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SPECIES LIMITS WITHIN THE MEXICAN GARTER SNAKES OF THE *THAMNOPHIS GODMANI* COMPLEX

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ABSTRACT: The highly variable *Thamnophis godmani* complex of southern Mexico, comprised of four apparently allopatric populations, was examined by using 28 morphological characters scored on 214 specimens. Character values were tested with univariate and multivariate statistics to determine if populations are morphologically distinct. The results suggest that the four populations represent independently evolving lineages. Four species, three previously undescribed,

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are recognized in the *T. godmani* complex. A lectotype is designated for *T. godmani*. For each species, a diagnosis, description of holotype or lectotype, summary of interspecific variation, and statement of distribution are provided. Comparisons are made with *T. errans*, alleged to be the closest relative to members of the complex.

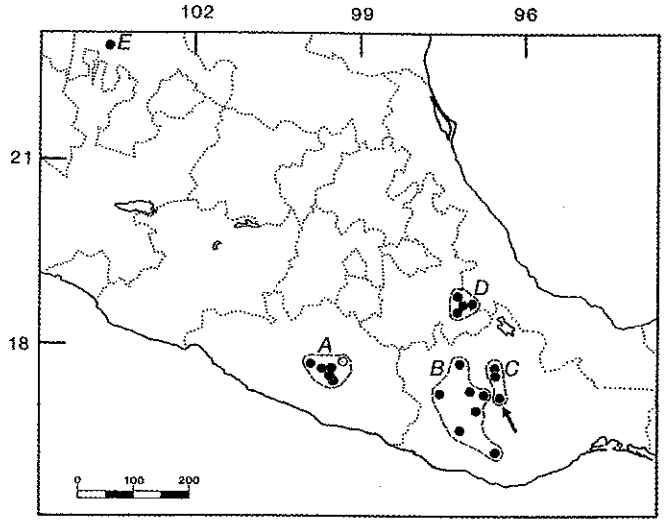

Figure 1. Distribution of the *Thamnophis godmani* complex (A-D) and *T. errans* (E) in south-central Mexico. Solid circles represent specimens examined, the hollow circle a literature record. The arrow indicates the cluster of specimens that were difficult to assign to one of the four populations of the *T. godmani* complex (see Methods and Materials).

INTRODUCTION

Species within the New World snake genus *Thamnophis* —the garter snakes—have long been known to be morphologically and behaviorally variable. Unquestionably that morphological variability prompted the following statement by Ruthven (1908): "... this genus has long stood in the minds of

herpetologists as a synonym for chaos." Almost a century has passed since this statement was made, and a number of studies have attempted to reduce the taxonomic confusion by documenting variability within many of the species and producing taxonomies that reflect evolutionary history (reviewed in Rossman et al., 1996). In this paper we examine the morphological variation and systematics of the *T. godmani* complex of southern Mexico in an attempt to clarify the taxonomy of this group.

First described as *Tropidonotus godmani* (Günther, 1894), Godman's garter snake was soon synonymized with *Thamnophis cyrtopsis* in Ruthven's (1908) classic monograph on the genus *Thamnophis*. There it remained until Smith's (1942) review of the Mexican and Central American members of the genus, in which he resurrected *godmani* as the southern subspecies of *T. scalaris*. Since 1979 (Rossman, in Varkey, 1979), it has been recognized that *T. godmani* is a distinct species, but no data to support that conclusion were presented prior to the studies of de Queiroz and Lawson (1994), Rossman *et al.* (1996), and de Queiroz et al. (2002), who provided either molecular or morphological evidence.

In the course of examining some 600 garter snake specimens to sort out the identities and relationships of the smaller Mexican montane taxa (*Thamnophis mendax* and *T. sumichrasti*, Rossman, 1992; *T. scalaris* and *T. scaliger*, Rossman and Lara-Góngora, 1997; *T. godmani*, the present study; *T. chrysocephalus*, in progress), it became apparent to the senior author that, while *T. godmani* is not conspecific with any of the other taxa, it is by no means geographically homogeneous in its morphology. Moreover, *T. godmani* occurs in at least four discrete geographic areas that are effectively separated at the present time by habitat disjunctions unsuitable for these residents of montane pine-oak forests (1768-3048 m). Therefore, the focus of this paper is to determine if

morphological variation within *T. godmani* is localized to these discrete geographic areas. We chose to examine frequency shifts in 33 morphological characters among these four geographic areas (populations). Significant differences in morphology among the four geographically separated and localized populations were used to infer a lack of genetic contact and subsequent lineage formation.

MATERIALS AND METHODS

We examined *T. godmani* from the following four geographic areas, which we considered to represent four distinct populations: A—the Sierra Madre del Sur in south-central Guerrero (30 males, 41 females); B—the Mesa del Sur in central Oaxaca, exclusive of the Sierra de Juárez (35 males, 33 females); C—the Sierra de Juárez in north-central Oaxaca (19 males, 16 females); and D—the southern interface of the Mesa Central and the Sierra Madre Oriental along the Puebla-Veracruz state line (12 males, 28 females) (Fig.1). Three individuals were difficult to assign to a specific population: AMNH 97890, a male from Oaxaca, 1.6 km NE Cuajimoloyas; AMNH 147650, a female from Oaxaca, 1.6 km NW Cuajimoloyas; AMNH 91105, a female from Oaxaca, 2.4 km S Carrizal. These three specimens were analyzed by using discriminant function analysis (DFA) to determine their putative population membership. Because de Queiroz and Lawson (1994) demonstrated that *T. godmani* and *T. errans* have identical allozyme character-states, we included a small sample (6 males, 13 females) of *T. errans* in order to compare the range of variation within *T. godmani* to this taxon.

The morphological characters we examined are those that have been demonstrated to be taxonomically useful in variational studies of other species within the genus *Thamnophis* (Rossman et al. 1996). We quantified the

dorsal scale rows at the level of the tenth ventral (DSR10), at midbody (DSRM), and at the penultimate ventral (DSRPen); as well as numbers of maxillary teeth (MT), ventrals (V), subcaudals (SC), and intergenials (IG). Scored mensural characters included: snout-vent length (SVL), tail length (T), head length (HL), frontal length (FL), parietal length (PL), eye diameter (ED), maximum anterior frontal width (FWA), posterior frontal width (where parietals meet supraoculars and frontal) (FWP), muzzle length (combined length of internasal and prefrontal median sutures) (ML), muzzle width (combined width of internasals at posterolateral corners) (MW), prefrontal suture length (PFL), internasal length (INL), combined internasorostral contact (INR), nasorostral contact (NR), total nasal length along ventral suture (TN), anterior nasal length (AN), posterior nasal length (PN), loreal length along ventral suture (LV), dorsal loreal length (LD), loreal height (LHT), anterior chin shield length (ACS), and posterior chin-shield length (PCS). Methods for making the various counts and measurements were figured and discussed in Rossman et al. (1996: pp. 19-29). In addition to these characters, we noted the proportion of black pigment in the nuchal blotches and the development of black barring along: the posterior suture of the fifth supralabial; the suture between the sixth and seventh supralabials; and the dorsal connection between these bars.

Basic descriptive statistics (N, mean, SD, Min and Max) were calculated on males and females separately for each population and all statistical analyses were performed with the program Systat 8.0 (SPSS, 1998). To produce a linear relationship between all variables and reduce the effect of individual size variation, mensural characters were log-transformed and residuals were produced by using either SVL or HL as the independent variable (Hills, 1978; Thorpe and Leamy, 1983; and Sokal and Rohlf, 1995; Burbrink 2001). Snout-vent length (SVL) was used as the independent variable when

overall body-size: T and HL. Head-length (HL) was used as the independent variable when obtaining size-free residuals for characters only associated with the head: FL, PL, ED, FWA, FWP, ML, MW, PFL, INL, INR, NR, TN, AN, PN, LV, LD, LHT, ACS, and PCS.

All raw meristic and transformed mensural characters were first examined for statistical significance among each of the four populations of *T. godmani* and *T. errans* by using ANOVA with a Bonferroni adjustment (Sokal and Rohlf, 1995). This assumes a null hypothesis that characters are not significantly different among groups while risking a Type I error at a frequency of 0.05. Student's *t*-test was used to determine if characters were significantly different between sexes within each population.

Discriminant function analysis (DFA) was performed on meristic variables and transformed mensural variables separately, after assessing multivariate normality for each character. We used DFA to determine if it is possible to statistically differentiate among groups with the characters defined above (Manly 1994). This technique maximizes the separation among groups and accounts for within-group variance and correlation. DFA has been used successfully in differentiating closely related lineages of snakes with morphological data (referred to as CVA in Thorpe 1976, 1980, 1983, 1987; Wüster and Thorpe 1992; Wüster et al. 1995). Discriminant function analysis also indicates those morphological characters that influence the inclusion of an individual in a specific population. Separate analyses were performed on female and male data. Classification matrices based on DFA scores were produced to determine how well individuals could be classified into their correct populations.

To assess if populations cluster by using uncorrelated

population designations, we used principal component analysis (PCA) on males and females. To determine if significant differences exist among populations in scores derived from principal component axes occupying the highest percentage of variance (the first and second axes), we used ANOVA with a Bonferroni correction.

To assess the diagnostic value of mensural variables, we calculated the following ratios: T/SV, HL/SVL, FL/PL, ED/FL, FWA/FL, FWP/FWA, ML/FL, MW/FL, PFL/INL, INR/NR, TN/ML, AN/PN, LV/ML, LD/LV, LHT/LV, and ACS/PCS.

RESULTS

Descriptive statistics of the raw characters are reported for males and females separately (these scores along with ANOVA *P* values may be obtained from FB or by accessing the web site: http://163.238.8.180/~fburbrink/). For males and females, respectively, 60.7% and 57.1% of the raw meristic and transformed mensural characters examined were significantly different as revealed by ANOVA with a Bonferroni correction. Within the four populations of male *T. godmani*, Population A had the highest number of character differences when compared to other populations: 32.6% of the characters differed statistically when comparing Population A to B or C, and 35.7% when compared to D. Fewer differences were noticed when comparing males of population B, C, and D: 14.2% of characters for B and C differed statistically, 3.6% of B and D differed statistically, and 18% of C and D differed statistically. Similarly for females within the four populations of *T. godmani*, Population A had the highest number of character differences when compared to other populations: 46.4% and 28.6% of characters differed statistically when comparing Population A to B and C, respectively, and 46% when A was compared to D. Also, fewer differences were noticed when comparing females

differed statistically, 17.9% of B and D differed statistically, and 21.4% of C and D differed statistically.

Population B and *Thamnophis errans* were highly sexually dimorphic, with 59% and 62% of the raw characters differing significantly for each population, respectively. Sexual dimorphism was much less pronounced in the other three populations.

By using the Mahalanobis distances produced from the DFA, Wilks' Lambda verified that there was significant dispersion among each of the *T. godmani* populations and *T. errans* at all four functions for both males and females ($P<0.001$) when using sets of meristic characters separately. Most variance was occupied by the first two axes, with 68.7% and 26.0% of the total variance for functions one and two, respectively, for males. Discriminant function one and two occupied 60% of variance and 38% of variance, respectively, for females. For males, the following meristic variables had the highest absolute correlation with function one and two: SC at 0.977 for function one and V at 0.848 and DSRM at 0.507 for function two. For females, the following meristic variables had the highest absolute correlation with function one: SC at 0.824 and DSR10 at 0.688. Three-dimensional plots of the discriminant function scores obtained from the first three functions by using meristic variables for males revealed that populations, although tightly grouped, do appear somewhat distinct (Fig. 2). For females, these same plots failed to demonstrate separation as clearly (Fig. 3).

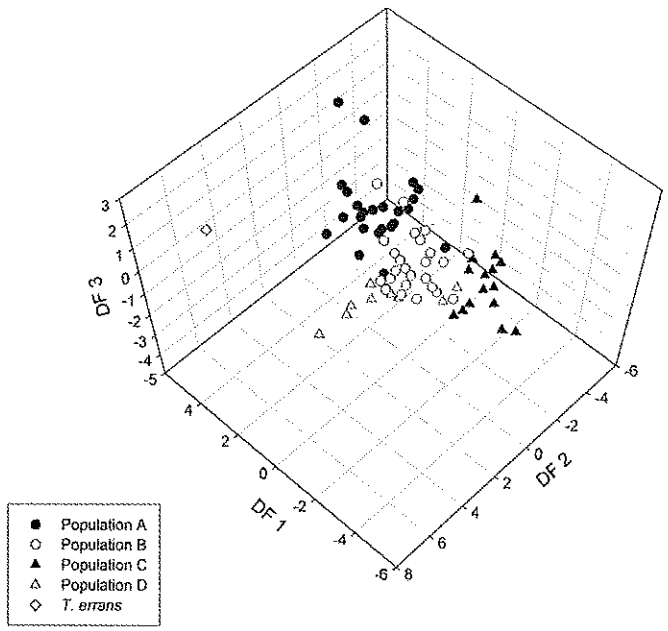

Figure 2. Three-dimensional plot of the first three discriminant function scores based meristic characters of males in the four populations of the *Thamnophis godmani* complex and *T. errans.*

Discriminant Function Analysis was also conducted separately for mensural variables. Significant dispersion among each of the *T. godmani* populations and *T. errans* for both males and females was verified by Wilks' Lambda ($P<0.001$) at all functions. Discriminant functions one, two and three occupied 39.8%, 33.2%, and 14.0% of the total variance, respectively, for males. Discriminant functions one, two and three occupied 39.6%, 38%, and 16.7% of the total variance, respectively, for females. Absolute correlation of variables with functions were not particularly high for males or females at any function. The highest absolute value for males was the character FWA on the third function at 0.472, and for females the character TN on the first function at -0.449. Three-dimensional plots of the

variables for both males and females revealed that populations appear somewhat distinct (Fig. 4 and 5). For females, Populations B and D appear tightly grouped (Fig. 5).

Population classification matrices based on DFA scores demonstrated that 87.2% of males and 77.4% of females could be classified into their correct populations consistently from meristic variables. With respect to mensural characters, 100% of males and 97.7% of females could be classified into their correct populations. The fact that there were 13 more mensural characters than meristic characters possibly accounts for the higher classification scores based on mensural characters. Additionally, the number of individuals included in the multivariate analysis was much smaller than the total number of individuals examined in this paper because only individuals with a complete data set were included in the DFA. It is possible that the higher classification score was the result of over-parameterization due to a large number of variables (characters) as compared to a small number of samples. Principal Components Analysis was used to reduce the dimensionality of the meristic and transformed mensural data sets for males and females separately. For male meristic characters, axis one occupied 38.3% of the total variance, axis two occupied 29.0% of the variance, and axis three 16.3% of the total variance. Additionally, for male mensural characters, axis one occupied 20.3% of the total variance, axis two occupied 17.9% of the variance, and axis three occupied 10.6% of the variance. For female meristic characters, axis one occupied 45.9% of the total variance, axis two 25.7%, and axis three 17.3%. Finally, for female mensural characters, axis occupied 25.5% of the total variance, axis two occupied 16.8%, and axis three 10.8%. The following meristic characters had the highest loadings on axis one for males: DSR1 at 0.827 and V at 0.738. The character SC, at 0.875, had the highest loadings on axis two for male meristic characters. For male mensural characters, the

TL at 0.671 and LHT at 0.623. The characters NR, at 0.649, and FL, at 0.616, had the highest loadings on axis two for male mensural characters. The following female meristic characters had the highest loadings on axis one: DSR10 and DSRM at 0.919 and 0.920, respectively. The character DSRPen, at 0.821, had the highest loading on axis two for all female meristic characters. For female mensural characters, the following characters produced the highest absolute value loadings on axis one: INR at –0.783 and TN at 0.835. The characters, INL at –0.694 and LH at –0.648, had the highest absolute value loadings on axis two for female mensural characters. Using ANOVAs to determine if populations differ with respect to scores obtained from the first three Principal Component (PC) axes revealed that only populations B and D were not significantly different at any axis using meristic characters for females. However, all populations were significantly different for males. Further, conducting ANOVAs on the first three PCs of mensural data revealed that populations B and D, as well as B and C, did not differ significantly at any of the first three axes for males, but only C and D were not significantly different for females.

All three individuals of unknown population membership, AMNH 97890, 91105, and 14760 (mentioned above), appear to group closely with Population C as determined by the between-group F-matrix of comparisons based on DF scores. The between-group F-matrix distances from Population C for those unknown individuals are 0.557, 0.726, and 0.680, respectively. Population B has the next closest distance with values of 1.062, 1.839, and 1.947, with respect to the order of the AMNH unknown specimens listed above.

Ratios of mensural data reveal that, although the ranges of variation within all characters do overlap (Tables 2 and 3), certain morphological trends exist that make it possible to

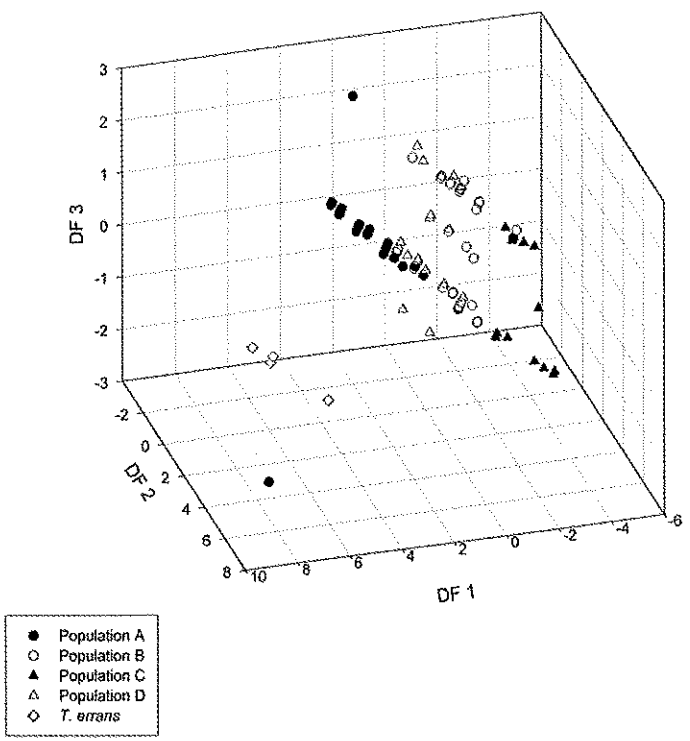

Figure 3. Three-dimensional plot of the first three discriminant function scores based meristic characters of females in the four populations of the *Thamnophis godmani* complex and *T. errans.*

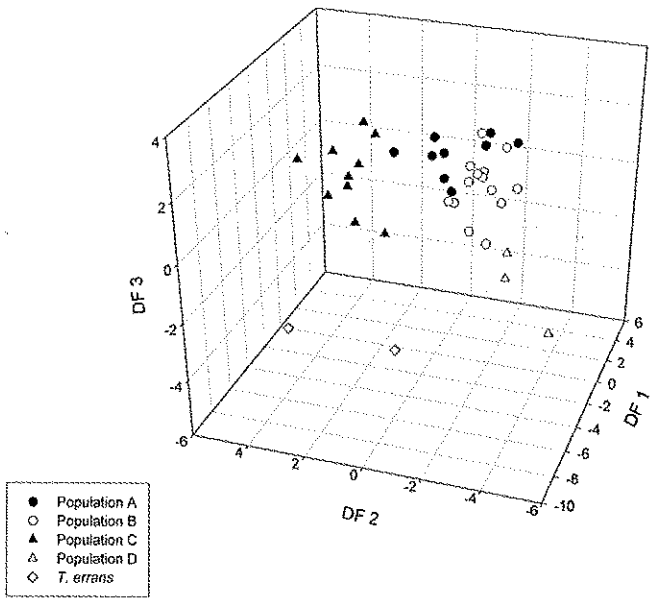

Figure 4. Three-dimensional plot of the first three discriminant function scores based mensural characters males in the four populations of the *Thamnophis godmani* complex and *T. errans.*

Morphological Characterization of Population Samples

Population A: Specimens in this sample have a longer tail, more subcaudals, more maxillary teeth, shorter parietals, longer internasals, a longer and more triangular loreal, a broader muzzle tip, more nearly equal anterior and posterior nasals, a shorter muzzle, and a narrower frontal posteriorly than do members of the other three populations. Moreover, the Guerrero specimens appear to reach a substantially greater SVL (the 10 longest presumptive adult females average 480 mm, the 10 longest males 427 mm), the nuchal blotches usually are black

(69% of specimens examined for this character; 8% are predominantly brown; 23% are black posteriorly, brown anteriorly), and the pattern of black barring on the posterior supralabials appears to be unique in having the bar along the posterior suture of the fifth supralabial equal to-or broader than-the one along the suture between the sixth and seventh supralabials (with the dorsal connection between these bars weakly developed at most).

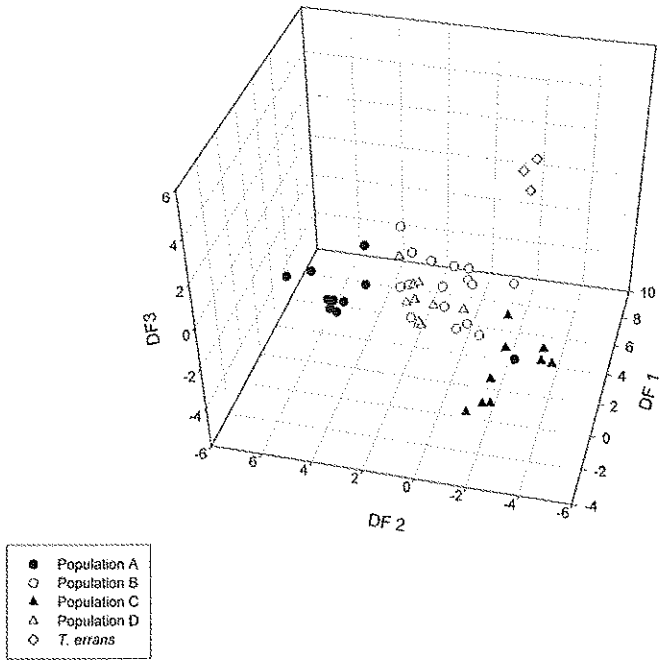

Figure 5. Three-dimensional plot of the first three discriminant function scores based on mensural characters of females in the four populations of the *Thamnophis godmani* complex and *T. errans*.

Population B: In addition to differing from Population A in the characters mentioned above, specimens from

Population C in having more ventrals, more subcaudals, a longer tail, and the barring on the posterior supralabials usually involving a bar along the fifth scale as well as between the sixth and seventh (with the dorsal connection well-developed and usually encroaching on the adjacent anterior temporal). Adult SVL appears to be greater than in Population C animals (the 10 longest presumptive adult females average 410 mm, the 10 longest males 342 mm). Nuchal blotch color is highly variable (55% are black; 15% are predominantly brown; 30% are black posteriorly, brown anteriorly). In comparison to Population D specimens, those in Population B have fewer ventrals, more maxillary teeth, and perhaps a slightly shorter muzzle.

Population C: These specimens differ from those in all other populations in having fewer ventrals, fewer subcaudals, a shorter tail, a wider frontal posteriorly, perhaps a slightly longer set of nasals, and a frequent loss of barring along the posterior suture of the fifth supralabial (although the dorsal connection along the lower edge of the anterior temporal to the bar along the sixth-seventh suture remains). Small sample size must be taken into consideration, but it does appear that adults in this population attain a shorter SVL than those in the other three populations (the six longest presumptive adult females average 330 mm, the 10 longest males 309 mm). The nuchal blotches usually are predominantly brown (92%; 8% are black posteriorly, brown anteriorly).

Population D: Members of this population differ from all others in having more ventrals, fewer maxillary teeth, and perhaps a slightly longer muzzle. In nearly all other features, including supralabial barring pattern and adult SVL length (the 10 longest presumptive adult females average 383 mm, the six longest males 337 mm), these snakes do not appear to differ significantly from those in Population B. However, like the snakes in Population C, those in D have predominantly brown

nuchal blotches (100% of specimens examined for this character).

Thamnophis errans (Fig. 6), which was shown by de Quieroz and Lawson (1994) to be indistinguishable from *T. godmani* from allozyme data, is morphologically distinguishable from members of the complex in a number of characters. Subsequently, *T. errans* and *T. godmani* have been shown to not be closely related when using mtDNA, (de Queiroz et al., 2002). *Thamnophis errans* has more DSR, more V, more SC, a larger eye, a wider muzzle and muzzle tip, and a shorter total nasal length than any of the four populations currently assigned to *T. godmani*. *Thamnophis errans* also has a longer tail than any of the *T. godmani* population samples—except for those in Population A, which demonstrates that the positive correlation existing between relative tail length and SC number is not always absolute. In contrast to members of populations B, C, and D, *T. errans* also shares with the members of Population A a very broad muzzle tip (that of *errans* is the broadest of any species of *Thamnophis*; that of Population A ranks third), and a longer, more triangular loreal. It may be worth noting in this context that Population A is the member of the complex geographically closest to *T. errans*, although their present ranges are some 665 km apart.

DISCUSSION

The results of our study demonstrate that each of the four population samples currently assigned to *Thamnophis godmani* can be distinguished to some degree morphologically by using univariate and multivariate statistical techniques on meristic and mensural data. Moreover, the populations also appear to be allopatric at the present time. Populations A and B are separated by 185 km, C and D by 125 km, and B and D by nearly 100 km. In the latter two instances, the mountain ranges

valleys (C and D by that of the Río Quiotepec, B and D by that of the Río Salado) that would pose formidable barriers to inhabitants of high-elevation pine-oak forest. These arid barriers

Figure 6. Dorsal pattern of *Thamnophis errans* (MSUM 3167), an adult female (375 mm SVL) from 1.6 km SW La Ciudad, Durango, México. From a kodachrome by Robert G. Webb.

to potential genetic connection among populations may have arisen during periods of warming and drying during the mid-and late Pleistocene (as reviewed in Rossman, 1992, and deQuieroz et al., 2002). As noted by de Quieroz et al. (2002), these arid trends may have led to speciation events in other members of the genus *Thamnophis*. With respect to the four distinct populations of *T. godmani*, it seems unlikely that they have experienced any interpopulation gene flow for a considerable period of time. However, without molecular data, the relative amount of gene flow and the timing of the genetic disconnection among populations cannot be determined.

While Population C is largely separated from Population B to the west by the valley of the Río Grande, there appears to be no obvious ecological barrier at the southern end of the Sierra de Juárez where representatives of the two populations have been collected within 33 km of each other. Three specimens from the southern end of the Sierra de Juárez initially proved difficult to assign collectively to a population and were grouped with Population C only following the multivariate analysis. AMNH 97890 and 147650, from just north of Cuajimoloyas, appeared to belong to Population C—but AMNH 91105, from 2.4 km S Carrizal (less than 6 km to the southeast), superficially resembled the members of Population B more than it did those of Population C. Although multivariate analysis assigned all three specimens to Population C, AMNH 91105 showed the lowest degree of affinity of the three. It cannot be determined if this situation reflects continued or residual gene flow between the two populations or is merely due to individual variation within Population C. Cuajimoloyas is situated in pine-oak forest and Carrizal in dry pine-oak forest (J. Campbell, pers. comm.). New material from this area, and a phylogeographic analysis of the entire group, might help to resolve the question relationships among these populations.

Taxonomic Conclusions

Since the four populations of *Thamnophis godmani* examined here appear to be allopatric and morphologically distinct, it can be inferred that they represent independently evolving lineages based on the criteria that they are distinguishable and each forms a cohesive group (de Queiroz, 1998). Therefore, we propose that each population should be recognized as separate species. *Thamnophis godmani* was originally described from Guerrero, so Population A will retain that name. No names are currently available for the other three

Thamnophis godmani (Günther)

Tropidonotus godmani Günther, 1894:133.

Type-locality: Mexico, Guerrero, Omilteme and Amula (lectotype: BM(NH) 1946.1.21.81, designated below).

Eutaenia godmanii: Cope, 1900:1232.

Thamnophis scalaris godmani: Smith, 1942:98.

Thamnophis godmani: Rossman, in Varkey, 1979:2.

Diagnosis. *Thamnophis godmani* can be distinguished from all other Mexican species of the genus by the following combination of characteristics: (1) maximum DSR 17; (2) maxillary teeth 17-21; (3) top of the head unpatterned; (4) two rows of relatively small black spots between light vertebral and lateral stripes; (5) nuchal blotches usually predominantly black; (6) prominence of black bar along posterior suture of SL 5 equal to, or greater than, bar along SL 6 and 7 suture; (7) V averaging 144 in males, 138 in females; (8) SC averaging 79 in males, 71 in females; (9) tail relatively long (mean T/TL 27% in males, 26% in females); (10) prefrontal suture usually slightly shorter than internasal suture (mean PFL/INL 94%); (11) muzzle tip usually very broad (mean INR/NR 134%); (12) anterior and posterior nasals usually subequal in length; (13) parietals shortest of all *Thamnophis* species (mean FL/PL 88%); and (14) frontal usually relatively narrow posteriorly (mean FWP/FWA 72%).

Designation of Lectotype. Günther (1894) based his description of *Thamnophis godmani* on a series of seven syntypes in the British Museum (Natural History), one of which (presumably the only specimen from Amula) was subsequently exchanged to the Museum of Comparative Zoology at Harvard (MCZ 28466) according to Smith, Nixon, and Smith (1950). We have examined the syntypes remaining in the British Museum and are here designating BM(NH) 1946.1.21.81 as the

Description of Lectotype. An adult female from Omilteme, Guerrero, Mexico, collected by H. H. Smith (date unknown) and purchased from F. D. Godman. SVL 418 mm, T length 136.5 mm (tip regenerated), T/TL 24.6%; DSR 17-17-15; V 138; SC 66; SL 7, third and fourth entering orbit; IL 11, first five in contact with ACS; oculars 1+3; maxillary teeth 20, most relatively short and stout for a *Thamnophis* — but last three greatly enlarged; HL/SVL 6.0%; FL/PL 85.0%; ED/FL 63.5%; FWA/FL 55.3%; FWP/FWA 75.6%; ML/FL 62.9%; MW/FL 74.1%; PFL/INL 87.8%; INR/NR 130.6%; TN/ML 62.2%; AN/PN 87.4%; LV/ML 39.3%; LD/LV 59.5%; LHT/LV 95.1%; ACS/PCS 83.8%.

The dorsum is brown with the only dark spotting being some scattered black flecks. The light vertebral stripe is distinct, confined to the vertebral row, and passes between the nuchal blotches to reach the interparietal notch (the four anteriormost scales are not as bright as those that follow). The nuchal blotches are black and extend ventrally to the upper edge of DSR 3. The light lateral stripes are grayish tan and confined to DSR 2 and lower DSR 3. DSR 1 and the outer edges of the ventrals are light brown (darker than the LS but lighter than the dorsal ground color). Vertically oriented, irregular black spotting is present on the anterior end of most scales in DSR 1. Prominent black barring on the posterior margins of SL 2-4 extends ventrally 60-80% of the height of each suture; on posterior SL 5 and SL 6 (the latter including anterior SL 7) the bars reach the lip. The IL are unmarked save for a black bar along the suture between IL 9 and 10. The venter is grayish green with an overlay of brown pigment.

Intraspecific Variation. Variation in *Thamnophis godmani* is summarized in Tables 2 and 3. The black dorsal spots are more prominent in juveniles and subadults (Fig. 7) than in adults. In TCWC 9538, the anteriormost spots fuse

stripe to the lateral stripes. The nuchal blotches are usually fused dorsomedially to form an unbroken, but indented, collar. The black barring on the supralabials usually is most prominent on SL 5, which occasionally is the only bar to reach the lip.

Distribution. *Thamnophis godmani* appears to be confined to pine-oak forest and cloud forest in the Sierra Madre del Sur of Guerrero (Fig. 1). Recorded elevations that are probably valid range from 1768-2438 m. A record from Acahuizotla at 853 m (TCWC 9533) is suspect because habitat suitable for this species would be unlikely to occur at such a low elevation.

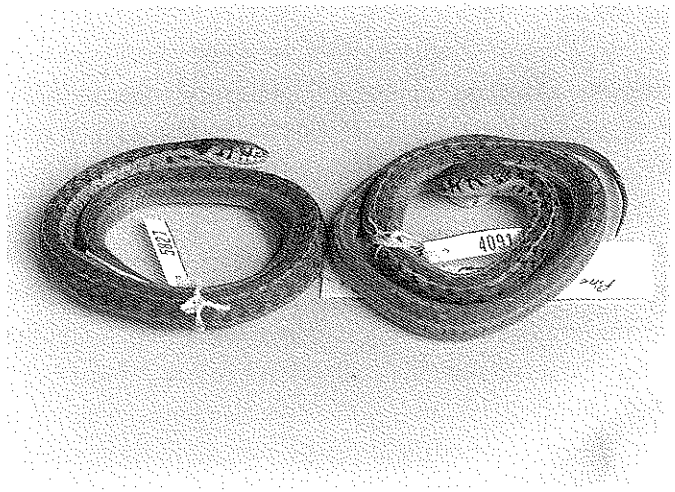

Figure 7. Dorsal pattern of two *Thamnophis godmani* (UTA R-5827, R-4091), subadult females (271 and 288.5 mm SVL, respectively) from Omilteme, Guerrero, Mexico. Photograph by Mark Kleiner.

Etymology.—Thamnophis godmani was named in honor of F. D. Godman, who obtained the type series for the British Museum (Natural History).

Thamnophis bogerti sp. nov.

Holotype. AMNH 93237, an adult male, from Mexico, Oaxaca, El Tejocote, 2377 m elevation; collected 11 October 1964 by C. M. Bogert.

Diagnosis. Thamnophis bogerti can be distinguished from all other Mexican species of the genus by the following combination of characteristics: (1) maximum DSR 17; (2) maxillary teeth 17-20; (3) top of head unpatterned; (4) two rows of relatively small black spots between light vertebral and lateral stripes; (5) nuchal blotch coloration variable, although only 15% have predominantly brown blotches; (6) prominence of black bar along posterior suture of SL 5 equal to, or less than, bar along SL 6 and 7 suture; (7) V averaging 145 in males, 140 in females; (8) SC averaging 70 in males, 62 in females; (9) tail of moderate length (mean T/TL 25% in males, 23% in females; (10) prefrontal suture usually slightly longer than internasal suture (mean PFL/INL 106%); (11) muzzle tip usually broad (mean INR/NR 115%); (12) anterior nasal usually shorter than posterior nasal (mean AN/PN 81%); (13) parietals usually of moderate length (mean FL/PL 77%); and (14) frontal usually relatively broad posteriorly (mean FWP/FWA 79%).

Description of Holotype. An adult male measuring 298.5 mm in SVL, T length 97.5 mm, T/TL 24.6%; DSR 17-17-15; V 143; SC 69; SL 8, fourth and fifth entering orbit; IL 10, first five in contact with ACS; oculars 1+3; maxillary teeth 20; HL/SVL 5.5%; FL/PL 76.1%; ED/FL 59.4%; FWA/FL 56.9%; FWP/FWA 83.0%; ML/FL 64.4%; MW/FL 66.5%; PFL/INL 92.3%; INR/NR 107.3%; TN/ML 59.3%; AN/PN 97.8%; LV/ML 40.3%; LD/LV 64.5%; LHT/LV 77.3%; ACS/PCS 83.6%. The dorsum is brown with small, irregular black spots that are barely visible (Fig. 8). The light vertebral stripe is confined to the vertebral row and is difficult to discern

lower edge of DSR 3. The nuchal blotches are predominantly black and fused middorsally (the vertebral stripe is separated from the interparietal notch by 4-1/2 scales). Prominent black barring along the posterior margins of SL 2-5 extends ventrally 50-75% of the height of each suture; along the posterior sutures of SL 6 and SL 7 (which includes anterior SL 8) the bars reach the lip. A black stripe extends along the lower margin of the anterior temporal connecting the two posteriormost SL bars. The IL are unmarked save for a black bar along the IL 9 and 10 suture.

Intraspecific Variation. Variation in *Thamnophis bogerti* is summarized in Tables 2 and 3. The distinctness of the light vertebral stripe and the dark dorsolateral spots is highly variable, and in many specimens they are much more distinct (Fig. 9) than they are in the holotype (Fig. 8). On the other hand, in AMNH 97861, 97886, 103103, 106998, and 113738 practically no trace of a light vertebral stripe is discernible. AMNH 103115 and 104394 differ from the holotype in not having the nuchal blotches fused middorsally. In most specimens, the vertebral stripe is confined to the vertebral row, but in a few the stripe involves part (but less than half the width) of the adjacent paravertebral scales as well. The light lateral stripes are occasionally absent or, at least, very difficult to see, and they sometimes appear to involve DSR 1 as well as DSR 2 and DSR 3. Two specimens (AMNH 100921, 100926) have the anterior dark spots fused vertically to form seven bars that extend ventrally from the vertebral stripe to interrupt the lateral stripes.

Distribution. Thamnophis bogerti is widely distributed in oak woodland, pine-oak forest, and pine-oak-madroño forest in the Mesa del Sur of Oaxaca, exclusive of the Sierra de Juárez (Fig. 1). Recorded elevations that are likely to be valid range

Figure 8. Dorsal pattern of *Thamnophis bogerti* (AMNH 93237 [holotype]), an adult male (298.5 mm SVL) from Tejocotes, Oaxaca, Mexico. Photograph by Mark Kleiner.

Etymology. We name Population B in honor of the late Charles M. Bogert of the American Museum of Natural History, who personally collected most of this material, and who very graciously ceded his interest in both the *Thamnophis godmani* and *T. scalaris* complexes to the senior author.

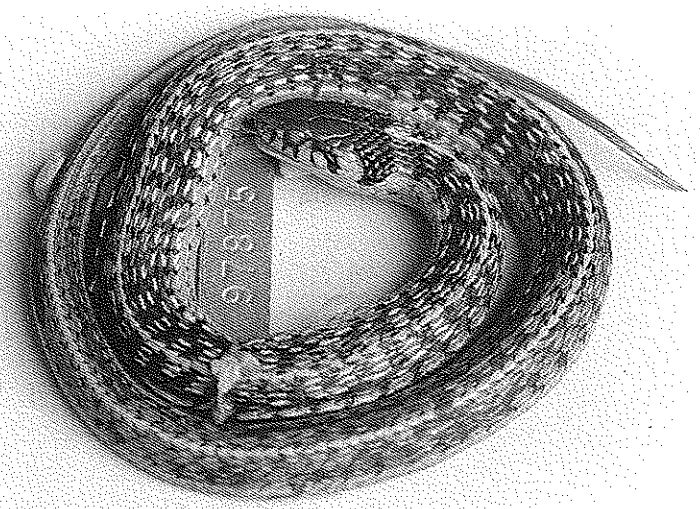

Figure 9. Dorsal pattern of *Thamnophis bogerti* (AMNH 97875), a subadult male (268 mm SVL) from Cofradía, Oaxaca, Mexico. Photograph by Mark Kleiner.

Thamnophis lineri sp. nov.

Holotype. UTA R-12482, an adult male, from Mexico, Oaxaca, Llano de las Flores, 2786 km elevation; collected 8 June 1983 by J. A. Campbell.

Diagnosis. Thamnophis lineri can be distinguished from all other Mexican species of the genus by the following combination of characteristics: (1) maximum DSR 17: (2) maxillary teeth 18-20; (3) top of head unpatterned; (4) two rows of relatively small black spots between light vertebral and lateral stripes; (5) nuchal blotches predominantly brown; (6) black bar along posterior suture of SL 5 frequently reduced or absent; (7) V averaging 140 in males, 136 in females; (8) SC

(mean T/TL 23.5% in males, 21.5% in females; (10) prefrontal suture usually slightly longer than internasal suture (mean PFL/INL 106%); (11) muzzle tip usually broad (mean INR/NR 116%); (12) anterior nasal usually shorter than posterior nasal (mean AN/PN 76%); (13) parietals usually of moderate length (mean FL/PL 80%); and (14) frontal usually very broad posteriorly (mean FWP/FWA 85%).

Description of Holotype. An adult male measuring 302.5 mm in SVL, T length 101.5 mm, T/TL 25.1%; DSR 17-17-15; V 143; SC 68; SL 7, third and fourth entering orbit; IL 9, first four in contact with ACS; oculars 1+3; maxillary teeth 18; HL/SVL 5.5%; FL/PL 82.2%; ED/FL 58.9%; FWA/FL 51.9%; FWP/FWA 91.2%; ML/FL 60.4%; MW/FL 76.7%; PFL/INL 117.1%; INR/NR 119.1%; TN/ML 66.7%; AN/PN 85.4%; LV/ML 38.5%; LD/LV 76.9%; LHT/LV 79.9%; ACS/PCS 85.2%.

The dorsum is brown with two alternating rows of moderately small black spots (Fig. 10, left). The light vertebral stripe is straw colored, barely distinct, and confined to the vertebral row. No light lateral stripes are visible. The nuchal blotches are brown with a black border (one scale long) posteriorly; the blotches are fused middorsally. There is very little black pigment along the posterior sutures of the SL anterior to that occurring along the common suture of SL 6 and SL 7, which is broad and reaches the lip. The IL are unmarked.

Intraspecific Variation. Variation in *Thamnophis lineri* is summarized in Tables 2 and 3. Distinctness of the dorsolateral dark spots and light vertebral and lateral stripes is highly variable (Fig. 10, right; Fig. 11), although most specimens tend to agree with the holotype in having a faintly visible vertebral stripe and no discernible lateral stripes. Some specimens have virtually no dorsolateral spotting visible. The presence or absence of black bars along the posterior SL

the holotype in having the most prominent bar along the SL 6-7 suture, and reduced or no barring on SL 5. Some individuals differ from the holotype in having dark IL barring.

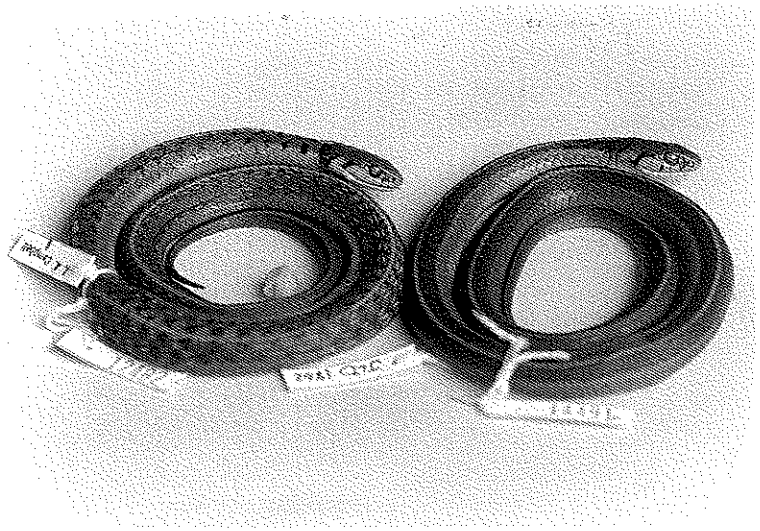

Figure 10. Dorsal pattern of two *Thamnophis lineri* (UTA R-12482 [holotype], R-14491), an adult male (302.5 mm SVL) and an adult female (331 mm SVL) from Llano de las Flores, Oaxaca, Mexico. Photograph by Mark Kleiner.

Color notes taken in the field on LSUMZ 11132-33 provide a partial glimpse of what *Thamnophis lineri* looks like in life. No description of dorsal ground color was given for either animal, but the vertebral stripe in LSUMZ 11132 was said to be "very dark tan, scarcely distinguishable from the dorsal ground color." In the other specimen, the vertebral row was characterized as being "dark tan." In both animals, DSR 1 and DSR 2 were said to be the same color as the vertebral stripe and "a shade lighter than the dorsal ground color," and the SL were

characterized as being "light grayish tan." The two venters were "grayish brown" with an "orange" (LSUMZ 11132) or "pale orange" (LSU11133) posterior margin on each V. The anal plate was predominantly "orange" in both. In general, the skin between the scales was "white," but in LSUMZ 11132 the skin immediately behind the nuchal blotches was "yellow." The tongue was "entirely black." A color photograph of a *T. lineri* (labeled as *T. godmani*) appears in Plate 6 of Rossman et al. (1996).

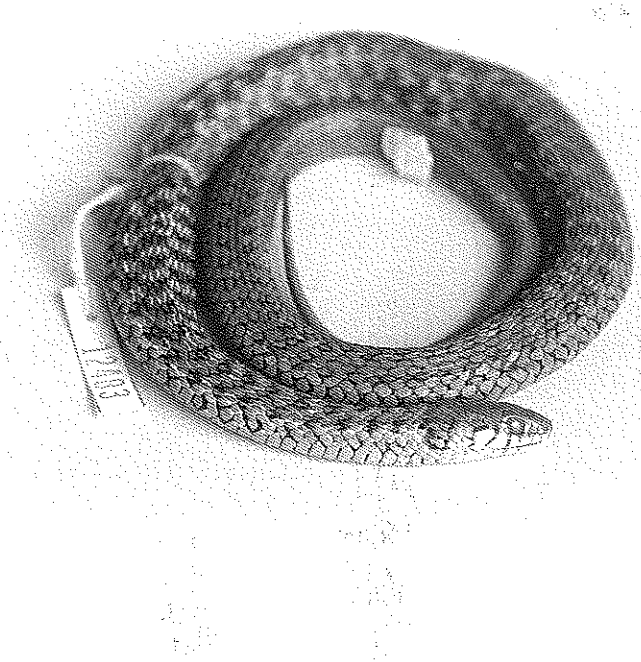

Figure 11. Dorsal pattern of *Thamnophis lineri* (UTA R-12483), an adult male (306 mm SVL) from Llano de las Flores, Oaxaca, Mexico. Photograph by Mark Kleiner.

Distribution. *Thamnophis lineri* apparently is confined to pine-oak forest and pine-oak-madroño forest in the Sierra de Juárez portion of the Mesa del Sur in Oaxaca (Fig. 1). Recorded elevations that are likely to be valid range from 2700-

Etymology. In recognition of his substantial contributions to Mexican herpetology, we take great pleasure in naming Population C after Ernest A. Liner.

Thamnophis conanti sp. nov.

Holotype. LSUMZ 75985 (originally USL 23933), an adult female, from Mexico, Puebla-Veracruz state line at Mexico Highway 125 [number in error, it is Highway 150 that extends north from Tehuacan, Puebla, to the state line at Puerto del Aire]; collected 15 August 1975 by Tom Hardaway.

Figure 12. Dorsal pattern of *Thamnophis conanti* (LSUMZ 75985), an adult female (317.5 mm SVL) from Puebla-Veracruz state line at Mexico Highway 150, Mexico. Photograph by Mark Kleiner.

Diagnosis. *Thamnophis conanti* can be distinguished from all other Mexican species of the genus by the following combination of characteristics: (1) maximum DSR 17; (2) maxillary teeth 16-18; (3) top of head unpatterned; (4) two rows

lateral stripes; (5) nuchal blotches predominantly brown; (6) prominence of black bar along posterior suture of SL 5 equal to, or less than, bar along SL 6 and 7 suture; (7) V averaging 150 in males, 144 in females; (8) SC averaging 72 in males, 64 in females; (9) tail of moderate length (mean T/TL 25% in males, 23% in females); (10) prefrontal suture usually slightly longer than the internasal suture (mean PFL/INL 105%); (11) muzzle tip usually moderately broad (mean INR/NR 107%); (12) anterior nasal usually shorter than posterior nasal (mean AN/PN 77%); (13) parietals usually of moderate length (mean FL/PL 75%); and (14) frontal usually of moderate width posteriorly (mean FWP/FWA 75%).

Description of Holotype. An adult female measuring 317.5 mm in SVL, T length 97 mm, T/TL 23.4%; DSR 17-17-16; V 146; SC 65; SL 7, third and fourth entering orbit; IL 10, first five in contact with ACS; oculars 1+2, 3; maxillary teeth 18; HL/SVL 5.5%; FL/PL 74.6%; ED/FL 61.4%; FWA/FL 58.8%; FWP/FWA 82.1%; ML/FL 72.4%; MW/FL 77.4%; PFL/INL 100.0%; INR/NR 94.8%; TN/ML 63.4%; AN/PN 70.4%; LV/ML 34.8%; LD/LV 63.2%; LHT/LV 85.0%; ACS/PCS 86.4%.

The dorsum is light grayish brown with two alternating rows of very small black spots visible only on the neck (Fig. 12). The light vertebral stripe is distinct, but not bright, and involves the vertebral row and the adjacent edges of the paravertebral rows. The light lateral stripes are barely discernible but apparently involve DSR 1-3. The nuchal blotches are brown with a black border (one scale long) posteriorly, and they are not fused middorsally. There are short black bars along the posterior sutures of SL 2-4, a narrow bar along SL 5 that reaches the lip, and a broad bar along the common suture of SL 6 and 7 that reaches the lip. The last two bars are joined dorsally by a black stripe along the lower

Intraspecific Variation. Variation in *Thamnophis conanti* is summarized in Tables 2 and 3. Distinctness of the dorsolateral spots and light vertebral and lateral stripes is variable, although the spotting is usually very faint or nearly absent, and the lateral stripes usually indistinct or lacking. Some individuals differ from the holotype in having dark barring along the suture between the posteriormost IL.

Color notes taken in the field on LSUMZ 11123-26, 11131 provide a partial glimpse of what *Thamnophis conanti* looks like in life. No mention was made of the dorsal ground color in any of these five snakes, but the skin between the scales was said to be "bright light yellow." The light vertebral stripe was characterized as being "pale tan" or "very pale tan" (it was confined to the vertebral row in three individuals, and involved the adjacent edges of the paravertebral rows in two). The SL were "pale grayish white," "light gray," or "light gray brown." The venters were variable ("pale gray, becoming grayish brown posteriorly," "orange suffused with brown," "orange flecked with gray," "deep orange anteromedially, gray-brown posteriorly and laterally"). The tongue was "entirely black."

Distribution. *Thamnophis conanti* apparently is confined to the southern interface of the Mesa Central and Sierra Madre Oriental near the Puebla-Veracruz state line (Fig. 1), where it has been taken in oak woodland. Recorded elevations likely to be valid range from 2134-2256 m.

Etymology. In recognition of the late Roger Conant's many contributions to our understanding of Mexican thamnophiine snakes—including a number of species of *Thamnophis*, we take great pleasure in naming Population D in his honor.

ACKNOWLEDGMENTS

We are indebted to the curators and collection managers of the eleven museums who loaned us the material listed in Appendix I. We also wish to thank the late Charles M. Bogert for relinquishing his own studies on this complex and making available the extensive collections he had accumulated; Hobart M. Smith for helping us find several obscure localities; Robert G. Webb for providing the kodachrome of a living *T. errans* from which Fig. 6 was made; Mark Kleiner for photographing the preserved specimens appearing in the other figures; Linda S. Ford for expediting the discovery and cataloguing of a critical specimen from Oaxaca (AMNH 147650) residing at that time in an uncatalogued collection from the late Sherman A. Minton; Jeff Boundy and Jonathan A. Campbell, for reading the manuscript and providing constructive criticism; and the Mexican government for issuing the scientific collecting permit in 1965 that made it possible for the senior author to become familiar with *T. lineri* and *T. conanti* in the field (the fieldwork was made possible by a grant from the National Science Foundation). We are grateful for the helpful advice concerning species lineages provided by Jim McGuire.

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APPENDIX I

Specimens Examined

Specimens were borrowed from the following institutional collections: American Museum of Natural History, New York (AMNH); British Museum (Natural History), London (BM[NH]); Monte L. Bean Museum, Brigham Young University, Provo, Utah (BYU); California Academy of Sciences, San Francisco (CAS); Field Museum of Natural History, Chicago (FMNH); Los Angeles County Museum of Natural History (LACM); Louisiana State University Museum of Natural Science, Baton Rouge (LSUMZ); University of Illinois Museum of Natural History, Urbana (UIMNH); University of Michigan Museum of Zoology, Ann Arbor (UMMZ); National Museum of Natural History, Smithsonian

Institution, Washington (USNM); University of Texas at Arlington Collection of Vertebrates (UTA).

Thamnophis errans MEXICO: Chihuahua: BYU 14493, 15721, 17076-77; Durango: AMNH 91106, BYU 13893-94, 15742, 15776, LSUMZ 16418-19, 40835-36, UMMZ 102509, 110880, UTA R-5941-42, R-5944, R-5957.

Thamnophis godmani MEXICO: Guerrero: AMNH 72500-02, 72505, BM(NH) 1946.1.21.80-85 (-.81, lectotype of *T. godmani)*, CAS 143956, FMNH 113736-37, TCWC 8580-81, 9533-48, 9550, UIMNH 35010-11, 35013, UMMZ 85734-35, 85738, UTA R-2818, R-2020-21, R-4019, R-4090-92, R-4417-22, R-4456-57, R-4926-27, R-4930-31, R-5827, R-6321-32.

Thamnophis bogerti MEXICO: Oaxaca: AMNH 89604, 89609, 93237 (holotype of *T. bogerti*), 97852-53, 97861, 97865, 97872-79, 97885-88, 100921-26, 103089-90, 103092-99, 103101, 103103-15, 104393-95, 106993-7000, 107002-05, CAS 140943, FMNH 113738, UMMZ 126828-29.

Thamnophis lineri MEXICO: Oaxaca: AMNH 65892, 89605-08, 91101-05, 97880, 97882-84, 97890, 100919, 103085-88, 147650, LACM 121861, LSUMZ 11132-34, UMMZ 125733 (2 spec.), 118788-89, 119627-30, USNM 224547-48, UTA R-12482 (holotype of *T. lineri*), R-12483, 14491.

Thamnophis conanti MEXICO: Puebla-Veracruz: AMNH 97892, BYU 13230, FMNH 70771-72, 103994-99, 105198, 113740-42, LACM 66902, 104261-62, 121856-60, LSUMZ 11123-26, 11131, 75985 (holotype of *T. conanti*), UIMNH 18901, 60820-23, UMMZ 88710, 105040-41, USNM 110807, 110809-11.

TABLES

Table 1. A checklist of sexually dimorphic characters for each population of the *T. godmani* complex and *T. errans*. The letter "R" indicates the raw characters that exhibit sexual dimorphism and the letter "L" indicates the log-transformed mensural characters that exhibit sexual dimorphism.

Character	Pop A	Pop B	Pop C	Pop D	*errans*
DSR 10					
DSR M					
DSR PEN					
V		R	R		
SC	R		R		R
TN		L			R, L
AN	R				R
PN		R, L			R
SVL					
T					
HL		R, L			R, L
ED		R, L			R
MW		R, L			R, L
ACS	R	R, L			R, L
PCS		R, L			R, L
FL				R, L	
FWA					R, L
FWP					
INR					
NR		R, L			R, L
PL		R, L			R, L
ML		R, L			R, L
PFL		R, L			R
INL		R, L			R, L
LD		R, L			R, L

LV	R, L	R, L
LHT	R,L	R, L
IG		

TABLE 2. Basic statistical information for males of the *T. godmani* complex and *T. errans*

Pop		T/ SVL	HL/ SVL	FL/ PL	EL/ FL	FWA/ FL	FWP/ FWA	ML/ FL	MW/ FL
A	N	27	22	21	21	21	14	21	13
	Minimum	0.34	0.05	0.77	0.53	0.54	0.64	0.48	0.68
	Maximum	0.42	0.06	0.97	0.72	0.65	0.81	0.73	0.75
	Mean	0.37	0.06	0.89	0.63	0.59	0.71	0.58	0.71
	SD	0.02	0.00	0.05	0.04	0.03	0.05	0.05	0.02
B	N	27	25	24	23	24	24	24	24
	Minimum	0.29	0.05	0.69	0.58	0.54	0.70	0.56	0.53
	Maximum	0.37	0.07	0.95	0.68	0.68	0.96	0.70	0.81
	Mean	0.33	0.06	0.78	0.63	0.60	0.81	0.63	0.71
	SD	0.02	0.00	0.06	0.03	0.03	0.06	0.04	0.05
C	N	16	12	12	12	12	12	12	12
	Minimum	0.27	0.05	0.76	0.57	0.52	0.80	0.53	0.67
	Maximum	0.37	0.06	0.89	0.67	0.59	0.94	0.65	0.79
	Mean	0.31	0.05	0.80	0.62	0.56	0.86	0.60	0.74
	SD	0.02	0.00	0.04	0.03	0.02	0.05	0.03	0.03
D	N	11	8	8	8	6	6	6	5
	Minimum	0.30	0.05	0.67	0.57	0.56	0.71	0.61	0.62
	Maximum	0.34	0.06	0.86	0.65	0.64	0.85	0.77	0.76
	Mean	0.32	0.05	0.75	0.61	0.61	0.77	0.68	0.71
errans	N	5	6	6	6	6	6	6	6
	Minimum	0.34	0.05	0.72	0.65	0.53	0.67	0.59	0.72
	Maximum	0.38	0.06	0.88	0.74	0.63	0.85	0.68	0.81
	Mean	0.36	0.05	0.81	0.69	0.58	0.77	0.64	0.78
	SD	0.02	0.00	0.05	0.03	0.03	0.06	0.04	0.04

Pop		PFL/ INL	INR/ NR	TN/ ML	AN/ PN	LV/ ML	LD/ LV	LHT/ LV	ACS/ PCS
A	N	14	21	11	11	12	12	11	21
	Minimum	0.76	1.02	0.53	0.85	0.34	0.56	0.74	0.69
	Maximum	1.43	1.62	0.76	1.19	0.49	0.72	0.84	0.90
	Mean	1.00	1.36	0.61	1.02	0.43	0.65	0.79	0.78
	SD	0.21	0.16	0.06	0.12	0.03	0.05	0.03	0.06
B	N	24	24	20	20	21	21	19	24
	Minimum	0.82	0.97	0.56	0.61	0.31	0.64	0.66	0.63
	Maximum	1.43	1.92	0.71	1.37	0.42	0.86	1.06	0.93
	Mean	1.09	1.19	0.63	0.85	0.37	0.75	0.82	0.79
	SD	0.15	0.20	0.04	0.18	0.03	0.06	0.09	0.07
C	N	12	12	12	12	11	11	11	12
	Minimum	0.68	0.96	0.66	0.60	0.26	0.65	0.74	0.70
	Maximum	1.21	1.41	0.75	0.91	0.46	0.88	1.12	0.92
	Mean	1.02	1.18	0.69	0.73	0.36	0.76	0.84	0.84
	SD	0.15	0.16	0.03	0.09	0.06	0.06	0.11	0.06
D	N	6	6	5	5	6	6	5	8

	Minimum	0.90	1.04	0.57	0.63	0.29	0.74	0.65	0.70
	Maximum	1.21	1.36	0.63	0.83	0.41	0.82	0.89	0.88
	Mean	1.07	1.14	0.60	0.74	0.35	0.76	0.75	0.80
	SD	0.12	0.12	0.02	0.10	0.04	0.03	0.09	0.06
errans	N	6	6	6	2	6	6	6	6
	Minimum	0.87	1.28	0.51	0.80	0.37	0.53	0.78	0.74
	Maximum	1.40	1.80	0.60	1.03	0.42	0.72	1.00	0.93
	Mean	1.16	1.59	0.54	0.91	0.40	0.62	0.88	0.86
	SD	0.20	0.21	0.03	0.16	0.02	0.08	0.08	0.07

Pop		DSR 10	DSR M	DSR	V	SC	MT
A	N	31	31	31	31	26	15
	Minimum	17	15	15	139	74	18
	Maximum	17	17	17	149.5	88	21
	Mean	17	16.7	15.1	143.4	78.9	19.4
	SD	0	0.70	0.40	2.78	3.81	0.83
B	N	35	35	35	35	27	9
	Minimum	17	17	15	139	64	17
	Maximum	17	17	17	151	79	20
	Mean	17	17	16	144.7	70.3	18.1
	SD	0	0	1	2.65	3.36	0.93
C	N	19	19	19	19	15	9
	Minimum	17	17	14	135	55	18
	Maximum	17	17	17	144	67	20
	Mean	17	17	15.9	139.5	61.3	18.8
	SD	0	0	1.08	2.48	2.89	0.57
D	N	11	11	11	13	11	7
	Minimum	17	17	15	142	64	16
	Maximum	17	17	17	157	77	20
	Mean	17	17	15.9	149.1	71.4	18.0
	SD	0	0	0.94	3.82	4.08	1.53

errans	N	5	5	5	2	2	NM
	Minimum	19	19	16	154	84	NM
	Maximum	19	19	17	159	85	NM
	Mean	19	19	16.8	156.5	84.5	NM
	SD	0	0	0.45	3.54	0.71	NM

TABLE 3. Basic statistical information for females of the *Thamnophis godmani* complex and *T. errans*.

Pop		T/ SVL	HL/ SVL	FL/ PVL	EL/ FL	FWA/ FL	FWP/ FWA	ML/ FL	MW/ FL
A	N	35	23	21	21	21	15	21	16
	Minimum	0.29	0.05	0.79	0.56	0.50	0.63	0.52	0.66
	Maximum	0.38	0.11	0.95	0.68	0.64	0.83	0.72	0.80
	Mean	0.35	0.06	0.87	0.63	0.58	0.72	0.62	0.72
	SD	0.02	0.01	0.04	0.03	0.04	0.06	0.05	0.04
B	N	27	2	24	24	23	23	24	24
	Minimum	0.26	0.05	0.65	0.58	0.54	0.70	0.57	0.67
	Maximum	0.34	0.07	0.89	0.71	0.68	1.10	0.77	0.81
	Mean	0.30	0.06	0.75	0.65	0.61	0.79	0.68	0.74
	SD	0.02	0.00	0.05	0.03	0.04	0.09	0.05	0.04
C	N	16	12	9	9	9	9	9	9
	Minimum	0.25	0.05	0.71	0.59	0.51	0.74	0.61	0.71
	Maximum	0.30	0.07	0.83	0.74	0.67	0.92	0.78	0.84
	Mean	0.27	0.06	0.79	0.64	0.59	0.84	0.68	0.78
	SD	0.02	0.00	0.04	0.04	0.05	0.06	0.06	0.04
D	N	22	19	18	18	14	14	14	14
	Minimum	0.27	0.05	0.70	0.56	0.54	0.67	0.63	0.69
	Maximum	0.32	0.08	0.84	0.68	0.68	0.82	0.78	0.80
	Mean	0.30	0.06	0.75	0.62	0.62	0.74	0.70	0.75
	SD	0.01	0.01	0.04	0.03	0.04	0.05	0.04	0.03
errans	N	10	13	13	13	13	13	13	13
	Minimum	0.31	0.05	0.72	0.64	0.52	0.68	0.59	0.76
	Maximum	0.34	0.06	0.84	0.73	0.64	0.88	0.79	0.86
	Mean	0.32	0.06	0.77	0.69	0.58	0.75	0.69	0.81
	SD	0.01	0.00	0.03	0.03	0.04	0.06	0.05	0.03

Pop		PFL/ INL	INR/ NR	TN/ ML	AN/ PN	LV/ ML	LD/ LV	LHT/ LV	ACS/ PCS
A	N	14	21	11	11	12	12	11	21
	Minimum	0.76	1.02	0.53	0.85	0.34	0.56	0.74	0.69
	Maximum	1.43	1.62	0.76	1.19	0.49	0.72	0.84	0.90
	Mean	1.00	1.36	0.61	1.02	0.43	0.65	0.79	0.78
	SD	0.21	0.16	0.06	0.12	0.03	0.05	0.03	0.06
B	N	24	24	20	20	21	21	19	24
	Minimum	0.82	0.97	0.56	0.61	0.31	0.64	0.66	0.63
	Maximum	1.43	1.92	0.71	1.37	0.42	0.86	1.06	0.93
	Mean	1.09	1.19	0.63	0.85	0.37	0.75	0.82	0.79
	SD	0.15	0.20	0.04	0.18	0.03	0.06	0.09	0.07
C	N	12	12	12	12	11	11	11	12
	Minimum	0.68	0.96	0.66	0.60	0.26	0.65	0.74	0.70
	Maximum	1.21	1.41	0.75	0.91	0.46	0.88	1.12	0.92
	Mean	1.02	1.18	0.69	0.73	0.36	0.76	0.84	0.84
	SD	0.15	0.16	0.03	0.09	0.06	0.06	0.11	0.06
D	N	6	6	5	5	6	6	5	8
	Minimum	0.90	1.04	0.57	0.63	0.29	0.74	0.65	0.70
	Maximum	1.21	1.36	0.63	0.83	0.41	0.82	0.89	0.88
	Mean	1.07	1.14	0.60	0.74	0.35	0.76	0.75	0.80
	SD	0.12	0.12	0.02	0.10	0.04	0.03	0.09	0.06
errans	N	6	6	6	2	6	6	6	6
	Minimum	0.87	1.28	0.51	0.80	0.37	0.53	0.78	0.74
	Maximum	1.40	1.80	0.60	1.03	0.42	0.72	1.00	0.93
	Mean	1.16	1.59	0.54	0.91	0.40	0.62	0.88	0.86
	SD	0.20	0.21	0.03	0.16	0.02	0.08	0.08	0.07

Pop		DSR 10	DSR M	DSR PEN	V	SC	MT
A	N	41	41	41	40	31	13
	Minimum	17	17	14	131.5	61	17
	Maximum	19	17	15	143	77	20
	Mean	17.1	17	14.9	137.8	70.6	18.8
	SD	0.35	0.00	0.16	3.26	3.58	0.93

B	N	34	34	34	34	26	12
	Minimum	17	17	15	133	56	17
	Maximum	17	17	17	149	68	19
	Mean	17	17	16.1	140.5	61.9	17.8
	SD	0.00	0.00	0.97	3.11	2.58	0.58
C	N	14	14	14	16	15	7
	Minimum	17	17	15	131	51	18
	Maximum	17	17	17	140	57	20
	Mean	17	17	5.8	135.9	54.1	18.6
	SD	0.00	0.00	0.9	2.76	2.26	0.79
D	N	23	23	23	28	22	10
	Minimum	16	17	14	139	59	16
	Maximum	17	17	17	150	68	18
	Mean	16.9	17.00	15.7	144.4	64.1	16.8
	SD	0.21	0.00	1.11	2.74	2.35	0.79
errans	N	9	9	9	5	5	NM
	Minimum	19	19	17	150	70	NM
	Maximum	19	19	17	156	78	NM
	Mean	19	19	17	153.2	74.8	NM
	SD	0.00	0.00	0.00	2.59	3.03	NM

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