorly; *scaliger* predominantly having 19 rows anteriorly, 17 rows posteriorly) and secondarily on the numbers of ventrals and subcaudals in males (*scalaris* rarely having more than 143 ventrals or fewer than 60 subcaudals, but with

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half the *scaliger* exhibiting those conditions). Those distinctions were based on a total of 69 specimens, 38 allocated to *scalaris* and 31 to *scaliger*.

In the course of our study of the *T. scalaris* complex using a much larger sample, we discovered that the previously emphasized differences in dorsal scale row numbers are not valid. At the same time, however, we also uncovered an array of other characters that not only serve to confirm the existence of two taxa, but which suggest that their relationship more appropriately should be regarded as one of sister-species rather than subspecies. Our preliminary findings have been reported previously (Rossman, 1992); the present paper provides documentation, formally resurrects *T. scaliger* as a valid species, and designates neotypes for both taxa (the holotypes having been lost).

#### MATERIALS AND METHODS

The three population samples used in this analysis were *T. scaliger*, and eastern and western groups of *T. scalaris*. *Thamnophis scalaris* was divided into two sets of populations ("eastern"=Veracruz; "western"=all other populations [except Tlaxcala, see below]-Figure 1) because of preliminary indications that they differ in numbers of dorsal scale rows and subcaudals.

We recorded color pattern, meristic, and mensural data for 39 specimens ultimately identified as *T. scaliger* and 145 as *T. scalaris*. Meristic characters included numbers of maxillary (Mx) teeth, ventrals (V), subcaudals (SC), supralabials (SL), infralabials (IL), and dorsal scale rows (at the level of V10, at midbody, and at the level of the penultimate V). Mensural characters included length of inverted hemipenis, tail length/total length (T/TL), head length/snout-vent length (HL/SV), frontal length/parietal length (FL/PL), eye diameter/frontal length (ED/FL), maximum anterior frontal width/frontal length (FW/FL), posterior frontal width (where parietals meet supraoculars and frontal)/maximum anterior frontal width (FWP/A), muzzle length (combined length of internasal and prefrontal medial sutures)/frontal length (ML/FL), muzzle width (combined width of internasals at posterolateral corners)/frontal length (MW/FL), prefrontal suture length/ internasal suture length (Prf/In), combined internasorostral contact/nasorostral contact (InR/NR), total nasal length along ventral suture/muzzle length (TN/ML), anterior nasal length/posterior nasal length (AN/PN), loreal length along ventral suture/muzzle length (LV/ML), dorsal loreal length/ventral loreal length (LD/LV), loreal height/ventral loreal length (LHt/LV), and anterior genial length/posterior genial length (AG/PG). The color pattern characters included width of the vertebral stripe, coloration of the last supralabial, nature of the dark barring on the supralabials, and coloration of the venter.

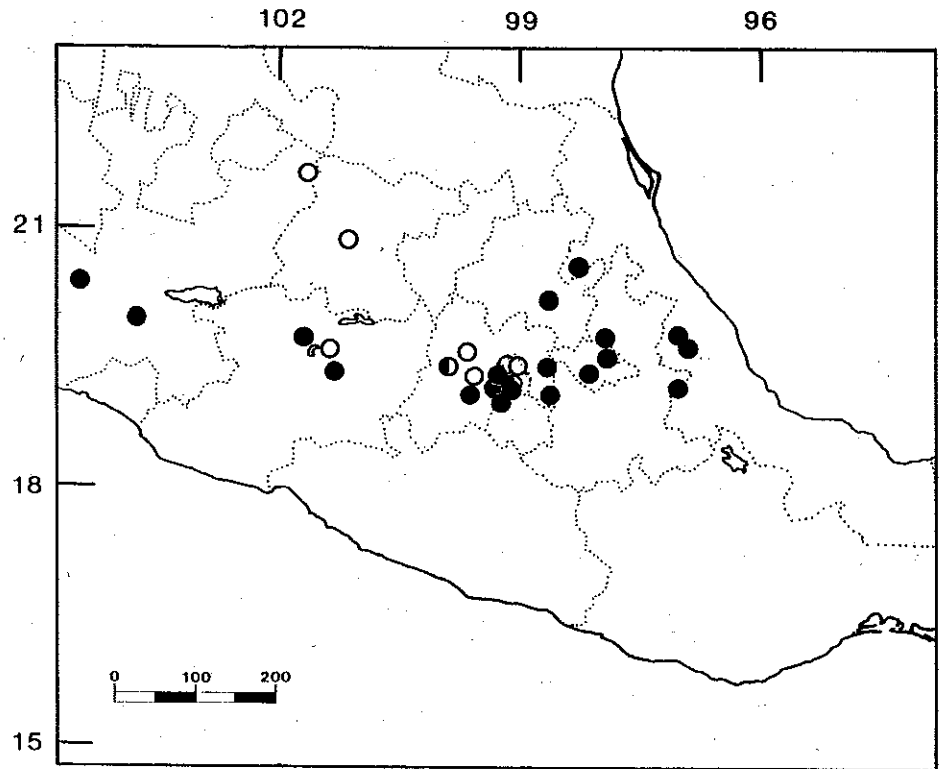


FIGURE 1. Distribution of *Thamnophis scalaris* (solid circles) and *T. scaliger* (open circles) in central México. The two semi-solid circles represent localities where both species occur sympatrically.

All of the mensural and meristic data (except for hemipenis length--see text--and the numbers of dorsal scale rows, supralabials, and infralabials--see Table 1) were treated statistically; Student's t-tests were used for pairwise statistical comparisons between *T. scaliger* and western *T. scalaris*, and between eastern and western *T. scalaris*. The 0.005 significance level (rather than the standard 0.05) was chosen to insure greater rigor in these comparisons, which are presented in Table 2. For those characters that are sexually dimorphic in at least one sample, data for each sex were treated separately.

Table 1. Comparison of the numbers of dorsal scale rows (DSR), supralabials (SL), and infralabials (IL) in *Thamnophis scaliger*, western *T. scalaris*, and eastern *T. scalaris*. Values indicate number of individuals followed by % in parentheses.

| Character     | <i>scaliger</i> |           | <i>scalaris</i> (West) |           | <i>scalaris</i> (East) |           |
|---------------|-----------------|-----------|------------------------|-----------|------------------------|-----------|
|               | Male            | Female    | Male                   | Female    | Male                   | Female    |
| Anterior DSR  |                 |           |                        |           |                        |           |
| 15            | --              | 1 (4.8)   | 1 (1.1)                | --        | --                     | --        |
| 16            | --              | --        | 1 (1.1)                | --        | --                     | --        |
| 17            | 2 (11.1)        | 4 (19.0)  | 9 (23.7)               | 10 (20.4) | 18 (69.2)              | 10 (34.5) |
| 18            | 1 (5.6)         | 1 (4.8)   | 2 (5.3)                | 3 (6.1)   | 4 (15.4)               | 3 (10.3)  |
| 19            | 15 (83.3)       | 15 (71.4) | 25 (65.8)              | 36 (73.5) | 4 (15.4)               | 16 (55.2) |
| Midbody DSR   |                 |           |                        |           |                        |           |
| 15            | --              | --        | 1 (2.6)                | --        | --                     | --        |
| 16            | --              | --        | --                     | --        | --                     | --        |
| 17            | 4 (22.2)        | 6 (28.6)  | 7 (18.4)               | 9 (18.4)  | 17 (63.0)              | 12 (41.4) |
| 18            | --              | --        | 2 (5.3)                | 1 (2.0)   | 2 (7.4)                | 1 (3.5)   |
| 19            | 14 (77.8)       | 15 (71.4) | 28 (73.7)              | 39 (79.6) | 8 (29.6)               | 16 (55.2) |
| Posterior DSR |                 |           |                        |           |                        |           |
| 13            | --              | --        | 1 (2.6)                | --        | --                     | 1 (3.4)   |
| 14            | --              | --        | --                     | --        | --                     | --        |
| 15            | 2 (11.1)        | 1 (4.8)   | 5 (13.2)               | 2 (4.1)   | 9 (33.3)               | 9 (31.0)  |
| 16            | 1 (5.6)         | --        | 2 (5.3)                | 6 (12.2)  | 3 (11.1)               | 2 (6.9)   |
| 17            | 15 (83.3)       | 20 (95.2) | 30 (78.9)              | 40 (81.6) | 15 (55.5)              | 17 (58.6) |
| 18            | --              | --        | --                     | 1 (2.0)   | --                     | --        |
| Character     | <i>scaliger</i> |           | <i>scalaris</i> (West) |           | <i>scalaris</i> (East) |           |
|               | Sexes combined  |           | Sexes combined         |           | Sexes combined         |           |
| Total SL      |                 |           |                        |           |                        |           |
| 12            |                 | 2 (5.1)   |                        | 1 (1.1)   |                        | 1 (1.8)   |
| 13            |                 | 3 (7.7)   |                        | --        |                        | 1 (1.8)   |
| 14            |                 | 34 (87.2) |                        | 67 (77.0) |                        | 48 (84.2) |
| 15            |                 | --        |                        | 12 (13.8) |                        | 7 (12.3)  |
| 16            |                 | --        |                        | 8 (9.2)   |                        | --        |
| Total IL      |                 |           |                        |           |                        |           |
| 16            |                 | 2 (5.3)   |                        | 3 (3.4)   |                        | 2 (3.6)   |
| 17            |                 | 4 (10.5)  |                        | 1 (1.1)   |                        | 4 (7.3)   |
| 18            |                 | 29 (76.3) |                        | 30 (34.1) |                        | 26 (47.3) |
| 19            |                 | 3 (7.9)   |                        | 18 (20.5) |                        | 14 (25.5) |
| 20            |                 | --        |                        | 34 (38.6) |                        | 7 (12.7)  |
| 21            |                 | --        |                        | 2 (2.3)   |                        | 2 (3.6)   |

## RESULTS

*Color Pattern.*--Superficially, *T. scalaris* (Fig. 2) and *T. scaliger* (Fig. 3) are remarkably similar in appearance. The two taxa are unique among garter snakes in having a dorsal pattern in which the three light stripes are connected anteriorly by large black-edged, brown blotches (usually in one row

Table 2. Comparison of the meristic and mensural characters of *Thamnophis scaltiger* and the western and eastern population samples of *T. scaltaris*. The numerical values presented represent the mean, standard deviation, range of variation, and sample size. An asterisk denotes statistically significant differences at  $p < 0.005$ . Where there is sexual dimorphism, the upper values refer to males, the lower to females.

| Character  | <i>scaltiger</i> |              | <i>scaltaris</i> (West) |             | <i>scaltaris</i> (East) |    |             |              |    |
|------------|------------------|--------------|-------------------------|-------------|-------------------------|----|-------------|--------------|----|
|            | Mean             | SD           | Mean                    | SD          | Mean                    | SD |             |              |    |
| Ventrals   | 142.6±4.46       | (135-151)    | 18                      | 137.5±3.95  | (130-147)               | 35 | 137.3±2.69  | (131-142)    | 24 |
| Subcaudals | 136.4±4.77       | (130-145)    | 21                      | 139.9±3.19  | (135-147)               | 47 | 140.3±3.66  | (132-146)    | 28 |
| T/TL (%)   | 53.5±2.83        | (49-58)      | 15                      | 71.1±4.19   | (64-83)                 | 34 | 74.9±4.77   | (64-85)      | 23 |
| Mx Teeth   | 45.4±2.37        | (40-49)      | 17                      | 57.0±4.02   | (50-66)                 | 43 | 61.6±4.70   | (53-69)      | 28 |
| HL/SV (%)  | 19.6±1.15        | (17.6-21.3)  | 15                      | 29.4±1.65   | (25.3-32.4)             | 25 | 30.2±1.68   | (25.9-33.2)  | 19 |
| FL/PL (%)  | 17.5±0.92        | (15.5-18.7)  | 17                      | 21.5±1.27   | (19.5-24.3)             | 43 | 22.9±1.30   | (20.2-25.0)  | 27 |
| ED/FL (%)  | 15.9±0.52        | (15-17)      | 15                      | 16.8±1.06   | (15-19)                 | 16 | 17.2±0.75   | (16-18)      | 6  |
| ML/FL (%)  | 15.3±0.46        | (15-16)      | 15                      | 16.3±0.55   | (16-18)                 | 20 | 16.7±0.95   | (15-18)      | 10 |
| AG/PC (%)  | 5.0±0.34         | (4.1-5.4)    | 19                      | 5.6±0.28    | (5.1-6.2)               | 53 | 5.5±0.24    | (5.1-6.0)    | 26 |
| FW/FL (%)  | 84.8±5.14        | (74.6-92.3)  | 15                      | 83.1±5.33   | (72.7-97.6)             | 26 | 86.1±5.44   | (74.6-93.2)  | 16 |
| FW/A (%)   | 79.2±6.41        | (70.1-92.9)  | 19                      | 79.8±5.14   | (69.4-88.4)             | 41 | 80.4±5.81   | (69.2-92.6)  | 18 |
| MW/FL (%)  | 60.6±4.19        | (54.4-68.2)  | 35                      | 62.7±3.66   | (56.0-72.0)             | 66 | 64.1±4.89   | (55.0-75.2)  | 34 |
| Prf/In (%) | 89.8±6.62        | (84.4-97.2)  | 34                      | 64.6±5.30   | (49.6-77.2)             | 66 | 63.7±6.73   | (46.0-79.7)  | 32 |
| InR/NR (%) | 63.1±4.81        | (52.3-73.6)  | 34                      | 90.1±8.70   | (70.7-112.7)            | 64 | 95.5±8.19   | (83.0-115.6) | 33 |
| LD/LV (%)  | 78.2±6.35        | (67.6-98.5)  | 34                      | 56.0±4.25   | (44.8-63.5)             | 66 | 54.9±3.97   | (44.3-61.1)  | 31 |
| LHt/LV (%) | 75.8±3.38        | (69.9-81.0)  | 15                      | 78.0±7.13   | (61.8-96.6)             | 52 | 80.6±7.51   | (62.6-95.6)  | 29 |
| LW/ML (%)  | 81.1±6.88        | (68.6-95.0)  | 20                      | 72.9±4.10   | (62.5-78.9)             | 22 | 74.6±3.71   | (69.5-82.4)  | 13 |
| TN/ML (%)  | 113.0±19.79      | (80.8-157.3) | 35                      | 73.6±3.88   | (63.0-79.4)             | 30 | 76.3±6.62   | (66.7-90.1)  | 16 |
| AN/PN (%)  | 122.6±16.64      | (88.9-160.0) | 34                      | 121.9±15.96 | (95.6-175.7)            | 54 | 110.6±21.51 | (52.1-164.7) | 32 |
|            | 54.0±7.08        | (35.3-67.9)  | 35                      | 129.1±12.83 | (103.4-159.2)           | 65 | 132.6±17.01 | (70.3-159.1) | 33 |
|            | 83.3±10.93       | (53.7-110.8) | 34                      | 65.4±6.04   | (53.0-78.7)             | 52 | 65.8±6.97   | (54.5-81.4)  | 30 |
|            | 48.6±4.93        | (38.0-58.9)  | 32                      | 80.2±9.10   | (62.5-102.4)            | 49 | 83.8±7.30   | (71.2-100.0) | 27 |
|            | 55.0±6.20        | (43.2-64.7)  | 32                      | 43.0±4.57   | (32.5-52.0)             | 21 | 42.3±4.35   | (32.8-49.4)  | 29 |
|            | 109.6±27.23      | (63.4-162.1) | 32                      | 55.2±4.71   | (46.6-62.7)             | 21 | 55.3±3.94   | (48.6-63.9)  | 23 |
|            |                  |              |                         | 74.2±23.03  | (53.4-159.8)            | 22 | 77.5±19.24  | (48.2-128.6) | 23 |

on each side, but occasionally in two alternating rows) that may or may not reduce to narrow black bars posteriorly. The prominent nuchal blotches also are brown with black borders, and they may or may not be continuous with the brown coloration of the parietals. Frequently, a light streak extends for varying distances along the interparietal suture to fork out along the frontoparietal suture, thus forming a Y-shaped marking (often irregular in shape).

The two taxa differ consistently in several details of color pattern. The vertebral stripe is confined to the vertebral row in *T. scaliger*, but it involves at least the adjacent margins of the paravertebral rows in *T. scalaris*. All supralabials have the same ground color in *T. scalaris*, but in *T. scaliger* a black-edged brown extension of the temporal coloration covers the ultimate supralabial and, in most specimens, the posterior portion of the one preceding it. There often are short, narrow, black wedge-shaped marks on the upper part of some anterior supralabial sutures in *T. scalaris*; in *T. scaliger*, most of the marks are brown with black margins and are greatly expanded (those on the subocular supralabials are actually joined dorsally). The ventral scales in *T. scaliger* usually have extensive black vermiculations along the anterior margin; when black pigment is present in *T. scalaris*, it is in the form of an irregular "dusting" or "peppering."

*Hemipenis Morphology.*--*Thamnophis scalaris* is unique among natricid snakes in having a hemipenis that is exceptionally long (on average, the *in situ* organ extending to the level of the 27th or 28th subcaudal) and has an unexpanded or only slightly expanded (see USNM 22436, 22439) apical region. The hemipenis of *T. scaliger*, on the other hand, is of moderate length for a garter snake (extending, on average, to the level of the 11th or 12th subcaudal) and has the broadly expanded apical region typical of most species of *Thamnophis* (see Rossman, *et al.*, 1996, Fig. 13). The two hemipenes differ so dramatically that it is difficult to imagine that *T. scalaris* and *T. scaliger* belong in the same genus; yet other evidence points to their being sister-species.

When injected with preservative, the organ of *T. scalaris* is everted in a corkscrew fashion, and it seems likely that it is inserted into the female cloaca in a similar manner. Because of its great length, the hemipenis obviously cannot fit in a female's cloaca (the dissected cloaca of LSUMZ 42641 is only six ventrals long) in a fully expanded form unless it lies in a spring-like coil. To do so would surely bring the tip of the *sulcus spermaticus* into proximity with only one of the oviducal openings; are eggs fertilized in only one oviduct in any given mating in this species? At this point, the questions outnumber the answers.

*Dorsal Scale Rows.*--*Thamnophis scaliger* and the western populations of *T. scalaris* have basically similar numbers of scale rows at all three positions along the body (Table 1), but the eastern populations of *T. scalaris* show a tendency toward reduction in number at all three positions (most

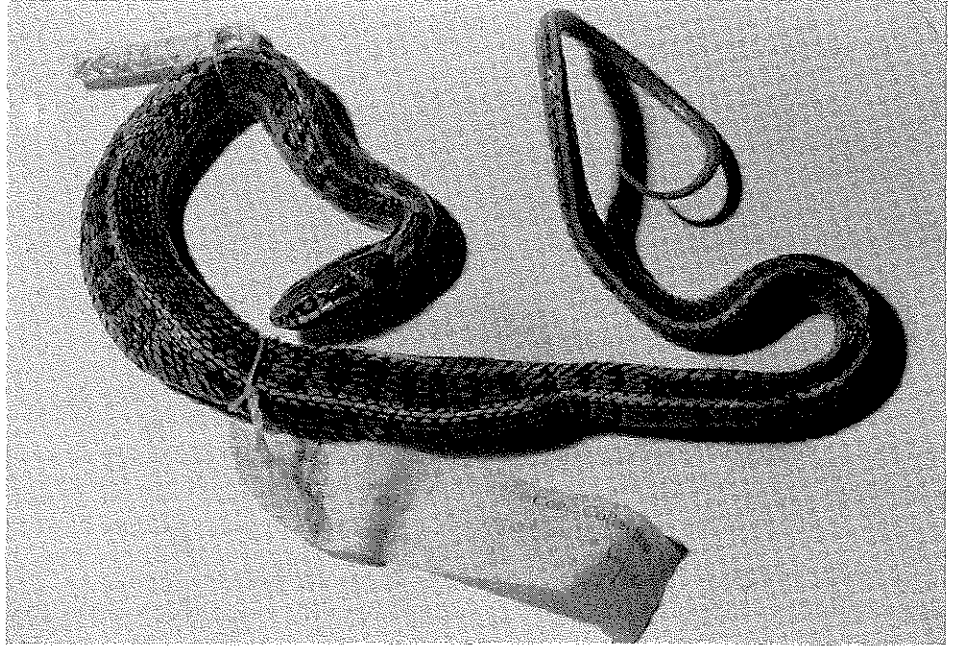


FIGURE 2. Dorsal pattern of the neotype of *Thamnophis scalaris* (ANSP 11694), a subadult (241 mm SVL) male from Jalapa, Veracruz, México. Photograph by Mark Kleiner.

dramatically in males, there being sexual dimorphism in the sample at the anterior and midbody positions). This is one of only two characters in which the western *T. scalaris* are similar to *T. scaliger* but dissimilar to eastern *T. scalaris* (AG/PG is the other). Because dorsal scale row number was the primary character Smith (1942) used to distinguish his *T. scalaris scaliger* from his *T. s. scalaris*, it led him to misidentify some of the western *T. scalaris* as *T. scaliger* (e. g., those from the vicinity of Río Frío, near the México-Puebla state line).

*Labials.*--Both *T. scaliger* and *T. scalaris* predominantly have seven supralabials on both sides of the head, but there is a slight tendency in both populations of the latter species to have eight on at least one side, whereas none of the *T. scaliger* examined showed this condition (Table 1). *Thamnophis scaliger* rarely has more than nine infralabials on either side of the head, whereas both eastern and especially western *T. scalaris* frequently have ten infralabials on at least one side (Table 1).

*Ventrals.*--There are significantly more ventrals in male, and fewer in female, *T. scaliger* than in *T. scalaris*, which is unique among garter snakes in

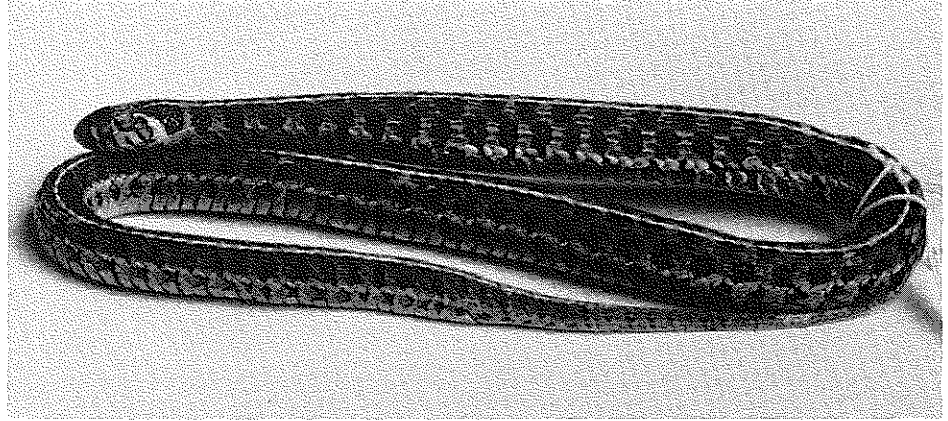


FIGURE 3. Dorsal pattern of the neotype of *Thamnophis scalaris* (MZFC 2001), an adult (408 mm SVL) female from Pedregal de San Angel, Distrito Federal, México. Photograph by Mark Kleiner.

having the males with significantly fewer ventrals than the females. The eastern and western samples of *T. scalaris* exhibit no difference in this character, but two males from Tlaxcala (TCWC 879, LACM 66900) have 151 and 150 ventrals, respectively, which well exceed the otherwise known range of variation for the species. The only Tlaxcala female examined (UIMNH 18895) has 144 ventrals, which is above the mean for the species but within the known range of variation. Obviously, larger samples from Tlaxcala are desirable.

*Subcaudals.*--As might be anticipated from the dramatic differences in hemipenis length between *T. scalaris* and *T. scalariger*, the former has a much longer tail (especially in males), which is reflected not only in T/TL but in subcaudal number (Table 2). The two samples of *T. scalaris* also differ significantly (the eastern sample having more subcaudals), but to a much smaller degree.

*Relative tail length (T/TL).*--The tail is proportionately much longer in *T. scalaris* than in *T. scalariger*, especially in the males (Table 2); the former having the greatest degree of sexual dimorphism in this character known for garter snakes (more than 7% in *T. scalaris* vs. less than 3.5% in all other garter snake species). The tail is also significantly longer in eastern than in western *T. scalaris* females, but not in the males of those samples. A surprising discovery was that relative tail length in juvenile male *T. scalaris* (<225 mm SVL) is significantly less than in larger males (averaging  $25.0 \pm 0.84$  in 11 western-sample juveniles,  $26.7 \pm 0.98$  in six eastern-sample individuals). There is no comparable allometric growth in female *T. scalaris*, so we suspect that the dramatic change in males is correlated with post-partem allometric growth of the hemipenes.



*Maxillary teeth.*--There are significantly more maxillary teeth in *T. scalaris* than in *T. scaliger*, which has the fewest teeth of any species of garter snake (Table 2).

*Relative head length (HL/SV).*--The head in adults (>260 mm SVL) is significantly shorter in *T. scaliger* than in *T. scalaris* (Table 2). Relative head length in juveniles and subadults is subject to the effects of allometric growth, so their values were not included in the statistical analysis.

*Relative genial length (AG/PG).*--The posterior genials are significantly shorter in eastern *T. scalaris* than in either western *T. scalaris* or *T. scaliger* (Table 2).

*Relative frontal width (FW/FL).*--The frontal is significantly narrower in *T. scalaris* than in *T. scaliger* (Table 2), but the overall shape of the frontal (as reflected by FWP/A) does not differ significantly among the three samples.

*Relative muzzle width (MW/FL).*--The proportionate muzzle width is similar in the males of all three samples, but female *T. scaliger* (the only sample exhibiting significant sexual dimorphism in this character) have a significantly wider muzzle (Table 2).

*Loreal shape (LD/LV).*--Because *T. scaliger* has a significantly shorter dorsal loreal border (Table 2), its loreal has a somewhat more triangular appearance than that of *T. scalaris*.

*Relative loreal length (LV/ML).*--The ventral border of the loreal is significantly longer in *T. scaliger* than in *T. scalaris* (Table 2).

*Nasal configuration (AN/PN).*--Although the variance is extremely high, *T. scaliger* differs significantly from *T. scalaris* in the relative proportions of the anterior and posterior nasal scales (Table 2). In *T. scalaris*, the anterior nasal is substantially shorter than the posterior; in *T. scaliger*, the anterior nasal is slightly longer than the posterior.

*Non-significant morphological variation.*--In seven of the mensural features examined (FL/PL, ED/FL, ML/FL, Prf/In, InR/NR, LHt/LV, TN/ML), we found no significant differences between either *T. scaliger* and *T. scalaris* or the two samples of the latter (Table 2).

*Allozymes.*--R. Lawson (pers. comm.) found a fixed allelic difference between *T. scaliger* and *T. scalaris* at the aspartate amino transferase (AAT-1) locus.

*DNA Sequences.*--A. de Queiroz (pers. comm.) found that, for a 139-base sequence of the mitochondrial cytochrome *b* gene, there is only one difference between an individual of *T. scaliger* and a composite sequence from two western *T. scalaris*. This amounts to a sequence difference of 0.7%, comparable to the variation seen within many species of *Thamnophis*. Not surprisingly, these sequences for *T. scalaris* and *T. scaliger* are more similar to each other than they are to those of any other species of *Thamnophis* de Queiroz examined. The *T. scaliger* sequence is from LSUMZ 42638 and the *T. scalaris* sequences are from LSUMZ 42641 and CU (Cornell University) 12551. The CU specimen was collected about 13 km west of Río Frío in the state of México.

## DISCUSSION

It seems clear from the broad array of color pattern, hemipenial, meristic, mensural, and allozyme differences existing between *Thamnophis scalaris* and *T. scaliger* that they are distinct species. Furthermore, where the two taxa have been collected microsympatrically west of Toluca (Fig. 1), there is no evidence of morphological or biochemical intermediacy.

Despite the differences in hemipenial morphology, *Thamnophis scalaris* and *T. scaliger* appear to be sister-species. On the basis of morphology (especially head and nape patterns), their closest relative would appear to be *T. exsul* (Rossman, 1969; Rossman *et al.*, 1989; Rossman, 1992), a conclusion consistent with mitochondrial DNA sequence analysis but not supported by allozyme analysis (de Queiroz and Lawson, 1994).

Two formalin-darkened specimens (UMMZ 105415-16) from Amoles in north-central Querétaro (a locality lying outside the Mesa Central, whence all other specimens of *T. scalaris* and *T. scaliger* are known) were catalogued as *T. scalaris* but defy identification. The juvenile female (UMMZ 105416) has 17-17-16 DSR, 145 V, 57 SC, 20.6% T/TL, 16 total SL, and 19 total IL. The adult male has 17-17-17 DSR, 143 V, 60 SC, 22.4% T/TL, 14 total SL, 20 total IL, 15 maxillary teeth, 59.3% FW/FL, 55.4% LD/LV, 53.3% MW/FL, 170.6% InR/NR, 89.5% Prf/In, 52.8% LV/ML, 80.1% AN/PN, and a hemipenis nine subcaudals long. The extremely low tooth count and basically unreduced DSR support the notion that these animals are related to *T. scalaris*. However, the combination of characteristics does not comfortably fit *T. scalaris*, *T. scaliger*, or *T. exsul*. The number of DSR is most like *T. exsul* or eastern *T. scalaris* but could fit a few *T. scaliger*. The number of maxillary teeth is typical of *T. scaliger*, is known to occur only once in *T. scalaris*, and is far too low for *T. exsul*. The length of the hemipenis would rule out *T. scalaris* but would be appropriate for either of the other species. No *T. scaliger* or *T. exsul* are known to have as many as 16 total supralabials, but a few western *T. scalaris* do. No *T. scaliger* or *T. exsul* are known to have as many as 20 total infralabials, but a substantial number of *T. scalaris* do. Until fresh material becomes available, it would seem prudent to defer judgement on the identity of these Querétaro specimens.

## DESIGNATION OF NEOTYPES

The holotype of *Thamnophis scalaris* Cope (1861) from Jalapa, Veracruz, Mexico, was originally housed in the Academy of Natural Sciences of Philadelphia, but apparently it has been lost (Malnate, 1971). In order to prevent any further confusion with *T. scaliger*, we are hereby designating as a neotype for *T. scalaris* another specimen examined by Cope from the same locality.

*Description of T. scalaris neotype.*--ANSP 11694, a subadult male from Jalapa, Veracruz, Mexico, collected by Dr. Flohr (date unknown). Snout-vent length 241 mm, tail length 93.5 mm, T/TL 28.0%; dorsal scale formula  $19 \frac{-4(99)}{3+4(100)} 17$ , DSR 1/vertebral row at midbody 3.0; V 137 (plus a half scute at V20); SC 73; SL 7, the third and fourth entering the orbit; IL 9, the first four in contact with the anterior genial; oculars 1+3; maxillary teeth 17; HL/SV 5.9%; ED/FL 60.4%; FL/PL 84.1%; FW/FL 59.4%; FWP/A 80.1%; ML/FL 62.3%; MW/FL 79.2%; Prf/In 103.1%; InR/NR 120.9%; TN/ML 54.8%; AN/PN 79.1%; LV/ML 42.2%; LD/LV 64.2%; LHt/LV 85.8%; AG/PG 95.2%.

The dorsum is light brown with a series of short, black-bordered, dark brown blotches lying between the light vertebral stripe and the light lateral stripe. The blotches are three scales long on the neck, shortening to one scale long by midbody (where the brown core disappears, leaving solid black bars posteriorly). The lighter interspaces are 1.5-2 scales long on the neck, 1-1.5 scales long by midbody. The vertebral stripe involves the vertebral scale row and slightly less than half of each paravertebral row. The lateral stripe is confined to DSR 2 and 3. The large, black-bordered brown nuchal blotches are separated by the vertebral stripe, but they are narrowly continuous with the brown ground color of the head anteromedially (Fig. 1). The light parietal spots are fused, and an irregular light streak extends anterolaterally from the center of the frontoparietal suture to a point about one-half the length of the left fork. A light crescentic streak extends along the posteromedial border of the right supraocular suture onto the frontal where it extends forward to a point just behind the anterior fourth of the frontal. The oculars are light. Vertical black bars lie along the posterior edge of the anterior nasal, the posterior edge of the posterior nasal, and the posterior edge of the loreal. The supralabials are uniformly light except for the narrow black wedges that lie anterior to the upper half (or less) of each supralabial suture. The infralabials are unmarked save for a small amount of black pigment along the suture between IL 8 and 9. The venter is unmarked.

*Tropidonotus scaliger* Jan (1863) was based on a specimen in the Museo Civico di Storia Naturale in Milan that was destroyed--along with the rest of the Jan collection--during World War II (M. Podesta, pers. comm.). Unfortunately, no locality data were associated with the holotype, and the descriptions provided by Jan (1863, 1865) do not permit *T. scaliger* to be unequivocally distinguished from all of its congeners. Under such circumstances, one alternative would be to declare *T. scaliger* a *nomen dubium* and to create a new name for the taxon. We have chosen another alternative, that of using *T. scaliger* to apply to the taxon with which the name has been associated by Smith (1942) and most subsequent workers (but acknowledging that they did make some misidentifications).

*Description of T. scaliger neotype.*--MZFC 2001, an adult female from Pedregal de San Angel, Ciudad Universitaria, Delegación Coyoacán, Distrito Federal, Mexico (collector and date unknown). Snout-vent length 408 mm, tail

length 82 mm, T/TL 16.7%; dorsal scale formula  $19 \frac{-4(87)}{-4(88)} 17$ , DSR 1/vertebral row at midbody 2.9; V 145; SC 48; SL 7, the third and fourth entering the orbit; IL 9, the first four in contact with the anterior genial; oculars 1+2; maxillary teeth 16; HL/SV 4.1%; ED/FL 64.1%; FL/PL 77.9%; FW/FL 63.4%; FWP/A 72.3%; ML/FL 72.4%; MW/FL 85.9%; Prf/In 123.8%; InR/NR 119.9%; TN/ML 51.8%; AN/PN 130.9%; LV/ML 46.0%; LD/LV 55.1%; Lht/LV 87.5%; AG/PG 85.2%.

The dorsum is light brown with two alternating rows (only one row on neck and posterior part of body) of very dark brown or black blotches lying between the light vertebral stripe and the light lateral stripe. The lower blotches (on DSR 3-6) are 1.25-1.5 scales long, the upper blotches (on DSR 7-9) 1-1.5 scales long. The lighter interspaces are 0.5-1 scale long between the lower blotches, 1-1.25 scales long between the upper blotches. The vertebral stripe is confined to the vertebral scale row. The lateral stripe is confined to DSR 2 and 3. The large, black-bordered dark brown nuchal blotches are separated by the vertebral stripe--which extends anteriorly to the frontoparietal suture--but are narrowly continuous with the brown ground color of the head anteromedially (Fig. 2). The oculars are light. The supralabials (other than SL 7) are uniformly light except for the broad black wedges that extend along the sutures to the ventral margins of the scales (the wedges on SL 3 and 4 are joined dorsally beneath the orbit). Supralabial 7 has the same brown ground color as the head. The venter is gray with black pigment extending across the anterior margin of each scute. The gular region is yellowish white, and contrasts with the rest of the venter.

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#### SPECIMENS EXAMINED

*Thamnophis scalaris*: Distrito Federal, LACM 121862, MSU 7120, MZFC 69, 3108; Hidalgo, FMNH 103225, LSUMZ 38543, MVZ 109499, UCM 50398, UMMZ 105044, 106436-37; Jalisco, KU 87472-73, UTA R-4040, 4932-34, 4936, 4945, 4947, 4949, 5991-93; México, AMNH 71315-16, 75934, 94714, FMNH 70767, 106286, KU 29312, LACM 109737, LSUMZ 24579, 40794-95, 42637, 42639, 42641, 42796-803, 43375-77, MVZ 112413, 143522, MZFC 340, 512, 573, 3265, 3460, TCWC 709, 874-76, 892, 898, UCM 52368, UF 11332, 12826, 51123, 52688-89, UIMNH 18898-99, 48064, UMMZ 112542, USNM 110815, UTA R-4578; Michoacán, FMNH 39064, UMMZ 99760, 101909, 105045, USNM 46553; Morelos, FMNH 106280-81, 106285, 65347, KU 182699, LACM 68883-84, TCWC 4122-25, 7388-89, 7394, UMMZ 113032, USNM 110816; Puebla, FMNH 106279, 206893, LSUMZ 49438, UMMZ 95119, 125737 (2), USNM 110817-18; Tlaxcala, LACM 66900, TCWC 879, UIMNH 18895; Veracruz, ANSP 11694 (neotype), CAS 98555, 98557-58, 103594, 156542-45, 156550, CM 8098, FMNH 1517, 1523, 70766, 105099, 206894-98, KU 26861-63, 26866-68, 26870-74, LSUMZ 11127-30, 24576-78, 28694, MCZ 67590-91, MVZ 131519, 144489, TCWC 893, TNHC 5153-54, UIMNH 18893, 48065, 60791, UMMZ 105043, USNM 7076, 12115-16, 30497, 110806, 224436-40, 496495.

*Thamnophis scaliger*: Distrito Federal, MZFC 67-68, 504-05, 630, 2001 (neotype)-06, 3267, USNM 12730; Guanajuato, USNM 12675; Jalisco, KU 95968; México, AMNH 91594-600, KU 67729-30, LSUMZ 42638, 42640, 43373-74, 43378-79, UF 12827, 52690-91, UMMZ 85367, USNM 32281, 110812; Michoacán, AMNH 8872, USNM 110782.

*Thamnophis incerta sedis*: Querétaro, UMMZ 105415-16.

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