

# Geographic variation in the garter snakes (*Thamnophis sirtalis*) of the north-central United States, a multivariate study

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A study of geographic variation in three subspecies of garter snake (*Thamnophis sirtalis sirtalis*, *T. s. parietalis*, *T. s. semifasciata*) in the north-central United States indicates patterns of irregular non-clinal microgeographic variation for 40 characters of coloration, scalation, and internal anatomy. Multivariate analyses show that geographically close populations are not always phenetically close and that overall differentiation of the phenotype is greater in males than in females. Univariate and multivariate studies indicate that *T. s. semifasciata* Cope 1892, restricted to the Chicago area, is not uniform within its small range and that it has no constant distinguishing features: it is shown to be taxonomically invalid.

KEY WORDS: — snakes — *Thamnophis sirtalis* — geographic variation — subspecies — multivariate analysis.

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## INTRODUCTION

The common garter snake (*Thamnophis sirtalis*) is an advanced colubrid which is abundant over much of North America. *T. sirtalis* displays considerable geographic variation over its range and it has been divided into at least 11 subspecies (Wright & Wright, 1957; Conant, 1975) on the basis of a few colour characters considered independently of one another.

Although *T. sirtalis* is well known for its confusing patterns of geographic variation (and as a result, its confused taxonomy), no multivariate studies of racial differentiation have yet been carried out. The present study relates to the north-central United States which is the transition zone between two subspecies of *T. sirtalis* and contains a problematical subspecies of very limited range (Fig. 1). The three subspecies in question and their distinguishing features (as defined by Cope, 1900: 1064–1079) are briefly as follows:

*Thamnophis sirtalis sirtalis* (Linnaeus, 1758)

No red marks on side; no black blotches across lateral stripe.

*Thamnophis sirtalis parietalis* (Say, 1823)

Dorsal black spots separated by red interspaces above lateral pale stripe.

*Thamnophis sirtalis semifasciata* (Cope, 1892)

Anterior dorsal black spots confluent with ventral spots, forming half crossbars across lateral stripe.

*T. s. sirtalis* (eastern garter snake) and *T. s. parietalis* (western or red-sided garter snake) are distributed over large areas. However, *T. s. semifasciata* (Chicago garter snake) has a very small range (Fig. 1), and its distinguishing character (side spots) is not present in all specimens from its range. In a major study of geographic variation in garter snakes, Ruthven (1908a) concluded that *semifasciata* was merely one of many colour phases without defined bounds of distribution. Many authors supported this view (Brown, 1901; Sperry, 1903; Smith, 1942; Pope, 1944; Wright & Wright, 1957: 834–866). However, Smith (1956) reviewed this question and concluded that the *semifasciata* pattern was constant around north-eastern Illinois and he mapped isophenes of the frequencies of occurrence of this pattern. This conclusion is supported in recent works (Smith, 1961: 231–235; Minton, 1972: 245–251) and in the standard field guide (Conant, 1975).

The aim of this work was to study geographic variation in colour pattern and other character systems and to test the validity of the subspecies *T. s. semifasciata*. The initial commitment was to measure as many characters as possible (to give an assessment of overall racial differentiation) from as many populations as possible. In the time available, however, only 26 continuously variable characters from six populations and 16 binary colour pattern characters from these and an additional 45 populations were measured.

## METHOD

*Specimens*

Eighty-seven male and female garter snakes from two populations within the ranges of each of *T. s. sirtalis*, *T. s. parietalis* and *T. s. semifasciata* were measured for the multivariate study (mapped in Fig. 1). The specimens are in the collections of

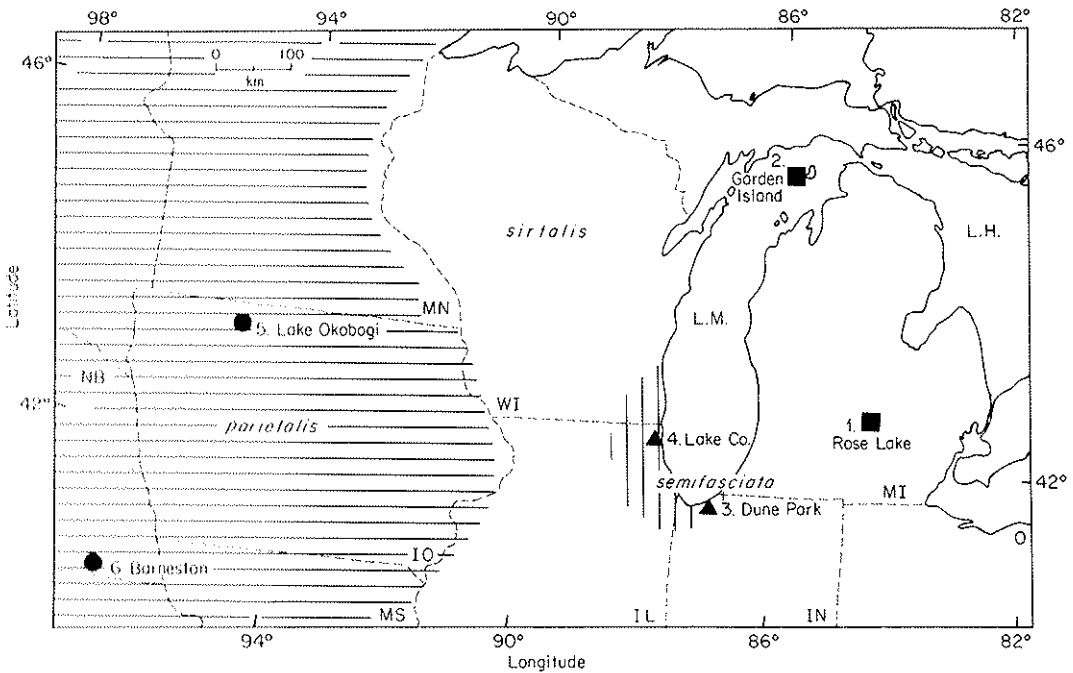


Figure 1. Map of the study area in the north-central United States, showing localities sampled in the present work (nos 1-6). Localities are coded as follows: ■ *sirtalis*; ▲ *semifasciata*; ● *parietalis*. The conventional subspecies ranges are indicated by shading: boundaries are taken from Conant (1975) and Smith (1956).

IL, Illinois; IN, Indiana; IO, Iowa; L. H., Lake Huron; L. M., Lake Michigan; MI, Michigan; MN, Minnesota; MS, Missouri; NB, Nebraska; O, Ohio; WI, Wisconsin.

Michigan State University, University of Michigan, Field Museum of Natural History, and University of Nebraska.

Seven hundred and twenty-five specimens from 51 localities were measured for the univariate study (552 from Michigan, 93 from Indiana, 19 from Illinois, 61 from Iowa). Individual localities were pooled and male and female data were combined so that there were at least ten specimens in each group. The final number of pooled 'localities' was 51, none of which had a radius greater than 50 km.

### Characters

Two kinds of characters were used in this study: continuously variable and binary. A univariate and a multivariate (canonical) analysis of the continuously variable characters was made and the binary (colour) characters were studied by means of isophene maps. Finally, both sets of characters were combined in a principal components analysis of sample means.

For each snake, four dentition, six scalation, and 14 internal organ characters were recorded as in Thorpe (1975a). Sixteen binary coloration characters were also noted. All internal organ characters were measured in terms of their ventral scale (V.S.) position and these values were converted to a %V.S. position in order to remove the effect of varying numbers of ventral scales in different individuals.

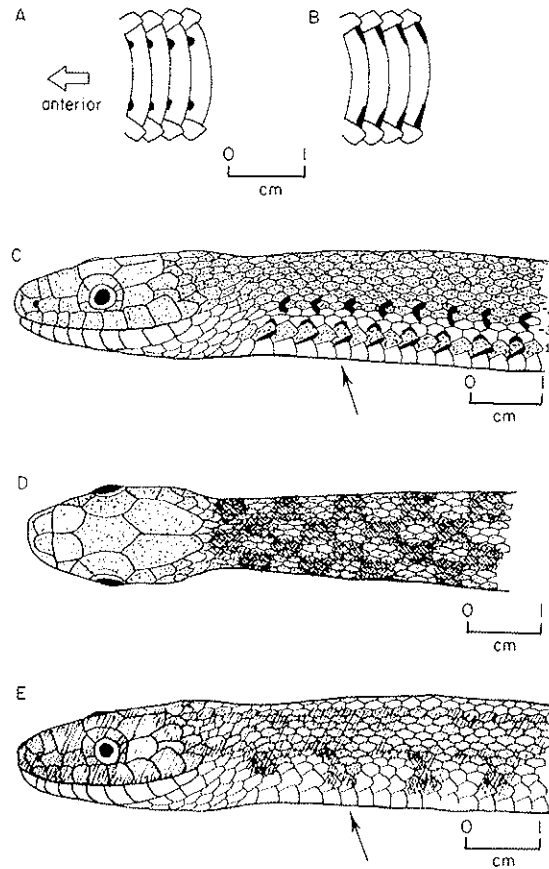


Figure 2. Colour pattern characters in garter snakes: A, ventral spots (character 42); B, ventral 'streaks' (character 43); C, black marks on dorsal scales of row 1, 2, 3 and 4 (characters 47-50), based on several specimens, one series is arrowed; D, 'checker' pattern (character 52), based on UM 61014; E, '*semifasciata*' blotches (character 53), based on UM 26297, one blotch is arrowed.

Table 1. Final reduced list of 21 continuously variable characters used in the multivariate study

1. Number of maxillary teeth	11. %V.S. anterior edge of thyroid gland
2. Number of pterygoid teeth	13. %V.S. posterior tip of left lung
3. Number of palatine teeth	15. %V.S. position at which right and left systemic arteries join
4. Number of dentary teeth	18. V.S. length of cystic duct
5. Number of ventral scales (measured according to the method of Dowling, 1951)	19. %V.S. anterior edge of pancreas
8. Number of sublabial scales, averaged for both sides	20. %V.S. posterior tip of right lung
9. Number of supralabial scales, averaged for both sides	23. %V.S. anterior tip of left kidney
10. %V.S. serial number of ventral scale (counted from anterior end) at which reduction of number of longitudinal rows of dorsal scales from 19 to 17 occurs	25. %V.S. anterior thyroid—posterior heart
	27. %V.S. join systemics—anterior liver
	28. %V.S. posterior liver—anterior pancreas
	30. %V.S. anterior right kidney—anterior left kidney
	36. %V.S. midpoint left kidney
	38. %V.S. separation of kidneys at midpoints

Some values for distance between internal organs and lengths of internal organs could be derived from these %V.S. positions. As far as possible, adults only were used in this study and gravid females were not measured since the embryos distorted the positions of some of the internal organs.

A one-way analysis of variance over the six localities was carried out for each of these continuously variable characters for each sex. This test indicates which characters show significant inter-locality variation and are thus suitable for use in a study of geographic variation. Characters with high F values (95% significant variation between localities) for both sexes or for either sex were selected for the multivariate analysis. Certain mutually exclusive characters had to be omitted (for example, anterior and posterior positions of an internal organ are mutually exclusive to length or midpoint of that organ) and the final list included 21 continuously variable characters (Table 1). The binary (coloration) characters are listed in Table 2.

#### *Univariate analysis*

Localities for the binary (colour) characters were pooled as described above ('Specimens'). The percentage of specimens displaying each of the 16 characters at each locality was computed and mapped and isophenes were inserted at 10% intervals.

In the univariate analysis of continuously variable characters, the least significant difference (LSD) was calculated (Snedecor & Cochran, 1967) for each sex and half the LSD value was plotted on either side of the mean character value at each locality. Overlaps of 95% confidence limits, separations of populations for particular characters, and clines were recorded.

#### *Multivariate analysis*

For each sex, two multivariate analyses were carried out: discriminant (canonical) analysis (of continuously variable characters only) and principal components analysis (Sneath & Sokal, 1973) of mean values for each sample (of continuously variable and binary characters together).

Table 2. List of 16 binary colour characters used in the univariate and multivariate studies

40. Colour of belly (more than, or less than 50% of total ventral area coloured)	49. Black marks on dorsal scales of longitudinal row 3 (present or absent) (Fig. 2C)
41. Colour of underside of tail (more than, or less than 50% of total subcaudal area coloured)	50. Black marks on dorsal scales of longitudinal row 4 (present or absent) (Fig. 2C)
42. Black spots on any of first 25 ventral scales (present or absent) (Fig. 2A)	51. Black marks on dorsal scales of longitudinal rows 5 and above (present or absent)
43. Dark streaks on posterior margins of ventral scales (present or absent) (Fig. 2B)	52. "Checker" pattern on dorsal surface (present or absent) (Fig. 2D)
44. Light mid-dorsal stripe (present or absent)	53. Black (" <i>semifasciata</i> ") blotches extending right across side stripe (present or absent) (Fig. 2C)
45. Light side stripes (clear or faint/absent)	54. Redsidedness—red or pink colour (in preserved specimens) between dorsal scales above side stripes ( <i>parietalis</i> character) (present or absent)
46. Light side stripes occupy dorsal scale rows 1–3 or 2–3.	55. White spaces between dorsal scales (present or absent) (see "Results" p. 315)
47. Black marks on dorsal scales of longitudinal row 1 (present or absent) (Fig. 2C)	
48. Black marks on dorsal scales of longitudinal row 2 (present or absent) (Fig. 2C)	

The Mahalanobis (1936) generalized distance ( $D^2$ ) was used in association with a canonical analysis (Program BMDP7M, Aberdeen University Honeywell Computer 66/80). The  $D^2$  statistic indicates the relative similarity of groups and it takes account of the within-group covariation between characters. The matrix of  $D^2$  values between populations may be summarized in several ways, namely: cluster analysis (Fig. 5), network diagrams (Fig. 6), and canonical analysis (Fig. 7) (Thorpe, 1976). Canonical analysis summarizes the variation between OTUs in a few axes (five in this case). Canonical variates 1 and 2 represent most of the variation (about 70% in the present study) and a two-dimensional scatter diagram plotted on these axes (Fig. 7) gives a summary of the variation in the groups.

Principal components analysis, like canonical analysis, summarizes variation between groups in a reduced number of axes. Two-dimensional scatter and centroid diagrams are plotted and degree of racial affinity is represented by the closeness of points in the plots. Thirty-four (females) and 35 (males) characters (means of continuously variable characters at each locality and % presence of each binary colour character at each locality) out of the original total of 36 were suitable for ordination using PCA for the six localities. The data were standardized to unit means and zero standard deviations and used in Program BMDP4M. Three scatter diagrams were plotted for the first three principal components and these diagrams were combined to produce a three-dimensional figure of scaled vectors (Fig. 8). Cluster analysis was based on the Pythagorean distances between centroids (computed from scaled eigenvectors).

## RESULTS

### *Geographic variation of continuously variable characters*

A review of some 80 maps of each continuously variable character for both sexes did not reveal any consistent patterns of geographic variation. The six localities form an approximately east-west series (1-6), but clinal variation occurs in only a few characters. (Increasing east-west: ventrals ♀, ♂; length left lung ♀; %V.S. anterior liver ♀; %V.S. anterior pancreas ♀, ♂; %V.S. anterior left kidney ♂; %V.S. join systematics — anterior liver ♀; %V.S. posterior liver — anterior pancreas ♂. Increasing west-east: %V.S. posterior heart ♀; %V.S. posterior left lung ♂; %V.S. posterior liver ♂; %V.S. total size kidneys ♂).

The six localities were selected so that two were located relatively close together within the conventional range of each of the three subspecies. However, in most cases, the mean values for both populations of a subspecies differ and the LSD values for separate subspecies overlap. In fact, the only characters which distinguish two subspecies at 95% significance are ventral scale count (females and males), and subcaudal scale count (males only). No character distinguishes all three subspecies, and no character separates any one subspecies from the other two. In a much larger number of characters (33 for females and 27 for males), the two populations within a subspecies are distinct at 95% significance: *sirtalis* is split 19 times, *semifasciata*, 15 times, and *parietalis*, 26 times. For only a few characters are the values for the two populations of a subspecies nearly identical (12 for females and 14 for males) and this is commonest in *semifasciata* (13 cases out of 26 in all), the two localities sampled for this subspecies being geographically closest.

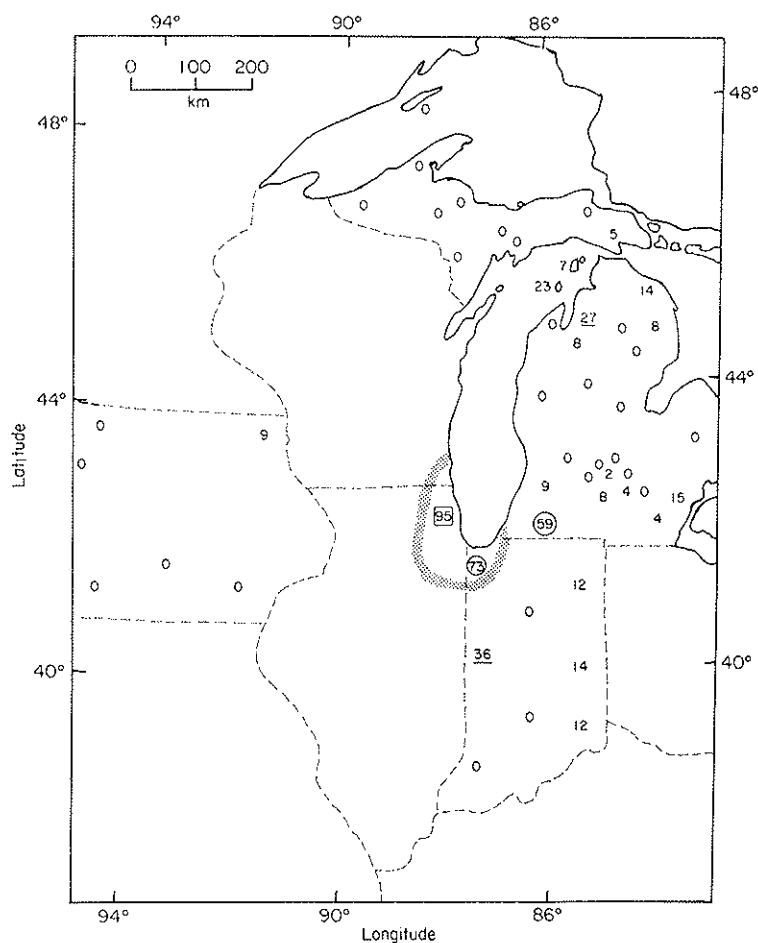


Figure 3. Distribution of garter snakes with "semifasciata" blotches (character 53). Map of study area showing percentage occurrence (averaged for males and females) at 51 localities. Conventional *semifasciata* range outlined. Values over 75% are boxed; over 50%, circled; over 25%, underlined.

#### *Geographic variation of binary (colour) characters*

Several colour characters appear to display trends showing, for example, high values in the range of one subspecies and low values in the range of another. Some examples of these rather ill-defined trends are given, but it should be stressed that they are all largely disrupted by irregular microgeographic variation and are not suitable characters for defining subspecies boundaries. *T. s. parietalis* (in Iowa, at least) had less than 50% of the underside of its tail coloured (character 41) and *T. s. sirtalis* generally had more than 50% coloured. There seemed to be a reduction from 90% to 0% from east to west. Similarly, *T. s. parietalis* in Iowa almost invariably had side stripes covering dorsal scale rows 2 and 3 only (character 46), whereas *T. s. sirtalis* frequently had side stripes on rows 1–3. There was apparently a reduction in the incidence of the lateral stripe on rows 1–3 from 90–100% to 0% from east to west. The presence of black marks on dorsal scales of rows 5 and above (character 51) showed a high point in north-eastern

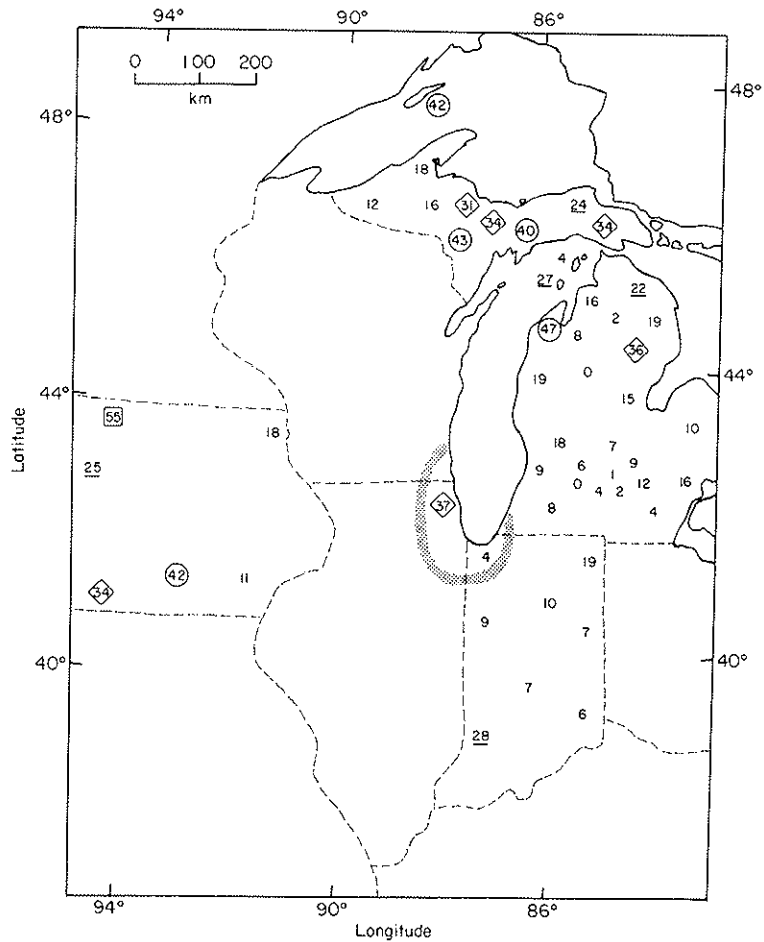


Figure 4. Distribution of "redsided" garter snakes. Map of study area showing percentage occurrence (averaged for males and females) of redsidedness (combined from data for characters 54 (redsidedness) and 55 ("whitesidedness")) at 51 localities. Conventional *semifasciata* range outlined. Values over 50% are boxed; over 40%, circled; over 30%, in diamonds; over 20%, underlined.

Illinois and values decreasing towards the east, west and south. In general, many *T. s. semifasciata* displayed this character and it was apparently absent in most *T. s. sirtalis* and *T. s. parietalis*. Finally, the 'checker' pattern (character 52) seemed to be restricted largely to Indiana. Minton (1972: 146) also noted this and figured a checkered garter snake from southern Indiana.

Some of the other colour characters recorded displayed little geographic variation in the study area, or if they did vary, there was seldom any clear pattern. Geographic variation was irregular for ventral colour (character 40), ventral spots (character 42), ventral streaks (character 43), mid-dorsal stripe (character 44), and spots on dorsal scales of rows 1–4 (characters 47–50). The maps for the last four characters showed similar irregular patterns of distribution.

The only published diagnostic character of *T. s. semifasciata* is the presence of several vertical black bars crossing the lateral pale stripe near the anterior end (character 53). This character is most common in north-eastern Illinois and



decreases in frequency of occurrence outwards from that point (Fig. 3). A population in northern Michigan and Garden Island, well outside the range normally given for *semifasciata*, also displays this feature.

The conventional diagnostic character of *T. s. parietalis* is red-sidedness (character 54). However, in most cases, the red colour fades to white in alcohol (cf. Brown, 1901: 28; Wright & Wright, 1957: 9) and this is recorded as 'whitesidedness' (character 55). Values for both characters are averaged to produce Fig. 4, which is probably a truer representation of the distribution of snakes with red sides. Western snakes display a greater frequency of red sides, but many specimens well within the range of *T. s. sirtalis* and *T. s. semifasciata* have red sides.

Thus, only a few colour characters displayed a pattern of geographic variation, but no one character state was restricted to a single subspecies. Five of the characters discussed above (nos 41, 45, 51, 53 and 54) were distributed approximately according to the conventional subspecies boundaries, but they certainly did not give an unequivocal indication of the latter.

#### Multivariate analysis of racial affinities

##### Canonical analysis

The mean Mahalanobis  $D^2$  values for distances between the six groups are given in Table 3.

An interesting feature of these matrices is that the  $D^2$  values tend to be lower and show less variation among females than among males. Since in females certain of the six populations are approximately equally different from each other, different groupings might arise from a different study. However, there are wider differences between  $D^2$  values in the male matrix.

Table 4 gives geographic distances between the localities sampled. These geographic distances do not correlate with the  $D^2$  values for either males or females in any regression model. The two populations of *T. s. semifasciata* are rather different from each other for females, the Indiana population (locality 3)

Table 3. Mahalanobis  $D^2$  values for females (a) and males (b)

(a)	2	50.9								
	3	37.8	61.1							
	4	38.8	38.0	40.6						
	5	57.6	60.6	40.3	44.9					
	6	53.1	61.1	36.1	41.7	43.1				
		1	2	3	4	5				
(b)	2	134.6								
	3	145.7	54.1							
	4	127.5	98.2	99.8						
	5	119.4	156.7	115.0	111.5					
	6	227.9	103.3	70.1	129.6	90.0				
		1	2	3	4	5				

Table 4. Geographic distances (to nearest 10 km) between localities sampled. Compare with matrices in Table 3

2	370				
3	280	520			
4	310	450	120		
5	880	840	720	620	
6	1060	1120	840	800	420
	1	2	3	4	5

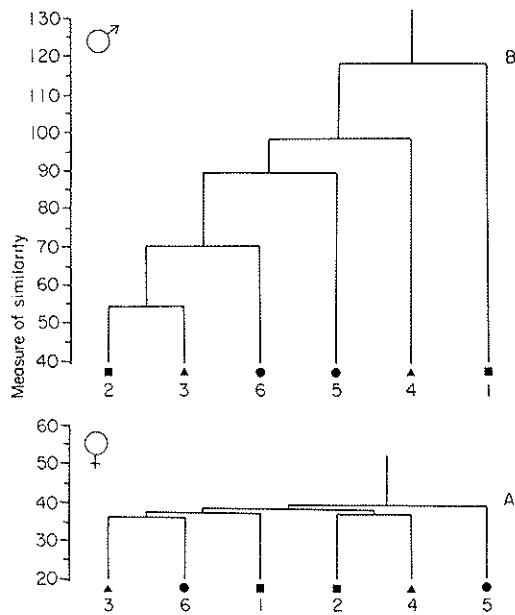


Figure 5. Cluster diagrams (dendrograms) produced by the pair-grouping method for canonical analysis results. A, Females; B, males. The populations are numbered and subspecies coded as in Fig. 1.

being closest (in terms of  $D^2$  values) to the Nebraska population of *T. s. parietalis* (locality 6), and the Illinois one (locality 4) being closest to the Garden Island population of *T. s. sirtalis* (locality 2). Males display a similar pattern.

Dendrograms (Fig. 5) are quite different for males and females, but neither clusters populations as might theoretically be expected from the conventional subspecies boundaries. Geographically distant populations (e.g. 3 and 6) cluster early, while geographically close populations (e.g. 3 and 4) appear to be phenetically distant. This is emphasized when network lines with Mahalanobis  $D^2$  values are added to a map (Fig. 6).

The canonical plots (Fig. 7) display rather similar patterns for males and females, but there is more overlap of the groups for females in these two dimensions. The lowest Mahalanobis  $D^2$  values are plotted on the network lines linking centroids. The 95% rings overlap in these two dimensions far more in females than in males, and this is related to the higher, more widely dispersed  $D^2$  values in the latter.

#### *Principal components analysis*

The three-dimensional plots of variation against the first three (out of five) reduced axes are given in Fig. 8. In both sexes, populations 3 and 4 are close phenetically, as are populations 1 and 2, and the dendrograms (Fig. 9) again indicate the relative phenetic closeness of populations 1 and 2, and 3 and 4, but in no way do they support a separation of subspecies as has been done in the past.

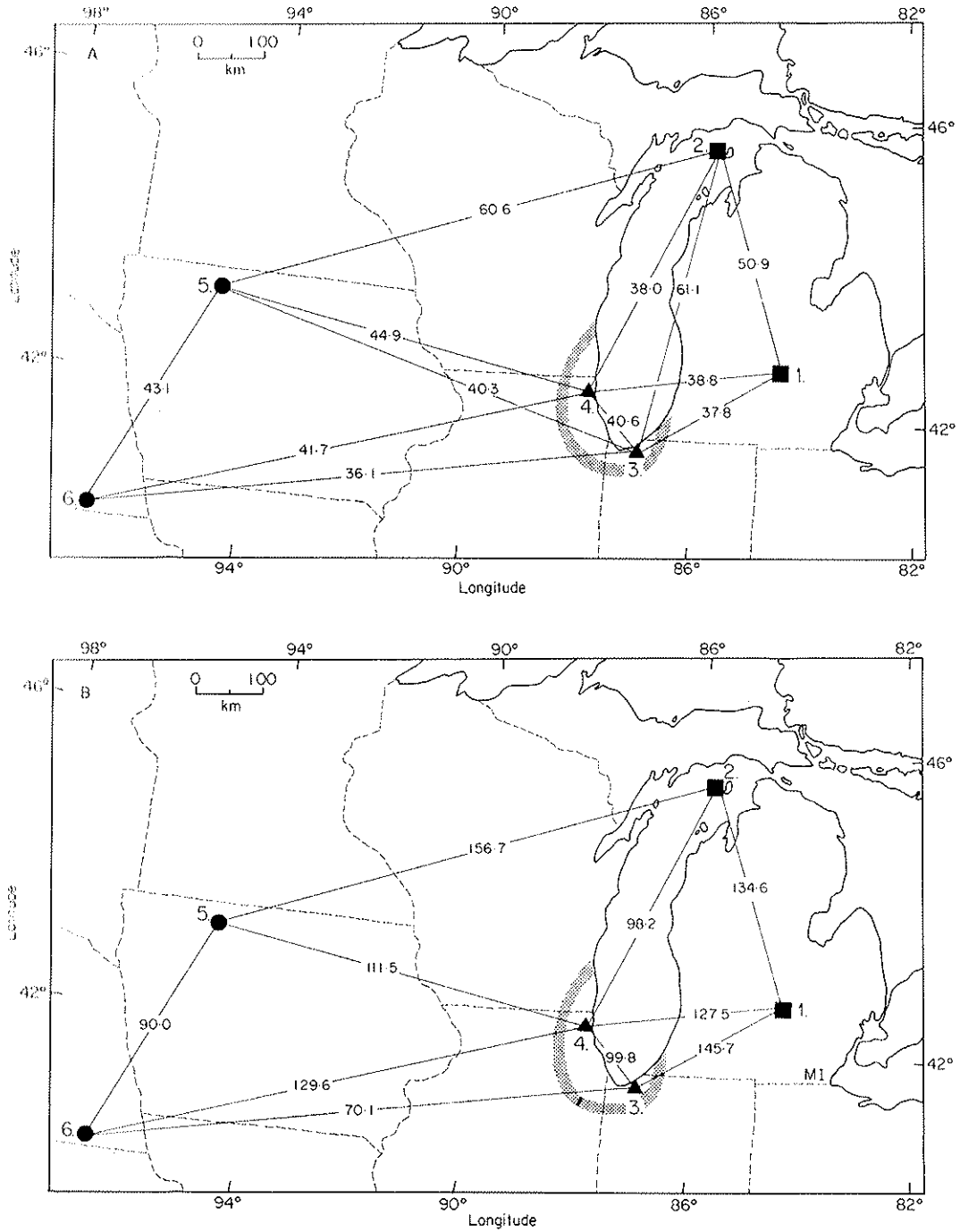


Figure 6. Phenetic similarities between populations derived from Mahalanobis  $D^2$  values. Maps showing the 6 localities sampled in this study (Fig. 1) for females (A) and males (B). The lowest  $D^2$  values are given on the network lines (cf. Fig. 7). The conventional *semifasciata* range is outlined and subspecies symbols are as in Fig. 1.

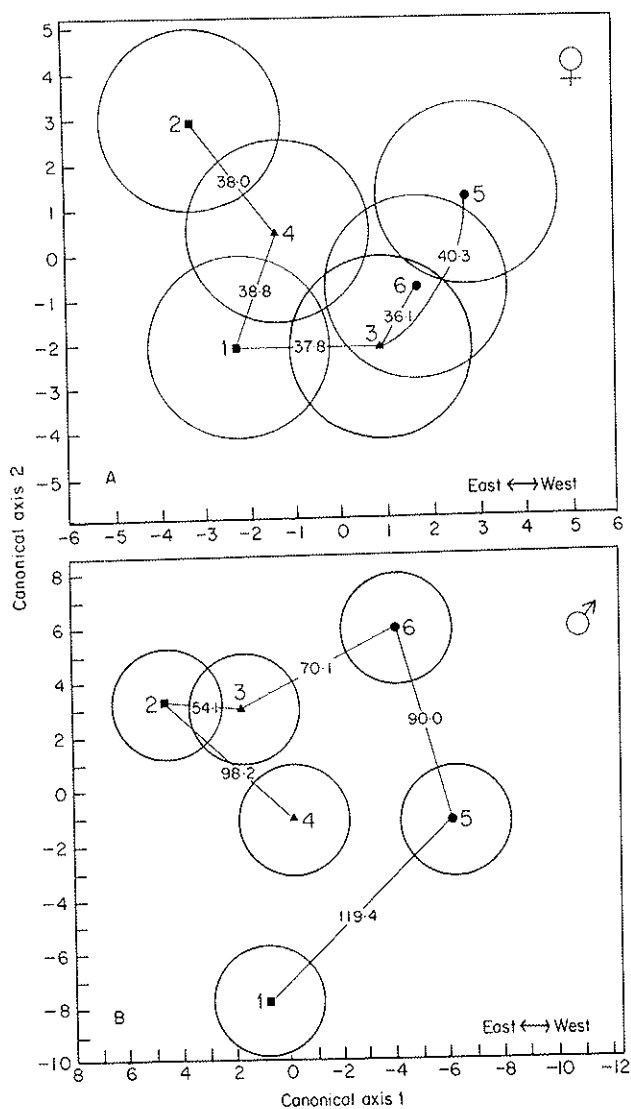


Figure 7. Canonical analysis plots for females (A) and males (B). The axes of the male figure are rotated for ease of comparison. First axis has 51.8% (females)/48.3% (males) discrimination. Second axis has 26.7% (females)/23.0% (males) discrimination. Locality names and subspecies symbols at centroids as in Fig. 1, 95% rings are added. The lowest  $D^2$  values are given on the network lines and an east-west direction is inserted.

#### DISCUSSION AND CONCLUSIONS

##### *Irregular microgeographic variation: problems in defining garter snake subspecies*

Garter snakes are well known for the complex geographic variation which they display. The genus *Thamnophis* "has long stood in the minds of herpetologists as a synonym for chaos" (Ruthven, 1908a: 3). This study shows how different characters display different patterns of geographic variation and emphasizes the

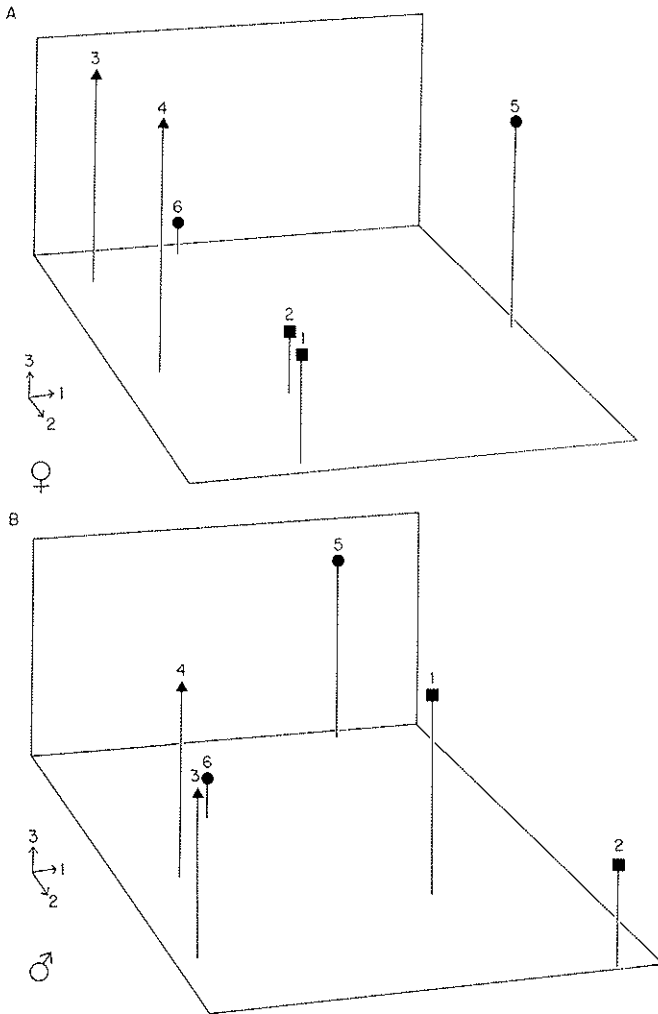


Figure 8. Principal components analysis results plotted for females (A) and males (B) along the first three (of five) canonical variates. Discrimination represented by axes 1, 2 and 3 respectively is: 32.5, 26.3, 21.5% (females) and 34.1, 28.7, 14.9% (males). Locality numbers and subspecies symbols as in Fig. 1.

futility of attempting to base subspecies on single characters. Conventionally, garter snake subspecies, like other snake subspecies, have been based on one or more characters of coloration or scalation considered independently. However, other characters which correlate with the present subspecific divisions of garter snakes are hard to find. Sperry (1903) suggested this 75 years ago when he tried to correlate scalation and coloration characters in a counterblast to the multiplication of garter snake subspecies by Cope.

Even 'diagnostic' characters themselves do not seem to have such well-marked patterns of geographic variation as might be expected. For example, the distribution of the diagnostic '*semifasciata* blotch' pattern shown in Fig. 3 agrees with the conventional range (Smith, 1956) except that a population in

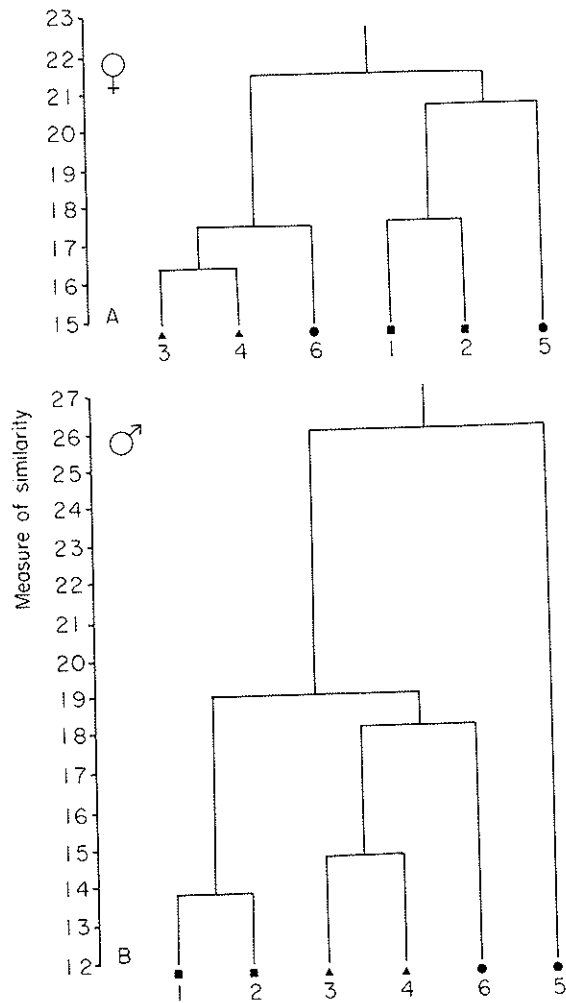


Figure 9. Dendrograms produced by the pair-grouping method for principal components analysis results, based on Pythagorean distances between centroids. A, females; B, males. Locality numbers and subspecies symbols as in Fig. 1.

northern Michigan also displays this feature, as do some specimens from Kansas (Branson, 1904: 370–371) and southern Indiana (Minton, 1972: 248). The diagnostic red-sided character of *T. s. parietalis* is also not restricted geographically to its conventional range. Well-developed red coloration is found in some snakes from north-eastern Illinois, south-western Indiana and Isle Royale, all well outside the conventional range of *T. s. parietalis*. Red sides have been recorded in the literature from Illinois (Garman, 1892: 267–268; Weed, 1922; Smith, 1961: 231–232), Indiana (Hay, 1892: 526), Isle Royale (Ruthven, 1908b), and northern Michigan (Carpenter, 1948).

Measurements from 725 specimens over the *sirtalis/parietalis* transition zone revealed little information other than that most colour characters display irregular microgeographic variation. Absence of ventral spots (character 42) was supposed

to be a distinguishing feature of *T. s. parietalis* (Cope, 1900: 1066, 1077), but it is shown that ventral spots are present in all populations examined, including those from Iowa and Nebraska.

At this point, it may be useful to consider an example of local geographic variation of colour morphs. Within the state of Michigan at least nine distinct colour morphs were observed, most with a restricted range, in a sample of over 500 specimens of *T. s. sirtalis*. Similarly, Fitch & Maslin (1961: 299–300) describe the considerable variety of colour patterns present in a living population of 520 *T. s. parietalis* at one locality in Nebraska. *T. s. semifasciata* is no more distinct than any of the colour varieties of these subspecies. Clearly it would lead to a great proliferation of names and consequent confusion if all colour morphs were named as subspecies.

#### *Evolution and biology*

An important biological boundary in the United States is the north-south line marking the eastern limit of the prairie, running from the southern end of Lake Michigan and across southern Illinois in the study area (Wright & Wright, 1957: 6). The *sirtalis/parietalis* conventional boundary is several hundred kilometres west of this line (Fig. 1), but coincides with it in the southern United States. However, it has been shown that the *parietalis* red-sided character occurs commonly in the study area up to the edge of the prairie, although diminishing in frequency going east. Presumably, garter snakes were absent from the area in question until well after the last Pleistocene glaciation and they must have migrated in and subspeciated within the last 7000 years. One might argue that the invaded area was invaded by two stocks of snakes that were already differentiated, as has been suggested for the ringed snake, *Natrix natrix*, in Europe (Thorpe, 1975b). However, *T. s. sirtalis* and *T. s. parietalis* are not distinct in this broad area of overlap and it would be easier to assume that we have an initial single population in the process of differentiating rather than two subspecies which have lost their genetic integrity and are becoming more similar. It would be tempting to associate the red coloration with the prairie habitat (note that nearly all the other western subspecies of *T. sirtalis* display marked red coloration) but it is harder to establish its adaptive advantage. Small local populations of garter snakes distinguished by slightly different colour patterns, of which *T. s. semifasciata* is one, occur all over North America (Wright & Wright, 1957: 842). There are rarely obvious physiographic or ecological features separating these populations (and this also applies to the Chicago garter snake) so that the maintenance of the constancy of these minor local colour variations indicates low gene flow and little movement of snakes between areas. This supports the conclusions of Ehrlich & Raven (1969) that large geographic barriers are not necessary to limit gene flow between populations.

Phenetic relations between populations are similar in both sexes of garter snakes but overall racial differentiation is greater among males than females in the region studied. These differences may be related to the different ecological requirements of both sexes. Garter snakes are viviparous and produce from 10 to 50 young at a time, which must impose considerable burdens on the females, which reach far greater size than males. Thus, both sexes are probably subject to different selection pressures which may explain the differences in the extent of

their variation. However, taxonomic conclusions derived from both sets of results are the same since neither indicates a division into subspecies, conventional or otherwise.

#### *Taxonomic conclusion*

A decision on the status of *T. s. sirtalis* and *T. s. parietalis* cannot be reached since the small number of populations studied here does not cover the conventional ranges adequately. However, since the range of *T. s. semifasciata* is very small, there is sufficient information in the present sample of two populations to indicate a taxonomic conclusion as to its status.

The canonical analysis and principal components analysis results indicate, as one would expect, that the two populations of the Chicago garter snake are phenetically intermediate between the populations sampled to east and west, but that they are not unequivocally distinct. The univariate maps show irregular patterns of geographic variation and the Chicago populations do not appear as distinct racial entities. Thus it is concluded that the subspecies *T. s. semifasciata* Cope 1892 should be regarded as invalid.

#### SUMMARY

A study of geographic variation in the common garter snakes (*Thamnophis sirtalis*, *T. s. parietalis*, *T. s. semifasciata*) of the north-central United States was carried out. Twenty-six continuously variable characters were recorded from 87 snakes in six populations and 16 binary colour characters were recorded from 725 snakes from 51 localities.

Univariate studies of each character showed irregular non-clinal patterns of geographic variation. Greater phenetic differentiation over the conventional subspecies boundaries was not apparent.

Multivariate studies (canonical analysis and principal components analysis) supported this view of the irregular nature of overall variation. Geographically closest populations were not always closest phenetically, suggesting that gene flow was often outweighed by local selection. Males showed considerably greater phenetic differentiation than females.

The multivariate studies also indicated, as one would expect, that the geographically intermediate Chicago garter snake, *T. s. semifasciata* Cope 1892, was phenetically intermediate between the other two subspecies to east and west. However, in the absence of any good distinguishing features, it is not a distinct racial entity and cannot be regarded as a valid subspecies.

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reporting the multivariate analyses, computer work and the presentation of the results.

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## NOT ADDED IN PROOF

Further to the comments on 'irregular microgeographic variation' and out-of-range occurrences of diagnostic characters, I have now seen a specimen of *Thamnophis sirtalis sirtalis* from Avondale, north-east Ohio, American Museum of Natural History (T. H. FOLEY), with the *semifasciata* character of side blotches, and a female of *T. s. sirtalis* from a water snake farm, Coldland County, south-east Michigan (T. H. FOLEY). I have also seen the male of *T. s. sirtalis* from Michigan