

GEOGRAPHIC VARIATION AND THE VALIDITY OF SUBSPECIES NAMES
FOR THE EASTERN GARTER SNAKE, *THAMNOPHIS SIRTALIS*

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Doubt has been expressed about the usefulness of the taxonomic subspecies concept. Detailed study of many particular examples has shown that it is hard to define subspecies boundaries and that different characters vary geographically in different ways. Multi-variate techniques that summarise the patterns of variation of a wide range of characters are one of the best ways to test the distinctness of conventional subspecies. Studied by these means, the eastern garter snake, *Thamnophis sirtalis*, of the northeastern United States, showed a complex pattern of interrelationships. The study also indicated that the Chicago garter snake, *T. sirtalis semifasciata* Cope, is no more a distinct entity than any of many local populations in Michigan.

Introduction

The eastern garter snake, *Thamnophis sirtalis*, is one of the most common North American reptiles. It occurs over nearly all of the United States and in Canada as far north as the 60° latitude. This vast distribution of a single species is divided into about 11 subspecies (Conant, 1975), of which some have very restricted ranges. Early herpetologists, like the renowned E. D. Cope, recognised even more subspecies. Cope was widely criticised in the early twentieth century, and most of his so-called subspecies were synonymised (or combined with each other). With reference to one of his subspecies, A. E. Brown (1901) wrote: "the only thing which appears to me out of the ordinary about this form, is that any one should have thought of giving it a name." Cope generally worked from a very few, usually pickled and often damaged specimens, and subspecies erected on this kind of material are hardly satisfactory. Are the 11 presently recognised subspecies of *Thamnophis sirtalis* more or less valid?

The Validity of the Subspecies Concept

Garter snake (and most reptile) subspecies classically have been founded on one or two apparently well-defined, geographically localised features of coloration or scalation. However, this method may not be valid for two reasons. Firstly, study of specimens from localities intermediate between the type localities of two neighbouring subspecies may show a gentle gradation between the two diagnostic states of the character (a morphological cline). Or the intermediate points might show a totally random distribution of the character states. In both cases it would be hard to define the dividing line between subspecies. Secondly, if one looks at any other character of the same snakes, it may well show a different pattern of geographic variation. In other words, different characters generally have different genetic control, and may respond to different selection pressures. Thus, subspecies would have

different geographic boundaries depending on which character is chosen. An infinite selection of geographic subspecies patterns could be drawn for garter snakes in North America using the classic one-character (univariate) technique. Is there a solution to this problem?

Multivariate Analysis of Geographic Variation

In the 1960s several authors followed this line of reasoning and decided that the "one-character" subspecies was not a useful concept. It was realized that subspecies based on many characters might be more acceptable, but how can one handle the vast amount of information produced?

During the 1960s and 1970s a large array of statistical techniques were developed to analyse just this kind of situation. The aim of most of these techniques is to simplify the patterns of variation of a large number of characters into 2 or 3 dimensional diagrams. These methods are collectively called "multivariate analysis" or "numerical taxonomy" (Sneath and Sokal, 1973). Although some of the techniques are complex, the results are usually easy to interpret. How do you set about analysing the multivariate geographical variation of a subspecies complex of snakes?

The first requirement is an adequate sample of specimens of each sex from each particular locality, and as many closely spaced localities as possible within the study area. These requirements are usually hard to meet because of the lack of specimens, but it can be surprising just how many specimens were collected by our Victorian predecessors and now lie unused in pickle jars in museums. Next, one must select a set of characters that can be recorded from most specimens. It has been estimated that perhaps 60 characters is a minimal number, but in practice far fewer characters are used. Even old pickled specimens can yield many useful characters of scalation, color pattern (although not color), teeth, bone, and internal organ measurements.

The resulting array ("matrix") of characters versus specimens is subject to preliminary statistical analysis to make sure that all the characters and specimens are useful (a headless specimen has to be excluded from analysis, and a totally invariable character adds nothing to the study).

Each character is given the same weight, and analysis of the matrix by appropriate standard computer programs will yield measures of resemblance between populations. Based on these measures, diagrams can be plotted that represent the relationships between populations, and the distances between points on these diagrams can be regarded as taxonomic distances.

Some of the multivariate methods used in the study of geographic variation of animals include cluster analysis, principal component analysis, and discriminant (canonical) analysis.

In cluster analysis individual populations are usually combined into progressively fewer and fewer sets according to the closeness of their relationship. Thus, the populations whose characters resemble each other most are paired together in subsets, which are paired progressively until an entire tree is built up.

Principal component analysis and canonical analysis, on the other hand, are both ordination techniques, that is, specimens or populations are placed in a space of many dimensions, equal to the number of characters or number of specimens minus one, whichever is the smaller. The information about relationships is summarised by various means so that the results can be represented in two or three dimensions with most variation contained in these first two or three axes.

Principal component analysis suggests groupings between closely related specimens or populations within the sample, while canonical analysis tests the closeness of relationship between known groups, by giving a numerical value (one such measure is called D^2) for the distance between means of any pair of populations in "character space".

The results from these analyses may be represented in various kinds of diagrams to make the relationships that have been worked out clear. Cluster analyses are often represented as dendograms ("tree diagrams") as in Fig. 5. Canonical analyses and principal component analyses may be displayed as scatter diagrams, in which all specimens are represented, or only the "average" individual of a population with a ring indicating the range of variation (e.g. Fig. 6). The taxonomic distances may be inserted to stress the relative separation of populations. The results of these analyses may be shown similarly as 3-dimensional figures with the "average" animals shown as "balls on poles" to give an impression of depth (e.g. Fig. 7). Other graphic methods include network lines on maps and contour diagrams.

More information on geographic variation and multivariate techniques and analysing it are given in Gould and Johnson (1972) and Thorpe (1976).

Thamnophis sirtalis in the North-Central United States

In the area of Michigan, Ohio, Indiana, Illinois, Wisconsin, and Iowa one finds three subspecies of the eastern garter snake represented on standard distribution maps (e.g. Conant, 1975, p. 157-160, map 116), see Fig. 1.

They are: *Thamnophis sirtalis sirtalis* (Linnaeus 1758), the eastern garter snake; *Thamnophis sirtalis parietalis* (Say, 1823), the red-sided garter snake, distinguished by red marks along the side; and *Thamnophis sirtalis semifasciata* (Cope, 1892), the Chicago garter snake, distinguished by black marks across the pale side stripe in the region just behind the head (Fig. 2).

The areas of distribution of *sirtalis* and *parietalis* are large

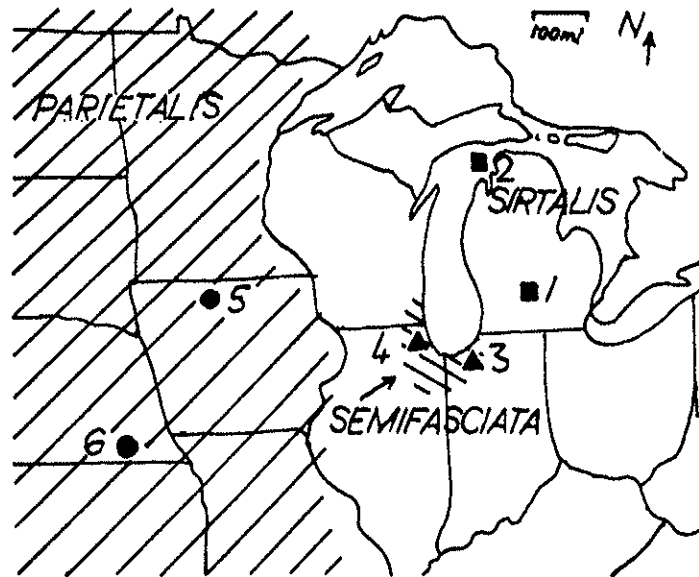


Fig. 1. Map of the study area in the north-central United States showing the ranges of the three conventional subspecies: *Thamnophis sirtalis sirtalis*, *T. s. parietalis*, and *T. s. semifasciata*.

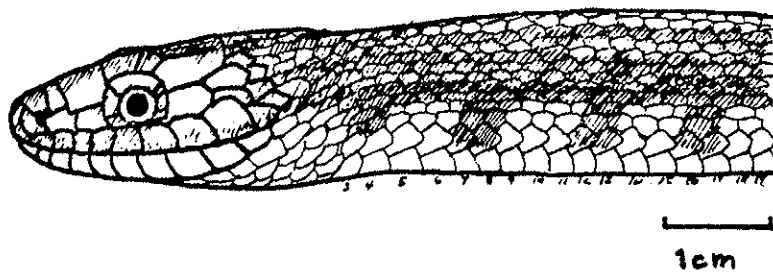


Fig. 2. Chicago side-blotch color pattern, based on UM 26297.

and apparently clearly defined conventionally. However, red-sided garter snakes have been reported outside their conventional range from NE Illinois (Smith, 1961), Indiana (Hay, 1892), Isle Royale (Ruthven, 1908), and northern Michigan (Carpenter, 1948). Similarly, *T. s. sirtalis* has been reported from Kansas (Collins, 1974). The much more restricted *T. s. semifasciata* has been regarded variously as a valid and an invalid subspecies. Smith (1956) argued that the *semifasciata* "Chicago side blotch" pattern is restricted geographically to the area of Illinois, Wisconsin, Indiana, and Michigan at the foot of Lake Michigan, but snakes displaying the diagnostic feature have been reported from Kansas (Branson, 1904) and southern Indiana (Minton, 1972). Can the subspecies boundaries be revised, and how well does the geographic variation of *Thamnophis sirtalis* in this area support the subspecies as a valid entity?

Geographic Variation and Taxonomy of *Thamnophis sirtalis* in the North-Central United States

In 1977, while at Michigan State University, I carried out a study of geographic variation in the garter snake, *T. sirtalis*, in the north-central U.S., examining 725 specimens held in Michigan State University (MSU), University of Michigan (UM), and the Field Museum of Natural History (FMNH). I recorded 16 color pattern characters from each of these, and a further 26 characters of scalation and internal organ length from 87 snakes in 6 populations spaced over the area (full details in Benton, 1980).

I plotted the percentage of occurrence of color characters for the 725 snakes (grouped into 51 populations) on maps and drew contours joining equivalent values. These showed that color characters seem to occur in a rather random fashion, since several high points may occur, and generally there is no geographic trend. Fig. 3 shows the relative presence of the red-sidedness character (diagnostic of *T. s. parietalis*), and highpoints in Isle Royale, southwest Indiana and north-eastern Illinois are well outside the normal range (c.f. Fig. 1). Should these specimens be called *parietalis*? I believe that if we accept the red-sided character as diagnostic we must call them *parietalis*. Herpetologists usually check the map in Conant (or Stebbins in the western states) and they will call them *sirtalis*, because that is easier than altering state boundaries, and we know, of course, that *parietalis* does not occur in Indiana.

Fig. 4 shows the occurrence of the diagnostic "Chicago side-blotch" character which is commonest in north-eastern Illinois, but shows an irregular distribution over south-eastern Michigan and north-western Indiana. Outlying populations occur on Lake Michigan islands (Garden and Beaver Islands), northern Michigan, south-eastern Michigan, south-eastern Indiana, and north-eastern Iowa.

Before making an assessment of the taxonomic value of the diagnostic color pattern characters, I examined the color patterns of 552 specimens from Michigan (all labeled *T. s. sirtalis*) and classified them into nine apparently distinct groups, each in a

Fig. 3. Distribution of red-sided character (diagnostic of *parietalis*). Map of study area showing percentage of occurrence by 10% contours. The highpoint in northern Iowa is 50 - 60 %. Note "outliers" is Isle Royale, northern Michigan, north-eastern Illinois, and south-west Indiana which are all outside the conventional *parietalis* range. Heavy dash lines outline conventional ranges. (c.f. Fig. 1).

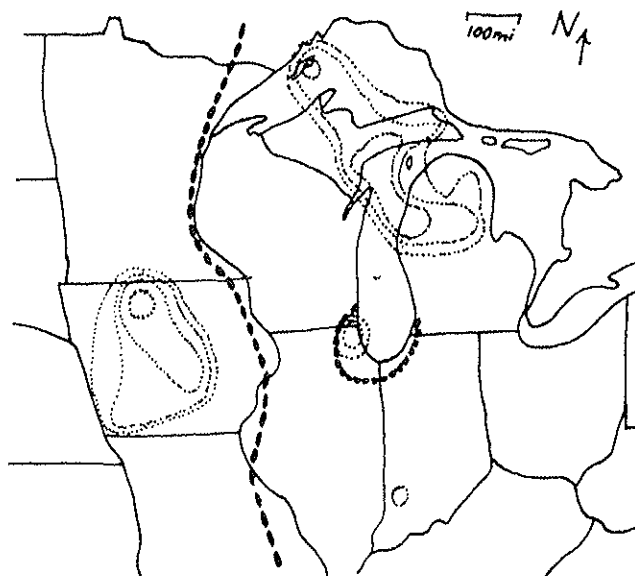
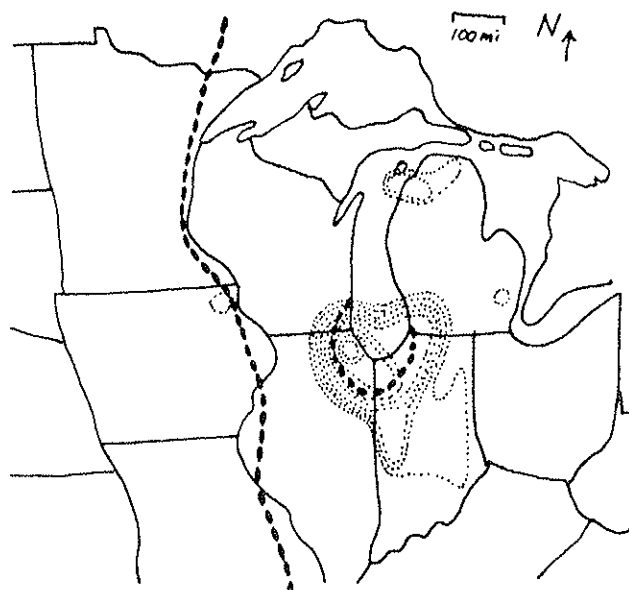


Fig. 4. Distribution of "Chicago side-blotch" character (diagnostic of *semifasciata*). Map of study area showing percentage of occurrence by 10% contours. The highpoint in north-eastern Illinois is 90 - 100%. Note "outliers" in northern Michigan, south-east Michigan, north-eastern Iowa, and eastern Indiana which are all outside the conventional *semifasciata* range. Heavy dashed lines outline conventional ranges (c.f. Fig. 1).



particular area (Tabel 1): Groups 3 and 9 are melanistic, but the others could be named as subspecies. Are they any more or less distinct than, say, *T. semifasciata*? If garter snakes show a similar kind of color variation over their whole range we would arrive at several hundred local subspecies.

The canonical analysis (Figs. 5, 6) and the principal components analysis (Fig. 7) of the six populations (87 snakes in all) showed different patterns of relationship between populations for males and females, and the patterns are not clear. They do not suggest that the six populations divide into three conventional subspecies. However, the evidence from this study is not sufficient to comment on the status of either *T. s. sirtalis* or *T. s. parietalis*. Measurements of more populations from further east and west would be needed.

The evidence is sufficient, however, to suggest that *T. s. semifasciata* is not distinct enough to be retained as a valid subspecies. It is equal in status to any of the several other local color pattern populations in Michigan, and elsewhere, and should be distinguished by no more than *T. s. sirtalis* (Chicago, or "side-blotched" race).

Evolution and Biology

If we accept that western garter snakes tend to be red-sided and eastern ones are not, can we connect this difference with any physical or environmental factor and can we explain the origin of the two forms?

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. The *sirtalis/parietalis* conventional boundary is several hundred miles 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 ice age glaciation and they may have migrated in and subspeciated within the last 7000 years. An alternative idea is that there were distinct subspecies before the ice ages that retreated to small areas (refugia) and then spread again when the climate improved, and proceeded to cross-breed at the boundary. It is hard to decide which idea is more correct. It is 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.

It was noted that males and females show slightly different patterns of variation for each character. This probably reflects the different ecological requirements of each sex. Female garter snakes are generally larger, and often much larger, than males (any *T. sirtalis* longer than 500 mm is almost always female). Since they are viviparous, a female bearing from 10-50 live young must be

Table 1. *T. sirtalis* color morphs in Michigan (data from 552 snakes in the museums of Michigan State University and the University of Michigan),

1. blue/steel, stripes faint or absent	southern lower peninsula
2. black/grey, stripes bright blue	south-east lower peninsula
3. black/dark blue, stripes bright blue	south-west lower peninsula
4. dark green/black, stripes yellow	central lower peninsula
5. purple-brown, stripes absent	central lower peninsula
6. dark/light blue, stripes light blue	central-north lower peninsula
7. steel, stripes yellow/cream	islands in Lake Michigan
8. black, stripes bright blue with black marks on all rows, ventral spots very marked	islands in Lake Michigan
9. black/grey, white between scales	upper peninsula, Isle Royale

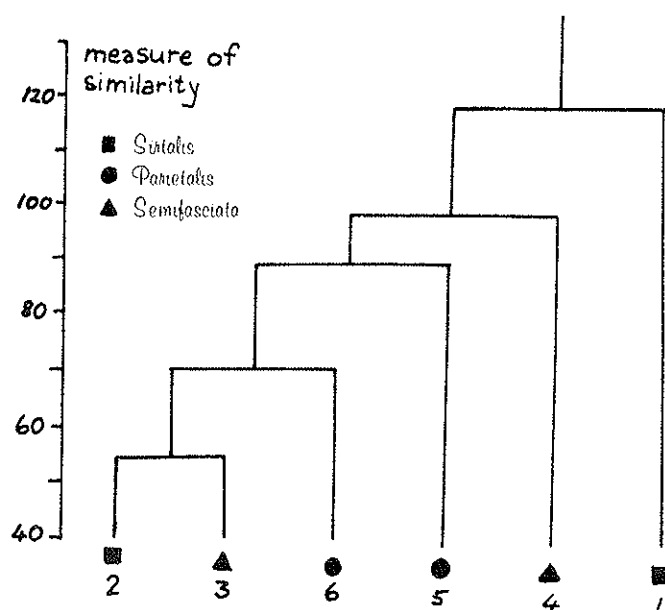


Fig. 5. Cluster diagram for canonical analysis D^2 values for male snakes. The horizontal line linking two populations corresponds to their degree of similarity. The populations are numbered and subspecies coded as in Fig. 1. According to this, populations 2 and 3 are most closely similar. No support is given for the conventional subspecies divisions.

Fig. 6. Canonical analysis plot for male snakes. This diagram is based on exactly the same data as Fig. 5 and both suggest the same conclusions. The first two canonical axes shown here summarise 71.3% of all variation measured. The circles include 95% of all specimens in a population and the central point represents the "average animal." The measure of similarity between populations is indicated by the numbers on the lines linking center points of circles (these numbers can be read off the "measure of similarity" axes in Fig. 5).

The populations are numbered and subspecies coded as in Fig. 1.

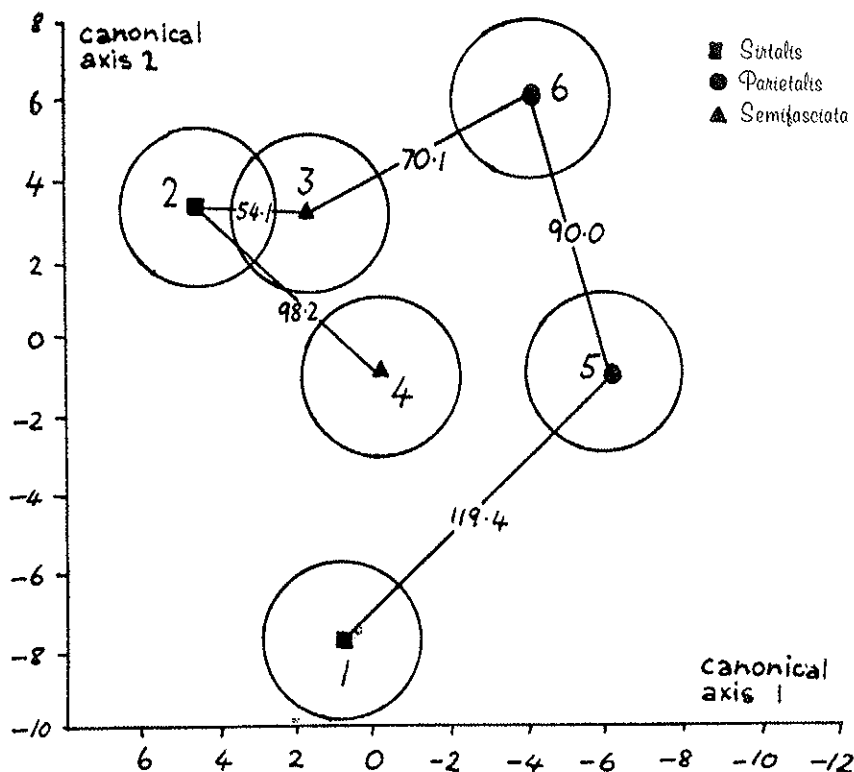
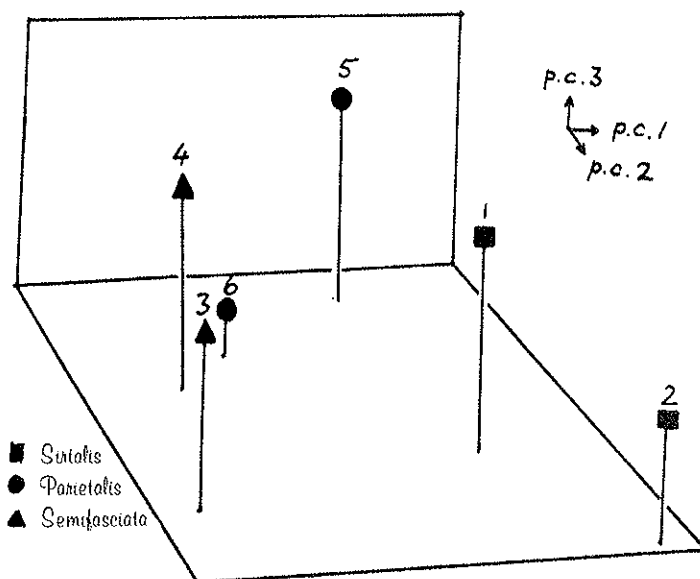


Fig. 7. Principal components analysis results plotted in 3 dimensions for male snakes along the first three axes (p.c.= principal component) which together summarise 77.7% of variation. The "average animal" of each population is indicated and the vertical lines are merely a guide to the eye in interpreting the 3-dimensional array of points. Locality numbers and subspecies symbols as in Fig. 1. Populations 1 and 2 (*sirtalis*) and 3 and 4 (*semi-fasciata*) appear to be close to each other, but they are not clearly distinguished from the other populations.



subject to different selection pressures than an adult male.

Conclusions

The subspecies concept is still of value in reptile taxonomy. However, this is only the case if we consider the variation in a reasonable number of characters based on an adequate number of specimens. Subspecies based on limited material and few characters will often be meaningless in biological terms. Unless a local population is isolated from the rest of its species by some barrier (even a very small one may be sufficient), it is likely that some interbreeding occurs and that we do not really have a distinct taxonomic entity. It is misleading in this situation to apply subspecies names.

In the example of the eastern garter snake from the north-central United States a local color pattern has developed mainly in the Chicago region, but it is also present in isolated populations elsewhere. It is considered unwise to establish a subspecies name on this feature. On the other hand, the eastern and red-sided garter snakes occur in generally well defined areas and a taxonomic distinction is helpful. However, we must recognise a very broad band of intergradation covering a width from Iowa to Indiana, and name *T. sirtalis* found in this area according to the presence or absence of redsidedness.

Appendix: Side Spots in Garter Snakes Studied

The Chicago side blotch pattern has not been well defined and some confusion could arise since black bars across the side stripes may be of two kinds.

Garter snakes from all parts of the study area had black marks on dorsal scales of row 1, the first row on the side above the single belly scale (Fig. 8a). In some cases, there were also marks on row 4 (Fig. 8b) and even on rows 2 and 3 (Fig. 8c). Thus, fairly extensive and regular black blotches arising from row 1 can partially cross the light-colored side stripe.

The Chicago side blotch pattern is different. It is a development of the dorsal "checkered" pattern especially well developed in some Indiana specimens (Fig. 8d). The light areas arise because the membranes between scales are white or cream-colored in restricted patches (Fig. 8 h). From the side (Fig. 8e), these light-colored patches can be seen to repeat regularly. In living specimens of *T. s. parietalis* these spaces between scales are light to dark red and, in addition, the red color often encroaches on the scales involved. In some specimens the dark areas descend onto the side stripe just behind the head (Fig. 8f). In *T. s. semifasciata*, 3 or 4 or more black patches move down over the side stripe to dorsal scale row 1 (Fig. 8g). These blotches repeat regularly along the snake behind the head every 3 or 4 dorsal scales and there may be up to 25 of them. This is the true Chicago side blotch pattern. In places, they occur between the previously described blotches arising from dorsal scale

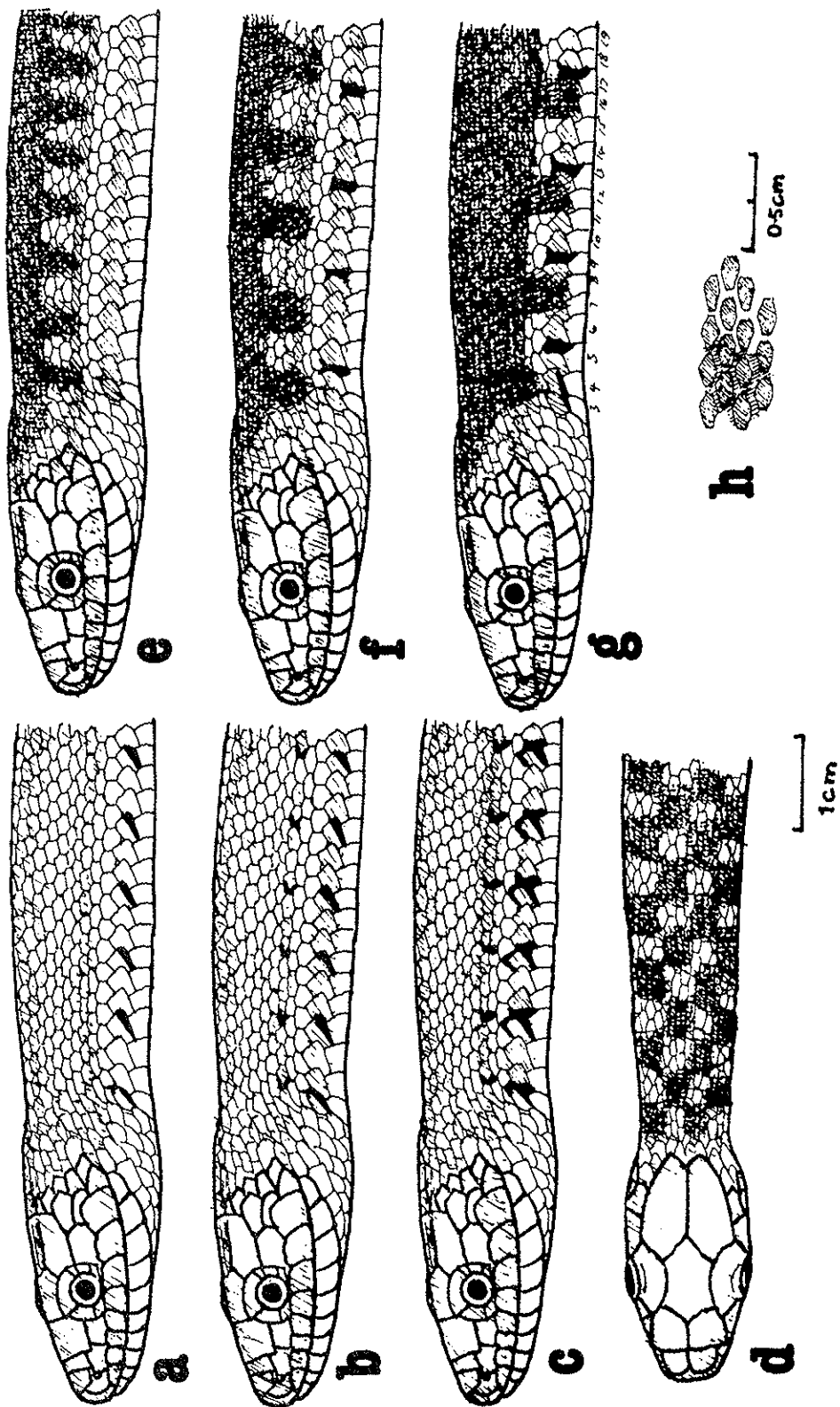


Fig. 8. Patterns of markings on the sides of *Thamnophis sirtalis* from the north-central United States. (a) spots on dorsal scales of row 1; (b) spots on dorsal scales of rows 1 and 4; (c) spots on dorsal scales of rows 1 and 4; (d) "checkered" pattern on dorsal surface (based on UM 61014); (e) incipient "Chicago side-blotches" (based on UM 100274); "Chicago side blotch" pattern fully developed (based on UM 26297); (h) enlargement of some dorsal scales showing how light and dark areas arise by absence or presence of pigment on membranes between scales.

row 1 and elsewhere they fuse with the blotches from row 1.

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The dwarf American toad, *Bufo americanus charlesmithi*, in amplexus. Eggs can be seen trailing the pair. For information on a new longevity record for this anuran see page 79. The photo was taken in an intermitten stream, in Union County, Illinois by John C. Murphy.