

PATTERNS OF GEOGRAPHIC VARIATION IN FLORIDA SNAKES

By

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Abstract of Dissertation Presented to the Graduate Council  
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I analyzed geographic variation in fifteen species of Florida snakes. Machine-produced contour maps were created for each of over 200 morphologic variables and 17 climatic variables. One hundred of the maps were factor analyzed, and seven major patterns of geographic variation extracted. These seven patterns were found to account for over 60% of the information contained in the original contour maps. Each of the patterns of geographic variation can be explained in terms of natural selection by past or present environments. Disjunct populations showing phenetic similarities are the result of an earlier widespread phenotype followed by differentiation in geographically intermediate regions. Recourse to land bridge hypotheses and retrogressive evolution are not necessary to explain polytopic phenotypes. Correlations between the patterns of variation and environment are discussed, but experimental verification of cause and effect relationships are not provided. The geographic localities of primitive character states and/or primitive species are not the centers of origin for the groups, but are considered to be areas in which evolution has proceeded relatively more slowly.

## INTRODUCTION

Darwin's theory of natural selection has as its keystone one important requirement: variation. Implicit in any interpretation of natural selection as the guiding force behind organic evolution is the assumption that organisms are not all alike. The members of a population of sexually-reproducing plants or animals are in fact (except for identical twins) all different, both genetically and phenotypically. Mutations and recombinations of existing genes insure the continuance of this variability.<sup>1</sup> Selection acts on the differences between organisms by eliminating unfit phenotypes (and hence their associated genotypes) from the reproductive effort of a population. However, phenotypes which are unfit in one part of a species' geographic distribution may be quite fit in another region. Thus geographic variation in selective pressures, brought about by geographic variation in environment, predisposes organisms to vary geographically in morphological, physiological and behavioral traits, even within a single biological species.

The process of speciation begins when differential selective pressures act on populations of a species in remote parts of its geographic range. Natural selection creates different phenotypes in response to these different selective regimes. When the degree of

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<sup>1</sup>But see Murray (1972) for a discussion of genetic diversity maintained by natural selection.

phenotypic divergence includes also reproductive incompatibility, the populations involved are said to have reached the species level.

Populations of organisms change phenotypically and genetically through time as they become better adapted to their environment and as their environment changes. This process is called evolution. Populations of organisms also change phenotypically and genetically through space as they adapt to different environments. This phenomenon has been called geographic variation, but it is really just another form of evolution. Albert Einstein has shown the equivalence of space and time in the physical world. Preston (1960, etc.) has pointed out analogies between space and time in ecology and species diversity. In this study, it is assumed that character variation through space is a form of organic evolution just as character variation through time is unquestionably so.

It is currently impossible to study the environmental factors responsible for character variation through time. We do not have accurate data on temperature or rainfall variations throughout the evolutionary history of any species. We are not able to assess the relative importance of various selective pressures that have brought about the species of today. However, we can study evolution through space. We do have accurate environmental measurements taken at many geographic points, and should be able to correlate these with character variation as we see it throughout a species' distribution. Assuming an analogy between space and time, I believe that patterns of character variation in space are brought about and maintained in the same ways as patterns of character variation through time (evolution, in the Darwinian sense).

Thus the key to an understanding of organic evolution lies in an understanding of geographic variation and the environmental factors responsible for its maintenance.

Although the study of geographic variation in living systems is not a new one, the use of modern multivariate methods to describe and compare patterns of variation has hardly begun. Most previous studies have simply described or illustrated the geographic variation of each of a set of characters pertaining to a single plant or animal species. A few very recent studies have utilized multivariate techniques to analyze the degree and type of covariation between characters of a single species. Still fewer investigators have attempted to demonstrate correlations between environmental parameters and intraspecific geographic variation. No previous study, to my knowledge, has attempted to quantitatively investigate patterns of geographic variation common to several species, and to compare these patterns with environmental variation. The present study does just that.

Florida is for the most part a peninsula with a warm temperate climate grading into that of a subtropical region. It has such diverse habitats as large swamps and marshes (prairies), forested pine lands, and scrubby chaparral-like deserts. It thus seems surprising that most studies concerned with the biogeography of Florida have concentrated on historical causation and left little credit to the power of natural selection as a factor in establishing patterns of geographic variation. Changing sea levels, "Ocala Islands," Suwannee Straits and the like have all been cited as influencing the patterns of distribution and variation in Florida plants and animals. No doubt many of the distributional

patterns and much of the variation seen in Florida organisms have been influenced by these historical phenomena. However, I believe that most of the variation within species represents adaptation to the present environment, brought about by natural selection that is still at work. Recent work by several authors has shown that demes or micro-geographic populations can and do differentiate as they become adapted to their own specialized environment. Species, in the conventional sense, are not panmictic. Rather, they are groups of populations, each adapted to its own particular portion of the total species distribution. Therefore, any analysis of geographic variation should include tests for correlation with components of the environment. Only after all possible correlations with environmental parameters have been eliminated, should historical phenomena be suggested as causation in biogeography.

Leon Croizat, in a series of works spanning the last thirty years (especially 1958, 1962) has advocated a method of biogeographical analysis which begins without *a priori* assumptions, and lets the data speak for itself. His method is to plot the distribution of the species of a given group on a map, and to connect the disjunct ranges with straight lines. When many groups are treated in this way, it is found that the lines of connection (tracks) do not form a random network over the map, but rather, they tend to follow the same routes. These routes, an aspect of the data, and in no way influenced by preconceived ideas of past geography or climate, can and must be interpreted as representing remnants of former wide-spread distributions.

By plotting the geographic patterns of morphologic variation of a particular species on a map, and then considering many such maps

together, one is, in effect, using a modification of Croizat's pan-biogeographic analysis on a micro scale. We begin with no assumptions of past dispersal routes, climate or geography. Instead, the data are mapped and the patterns emerging interpreted in the most parsimonious manner.

The method is simple: Computerized contour maps are produced depicting the geographic variation of each character to be investigated, one character per map. Next the maps are compared, and a smaller number of underlying patterns extracted and mapped. These patterns must be explained. By means of correlation analysis it is possible to compare the pattern maps with maps of environmental variables such as rainfall or temperature. In this manner, patterns of organic geographic variation can be identified and compared with geographic variation in environmental factors. Patterns of morphologic variation which do not correlate with the environmental variables may be correlated with untested environmental variables, or they may have received their present shape by past paleoclimatic or geographic factors.

## MATERIALS AND METHODS

### The Data

I analyzed character variation data on 3578 specimens of 15 species of Florida snakes. The species were chosen on the basis of availability of specimens or data, and, more importantly, because they are for the most part, wide-ranging, rather ubiquitous species with representatives (taxonomically distinct or not) in the southwestern United States and Mexico. It was assumed that species with wide distributions across the southern United States would be phenetically (and genetically) plastic throughout their ranges as they adapt to different environments. Geographic variation in a wide-ranging species is inevitable if we believe in evolution, and a species' ability to adapt to its environmental surroundings. Furthermore, it was hoped that some light could be shed on the postulated "Gulf Coast Corridor" phenomenon of Auffenberg and Milstead (1965) by studying character variation in species associated with the Gulf Coastal Plain.

The characters examined were primarily standard taxonomic variables with a history of application for the species studied. Although color is probably the single most important aspect of a snake's phenotype at the infraspecific level, this character was largely ignored, because of unpredictable color changes that specimens undergo in preservative. Aspects of pattern, carination and scutellation constitute the bulk of the characters employed in the present analysis. See Appendix A for a description of the characters examined.

Once the data were accumulated, they were coded, qualitative characters were ranked, and everything was punched on computer Hollerith cards. Various combinations of characters were utilized to produce new characters, such as ventrals plus caudals or percent tail, etc.

In addition to the data on snake morphology, I also recorded and analyzed summary data on Florida climate from the Climatic Summary of the United States, U.S. Department of Commerce. These data were also punched on computer cards. The environmental variables investigated are listed in Appendix B. Mean data from 196 weather stations in Florida, southern Georgia and southern Alabama were used. The average period of record on which means were based was 29 years.

In order to associate data from an individual snake or weather station with the appropriate geographic locality, it was necessary to develop a row and column coordinate system. This was done using as a base map, the 1972 edition of the American Automobile Association road map for Florida. Each specimen and weather station was assigned a latitude and longitude value representing its locality on the base map. These coordinates were punched on the cards along with the data. Although the use of the AAA road map for a base map may seem limiting, it is not, because the coordinates can easily be changed to any other system with the appropriate conversion factor. Actual latitude and longitude values could not be used because these vary in inter-line distance with the curvature of the earth, and the computational algorithms employed require that the grid system be uniform.

### The Problem of Samples and Populations

In every previous study of geographic variation that I know of, data on organisms from more or less nearby localities have been pooled and averaged, with the resultant average values applied to some point or area representing all the individuals included. This seems to me to be an arbitrary and unrealistic approach to the problem. Whether the method employed lumps specimens by state, county, circular or square grids, or the strange "splotch" system of Rossman (1963) and his students (Blaney, 1971a; Williams, 1970; etc.), the implication is that the values associated with the geographic units represent values for populations. There is no reason to believe that populations assume regular shapes any more than shapes determined by political boundaries. Nor is there any valid reason for lumping specimens with "similar" character states from "adjacent" localities. What are "similar" and "adjacent?"

The method used in the present study is, I believe, less arbitrary, and does not assume a knowledge of either population structure or geography. The character state for each specimen is plotted on a map at the point where the specimen was collected. If several specimens are available from the same point, they are averaged; otherwise, each specimen is plotted independently. The next step involves calculating hypothetical values for intermediate localities based only on the data available. Character values are weighted inversely according to the square of their distance from the point being considered. In this way values for all points on the map (or any fraction thereof) are calculated based on the points for which there are actual values. Contour lines can be con-

structured, and the areas of character change readily identified. Instead of *a priori* assumptions of geographic structure which are implicit in any scheme involving the means of putative populations, this method allows the patterns of geographic variation to emerge from considerations of individual specimens.

### The Mapping Procedure

This method of character mapping still suffers from the one drawback common to all methods: the map is only as good as the data. Obviously, the more points on the map with actual data values, the less interpolation will be necessary to identify the areas of character change. Ideally, we would like to have our specimens from regularly-spaced localities gridded over the entire map surface. This is simply not possible in the majority of cases, and probably never possible when studying snakes.

Throughout the following discussion, it is necessary to keep in mind that the mapping procedure employed does nothing more than map the data as they appear, and interpolate between data points, just as a cartographer would do, mentally, in constructing a contour map by hand. There is nothing mysterious or even very sophisticated in the method. It is faster than mapping manually, and it removes the element of bias from contour line placement.

The actual computer program used in the production of character variation maps was the SYMAP program developed by the Harvard University Laboratory for Computer Graphics. This program has been used previously in geographic variation studies by Jackson (1970) and Johnston and Selander (1971), and is described in some detail in Peucker (1972).

### Multivariate Analysis

The SPSS factor analysis procedure (Nie *et al.*, 1970) was employed to extract factor scores from the data set for each species studied. If morphological characteristics of an organism co-vary, then there is some underlying component or "factor" that will explain the variation in the suite of characters that are varying together. This is the assumption behind factor analysis. First a matrix of product-moment correlation coefficients between the variables was calculated. R-type factor analysis was employed to extract a smaller number of summarizing axes that explain the covariation in the characters. These axes represent a "summary" of the variation in a larger number of variables. Based on these factor axes, factor scores were assigned to each specimen, and these values mapped like univariate characters. The finished product is a map of the geographic variation of a factor, which is, by definition, a map of the underlying trends of geographic variation in a suite of characters, where such underlying trends exist. A more detailed discussion of Factor Analysis may be found in Harmon (1962).

### Comparison of Mapped Data

The problem of comparing mapped data is a complex one. Prior to this study there were no available methods for analyzing maps or performing correlation analysis between maps. If the variables to be analyzed were located geographically at the same point, simple product-moment correlation analysis could be performed and any correlative tendencies readily discovered. However, when the maps to be compared have different data points, a preliminary step to standardize the reference points is

necessary. That is, given two maps of Florida, one with X data points (set A) and the other with Y data points (located at different points, set B), it is necessary to interpolate each data set to a standard grid system, or to interpolate one data set so that its new grid system corresponds with the other. If the data are treated in this manner, it is possible to compare climatic variables from U.S. weather stations, with morphological variables of snakes from wherever they were collected (usually not weather stations).

The SYMAP mapping routine, discussed above, calculates estimated data values for a finite number of points on a map based on the values associated with actual data points. It is possible to output the values so calculated for one data set, and compare these with values output from another data set run in the same way at another time. In this way, multiple sets of geographic data can be standardized to a grid system by non-arbitrary, reproducible methods (SYMAP) and the resulting grids can be treated as matrices in correlation, cluster, or factor analysis.

A computer program to handle the SYMAP-produced data point values and store these on magnetic tape for later analysis was written for this study by William Ingram.

### Geography

Regional and place names used in this study are located on Fig. 1. The major rivers of Florida are shown on Fig. 2. Figs. 1 and 2 should enable the reader not familiar with Florida to follow easily the results and discussions presented below.

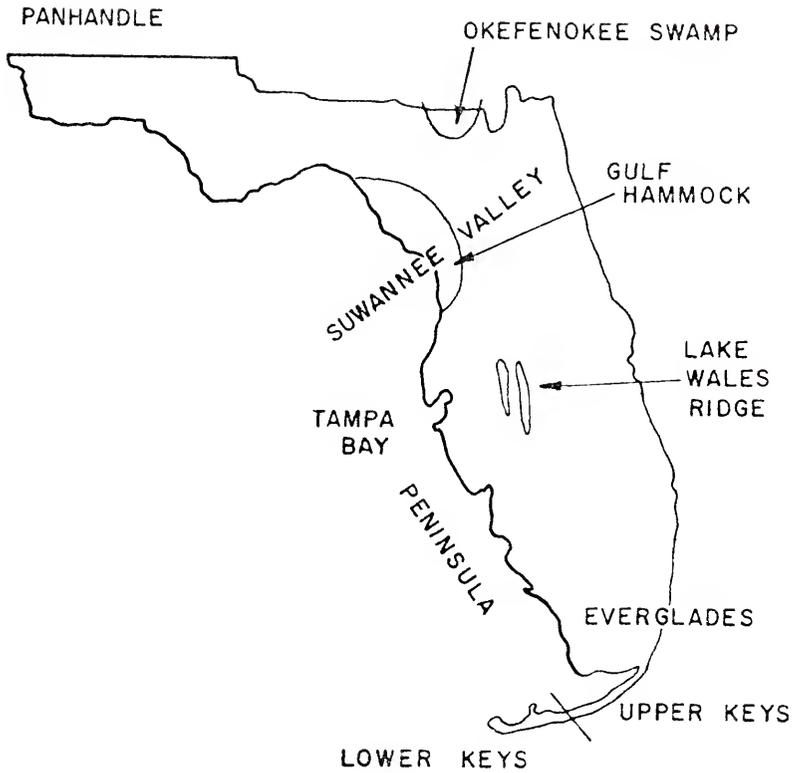


Figure 1. Regional and place names referred to in the text.

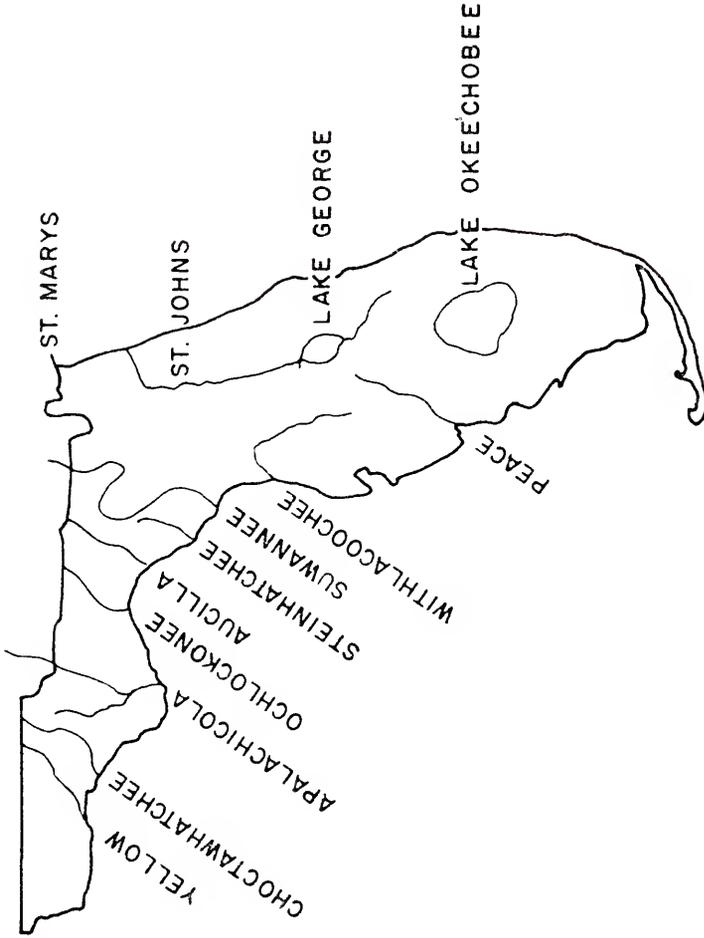


Figure 2. Important rivers in Florida.

## RESULTS

Pearson Product-Moment correlation coefficients were calculated between every character and sex and snout-vent length for each species. Unless otherwise noted, all characters mapped showed no correlation with sex or body size. Note that the mapping procedure employed does nothing more than assign a given value to the appropriate locality, then interpolate between the localities to predict the location of a change in character state. Each specimen is weighted equally, so geographically isolated specimens may contribute more heavily in the analysis than individual specimens from better-collected regions. That is, if only a single specimen is available from region A, then that region will be shaded as though the population had the characteristics of that specimen. If 20 specimens were available from the same region, the shading would reflect the average of those 20 specimens. When interpreting the maps in this section, it is important to bear this in mind, and to refer to the specimen locality maps presented for each species.

Results are presented first by species, and compared with previous studies. Patterns of geographic variation are discussed in the second section, and finally, a third section deals with correlations between observed patterns and environmental factors. A description of each of the characters examined appears in Appendix A. Actual raw values may be obtained from the author.

### The Species

#### *Storeria dekayi* (Holbrook)

I examined 151 specimens of *Storeria dekayi* from Florida and southern Georgia (Map 1) for possible geographic variation in each of 21 characters (Appendix A). The numbers of supralabials and infralabials are essentially unvarying over the study area. More than 93% of the specimens examined had 14 supralabial combining both sides, and 87.4% had 14 infralabials. The number of postocular scales was usually four (88.3%). None of the characters examined was found to be size-correlated. The following characters showed apparent geographic variation.

Number of ventrals. The number of ventral scales in Florida *Storeria dekayi* was only slightly correlated with sex, with the males usually having lower counts ( $r = 0.3559$ ). Nevertheless, the sexes were mapped separately as shown in Maps 2 and 3. In general, the number of ventrals increases southward on the peninsula and drops again on the Lower Keys. The highest ventral counts are observed on snakes from the Everglades region, while the lowest values are found on the Lower Keys and in the Panhandle. A reasonable degree of concurrent variation between the sexes suggests that they are responding similarly in ventral count expression.

Number of subcaudals. Males tend to have more subcaudals than females ( $r = 0.5167$ ). Geographic variation in the number of subcaudals in Florida *S. dekayi* is shown in Maps 4 and 5. Variation is similar to that described for ventrals, above. Snakes from the Panhandle and from

the Lower Keys have the lowest subcaudal counts. Otherwise, the variation is clinal, increasing southward on the Florida peninsula. Brown snakes from the Apalachicola Valley may be more similar to snakes from Central Florida as regards this character. Again, concordance in the patterns of variation observed in the sexes is very good.

Number of ventrals plus caudals. Although both the number of ventrals and the number of subcaudals are correlated with sex (see above) their sum is not ( $r = 0.1522$ ). Therefore, the sexes can be lumped to increase sample size, producing Map 6. Geographic variation in this character consists of increasing counts southward on the peninsula, and a major drop on the Lower Keys. Snakes from west of the Suwannee River in the Panhandle also have low values for this character. (Note that the area west of the Yellow River is represented by only a single specimen, and is therefore an inadequate sampling.)

Percent tail. Males tend to have proportionately longer tails ( $r = 0.7214$ ), and so the sexes have been mapped separately in Maps 7 and 8. Brown snakes from the southern mainland have the longest tails proportionate to body length. Snakes from the Lower Keys have somewhat shorter tails, more like specimens from northern Florida.

Dorsal scale rows. Dorsal scales were counted at the standard three places along the body, but all three varied the same way, so only midbody scale rows are mapped (Map 9). Brown snakes from the Panhandle east to the vicinity of the Suwannee River have 17 scale rows around the body, while those from the remainder of the state have 15.

Preocular scales. Generally, *Storeria dekayi* has a single preocular scale on each side of the head. However, individuals from the Lower Keys

typically have two preoculars on each side. In addition, a high proportion of specimens from near Jacksonville and Gainesville in northern Florida have two preoculars on each side. See Map 10.

Ventral dark pigmentation. Geographic variation in the qualitative assessment of the amount of dark pigment ventrally in Florida *S. dekayi* is presented in Map 11. Generally speaking, brown snakes from the south-west coast of the peninsula have the darkest bellies, while those from the Lower Keys have the lightest.

Temporal pigmentation. Dark pigment on the temporal scale in *S. dekayi* may be in a tear-shaped blotch with one end wider and continuing onto adjacent scales (see Appendix A). The wider end may be directed posteriorly as in most snakes from the Panhandle, or it may be directed to the front as in specimens from the Florida peninsula. Brown snakes from the Lower Keys often have the temporal pigment so reduced as to have no obvious orientation, but when present, the wider end is directed to the front. See Map 12.

Subocular pigmentation. The number of supralabial scales contained within the subocular dark blotch in Florida *S. dekayi* varies geographically as shown in Map 13. Generally, snakes from the peninsula tend to have larger subocular spots than specimens from the Panhandle. Many individuals from the Everglades region have very small or absent subocular spots. Subocular spots on specimens from the Lower Keys are diffuse and faint, but cover three to five supralabials.

Factor 1. The first factor accounts for 24% of the variation in 18 characters. It accounts for most of the variation in the three dorsal scale row counts, the sum of ventrals plus caudals, temporal pigmentation,

ventral pigmentation, and supralabial pigmentation. The first factor discriminates between two phenotypes of *Storeria* in Florida: snakes with 17 dorsal scale rows, fewer than 187 ventrals plus caudals, a temporal blotch with its wider end directed posteriorly, reduced ventral pigment, and fewer supralabials with black pigment occur in the Panhandle, while snakes of a contrasting phenotype occur on the peninsula. See Map 14.

*Thamnophis sirtalis* (Linnaeus)

Data on 192 specimens of *Thamnophis sirtalis* from Florida (Map 15) were analyzed for possible geographic variation in each of 13 characters (Appendix A). Dorsal scale rows varied little throughout the study area, with most specimens having 19-19-17 scale rows (94.7%, 95.7%, and 96.8% respectively). Ninety-one percent of the *T. sirtalis* examined had 14 supralabials and 92.4% had 20 infralabials. None of the characters examined was size- or sex-correlated. The following characters appear to show trends of geographic variation within Florida.

Numbers of ventrals. Geographic variation in the number of ventral scales in *T. sirtalis* is shown in Maps 16 and 17. Although differentiation within Florida for this character is minimal, some trends are apparent. In general, garter snakes from Lake Okeechobee southward have the highest ventral counts. Snakes from the Panhandle tend to have low counts. It is not possible, however, to discern a well-developed cline within the state of Florida.

Number of subcaudals. Trends in the geography of subcaudal count variation in Florida garter snakes are not clear. Maps 18 and 19 show

the general lack of concordance between the sexes for this character. Patterns like these may imply that the sexes are responding differently in subcaudal count expression, or they may be the result of sampling bias due to inadequate sample sizes (51 males, 62 females). Alternatively, the number of subcaudal scales in Florida *T. sirtalis* may not correspond with anything that varies geographically.

Number of ventrals plus caudals. The summation of the preceding two characters varies geographically as shown in Map 20. Garter snakes tend to have the highest counts in the northern peninsula and extreme southern peninsula, with lower counts found in the intervening region, and in the Panhandle.

Percent tail. Tail length divided by total length varies as shown in Maps 21 and 22. In general, specimens from Apalachicola Valley, the northern peninsula, and the southern peninsula have proportionately longer tails than snakes from elsewhere. Although the pattern appears complex, the concordance between the sexes is quite good, supporting the reality of the trends, based, as they are, on different sets of specimens.

Dorsal spotting. That some individuals of *Thamnophis sirtalis* are marked with black spots dorsally is well known. Linnaeus (1766) described the phase as *Coluber ordinatus*; Cope (1900) considered it a subspecies of *T. sirtalis*, and more recent authors have considered it little more than an occasional pattern variant without geographic correlation (Rossman, 1965). Maps 23, 24, and 25 show the geographic variation in this character for Florida specimens. Garter snakes from the western Panhandle usually have a well-developed pattern of dorsal checks, sometimes to the complete exclusion of longitudinal stripes. Additionally, the west coast of the

peninsula and parts of the Central Highlands support populations of *T. sirtalis* with dorsal checking. Specimens from the southern Everglades are almost invariably heavily spotted.

Parietal spots. Rossman (1963) considered the nature of the paired parietal light spots important to the taxonomy of the genus *Thamnophis*. The pattern of geographic variation in this character is remarkably similar to that seen in the previous character, dorsal spotting. Maps 26, 27, and 28 show the geographic variation as interpreted in the present study. Again, the Panhandle, the southwest coast of the peninsula and the southern Everglades stand out as areas with higher states for this character. Concordance between the sexes is good.

Factor 1. The first factor extracted from the correlation matrix of eleven characters accounts for 18.5% of the total variation, and much of the variation in dorsal spotting and parietal spots. Map 29 shows how factor 1 varies in Florida. The western half of the Panhandle, the southwestern coast of the peninsula, and much of the Central Highlands and southern Everglades support populations of garter snakes characterized by well-developed dorsal and parietal spots.

*Thamnophis sauritus* (Linnaeus)

I analyzed data on 279 specimens of *Thamnophis sauritus* from Florida and southern Georgia (Map 30) for possible geographic variation in each of 13 characters (Appendix A). Another 12 specimens from the Lower Florida Keys were examined and included in the discussion, but were not available at the time of mapping. The number of infralabials was essentially unvarying throughout the study area (92.6% had ten on each side). None

of the characters investigated was correlated with snout-vent length. Those characters which showed trends of geographic variation follow.

Number of ventrals. Males and females do not differ significantly in ventral counts ( $r = 0.2910$ ). Maps 31 and 32 show the apparent clinal increase in ventral counts for both sexes southward on the Florida peninsula. Higher ventral counts tend to extend farther northward along the coasts, and specimens from the Gulf Hammock region on the east coast have ventral counts comparable to snakes from the most southerly localities. Data from Paulson (1968) and from the present study indicate that *T. saxritus* from the Lower Keys have ventral counts like those seen in specimens from the southern mainland. Seven males from the Lower Keys averaged 163.4 ventrals and five females averaged 160.2.

Number of subcaudals. Males usually have more subcaudal scales than females ( $r = 0.5801$ ), and the sexes have been mapped separately in Maps 33 and 34. Ribbon snakes from the Panhandle west of the Choctawhatchee River tend to have more subcaudals than specimens from the remainder of the Panhandle and northern peninsula. Snakes from the peninsula usually have higher counts than specimens from the Panhandle, and there seems to be a weakly differentiated cline of increasing counts southward on the peninsula. Specimens examined from the Lower Florida Keys have higher subcaudal counts than ribbon snakes from anywhere else in Florida. Seven males averaged 137.9 subcaudals and three females averaged 126.0.

Number of ventrals plus caudals. The summation of the two previous counts was found to correlate with sex ( $r = 0.5201$ ), with males having more total ventral and subcaudal scutes. Maps 35 and 36 show how this

character varies in Florida. The variation tends to be clinal, with values increasing southward. Higher values extend farther north along the coasts of the peninsula. The highest values observed in Florida ribbon snakes are associated with specimens from the Lower Keys. Seven males from the Lower Keys had an average ventral plus caudal value of 301.3, and three females averaged 286.2 ventrals plus caudals.

Percent tail. Ribbon snakes with the longest tails relative to snout-vent length tend to occur in the central part of the peninsula, with specimens having lower values occurring both north and south. In addition, the few specimens available from the extreme western Panhandle and the Lower Keys suggest that snakes from these areas also have longer relative tail lengths.

Supralabials. Ribbon snakes from the Panhandle generally have seven upper labials on each side, while those from the peninsula have eight. Although not mapped, the ribbon snakes from the Lower Keys occasionally have seven supralabials as well. Map 37 shows the geographic variation in supralabial number for both sexes of *Thamnophis sauritus* from Florida.

Dorsal stripe edge. Geographic variation in the width and development of the black border of the dorsal stripe is figured in Maps 38, 39, and 40. Although the pattern is complex, congruence between the sexes is good. *Thamnophis sauritus* from the Panhandle west of the Apalachicola River and from parts of the central peninsula tend to have well-developed dorsal stripe edges. Snakes examined from the Lower Keys have extremely well-developed black dorsal stripe borders. Many specimens from the northern half of the Florida peninsula lack a stripe border

altogether, and some lack even the mid-dorsal yellow stripe (Rossman, 1963).

Parietal spot. Although Rossman (1963) stated that the nature of the paired parietal light spots in *T. sauritus* does not vary geographically, my analysis of his data indicates that it does. Maps 41, 42, and 43 show this variation. Most Florida *T. sauritus* lack a distinct parietal spot. However, specimens from the extreme northern Florida peninsula, at the edge of the Okefenokee Swamp, the area east of Tampa Bay, and the southern tip of the peninsula have distinct parietal spots. The concordance between the sexes in the geographic pattern of variation observed in this character support the reality of the pattern. The few specimens available from the Lower Keys have weakly developed parietal spots.

Ground color. Most ribbon snakes from Florida have a tan or light brown ground color. However specimens from the Gulf Hammock region usually have a very dark brown or black ground color. Some specimens from the Everglades and southern mainland also have a darker ground color, but specimens seen from the Lower Keys are light brown or tan. See Map 44.

Factor 1. The first factor extracted from the correlation matrix of ten characters accounts for 22.3% of the total variation, and most of the variation in parietal spot distinctiveness and parietal spot size. Map 45 shows how the first factor varies geographically. Higher states are associated with snakes from the northern peninsula, the area east of Tampa Bay, and the southern tip of the peninsula.

*Coluber constrictor* Linnaeus

I examined 440 specimens of *Coluber constrictor* from Florida (Map 46) for possible geographic variation in each of 18 characters

(Appendix A). The numbers of supralabials and infralabials were practically nonvariant with seven and eight respectively on each side. Aspects of the color and pattern were scored only on adult snakes (over 70 cm). With ontogenetic change in color and pattern thus taken out of the picture, none of the characters investigated was found to correlate with snout-vent length. Those variables that showed trends of geographic variation within the study area are discussed below.

Number of ventrals. There is no significant difference between males and females in ventral counts ( $r = 0.2253$ ), and the sexes have been lumped to produce Map 49. Maps 47 and 48 show the good degree of concordance between the patterns of variation in the two sexes. There is a well-developed clinal increase in number of ventrals as one proceeds southward down the peninsula. Specimens from the Lower Keys do not follow this trend, however, having much lower ventral counts than specimens from the southern tip of the mainland. It is also noteworthy that occasional specimens from the Apalachicola River Valley have higher than expected ventral counts, being more like specimens from farther south on the peninsula in this regard.

Number of subcaudals. Males tend to have more subcaudal scales than females ( $r = 0.3898$ ), although the correlation is not a strong one. Maps 50 and 51 show the geographic variation in subcaudal counts for Florida *Coluber constrictor*. Specimens from the Panhandle usually have lower counts than those from the peninsula. On the peninsula, there may be a very weakly defined clinal increase in subcaudal numbers for each sex, but any tendency in that direction is well masked.

Number of ventrals plus caudals. Map 52 shows the cline on the Florida peninsula of increasing ventral scute counts southward, except

for a dip on the Lower Keys. The sexes could be lumped in this map because ventrals plus caudals is independent of sex ( $r = 0.1618$ ).

Supralabial - loreal contact. Auffenberg (1955) first noted the variability of this character. In some specimens of *Coluber*, especially in the south-eastern United States, the first supralabial is in contact with the loreal. Although Auffenberg did not believe that this character varied with any degree of geographic regularity, my analysis has shown that it does. Map 53 shows that specimens from extreme northern Florida, the area east of Tampa Bay and extreme southern Florida, including the Middle Keys tend to have the first supralabial in contact with the loreal more frequently than specimens from the remainder of the state. This pattern occurs repeatedly in Florida snakes and must be considered indicative of some geographic factor based on present or past environments.

Ventral white. Geographic variation in the amount of white on the ventral surface in Florida *C. constrictor* is shown in Maps 54, 55, and 56. Snakes under 70 cm have been excluded from this analysis. Black snakes from south Florida and the Everglades region have almost totally white undersides. Snakes with the darkest bellies (*i.e.* the least white) are found on the Lower Keys and extreme northern Florida. Lighter colored ventrums seem to be associated with the coastal and treeless areas of the state. The black snakes on the Upper Keys are intermediate between Lower Keys and south Florida mainland specimens. The correspondence between the sexes is excellent.

Gular brown pigmentation. Map 57 displays the geographic variation in the presence or absence of brown pigment on the gular scales in Florida

*Coluber*. Most black snakes from the Lower Apalachicola River Valley have brown pigment on the gulars. Snakes from the remainder of the state seldom have such pigment. When the sexes were mapped separately, the patterns were virtually identical.

Supralabial brown pigmentation. See Maps 58, 59, and 60 for the geographic variation in this character. Black snakes from the lower Apalachicola Valley have the most brown pigment on the supralabial scales. Snakes from the southern part of Florida peninsula and the Everglades tend to have some supralabial brown, but not as much. Black snakes from the extreme southern tip of the peninsula and from the Lower Keys generally do not have any brown pigment on the upper labials.

Gular black pigmentation. The presence or absence of black on the gular scales in Florida *Coluber* varies geographically as shown in Map 61. The extreme northern base of the peninsula just south of the Okefenokee Swamp, the area east of Tampa Bay, and the Lower Keys support populations of *C. constrictor* with black on the gular scales.

Supralabial black pigmentation. The amount of black pigmentation on the supralabial scales varies geographically much like the previous character (see Maps 62, 63, and 64). The congruence between the sexes is remarkable, and can be considered as very strong evidence for the reality of the pattern. Black snakes from extreme northern Florida, the area east of Tampa Bay and the Lower Florida Keys have more black pigment on the supralabial scales than specimens from anywhere else in Florida.

Factor 1. The first factor accounts for 17.4% of the total variation in 16 characters. This factor accounts for most of the variation in gular black pigmentation and supralabial black pigmentation as well

as much of the variation in ventral white pigmentation. Its geography (Map 65) shows regions with similar phenetic responses in northern Florida, the area east of Tampa Bay and the Lower Florida Keys.

Factor 3. This factor accounts for 13.2% of the total variation in 16 characters, and most of the variation in gular and supralabial brown pigmentation as well as part of the variation in the number of ventrals plus caudals. Snakes with high factor 3 scores (higher values for brown pigmentation characters and lower ventral plus caudal counts) tend to occur in the Apalachicola River Valley, especially the lower valley, and the Everglades region of south Florida. See Map 66.

*Masticophis flagellum* (Shaw)

I analyzed data on 85 specimens of *Masticophis flagellum* from Florida, southern Alabama and southern Georgia (Map 67) for possible geographic variation in each of nine characters (Appendix A). Over 96% of the specimens examined had 16 supralabials. None of the characters was size-correlated. Those which appear to vary geographically follow.

Number of ventrals. Male coachwhips usually have more ventrals than females ( $r = 0.4010$ ). Maps 68 and 69 show that in general, the highest ventral counts are found in snakes from the peninsula, and especially the western half of the peninsula. Correspondence between the sexes is weak.

Number of subcaudals. Males and females are not significantly different in subcaudal counts ( $r = 0.2425$ ), and have been lumped to produce Map 70. It appears that specimens from the Panhandle and western parts of the peninsula usually have more subcaudal scales than snakes from the eastern peninsula.

Ventrals plus caudals. The summation of the preceding two characters is not correlated with sex ( $r = 0.3219$ ) and varies geographically as in Map 71. Again, the Panhandle and western part of the peninsula are characterized by coachwhips with higher ventral counts.

Percent tail. Tail length divided by total length is not correlated with sex ( $r = 0.2422$ ), and the sexes have been lumped to produce Map 72. Longer tails seem to be associated with specimens from the Panhandle and western parts of the peninsula.

Color phase. Most *Masticophis* from the Panhandle of Florida are of the light color phase, and most from the peninsula are dark. However, as shown in Maps 73, 74, and 75 there is some individual variation in this character. Furthermore, there appears to be two areas in peninsular Florida where snakes of the light phase are more common. This same pattern appears in both sexes, lending credence to its reality. Unfortunately, the sample sizes are very small.

Factor 1. The first factor accounts for 43.0% of the total variation in five characters, and most of the variation in ventrals plus caudals, and part of the variation in number of infralabials. Its geography, depicted in Map 76, shows a pattern of high factor 1 scores in the Panhandle and northern peninsula separated from another area of high values in southern Florida by an intervening region where the coachwhips tend to have fewer ventral scutes and infralabial scales.

*Opheodrys aestivus* (Linnaeus)

I examined 176 specimens of *Opheodrys aestivus* from Florida (Map 77) for geographic variation in each of 16 characters (Appendix A).

Supralabial and infralabial counts remained essentially constant throughout the study area with 87.4% having 14 supralabials and 75.6% having 16 infralabials. Dorsal scale rows were found to be 17-17-15 for over 95% of the specimens examined. Three measurements of the frontal scale were found to correlate with snout-vent length even after standardization by dividing by snout-vent length. The characters which appear to show geographic variation are discussed below.

Number of ventrals. Female green snakes typically have more ventral scales than males ( $r = 0.3991$ ). There is no obvious well-developed cline in ventral counts for Florida *Ophiodrys*. However, specimens from the southern parts of the state, and especially the south-west usually do have the highest counts.

Number of subcaudals. Green snake males tend to have higher subcaudal counts than females ( $r = 0.5513$ ). Specimens from the western Panhandle east to the Apalachicola River tend to have the most subcaudal scales, while specimens from the Everglades and southern peninsula have the least.

Ventrals plus caudals. Although both ventrals and caudals were found to be correlated with sex, their summation was not ( $r = 0.2807$ ). Map 78 shows the geographic variation in this character for the combined sexes. Highest values are associated with snakes from the western Panhandle and parts of South Florida. Snakes from the Everglades region have the lowest ventral scute values. The variation is complex, and it is not possible to discern a simple north-south cline in this character.

Percent tail. Relative tail length in Florida green snakes varies with sex. Males usually have proportionately longer tails ( $r = 0.5211$ ).

Concordance between the sexes is poor. In general, however, both sexes tend to have slightly longer tails in the Panhandle, and shorter tails south of Lake Okeechobee. In addition, the males show a pattern of longer tails on the Lower Keys, while the females do not.

Keeling of the second dorsal scale row. Maps 79, 80, and 81 show the geographic variation in the development of the keel on the scales of the second dorsal row at midbody. The maps for the two sexes indicate that the variation is very similar. North of central Florida and in the Panhandle green snakes tend to have reduced or no keeling on these scales. In central Florida, south throughout the peninsula, states for this character tend to be higher, with the highest states frequently associated with snakes from coastal regions. On the Lower Keys, the males have keeled scales on the second row, but the females apparently do not.

Supralabial pigmentation. Maps 82, 83, and 84 show the geographic variation in the amount of dark pigmentation on the upper labial scales in Florida *Ophiodrys aestivus*. The strong degree of concordance between the sexes may be taken as evidence for the reality of the pattern, since the two maps are based on separate sets of specimens. In general, snakes with more dark pigment on the supralabials occur in the Panhandle, the northern parts of the peninsula, and southward along the west coast. Green snakes from the Keys have very light colored upper labials.

Factor 3. This multivariate character varies geographically as shown in Map 85. It accounts for 12.6% of the total variation in ten characters, and most of the variation in keels of the second dorsal scale row and supralabial pigmentation. Green snakes from the southern half of the peninsula have less supralabial pigment, and better developed keels on their second

scale row. Snakes from extreme northern Florida may have higher Factor 3 scores, like specimens from the south.

*Elaphe guttata* (Linnaeus)

I examined 455 specimens of *Elaphe guttata* from Florida, southern Georgia, and southern Alabama (Map 86) for possible geographic variation in each of 16 characters (Appendix A). Some of the characters varied little throughout the study area. Dorsal scale rows counted at three points along the body were almost always 25-27-19. Measurements of the frontal scale were divided by snout-vent length, and found to correlate with snout-vent length. These characters were excluded from the analysis that follows.

Number of ventrals. Females usually have more ventral scales than males ( $r = 0.5933$ ). In both sexes, ventral counts increase southward on the Florida peninsula, with the highest values associated with snakes from the Lower Keys. Coastal areas also seem to support *E. guttata* with higher ventral counts. Maps 87 and 88 depict the geographic variation in ventral numbers for *E. guttata* from Florida.

Number of subcaudals. Males tend to have more subcaudal scales than females ( $r = 0.5015$ ). The number of subcaudals in Florida corn snakes appears to increase southward on the peninsula, but the trend is not as clear-cut as in the preceding character. See Maps 89 and 90.

Ventrals plus caudals. The summation of ventrals and caudals is not correlated with sex ( $r = 0.1118$ ), and so the sexes could be lumped to increase sample size (Map 91).

The highest counts occur on snakes from the Florida Keys and adjacent mainland. Higher counts are frequently associated with coastal

areas as well. The lowest ventral plus caudal counts occur on snakes from the northern peninsula and Panhandle.

Number of body blotches. *Elaphe guttata* from the Lower Keys have the highest dorsal blotch counts. Specimens from the Panhandle and northern peninsula have the lowest. Higher counts reach farther northward on the peninsula along both coasts. Maps 92 and 93 show the geographic variation in number of body blotches in Florida *E. guttata*. The rather high degree of individual variation in this character partially obscures the clinal nature of its geography.

Number of tail blotches. Corn snakes from the Lower Keys and south Florida mainland have the highest tail blotch counts. Maps 94 and 95 show the geography of this character. The lowest tail blotch counts are seen in snakes from the Panhandle, and the increase southward is probably clinal, although complicated by individual variation from snake to snake.

Blotch border. The red blotches on the dorsum of Florida corn snakes are usually surrounded by a narrow black border. The width of this border varies geographically as shown in Map 96. Snakes from the extreme south Florida mainland and parts of the western Panhandle have wider blotch borders.

Lateral blotch shape. Corn snakes from the Panhandle of Florida east to the Aucilla River frequently have the border of the lateral blotch open ventrally, suggesting an inverted U rather than a complete circle. The character occurs sporadically throughout Florida, but is almost universal among Panhandle specimens. See Map 97.

Ventral pigmentation. Corn snakes from the Lower Florida Keys have the least dark pigment ventrally. Snakes in coastal areas and

other off shore islands have reduced pigment, while the majority of specimens from the remainder of the peninsula and Panhandle tend to have much black pigment on their ventral surfaces. Maps 98, 99, and 100 show the geographic variation of this character in Florida *E.*

*guttata*.

Ventral check shape. The ventral dark pigmentation is generally confined to discrete rectangles. Snakes from the Lower Florida Keys and coastal regions (especially the south-west coast) have small, often square pigment spots ventrally. Specimens examined from more interior regions, especially in the northern parts of the state, have their ventral pigment in elongated rectangles. Many specimens from the Panhandle and extreme northern Florida have wide rectangular pigment spots covering entire ventral scutes.

Factor 1. The first factor accounts for 19% of the total variation in 12 characters. Factor 1 accounts for most of the variation in ventrals plus caudals, number of body blotches and number of tail blotches. Map 101 shows how this multivariate character varies geographically in Florida. Snakes from the Florida Keys and southern parts of the peninsula tend to have high factor 1 scores, while the lowest values are associated with Panhandle specimens.

Factor 2. The second factor accounts for 15.0% of the total variation, and most of the variation in the amount of ventral dark pigmentation, and the shape of the ventral pigment blotches. Low values (that is, lighter bellies with smaller blotches) are associated with corn snakes from coastal areas, and the lowest values of all are seen in specimens from the Lower Keys. See Map 102.

*Elaphe obsoleta* (Say)

I analyzed data on 370 specimens of *Elaphe obsoleta* from Florida (Map 103) for potential geographic variation in each of six characters (Appendix A). None of the characters investigated was correlated with size. The sex of the specimens was not determined.

Number of dorsal blotches. The number of body blotches in *E. obsoleta* increases clinally on the Florida peninsula to the south. Map 104 shows the variation in this count.

Ground color. The dorsal ground color of Florida *E. obsoleta* varies geographically as shown in Map 105. This character attempts to describe the amount of melanin or dark pigmentation on the dorsum of these snakes. In general, specimens from coastal areas have the lightest ground colors. Most chicken snakes from the interior of the peninsula, the Panhandle, and the Upper Keys have darker dorsums. (The species does not occur on the Lower Keys.)

Stripe development. *Elaphe obsoleta* from the Panhandle east to the vicinity of the Suwannee River generally lack dorsal stripes. Within the peninsula, specimens from more northerly regions have the most well-defined stripes, while most examples from southern Florida have moderately-developed dorsal stripes. See Map 106.

Blotch development. Chicken snakes from the Florida Panhandle east to the vicinity of the Suwannee River, and southward along the west coast to the vicinity of the Withlacoochee River have dorsal blotches. Those specimens south of the Suwannee have dorsal stripes as well, and are recognized as the subspecies *E. obsoleta williamsi*. In addition, *E. obsoleta* from the Upper Keys and extreme southern

Florida mainland have fairly well-developed dorsal blotches, and have been called *E. o. deckerti*. See Map 107.

Ventral pigmentation. Map 108 shows the geographic variation in the amount of dark pigment in the ventral pattern of Florida chicken snakes. Specimens from the Panhandle east to the Suwannee River have the darkest bellies.

Supralabial pigmentation. The geographic variation in the amount of dark pigment on the upper labial scales in this species varies geographically as in Map 109. Its variation is almost identical to that seen in ventral pigmentation except that snakes with dark supralabials occur also on the Upper Keys.

Factor 1. The first factor accounts for 51.6% of the total variation in four characters, and most of the variation in ventral and supralabial pigmentation, as well as part of the variation in number of dorsal blotches. Map 110 shows how this character varies within Florida. Snakes from the Panhandle receive the highest factor scores, implying darker labial and ventral pigment and fewer dorsal blotches.

*Lampropeltis getulus* (Linnaeus)

I analyzed data on 207 specimens of *Lampropeltis getulus* from Florida, southern Georgia and southern Alabama (Map 111). A total of eleven characters were investigated for geographic variation (Appendix A). Head length was divided by snout-vent length and the resulting ratio found to correlate with snout-vent length. Further consideration of this character has been omitted. The characters which seem to vary geographically are discussed below.

Number of ventrals. The number of ventral scales in Florida kingsnakes does not correlate with sex ( $r = 0.1392$ ). Therefore, the sexes could be lumped to increase the sample size. Kingsnakes from the Panhandle tend to have fewer ventrals than those from the peninsula. The tendency is not pronounced, however, and if any geographic pattern of variation exists within the peninsula, it does not emerge from examination of the maps.

Number of subcaudals. Male *L. getulus* usually have more subcaudals than females ( $r = 0.6306$ ). There is little geographic concordance between the sexes. There is a very generalized tendency for subcaudal counts to be higher in the southern parts of the peninsula.

Percent tail. Tail length divided by total length varies as shown in Maps 112 and 113. Males have proportionately longer tails than females ( $r = 0.4837$ ), thus the sexes have been treated separately in the geographical analysis. Snakes with proportionately longer tails occur in extreme southern Florida and apparently the Apalachicola River Valley.

Dorsal scale rows. The number of scale rows at midbody varies geographically as shown in Map 114. Kingsnakes from the Panhandle east to the vicinity of the Aucilla River have 21 midbody scale rows, while specimens from the peninsula usually have 23. It is apparent that a large percent of kingsnakes from extreme southern Florida have 21 scale rows as well.

Number of infralabials. Most Florida kingsnakes have 18 lower labial scales, counting both sides. However, many from extreme northern parts of the state have 19 or 20 infralabial scales. In addition, kingsnakes from the east coast of the peninsula frequently have 20 lower labials. See Map 115.

Number of cross bands. Maps 116, 117, and 118 show the geographic variation in the number of dorsal precaudal cross bands in Florida *L. getulus*. The concordance between the sexes is remarkable, and suggests that the sexes are responding similarly to whatever environmental factor selects for cross band counts. There is a very weak ( $r = -0.4038$ ) correlation between snout-vent length and number of cross bands, implying that larger snakes tend to have fewer cross bands. In the present case, however, there is no correlation between snout-vent length and latitude in Florida ( $r = 0.1678$ ), so the variation described is not due to variation in snout-vent length, but to inherent variation in cross band counts. In other words, snout-vent length does not vary geographically in Florida, based on the present sample. The number of cross bands increases in a regular cline southward on the Florida peninsula.

Dorsal pattern. The amount of light pigment in the dorsal pattern of Florida kingsnakes varies geographically as shown in Maps 119, 120, and 121. Congruence between the sexes is quite good. Areas in which the kingsnakes tend to have more light pigment dorsally include the Everglades and southern peninsula, the Lower Apalachicola Valley, and extreme northern Florida. Frequently, the kingsnakes from the region to the east of Tampa Bay are light colored, as well.

Factor 2. The second factor accounts for 27% of the total variation in five characters, and much of the variation in number of ventrals and midbody scale rows. Map 122 shows the geographic variation for this multivariate character. Specimens with higher factor 2 scores tend usually to occur in the peninsula as opposed to the Panhandle.

Factor 3. Factor 3 accounts for 23% of the total variation in five characters, and much of the variation in dorsal scale rows and

light pigment in the pattern. Snakes from extreme northern Florida, parts of southern Florida, and certain other regions in the peninsula have high factor 3 scores. See Map 123.

*Lampropeltis triangulum* (Lacepede)

I analyzed data on 120 specimens of *Lampropeltis triangulum* from Florida, southern Georgia and southern Alabama (Map 124) looking for trends of geographic variation in each of 15 characters (Appendix A). None of the characters investigated showed correlations with snout-vent length. Those characters which seem to vary geographically are discussed below.

Number of ventrals. Males and females do not differ appreciably in number of ventral scales ( $r = 0.2330$ ). However they do seem to differ in their patterns of geographic variation. Sample sizes are admittedly small, and trends uncovered by the mapping techniques may be a result of sampling bias. However, based on the data available (Maps 125 and 126) male milk snakes seem to have higher ventral counts in northern Florida and the peninsula, while females have lower counts there.

Number of subcaudals. Males generally have more subcaudal scales than females ( $r = 0.6352$ ). Maps 127 and 128 show the geographic variation of this character. Concordance between the sexes is fair. If there is any geographic tendency, it is for snakes from the Panhandle and parts of southern Florida around Lake Okeechobee to have higher subcaudal counts.

Ventrals plus caudals. The summation of the preceeding two characters does not correlate with sex ( $r = 0.1106$ ), and samples could be lumped to produce Map 131. In addition, Maps 129 and 130 are provided to show

the degree of correspondence between the sexes. Generally speaking, milk snakes from the Panhandle have higher ventral and caudal counts than specimens from most of the peninsula. However, snakes from the east coast and areas around Lake Okeechobee seem to have high ventral plus caudal counts as well.

Percent tail. Relative tail length varies geographically as shown in Maps 132 and 133. Males have proportionately longer tails ( $r = 0.6537$ ). The variation does not have a clear-cut pattern, but there seems to be a slight tendency for relative tail length to increase clinally to the south on the Florida peninsula.

Dorsal scale rows. Female *L. triangulum* from Florida usually have 19 midbody scale rows, while males may have either 19 or 17. Maps 134 and 135 show the geographic variation in midbody scale rows. Male specimens from the Panhandle usually have 19 scale rows at midbody, and males from the peninsula may have either 19 or 17.

Body bands. The number of red precaudal cross bands varies geographically as shown in Maps 136, 137, and 138. High band counts are associated with milk snakes from northern Florida, including the Panhandle, the area east of Tampa Bay on the central Highlands, and apparently, the region around Miami in southern Florida.

Tail bands. Maps 139, 140, and 141 show the geographic variation in number of red tail cross bands in Florida milk snakes. In general, specimens from the Panhandle and northern peninsula have higher tail band counts than those from the remainder of the state.

Total bands. The summation of precaudal and caudal red bands varies geographically as shown in Map 142. Highest counts occur on

snakes from northern Florida, the area east of Tampa Bay and the southeastern peninsula region. Milk snakes from the southern half of the peninsula (not counting the Miami rim area) have low band counts compared with specimens from the Panhandle and northern half of the peninsula.

Factor 3. This multivariate character accounts for 16.6% of the total variation in 10 characters and most of the variation in the number of red cross bands on the body and the tail. Its variation is shown in Map 143 and is very similar to the variation seen in total band counts.

*Diadophis punctatus* (Linnaeus)

I examined 295 specimens of *Diadophis punctatus* from Florida, southern Georgia and southern Alabama (Map 144) for potential geographic variation in each of 23 characters (see Appendix A). None of the characters examined was found to be correlated with body size. Those characteristics which show apparent patterns of geographic variation are discussed below.

Number of ventrals. Maps 145 and 146 show the geographic variation in ventral numbers for male and female ringneck snakes from Florida. The correlation coefficient between ventral counts and sex was found to be 0.6314. Snakes from the Panhandle and northern peninsula have the highest ventral counts. Concordance between the sexes is very good.

Number of subcaudals. Males have more subcaudal scales than females ( $r = 0.7425$ ). The geographic variation in subcaudal counts is presented in Maps 147 and 148. Its variation is more complex than that observed in ventral count variation.

Ventrals plus caudals. The summation of ventrals and subcaudals is not correlated with sex ( $r = 0.0624$ ), and the samples could be lumped to produce Map 149. The highest ventral scute counts occur in snakes from the Panhandle and northern peninsula. Snakes with intermediate values occur in the southern tip of the peninsula, and specimens with low ventral plus caudal counts are found on the Lower Keys and most of the south-central Florida peninsula.

Percent tail. Relative tail length was found to be correlated with sex ( $r = 0.8058$ ), and the males and females have been mapped separately (Maps 150 and 151). Generally speaking, *Diadophis* from the southern half of the peninsula and the Keys have proportionately longer tails than specimens from the remainder of the state.

Numer of supralabials. Most southeastern ringneck snakes have 16 total supralabial scales. Occasional specimens have only 14 upper labials, and these tend to occur more frequently in the Panhandle and northern parts of the Florida peninsula. See Map 152.

Subcaudal spots. The number of small black spots on the underside of the tail varies geographically as shown in Map 153. *Diadophis punctatus* from the Florida Panhandle, the Gulf Hammock region and the Lower Keys often have such spots. Specimens from the remainder of the state usually lack these black spots.

Labial pigmentation. Pigment on the labials of Florida *D. punctatus* may be in discrete spots, diffuse smudges or lacking altogether. Map 154 shows the geographic variation of this character for both sexes of Florida ringnecks. Specimens from the Lower Keys have no such pigment or it is very diffuse. Specimens from the southern Everglades and parts of the

Gulf Hammock region usually have diffuse labial pigment. The majority of Florida ringneck snakes have labial pigment confined to discrete spots.

Pigmented supralabials. The number of upper labial scales with black pigment varies geographically as in Maps 155, 156, and 157. Specimens from South Florida and the Keys as well as many from the Gulf Hammock region score high for this character. Snakes from the Panhandle have the lowest states for this character, while specimens from the remainder of the state receive intermediate scores for number of pigmented supralabials.

Pigmented labials. This character is the summation of labials, supra- and infra, with black pigment. Its geography is depicted in Map 158. Ringneck snakes from the Gulf Hammock region and the southern tip of the peninsula including the Keys have the highest states for this character. Specimens from the Panhandle have the least pigment on the labials and most peninsular specimens are intermediate for pigmented labials.

Ring interruption. Most ringneck snakes from the Florida peninsula have a middorsal break in the neck ring. Map 159 shows, however, that the geographic variation in this character is more complex. Specimens from the Lower Keys and the Gulf Hammock may lack a nuchal ring altogether. Many ringnecks from coastal areas do not have a middorsal ring interruption. Most *Diadophis* from the Panhandle have complete neck rings.

Ring width. The width of the nuchal ring varies geographically as shown in Maps 160, 161, and 162. *Diadophis* from the Panhandle and northern parts of the peninsula have the widest nuchal rings.

Ring displacement. The position of the nuchal ring relative to the parietal scales varies geographically as shown in Map 163. Snakes from the Panhandle and northern peninsula tend to have their neck rings originating nearer to the parietals than do more southerly specimens.

Factor 2. The second factor extracted from a matrix of 19 characters accounted for 13.2% of the total variation, and much of the variation in number of pigmented supralabials and infralabials as well as labial pigmentation type. Map 164 shows that *Diadophis* from the Gulf Hammock region and the southern peninsula including the Keys have the highest scores for factor 2. Snakes from the Panhandle have the lowest scores, and specimens from the remainder of the peninsula have intermediate values.

Factor 4. This multivariate character describes 7.8% of the variation in 19 characters as well as part of the variation in numbers of labials with pigment. Again, high factor 4 scores are associated with snakes from the Gulf Hammock region and the Keys. Snakes from most of the Panhandle and northern peninsula get low scores for this factor, implying wider, interrupted, more anterior rings. Map 165 shows the geographic variation of factor 4.

*Cemophora coccinea* (Blumenbach)

I analyzed data on 90 specimens of *Cemophora coccinea* from Florida and southern Georgia (Map 166) for geographic variation in each of 17 characters (Appendix A). The sample size is unfortunately small. The characters examined which seem to have patterns of geographic variation are discussed below.

Number of ventrals. The number of ventral scales in Florida scarlet snakes correlates with sex ( $r = 0.4144$ ), and the sexes have been mapped separately (Maps 167 and 168). The correspondence between the sexes is very good. Sample sizes are small, but scarlet snakes from the Panhandle and the southern end of the peninsula tend to have fewer ventral scales than specimens from the middle of the peninsula.

Number of subcaudals. Maps 169 and 170 show the geographic variation for male and female *Cemophora* subcaudal counts. The number of subcaudals correlates only weakly with sex ( $r = 0.3385$ ), with males having the higher counts. In both sexes, snakes from the Panhandle tend to have fewer subcaudals than specimens from the peninsula. The sample sizes are small, but it seems that specimens from the southern tip of the state also have low subcaudal counts.

Ventrals plus caudals. This character summarizes nicely the variation apparent in the two preceding counts, and is not correlated with sex ( $r = 0.2240$ ). Map 171 shows the pattern of geographic variation in ventral plus caudal counts for both sexes of Florida *C. coccinea*. Lowest counts are associated with snakes from the Panhandle east to the Suwannee River and from the southern end of the peninsula, south of Lake Okeechobee. Scarlet snakes from the remainder of the peninsula between the Suwannee River and Lake Okeechobee have higher ventral scute counts.

Percent tail. Tail length divided by total length varies geographically as shown in Maps 172 and 173. There is no significant difference between relative tail lengths in the two sexes for this species. In general, scarlet snakes from more southern localities tend to have pro-

portionately longer tails, although the tendency is not sharply defined. In the Panhandle, females have relatively longer tails, but males have shorter tails. The result of this is that sexual dimorphism is pronounced in the few Panhandle specimens examined but lacking in the peninsular specimens. The two Panhandle females have longer tail length/snout vent ratios (mean = 0.158) than the three males available (mean = 0.140).

Infralabials. Florida *C. coccinea* may have 14, 16 or 18 lower labial scales. Specimens from the Everglades Region frequently have 14 infralabials, while many specimens from the central and north-central peninsula have 18.

Supralabials. Map 174 shows the geographic variation in the number of supralabial scales in Florida *Cemophora*. Snakes from the Panhandle west of the Aucilla River, northeast Florida, and the Everglades usually have 11 to 13 upper labials. Snakes from the central peninsula tend to have 14 or 15.

Number of red body bands. Map 181 depicts geographic variation in the number of red cross bands in Florida scarlet snakes. Snakes from northern Florida and the Osceola National Forest region, just south of Tampa Bay, and the Everglades have fewer cross bands than snakes from the rest of the state.

Number of red tail bands. The number of cross bands on the tail in Florida *Cemophora* correlates with sex ( $r = 0.5179$ ). Maps 182 and 183 show the nature of variation in this character. Although concordance between the sexes is poorly developed, a general tendency for scarlet snakes from more northern localities to have more tail bands is apparent.

Dorsal scale rows. Ninety and four-tenths percent of Florida *Cemophora* have 19 dorsal scale rows at mid body. Specimens studied from the Everglades have 17 anterior scale rows, and specimens from extreme northern Florida tend to have 21, while those from the remainder of Florida usually have 19 anterior scale rows. All *Cemophora* examined from the Panhandle have 19 posterior scale rows. In the peninsula, many specimens have fewer than 19. See Maps 175 and 176.

Length of the white bands. Maps 177, 178, and 179 show the variation in the length (in scale-lengths) of the first and fifth white bands in Florida *Cemophora*. The geographic patterns will be discussed multivariately under factor 1.

Length of red bands. There seems to be three areas where longer red bands are the rule: northern Florida, especially the northern parts of the Panhandle, around Lake Okeechobee, and the extreme southern Everglades. See Map 180.

Number of red cross bands. The only consistent tendency between the sexes in the geography of the variation in number of red body bands is that specimens from the Everglades region usually have fewer such bands (Map 181). The number of tail bands varies geographically as shown in Maps 182 and 183. In this character, it is difficult to discern a pattern that is common to both sexes.

Factor 1. The first factor accounts for 24.7% of the total variation in 14 characters, and 80% of the variation in length of the first white band and 64% of the variation in length of the fifth white band. Thus factor 1 describes variation in the length of the white bands in *C. coccinea*. Its geographic variation is figured in Map 184. Snakes from

the western Panhandle, north central peninsula, and west coast tend to have longer white bands.

Factor 2. The second factor represents a multivariate assessment of red bands in *Cemophora*. It accounts for much of the variation in number of red body bands, and length of the first and fifth red bands. It represents 16% of the total variation, and is mapped in Map 185. The southern half of the peninsula tends to support populations of scarlet snakes with fewer but longer red bands, while the pattern in the rest of Florida is unclear.

Factor 3. Accounting for much of the variation in number of supra- and infralabials and ventrals plus caudals, the third factor represents 13.5% of the total variation, and is figured in Map 186. The Panhandle and north Florida as well as the Everglades are separated out with low values for factor 3. These areas have *Cemophora* with fewer labials and fewer ventrals plus caudals.

Factor 4. This factor accounts for 10.3% of the total variation, and gets high loadings from the three dorsal scale row variables. *Cemophora* with higher scale row counts occur in much of the Panhandle and northern half of the peninsula. See Map 187.

*Tantilla coronata* (Baird and Girard), *Tantilla relicta* Telford, and *Tantilla oolitic* Telford

I analyzed data on 198 specimens of *Tantilla* from Florida (Map 188) for possible geographic variation in each of 11 characters (Appendix A). Those characters which seem to vary geographically are discussed below.

Number of ventrals. Females generally have more ventrals than males ( $r = 0.4150$ ). The sexes have been mapped separately in Maps 189 and 190.

In both sexes, the number of ventral scales decreases southward on the peninsula until the southernmost localities in Florida. Specimens examined from Miami and Key Largo have high ventral counts, reminiscent of northern populations.

Number of subcaudals. The highest subcaudal counts occur on snakes from the Big Bend region of northern Florida and decrease quickly to the west and more gradually to the south. Maps 191 and 192 show the variation for males and females which differ in mean subcaudal counts ( $r = 0.4194$ ).

Ventrals plus caudals. The summation of the preceding two counts produces a variable which does not correlate with sex ( $r = 0.0783$ ). Maps 193, 194, and 195 show how this character varies geographically. *Tantilla* from the Panhandle and northern peninsula have the highest counts, decreasing clinally southward on the peninsula. *Tantilla* from the Miami area are more like northern populations in this character, with higher ventral scute counts.

Percent tail. Relative tail length varies geographically as shown in Maps 196 and 197. Males usually have proportionately longer tails than females ( $r = 0.6339$ ). Both sexes vary geographically with relatively longer tails occurring in populations inhabiting the Big Bend region and the western coast of the peninsula.

Supralabials. *Tantilla* from Highlands County often have six upper labials on each side, while specimens from the remainder of the state usually have seven. Map 198 shows this variation.

Parietal pigmentation. *Tantilla* examined from the Miami area and parts of the Big Bend region of northern Florida lack light spots on the parietal scales. Maps 199, 200, and 201 show the geographic variation

of this character. Specimens from the Panhandle east to the Ochlockonee River, Highlands County, and the lower east coast of the peninsula have extensive parietal light markings, often forming a partial nuchal ring. Snakes with intermediate amounts of light pigment in the parietal region occur throughout most of the Florida peninsula.

Snout pigmentation. Map 202 shows the geographic variation in the amount of light pigment on the snout in Florida *Tantilla*. Most specimens examined from the lower east coast of the peninsula have a large white spot on the rostral and internasal scales. *Tantilla* from Highlands County have some light pigment on the snout, while the majority of *Tantilla* populations studied lack this characteristic.

Factor 2. This multivariate character accounts for 18.1% of the total variation in eight characters and most of the variation in number of ventrals plus caudals and parietal and snout pigmentation. Map 203 summarizes the geographic variation in factor 2. The specimens examined from the Miami area and the Big Bend region receive the highest factor 2 scores, implying reduced light pigmentation and more ventrals plus caudals in these areas. Panhandle *Tantilla* and those from Highlands County have the lowest factor 2 scores. Intermediate values are seen in specimens from the remainder of the state.

#### *Sistrurus miliarius* (Linnaeus)

I examined 320 specimens of *Sistrurus miliarius* from Florida, southern Georgia and southern Alabama (Map 204) for possible variation in each of 22 characters (see Appendix A). Much of the variation studied in this species was very noisy owing to a large degree of individual

variation among snakes from nearby localities. Smoothing algorithms might help clarify the picture by plotting averages of adjacent specimens. However, the mapping procedure employed here does not smooth, but rather plots the data exactly as they appear. Three ratios concerned with the frontal scale and snout-vent length were correlated with snout-vent length and excluded from further consideration. Those characters for which geographic trends were noted are discussed below.

Number of ventrals. Females tend to have more ventral scales than males ( $r = 0.4672$ ), and the sexes have been treated separately in Maps 205 and 206. The lowest ventral counts are apparently associated with snakes from the Panhandle, while the highest occur in snakes from the central peninsula.

Number of subcaudals. Males usually have more subcaudal scales than females ( $r = 0.6267$ ). Maps 207 and 208 show the geographic variation in subcaudal counts for Florida pigmy rattlesnakes. The pattern is like that seen in the variation of ventral counts. Specimens from the Panhandle have the lowest counts, and specimens from the central part of the peninsula tend to have the most subcaudal scales. As with the preceding character, pigmys from the lowland region south of Lake Okeechobee tend to have lower counts than specimens occurring just north and south of this region.

Ventrals plus caudals. Although ventrals and caudals are both correlated with sex, their summation is not ( $r = 0.0570$ ). The variation in this character is depicted in Map 209 for the combined sexes. Snakes from the Panhandle east to the vicinity of the Aucilla River and in the Everglades region south of Lake Okeechobee tend to have the lowest ventral

scute values. *Sistrurus* from the peninsula excluding the Everglades seem to show a clinal increase in ventral and subcaudal counts to the south.

Dorsal scale rows. Maps 210 and 211 show the geographic variation in the number of dorsal scale rows at two points along the body in Florida *Sistrurus*. The lowest scale counts tend to be associated with specimens from the Florida Panhandle and the highest with specimens from coastal areas along the peninsula. Snakes with intermediate counts occur in most of the interior peninsula. A lot of individual variation among snakes from closely separated localities creates the noisy surfaces depicted in the maps.

Number of blotches. Pigmy rattlesnakes from the Panhandle west of the Ochlockonee River and from many coastal areas on the peninsula frequently have more dorsal body blotches than specimens from the remainder of the study area. Maps 212 and 213 show the patterns of geographic variation for male and female *S. miliarius*.

Spot/space ratio. This character varies geographically as shown in Map 214. Pigmys occurring west of the Ochlockonee River in the Panhandle and in the Everglades usually have crossband-like body blotches that are more narrow than their inter-blotch spaces. Snakes from coastal areas in the peninsula tend to have larger blotches with very narrow spaces between. Many specimens from interior localities on the peninsula have spot/space ratios intermediate between these.

Spot shape. When the length (in scale lengths) of a typical mid-body dorsal blotch is divided by its width, the resulting ratio varies geographically as depicted in Map 215. *Sistrurus* from the Panhandle and Everglades tend to have dorsal blotches that are more like crossbands. Specimens from most of the peninsula have blotches that are more roundish.

Dorsal contrast. *Sistrurus* from the Panhandle and parts of southern Florida including the Everglades have more contrast between their dorsal blotches and their ground color, resulting in a more distinctive dorsal pattern. There may also be a tendency for snakes from coastal areas to have higher values for this character as well. See Map 216.

Ventral pigmentation. Pigmy rattlers from much of the Panhandle west of the Ochlockonee and from South Florida tend to have more white ventrally than specimens from the remainder of the state. The geographic variation of this character is displayed in Maps 217 and 218.

*Crotalus adamanteus* Beauvois

I examined 194 specimens of *Crotalus adamanteus* from Florida (Map 219) for possible geographic variation in each of 18 characters (Appendix A). There is a large amount of individual variation in most of the characters examined. Patterns of geographic variation are obscured by this individual variation, with the result that many of the maps appear noisy. Several of the characters examined appeared not to vary geographically within the study area. Those for which geographic patterns could be recognized are discussed below.

Number of ventrals. Female rattlesnakes usually have more ventral scales than males ( $r = 0.6808$ ). The only geographic trend apparent in the variation of ventral counts is that snakes from the Florida Keys and adjacent mainland consistently have more ventrals than specimens from elsewhere in the study area. There is apparently no cline within Florida.

Number of subcaudals. Males have more subcaudals than females ( $r = 0.7971$ ). The variation in subcaudal counts within Florida is complex and seems to have no geographic component based on the sample available.

Dorsal scale rows. I can discern no geographic trend in the variation of dorsal scale row counts in Florida *C. adamanteus*. Map 220 shows the spotty occurrence of specimens with higher scale row counts.

Number of infralabials. The variation in this character is also noisy, but some geographic trends appear to exist. Maps of the variation in each sex are provided (Maps 221 and 222), and some correspondence is apparent. Rattlesnakes from northern Florida and from the Lower Keys typically have more lower labials than specimens from the central peninsula. Map 223 shows the variation in infralabial counts for the combined sexes.

Dorsal blotches. The number of diamonds on Florida *Crotalus* varies geographically as shown in Map 224. There seems to be a tendency for specimens from the Panhandle, the Keys, and the west coast of the peninsula to have fewer dorsal blotches than specimens from interior localities on the peninsula.

Labial pigmentation. The number of immaculate supralabials in Florida *C. adamanteus* varies geographically as shown in Maps 225, 226, and 227. There is a tendency for specimens from the western Panhandle, the Upper Keys and the Everglades region to have dark pigmentation on all upper labial scales. Rattlesnakes from the Central Ridge east of Tampa Bay and from the Lower Keys frequently have the most immaculate labials.

Ventral pigmentation. Maps 228, 229, and 230 depict the geographic variation in the degree of ventral dark smudging in Florida rattlesnakes. There is a tendency for *Crotalus* from the Panhandle, the Everglades region and the western coast of the peninsula to have lighter ventral patterns than specimens from the interior of the peninsula. Snakes from the

Lower Keys usually have darker ventral patterns, more like specimens from north-central Florida.

Factor 1. The first factor accounts for 16.7% of the total variation in 14 characters, and most of the variation in labial pigmentation and the number of immaculate supralabials. Map 231 shows its geographic variation in Florida. Snakes from the western Panhandle, the Everglades region and the Keys typically have darker supralabials. Specimens examined from the Central Ridge consistently have the least labial pigmentation.

Factor 2. The second factor accounts for 12.8% of the total variation in 14 characters, and most of the variation in infralabial number. Factor 2 also receives a contribution from the variation in the number of supralabial scales. Map 232 shows how factor 2 varies geographically. Specimens from the Florida Keys and parts of northern Florida tend to receive higher factor 2 scores, and specimens from the southern half of the peninsula usually score the lowest.

### Environmental Data

I mapped environmental data from 196 weather stations in Florida, Georgia and Alabama (Map 233). Maps 234 through 245 show the results of the variables examined.

### The Patterns

I used factor analysis to compare one hundred maps of morphological variation in fifteen species of Florida snakes. The SPSS factor analysis procedure extracted 24 factors (patterns of geographic variation) which accounted for 76.9% of the total information in the maps. The maps

(characters) analyzed and their communalities (percentage of variation accounted for) are presented in Table 1. Table 1 also gives the factor (pattern of geographic variation) with which each character is most closely associated.

Most of the geographic variation observed in Florida snakes is distributed along a north-south axis. Factor 1 accounted for 26.7% of the variation explained by the factor analysis procedure, and most of the variation in those characters which showed distinct north-south changes in character states. Of the 100 maps analyzed, factor 1 accounted for more than half of the variation in ten maps, and was the principal pattern of variation for 38 characters (Table 1). In all the maps, factor 1 accounts for that part of the geographic variation that is north-south oriented. Factor 1 actually identifies two important patterns of geographic variation. The Suwannee River Pattern is shared by those species which demonstrate distinct character state changes occurring in the region of the present Suwannee River. The North-South Pattern includes those species which show clinal changes in character states southward on the Florida peninsula.

Table 2 presents the characters (maps) and their factor loadings on factor 1. These factor loadings may be interpreted as the relative importance of the various characters (*i.e.* maps) to the definition of the factor. Their square is the percentage of variation accounted for by the factor. The important observation to be made here is that nearly all of the characters analyzed have a significant portion of their variation which may be described as a north-south gradient or a character shift along north-south lines.

The North-South Pattern is the most important pattern of geographic variation observed in Florida snakes. Table 2 presents the factor loadings for all maps analyzed. Even characters which are primarily varying in some other pattern usually have some component of their variation which can be described as north-south oriented. Many characters (e.g. ventrals plus caudals in *Storeria dekayi*, *Thamnophis sirtalis*, *Coluber constrictor*, *Elaphe guttata*, *Lampropeltis getulus*, *Lampropeltis triangulum*, *Cemophora coccinea*, *Diadophis punctatus*, and *Sistrurus miliarius*, and blotches or crossbands in *Elaphe guttata*, *Elaphe obsoleta*, and *Lampropeltis getulus*) vary primarily in the North-South Pattern. Figure 3 diagrammatically represents this important pattern of geographic variation.

The Suwannee River Pattern is presented in Figure 4, and is best exemplified by the geographic variation observed in such characters as midbody scale rows in *Storeria dekayi*, number of supralabials in *Thamnophis saxritus*, midbody scale rows in *Lampropeltis getulus*, and dorsal blotch development in *Elaphe obsoleta*. Like the North-South Pattern, this pattern is occasionally superimposed on other patterns of geographic variation (e.g. number of labial spots in *Diadophis punctatus*).

The second factor extracted from the matrix of 100 maps accounted for another large proportion of the information. Table 3 presents factor loadings on factor 2 for the variables which were important in its construction. This pattern of geographic variation may be called the Everglades Pattern and is the principal pattern of variation for such characters as the number of immaculate labials in *Crotalus adamanteus*, development of the dorsal blotch border in *Elaphe guttata*, and number

of crossbands, number of infralabials, and length of the red bands in *Cemophora coccinea*. A diagrammatic representation of the Everglades Pattern is provided in Figure 5.

Factor 3 describes a North Florida-Lower Keys Pattern, and is best illustrated by the variation seen in supralabial and gular black pigmentation in *Coluber constrictor*, and number of preocular scales in *Storeria dekayi*. This pattern is concerned with a phenetic resemblance between populations in northern Florida, the region east of Tampa Bay and the Lower Florida Keys. Ventral white in *Coluber constrictor*, ventrals plus caudals in *Storeria dekayi*, and supralabial-loreal contact in *Coluber constrictor* also have elements of this pattern in their geographic variation. Factor loadings for significant characters are presented in Table 4, and Figure 6 illustrates the Lower Keys Pattern.

The fourth factor is the principal pattern of variation for number of infralabials in *Masticophis flagellum*, number of infralabials in *Lampropeltis triangulum*, and the amount of white in the ventral pattern of *Sistrurus miliarius*. The Panhandle-Everglades Pattern describes the situation in which infraspecific populations in the Florida Panhandle and the Everglades region are more similar to each other than either is to geographically intermediate populations. Spot shape in *Sistrurus miliarius*, supralabial brown pigment in *Coluber constrictor*, and ring separation in *Diadophis punctatus* also have elements of this pattern in their geographic variation. Table 5 gives the factor loadings for characters with significant contributions to factor 4, and Figure 7 illustrates the Panhandle-Everglades Pattern.

The Coastal Pattern is defined by factor 5, and illustrated in Figure 9. Table 6 presents the factor loadings for important characters

varying in a coastal manner. Such characters as ventral pigmentation in *Elaphe guttata*, dorsal blotch border in the same species, labial pigmentation in *Diadophis punctatus*, dorsal scale rows in *Sistrurus miliarius*, and body blotches in *Sistrurus* load highly on factor 5. In this pattern, populations from coastal regions and the Florida Keys (when they occur there) tend to form a phenetic entity distinct from populations farther inland.

Factor 6 represents the Okeechobee Pattern and is illustrated in Figure 8. This pattern of geographic variation is seen in the number of midbody scale rows in *Lampropeltis triangulum*, number of supralabial scales in Florida *tantilla*, and nuchal pigmentation in *Tantilla*. The Okeechobee Pattern is characterized by geographic variation in which the region around Lake Okeechobee, and especially the high ridge immediately to the west, is inhabited by snakes phenetically different from conspecifics to the north and to the south. Table 7 gives the factor loadings for important characters in factor 6.

The remaining factors produced by the statistical procedure account for smaller amounts of the information in the maps, and their interpretation is omitted.

The multivariate analysis of contour maps of geographic variation in Florida snakes has shown that the variation can be reduced to seven major patterns. There are other patterns, but these are of less importance, and are shared by fewer species. For example, *Thamnophis sauritus* ground color is distinctive in the Gulf Hammock region of central Florida. This character fell out of the analysis in factor 22, which also received significant loadings from *Crotalus adamanteus* ventral pigmentation and

*T. sauritus* parietal spot size. However, factor 22 accounted for only 1.2% of the variation explained in the analysis. Tables 8 through 11 present the factor loadings on factors 7 through 10 for the characters which showed correlations with these factors.

The major patterns of geographic variation in Florida snakes (North-South Pattern, Suwannee River Pattern, Everglades Pattern, North Florida-Lower Keys Pattern, Panhandle-Everglades Pattern, Coastal Pattern, and Okeechobee Pattern) account for 60.4% of the information contained in the original contour maps. The remaining information is partitioned into lesser patterns, and in some cases represents variation unique to a particular species or character.

#### The Correlations

In order to search for correlations between the patterns of geographic variation and environmental factors, I analyzed 17 parameters of environmental variation. When these variables were factor analyzed, three factors were extracted that accounted for 74.4% of the variation. These factors are clearly defined as 1) average temperature, 2) maximum summer temperatures, and 3) average rainfall. When the factor analysis of the snake morphological data was carried out, representative variables from the climatic data matrix were included.

Average annual temperature loads vary highly on factor 1 (Table 1). Inspection of Map 235 reveals that average annual temperature belongs in the North-South Pattern. Thus the North-South Pattern of geographic variation is highly correlated with mean annual temperature. Similarly, The Panhandle-Everglades Pattern is correlated with mean annual rainfall,

and the Coastal Pattern is correlated with maximum summer temperatures (Table 1).

Although correlation does not prove cause and effect, its existence does suggest the possibility of just such a relationship. Until experimental falsification is at hand, I would hypothesize that the influence of mean annual temperature on morphological variation in Florida snakes is a great one. Using the same line of reasoning, very high summer maximum temperatures may be responsible for the Coastal Pattern of geographic variation, and mean annual rainfall may influence snake morphology to vary in the Panhandle-Everglades Pattern.

The remaining patterns of variation are not highly correlated with any environmental variables tested. These patterns may be maintained by some other environmental variables (biotic or physical) that were not examined, or they may be remnants of previous environmental conditions. If the latter were the case, then we would have to believe that present selective regimes have been insufficient to direct changes in phenotypes towards adaptation to present conditions. For example, the Suwannee River Pattern does not seem to correlate with any of the environmental variables tested. Snakes showing this pattern of geographic variation may be a result of past adaptations to an insular environment during Pleistocene high sea levels. The Florida peninsula is no longer an island, but selection has not been strong enough to eliminate (or "spread out") the abrupt character changes in the region of the former "Suwannee Straits." Furthermore, adaptations acquired during periods of former isolation may have been accompanied by reduced reproductive compatibility with mainland populations. This process (speciation) would

tend to preserve character states in both populations even after they became geographically rejoined. Such a pattern would not necessarily be expected to correlate with any present environmental parameter, and would have to be interpreted as a remnant of some past selective influence.

Table 1. Variables used in the factor analysis, their communalities, and the principal pattern to which each belongs. Note that most of the variables belong to several patterns, but only the principal pattern is included here.

| Variable                  | Communality | Principal Pattern    |
|---------------------------|-------------|----------------------|
| <i>Storeria</i> .ScIsmid  | .95369      | Suwannee River       |
| <i>Storeria</i> .Ventrum  | .68403      | Suwannee River       |
| <i>Storeria</i> .Temppig  | .58571      | Factor 20            |
| <i>Storeria</i> .Tempornt | .80744      | Suwannee River       |
| <i>Storeria</i> .Subocspt | .83800      | Suwannee River       |
| <i>Storeria</i> .Ventcaud | .82341      | North-South          |
| <i>Storeria</i> .Preocs   | .54303      | Keys                 |
| <i>Storeria</i> .Postocs  | .71416      | Factor 13            |
| <i>Storeria</i> .Blklabs  | .73975      | Factor 18            |
| <i>Sirtalis</i> .Parietal | .62678      | Factor 9             |
| <i>Sirtalis</i> .Dorspot  | .73091      | Factor 9             |
| <i>Sirtalis</i> .Ventcaud | .54009      | North-South          |
| <i>Sirtalis</i> .Suplabs  | .95685      | Factor 13            |
| <i>Sauritus</i> .Parsize  | .57189      | Factor 22            |
| <i>Sauritus</i> .Dorbrn   | .48245      | None                 |
| <i>Sauritus</i> .Stripe   | .66962      | Factor 19            |
| <i>Sauritus</i> .Ventcaud | .63856      | Factor 22            |
| <i>Sauritus</i> .Suplabs  | .91204      | Suwannee River       |
| <i>Coluber</i> .Ventrum   | .76578      | Everglades, Keys     |
| <i>Coluber</i> .Gulbrn    | .46922      | None                 |
| <i>Coluber</i> .Gulblk    | .80162      | Keys                 |
| <i>Coluber</i> .Slbrn     | .79836      | None                 |
| <i>Coluber</i> .Slblk     | .84235      | Keys                 |
| <i>Coluber</i> .Slloreal  | .42071      | Factor 19            |
| <i>Coluber</i> .Vencaud   | .78969      | North-South          |
| <i>Masticop</i> .Phase    | .75184      | Suwannee River       |
| <i>Masticop</i> .Ventcaud | .77890      | Factor 15            |
| <i>Masticop</i> .Inflabs  | .69603      | Panhandle-Everglades |

Table 1 - Continued.

| Variable                  | Communality | Principal Pattern          |
|---------------------------|-------------|----------------------------|
| <i>Ophiodry</i> .Slpig    | .51104      | Factor 7                   |
| <i>Ophiodry</i> .Keels2nd | .76185      | North-South, Factor 7      |
| <i>Ophiodry</i> .Ventcaud | .75063      | None                       |
| <i>Ophiodry</i> .Inflabs  | .54415      | Factor 24                  |
| <i>Guttata</i> .Bodyspts  | .62129      | North-South                |
| <i>Guttata</i> .Tailspts  | .58125      | North-South                |
| <i>Guttata</i> .Sc1smid   | .40211      | Factor 16                  |
| <i>Guttata</i> .Ventrum   | .54088      | Coastal                    |
| <i>Guttata</i> .Spotbord  | .62571      | Everglades                 |
| <i>Guttata</i> .Checks    | .39840      | Coastal                    |
| <i>Guttata</i> .Ventcaud  | .59094      | North-South                |
| <i>Obsoleta</i> .Blotches | .73191      | North-South                |
| <i>Obsoleta</i> .Stripe   | .70248      | Suwannee River             |
| <i>Obsoleta</i> .Spot     | .81187      | Suwannee River             |
| <i>Obsoleta</i> .Ventrum  | .87962      | Suwannee River             |
| <i>Obsoleta</i> .Labpig   | .84859      | Suwannee River             |
| <i>Getulus</i> .Blotches  | .92423      | North-South                |
| <i>Getulus</i> .Sc1smid   | .86965      | Suwannee River             |
| <i>Getulus</i> .Pattern   | .70095      | North-South, Everglades    |
| <i>Getulus</i> .Vencaud   | .66946      | North-South                |
| <i>Getulus</i> .Inflabs   | .68396      | Factor 10                  |
| <i>Triangul</i> .Sc1smid  | .58845      | Okeechobee                 |
| <i>Triangul</i> .Bodybnds | .74186      | Factor 7                   |
| <i>Triangul</i> .Tailbnds | .74450      | Factor 7                   |
| <i>Triangul</i> .Ventcaud | .77099      | North-South                |
| <i>Triangul</i> .Inflabs  | .76916      | Panhandle-Everglades       |
| <i>Triangul</i> .Loreals  | .65063      | Factor 11                  |
| <i>Cemophor</i> .Sc1sant  | .65221      | Factor 20                  |
| <i>Cemophor</i> .Sc1spost | .86221      | Suwannee River, Everglades |
| <i>Cemophor</i> .Bodybnds | .88621      | Everglades                 |
| <i>Cemophor</i> .Tailbnds | .77072      | Factor 11                  |
| <i>Cemophor</i> .5thred   | .77706      | Everglades                 |

Table 1 - Continued.

| Variable                   | Communality | Principal Patterns                   |
|----------------------------|-------------|--------------------------------------|
| <i>Cemophor</i> .5thwht    | .86478      | Suwannee River                       |
| <i>Cemophor</i> .Suplabs   | .92083      | Suwannee River                       |
| <i>Cemophor</i> .Inflabs   | .86708      | Everglades                           |
| <i>Cemophor</i> .Ventcaud  | .85531      | North-South, Everglades              |
| <i>Diadophi</i> .Ventrum   | .68257      | Factor 8                             |
| <i>Diadophi</i> .Spotshap  | .58628      | Factor 8                             |
| <i>Diadophi</i> .Ringsep   | .51227      | Suwannee River, Panhandle-Everglades |
| <i>Diadophi</i> .Ringwdth  | .52656      | Suwannee River                       |
| <i>Diadophi</i> .Labpig    | .59992      | Coastal                              |
| <i>Diadophi</i> .Clrvnts   | .55130      | Factor 8                             |
| <i>Diadophi</i> .Ventcaud  | .57328      | North-South                          |
| <i>Diadophi</i> .Suplabs   | .30275      | Suwannee River                       |
| <i>Diadophi</i> .Labspts   | .64861      | North-South, Suwannee River          |
| <i>Tantilla</i> .Ilfour    | .65249      | Factor 23                            |
| <i>Tantilla</i> .Parietal  | .77002      | North-South                          |
| <i>Tantilla</i> .Snout     | .65309      | Factor 7                             |
| <i>Tantilla</i> .Nuchal    | .71403      | Okeechobee                           |
| <i>Tantilla</i> .Ventcaud  | .80101      | North-South                          |
| <i>Tantilla</i> .Suplabs   | .77949      | Okeechobee                           |
| <i>Sistruru</i> .Bodyspts  | .53895      | Factor 19                            |
| <i>Sistruru</i> .Tailbnds  | .44302      | Factor 19                            |
| <i>Sistruru</i> .ScIsant   | .71182      | North-South                          |
| <i>Sistruru</i> .ScIsmid   | .46439      | Factor 18                            |
| <i>Sistruru</i> .Contrast  | .40396      | Factor 21                            |
| <i>Sistruru</i> .Ventrum   | .46360      | Panhandle, Everglades                |
| <i>Sistruru</i> .Ventcaud. | .75488      | North-South                          |
| <i>Sistruru</i> .Suplabs   | .50758      | Factor 17                            |
| <i>Sistruru</i> .Inflabs   | .49931      | Factor 17                            |
| <i>Sistruru</i> .Sptshape  | .56716      | North-South, Panhandle-Everglades    |
| <i>Sistruru</i> .Sptspace  | .52296      | North-South                          |
| <i>Crotalus</i> .Diamonds  | .55132      | Factor 14                            |

Table 1 - Continued.

| Variable                  | Communality | Principal Patterns               |
|---------------------------|-------------|----------------------------------|
| <i>Crotalus</i> .Blkcauds | .41927      | None                             |
| <i>Crotalus</i> .Ventrum  | .51970      | Factor 22                        |
| <i>Crotalus</i> .Clrlabs  | .44236      | Everglades, Panhandle-Everglades |
| <i>Crotalus</i> .Ventcaud | .48915      | Factor 23                        |
| <i>Crotalus</i> .Suplabs  | .70976      | Factor 12                        |
| <i>Crotalus</i> .Inflabs  | .61233      | Factor 12                        |
| Florida.Anntemp           | .76211      | North-South                      |
| Florida.Annrain           | .59495      | Panhandle-Everglades             |
| Florida.over 90           | .67363      | Coastal                          |

Table 2. North-South pattern and Suwannee River pattern (Factor 1). Variables followed by an asterisk (\*) have factor 1 as their principal pattern.

| Variable                   | Factor Loading |
|----------------------------|----------------|
| <i>Storeria</i> .Sc1smid*  | - 0.88912      |
| <i>Storeria</i> .Ventrum*  | 0.58711        |
| <i>Storeria</i> .Tempig    | 0.03903        |
| <i>Storeria</i> .Tempornt* | 0.73400        |
| <i>Storeria</i> .Supocspt* | 0.59878        |
| <i>Storeria</i> .Ventcaud* | 0.68715        |
| <i>Storeria</i> .Preocs    | - 0.09941      |
| <i>Storeria</i> .Postocs   | - 0.02662      |
| <i>Storeria</i> .Blklabs   | 0.15218        |
| <i>Sirtalis</i> .Parietal  | - 0.17929      |
| <i>Sirtalis</i> .Dorspt    | - 0.02442      |
| <i>Sirtalis</i> .Ventcaud* | 0.50298        |
| <i>Sirtalis</i> .Suplabs   | 0.23957        |
| <i>Sauritus</i> .Parsize   | 0.02563        |
| <i>Sauritus</i> .Dorbrn    | - 0.24255      |
| <i>Sauritus</i> .Stripe    | 0.03231        |
| <i>Sauritus</i> .Ventcaud  | 0.30364        |
| <i>Sauritus</i> .Suplabs*  | 0.77160        |
| <i>Coluber</i> .Ventrum    | 0.29000        |
| <i>Coluber</i> .Gulbrn     | - 0.36889      |
| <i>Coluber</i> .Gulblk     | 0.01574        |
| <i>Coluber</i> .Slbrn      | - 0.34031      |
| <i>Coluber</i> .Slblk      | - 0.03129      |
| <i>Coluber</i> .Slloreal   | 0.13485        |
| <i>Coluber</i> .Ventcaud*  | 0.73851        |
| <i>Masticop</i> .Phase*    | 0.39039        |
| <i>Masticop</i> .Ventcaud  | - 0.31311      |
| <i>Masticop</i> .Inflabs   | 0.01632        |
| <i>Opheodry</i> .Slpig     | - 0.26689      |
| <i>Opheodry</i> .Keels2nd* | 0.48867        |

Table 2 - Continued

| Variable                   | Factor Loading |
|----------------------------|----------------|
| <i>Ophiodry</i> .Ventcaud  | - 0.31820      |
| <i>Ophiodry</i> .Inflabs   | 0.08321        |
| <i>Guttata</i> .Bodyspts*  | 0.51736        |
| <i>Guttata</i> .Tailspts*  | 0.38104        |
| <i>Guttata</i> .ScIsmid    | 0.06079        |
| <i>Guttata</i> .Ventrum    | - 0.35622      |
| <i>Guttata</i> .Spotbord   | - 0.03501      |
| <i>Guttata</i> .Checks     | - 0.01880      |
| <i>Guttata</i> .Ventcaud*  | 0.45058        |
| <i>Obsoleta</i> .Blotches* | 0.70040        |
| <i>Obsoleta</i> .Stripe*   | 0.68599        |
| <i>Obsoleta</i> .Spot*     | - 0.81544      |
| <i>Obsoleta</i> .Ventrum*  | - 0.84751      |
| <i>Obsoleta</i> .Labpig*   | - 0.84396      |
| <i>Getulus</i> .Blotches*  | 0.77272        |
| <i>Getulus</i> .ScIsmid*   | 0.78203        |
| <i>Getulus</i> .Pattern*   | 0.38190        |
| <i>Getulus</i> .Ventcaud*  | 0.47711        |
| <i>Getulus</i> .Inflabs    | - 0.00146      |
| <i>Triangul</i> .ScIsmid   | - 0.30452      |
| <i>Triangul</i> .Bodybnds  | - 0.23409      |
| <i>Triangul</i> .Tailbuds  | - 0.28188      |
| <i>Triangul</i> .Ventcaud* | - 0.43181      |
| <i>Triangul</i> .Inflabs   | 0.29109        |
| <i>Triangul</i> .Loreals   | - 0.14573      |
| <i>Cemophor</i> .ScIsant   | - 0.16574      |
| <i>Cemophor</i> .ScIspost* | - 0.45041      |
| <i>Cemophor</i> .Bodybnds  | - 0.08845      |
| <i>Cemophor</i> .Tailbnds  | - 0.31636      |
| <i>Cemophor</i> .5thred    | - 0.25570      |
| <i>Cemophor</i> .5thwht*   | 0.49114        |
| <i>Cemophor</i> .Suplabs*  | 0.72762        |
| <i>Cemophor</i> .Inflabs   | 0.05655        |

Table 2 - Continued

| Variable                   | Factor Loading |
|----------------------------|----------------|
| <i>Cemophor</i> .Ventcaud* | 0.53298        |
| <i>Diadophi</i> .Ventrum   | 0.00094        |
| <i>Diadophi</i> .Sptshape  | - 0.20558      |
| <i>Diadophi</i> .Ringsep*  | 0.30422        |
| <i>Diadophi</i> .Ringwdth* | - 0.53219      |
| <i>Diadophi</i> .Labpig    | - 0.15822      |
| <i>Diadophi</i> .Clrvnts   | - 0.05158      |
| <i>Diadophi</i> .Ventcaud* | - 0.58642      |
| <i>Diadophi</i> .Suplabs*  | 0.31443        |
| <i>Diadophi</i> .Labspts*  | 0.41560        |
| <i>Tantilla</i> .Ilfour    | - 0.17786      |
| <i>Tantilla</i> .Parietal* | - 0.40090      |
| <i>Tantilla</i> .Snout     | 0.35250        |
| <i>Tantilla</i> .Nuchal    | - 0.20308      |
| <i>Tantilla</i> .Ventcaud* | - 0.55866      |
| <i>Tantilla</i> .Suplabs   | - 0.03635      |
| <i>Sistruru</i> .Bodyspts  | - 0.07901      |
| <i>Sistruru</i> .Tailbnds  | - 0.15767      |
| <i>Sistruru</i> .ScIsant*  | 0.48877        |
| <i>Sistruru</i> .ScIsmid   | 0.28273        |
| <i>Sistruru</i> .Contrast  | - 0.30038      |
| <i>Sistruru</i> .Ventrum   | - 0.01047      |
| <i>Sistruru</i> .Ventcaud* | 0.58554        |
| <i>Sistruru</i> .Suplabs   | 0.16292        |
| <i>Sistruru</i> .Inflabs   | 0.15802        |
| <i>Sistruru</i> .Sptshape* | 0.42178        |
| <i>Sistruru</i> .Sptspace* | 0.41702        |
| <i>Crotalus</i> .Diamonds  | 0.14065        |
| <i>Crotalus</i> .Blkcauds  | - 0.18888      |
| <i>Crotalus</i> .Ventrum   | - 0.05286      |
| <i>Crotalus</i> .Clrlabs   | 0.17053        |

Table 2 - Continued

| Variable                 | Factor Loading |
|--------------------------|----------------|
| <i>Crotalus.Ventcaud</i> | 0.14411        |
| <i>Crotalus.Suplabs</i>  | 0.10392        |
| <i>Crotalus.Inflabs</i>  | - 0.20077      |
| Florida.Anntemp*         | 0.82022        |
| Florida.Annrain          | - 0.35357      |
| Florida.Over 90          | 0.23942        |

Table 3. Everglades pattern (Factor 2). Variables followed by an asterisk have factor 2 as their principal pattern.

| Variable                  | Factor Loading |
|---------------------------|----------------|
| <i>Coluber.Ventrum</i>    | - 0.42099      |
| <i>Guttata.Spotbord</i>   | - 0.45133      |
| <i>Guttata.Ventcaud</i>   | - 0.29934      |
| <i>Getulus.Pattern</i>    | - 0.28488      |
| <i>Cemophor.Sc1spost</i>  | 0.37496        |
| <i>Cemophor.Bodybnds*</i> | 0.74285        |
| <i>Cemophor.5thred*</i>   | - 0.56371      |
| <i>Cemophor.Inflabs*</i>  | 0.84919        |
| <i>Cemophor.Ventcaud</i>  | 0.45206        |
| <i>Crotalus.Clrlabs*</i>  | 0.36125        |

Table 4. Keys pattern (Factor 3). Variables followed by an asterisk have factor 3 as their principal pattern.

| Variable                 | Factor Loading |
|--------------------------|----------------|
| <i>Storeria.Ventcaud</i> | - 0.23989      |
| <i>Storeria.Preocs*</i>  | 0.40677        |
| <i>Storeria.Bklabs</i>   | 0.23295        |
| <i>Coluber.Ventrum</i>   | 0.45636        |
| <i>Coluber.Gulblk*</i>   | 0.85700        |
| <i>Coluber.Slblk*</i>    | 0.88389        |
| <i>Coluber.Slbrn</i>     | - 0.32688      |
| <i>Coluber.Slloreal</i>  | 0.28467        |
| <i>Opheodry.Ventcaud</i> | - 0.27052      |

Table 5. Panhandle-Everglades pattern (Factor 4).  
 Variables followed by an asterisk (\*) have  
 factor 4 as their principal pattern.

| Variable                  | Factor Loading |
|---------------------------|----------------|
| <i>Masticop</i> .Phase    | - 0.31427      |
| <i>Masticop</i> .Inflabs* | 0.72896        |
| <i>Opheodry</i> .Ventcaud | - 0.28898      |
| <i>Opheodry</i> .Keels2nd | - 0.24849      |
| <i>Guttata</i> .Bodyspts  | - 0.27224      |
| <i>Triangul</i> .Inflabs* | - 0.46470      |
| <i>Triangul</i> .Ventcaud | 0.27908        |
| <i>Diadophi</i> .Ringsep  | 0.30168        |
| <i>Tantilla</i> .Suplabs  | 0.28222        |
| <i>Sistruru</i> .Ventrum* | - 0.44881      |
| <i>Sistruru</i> .Sptshape | 0.31826        |
| <i>Crotalus</i> .Blkcauds | 0.26556        |
| <i>Crotalus</i> .Clrlabs  | 0.30508        |
| Florida.Annrain*          | - 0.37981      |

Table 6. Coastal pattern (Factor 5). Variables followed by an asterisk (\*) have factor 5 as their principal pattern.

| Variable                  | Factor Loading |
|---------------------------|----------------|
| <i>Masticop</i> .Phase    | 0.28903        |
| <i>Guttata</i> .Ventrums* | - 0.46907      |
| <i>Guttata</i> .Spotbord  | - 0.34480      |
| <i>Guttata</i> .Checks*   | - 0.61322      |
| <i>Diadophi</i> .Labpig*  | - 0.44062      |
| <i>Sistruru</i> .Bodyspts | 0.25744        |
| <i>Sistruru</i> .ScIsant  | 0.34333        |
| Florida.over 90*          | - 0.40011      |
| <i>Sistruru</i> .ScIsmid  | 0.22124        |
| <i>Triangul</i> .ScIsmid  | - 0.23046      |
| <i>Crotalus</i> .Clrlabs  | - 0.24009      |

Table 7. Okeechobee pattern (Factor 6). Variables followed by an asterisk (\*) have factor 6 as their principal pattern.

| Variable                  | Factor Loading |
|---------------------------|----------------|
| <i>Storeria</i> .Tempig   | 0.28584        |
| <i>Sauritus</i> .Stripe   | 0.25478        |
| <i>Opheodrys</i> .Inflabs | 0.23024        |
| <i>Guttata</i> .Ventrum   | - 0.23154      |
| <i>Getulus</i> .Ventcaud  | 0.25687        |
| <i>Trairgul</i> .ScIsmid* | 0.41243        |
| <i>Tantilla</i> .Nuchal*  | 0.71364        |
| <i>Tantilla</i> .Ventcaud | 0.41977        |
| <i>Tantilla</i> .Suplabs* | 0.65938        |
| <i>Tantilla</i> .Ilfour   | 0.23273        |

Table 8. Factor 7. Variables followed by an asterisk (\*) have factor 7 as their principal pattern.

| Variable                   | Factor Loading |
|----------------------------|----------------|
| <i>Sauritus</i> .Parsize   | 0.24072        |
| <i>Sauritus</i> .Ventcaud  | 0.33728        |
| <i>Coluber</i> .Ventrum    | 0.25387        |
| <i>Coluber</i> .Slloreal   | - 0.23442      |
| <i>Masticop</i> .Phase     | 0.28746        |
| <i>Opheodry</i> .Slpig*    | - 0.43284      |
| <i>Opheodry</i> .Keels2nd  | 0.44881        |
| <i>Guttata</i> .Ventcaud   | 0.27252        |
| <i>Getulus</i> .Blotches   | 0.36369        |
| <i>Getulus</i> .Pattern    | 0.34378        |
| <i>Triangul</i> .Bodybnds* | - 0.71653      |
| <i>Triangul</i> .Tailbnds* | - 0.61504      |
| <i>Cemophor</i> .Bodyspts  | - 0.22212      |
| <i>Cemophor</i> .Suplabs   | 0.26222        |
| <i>Tantilla</i> .Snout*    | 0.60343        |
| <i>Tantilla</i> .Ventcaud  | 0.29430        |
| <i>Sistruru</i> .ScIsant   | 0.33893        |
| <i>Sistruru</i> .ScIsmid   | 0.25518        |
| <i>Sistruru</i> .Spotspac  | 0.29105        |
| <i>Crotalus</i> .Blkcauds  | - 0.24405      |
| Florida.Anntemp            | 0.32135        |

Table 9. Factor 8. Variables followed by an asterisk (\*) have factor 8 as their principal pattern.

| Variable                   | Factor Loading |
|----------------------------|----------------|
| <i>Storeria</i> .Blklabs   | - 0.32766      |
| <i>Diadophi</i> .Ventrum*  | 0.77950        |
| <i>Diadophi</i> .Sptshape* | 0.67326        |
| <i>Diadophi</i> .Clrvents* | - 0.63635      |

Table 10. Factor 9. Variables followed by an asterisk (\*) have factor 9 as their principal pattern.

| Variables                  | Factor Loading |
|----------------------------|----------------|
| <i>Cemophor</i> .5thred    | 0.32272        |
| <i>Diadophi</i> .Ringsep   | - 0.27036      |
| <i>Diadophi</i> .Labspts   | - 0.28795      |
| <i>Storeria</i> .Postovd   | 0.28601        |
| <i>Sirtalis</i> .Parietal* | 0.71245        |
| <i>Sirtalis</i> .Dorspot*  | 0.79233        |
| <i>Sirtalis</i> .Ventcaud  | - 0.29031      |
| <i>Sauritus</i> .Dorbrn    | - 0.27573      |
| <i>Sauritus</i> .Stripe    | 0.24338        |
| <i>Opheodry</i> .Ventcaud* | 0.33016        |

Table 11. Factor 10. Variable followed by an asterisk (\*) has factor 10 as its principal pattern.

| Variable                 | Factor Loading |
|--------------------------|----------------|
| <i>Storeria.Ventcaud</i> | - 0.27751      |
| <i>Guttata.Bodyspts</i>  | 0.24571        |
| <i>Guttata.Tailspts</i>  | 0.25619        |
| <i>Getulus.Inflabs*</i>  | 0.74571        |
| <i>Triangul.Sclsmid</i>  | 0.28497        |
| <i>Triangul.Inflabs</i>  | 0.53247        |



Figure 3. North-South Pattern (Factor 1, in part).



Figure 4. Suwannee River Pattern (Factor 1, in part).



Figure 5. Everglades Pattern (Factor 2).



Figure 6. Keys Pattern (Factor 3).



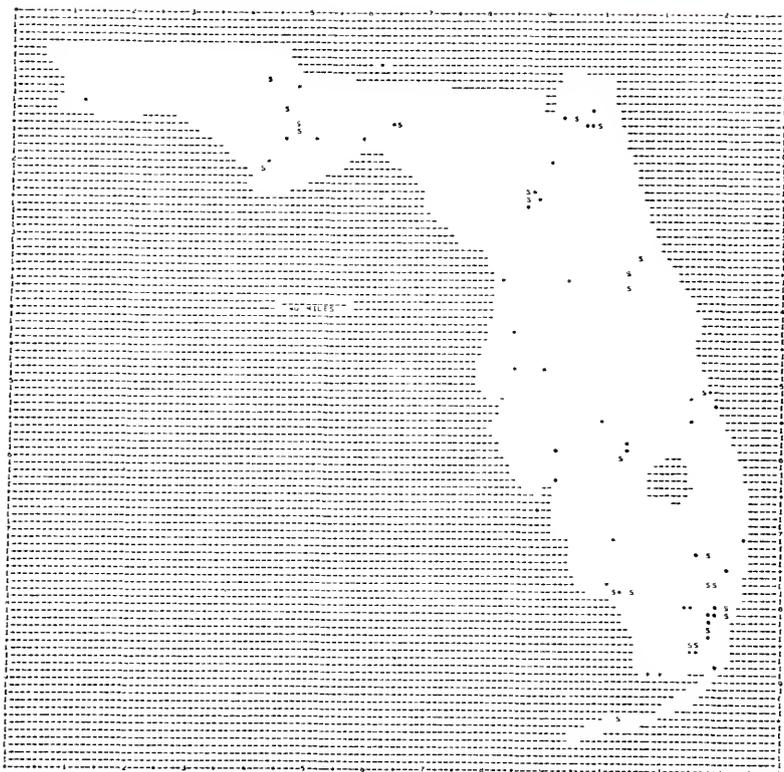
Figure 7. Panhandle-Everglades Pattern (Factor 4).



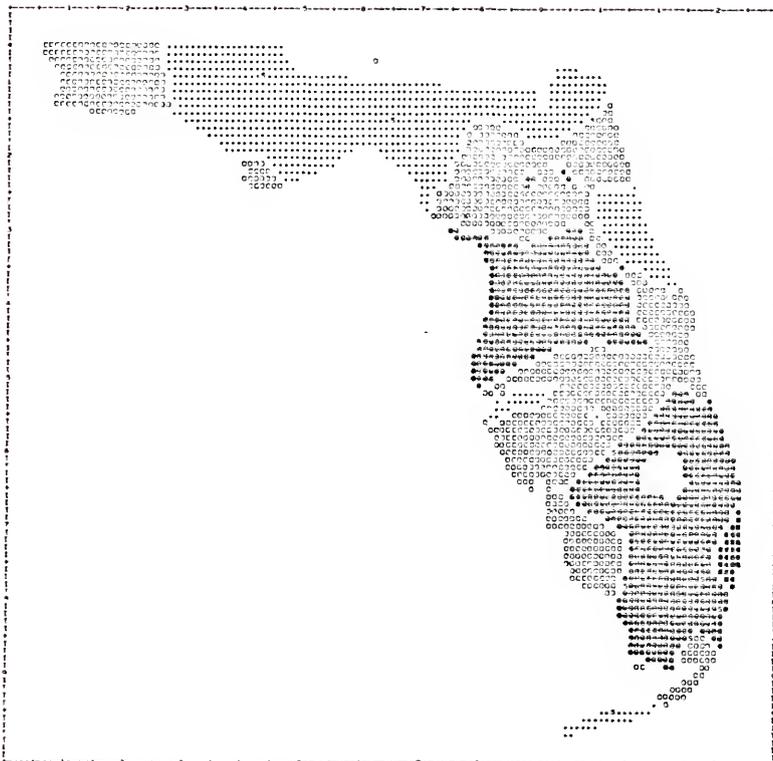
Figure 8. Okeechobee Pattern (Factor 5).



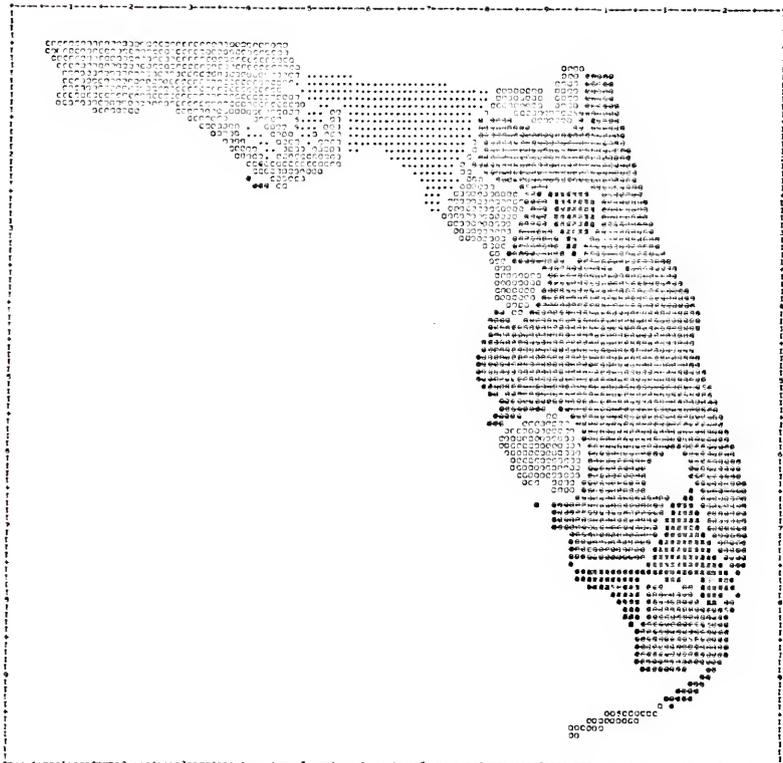
Figure 9. Coastal Pattern (Factor 6).



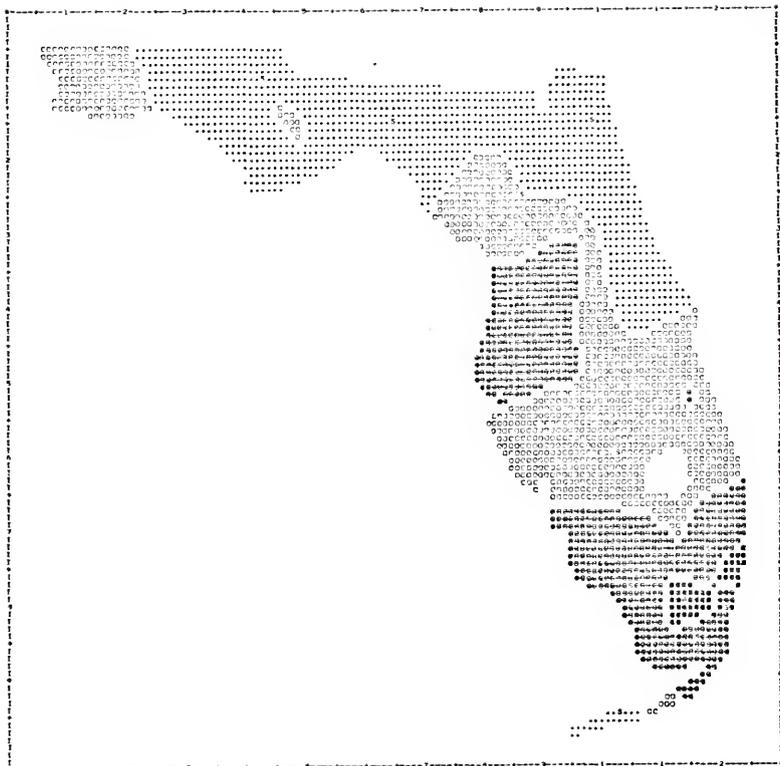
MAP 1. Localities of 151 *Storeria dekayi* specimens examined. An asterisk represents one specimen; an S represents more than one.



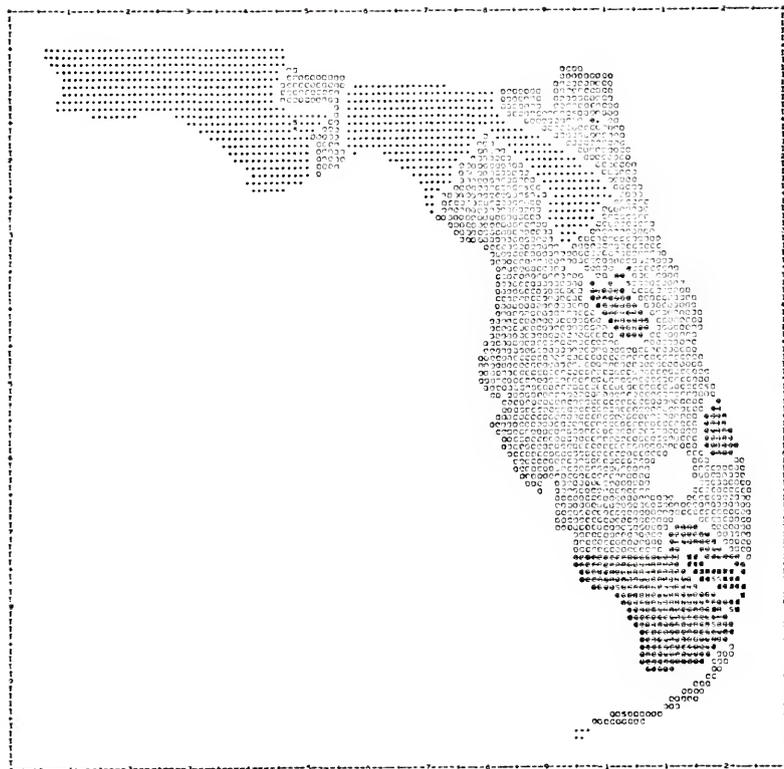
MAP 2. Geographic variation in number of ventral scales in *Storeria dekayi*, males only. Levels by increased shading are: 124-131, 132-138, 139-145, 146-153. Based on 69 specimens.



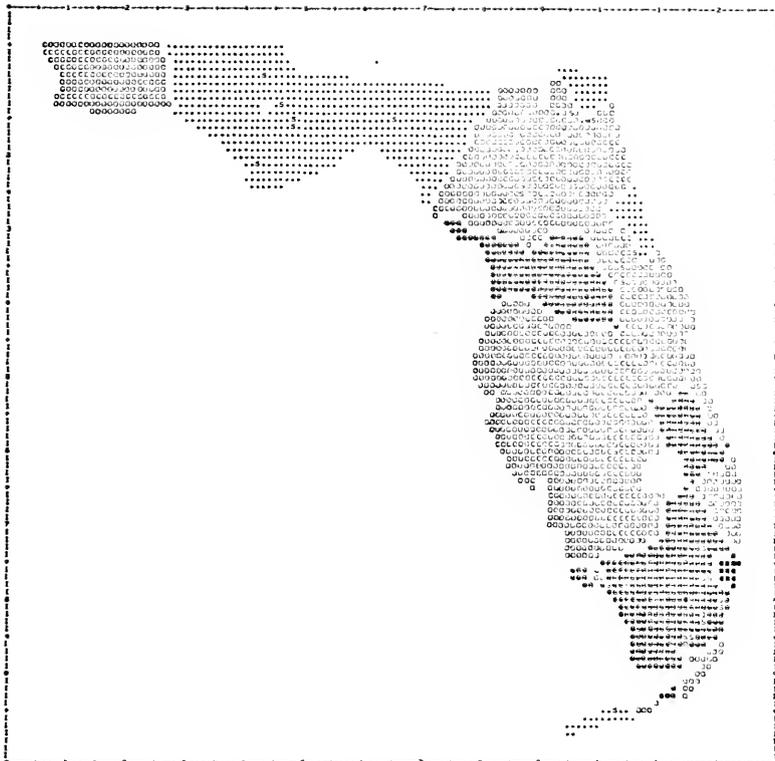
MAP 3. Geographic variation in number of ventral scales in *Storeria dekayi*, females only. Levels by increasing shading are: 126-131, 132-139, 139-145, 146-152. Based on 80 specimens.



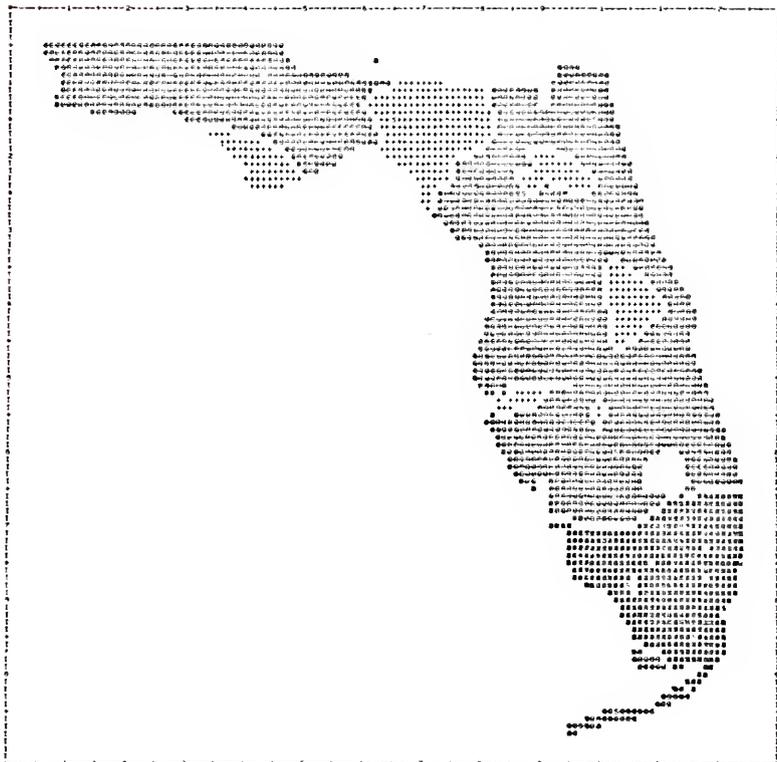
MAP 4. Geographic variation in number of subcaudal scales in *Storeria dekayi*, males only. Levels by increasing shading are: 56-63, 64-70, 71-77. Based on 63 specimens.



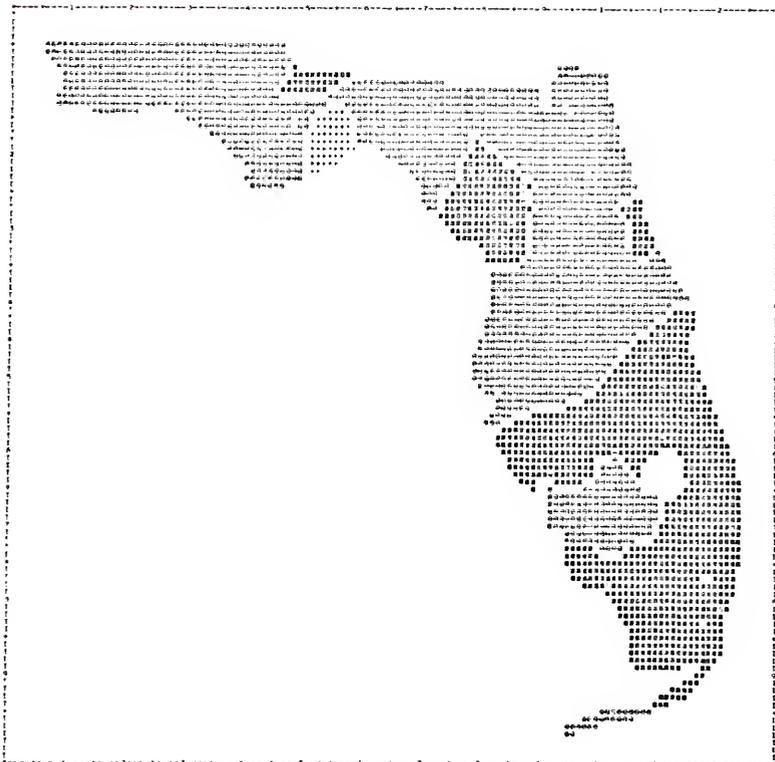
MAP 5. Geographic variation in number of subcaudal scales in *Storeria dekayi*, females only. Levels by increasing shading are: 43-49, 50-55, 56-61, 62-68. Based on 77 specimens.



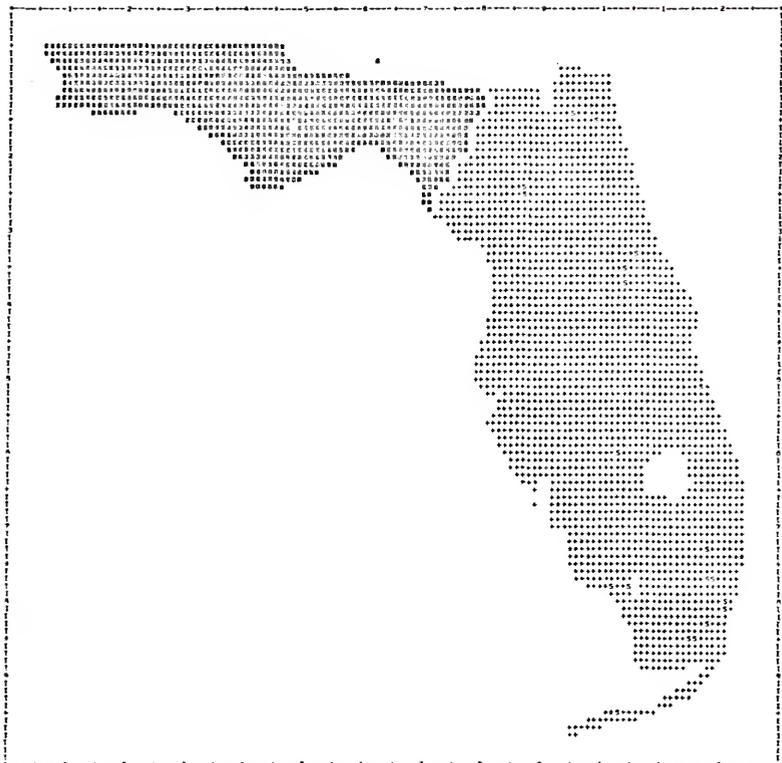
MAP 6. Geographic variation in the sum of ventrals plus caudals in *Storeria dekayi*, both sexes. Levels by increasing shading are: 169-186, 187-200, 201-215, 216-227. Based on 138 specimens.



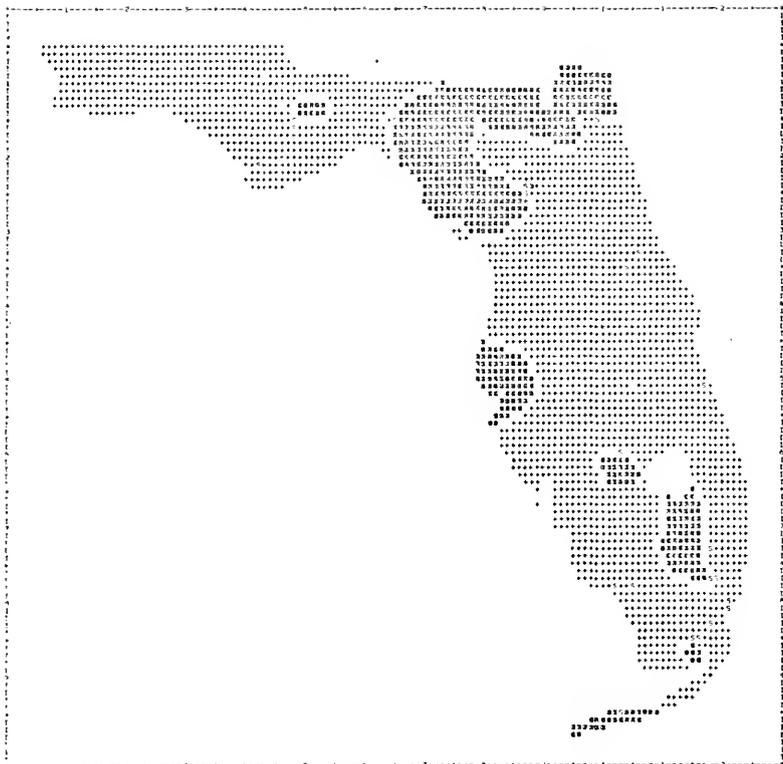
MAP 7. Geographic variation in tail length divided by total length in *Storeria dekayi*, males only. Darker shading represents proportionately longer tails. Based on 67 specimens.



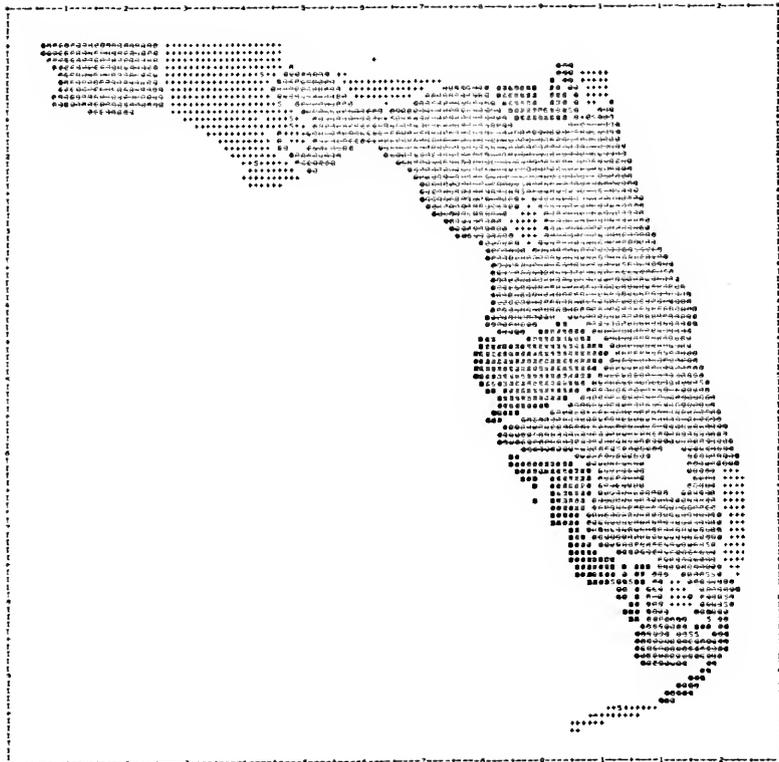
MAP 8. Geographic variation in tail length divided by total length in *Storeria dekayi*, females only. Darker shading represents proportionately longer tails. Based on 75 specimens.



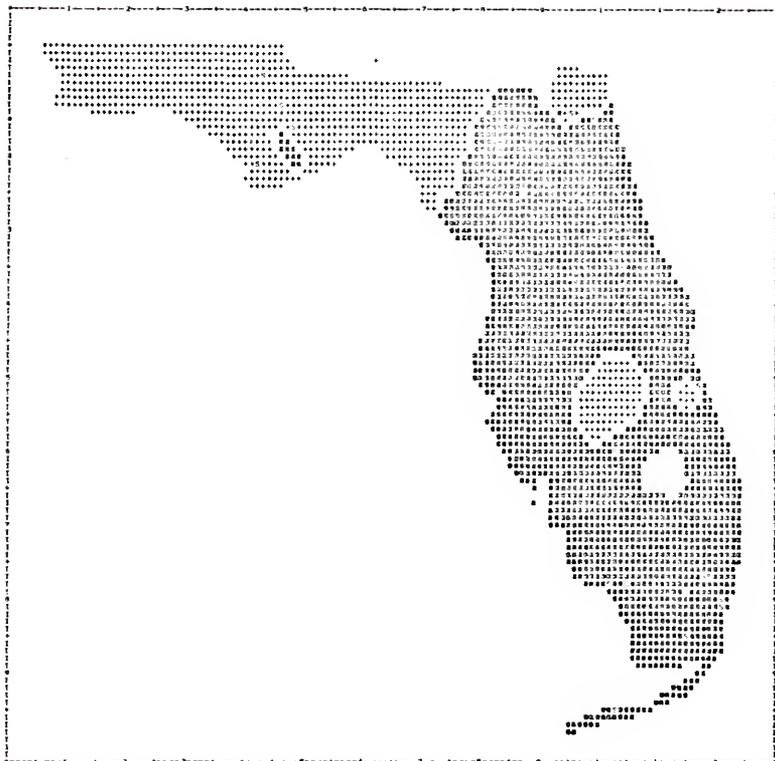
MAP 9. Geographic variation in number of dorsal scale rows at mid-body in *Storeria dekayi*, both sexes. Lighter shading represents 15 scale rows; darker shading represents 17. Based on 151 specimens.



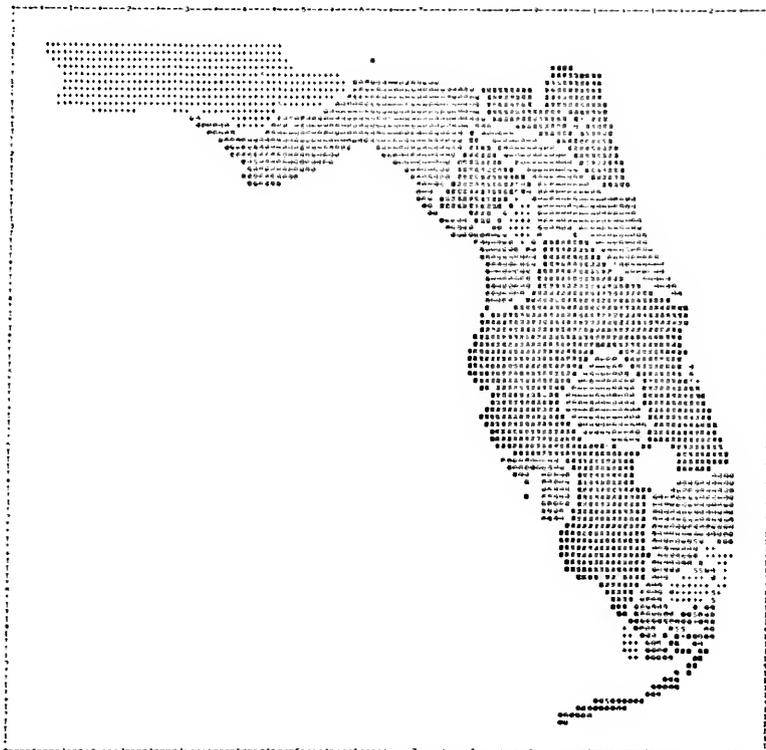
MAP 10. Geographic variation in number of preoculars (both sides) in *Storeria dekayi*, both sexes. Lighter shading represents 2 preocular scales; darker shading represents 3 or 4. Based on 149 specimens.



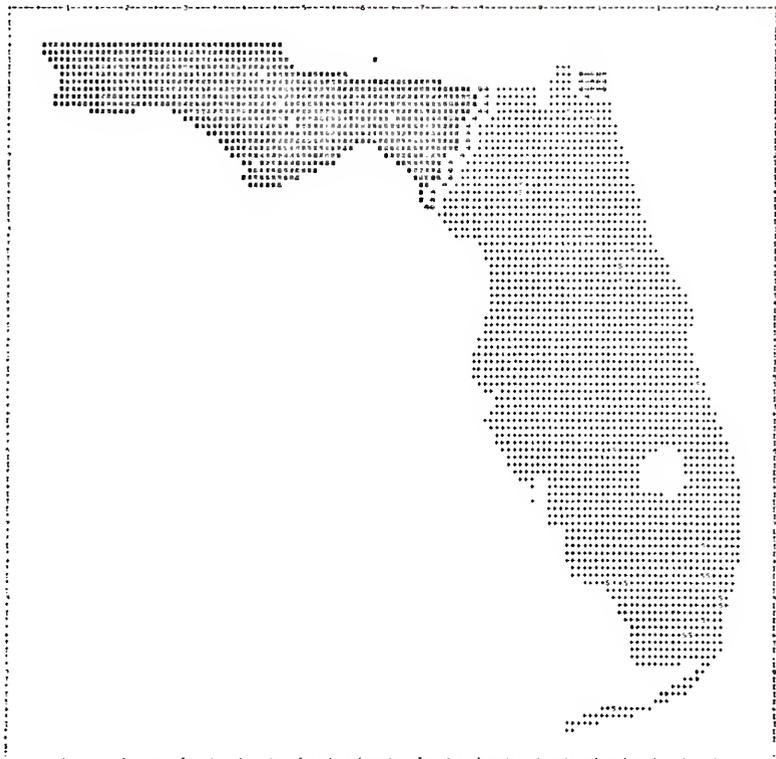
MAP 11. Geographic variation in extent and development of ventral dark pigment in *Storeria dekayi*, both sexes. Increased shading represents increased dark pigment on the ventral surface. Based on 149 specimens.



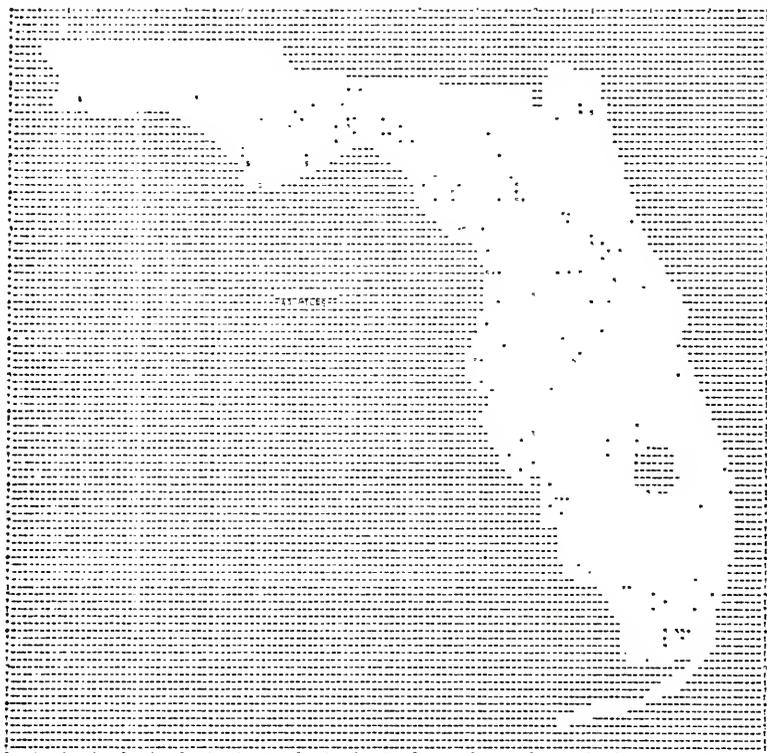
MAP 12. Geographic variation in the orientation of the dark temporal spot in *Storeria dekayi*, both sexes. Lighter shading represents a spot with the wider end directed posteriorly; darker shading represents spot with wider end directed anteriorly. Based on 99 specimens.



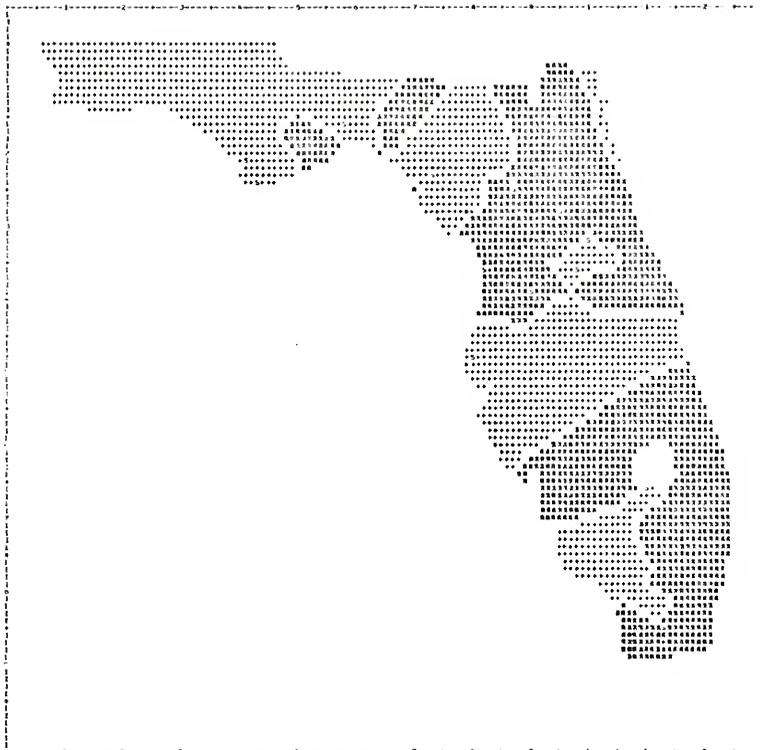
MAP 13. Geographic variation in the number of supralabials included in the subocular dark spot in *Storeria dekayi*, both sexes. Levels by increasing shading are: 0, 1-2, 3-5. Based on 148 specimens.



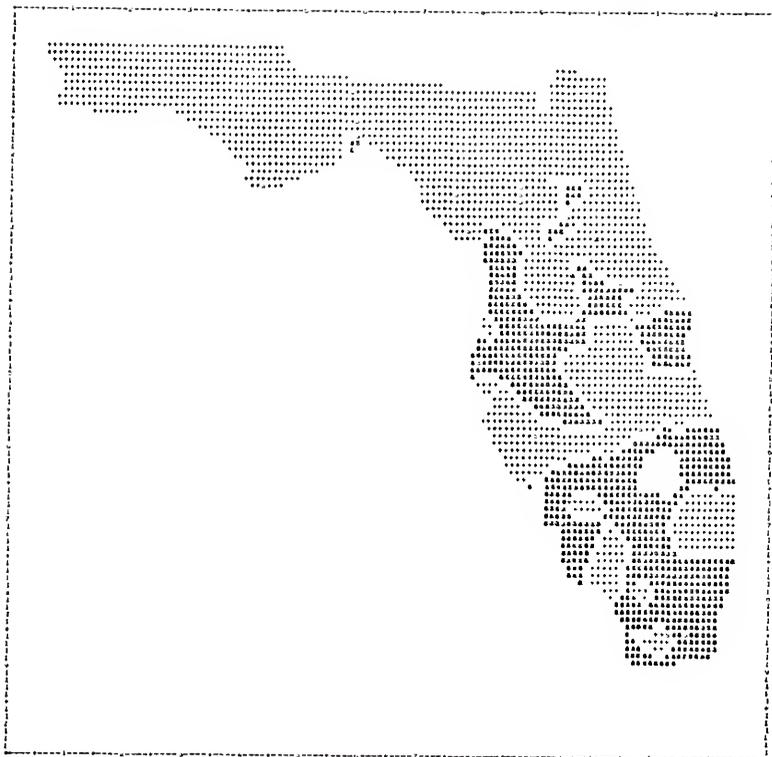
MAP 14. Geographic variation in Factor 1 for *Storeria dekayi* both sexes. Factor 1 accounts for most of the variation in the three dorsal scale row counts, the sum of ventrals plus caudals, temporal pigment orientation, extent of ventral pigment, and number of black supralabials. Darker shading represents generally higher values for the scale row counts and number of black supralabials, and lower values for the other three characters. Total variation accounted for by factor 1: 23.9% (18 characters). Based on 151 specimens.



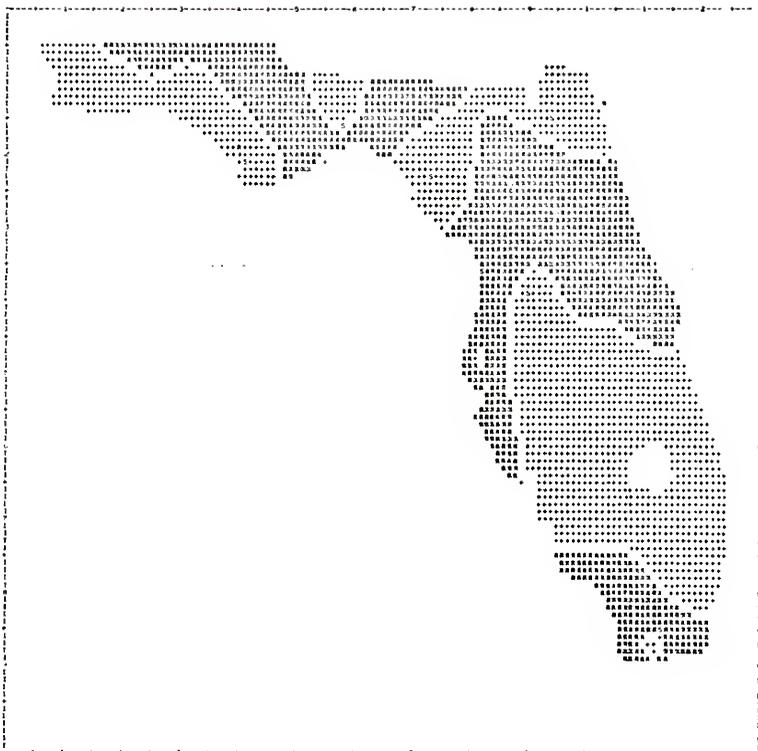
MAP 15. Localities of 192 Thamnophis sirtalis specimens examined. An asterisk represents one specimen; an S represents more than one.



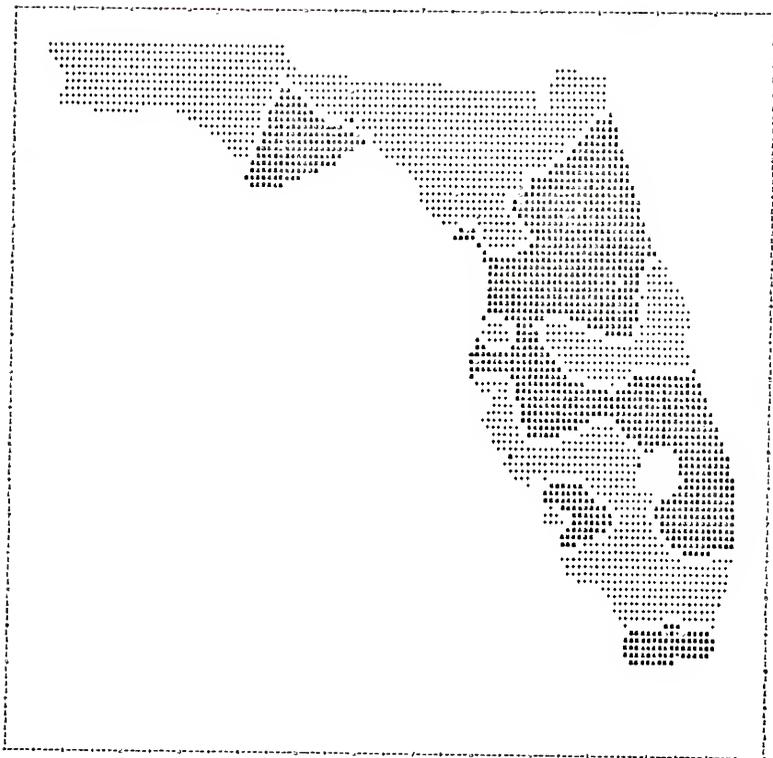
MAP 16. Geographic variation in number of ventral scales in Thamnophis sirtalis, males only. Lighter shading represents from 133 to 144 ventrals; darker shading represents from 145 to 172. Based on 74 specimens.



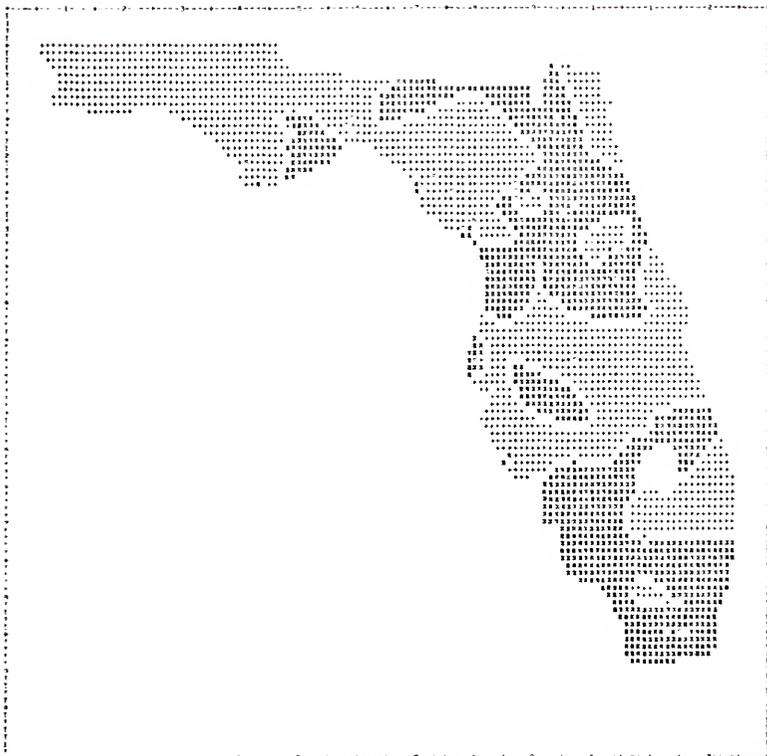
MAP 17. Geographic variation in number of ventral scales in Thamnophis sirtalis, females only. Lighter shading represents from 127 to 144; darker shading represents from 145 to 164. Based on 118 specimens.



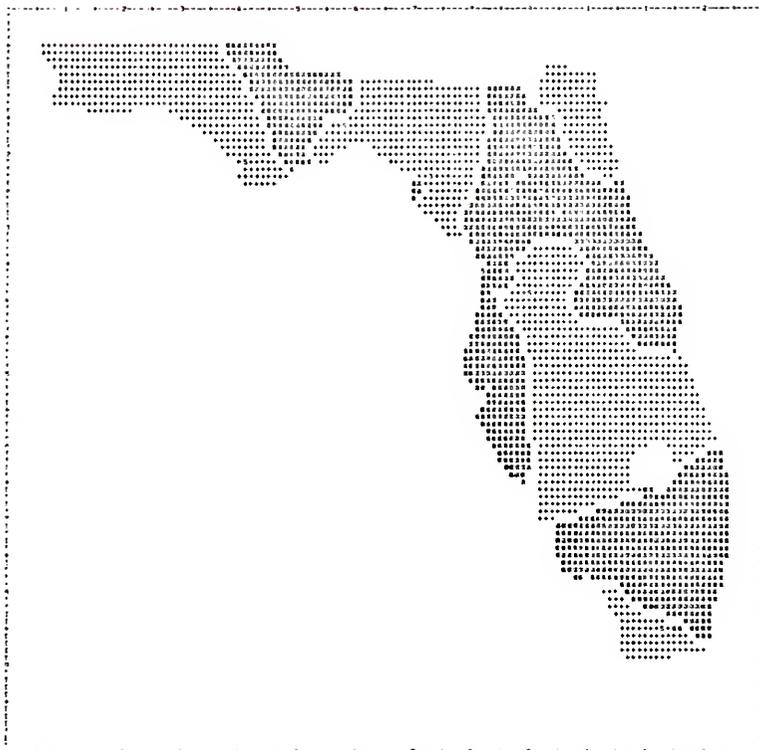
MAP 18. Geographic variation in number of subcaudal scales in *Thamnophis sirtalis*, males only. Lighter shading represents from 58 to 73 subcaudals; darker shading represents from 74 to 98. Based on 51 specimens.



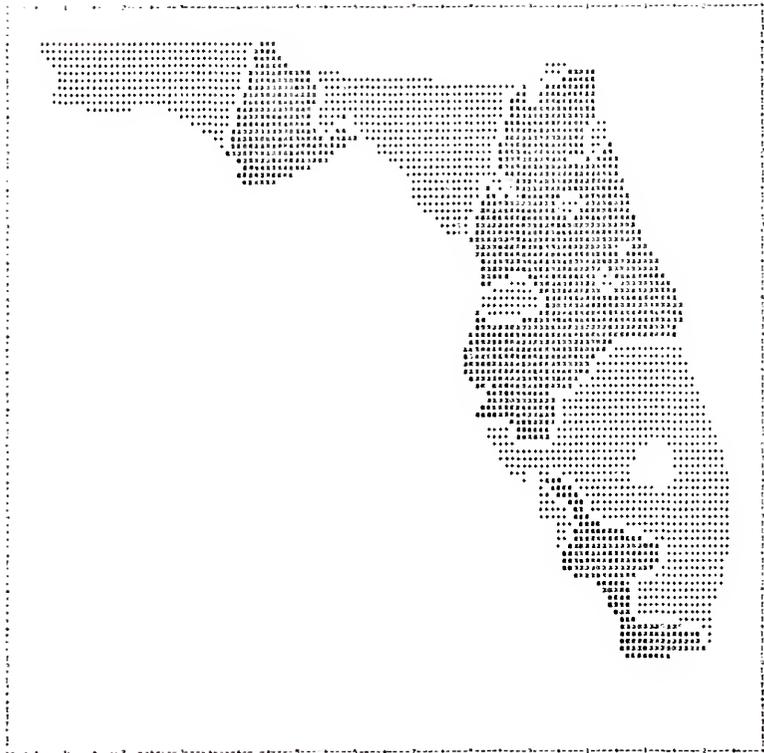
MAP 19. Geographic variation in number of subcaudal scales in Thamnophis sirtalis, females only. Lighter shading represents from 58 to 71 subcaudals; darker shading represents from 72 to 86. Based on 62 specimens.



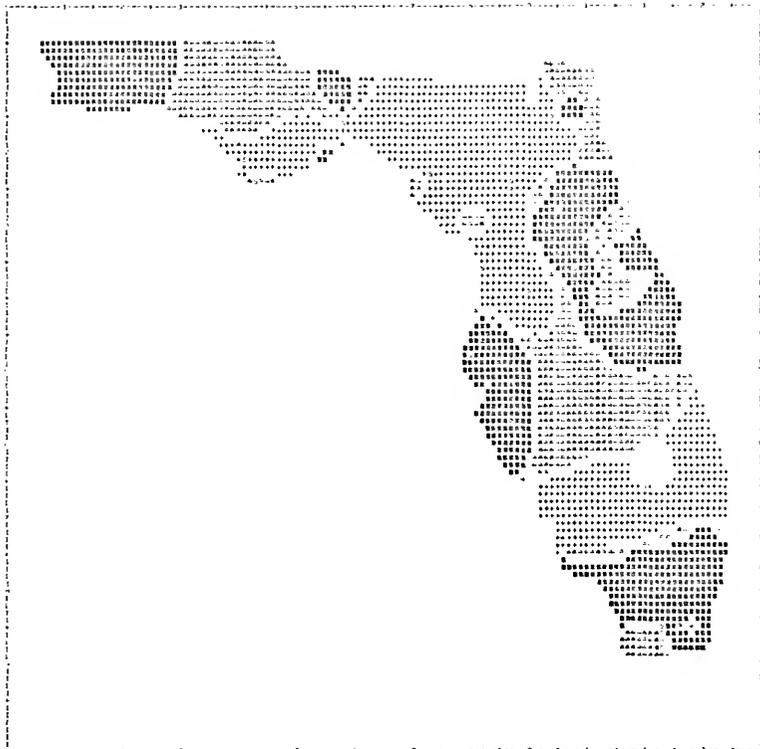
MAP 20. Geographic variation in the sum of ventrals plus caudals in Thamnophis sirtalis, both sexes. Lighter shading represents from 193 to 216; darker shading represents from 217 to 249. Based on 113 specimens.



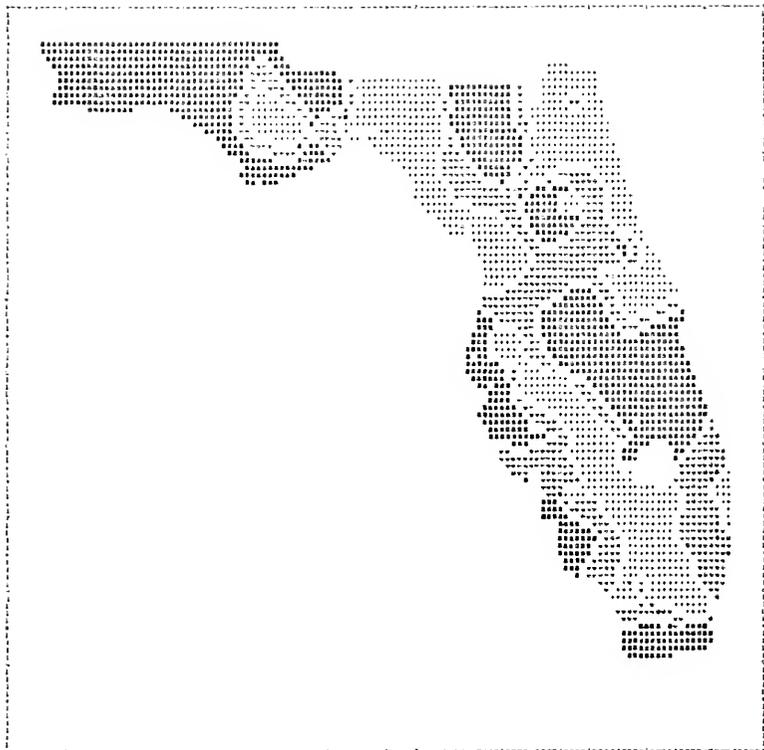
MAP 21. Geographic variation in tail length divided by total length in *Thamnophis sirtalis*, males only. Lighter shading represents from 0.22 to 0.24; darker shading represents from 0.25 to 0.33. Based on 53 specimens.



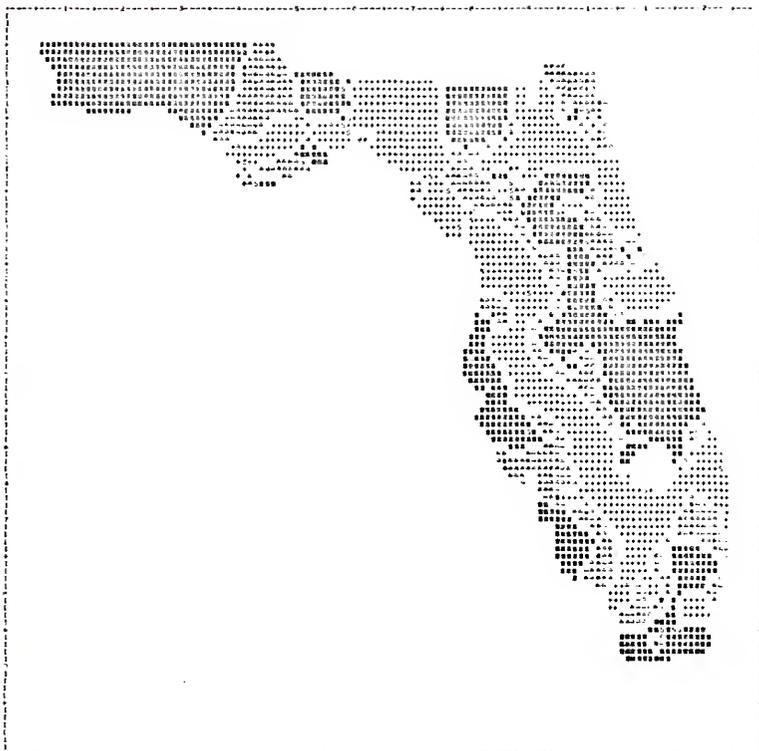
MAP 22. Geographic variation in tail length divided by total length in *Thamnophis sirtalis*, females only. Lighter shading represents from 0.16 to 0.22; darker shading represents from 0.23 to 0.33. Based on 65 specimens.



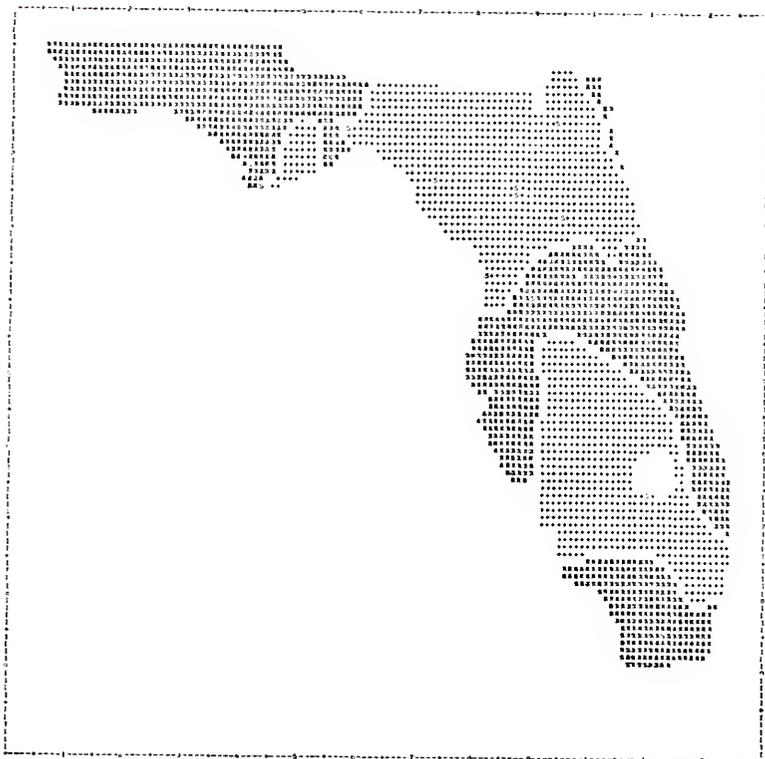
MAP 23. Geographic variation in development of the dorsal checking pattern in *Thamnophis sirtalis*, males only. Increased shading represents increased check development. Based on 74 specimens.



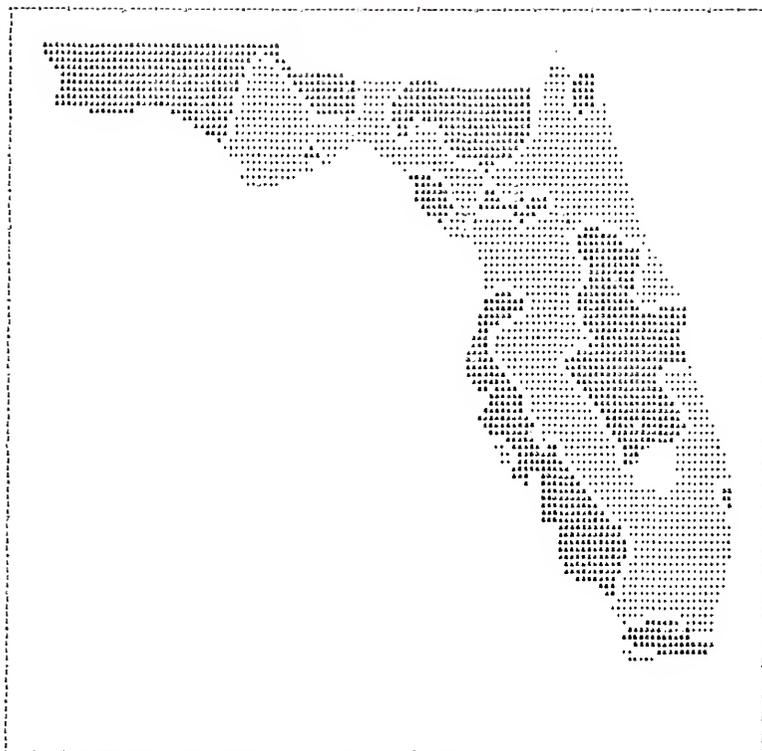
MAP 24. Geographic variation in development of dorsal checking in *Thamnophis sirtalis*, females only. Lightest shading represents no or very obscure dorsal checking; darkest shading represents well-developed pattern of dorsal checks; intermediate shading represents the intermediate condition. Based on 113 specimens.



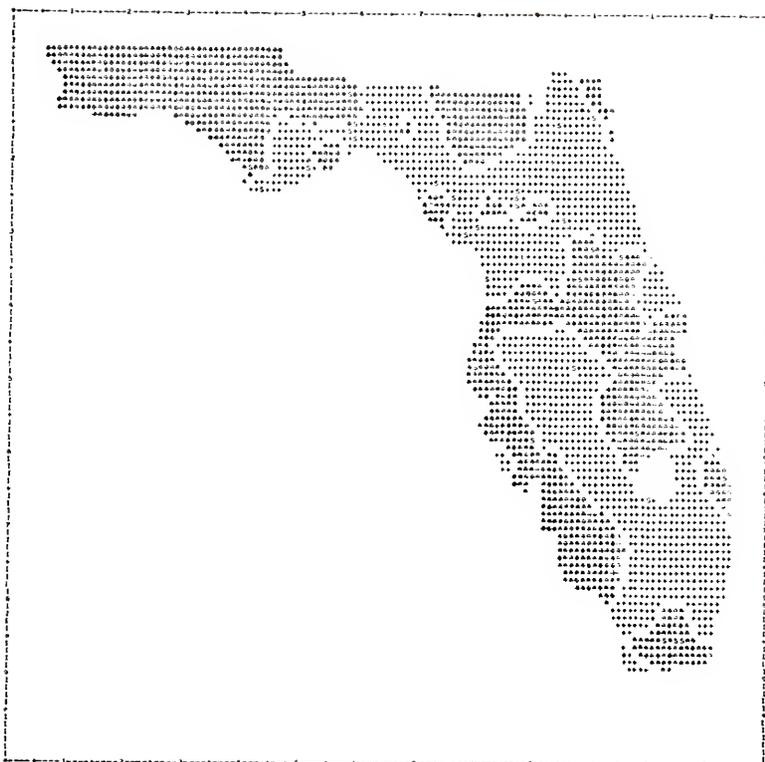
MAP 25. Geographic variation in development of dorsal checks in *Thamnophis sirtalis*, both sexes. Increasing shading represents increasing development of the dorsal checking pattern. Based on 192 specimens.



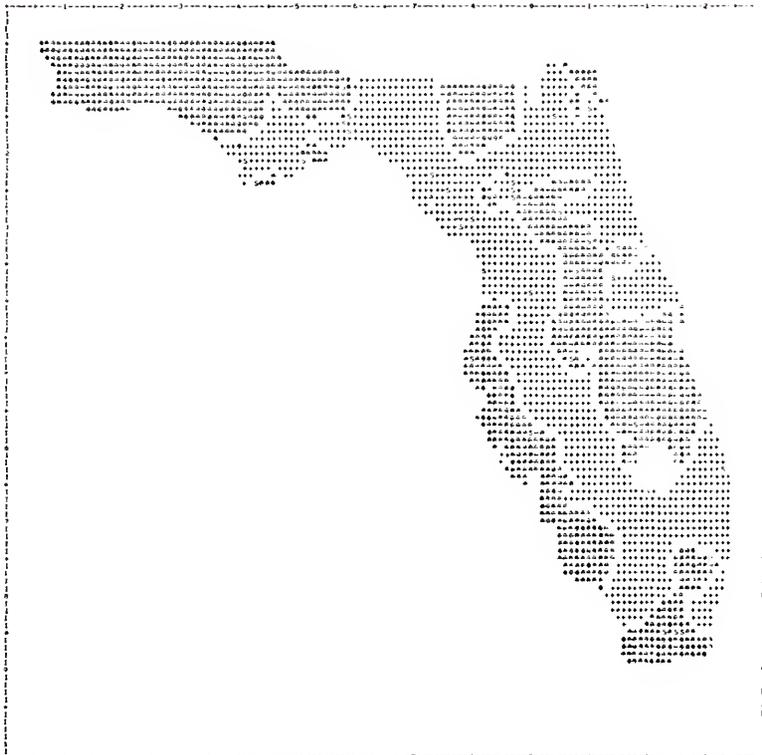
MAP 26. Geographic variation in the development of the parietal light spot in *Thamnophis sirtalis*, males only. Lighter shading represents poorly developed or absent parietal light spot; darker shading represents well-developed spot. Based on 71 specimens.



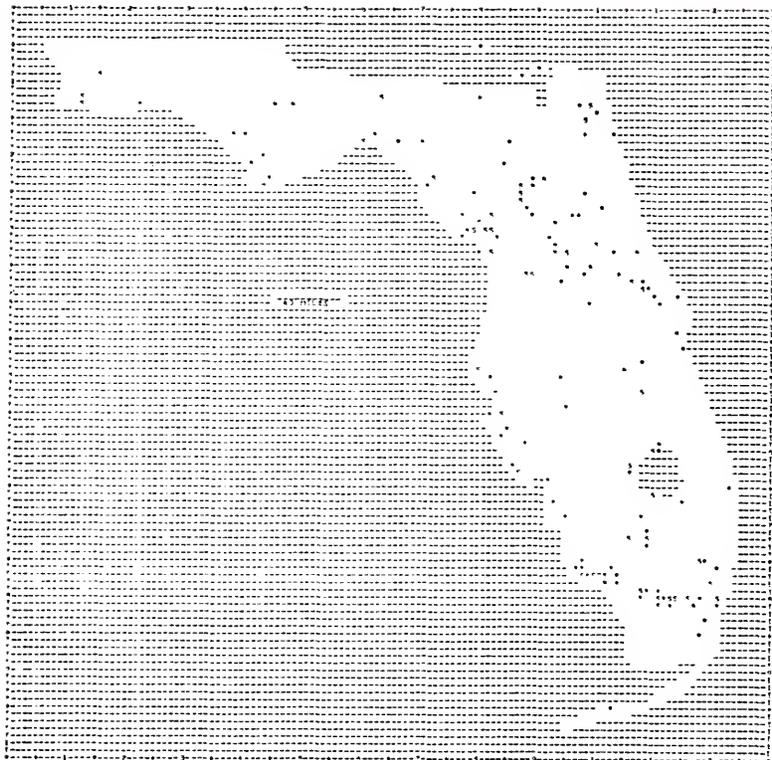
MAP 27. Geographic variation in the development of the parietal light spot in *Thamnophis sirtalis*, females only. Lighter shading represents poorly developed or absent parietal light spot; darker shading represents well-developed spot. Based on 116 specimens.



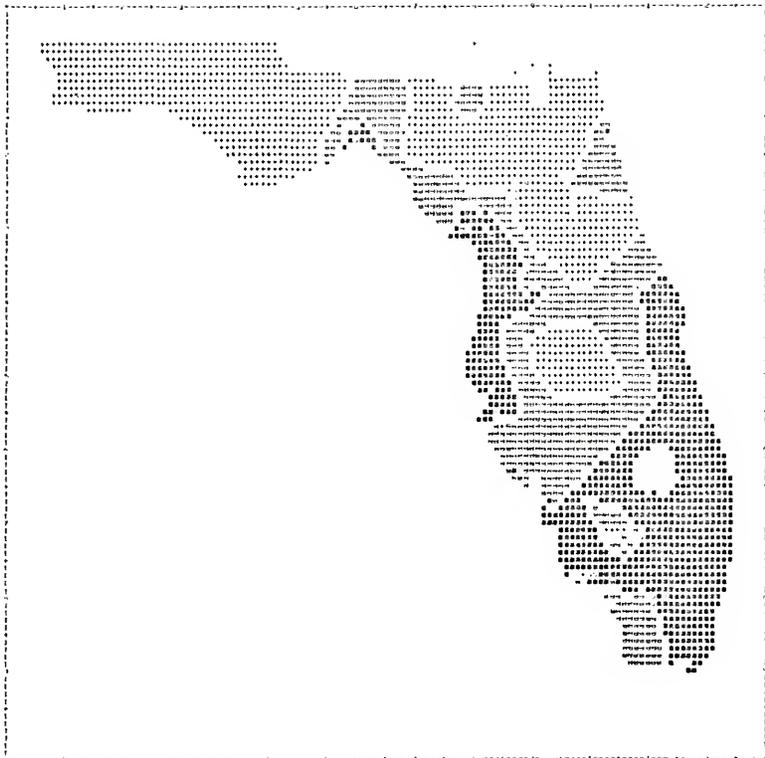
MAP 28. Geographic variation in development of the parietal light spot in *Thamnophis sirtalis*, both sexes. Lighter shading represents poorly developed or absent parietal light spot; darker shading represents well-developed spot. Based on 187 specimens.



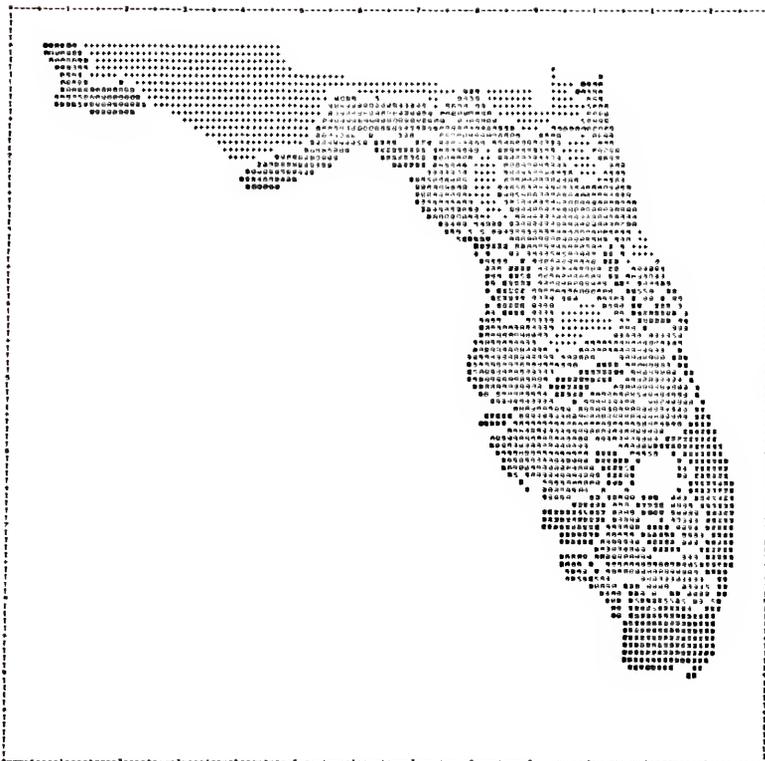
MAP 29. Geographic variation in factor 1 for *Thamnophis sirtalis*, both sexes. Factor 1 accounts for much of the variation in development of the parietal spot and development of the dorsal checking pattern. Darker shading represents generally better defined parietal spot and dorsal checking. Total variation accounted for by factor 1: 18.5% (11 characters). Based on 192 specimens.



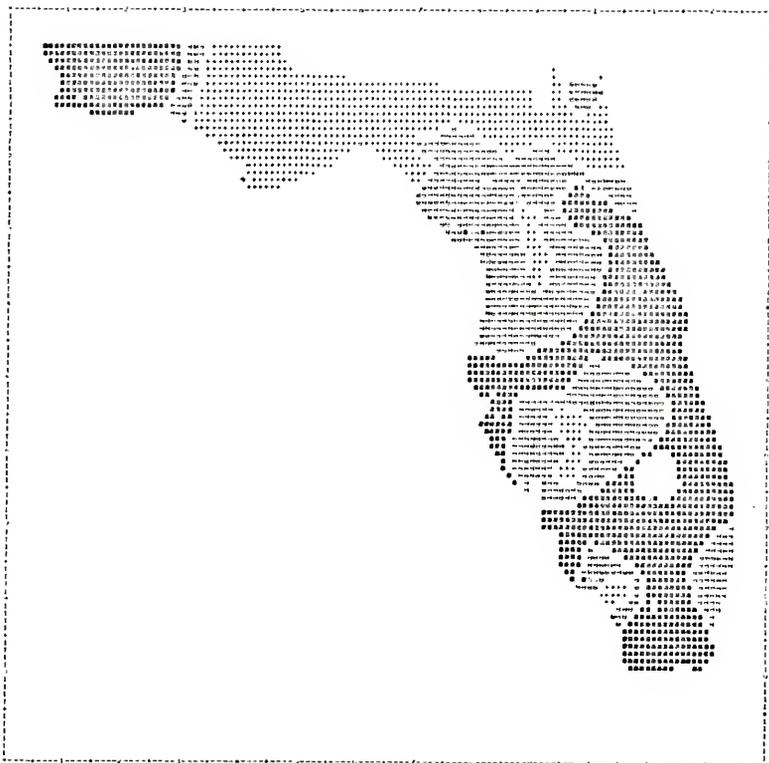
MAP 30. Localities of 279 *Thamnophis sauritus*, specimens examined. An asterisk represents one specimen; an S represents more than one.



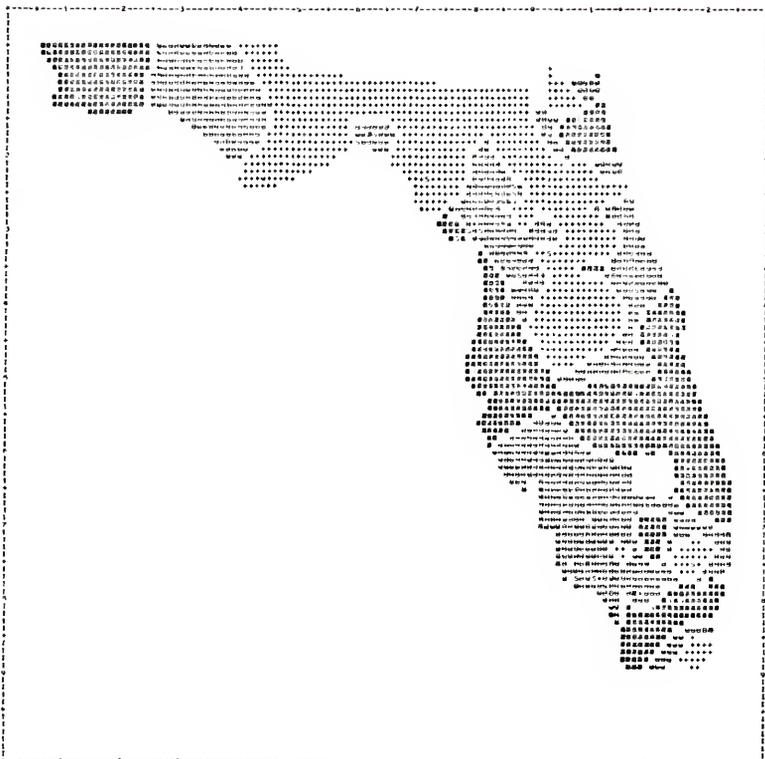
MAP 31. Geographic variation in number of ventral scales in *Thamnophis sauritus*, males only, Florida Keys specimens excluded. Levels by increasing shading are: 147-158; 159-162; 163-171. Based on 101 specimens.



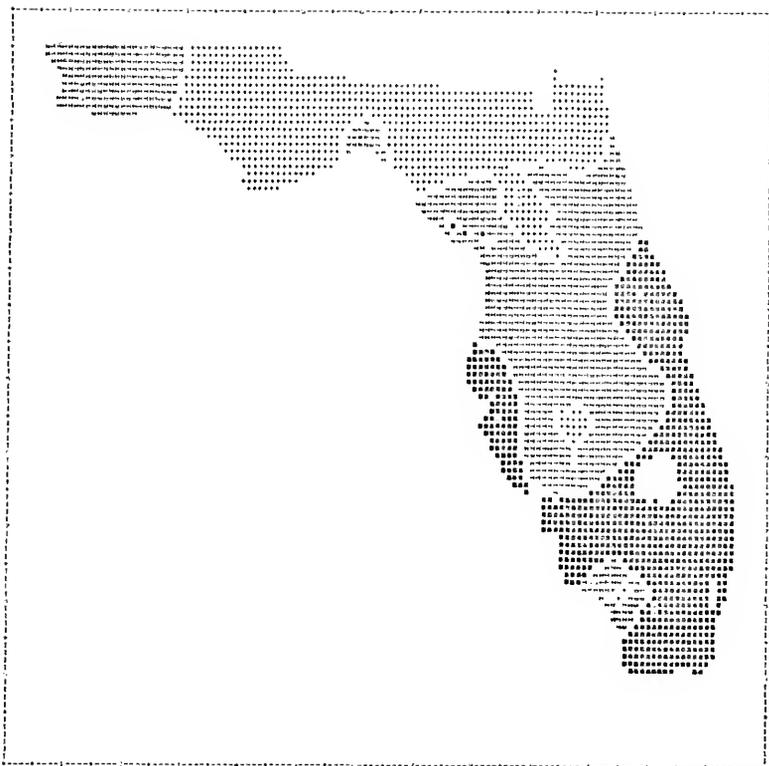
MAP 32. Geographic variation in number of ventral scales in *Thamnophis sauritus*, females only, excluding specimens from the Florida Keys. Levels by increased shading are: 145-152; 153-159; 160-167. Based on 178 specimens.



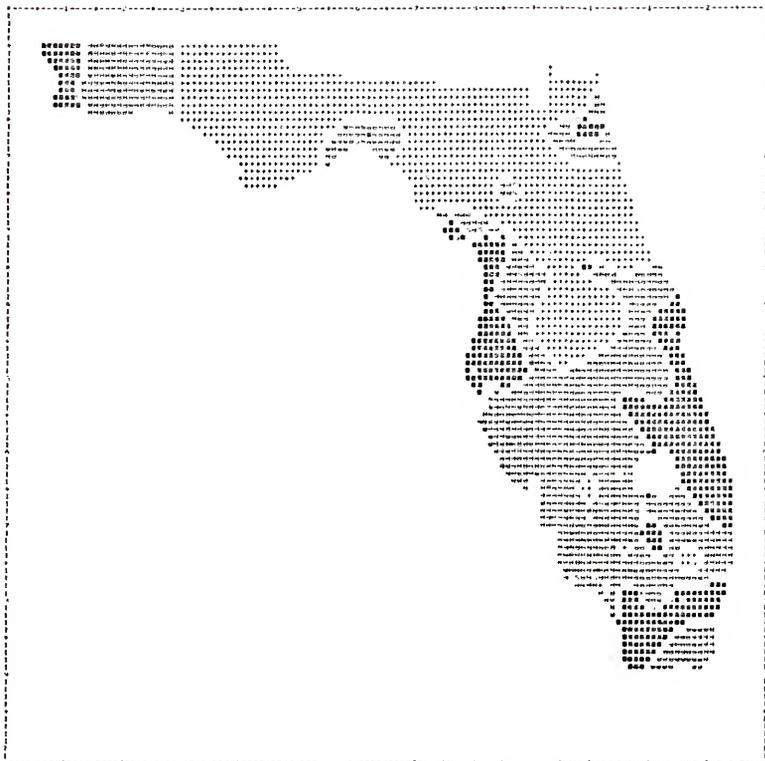
MAP 33. Geographic variation in number of subcaudal scales in *Thamnophis sauritus*, males only, Florida Keys specimens excluded. Levels by increasing shading are: 117-121; 122-128; 129-135. Based on 58 specimens.



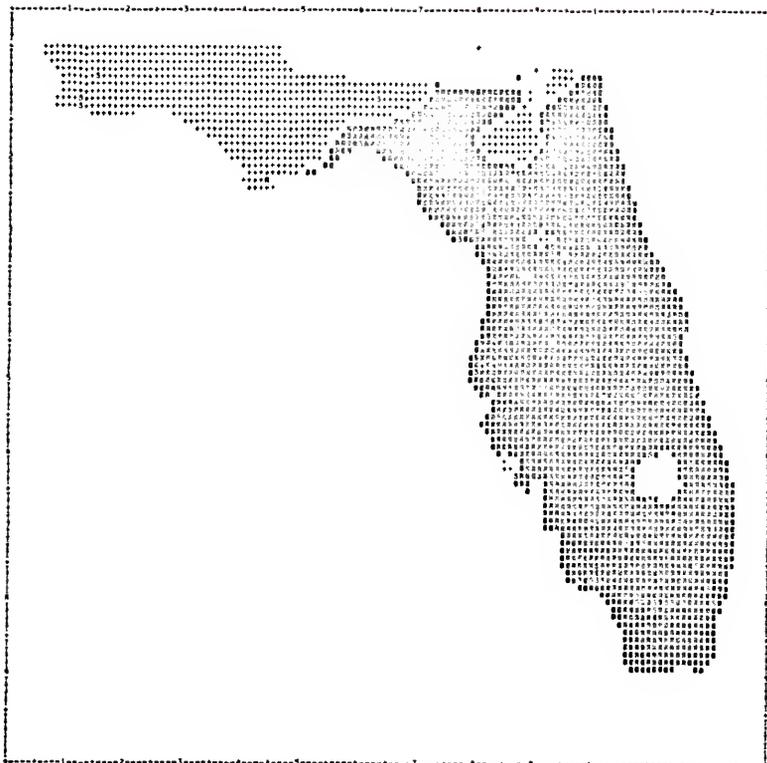
MAP 34. Geographic variation in number of subcaudal scales in *Thamnophis sauritus*, females only, Florida Keys specimens excluded. Levels by increasing shading: 105-110; 111-119; 120-130. Based on 91 specimens.



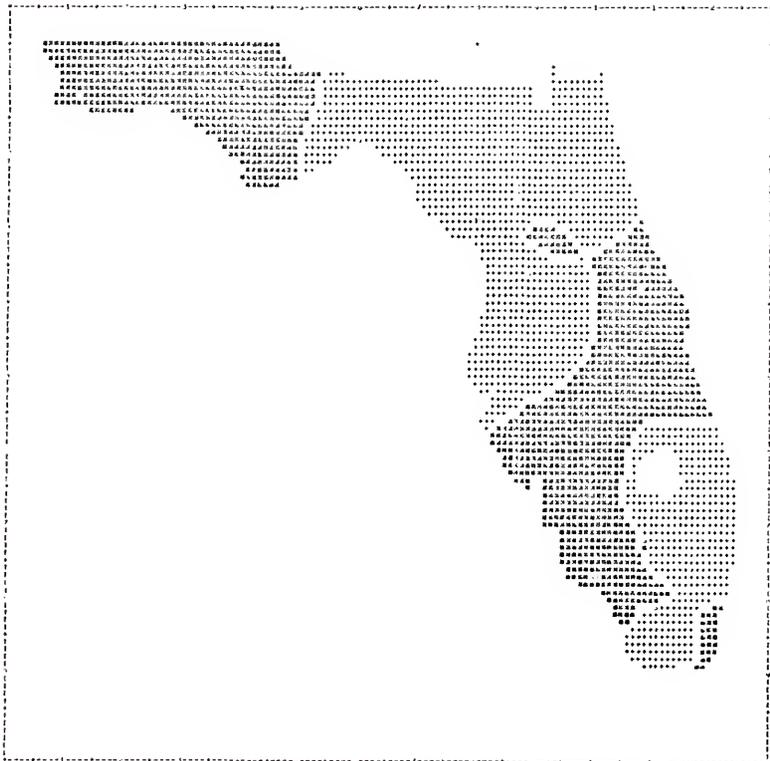
MAP 35. Geographic variation in number of ventrals plus caudals in *Thamnophis sauritus*, males only, exclusive of Florida Keys specimens. Levels by increasing shading are: 268-281; 282-290; 291-300. Based on 58 specimens.



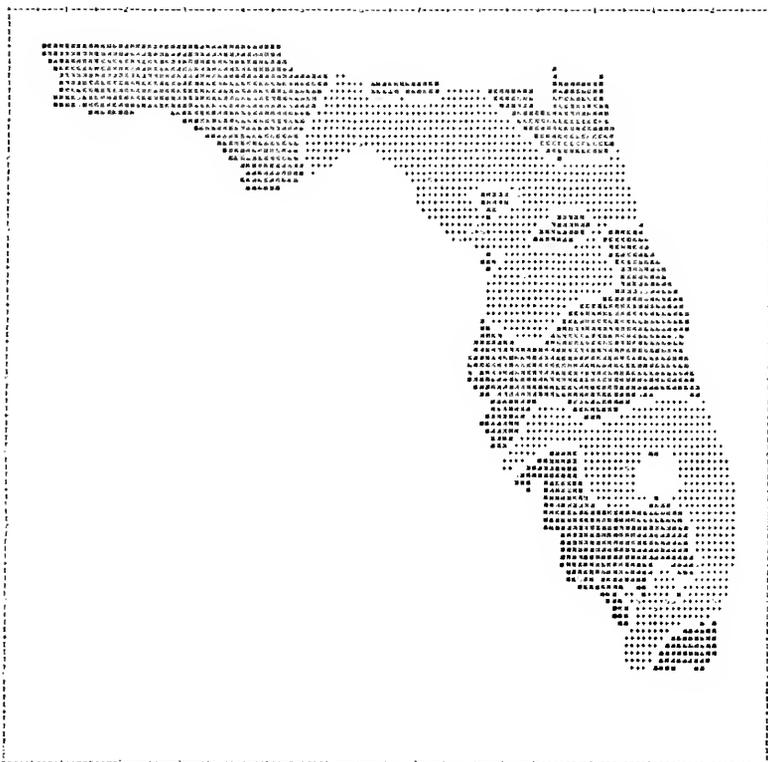
MAP 36. Geographic variation in number of ventrals plus caudals in *Thamnophis sauritus*, females only, exclusive of Florida Keys specimens. Levels by increasing shading are: 256-271; 272-279; 280-293. Based on 91 specimens.



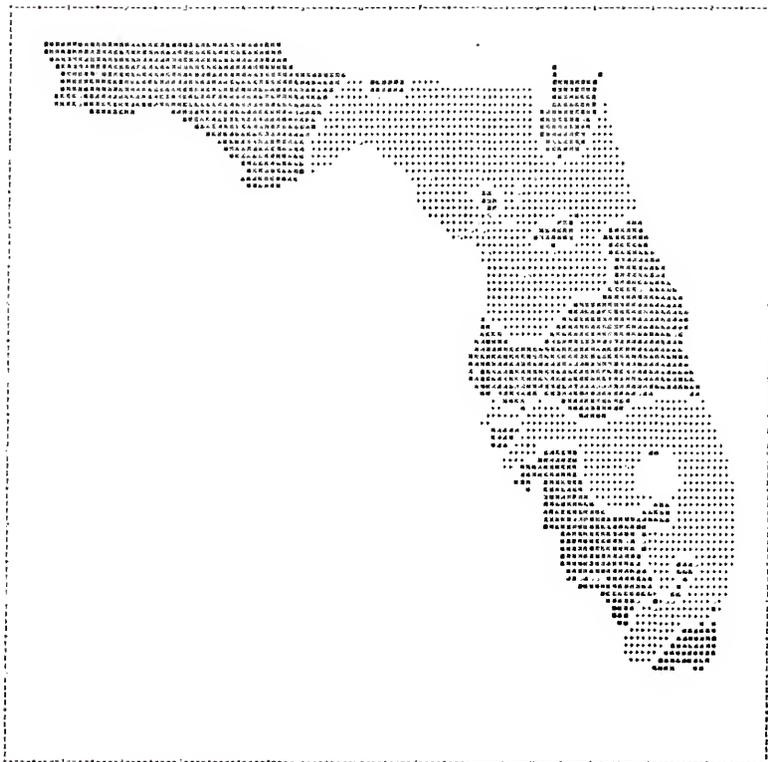
MAP 37. Geographic variation in number of supralabial scales in *Thamnophis sauritus*, both sexes, Florida Keys specimens excluded. Lighter shading represents 14 supralabials; darker shading, 15. Based on 271 specimens.



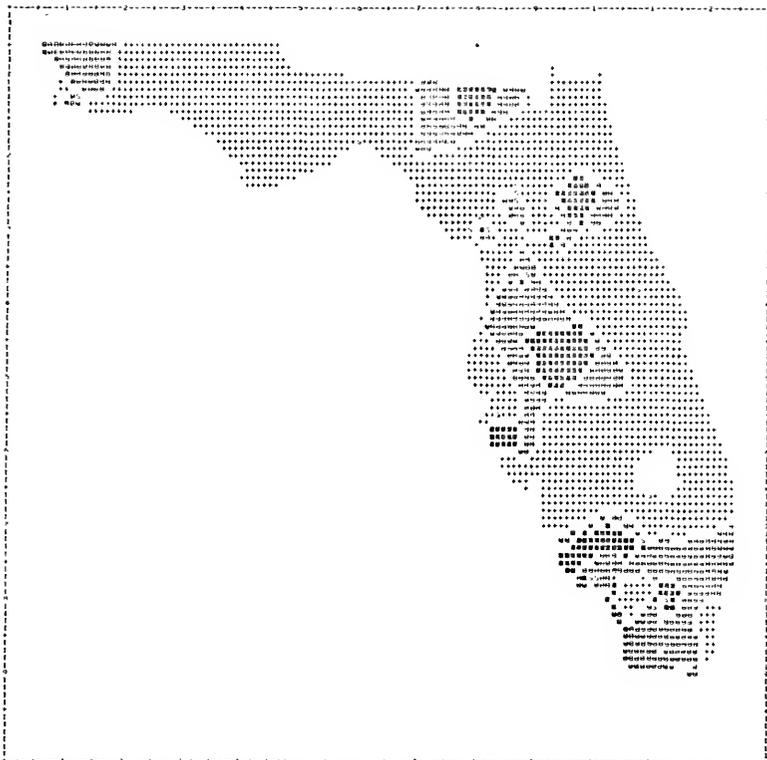
MAP 38. Geographic variation in development of the black edge of the mid-dorsal stripe in Thamnophis sauritus, males only, exclusive of specimens from the Florida Keys. Darker shading represents a well-developed stripe edge, and light shading represents no black edge on the dorsal stripe, or a very thin edge. Based on 62 specimens.



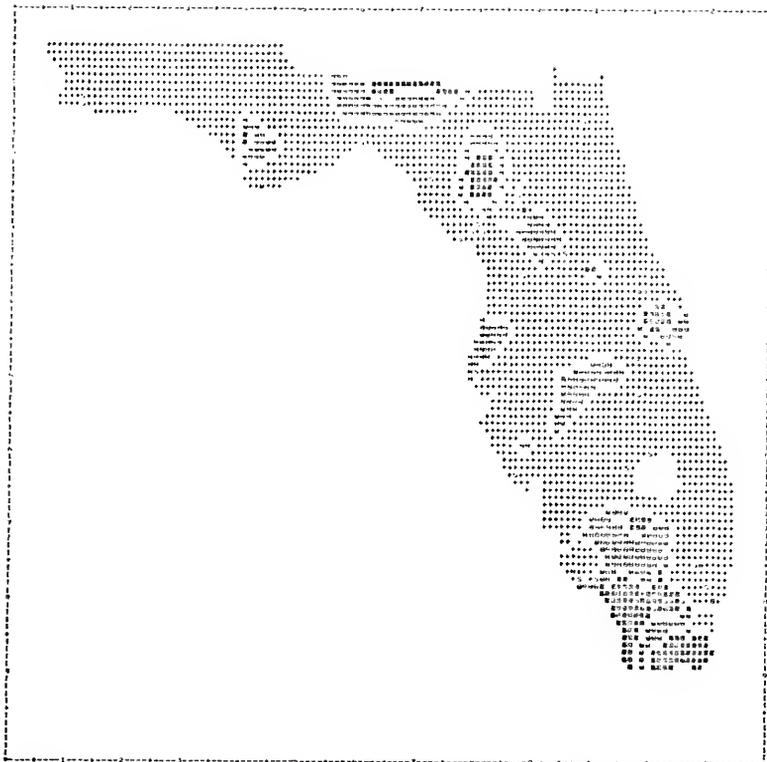
MAP 39. Geographic variation in development of the black edge of the mid-dorsal stripe in *Thamnophis sauritus*, females only, with specimens from the Florida Keys excluded. Darker shading represents a well-developed black edge on the dorsal stripe, and lighter shading represents no such edge, or a very weakly defined one. Based on 117 specimens.



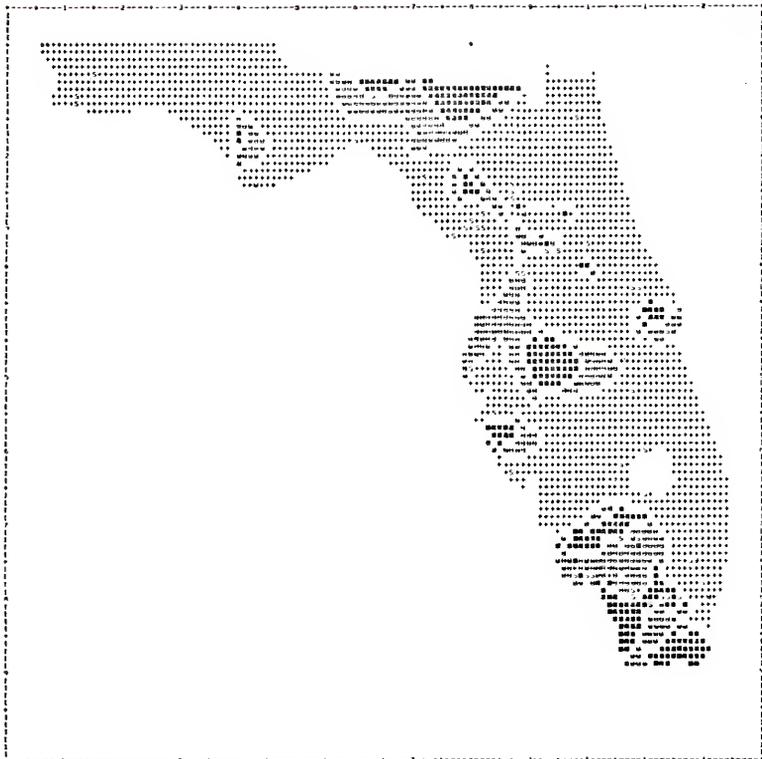
MAP 40. Geographic variation in development of the black edge of the mid-dorsal stripe in *Thamnophis sauritus*, both sexes, specimens from the Florida Keys excluded. Darker shading represents a well-developed stripe edge, and lighter shading represents no such edge, or a very weakly defined one. Based on 179 specimens.



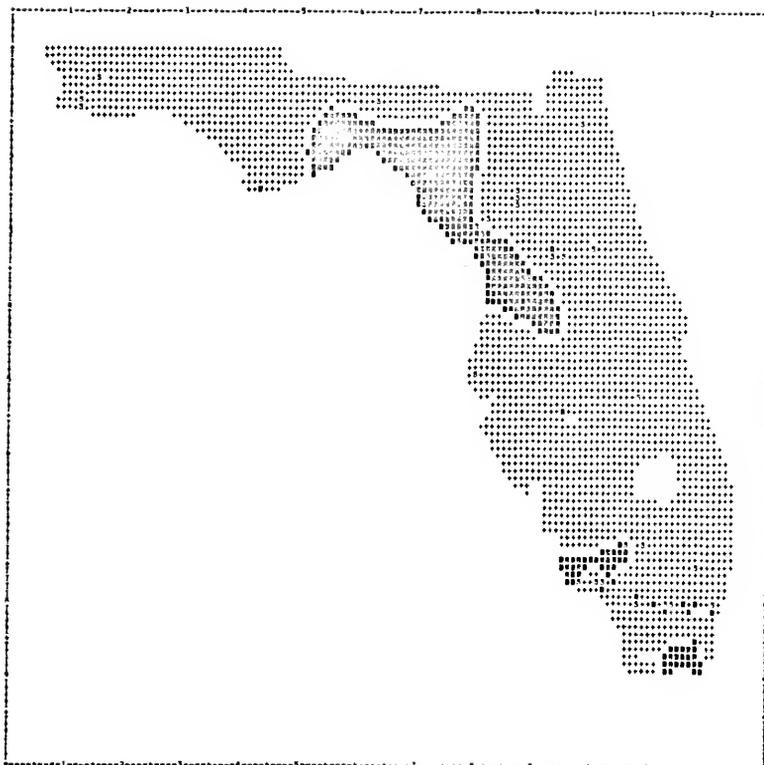
MAP 41. Geographic variation in the size of the parietal light spot in *Thamnophis sauritus*, males only, Florida. Keys specimens excluded. Lightest shading represents snakes with no parietal light spots; darkest shading, snakes with well-developed and large parietal spots, and intermediate shading, the intermediate condition. Based on 91 specimens.



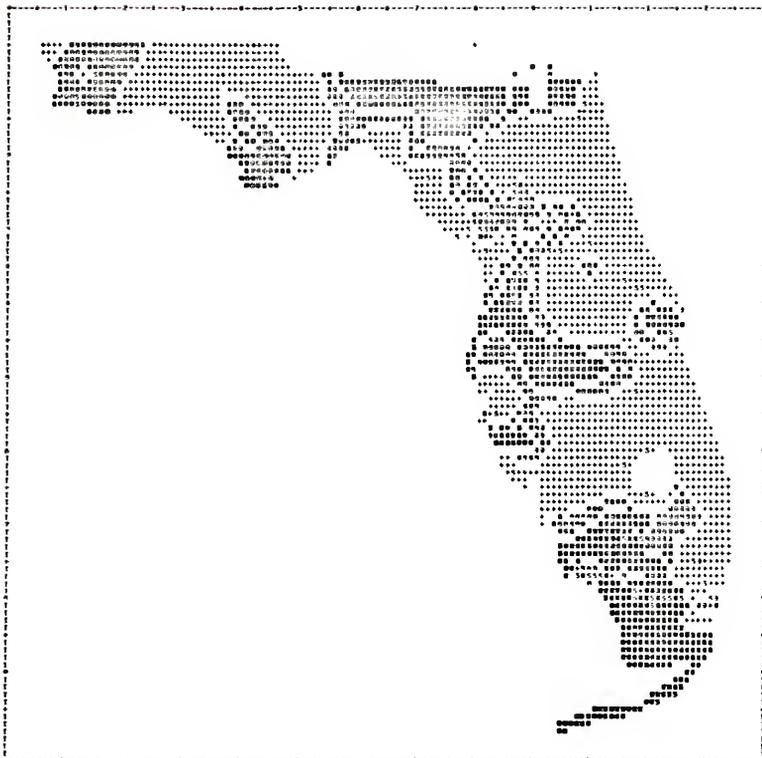
MAP 42. Geographic variation in size of the parietal light spot in *Thamnophis sauritus*, females only, Florida Keys specimens excluded. Lightest shading represents no parietal spot; darkest shading, a well-developed spot, and intermediate shading, the intermediate condition. Based on 165 specimens.



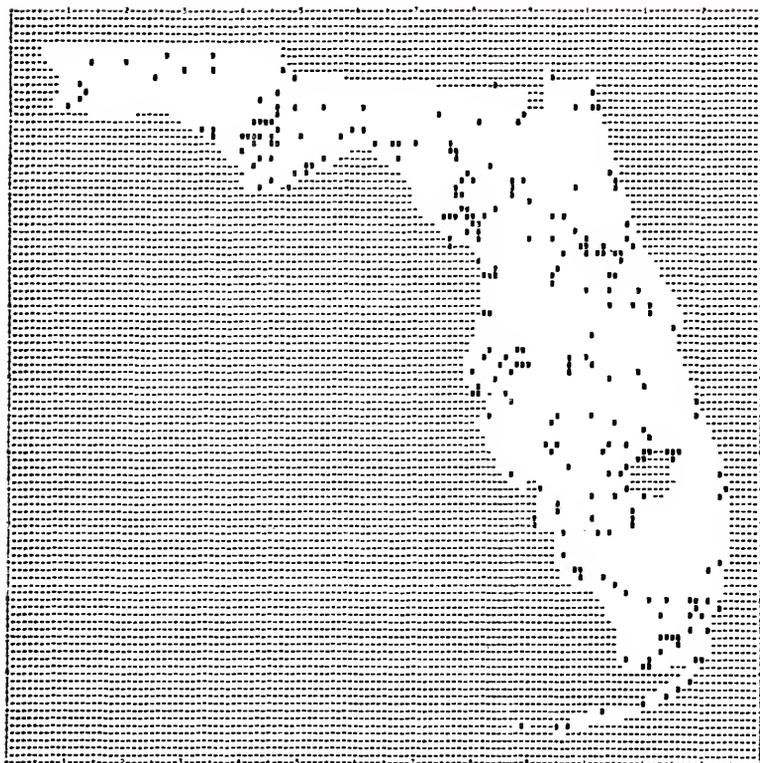
MAP 43. Geographic variation in size of the parietal light spot in *Thamnophis sauritus*, both sexes, Florida Keys specimens secluded. Lightest shading represents no parietal spot; darkest shading, a well-developed parietal spot, and the intermediate shading, the intermediate condition. Based on 256 specimens.



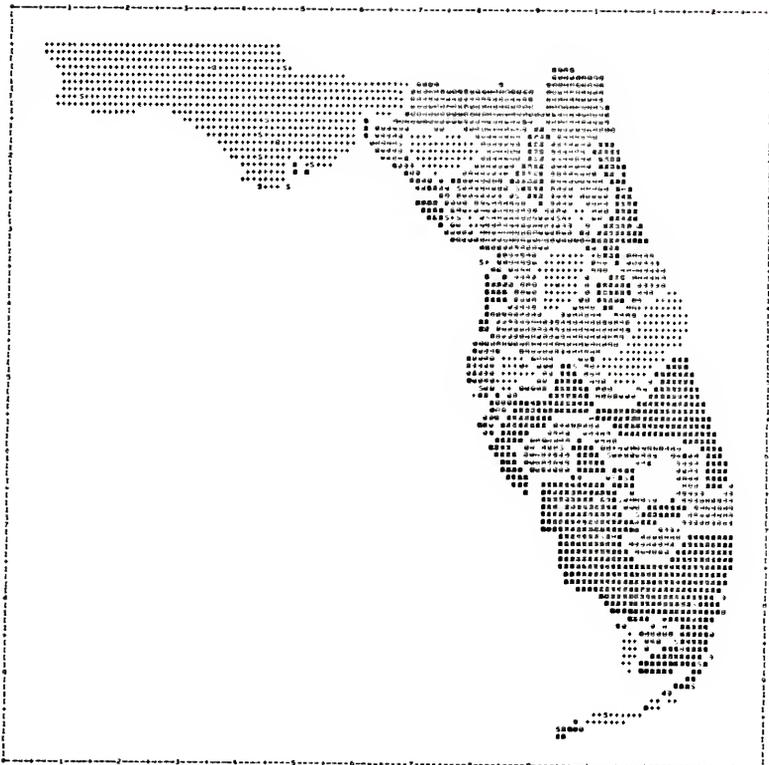
MAP 44. Geographic variation in darkness of the ground color in *Thamnophis sauritus*, both sexes, Florida Keys specimens excluded. Lighter shading represents a light brown or gray ground color, and darker shading represents a dark brown ground color. Based on 146 specimens.



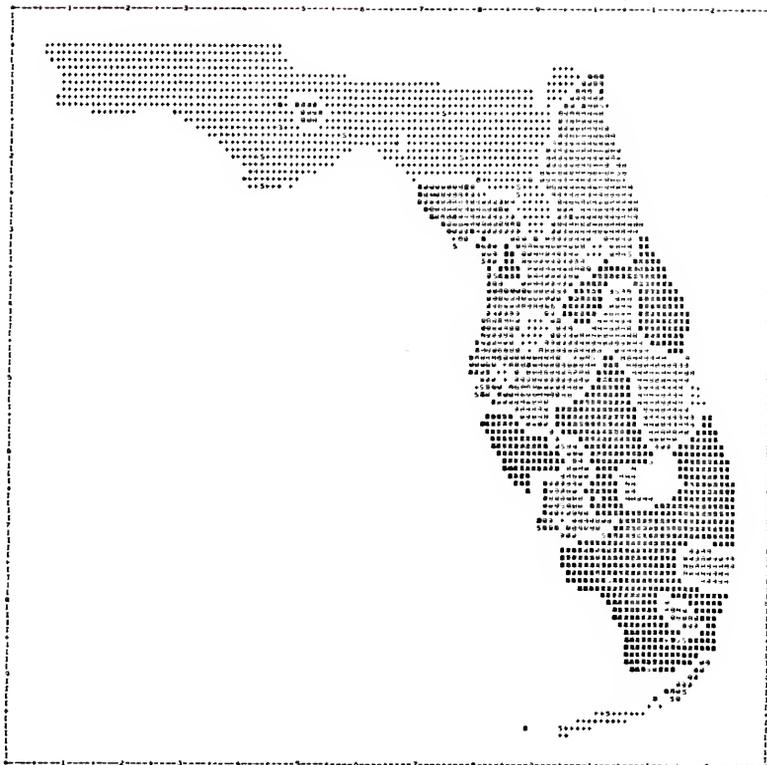
MAP 45. Geographic variation in Factor 1 for *Thamnoophis sauritus*, both sexes. Factor 1 accounts for 22.3% of the variation in 10 characters, and most of the variation in parietal spot distinctness and parietal spot size. Darker shading implies generally larger and more distinct parietal spots. Based on 278 specimens.



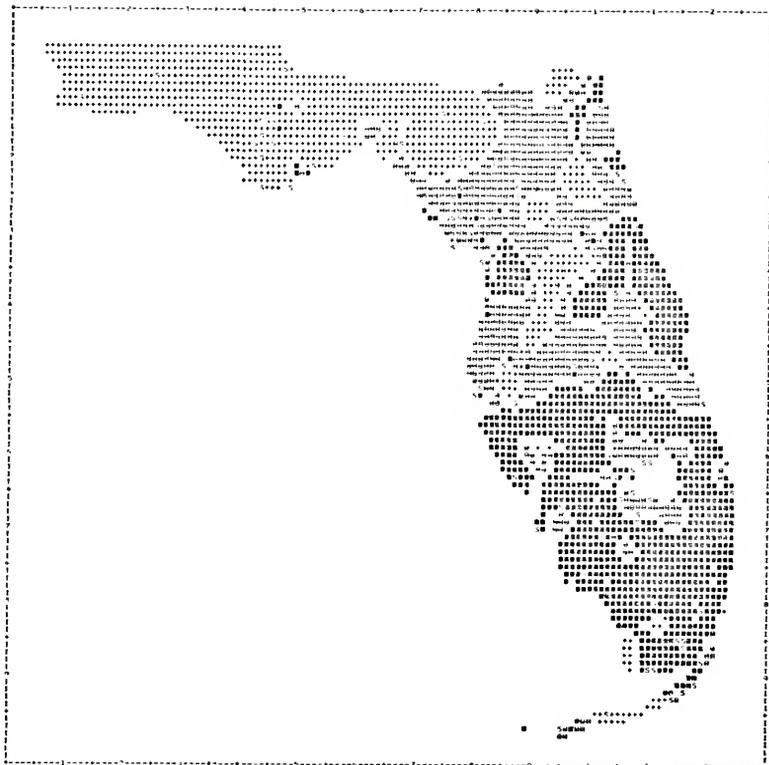
MAP 46. Localities of 440 Coluber constrictor specimens examined.



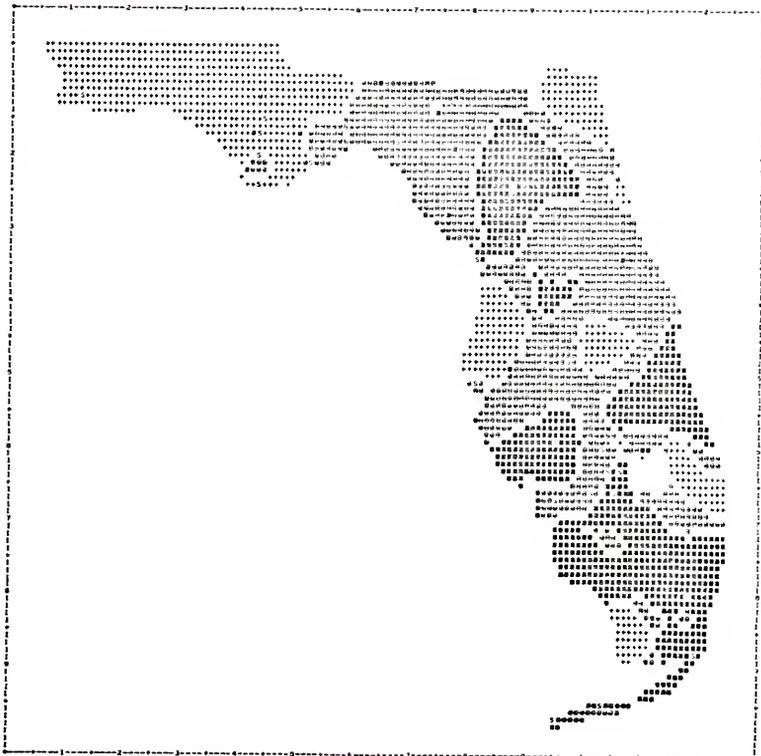
MAP 47. Geographic variation in the number of ventral scales in *Coluber constrictor*, males only. Levels by increasing shading are: 164-175; 176-179; 180-187. Based on 238 specimens.



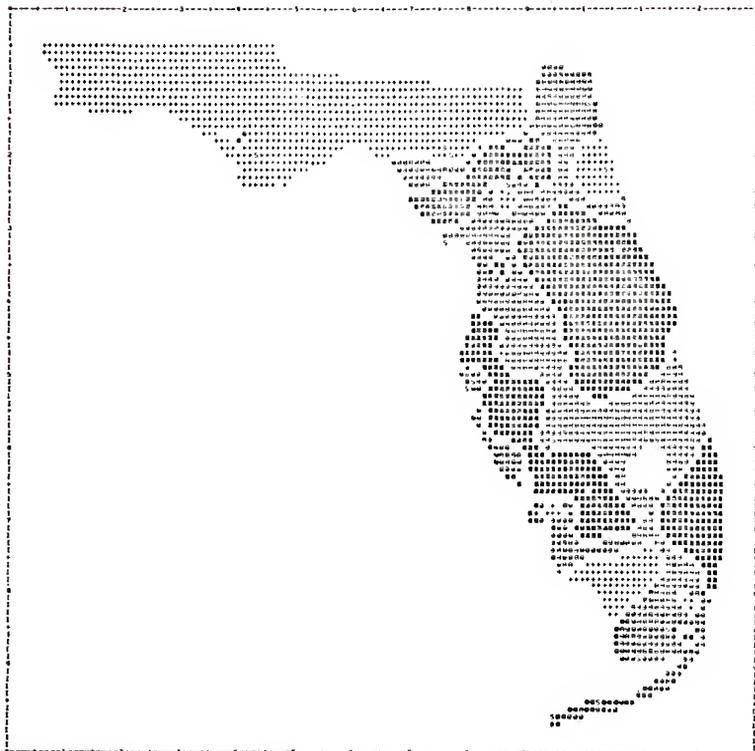
MAP 48. Geographic variation in number of ventral scales for *Coluber constrictor*, females only. Levels by increasing shading are: 165-177; 178-182; 183-191. Based on 200 specimens.



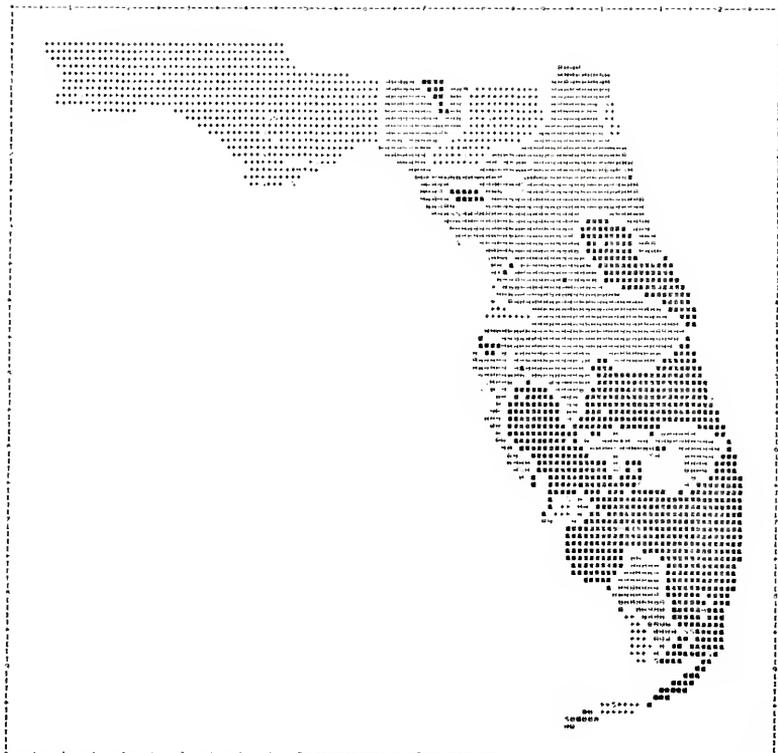
MAP 49. Geographic variation in the number of ventral scales in *Coluber constrictor*, both sexes. Levels by increasing shading are: 164-176; 177-180; 181-191. Based on 440 specimens.



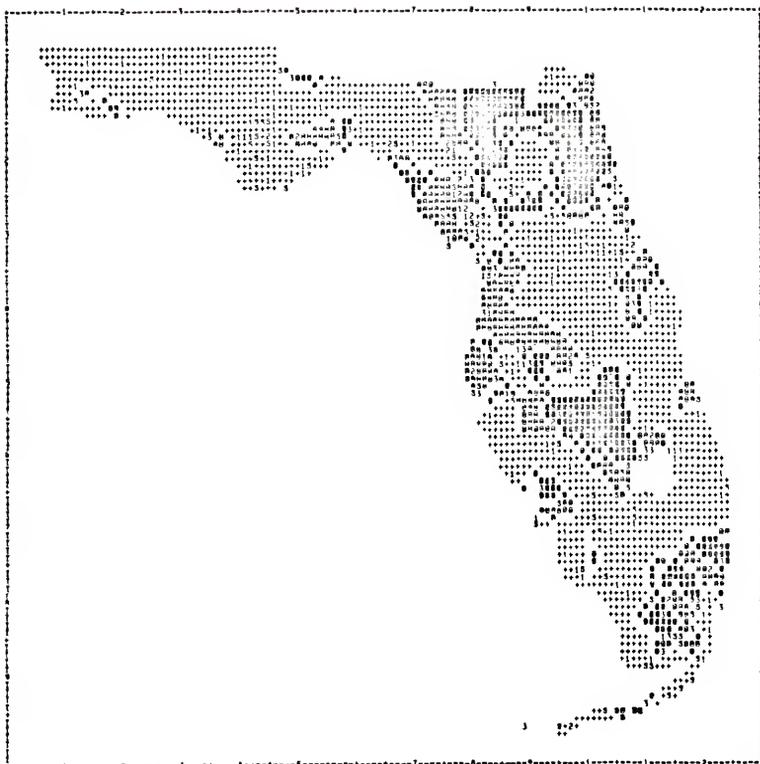
MAP 50. Geographic variation in number of subcaudal scales in *Coluber constrictor*, males only. Levels by increased shading are: 91-105; 106-110; 111-123. Based on 106 specimens.



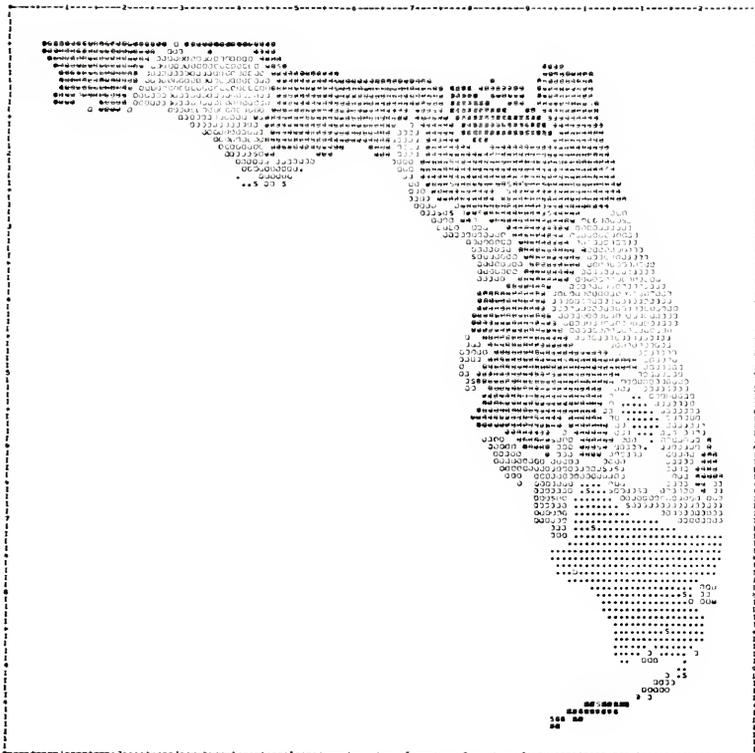
MAP 51. Geographic variation in number of subcaudal scales in *Coluber constrictor*, females only. Levels by increasing shading are: 90-100; 101-105; 106-118. Based on 87 specimens.



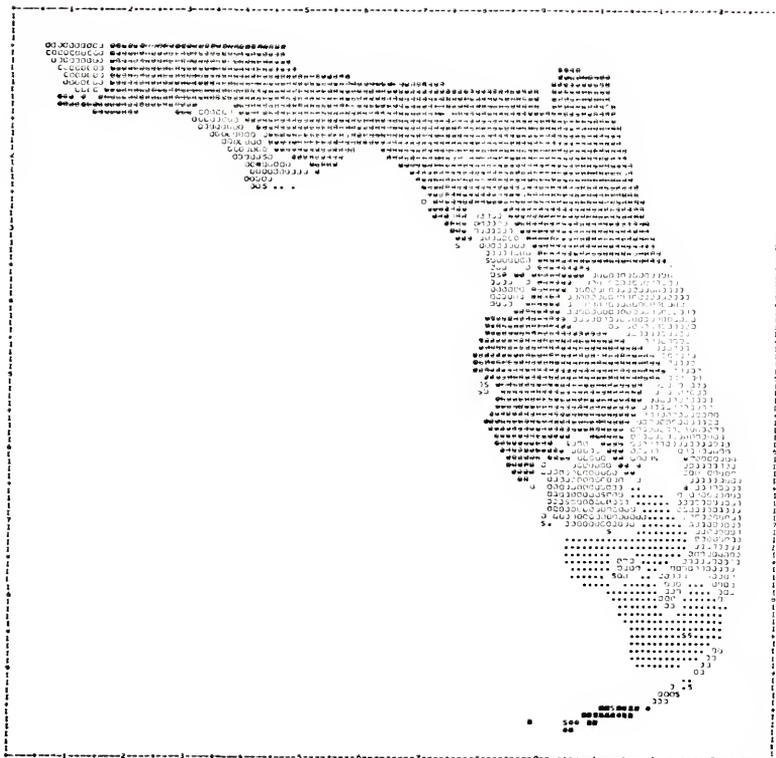
MAP 52. Geographic variation in number of ventrals plus caudals for *Coluber constrictor*, both sexes. Levels by increasing shading are: 258-280; 281-288; 289-307. Based on 193 specimens.



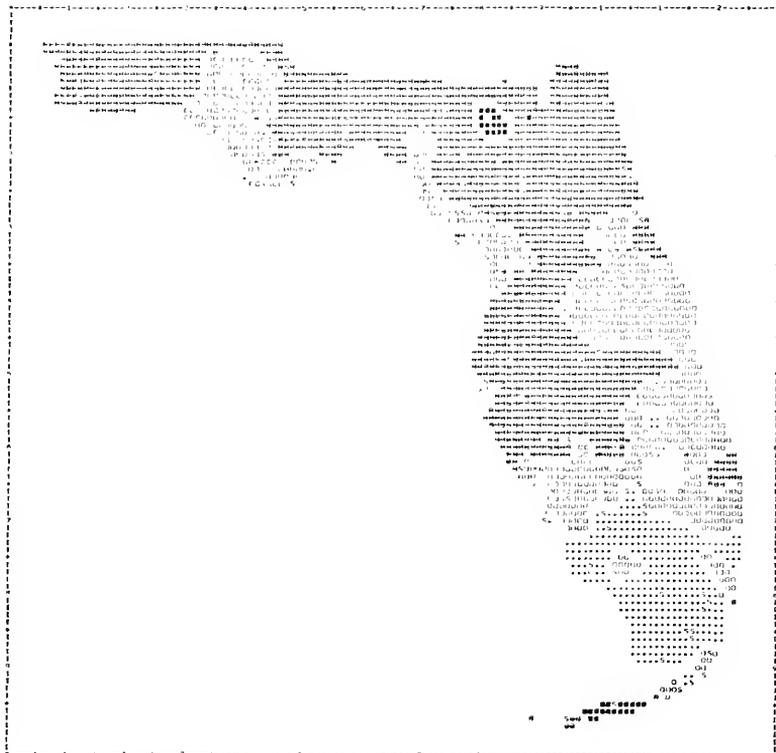
MAP 53. Geographic variation in the contact between the first supralabial and the loreal in Coluber constrictor, both sexes. Lightest shading represents no such contact, and darkest shading represents specimens with the loreal and first supralabial scales in contact on both sides of the head. Based on 436 specimens.



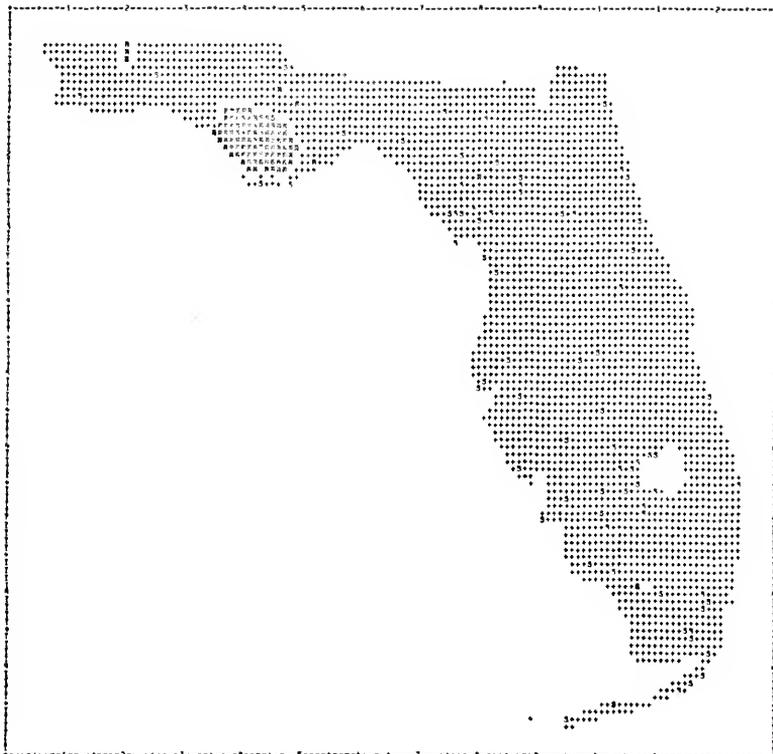
MAP 54. Geographic variation in amount of ventral white in *Coluber constrictor*, males only. The lighter the shading, the more white ventrally. The darkest shading represents snakes with essentially no ventral white, and the lightest shading represents specimens with the entire ventral surface light colored. Based on 208 specimens.



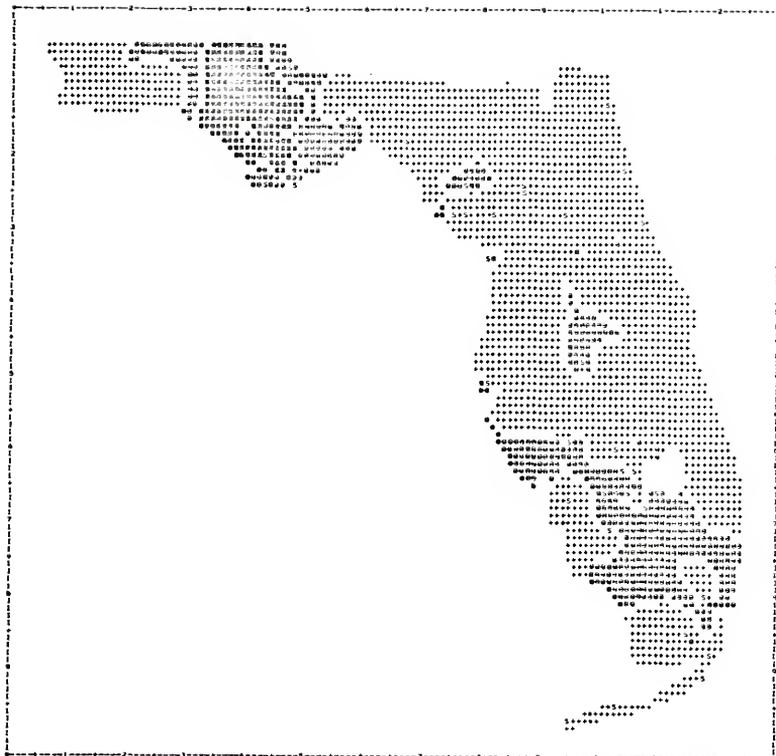
MAP 55. Geographic variation in the amount of white on the ventral surface in *Coluber constrictor*, females only. Darkest shading represents no or almost no white pigment ventrally. The lighter the shading, the more white pigment ventrally. The lightest shading represents snakes with essentially all white venters. Based on 183 specimens.



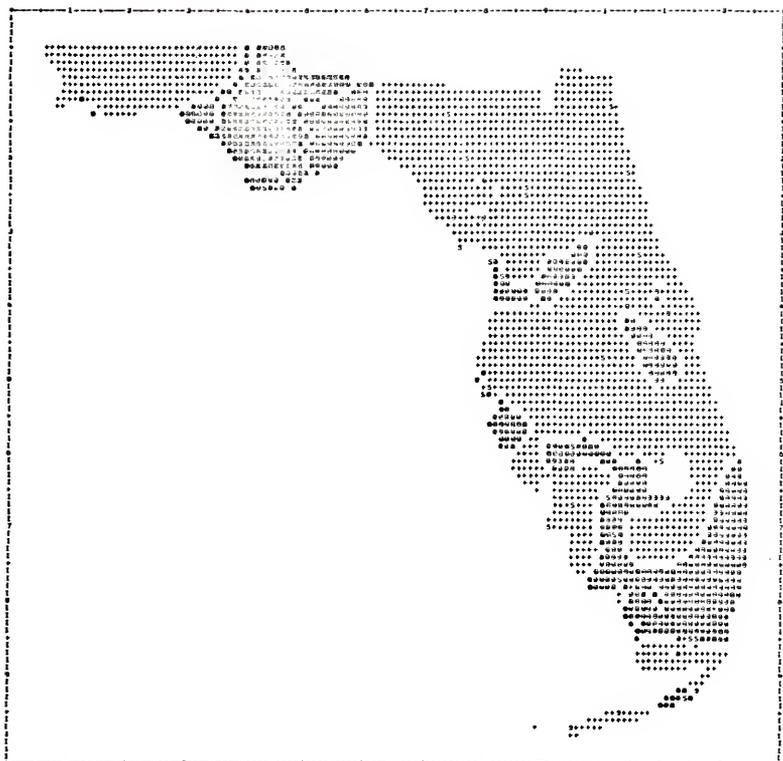
MAP 56. Geographic variation in the amount of ventral white in *Coluber constrictor*, both sexes. Lightest shading represents snakes with white venters; darkest shading snakes with very little or no white ventrally. Based on 393 specimens.



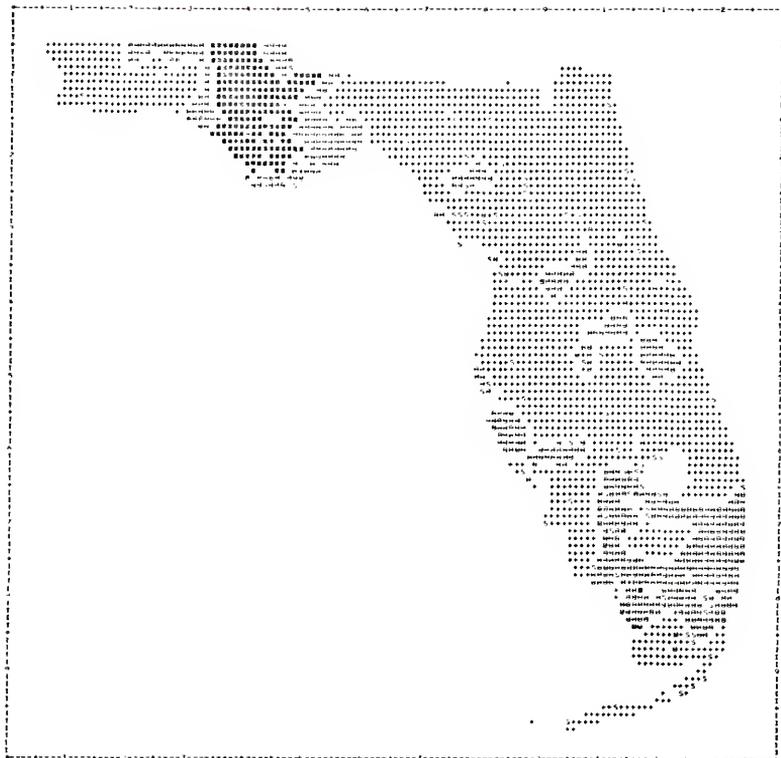
MAP 57. Geographic variation in presence or absence of brown pigment on the gular scales in Coluber constrictor, both sexes. Darker shading indicates the presence of such pigment. Based on 404 specimens.



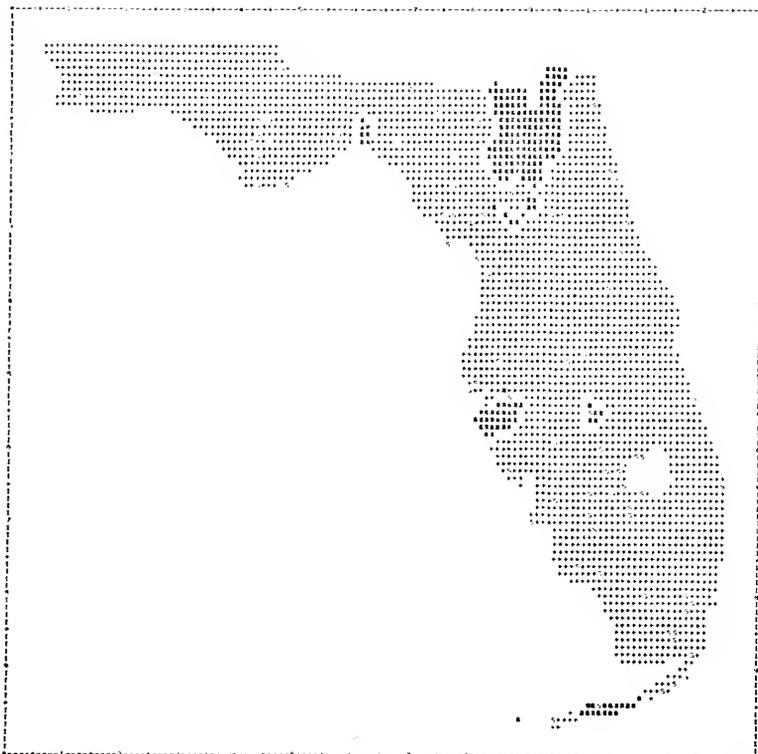
MAP 58. Geographic variation in the amount of brown pigment on the supralabial scales in *Coluber constrictor*, males only. Lightest shading represents no brown pigment on the supralabials; darkest shading represents much supralabial brown; intermediate shading, the intermediate condition. Based on 215 specimens.



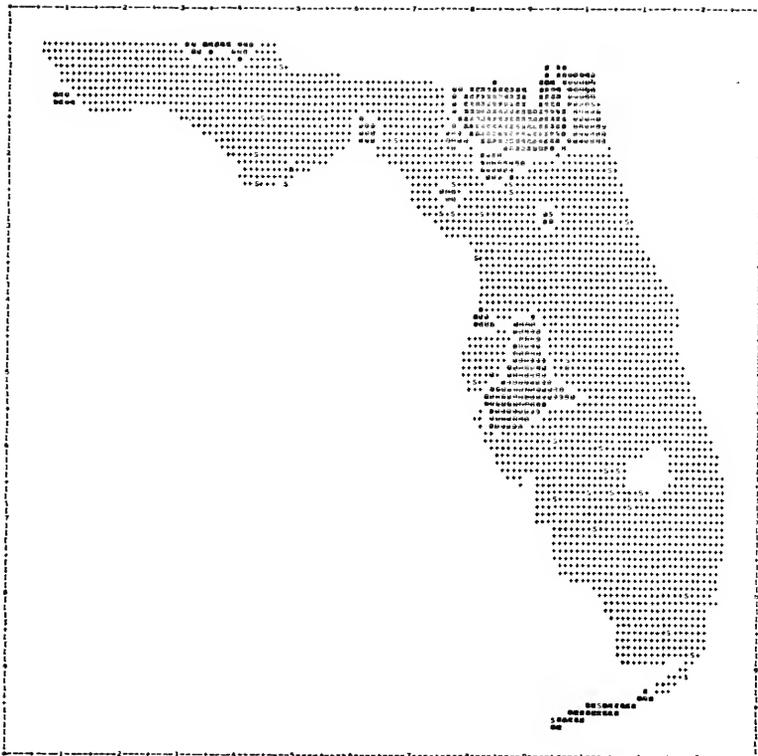
MAP 59. Geographic variation in the amount of brown pigment on the supralabial scales in *Coluber constrictor*, females only. Lightest shading represents no brown pigment on the supralabials; darkest shading represents much supralabial brown; intermediate shading, the intermediate condition. Based on 186 specimens.



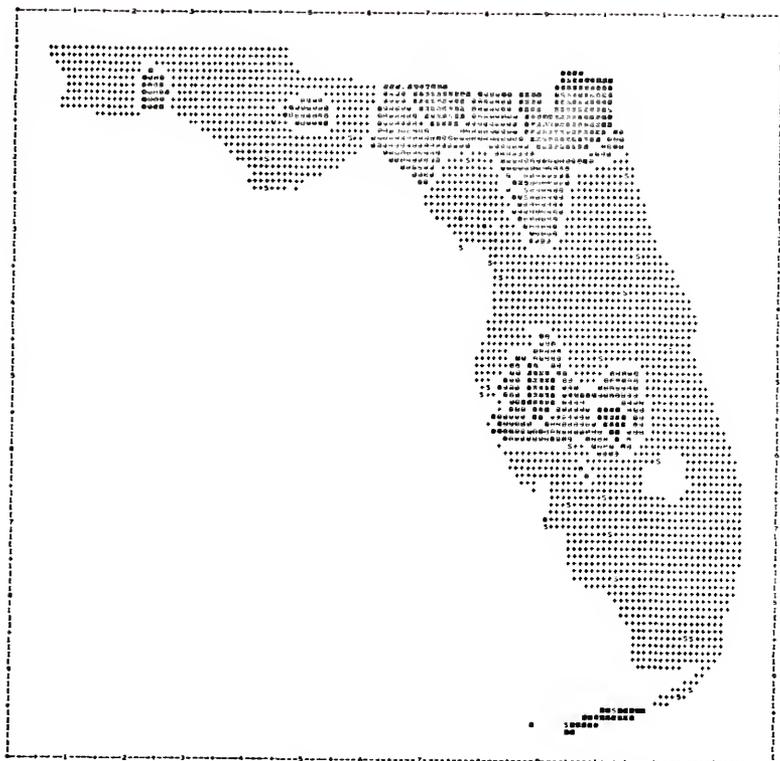
MAP 60. Geographic variation in the amount of brown pigment on the supralabial scales in *Coluber constrictor*, both sexes. Lightest shading represents no brown pigment on the supralabials; darkest shading represents much supralabial brown pigment; intermediate shading, the intermediate condition. Based on 403 specimens.



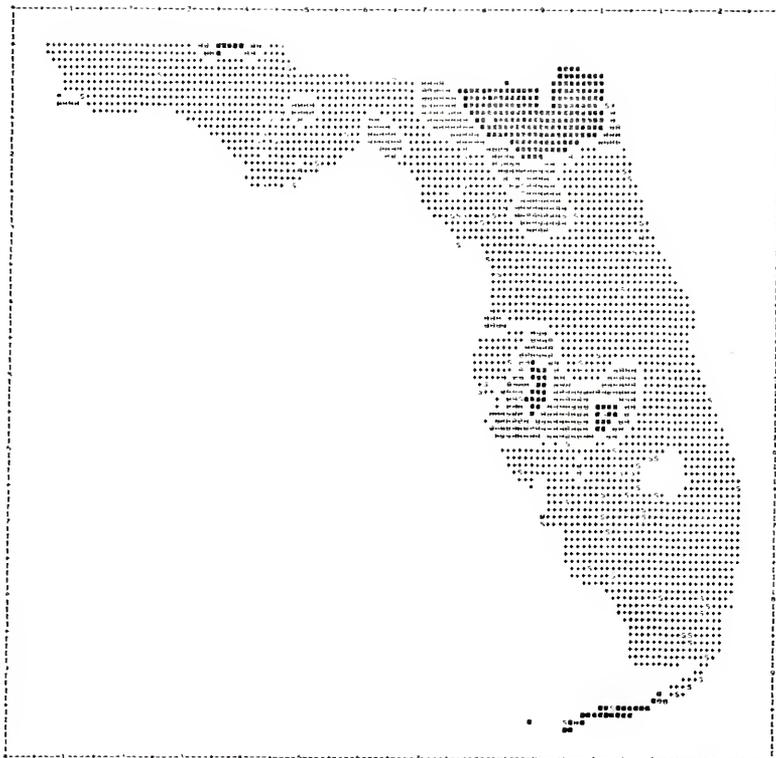
MAP 61. Geographic variation in the presence or absence of black pigment on the gular scales in Coluber constrictor, both sexes. Darker shading represents snakes with black pigment on the gulars. Based on 434 specimens.



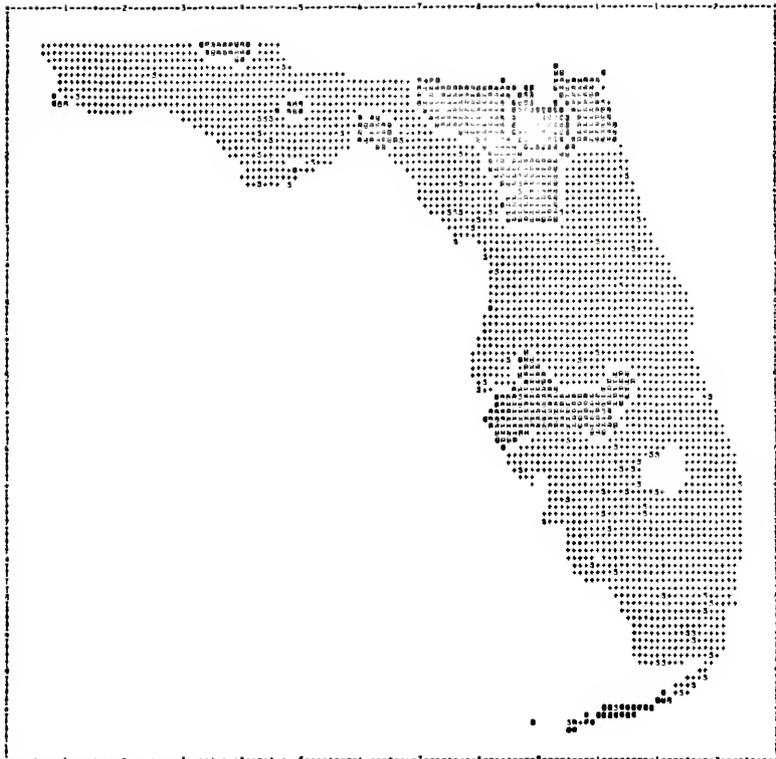
MAP 62. Geographic variation in the amount of black pigmentation on the supralabials in *Coluber constrictor*, males only. The lightest shading represents no black on the supralabials and the darkest shading essentially all black supralabials. Based on 215 specimens.



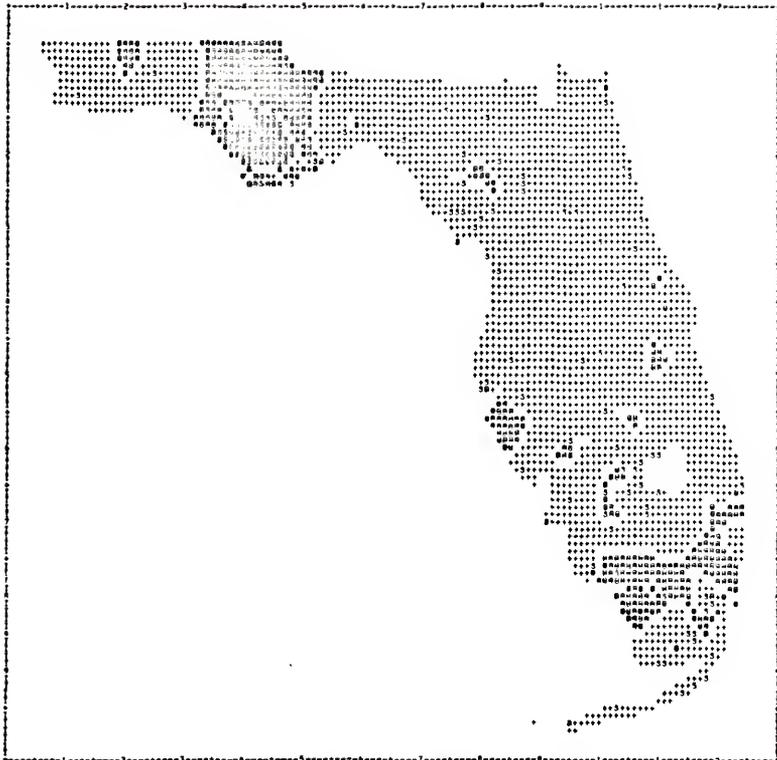
MAP 63. Geographic variation in amount of black pigmentation on the supralabials in *Coluber constrictor*, females only. The lightest shading represents essentially no black pigment and the darkest shading essentially all black supralabials. Based on 186 specimens.



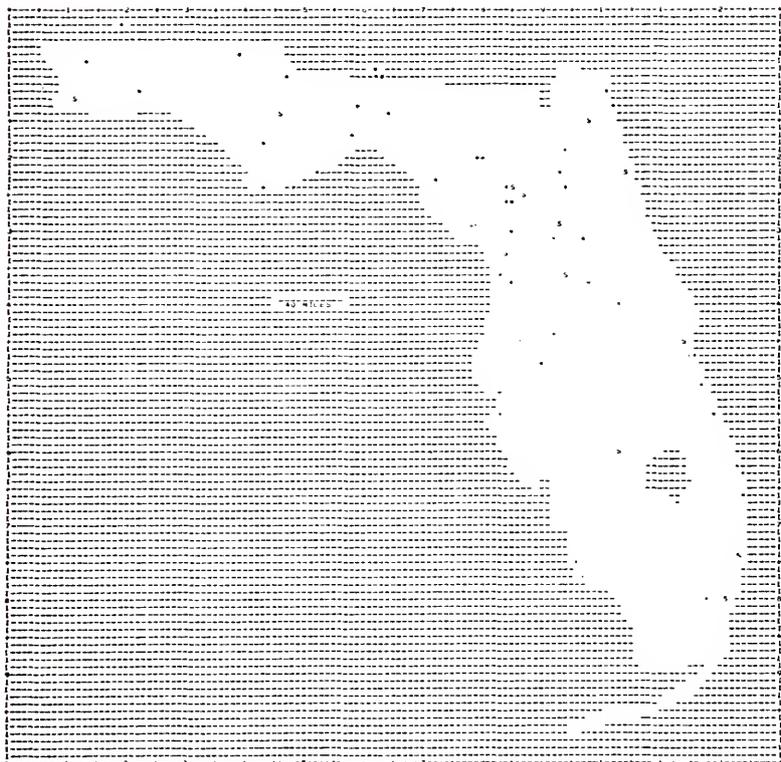
MAP 64. Geographic variation in amount of black pigment on the supralabials in *Coluber constrictor*, both sexes. The darkest shading represents essentially all black supralabials and the lightest shading, supralabials without black pigment. Based on 403 specimens.



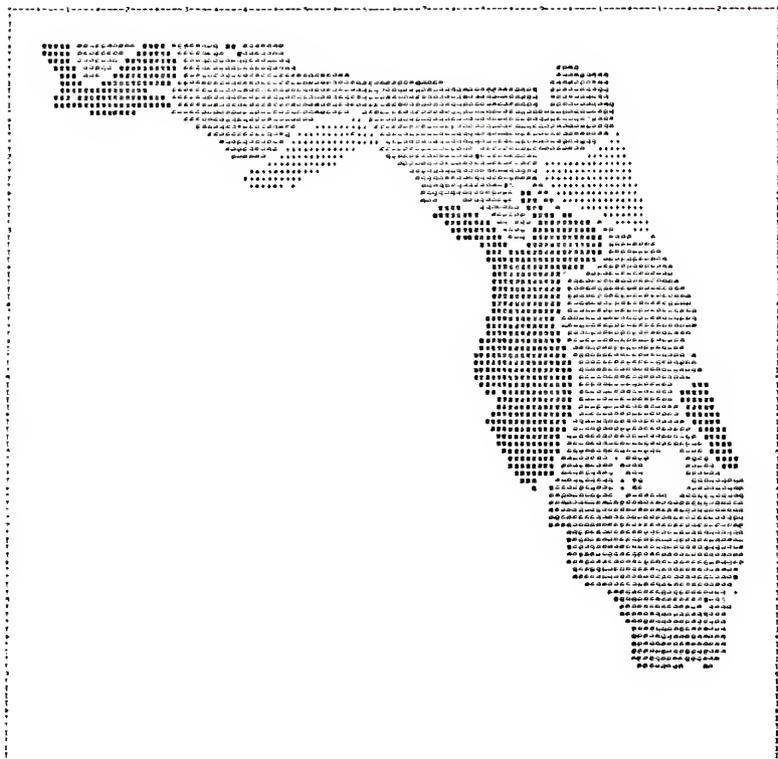
MAP 65. Geographic variation in Factor 1 for *Coluber constrictor*, both sexes. Factor 1 accounts for 17.4% of the variation in 16 characters, and most of the variation in gular black pigment and supralabial pigment, with some contribution from ventral white pigment. Darker shading implies generally more black on the labials and gulars and less white on the ventrum. Based on 440 specimens.



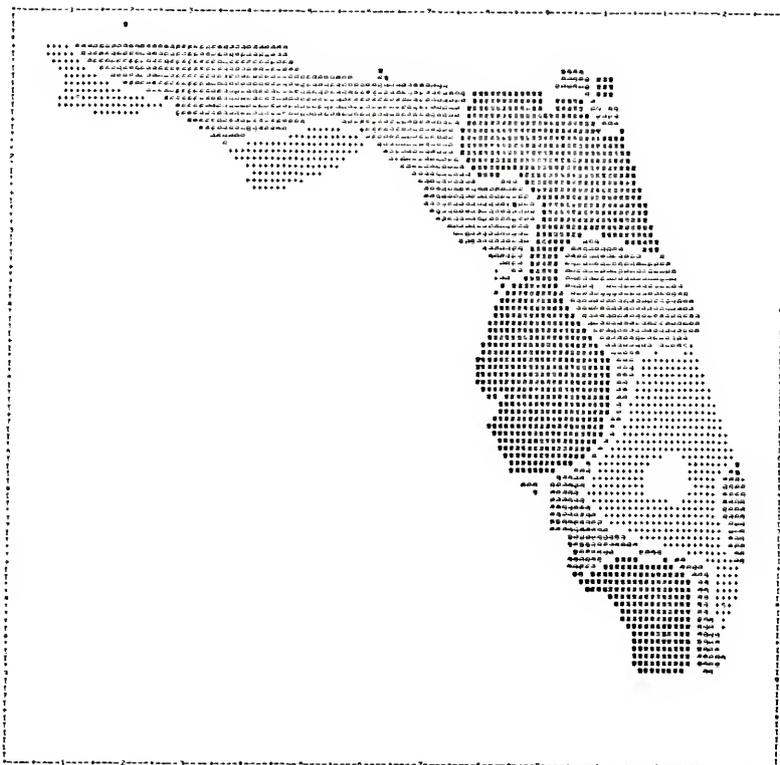
MAP 66. Geographic variation in Factor 3 for Coluber constrictor, both sexes. Factor 3 accounts for 13.2% of the total variation in 17 characters and most of the variation in gular and supralabial brown pigmentation, with a contribution from the number of ventrals plus caudals. Darker shading implies generally more brown pigment and fewer ventrals and caudals. Based on 440 specimens.



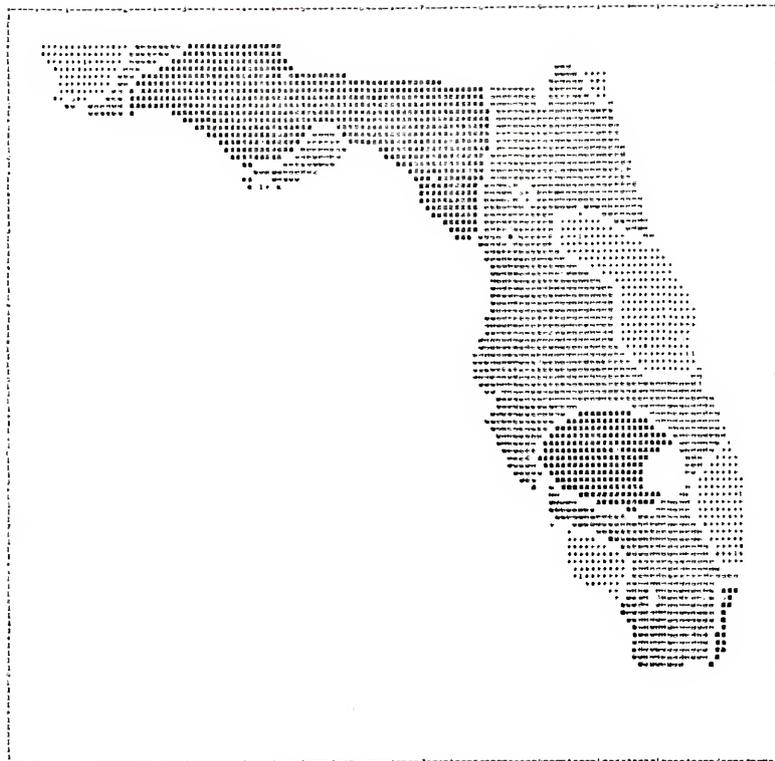
MAP 67. Localities of 85 *Masticophis flagellum* specimens examined. An asterisk represents one specimen; an S represents more than one.



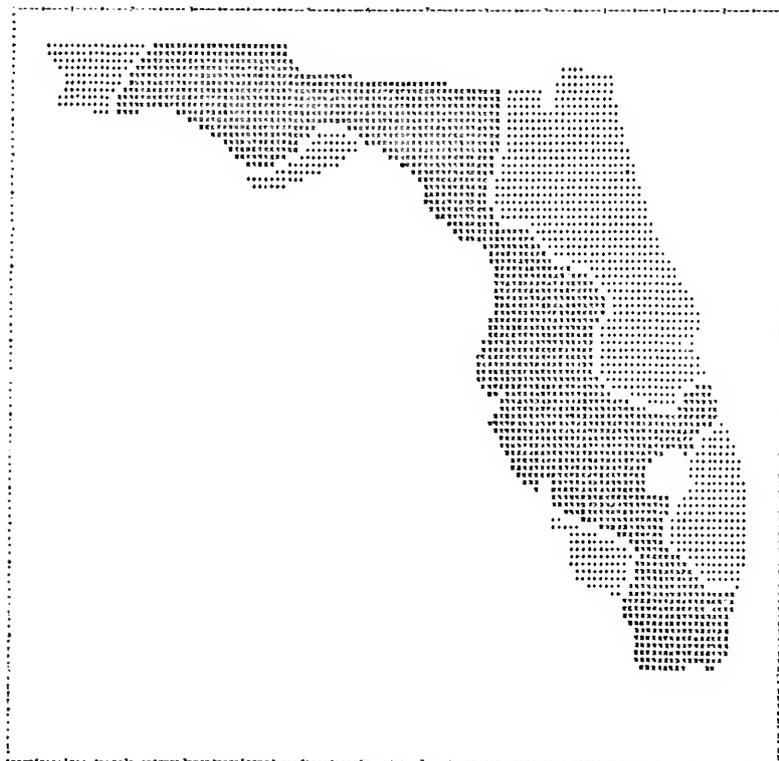
MAP 68. Geographic variation in number of ventral scales in *Masticophis flagellum*, males only. Levels by increasing shading are: 198-201; 202-203; 204-212. Based on 39 specimens.



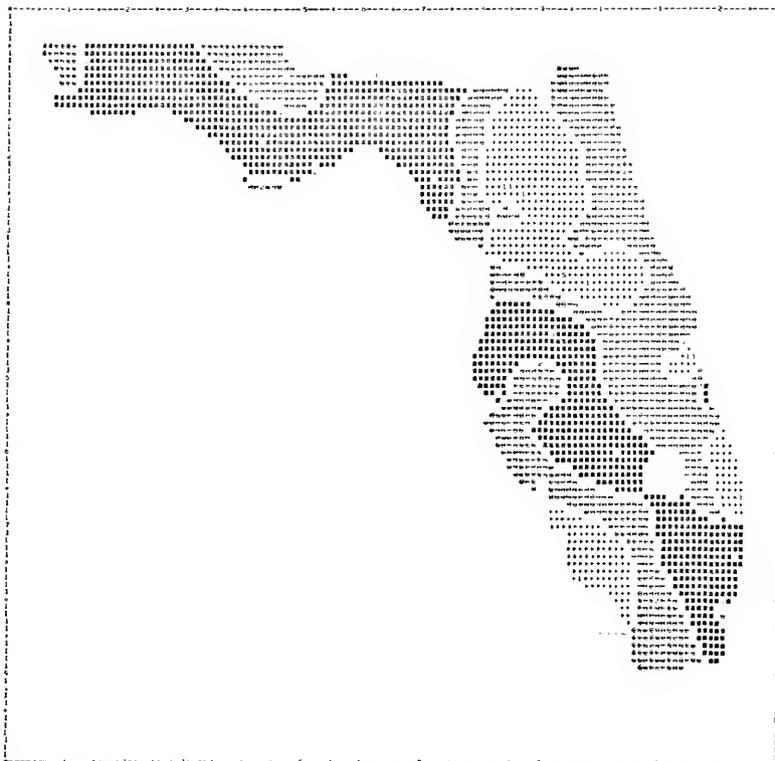
MAP 69. Geographic variation in number of ventral scales in *Masticophis flagellum*, females only. Levels by increasing shading are: 194-199; 200-201; 202-207. Based on 42 specimens.



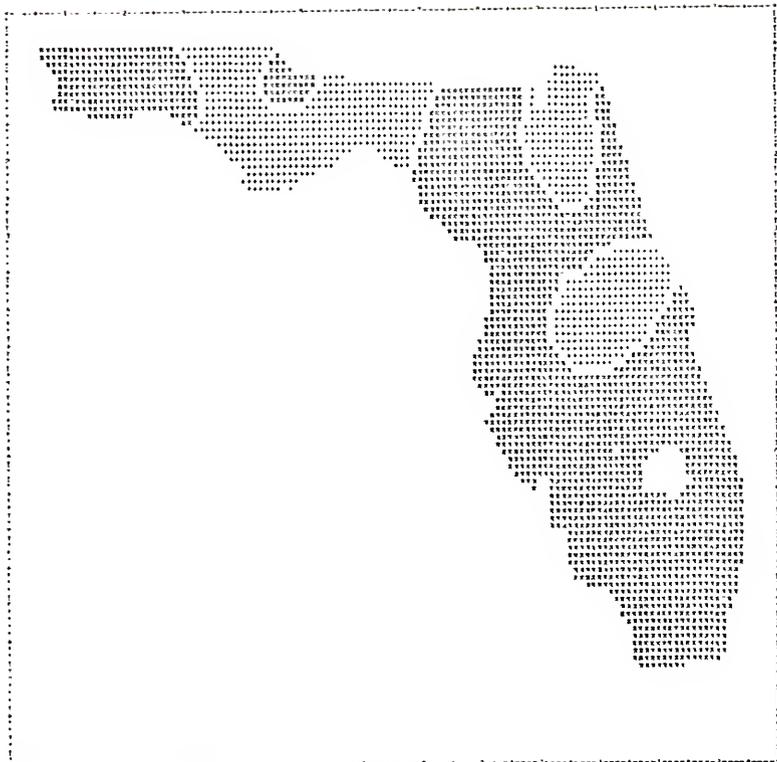
MAP 70. Geographic variation in number of subcaudal scales for *Masticophis flagellum*, both sexes. Levels by increasing shading are: 102-110; 111-114; 115-123. Based on 32 specimens.



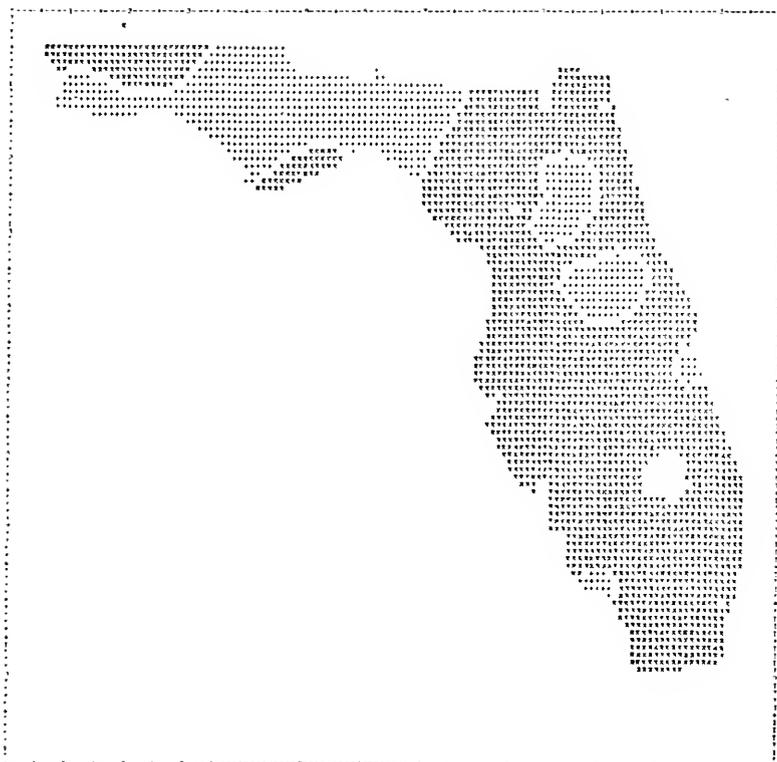
MAP 71. Geographic variation in the sum of ventrals plus caudals in *Masticophis flagellum*, both sexes. Levels by increasing shading are: 303-314; 315-325. Based on 31 specimens.



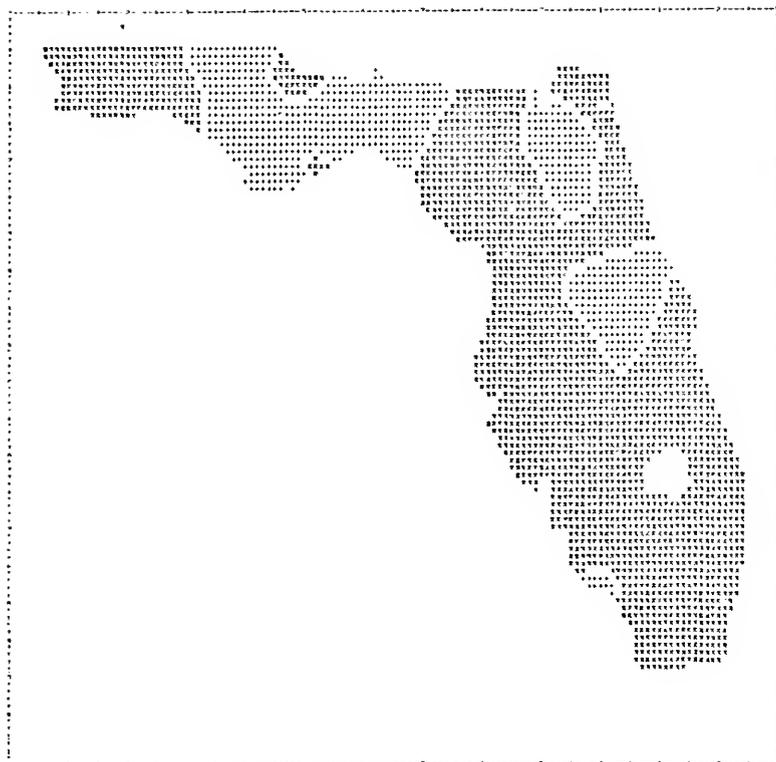
MAP 72. Geographic variation in tail length divided by total length in *Masticophis flagellum*, both sexes. Levels by increasing shading are: 0.23-0.24; 0.25-0.26; 0.27-0.30. Based on 31 specimens.



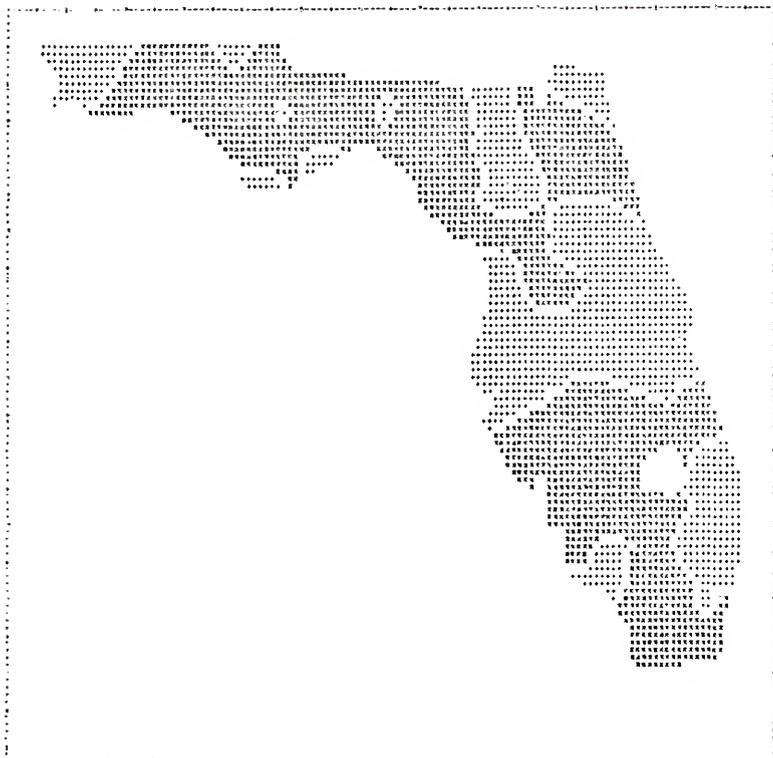
MAP 73. Geographic variation in color phase for *Masticophis flagellum*, males only. Light shading refers to light phase, and dark shading to the dark phase. Based on 40 specimens.



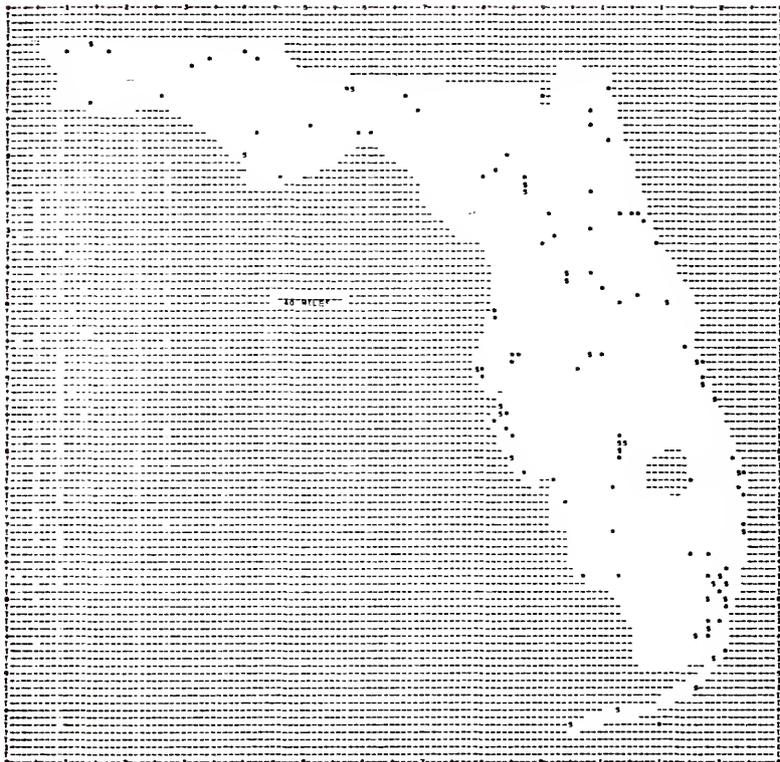
MAP 74. Geographic variation in color phase for *Mastigophis flagellum*, females only. Light shading represents the light phase, dark shading the dark phase. Based on 42 specimens.



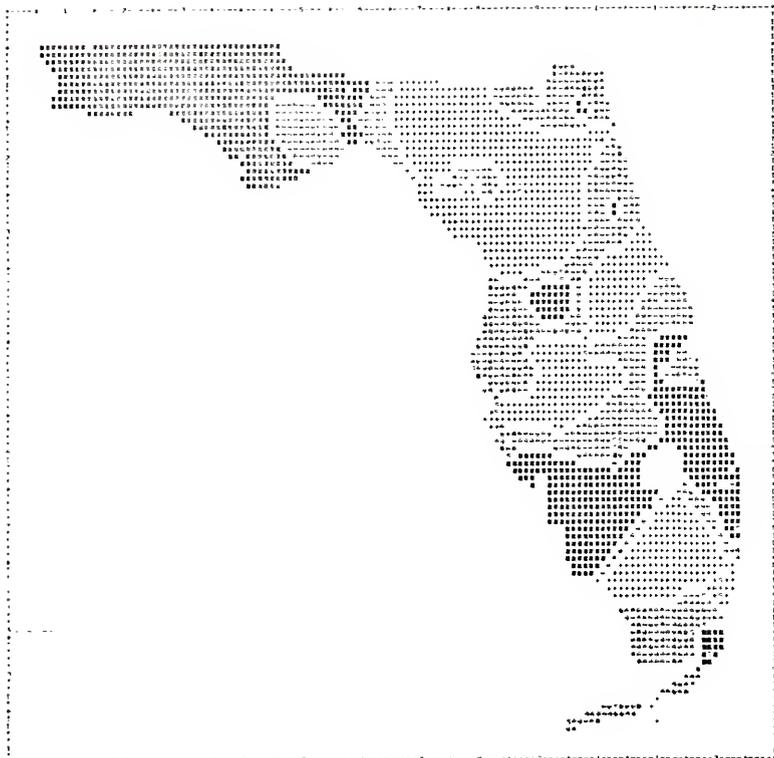
MAP 75. Geographic variation in color phase for Mastigophis flagellum, both sexes. Light shading represents the light phase and dark shading the dark phase. Based on 84 specimens.



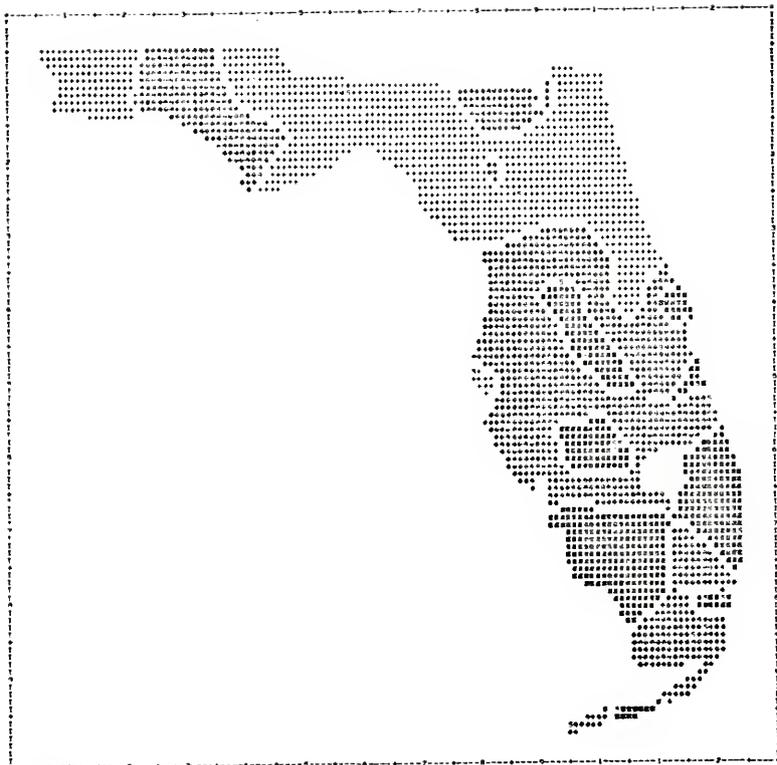
MAP 76. Geographic variation in Factor 1 for Masticophis flagellum, both sexes. Factor 1 accounts for 43.0% of the total variation in 5 characters, and most of the variation in number of caudals and ventrals. Darker shading represents higher values for both. Based on 69 specimens.



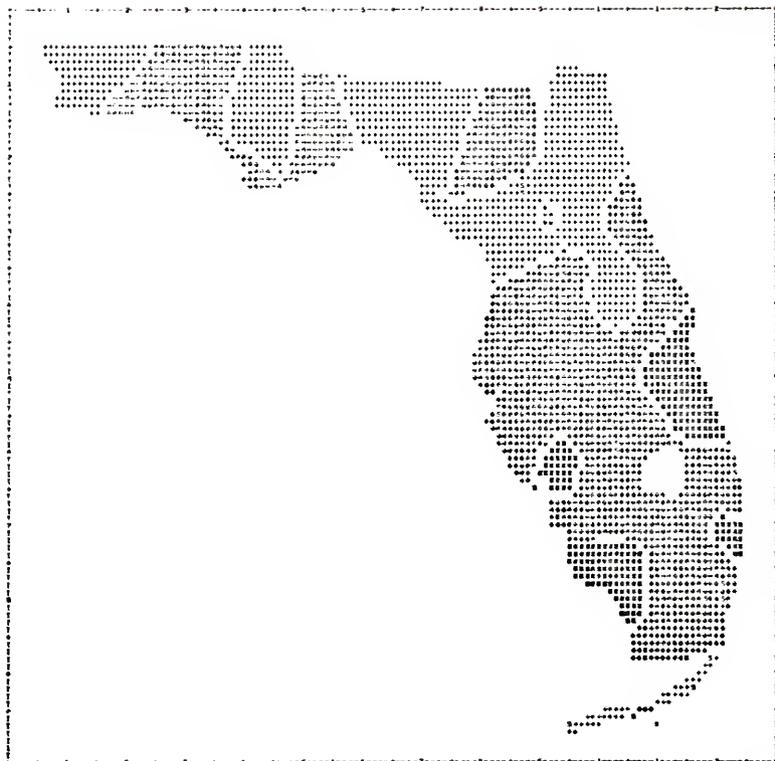
MAP 77. Localities of 176 *Ophiodrys aestivus* specimens examined. An asterisk represents a single specimen; an S represents more than one specimen.



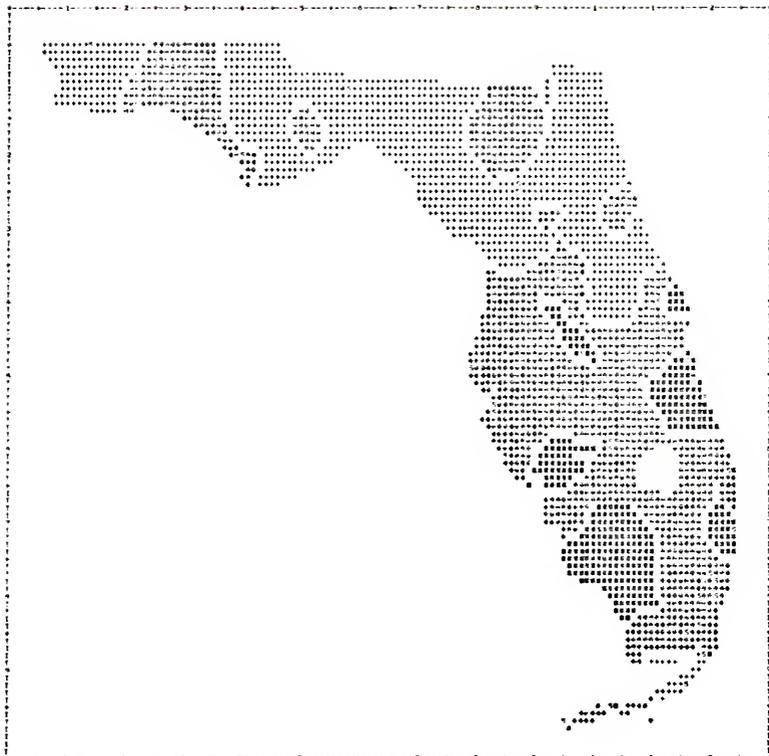
MAP 78. Geographic variation in the sum of ventrals plus caudals in *Opheodrys aestivus*, both sexes. Levels by increasing shading are: 282-295; 296-303; 304-322. Based on 138 specimens.



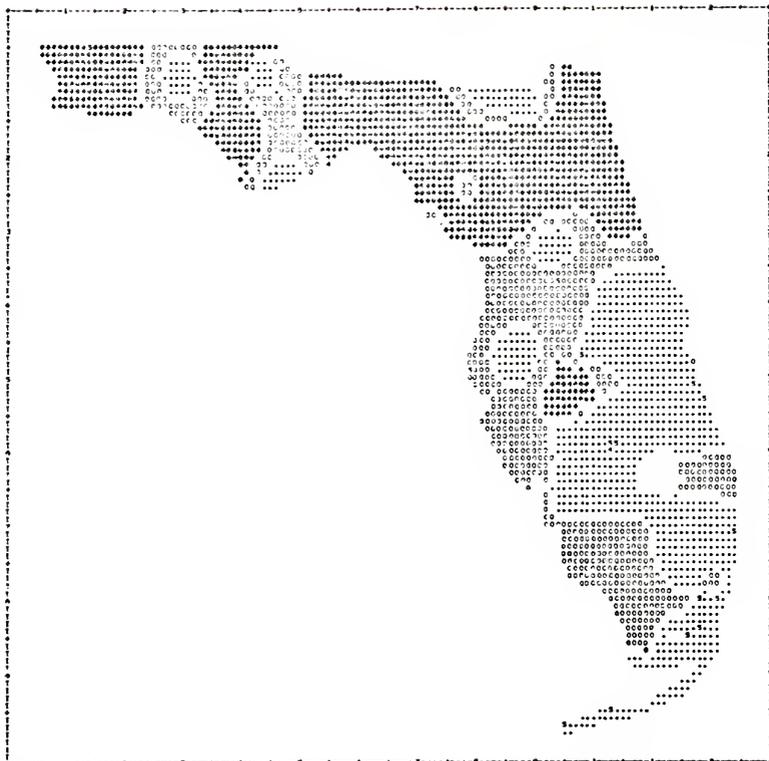
MAP 79. Geographic variation in the development of the keel on the scales of the second dorsal row at mid-body in *Ophiodrys aestivus*, males only. Lightest shading represents no keel; darkest shading represents a well-developed keel, and intermediate shading the intermediate condition. Based on 79 specimens.



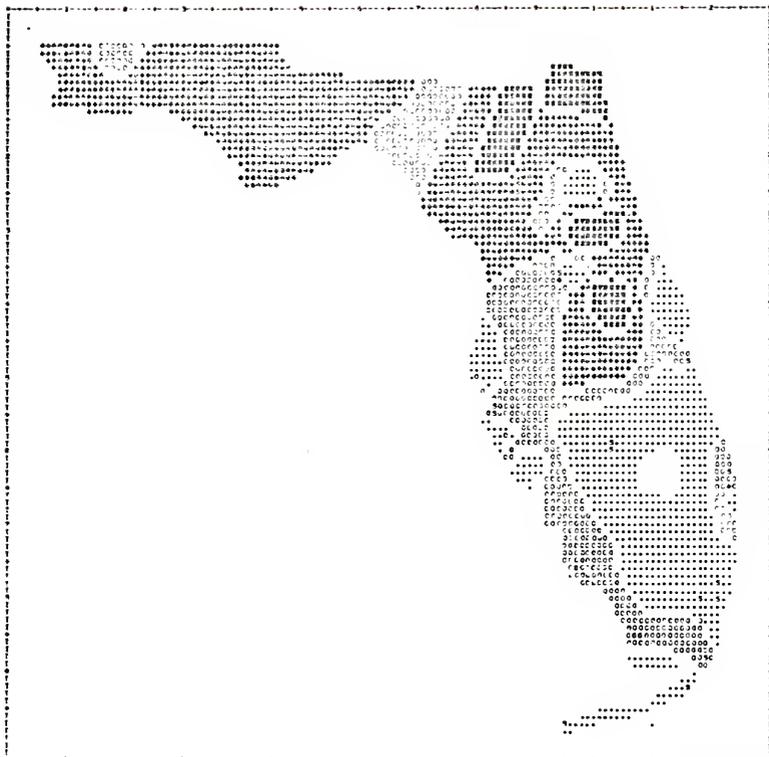
MAP 80. Geographic variation in the development of the keel on the scales of the second dorsal row at mid-body in *Opheodrys aestivus*, females only. Lightest shading represents no keel on the scales of the second dorsal row at mid-body; darkest shading represents a well-developed keel, and intermediate shading, the intermediate condition. Based on 97 specimens.



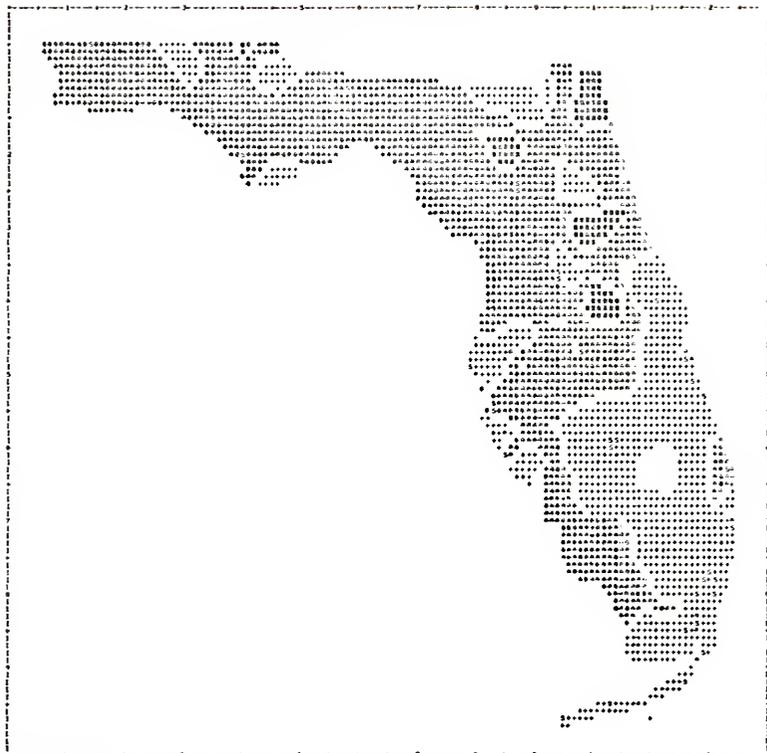
MAP 81. Geographic variation in development of the keel on the scales of the second dorsal row at mid-body in Opheodrys aestivus, both sexes. Lightest shading represents no keel on the scales of the second dorsal row at mid-body; darkest shading represents a well-developed keel present, and intermediate shading the intermediate condition. Based on 176 specimens.



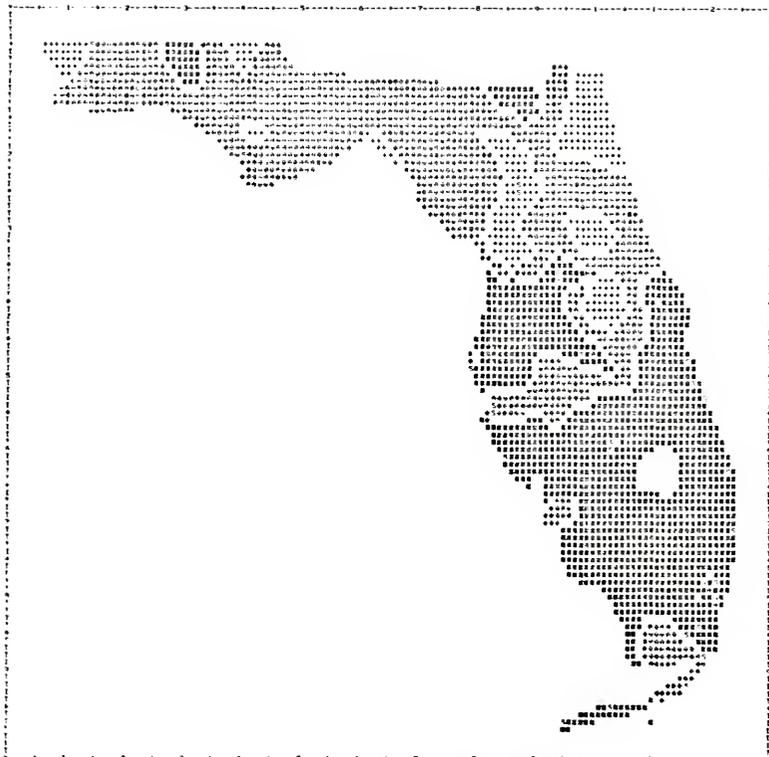
MAP 82. Geographic variation in the amount of dark pigmentation on the supralabial scales in *Ophedrysd aestivus*, males only. Darker shading implies more dark pigment on the supralabials. Based on 79 specimens.



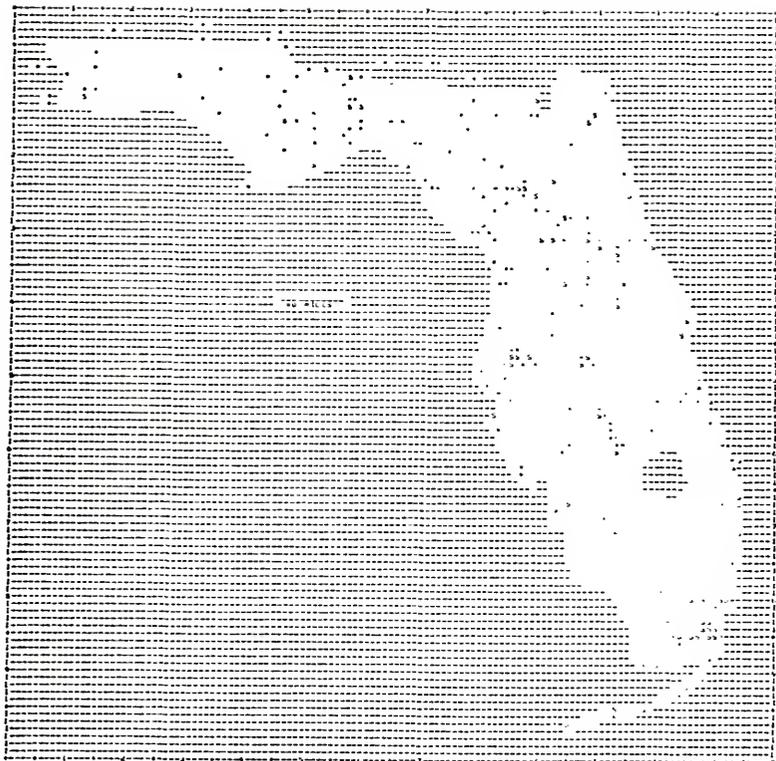
MAP 83. Geographic variation in the amount of dark pigmentation on the supralabial scales in *Ophedrys aestivus*, females only. Darker shading implies more dark pigment on the supralabials. Based on 96 specimens.



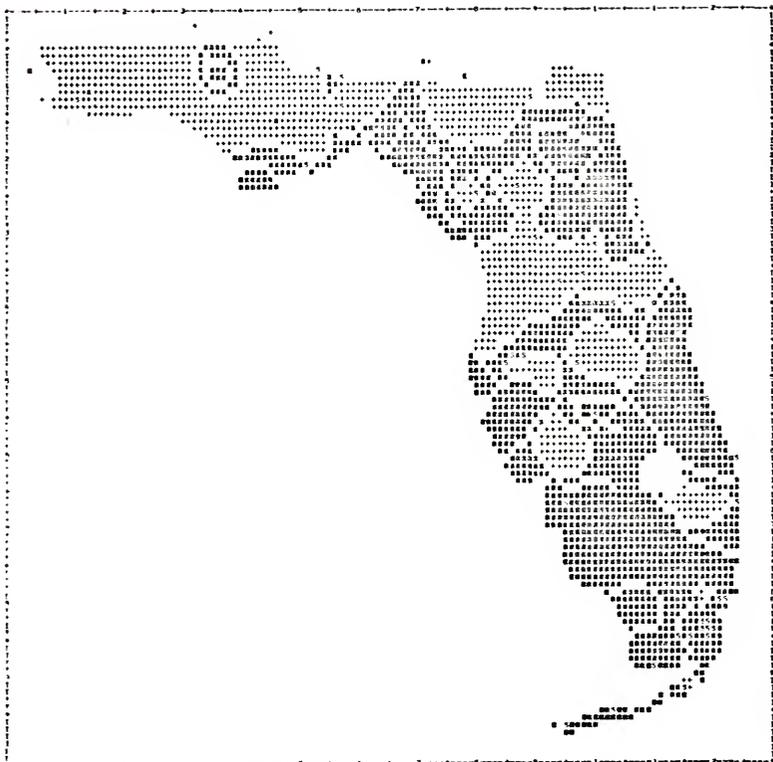
MAP 84. Geographic variation in extent of supralabial dark pigmentation in *Opheodrys aestivus*, both sexes. Increased shading represents increased labial pigmentation. Based on 175 specimens.



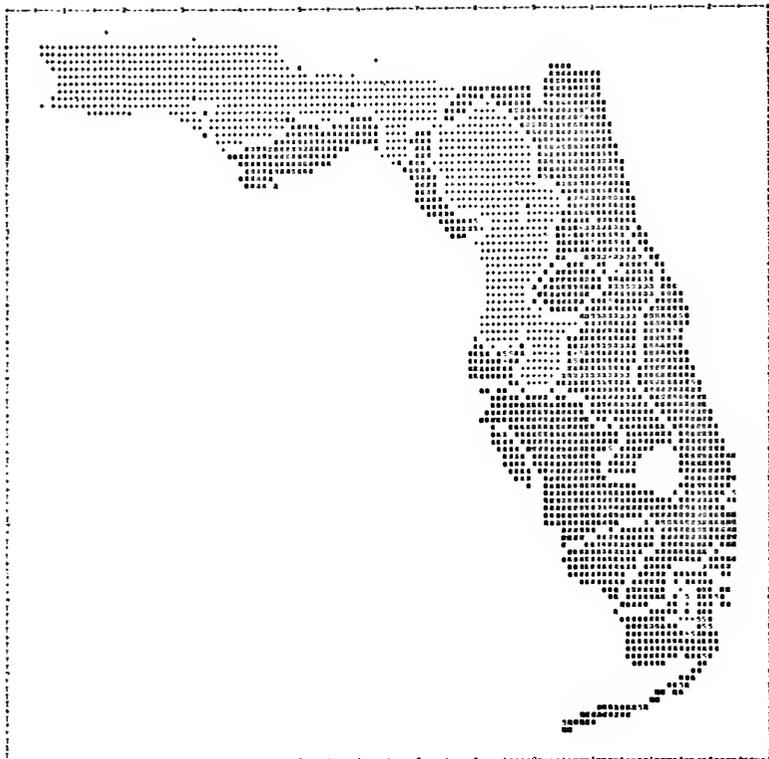
MAP 35. Geographic variation in Factor 3 for *Opheodryx aestivus*, both sexes. Factor 3 accounts for most of the variation in supralabial pigmentation and keels on the scales of the second dorsal row at mid-body. Darker shading represents generally lower values for supralabial pigmentation and higher values for keeling of the second scale row. Total variation accounted for by Factor 3: 12.6% (10 characters). Based on 176 specimens.



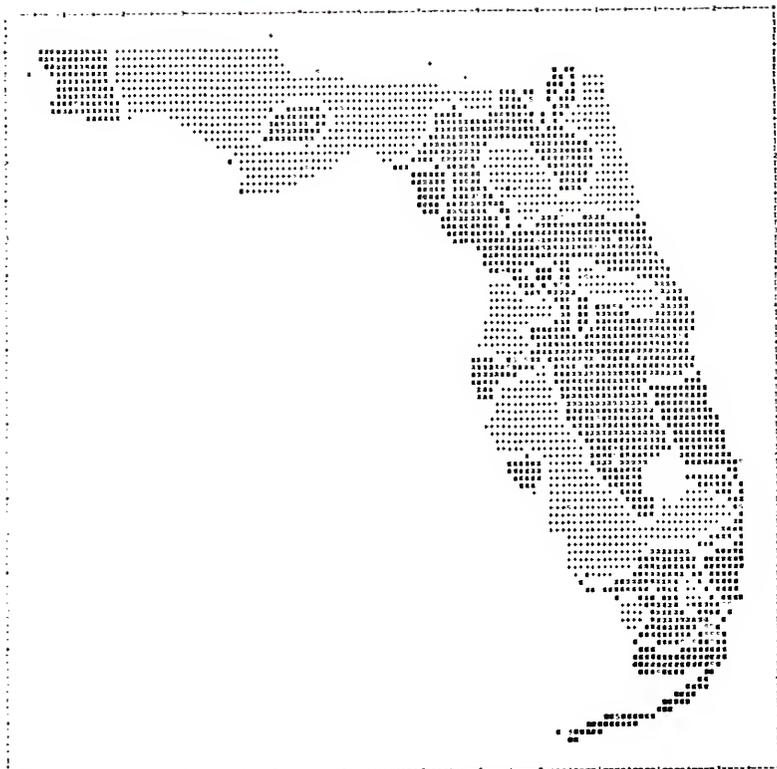
MAP 86. Localities of 455 *Elaphe guttata* specimens examined. An asterisk represents one specimen; an S represents more than one.



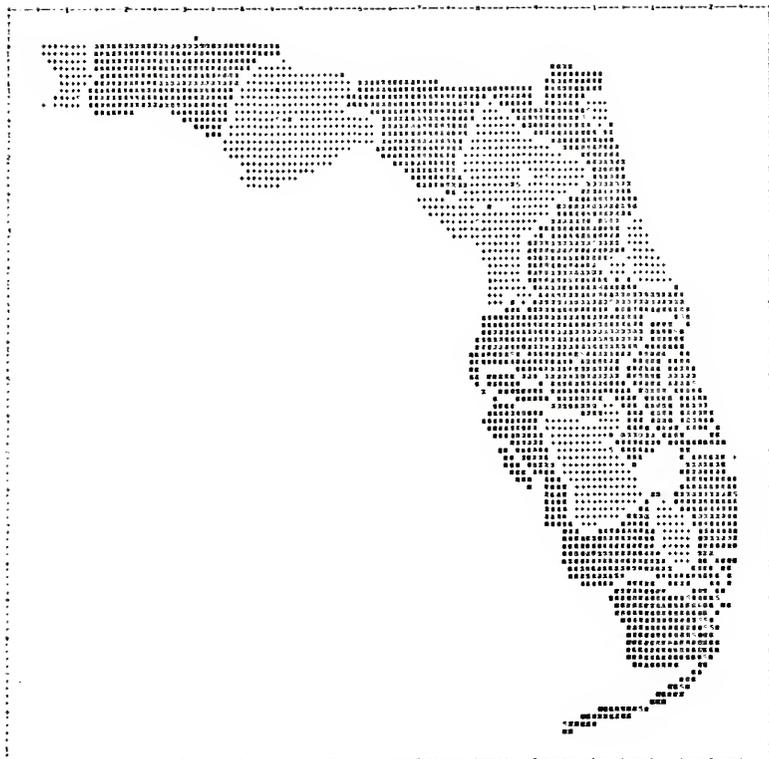
MAP 87. Geographic variation in number of ventral scales in *Elaphe guttata*, males only. Levels by increasing shading are: 210-220; 221-224; 225-241. Based on 264 specimens.



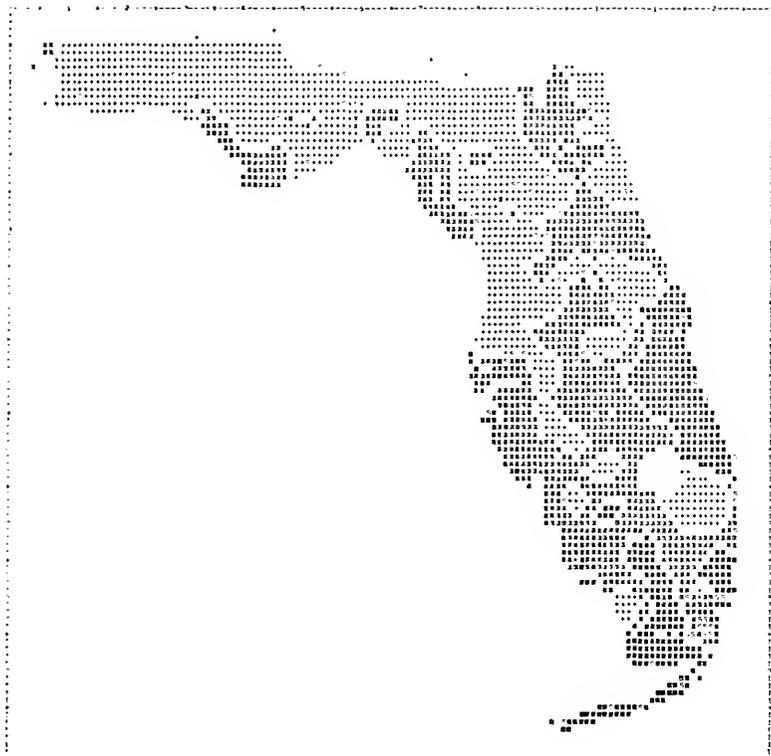
MAP 88. Geographic variation in number of ventral scales in *Elaphe guttata*, females only. Levels by increasing shading are: 218-227; 228-233; 234-247. Based on 183 specimens.



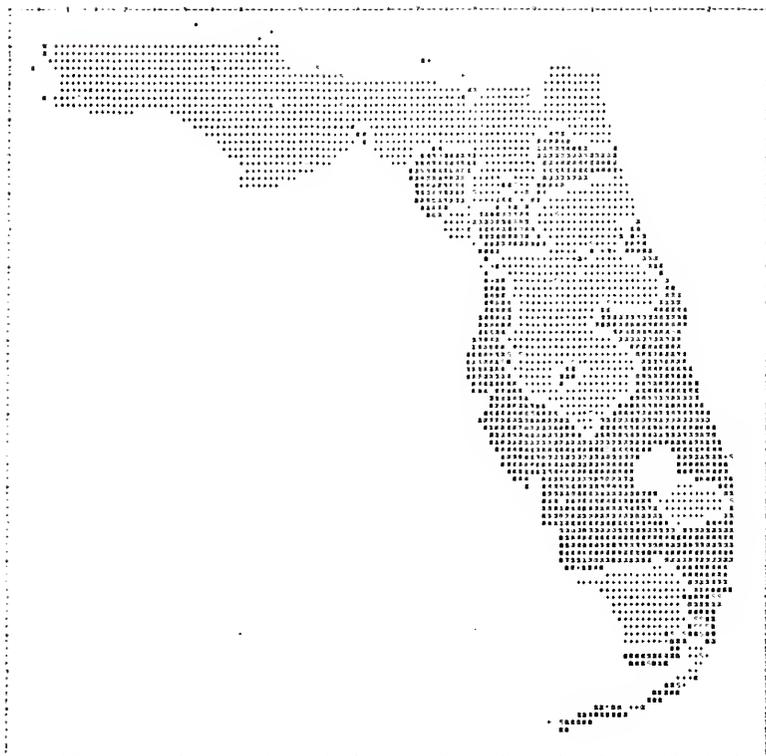
MAP 89. Geographic variation in number of subcaudal scales in *Elaphe guttata*, males only. Levels by increasing shading are: 60-69; 70-73; 74-87. Based on 217 specimens.



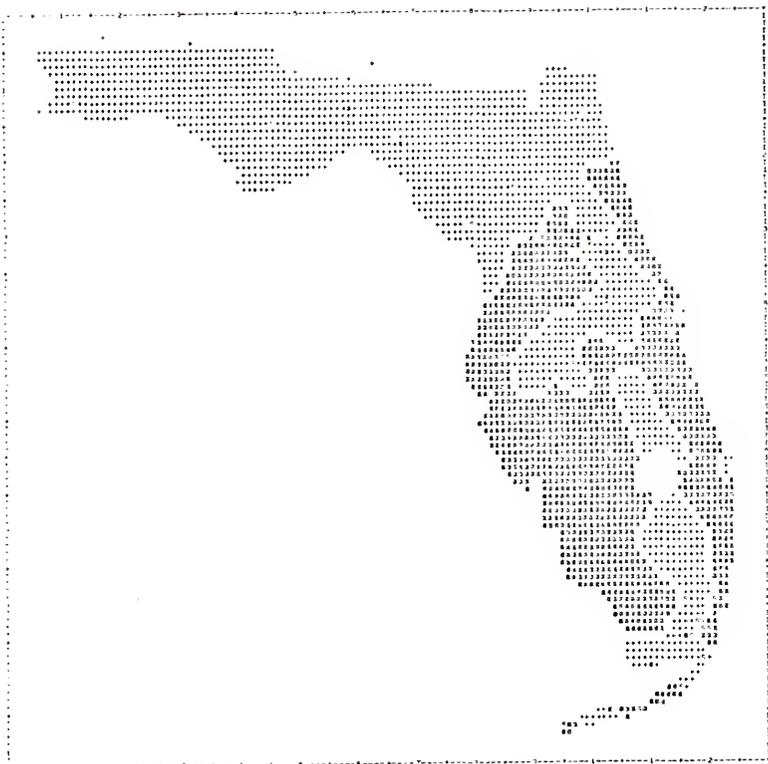
MAP 90. Geographic variation in number of subcaudal scales in *Elaphe guttata*, females only. Levels by increasing shading are: 47-63; 64-67; 68-81. Based on 153 specimens.



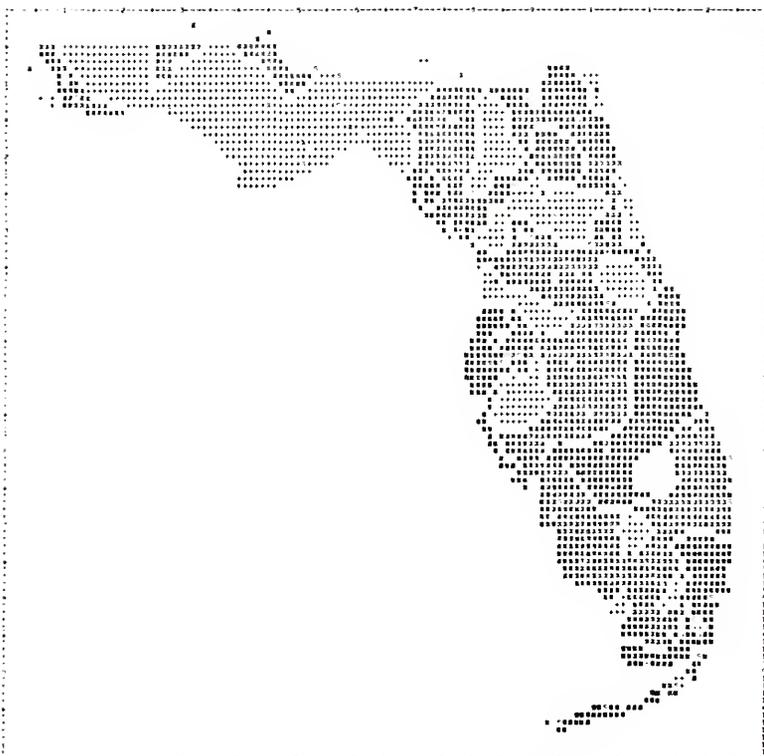
MAP 91. Geographic variation in the sum of ventrals plus caudals in *Elaphe guttata*, both sexes. Levels by increased shading are: 273-292; 293-299; 300-319. Based on 367 specimens.



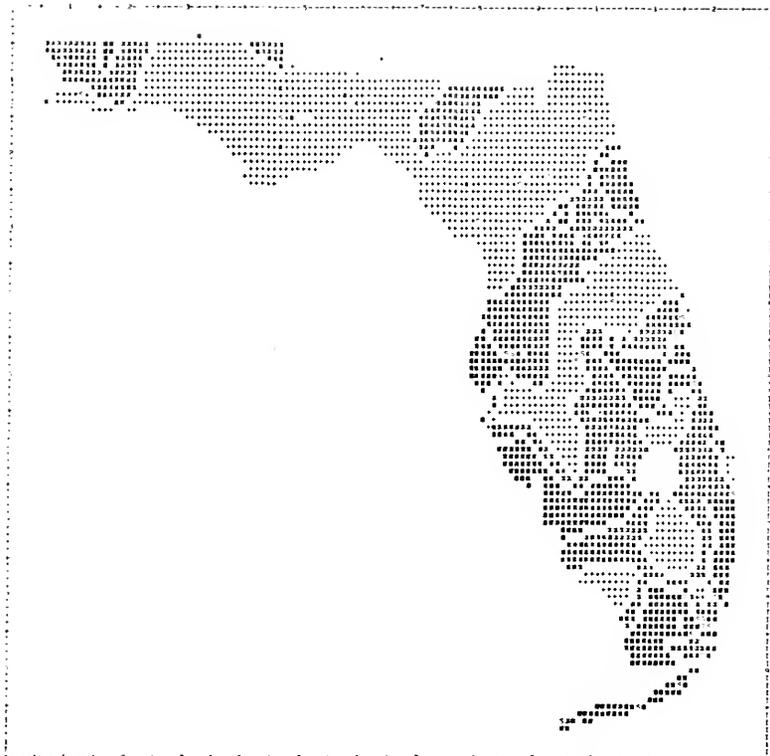
MAP 92. Geographic variation in number of body blotches in *Elaphe guttata*, males only. Lighter shading represents from 26 to 34 body blotches; darker shading represents from 35 to 46. Based on 266 specimens.



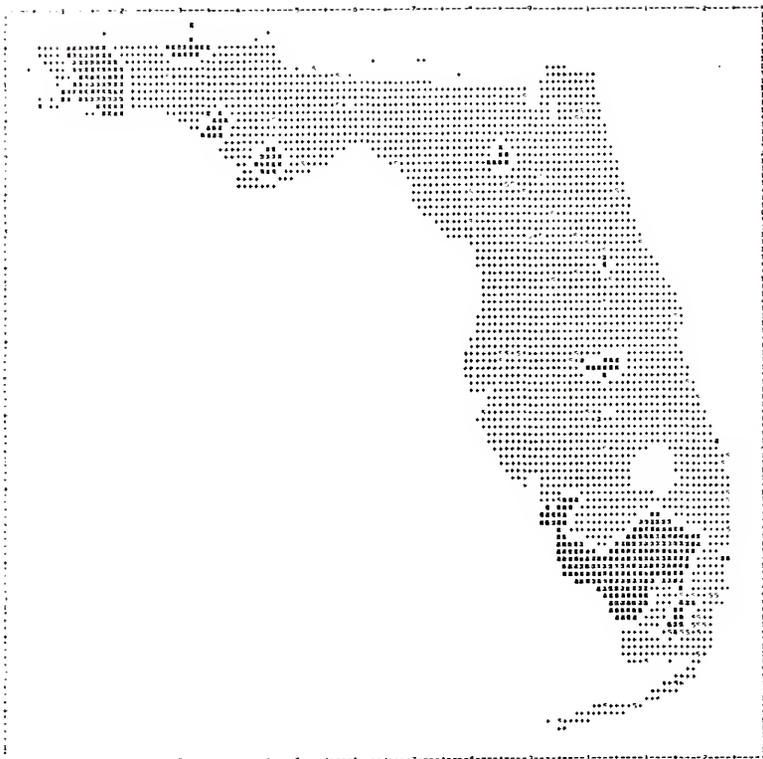
MAP 93. Geographic variation in number of body blotches in *Elaphe guttata*, females only. Lighter shading represents from 26 to 34 body blotches; darker shading represents from 35 to 50. Based on 186 specimens.



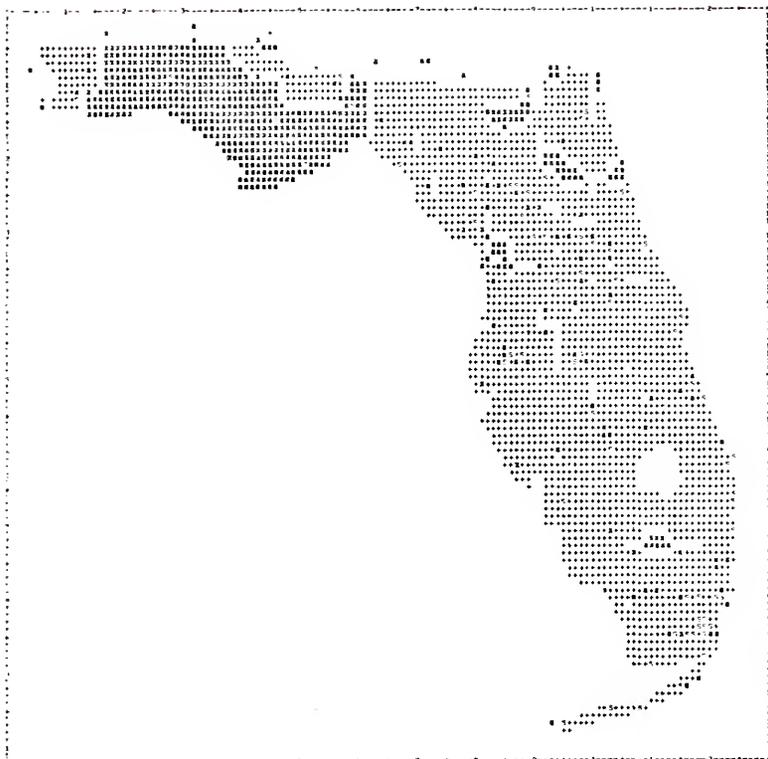
MAP 94. Geographic variation in number of tail blotches in *Elaphe guttata*, males only. Levels by increased shading are: 9-12; 13-14; 15-23. Based on 252 specimens.



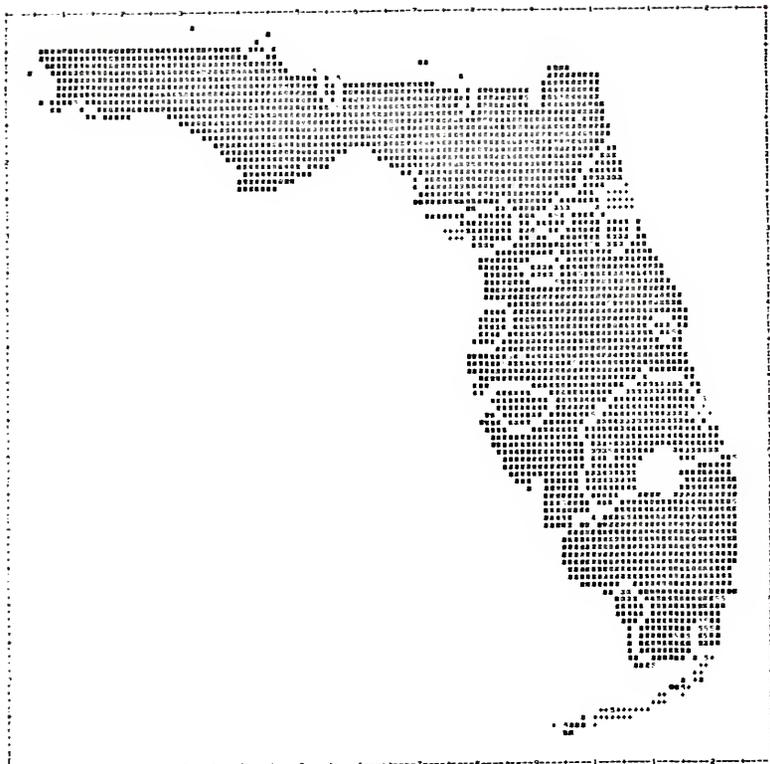
MAP 95. Geographic variation in number of tail blotches in *Elaphe guttata*, females only. Levels by increasing shading are: 8-11; 12-13; 14-22. Based on 173 specimens.



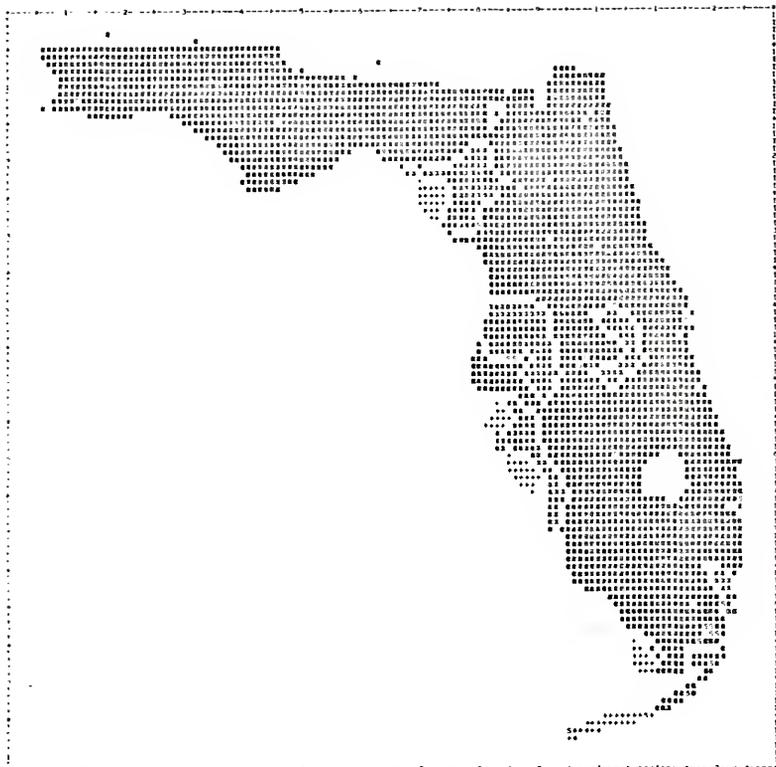
MAP 96. Geographic variation in width of the black dorsal blotch border in *Elaphe guttata*, both sexes. Lighter shading represents narrow or absent blotch border; darker shading represents blotch borders more than one scale in width. Based on 453 specimens.



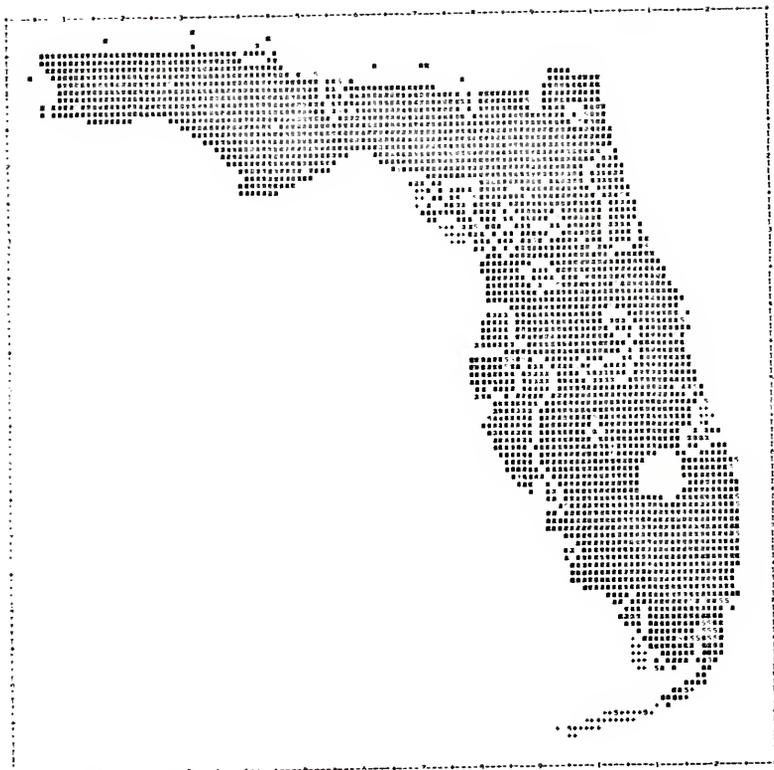
MAP 97. Geographic variation in lateral spot shape in *Elaphe guttata*, both sexes. Lighter shading represents more or less complete lateral spots; darker shading represents spots which are open on the bottom, resembling an inverted U. Based on 423 specimens.



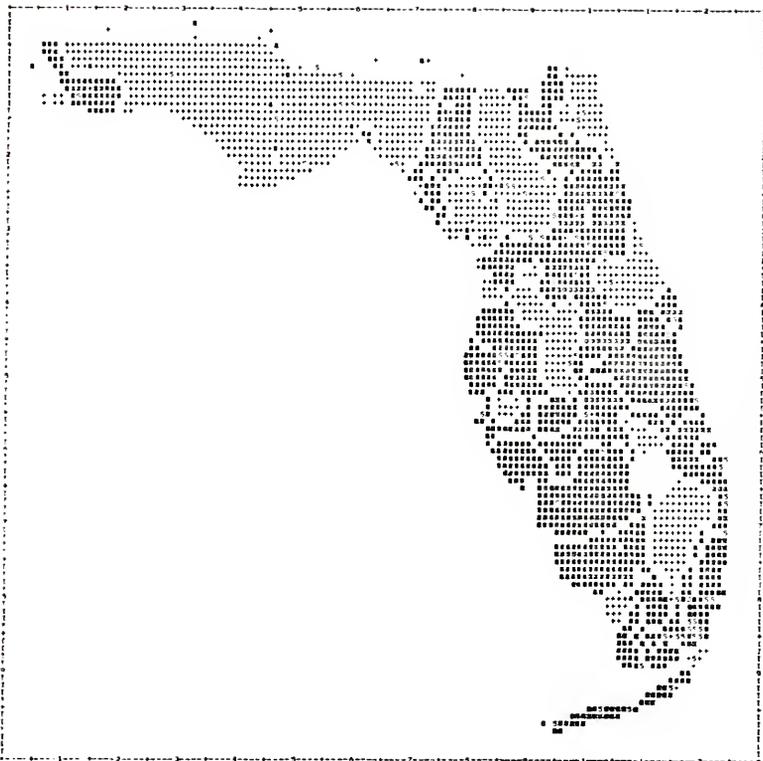
MAP 98. Geographic variation in relative extent of ventral dark pigmentation in *Elaphe guttata*, males only. Darker shading implies increased dark pigment ventrally. Based on 267 specimens.



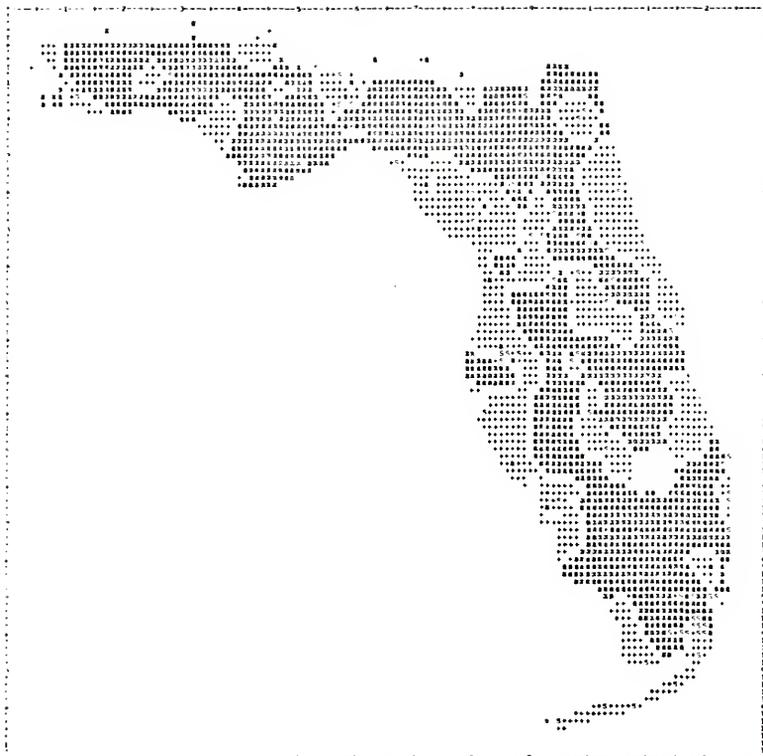
MAP 99. Geographic variation in relative extent of dark ventral pigmentation in *Elaphe guttata*, females only. Darker shading implies increased ventral pigment. Based on 188 specimens.



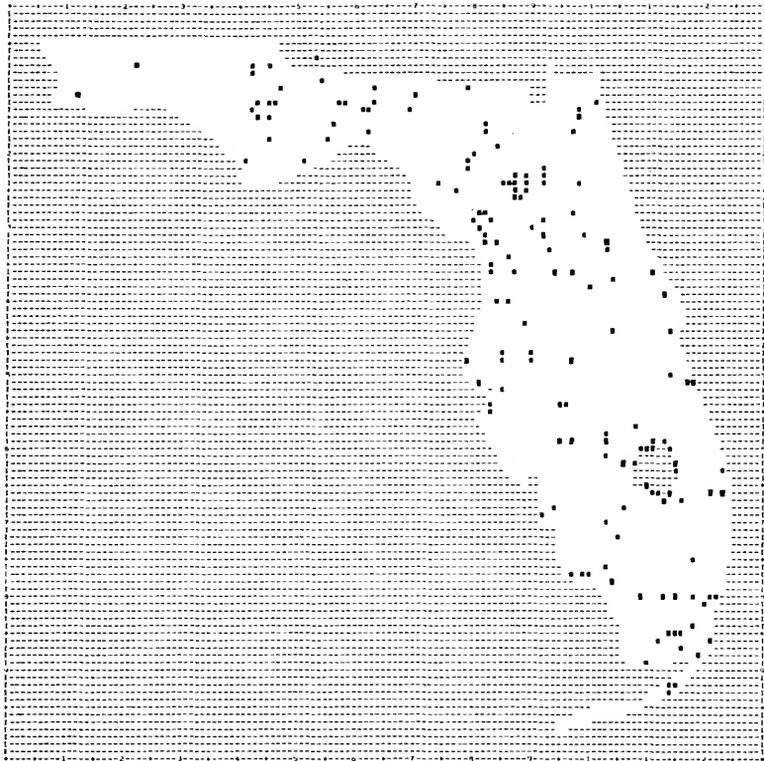
MAP 100. Geographic variation in relative extent of ventral dark pigmentation in *Elaphe guttata*, both sexes. Darker shading implies increased dark pigment ventrally. Based on 455 specimens.



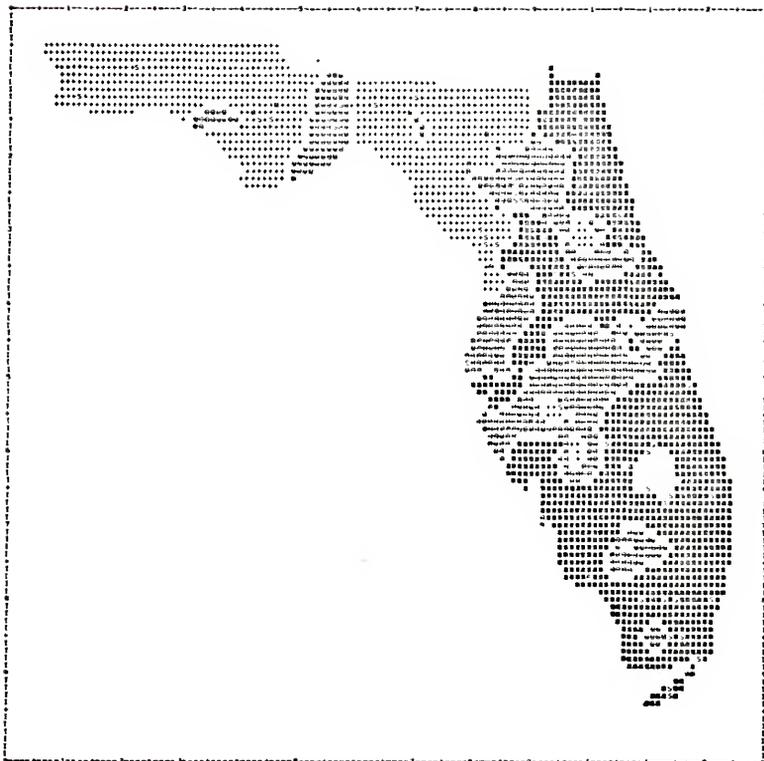
MAP 101. Geographic variation in Factor 1 for *Elaphe guttata*, both sexes. Factor 1 accounts for most of the variation in body spots, tail spots and sum of ventrals plus caudals. Darker shading represents generally higher values for all three. Total variation accounted for by Factor 1: 19.9% (12 characters). Based on 455 specimens.



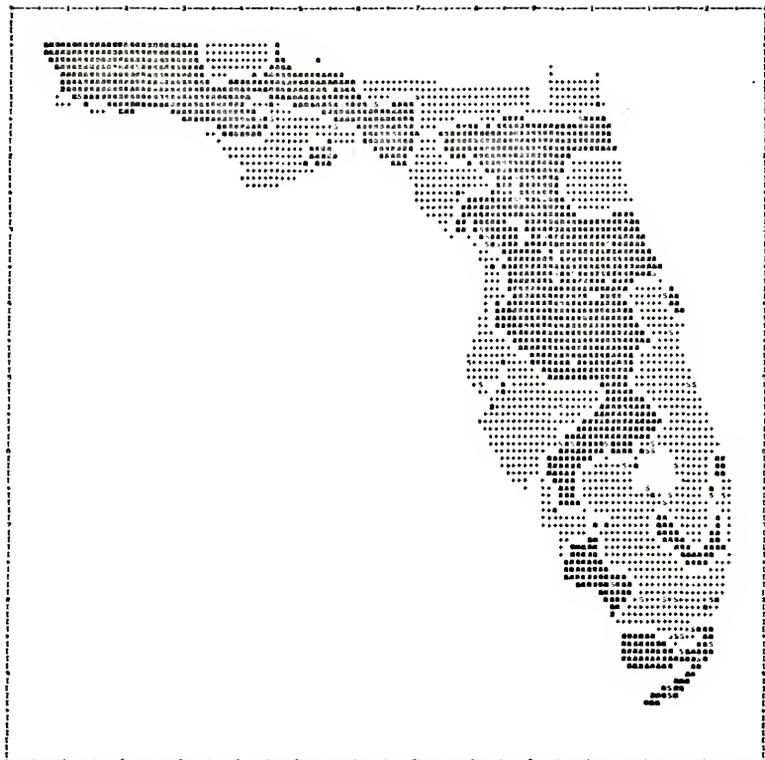
MAP 102. Geographic variation in Factor 2 for *Elaphe guttata*, both sexes. Factor 2 accounts for most of the variation in extent of ventral pigment, and shape of the ventral checks. It also receives a contribution from width of the dorsal blotch border. Darker shading represents generally more dark pigment ventrally and wider ventral checks as well as wider dorsal blotch borders. Total variation accounted for by Factor 2: 15.0% (12 characters). Based on 455 specimens.



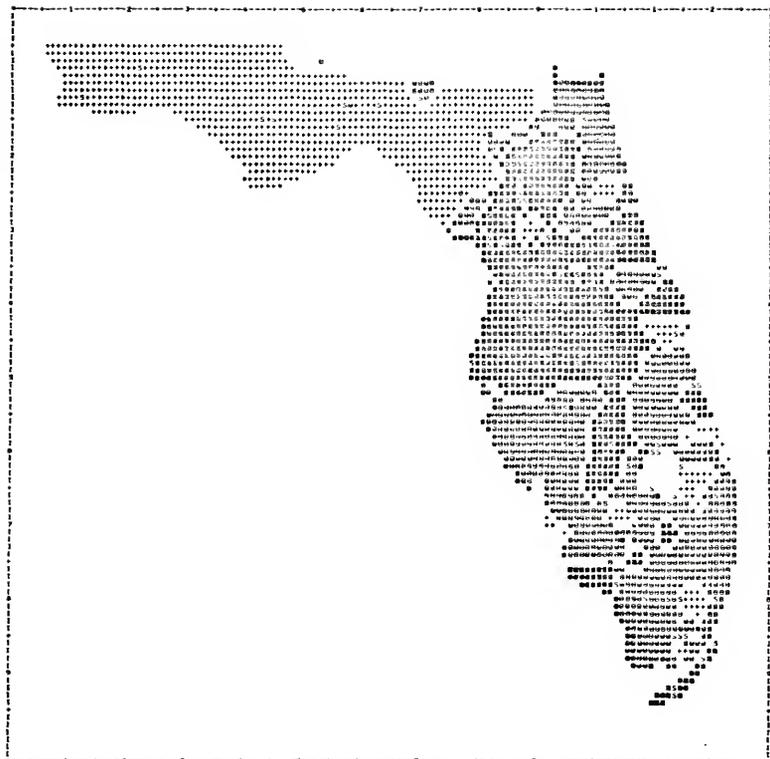
MAP 103. Localities of 370 *Elaphe obsoleta* specimens examined.



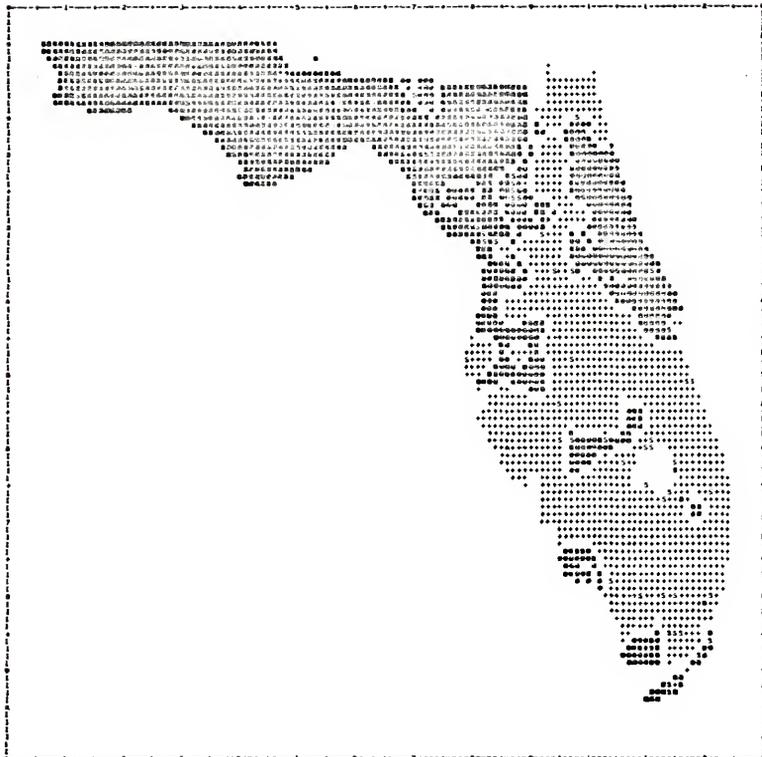
MAP 104. Geographic variation in number of dorsal body blotches in *Elaphe obsoleta*, both sexes. Levels by increasing shading are: 28-35; 36-38; 39-49. Based on 222 specimens.



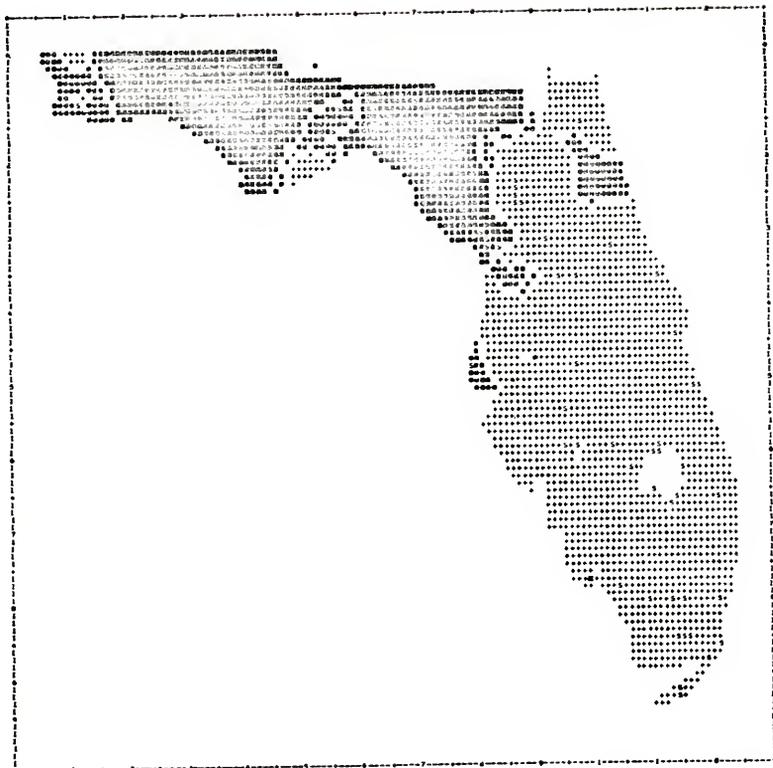
MAP 105. Geographic variation in ground color for *Elaphe obsoleta*, both sexes. Darker shading represents a darker ground color. Based on 370 specimens.



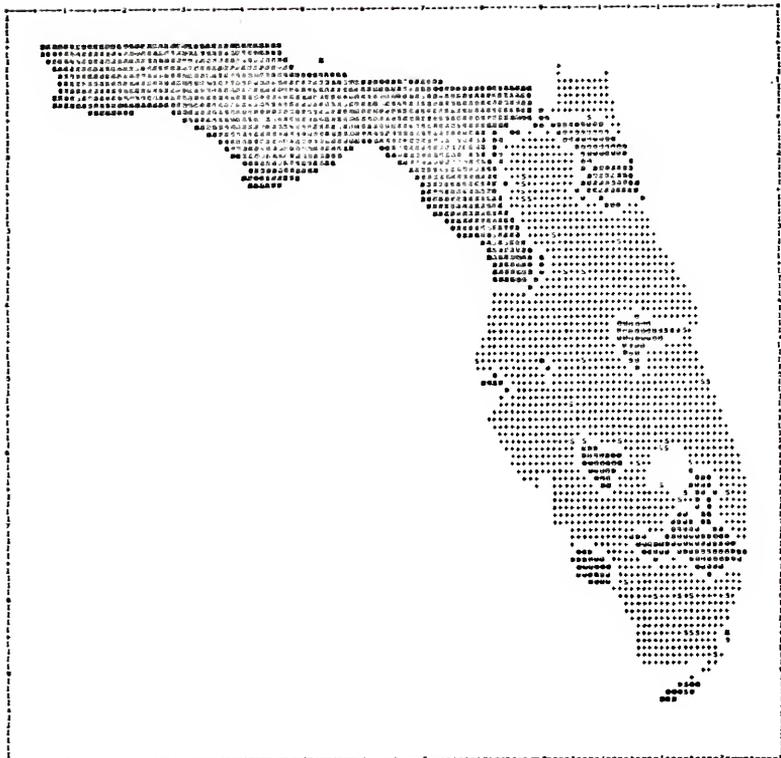
MAP 106. Geographic variation in development of the dorsal stripes in *Elaphe obsoleta*, both sexes, excluding juveniles. The darker the shading the better defined the dorsal stripes. Based on 322 specimens.



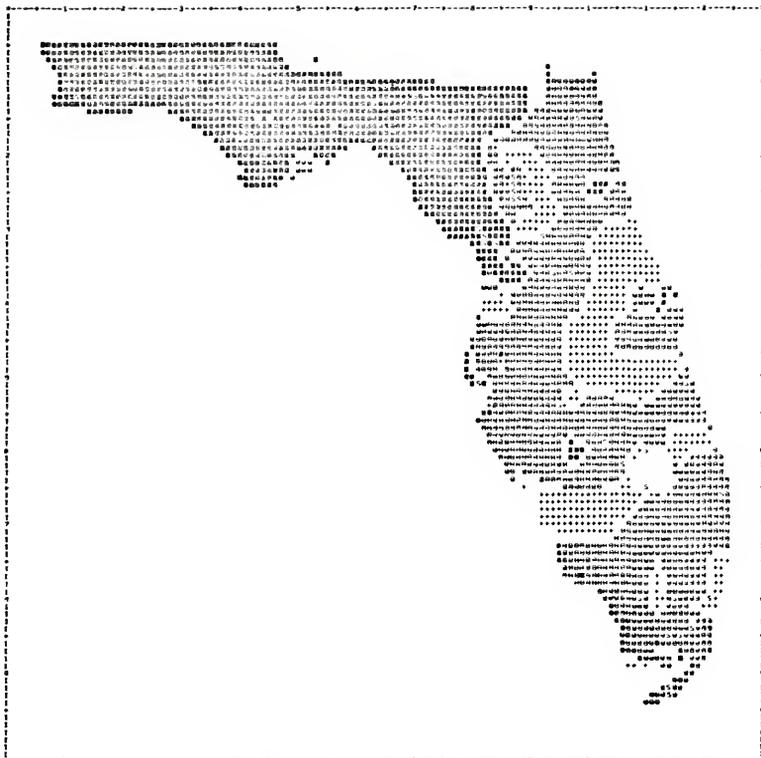
MAP 107. Geographic variation in development of the dorsal blotches in *Elaphe obsoleta*, both sexes, excluding juveniles. Darker shading represents snakes with better defined dorsal blotches. Based on 323 specimens.



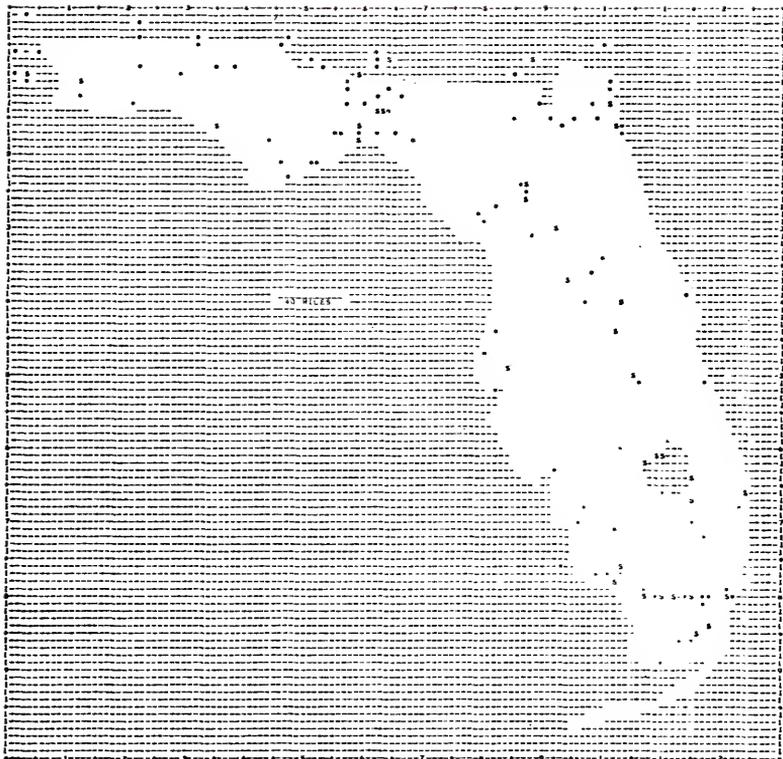
MAP 108. Geographic variation in amount of dark ventral pigmentation in *Elaphe obsoleta*, both sexes, excluding juveniles. The darker the shading, the more dark ventral pigment. Based on 323 specimens.



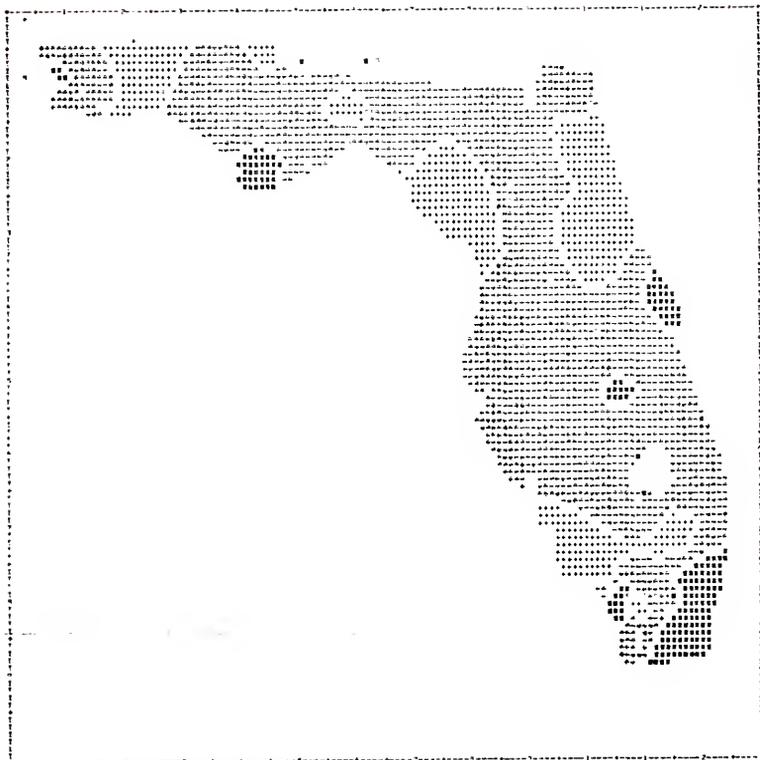
MAP 109. Geographic variation in amount of dark labial pigmentation in *Elaphe obsoleta*, both sexes, excluding juveniles. The darker the shading, the more labial dark pigment. Based on 323 specimens.



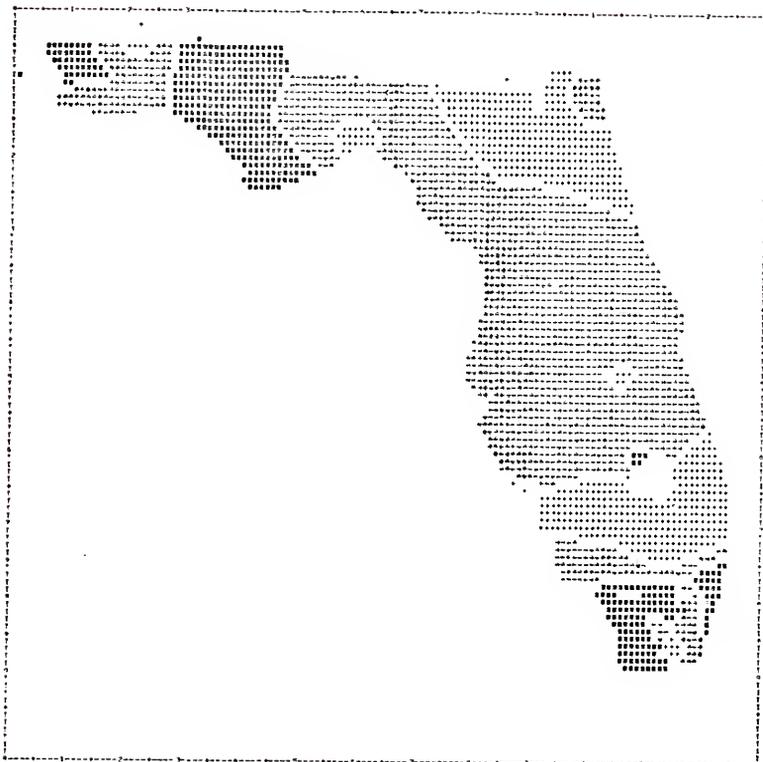
MAP 110. Geographic variation in Factor 1 for *Elaphe obsoleta*, both sexes. Factor 1 accounts for 51.6% of the variation in four characters, and most of the variation in number of dorsal blotches (when present), amount of dark pigment on the labials, and dark pigment on the venter. Darker shading represents snakes with fewer blotches (when present) and more dark pigment. Based on 370 specimens.



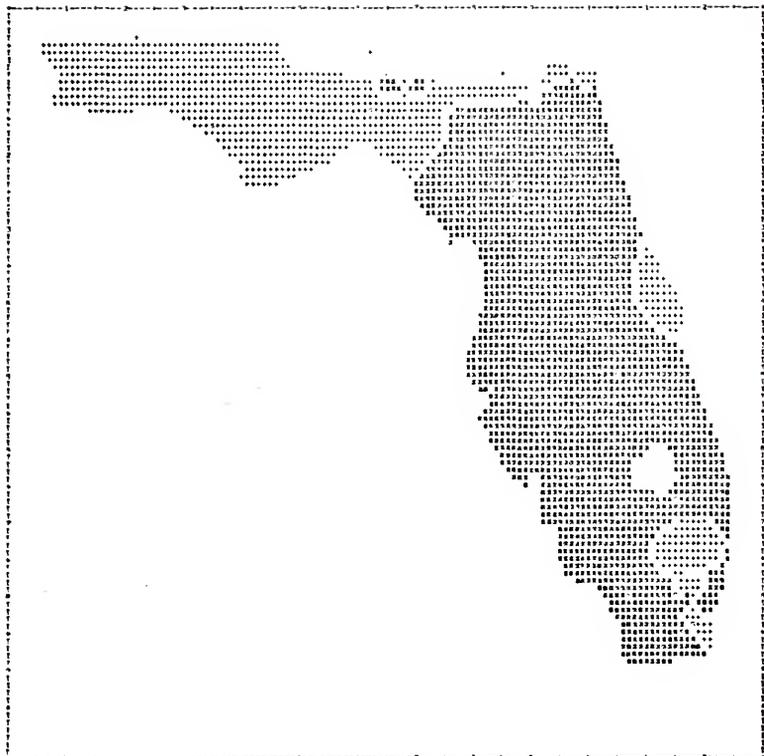
MAP 111. Localities of 207 *Lampropeltis getulus* specimens examined. An asterisk represents a single specimen; an S represents more than one specimen.



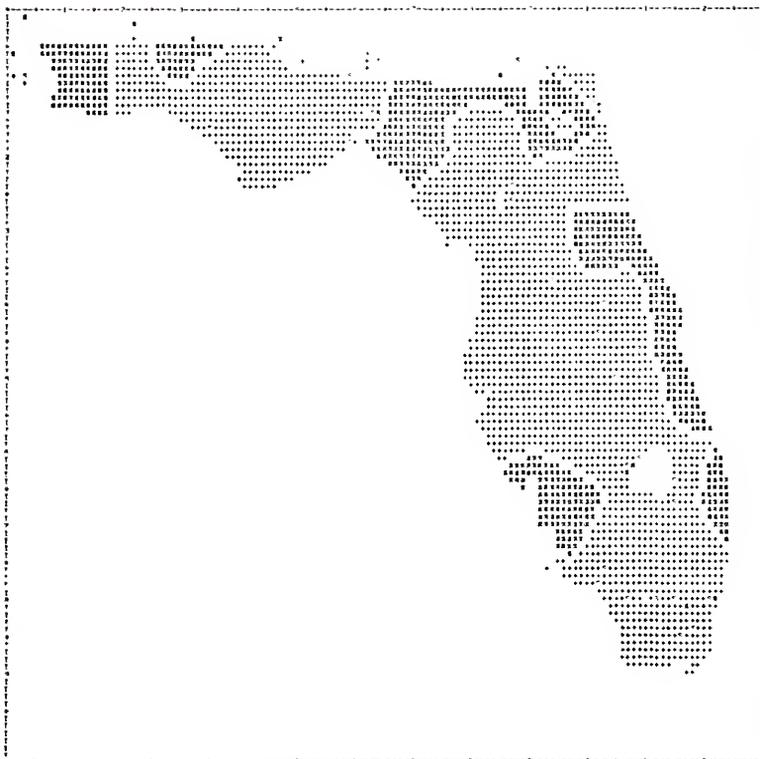
MAP 112. Geographic variation in tail length divided by total length in *Lampropeltis getulus*, males only. Darker shading represents proportionately longer tails. Based on 63 specimens.



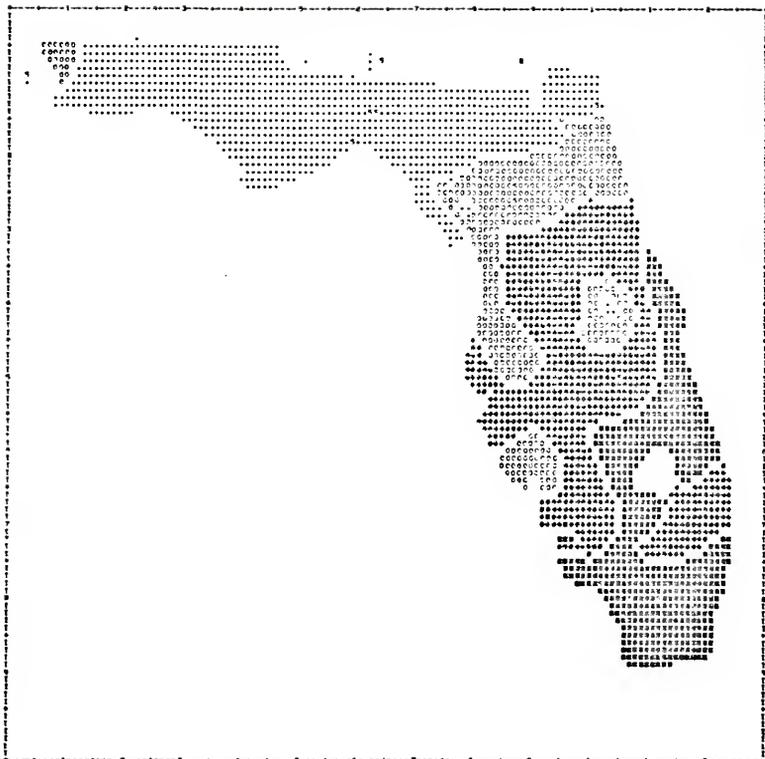
MAP 113. Geographic variation in tail length divided by total length in Lampropeltis getulus, females only. Darker shading represents proportionately longer tails. Based on 33 specimens.



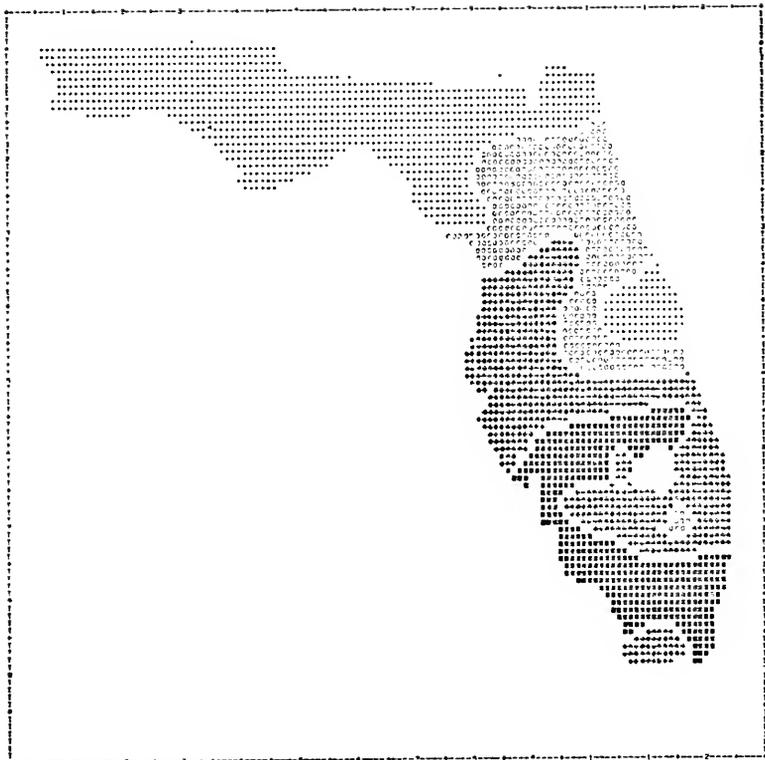
MAP 114. Geographic variation in the number of dorsal scale rows at mid body in *Lampropeltis getulus*, both sexes. Lighter shading represents 21 scale rows; darker shading represents 23. Based on 71 specimens.



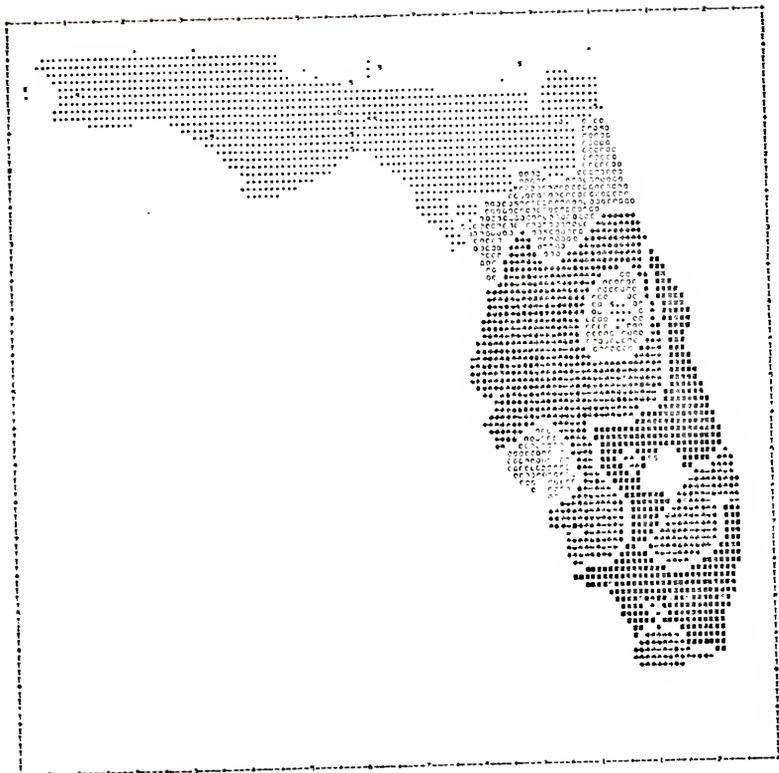
MAP 115. Geographic variation in number of infralabial scales, both sides, in *Lampropeltis getulus*, both sexes. Lighter shading represents 18 infralabials; darker shading 20. Based on 162 specimens.



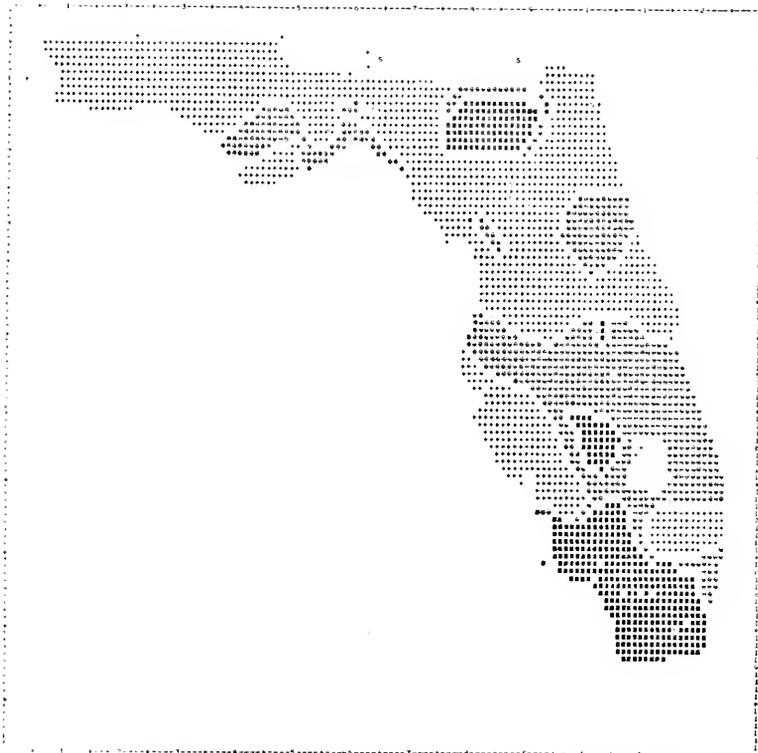
MAP 116. Geographic variation in number of body bands in Lampropeltis getulus, males only. Levels by increased shading are: 15-26; 27-38; 39-50; 51-62. Based on 90 specimens.



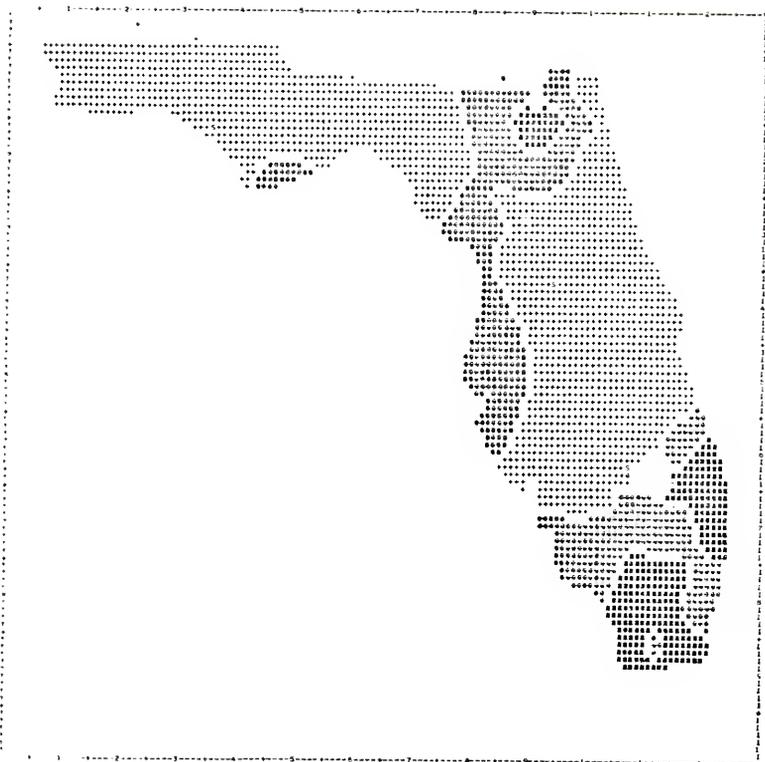
MAP 117. Geographic variation in number of body bands in *Lampropeltis getulus*, females only. Levels by increasing shading are: 17-28; 29-39; 40-51; 52-63. Based on 42 specimens.



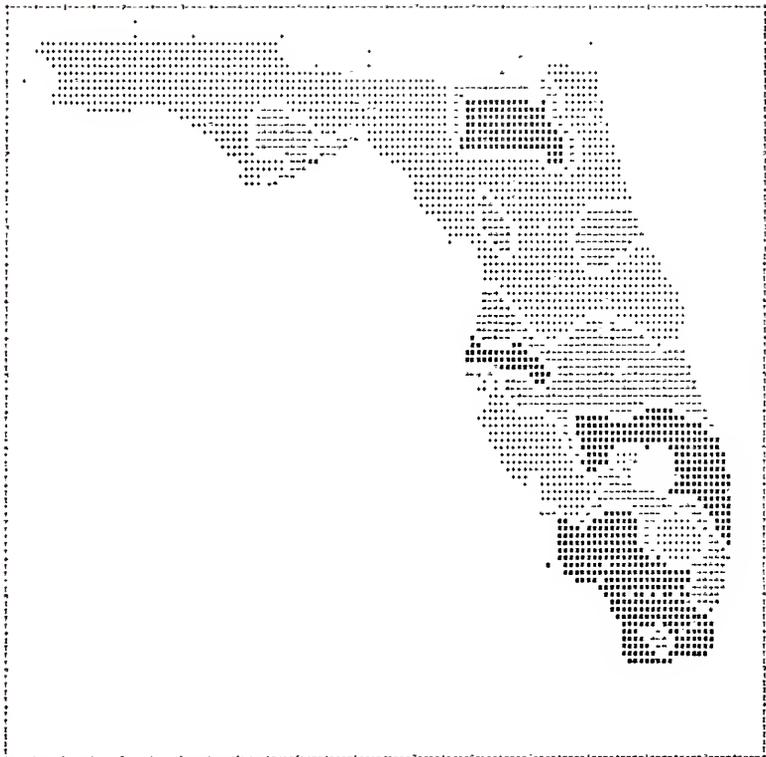
MAP 118. Geographic variation in number of body bands in Lampropeltis getulus, both sexes. Levels by increased shading are: 15-26; 27-38; 39-50; 51-63. Based on 160 specimens.



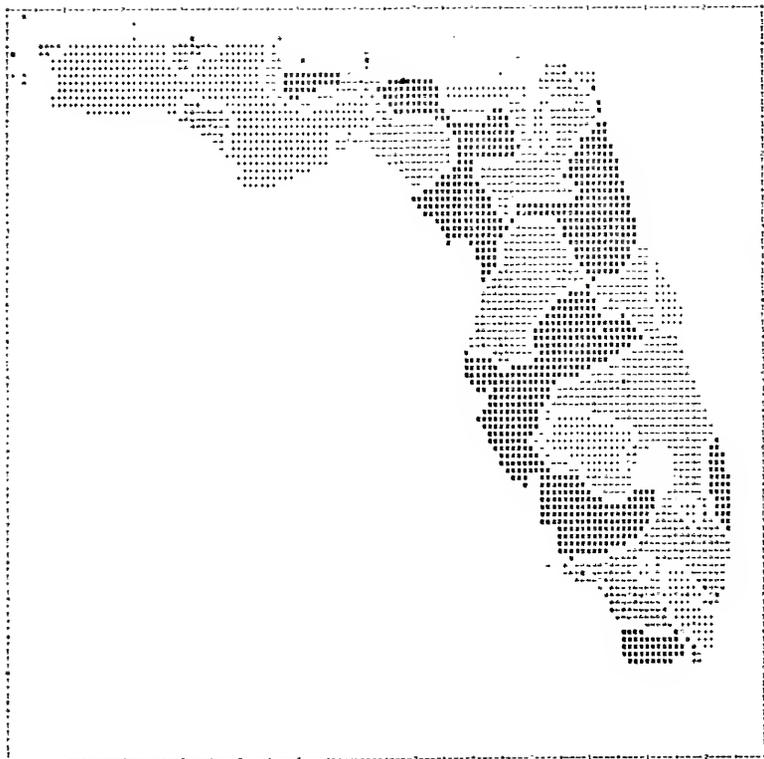
MAP 119. Geographic variation in the amount of light pigment in the dorsal pattern in *Lampropeltis getulus*, males only. Increased shading represents more light pigment. Based on 95 specimens.



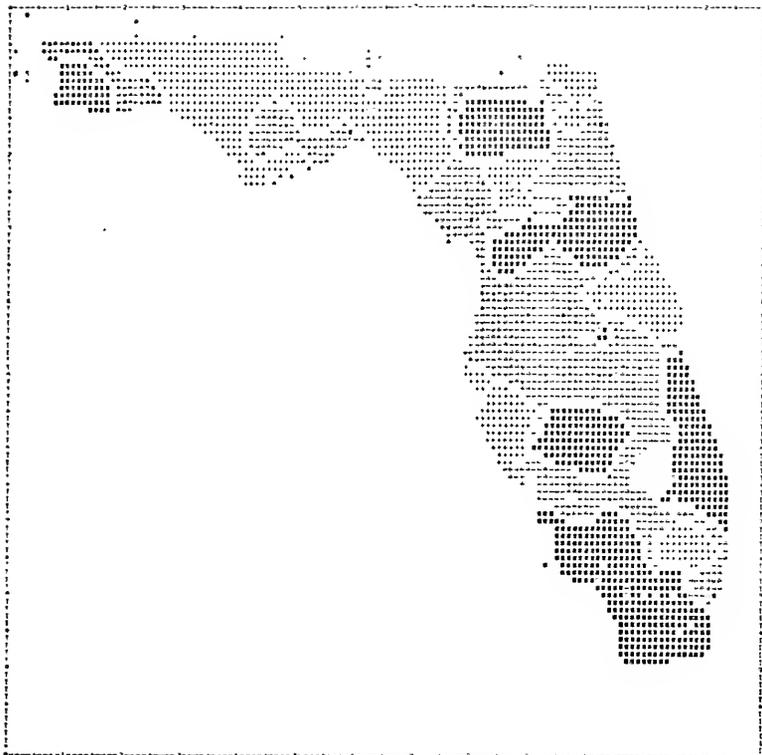
MAP 120. Geographic variation in the amount of light pigment in the dorsal pattern of *Lampropeltis getulus*, females only. Increased shading represents increased light pigment. Based on 43 specimens.



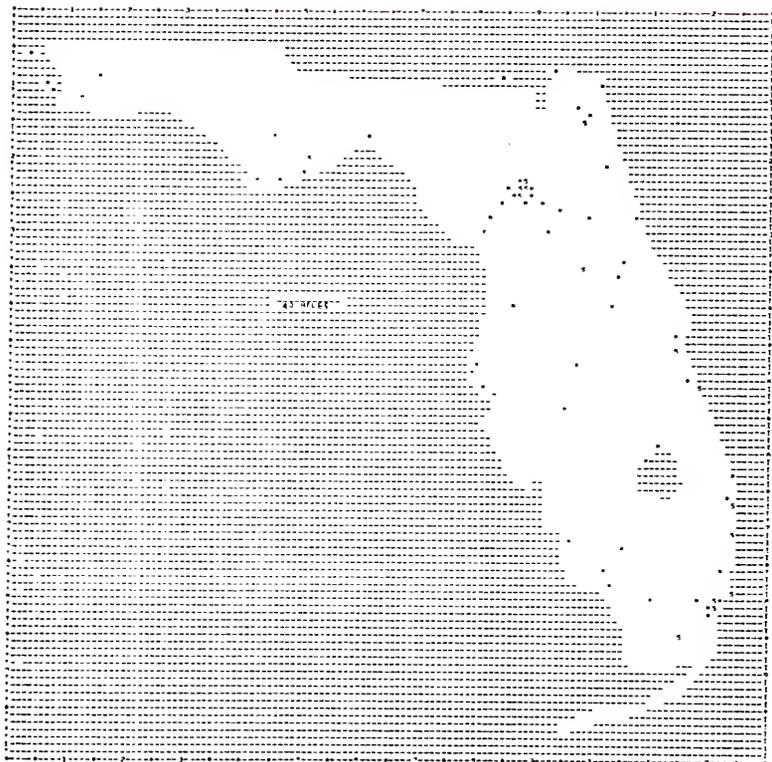
MAP 121. Geographic variation in the amount of light pigment in the dorsal pattern in *Lampropeltis getulus*, both sexes. Increased shading represents increased amounts of light pigment. Based on 172 specimens.



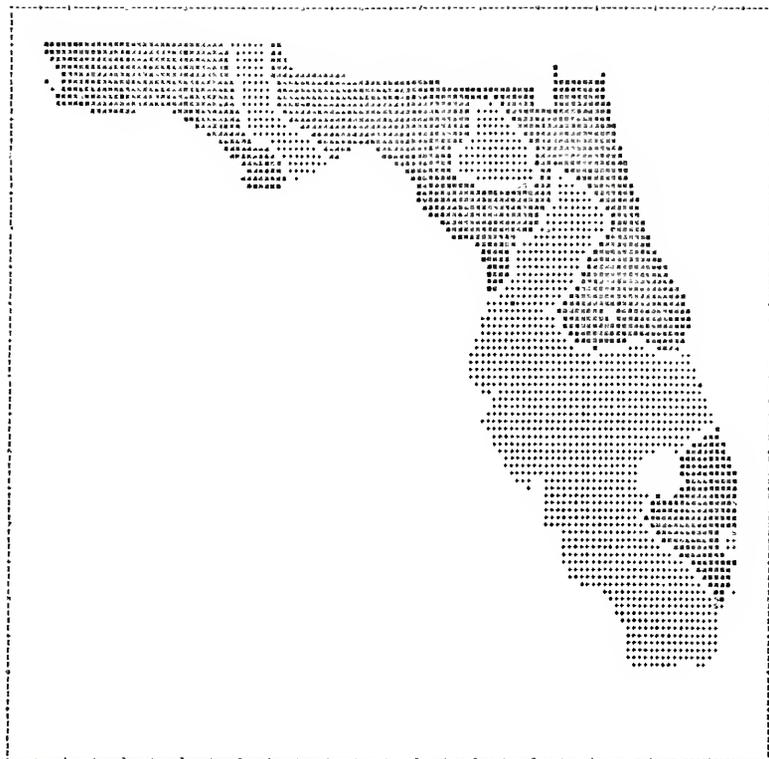
MAP 122. Geographic variation in Factor 2 for Lampropeltis getulus, both sexes. Factor 2 accounts for much of the variation in number of ventrals and number of mid-body dorsal scale rows. Darker shading represents higher values for both. Total variation accounted for by Factor 2: 27.4% (5 characters). Based on 162 specimens.



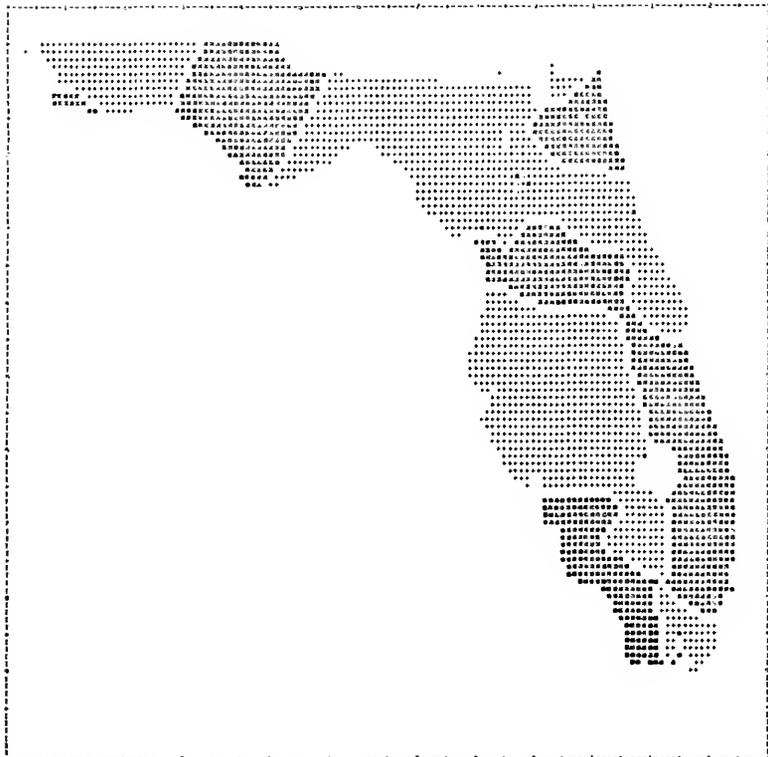
MAP 123. Geographic variation in Factor 3 for *Lampropeltis getulus*, both sexes. Factor 3 accounts for much of the variation in mid-body dorsal scale rows and amount of light pigment in the dorsal pattern. Darker shading represents generally more light pigment and more scale rows. Total variation accounted for by Factor 3: 20.9% (5 characters). Based on 162 specimens.



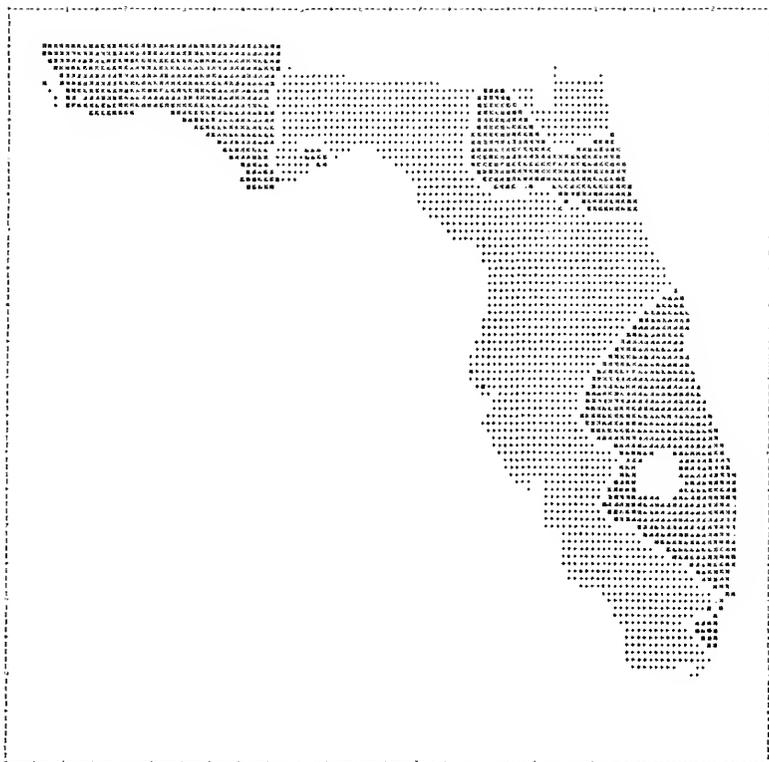
MAP 124. Localities of 120 *Lampropeltis triangulum* specimens examined. An asterisk represents one specimen; an S represents more than one.



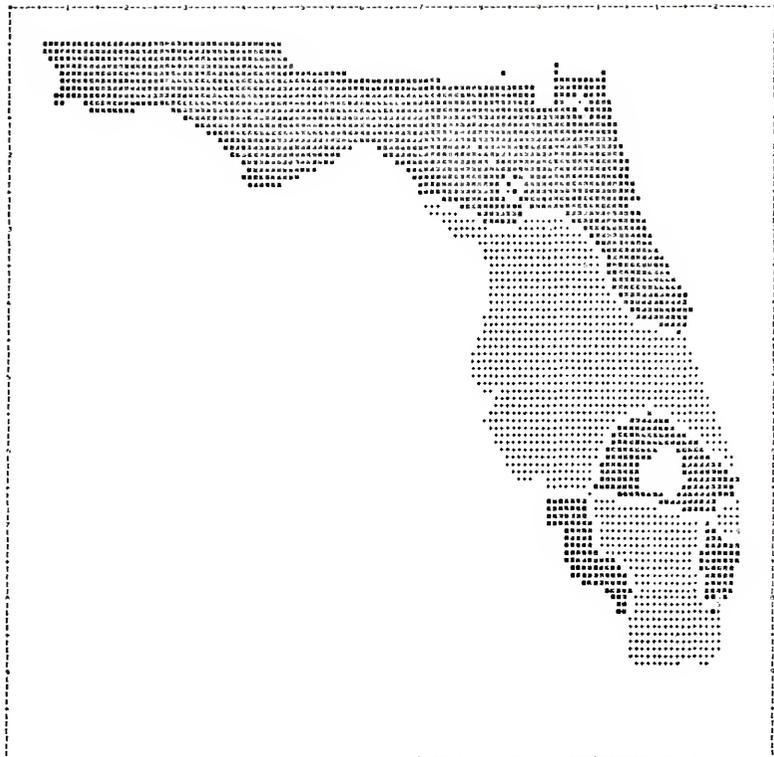
MAP 125. Geographic variation in the number of ventral scales in *Lampropeltis triangulum*, males only. Levels by increasing shading are: 159-169; 170-185. Based on 56 specimens.



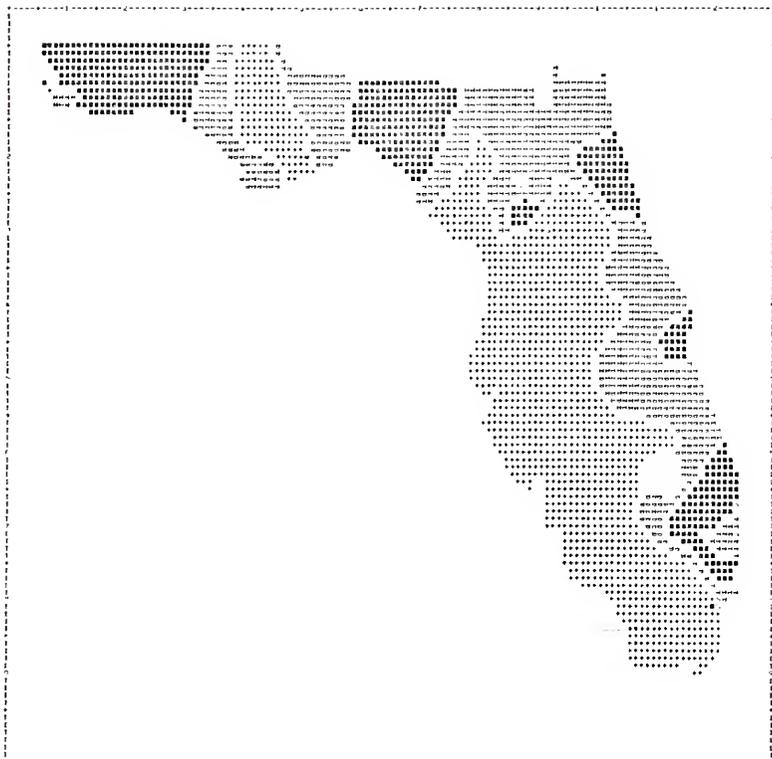
MAP 126. Geographic variation in number of ventral scales in *Lampropeltis triangulum*, females only. Levels by increasing shading are: 162-174; 175-185. Based on 61 specimens.



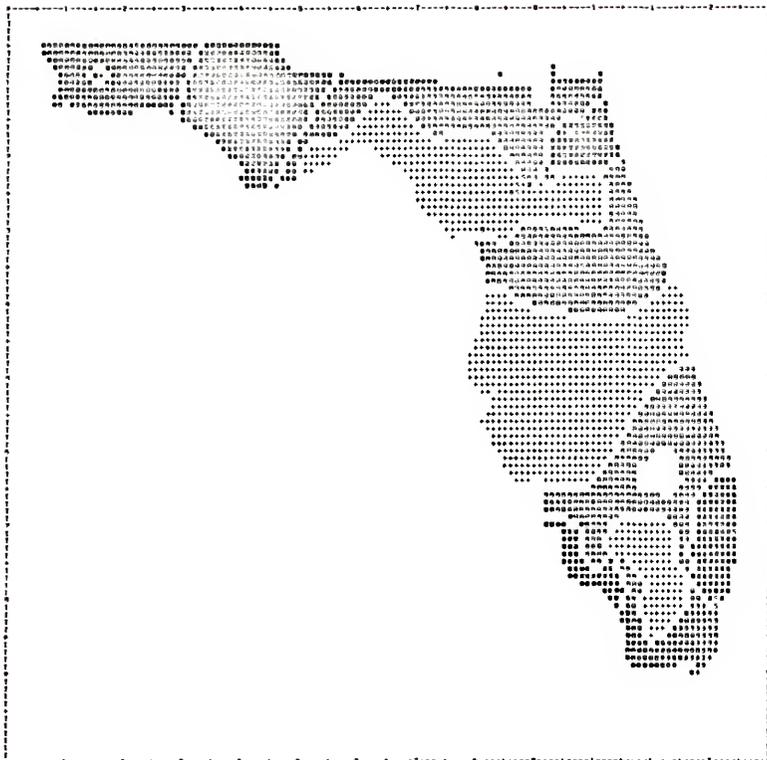
MAP 127. Geographic variation in number of subcaudal scales in *Lampropeltis triangulum*, males only. Lighter shading represents 37 to 40 subcaudals and darker shading 41 to 47. Based on 55 specimens.



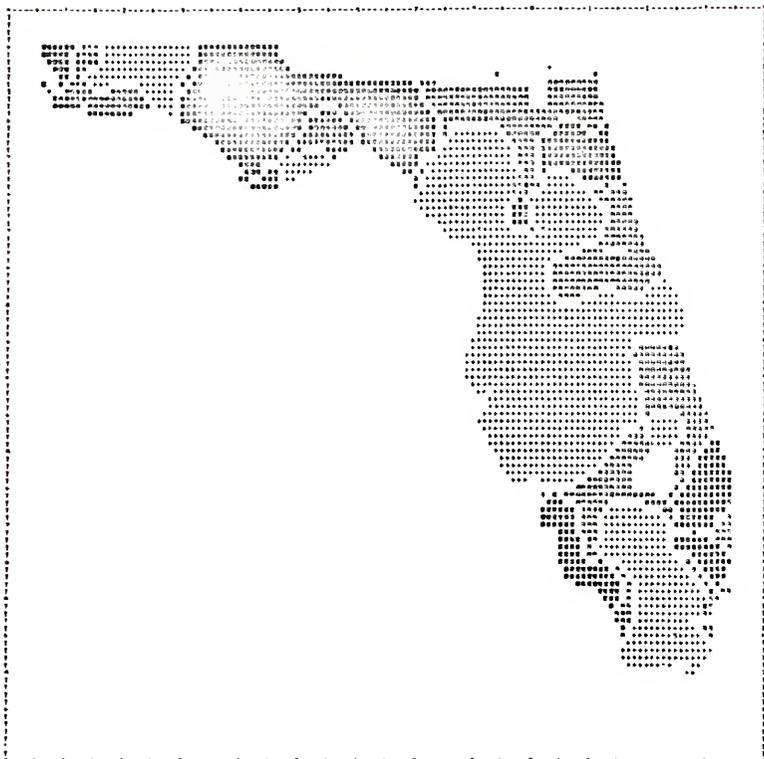
MAP 128. Geographic variation in number of subcaudal scales in *Lampropeltis triangulum*, females only. Levels by increasing shading are: 32-36 and 37-43. Based on 55 specimens.



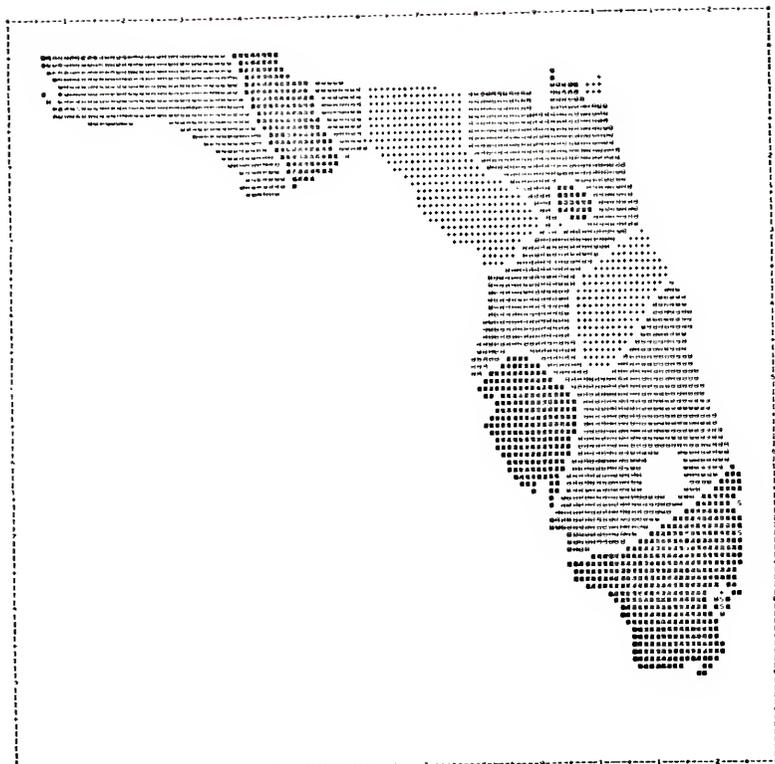
MAP 129. Geographic variation in the number of ventrals plus caudals in *Lampropeltis triangulum*, males only. Levels by increasing shading are: 199-210; 211-214; 215-227. Based on 52 specimens.



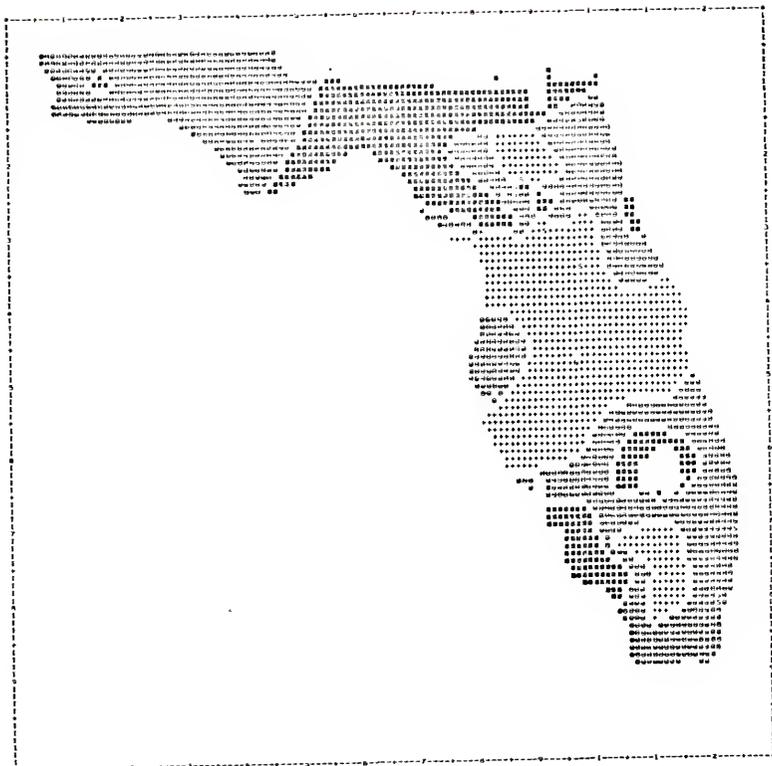
MAP 130. Geographic variation in sum of ventrals plus caudals in *Lampropeltis triangulum*, females only. Levels by increasing shading are: 197-209; 210-215; 216-223. Based on 55 specimens.



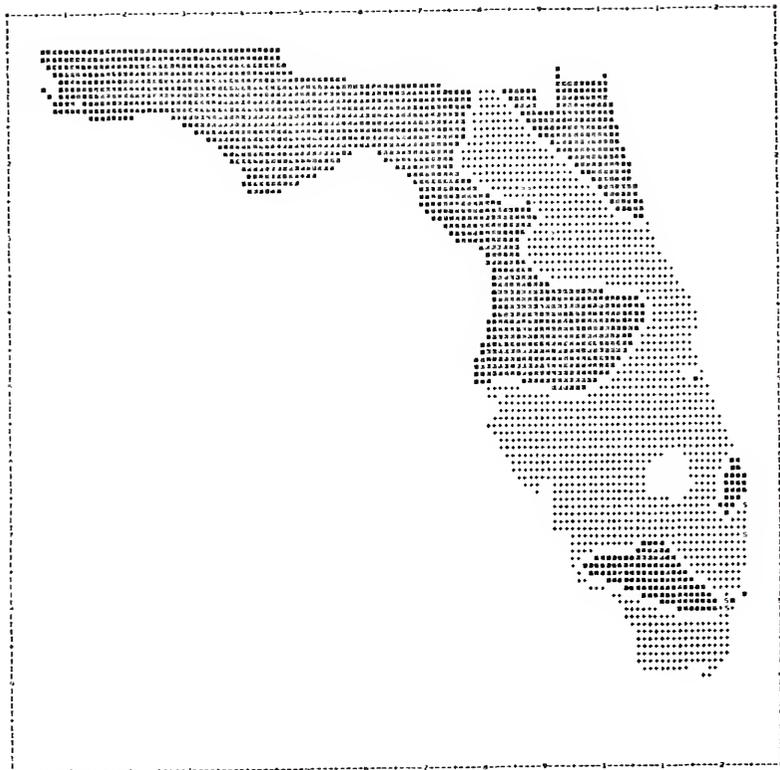
MAP 131. Geographic variation in sum of ventrals plus caudals in *Lampropeltis triangulum*, both sexes. Levels by increasing shading are: 197-211; 212-214; 215-227. Based on 107 specimens.



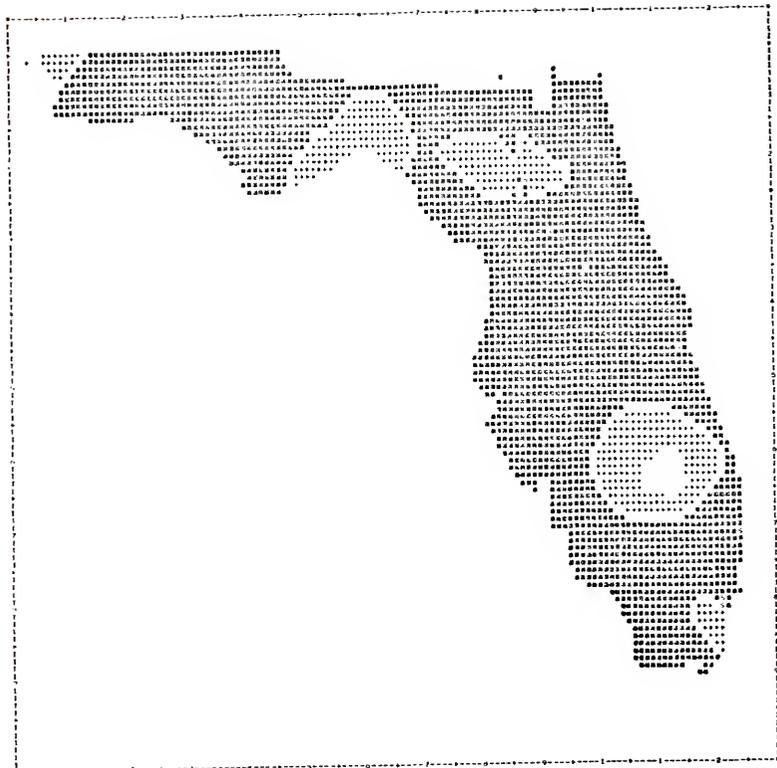
MAP 132. Geographic variation in tail length divided by total length in *Lampropeltis triangulum*, males only. Levels by increasing shading are: 0.13-0.14; 0.15-0.16; 0.16-0.17. Based on 55 specimens.



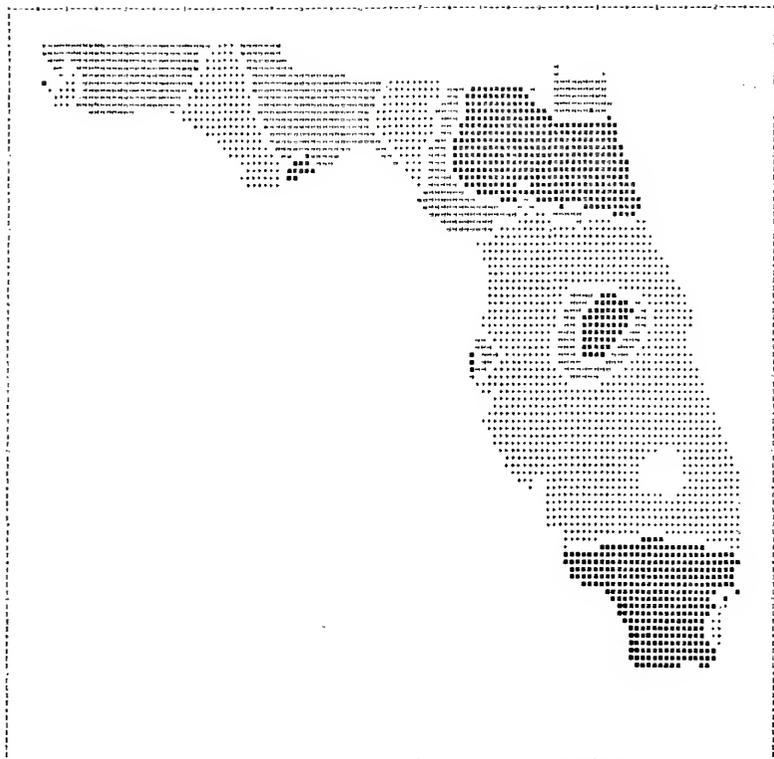
MAP 133. Geographic variation in tail length divided by total length in *Lampropeltis triangulum*, females only. Levels by increasing shading are: 0.11-0.13; 0.13-0.14; 0.14-0.16. Based on 56 specimens.



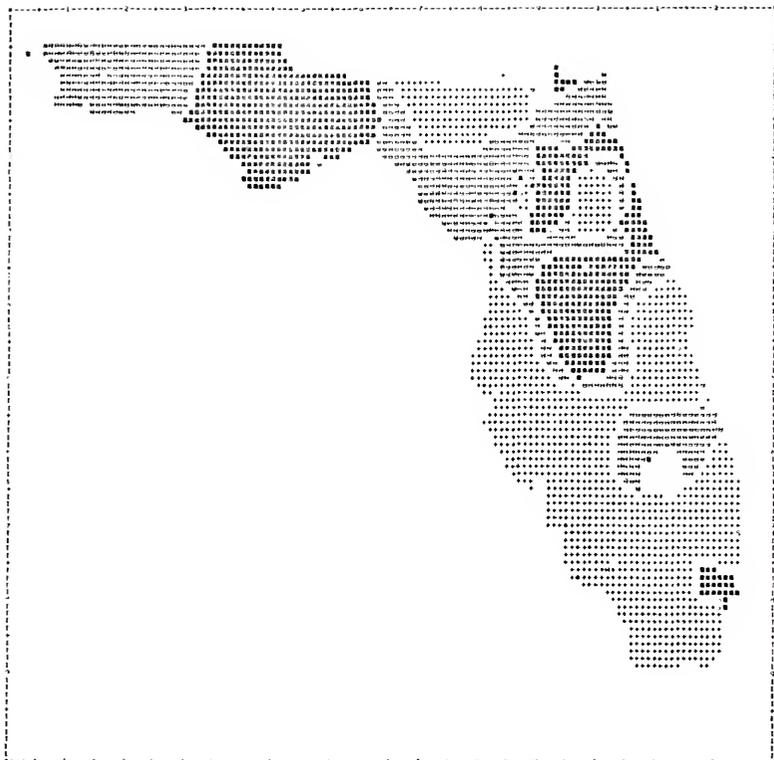
MAP 134. Geographic variation in number of dorsal scale rows at mid body in *Lampropeltis triangulum*, males only. Lighter shading represents 17 scale rows; darker shading represents 19 scale rows. Based on 59 specimens.



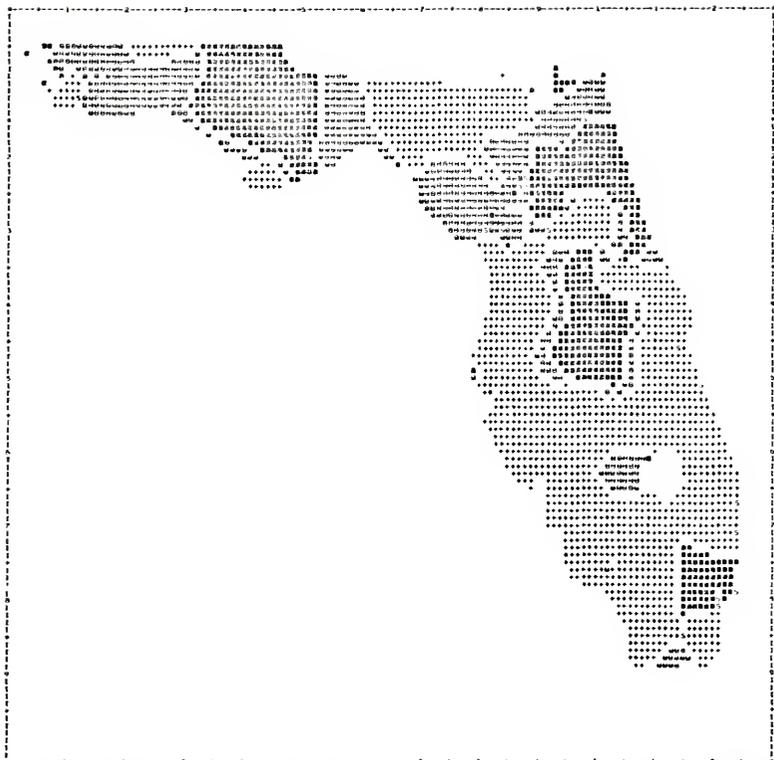
MAP 135. Geographic variation in number of dorsal scale rows at midbody in *Lampropeltis triangulum*, females only. Lighter shading represents 17 scale rows; darker shading represents 19 scale rows. Based on 59 specimens.



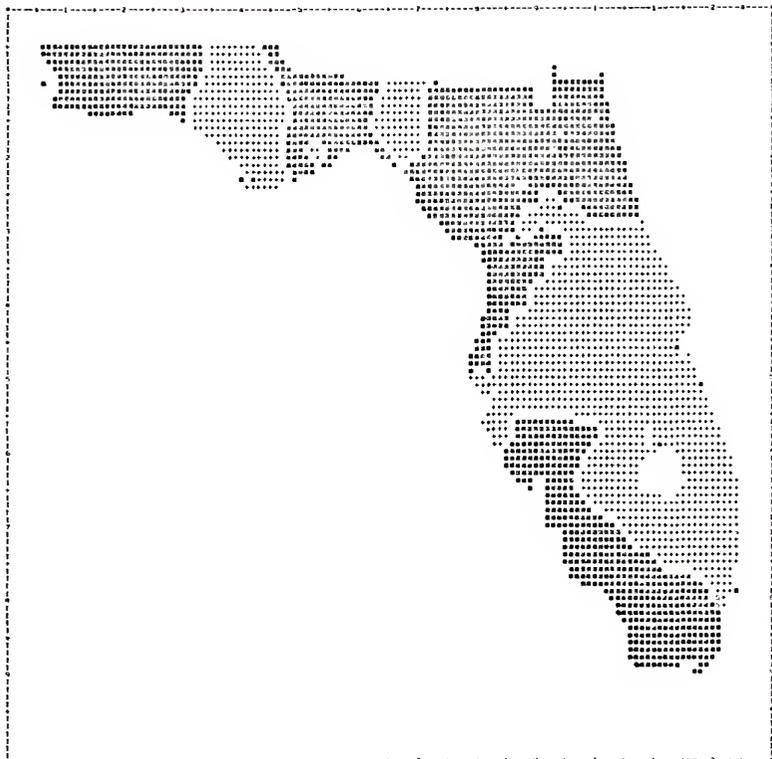
MAP 136. Geographic variation in number of red body bands in *Lampropeltis triangulum*, males only. Levels by increasing shading are: 12-15; 16; 17-20. Based on 59 specimens.



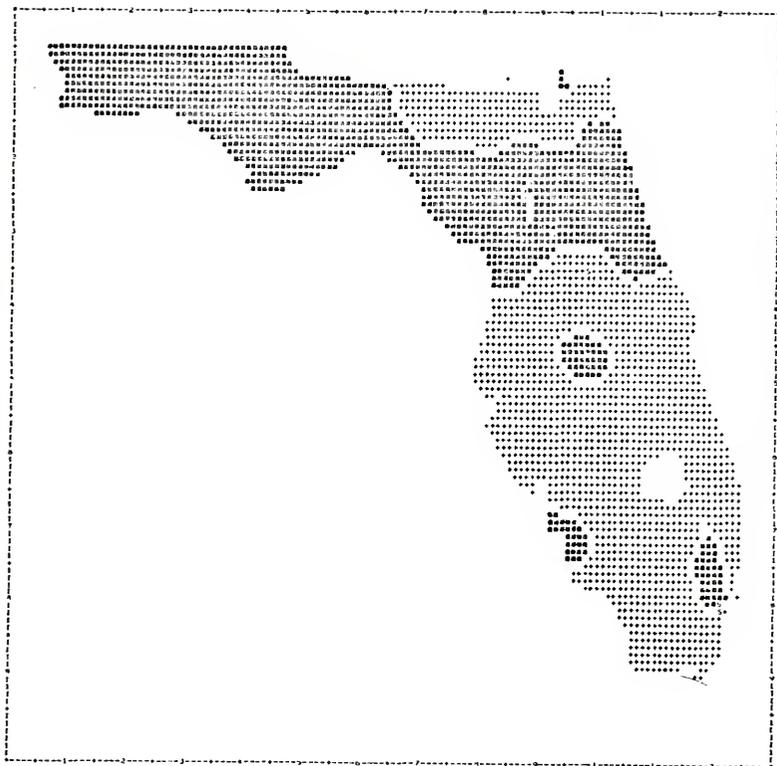
MAP 137. Geographic variation in number of red body bands in *Lampropeltis triangulum*, females only. Levels by increasing shading are: 12-15; 16; 17-20. Based on 61 specimens.



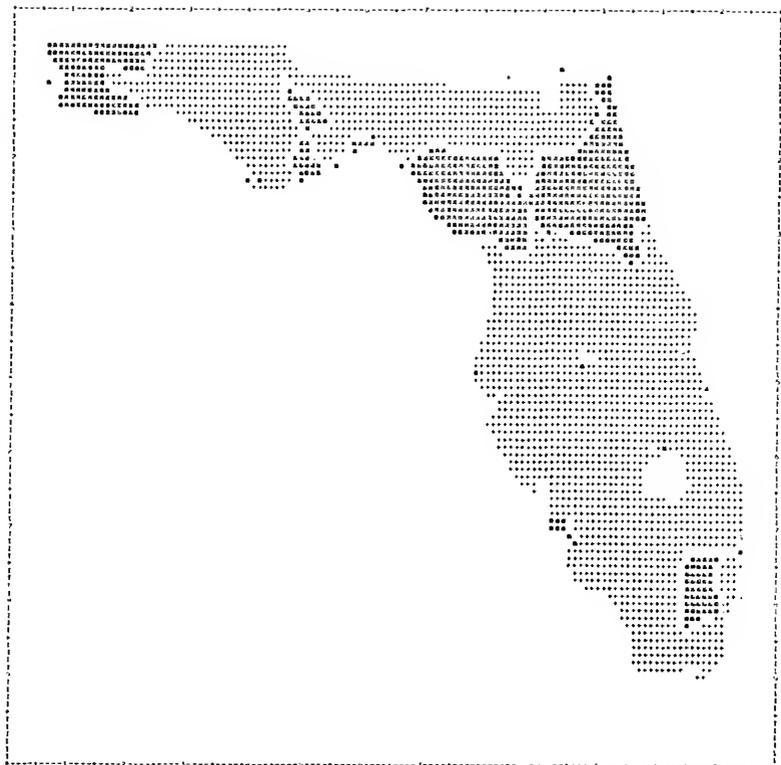
MAP 138. Geographic variation in number of red body bands in *Lampropeltis triangulum*, both sexes. Levels by increasing shading are: 12-15; 16; 17-20. Based on 120 specimens.



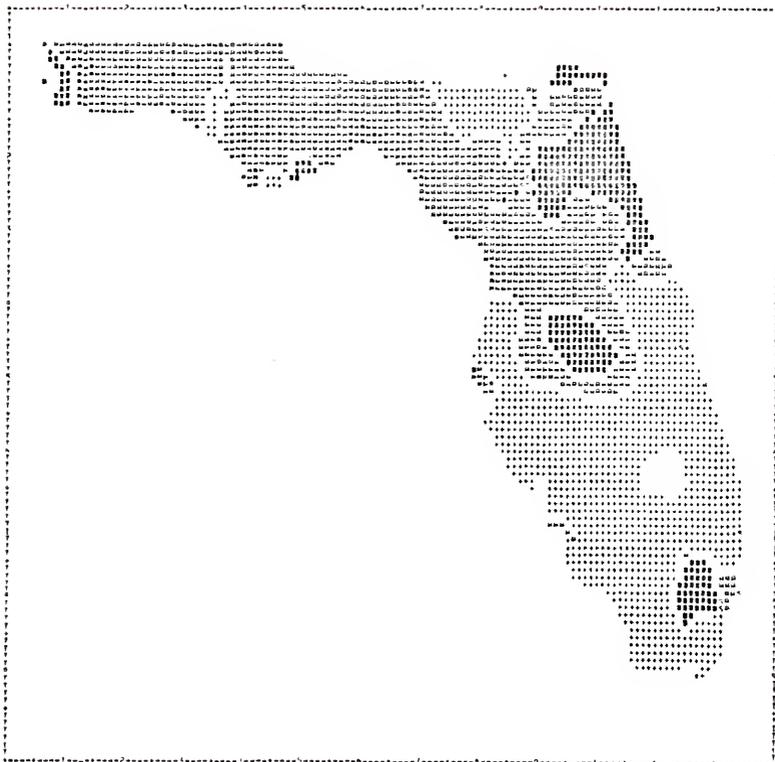
MAP 139. Geographic variation in number of red tail bands in *Lampropeltis triangulum*, males only. Lighter shading represents 2 or 3 tail bands, and darker shading, 4 to 6. Based on 35 specimens.



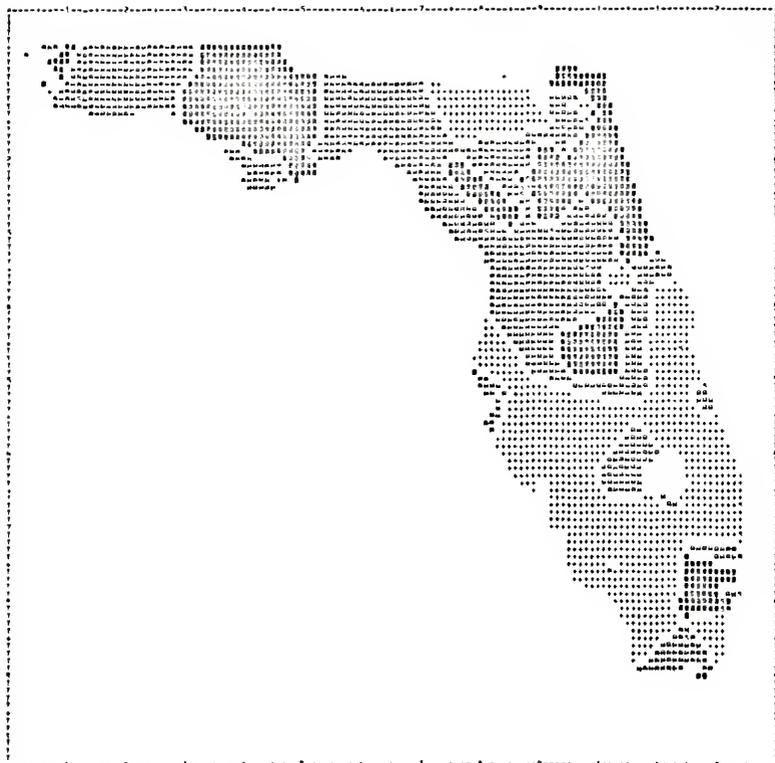
MAP 140. Geographic variation in the number of red tail bands in *Lampropeltis triangulum*, females only. Lighter shading represents 2 1/2 to 3 tail bands, and darker shading represents 3 1/2 to 5. Based on 45 specimens.



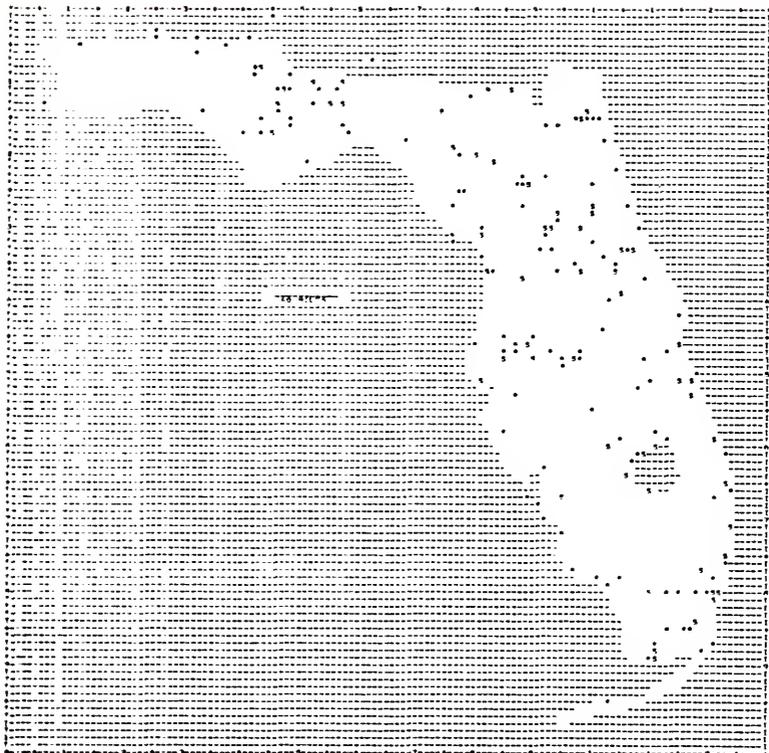
MAP 141. Geographic variation in number of red tail bands in *Lampropeltis triangulum*, both sexes. Lighter shading represents 2 or 3 tail bands and darker shading represents 4 to 6. Based on 80 specimens.



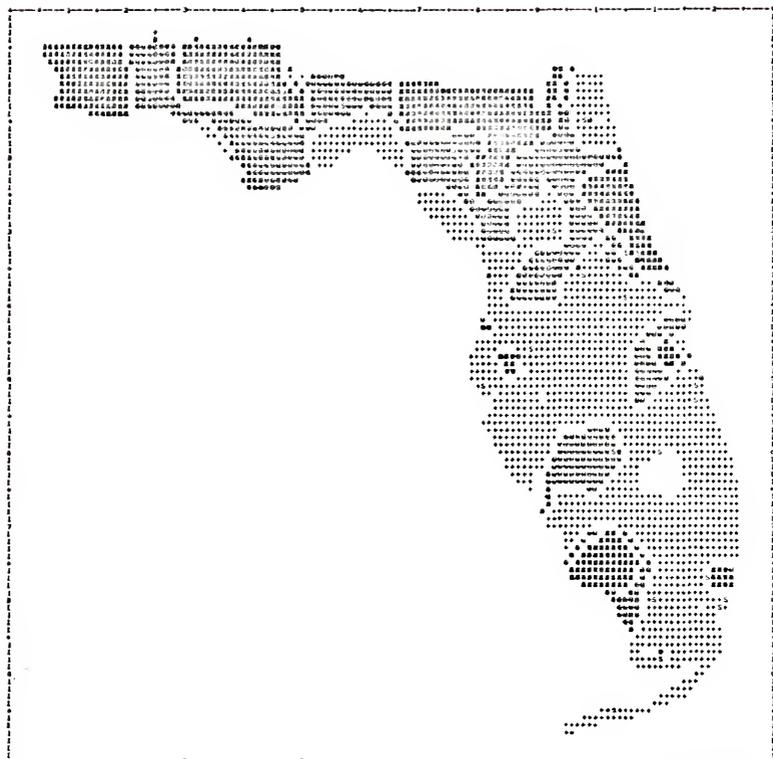
MAP 142. Geographic variation in the number of red bands, body and tail, in *Lampropeltis triangulum*, both sexes. Levels by increasing shading are: 15-18; 19-20; 21-25. Based on 80 specimens.



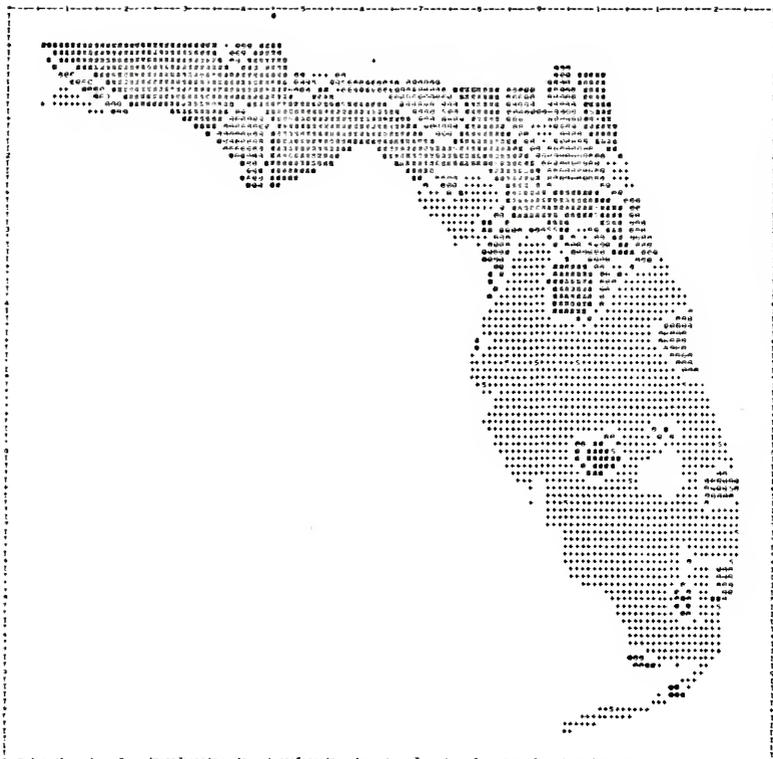
MAP 143. Geographic variation in Factor 3 for *Lampropeltis triangulum*, both sexes. Factor 3 accounts for most of the variation in number of red body bands and red tail bands. Darker shading represents generally higher values for both. Total variation accounted for by Factor 3: 16.6% (10 characters). Based on 120 specimens.



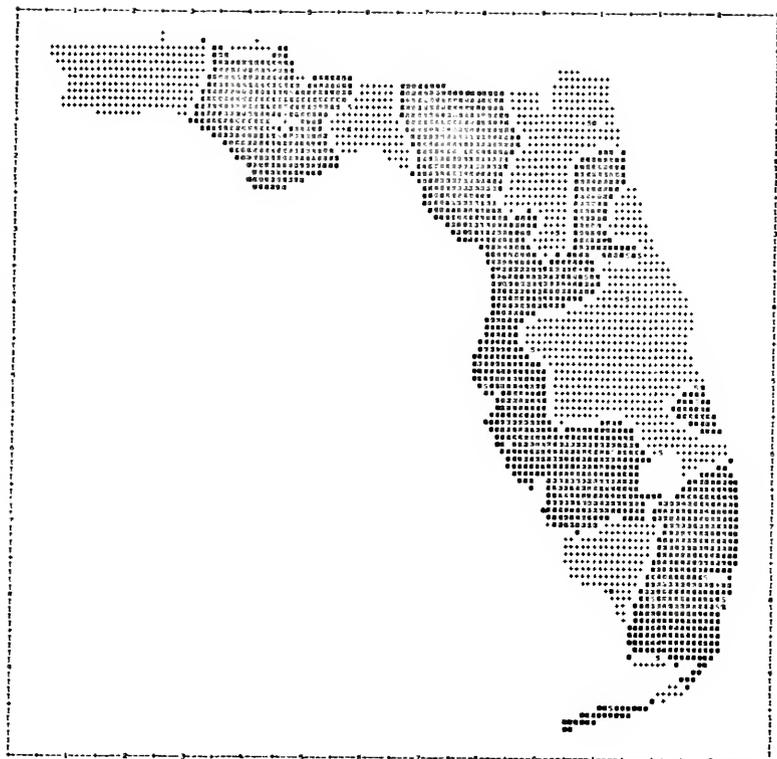
MAP 144. Localities of 295 Diadophis punctatus specimens examined. An asterisk represents one specimen; and S represents more than one.



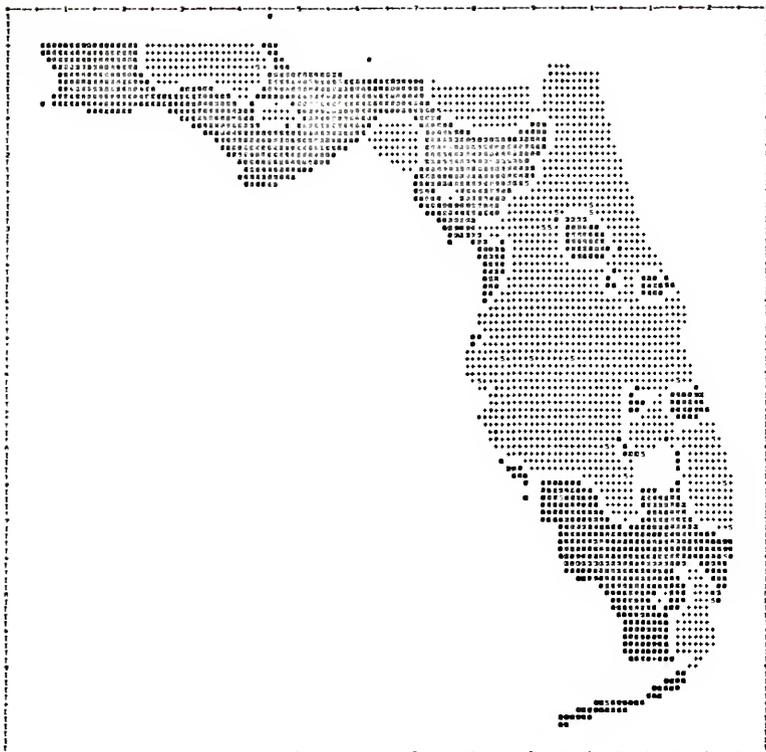
MAP 145. Geographic variation in number of ventral scales in *Diadophis punctatus*, males only. Levels by increasing shading are: 124-135; 136-138; 139-148. Based on 132 specimens.



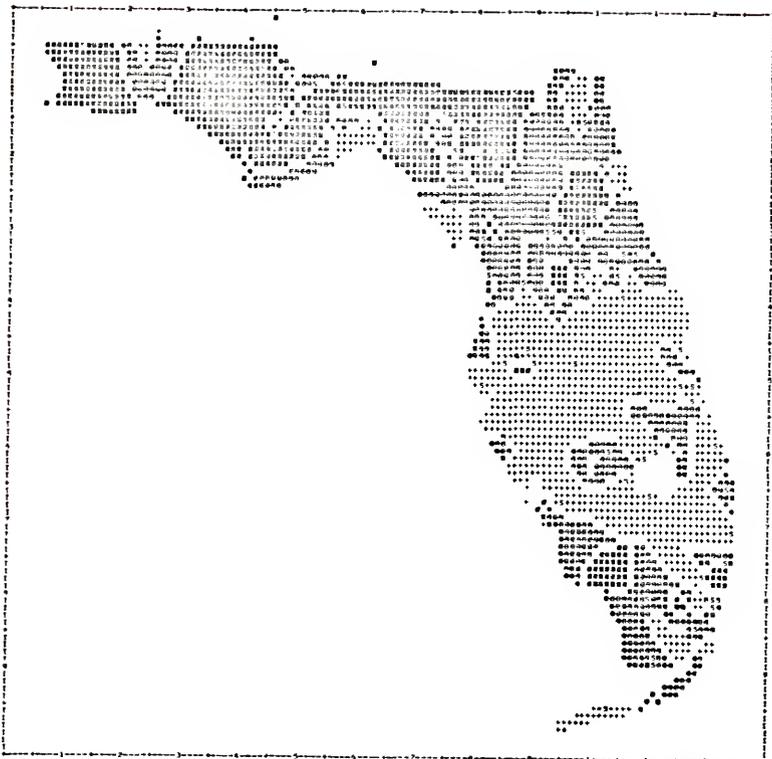
MAP 146. Geographic variation in number of ventral scales in *Diadophis punctatus*, females only. Levels by increasing shading are: 133-142; 143-144; 145-154. Based on 162 specimens.



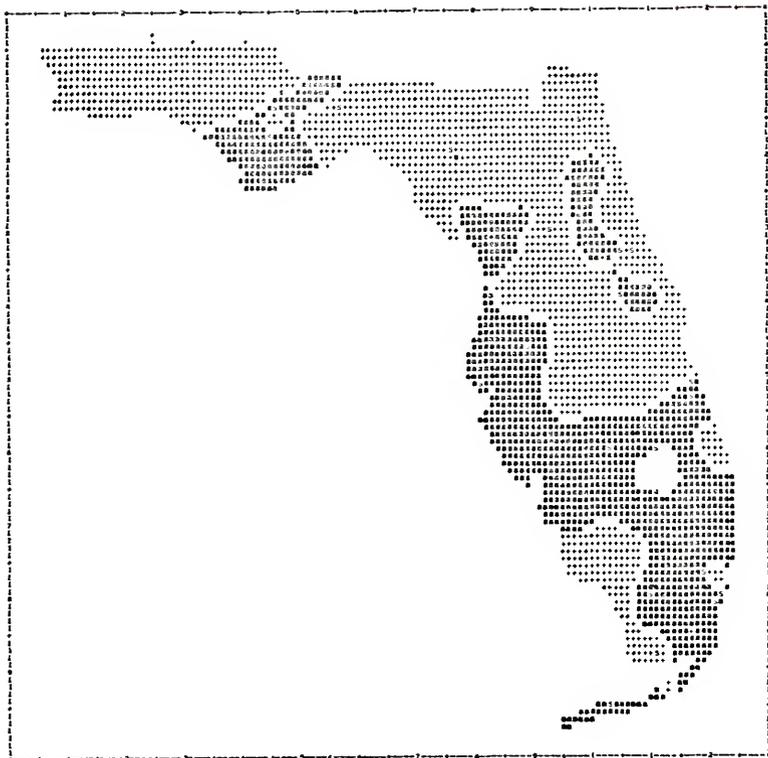
MAP 147. Geographic variation in the number of subcaudal scales in *Diadophis punctatus*, males only. Lighter shading represents 39-46 subcaudals; darker shading, 47-55. Based on 125 specimens.



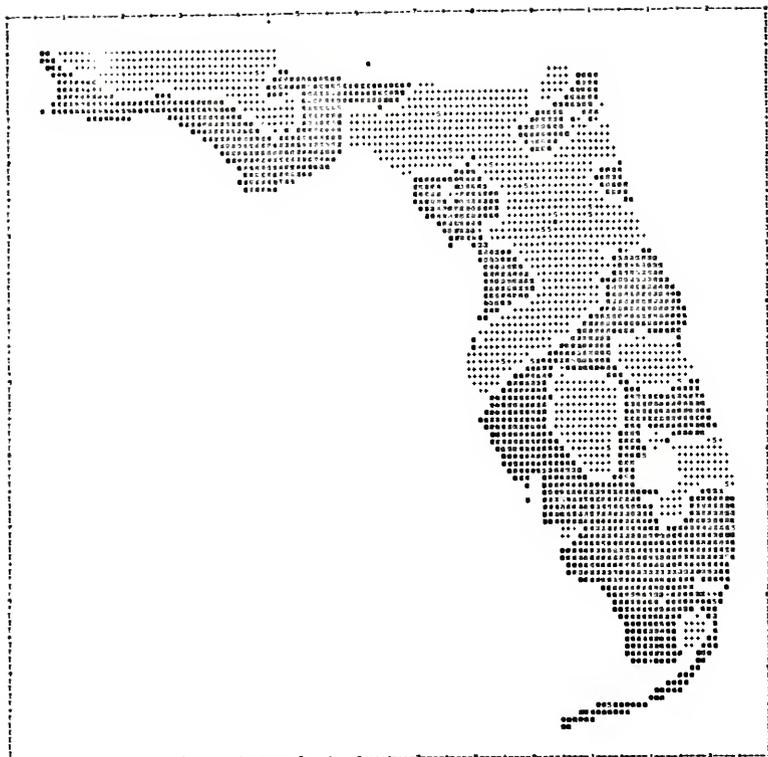
MAP 148. Geographic variation in number of subcaudal scales in *Diadophis punctatus*, females only. Lighter shading represents 34-41 subcaudals; darker shading, 42-49. Based on 154 specimens.



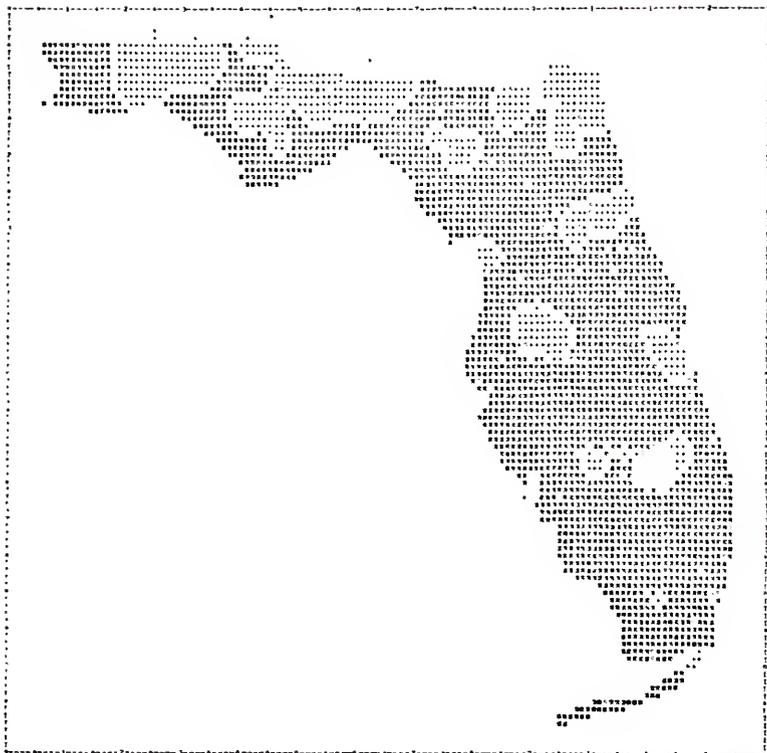
MAP 149. Geographic variation in the sum of ventrals plus caudals for *Diadophis punctatus*, both sexes. Levels by increasing shading are: 171-181; 182-186; 187-198. Based on 280 specimens.



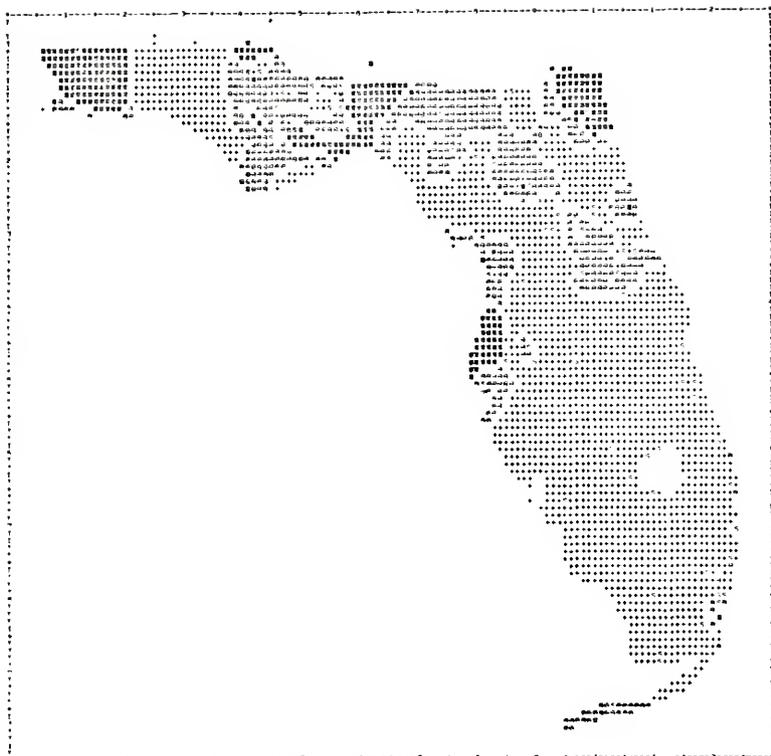
MAP 150. Geographic variation in tail length divided by total length in *Diadophis punctatus*, males only. Lighter shading represents 0.16 to 0.20; darker shading, 0.21 to 0.25. Based on 123 specimens.



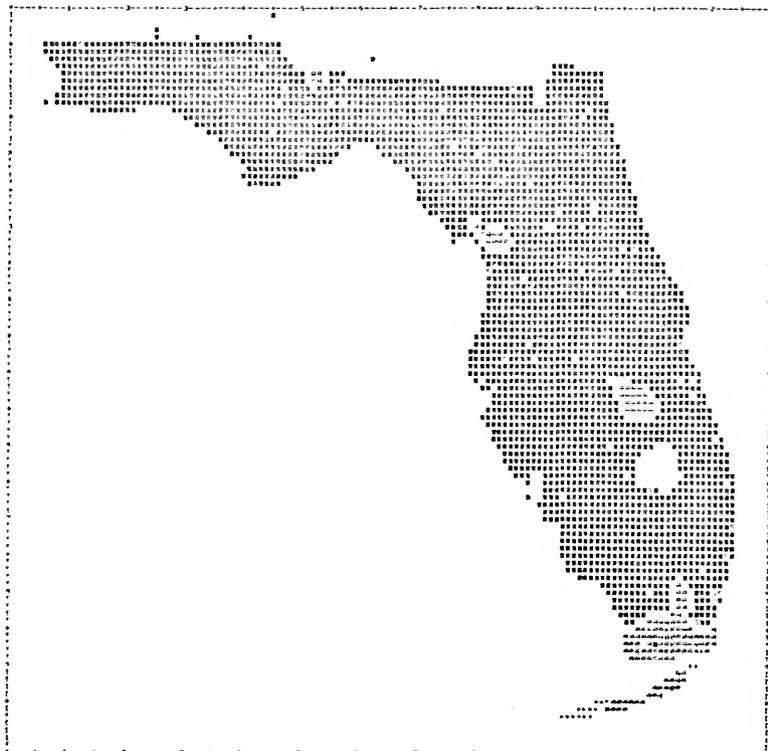
MAP 151. Geographic variation in tail length divided by total length in *Diadophis punctatus*, females only. Levels by increased shading are: 0.14-0.17; 0.18-0.22. Based on 152 specimens.



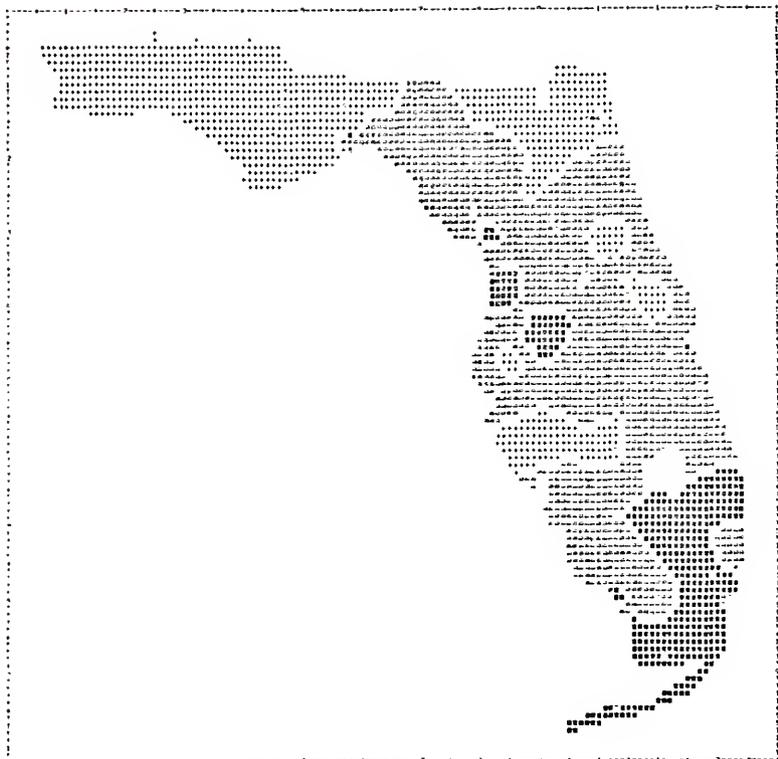
MAP 152. Geographic variation in number of supralabial scales in *Diadophis punctatus*, both sexes. Lighter shading represents 14 or 15 supralabials; darker shading represents 16 or 17. Based on 280 specimens.



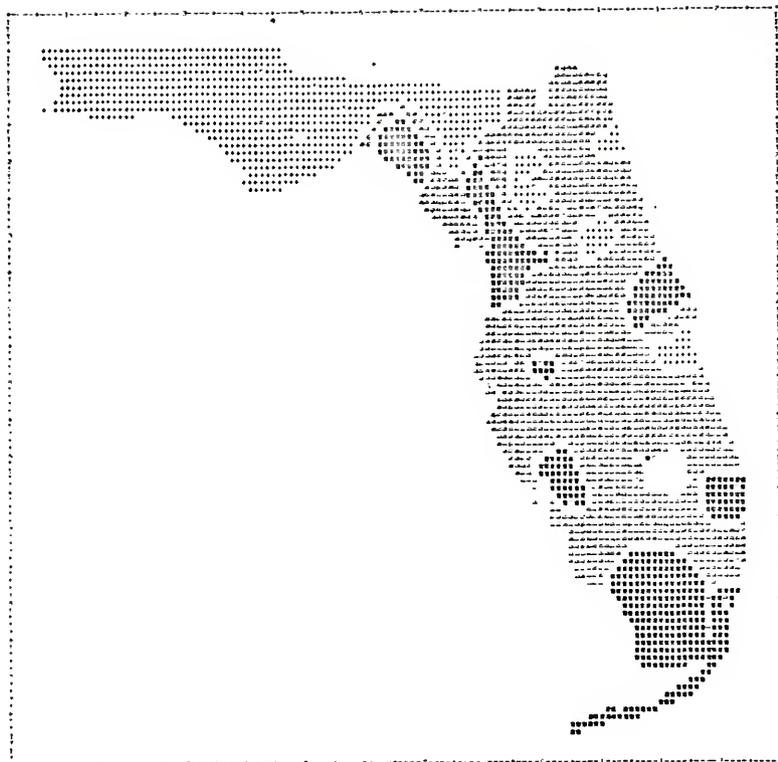
MAP 153. Geographic variation in the number of subcaudal black spots in *Diadophis punctatus*, both sexes. Lightest shading represents no black spots on the underside of the tail. Intermediate shading represents from 1 to 5 spots, and the darkest shading from 6 to 59. Based on 293 specimens.



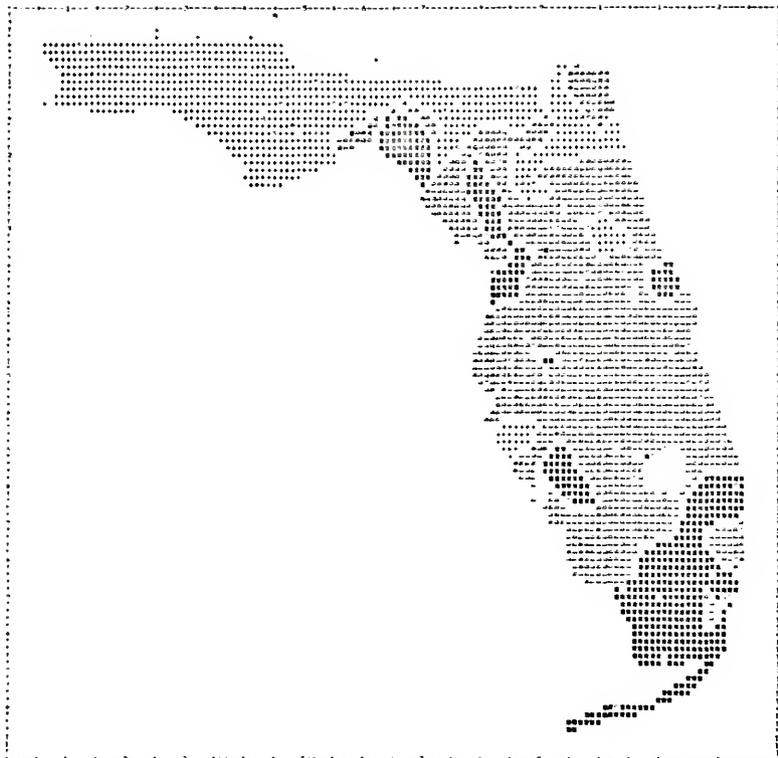
MAP 154. Geographic variation in the nature of the labial pigmentation in *Diadophis punctatus*, both sexes. Darkest shading represents labial pigment in discrete spots; lightest shading represents either no labial pigment, or pigment that is very diffuse; intermediate shading represents the intermediate condition. Based on 291 specimens.



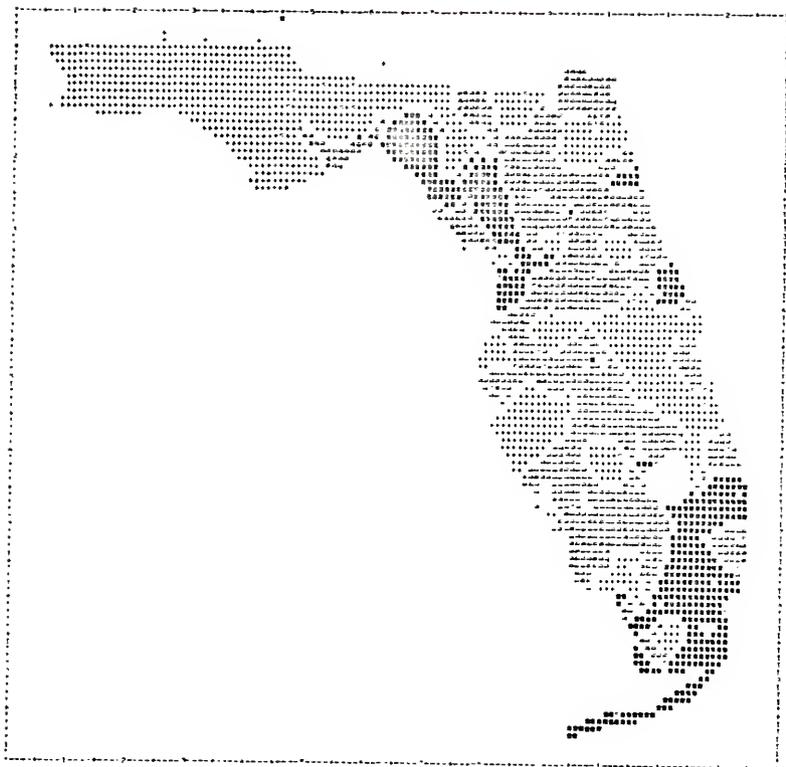
MAP 155. Geographic variation in number of supralabial spots, right side, in *Diadophis punctatus*, males only. Levels by increasing shading are: 0-1, 2-4, 5-7. Based on 130 specimens.



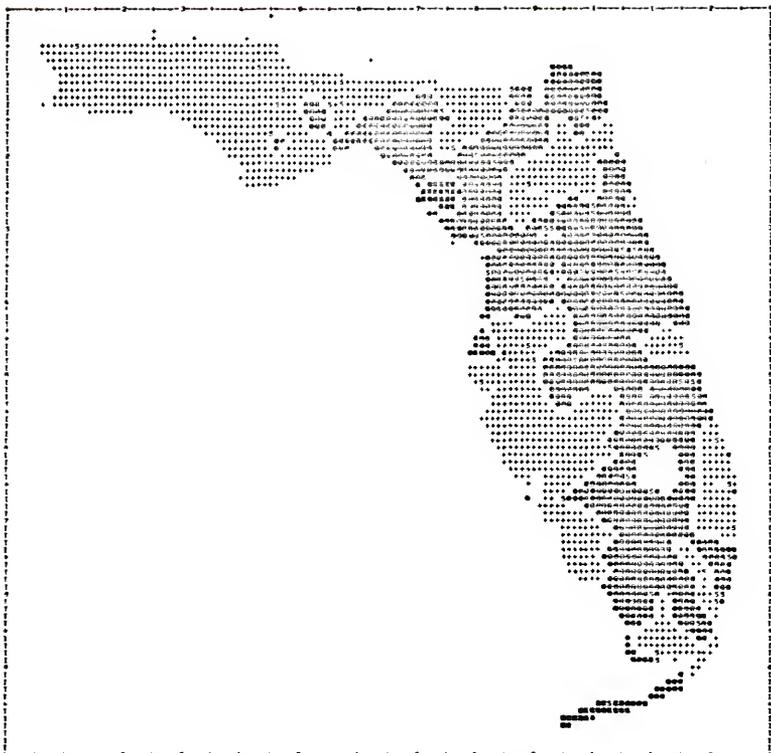
MAP 156. Geographic variation in number of supralabial spots, right side, in *Diadophis punctatus*, females only. Levels by increasing shading are: 0-1; 2-4; 5-7. Based on 159 specimens.



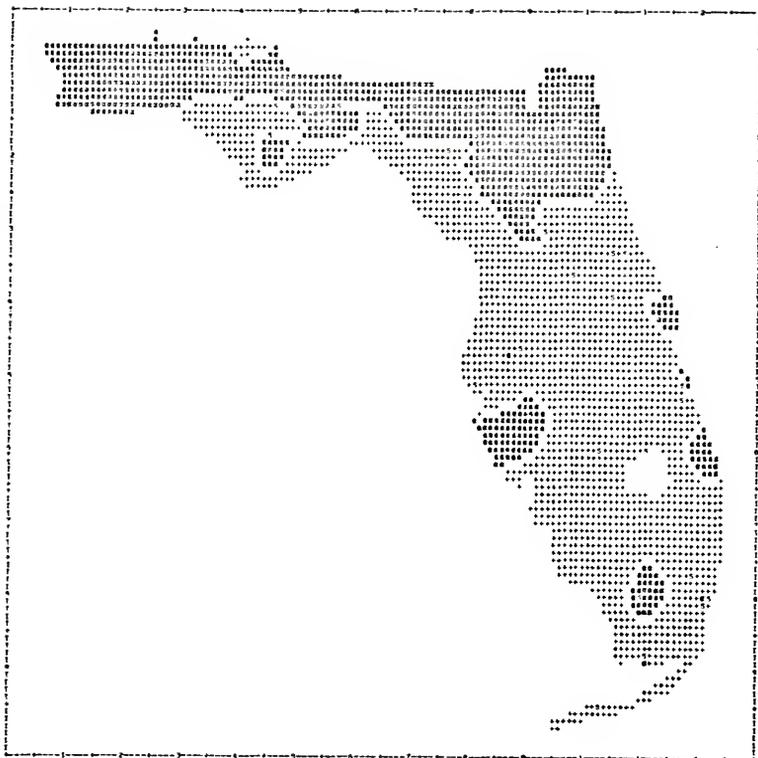
MAP 157. Geographic variation in number of supralabial black spots, right side, in *Diadophis punctatus*, both sexes. Levels by increasing shading are: 0-1; 2-4; 5-7. Based on 295 specimens.



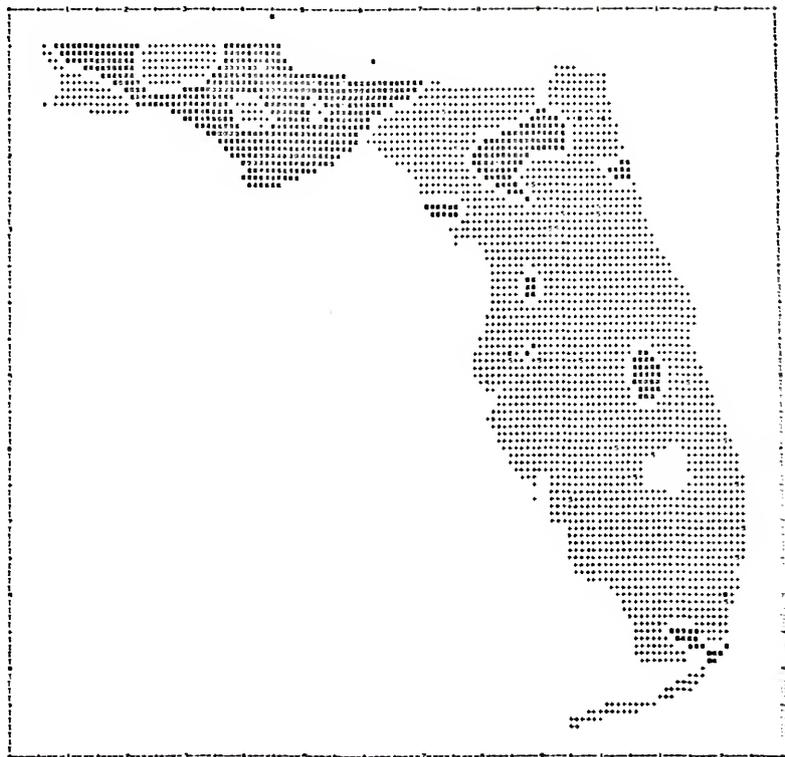
MAP 158. Geographic variation in total number of labials with pigment, right side, for *Diadophis punctatus*, both sexes. Levels by increasing shading are: 0-6; 7-9; 10-13. Based on 295 specimens.



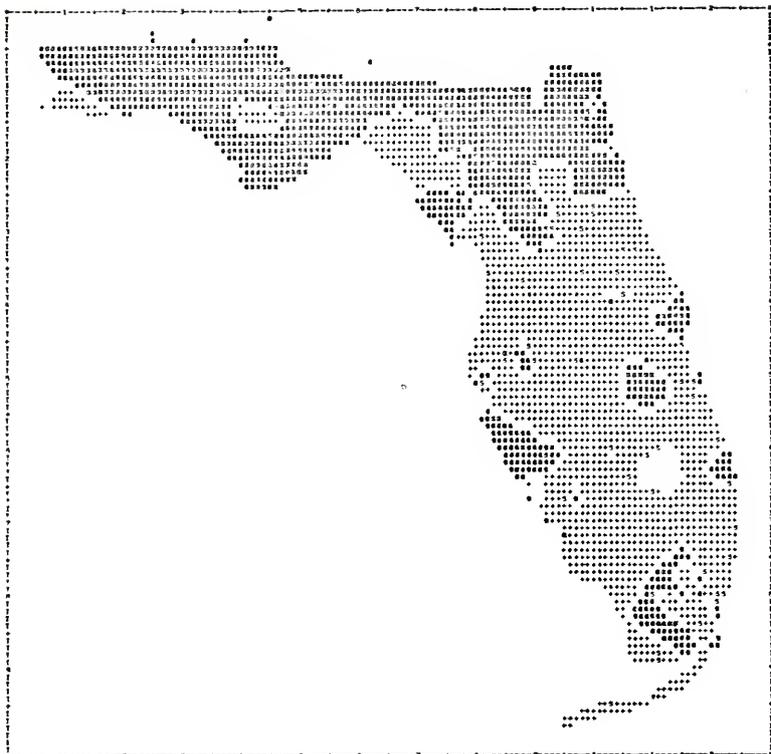
MAP 159. Geographic variation in the mid-dorsal break in the nuchal ring in *Diadophis punctatus*, both sexes. Light shading represents a complete neck ring; intermediate shading a ring with a mid-dorsal interruption of from 1 to 5 scales in width; darkest shading represents a ring that is interrupted mid-dorsally by more than five scale widths, or the absence of the nuchal ring. Based on 293 specimens.



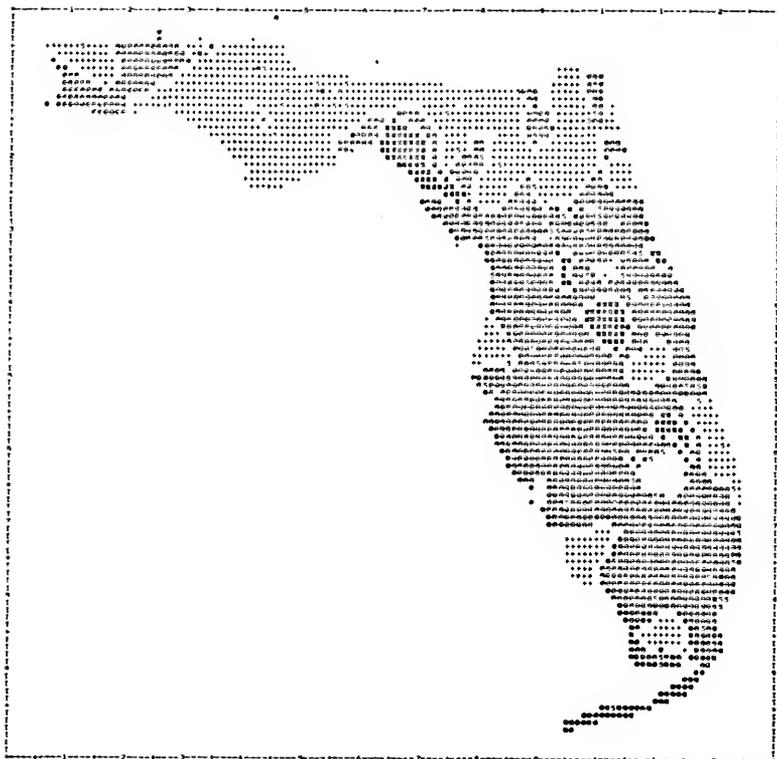
MAP 160. Geographic variation in the width of the nuchal ring in *Diadophis punctatus*, males only. The lighter shading represents a narrow ring, 0.5 to 1.75 scales in width, and the darker shading represents a neck ring 1.75 to 3 scale lengths long. Based on 131 specimens.



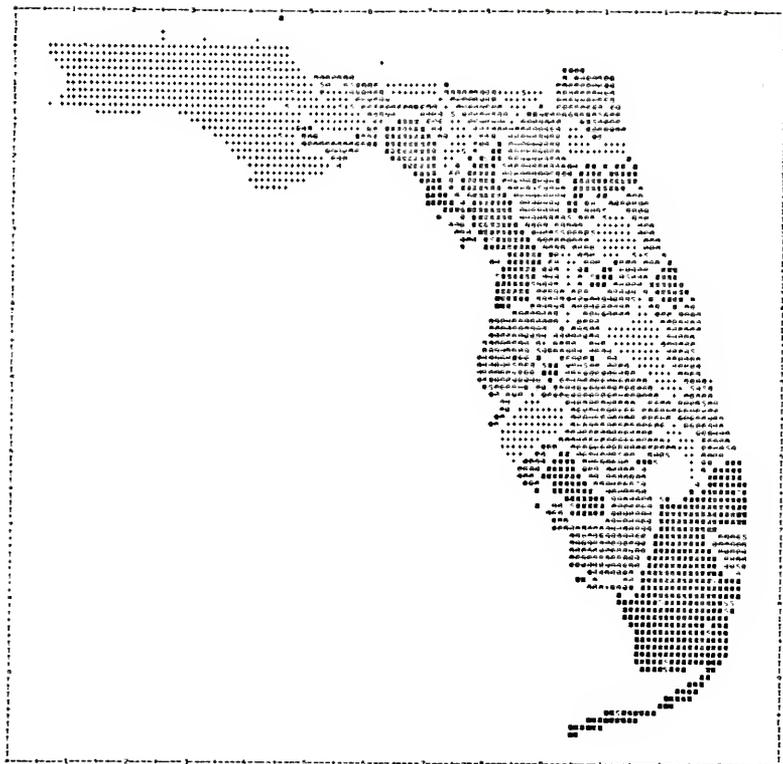
MAP 161. Geographic variation in the width of the nuchal ring in *Diadophis punctatus*, females only. Lighter shading represents a ring width of 0.5 to 1.75 scale lengths; darker shading, a width of 1.75 to 3 scale lengths. Based on 159 specimens.



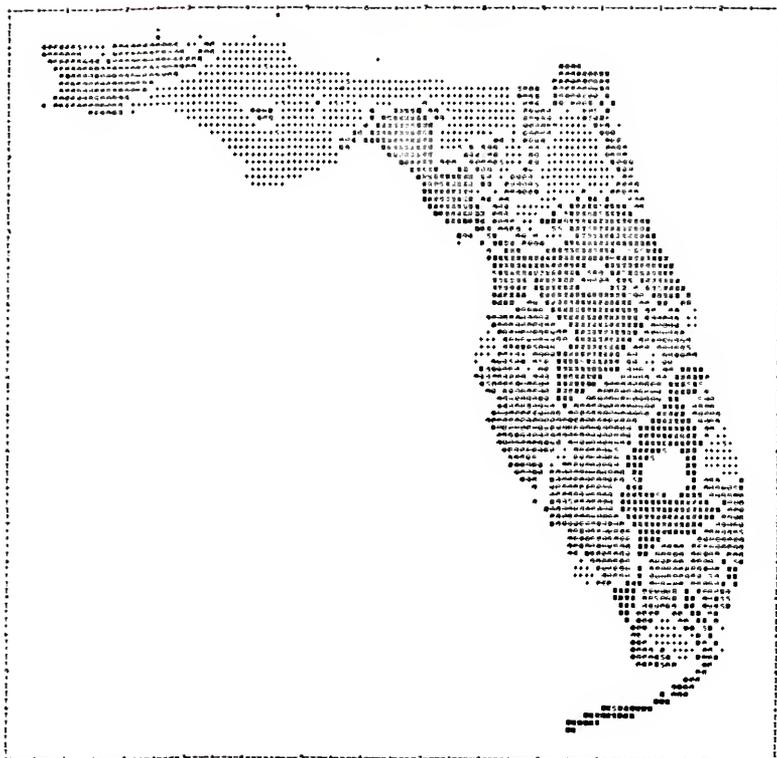
MAP 162. Geographic variation in the width of the nuchal ring in Diadophis punctatus, both sexes. Lighter shading represents a narrow ring, 0.5 to 1.5 scale lengths long, and darker shading represents a neck ring 1.5 to 3 scale lengths long. Based on 291 specimens.



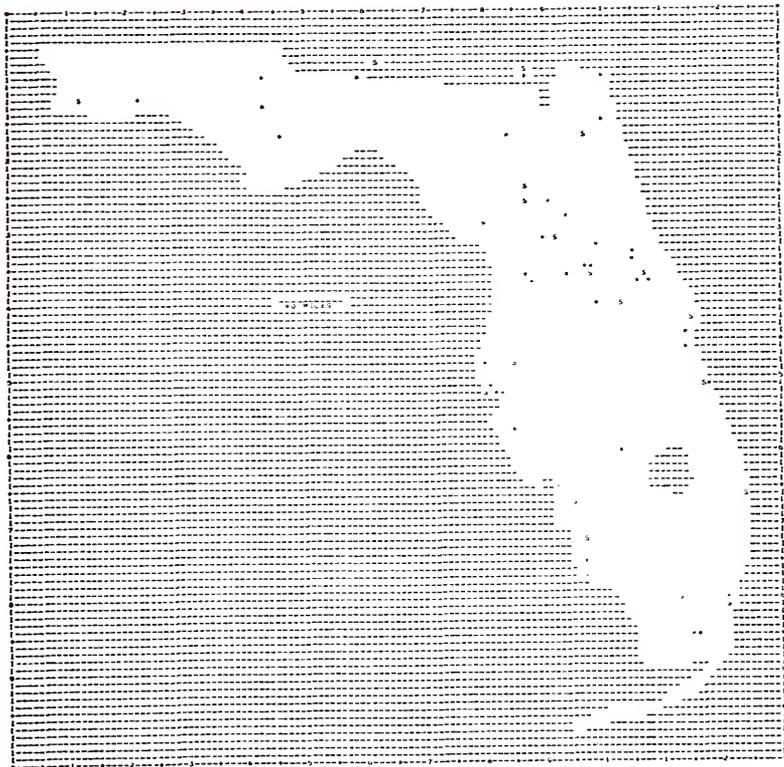
MAP 163. Geographic variation in the displacement of the nuchal ring behind the parietal scales in *Diadophis punctatus*, both sexes. Lightest shading represents neck rings 0.75 to 1.75 scale lengths behind the parietals; intermediate shading, 1.75 to 2.5; and the darkest shading represents snakes with neck rings 2.75 to 3.5 scale lengths behind the parietal scales. Based on 291 specimens.



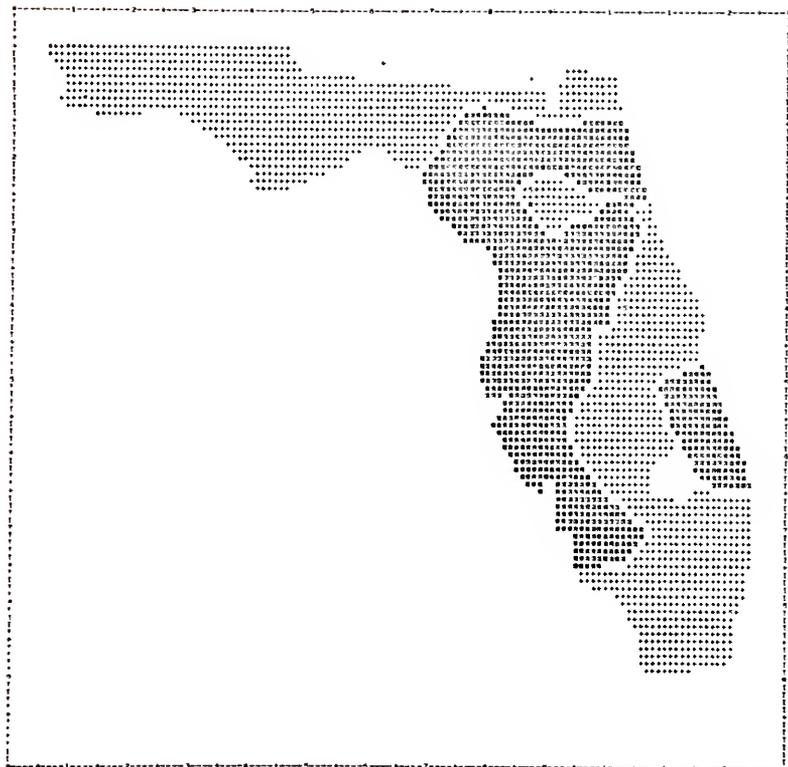
MAP 164. Geographic variation in Factor 2 for *Diadophis punctatus*, both sexes. This factor accounts for 13.2% of the variation in 19 characters, and most of the variation in labial pigment distinctiveness and number of spots on the supra- and infralabials. Darker shading implies labial pigment less distinct, or in diffuse patches rather than discrete spots, and more labial pigment spots, when present. Based on 295 specimens.



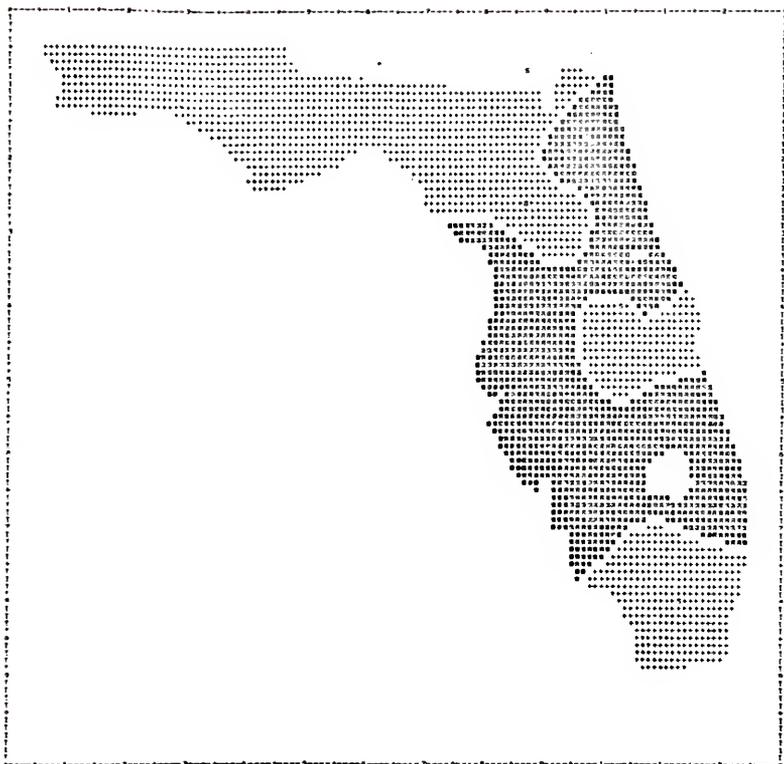
MAP 165. Geographic variation in Factor 4 for *Diadophis punctatus*, both sexes. This factor accounts for 7.8% of the total variation in 19 characters, and most of the variation in ring interruption, ring displacement behind the parietal, and ring width. It also receives small contributions from supralabial and infralabial spots. Darker shading means generally narrower rings, wider ring interruptions, rings displaced farther posteriorly, and a tendency for more labial spots. Based on 295 specimens.



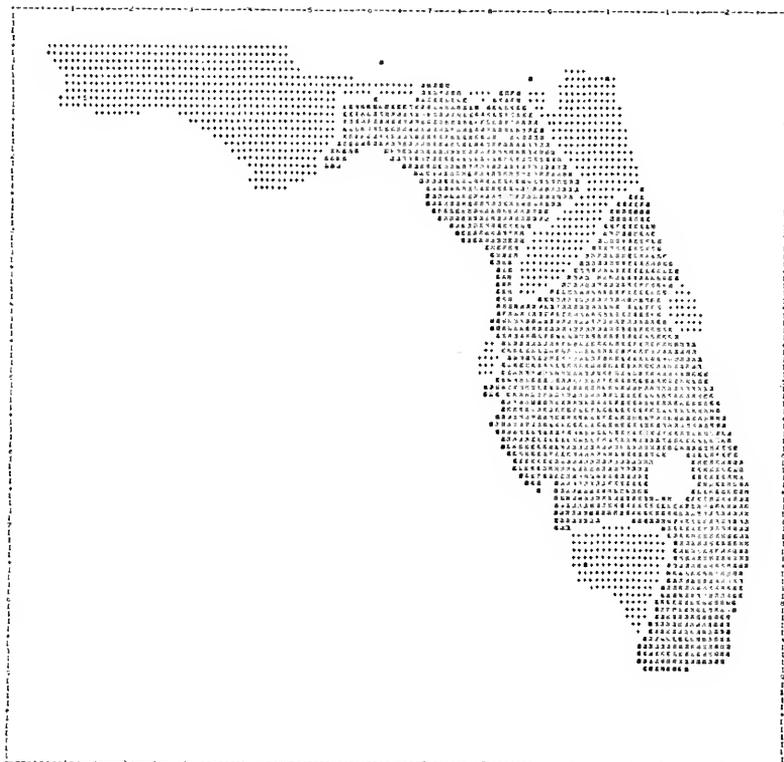
MAP 166. Localities of 90 *Cemophora coccinea* specimens examined. An asterisk represents one specimen; an S represents more than one.



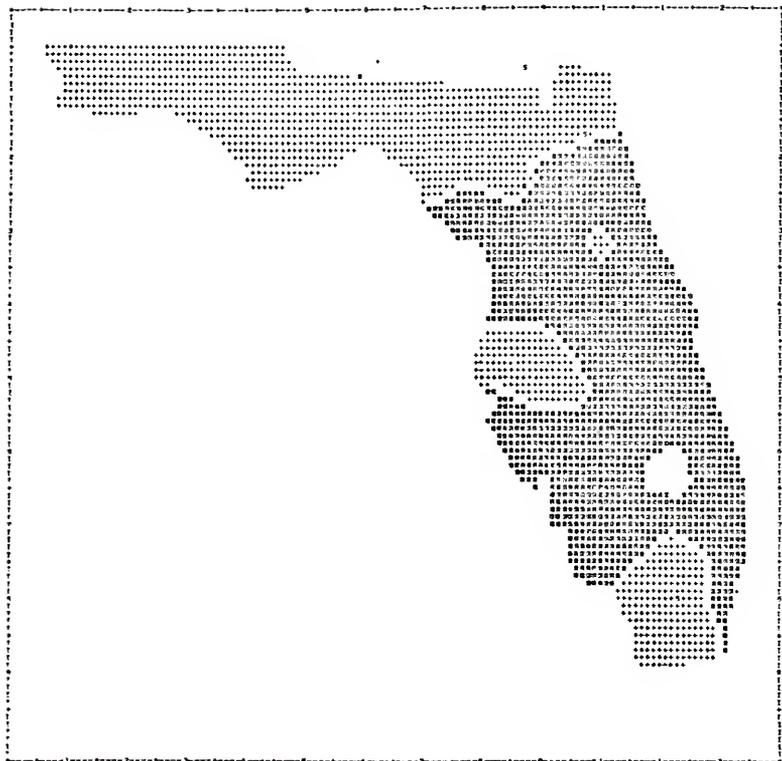
MAP 167. Geographic variation in number of ventral scales in *Cemophora coccinea*, males only. Light shading represents from 158 to 170; darker shading represents from 171 to 182 ventral scales. Based on 41 specimens.



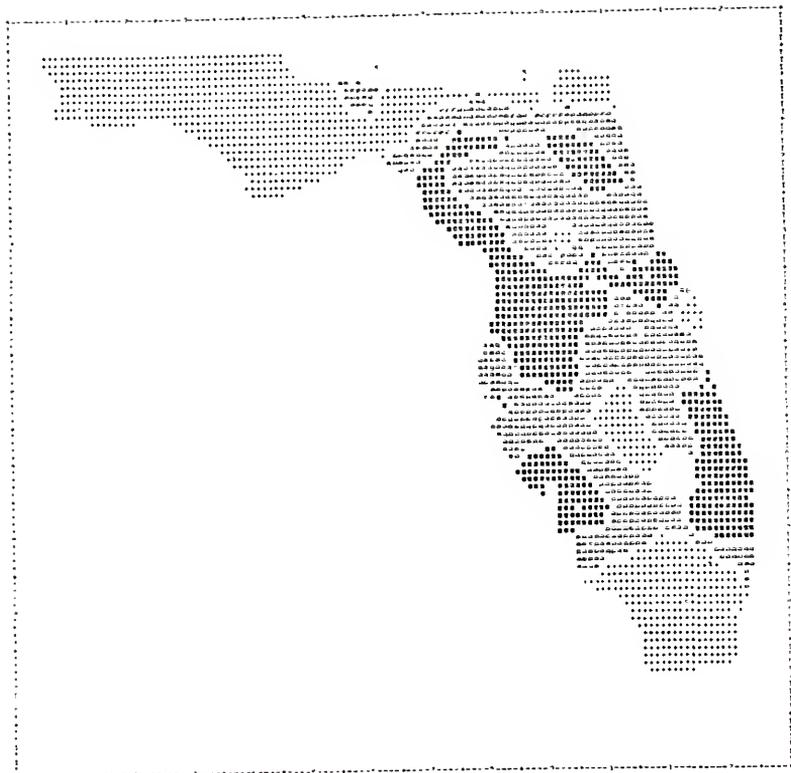
MAP 168. Geographic variation in the number of ventral scales in *Cemophora coccinea*, females only. Lighter shading represents from 165 to 174 ventrals; darker shading represents from 175 to 185. Based on 37 specimens.



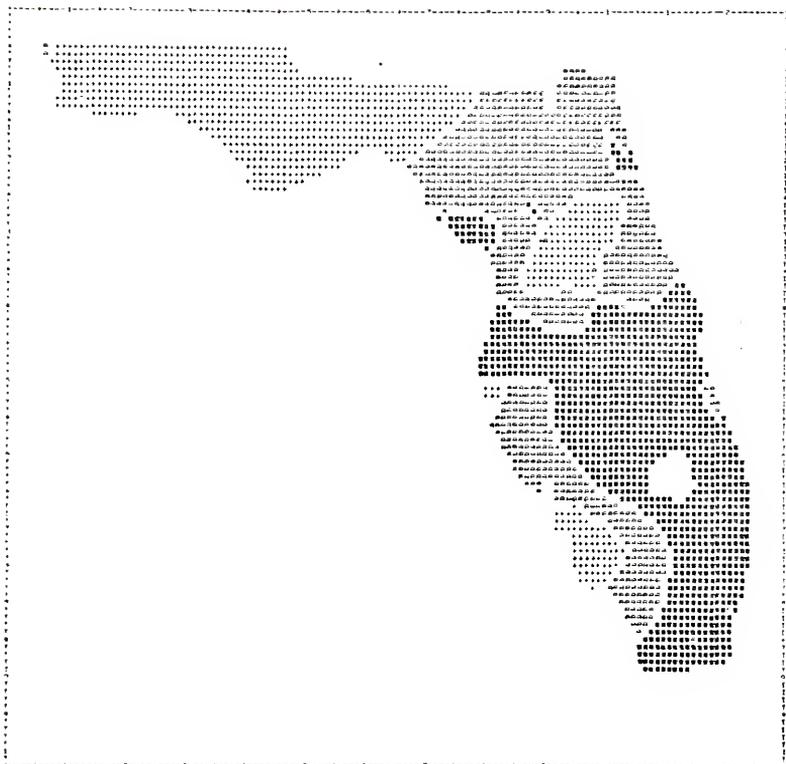
MAP 169. Geographic variation in number of subcaudal scales in *Cemophora coccinea*, males only. Lighter shading represents from 36 to 42; darker shading represents from 43 to 50 subcaudal scales. Based on 42 specimens.



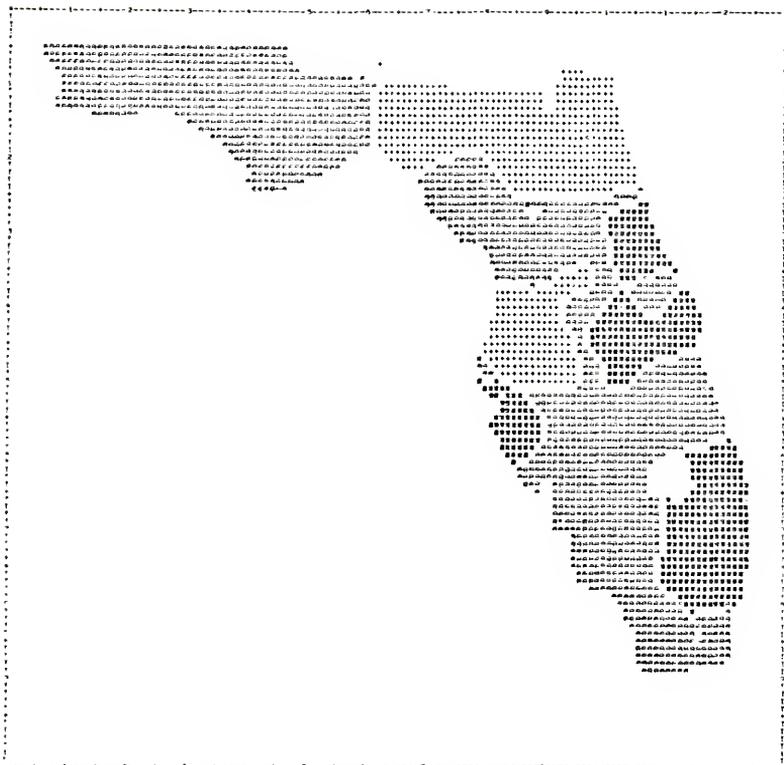
MAP 170. Geographic variation in number of subcaudal scales in *Cemophora coccinea*, females only. Lighter shading represents from 33 to 40 subcaudals; darker shading represents from 41 to 47. Based on 38 specimens.



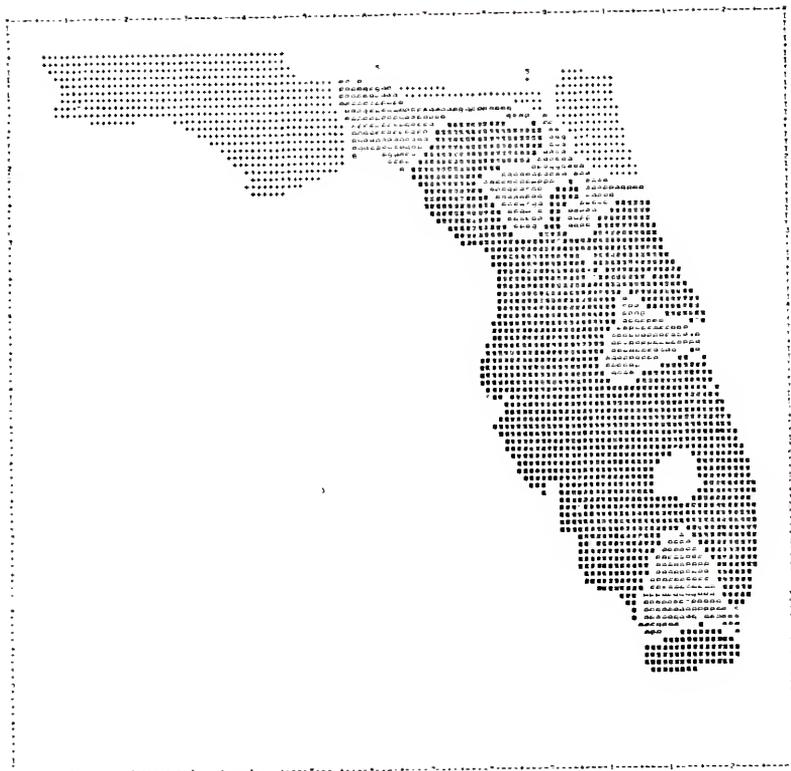
MAP 171. Geographic variation in the sum of ventrals plus caudals in *Cemphora coccinea*, both sexes. Levels by increased shading are: 197-212, 213-218, 219-228. Based on 84 specimens.



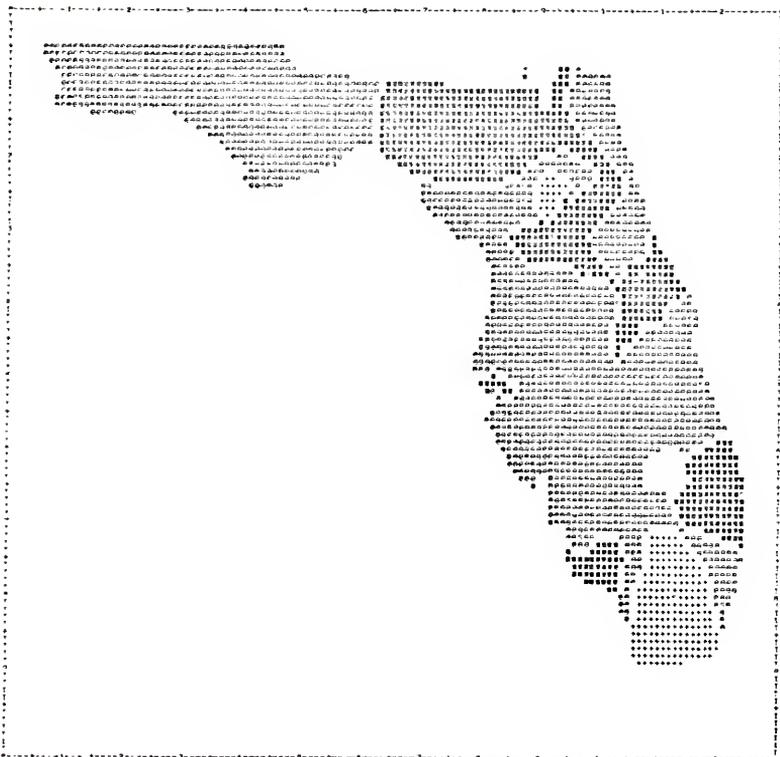
MAP 172. Geographic variation in tail length divided by total length in *Cemophora coccinea*, males only. Increasing shading represents increasing proportionate tail length. Based on 37 specimens.



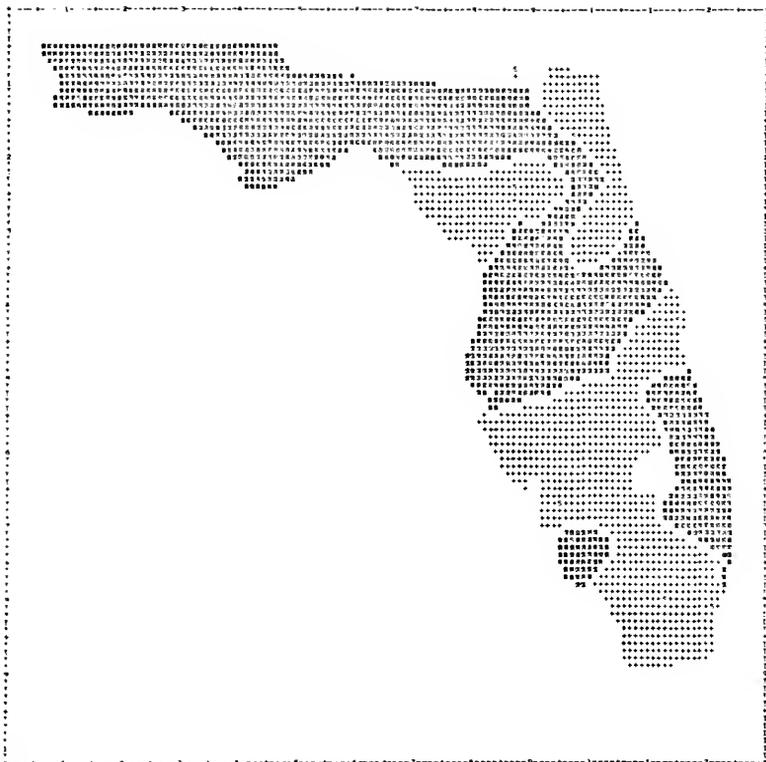
MAP 173. Geographic variation in tail length divided by total length in *Cemophora coccinea*, females only. Increasing shading represents proportionately longer tails. Based on 31 specimens.



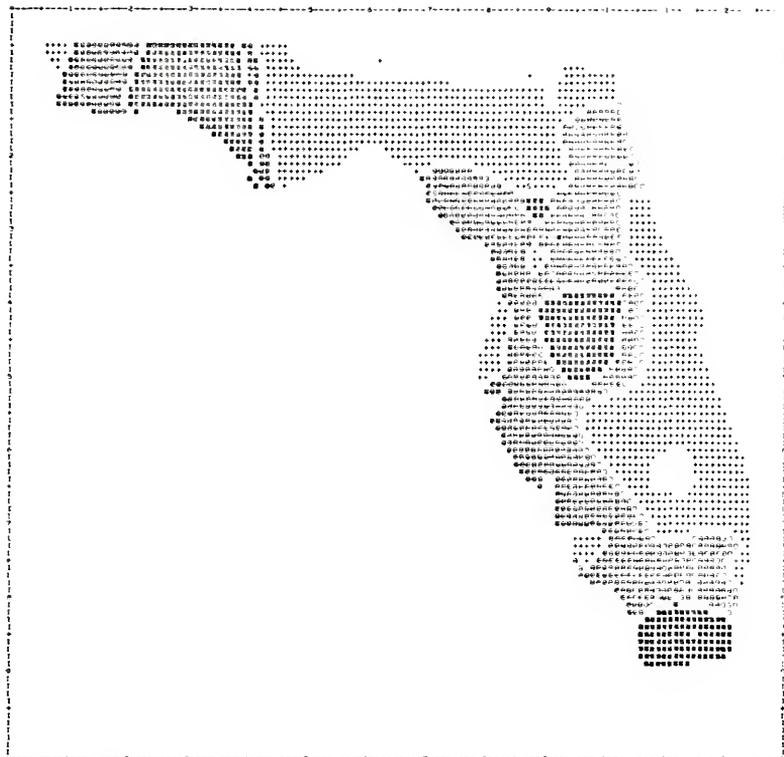
MAP 174. Geographic variation in number of supralabial scales (both sides) in *Cemophora coccinea*, both sexes. Levels by increasing shading are: 11-12, 13, 14-15. Based on 85 specimens.



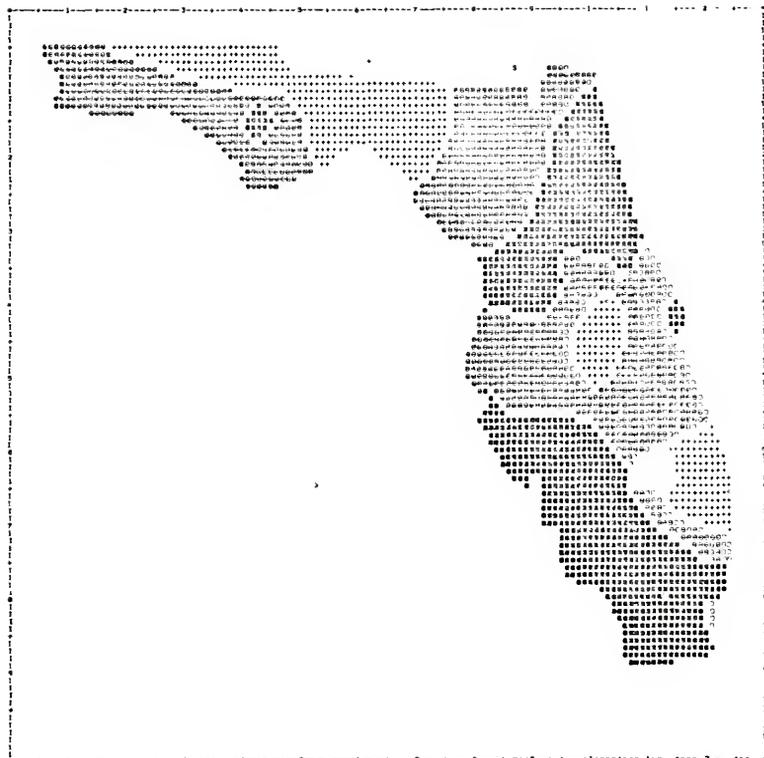
MAP 175. Geographic variation in number of dorsal scale rows one head length behind the head in *Cemophora coccinea*, both sexes. Levels by increasing shading are 17, 19, and 21. Based on 64 specimens.



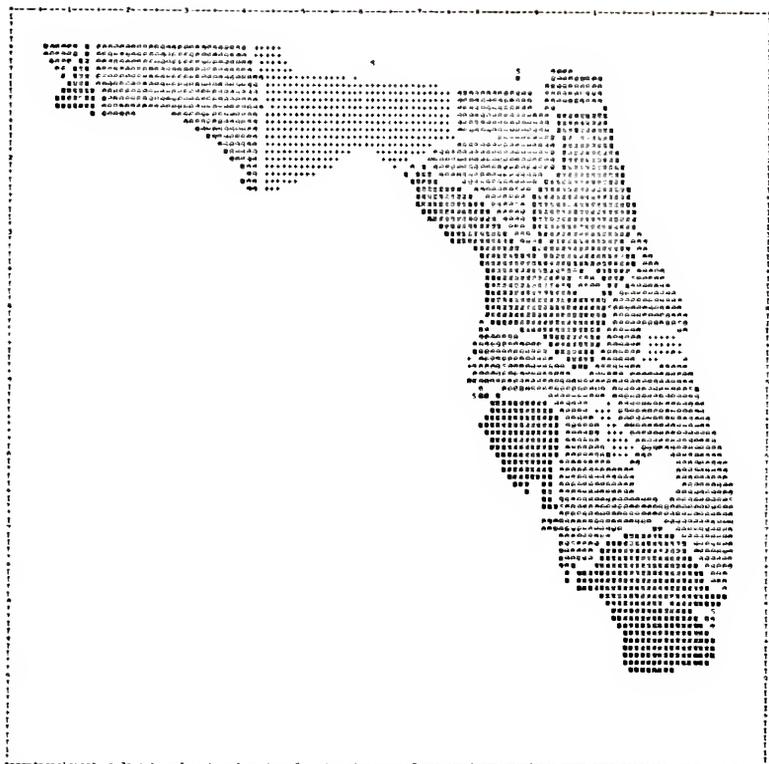
MAP 176. Geographic variation in number of dorsal scale rows one head length anterior to the vent in *Cemophora coccinea*, both sexes. Lighter shading represents fewer than 19 posterior scale rows; darker shading represents 19. Based on 64 specimens.



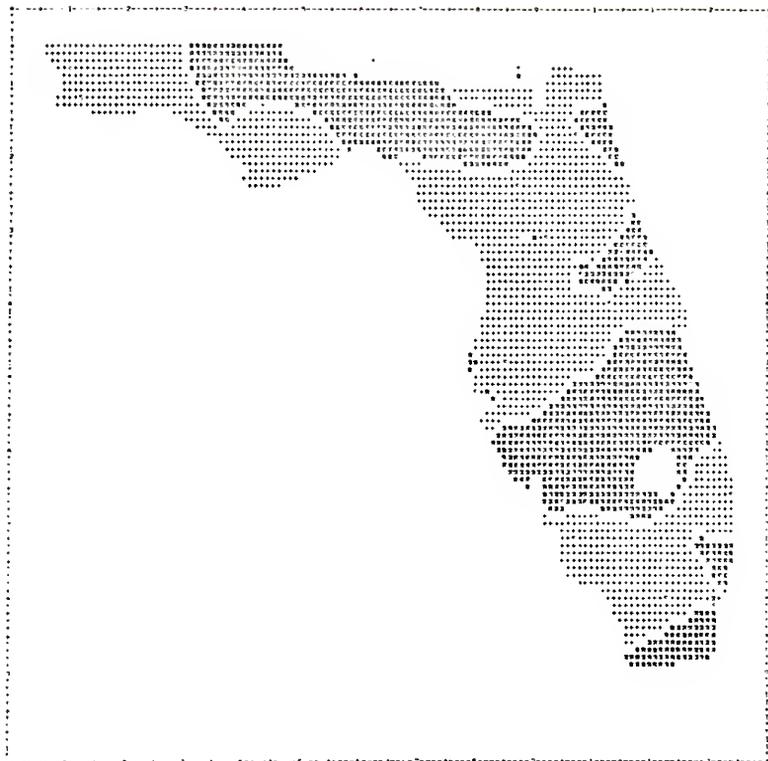
MAP 177. Geographic variation in length of the first white band in *Cemophora coccinea*, males only. Levels by increasing shading are (in scale lengths): 1.7-2.6, 3.0, 3.2-4.0. Based on 42 specimens.



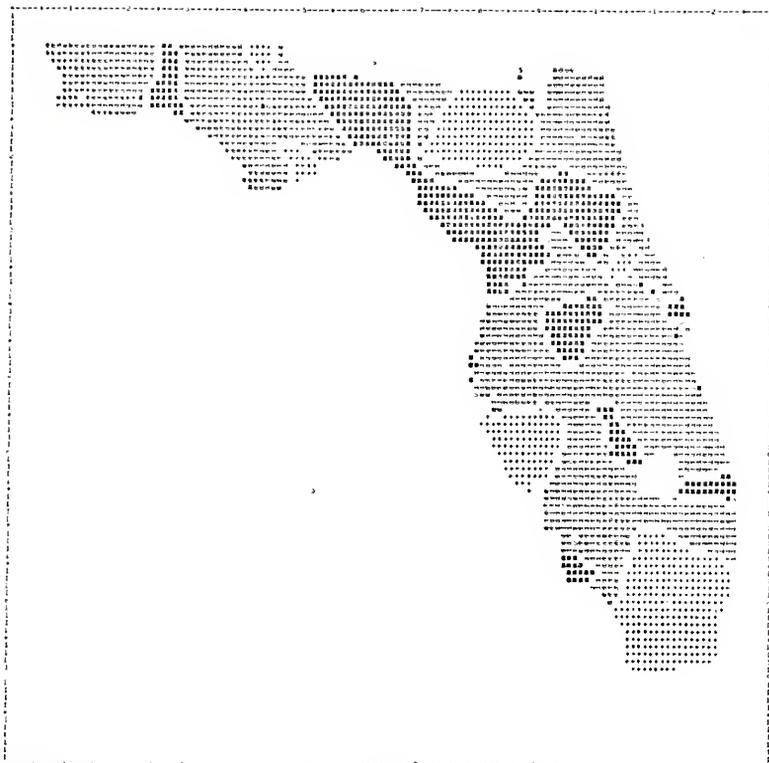
MAP 178. Geographic variation in length of the first white band in *Cemophora coccinea*, females only. Levels by increasing shading are (in scale lengths): 1.2-2.3, 2.5-2.8, 3.0-4.0. Based on 39 specimens.



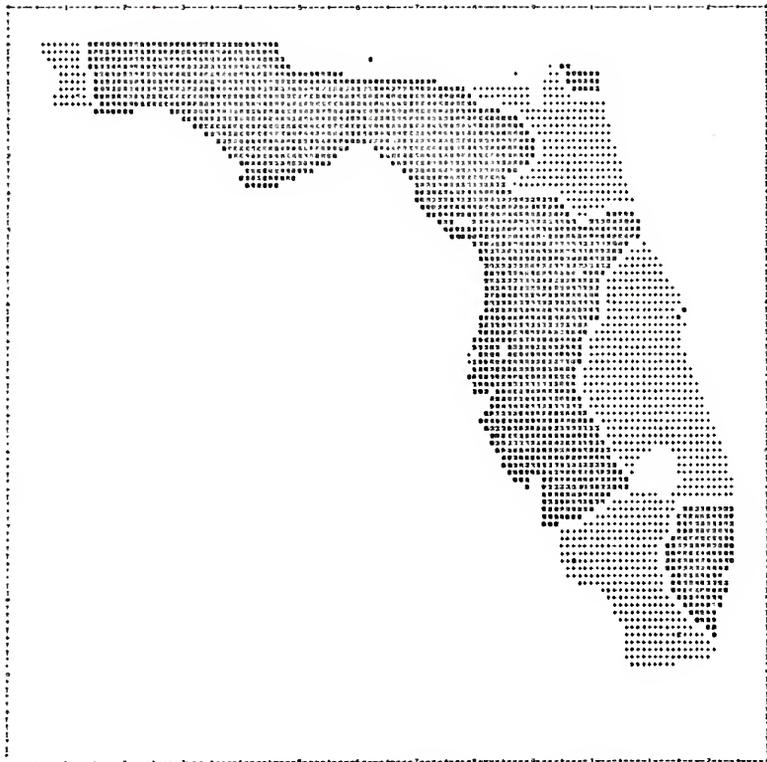
MAP 179. Geographic variation in length of the fifth white band in *Cemophora coccinea*, both sexes. Levels by increasing shading are (in scale length): 1.0-1.8, 2.0-2.4, 2.5-3.5. Based on 88 specimens.



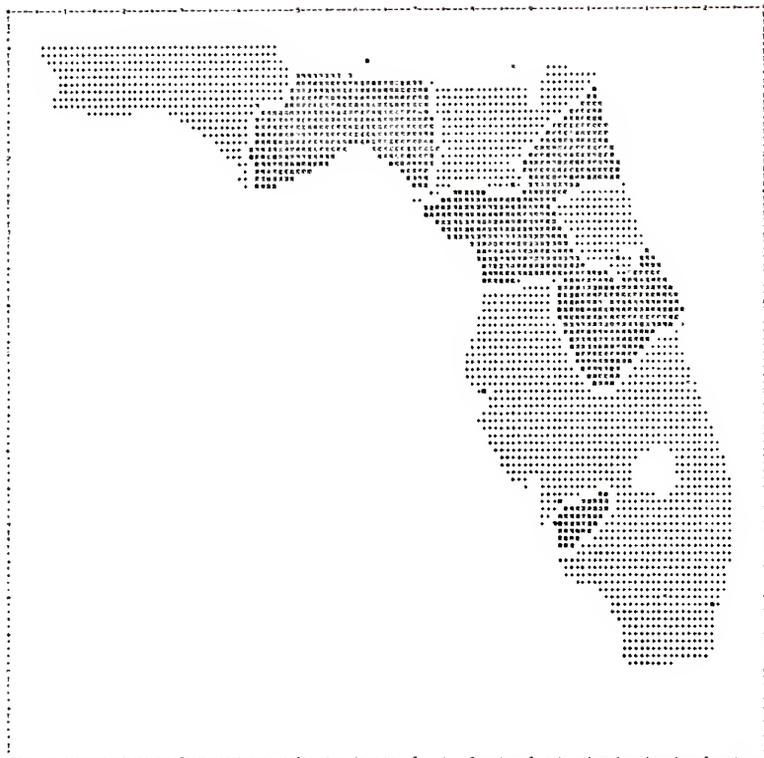
MAP 180. Geographic variation in length of the first red band in *Cemophora coccinea*, both sexes. Lighter shading represents from 4 to 8 scale lengths; darker shading represents from 9 to 12 scale lengths. Based on 89 specimens.



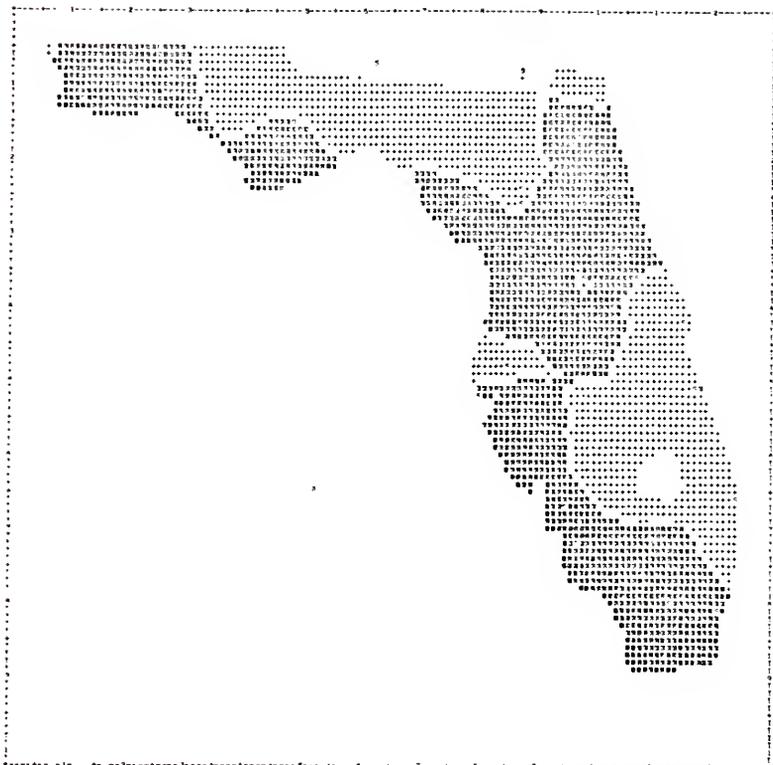
MAP 181. Geographic variation in number of red body bands in *Cemophora coccinea*, both sexes. Levels by increasing shading are: 12-16, 17-18, 19-24. Based on 89 specimens.



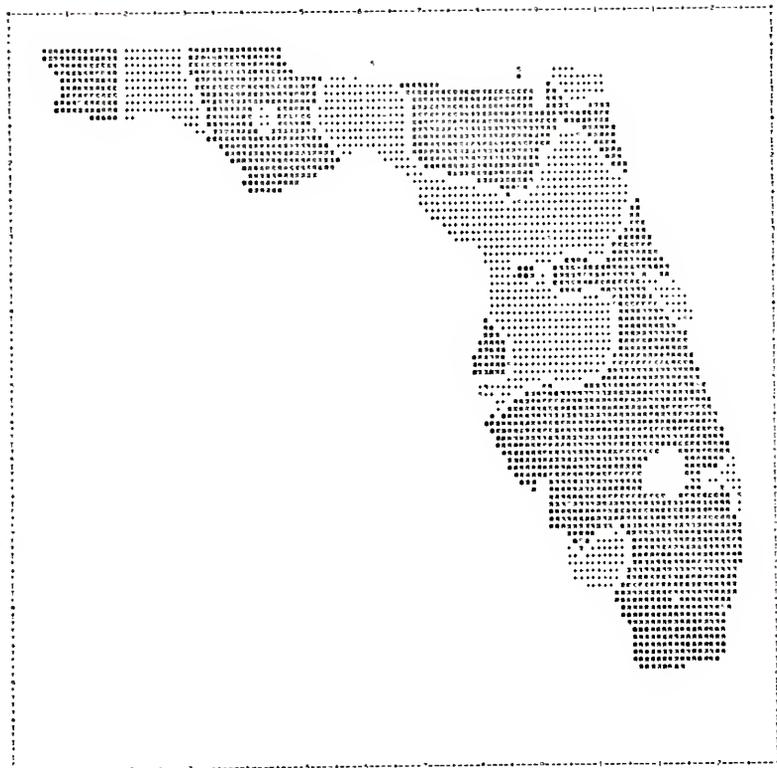
MAP 182. Geographic variation in number of tail bands in *Cemophora coccinea*, males only. Lighter shading represents from 4 to 5 tail bands; darker shading represents from 6 to 8. Based on 42 specimens.



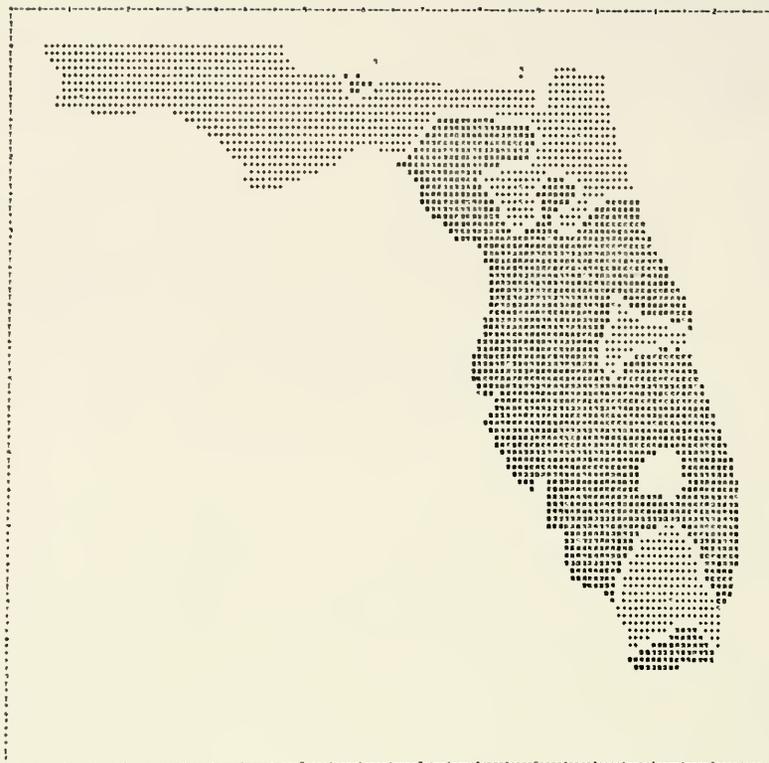
MAP 183. Geographic variation in number of tail bands in *Cemophora coccinea*, females only. Lighter shading represents from 3 to 4 tail bands; darker shading represents from 5 to 7. Based on 38 specimens.



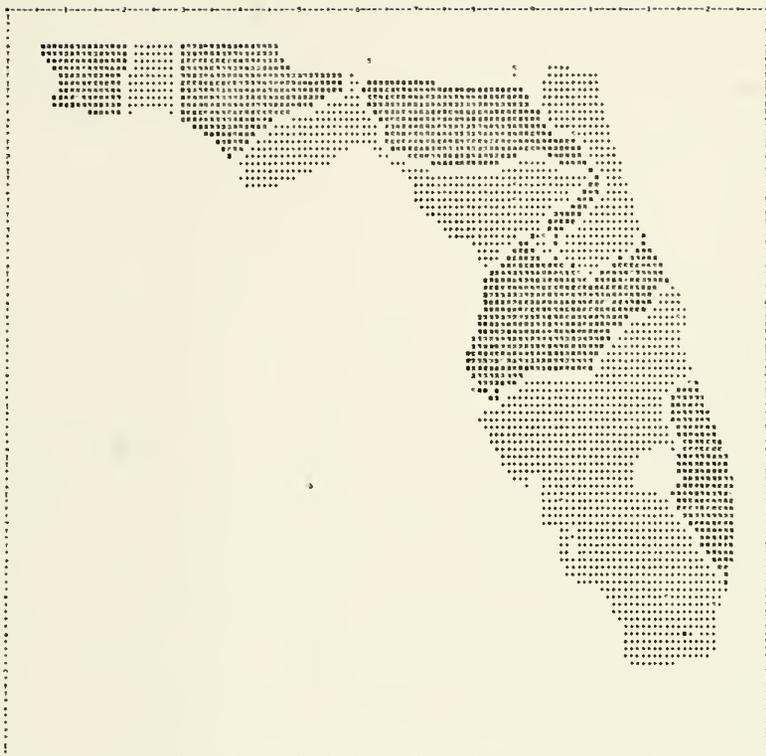
MAP 184. Geographic variation in Factor 1 in *Cemophora coccinea*, both sexes. Factor 1 accounts for most of the variation in length of the first and fifth white bands. Darker shading represents longer white bands. Total variation accounted for by Factor 1: 24.7% (14 characters). Based on 90 specimens.



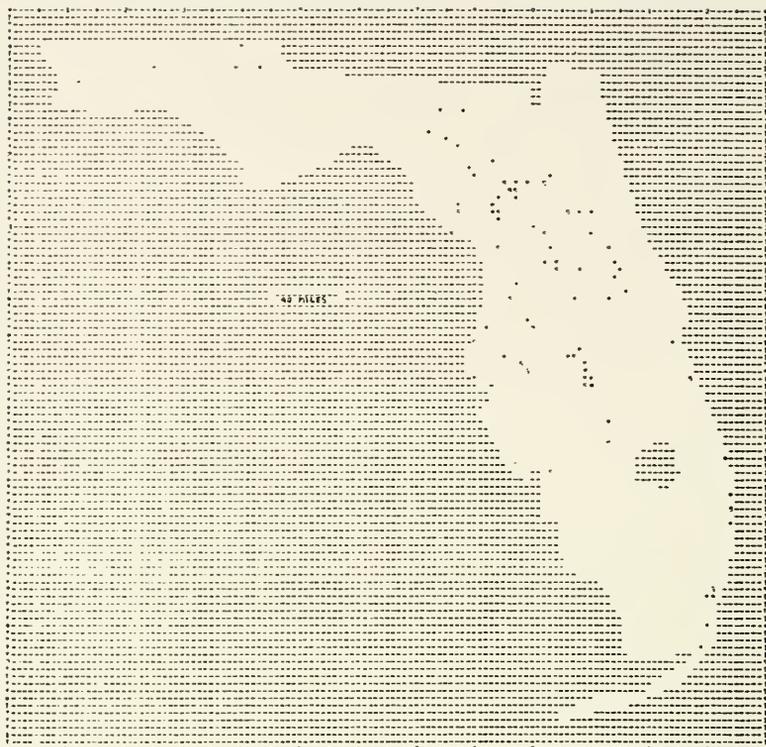
MAP 185. Geographic variation in Factor 2 for Cemophora coccinea, both sexes. Factor 2 accounts for much of the variation in number of red bands, and length of the first and fifth red bands. Darker shading represents generally fewer and longer red bands. Total variation accounted for by Factor 2: 16.0% (14 characters). Based on 90 specimens.



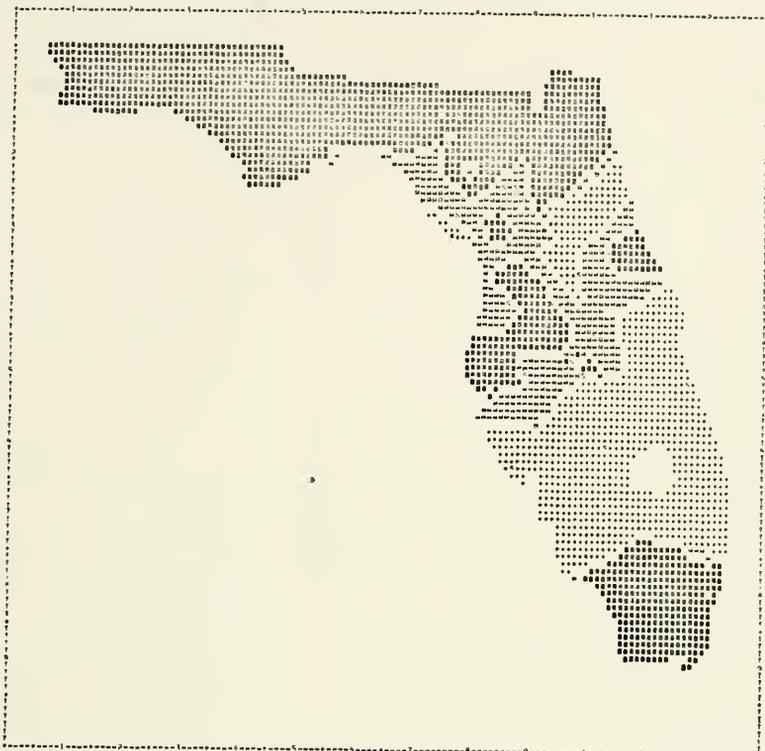
MAP 186. Geographic variation in Factor 3 for *Cemophora coccinea*, both sexes. Factor 3 accounts for much of the variation in infralabials, supralabials, and ventrals plus caudals. Darker shading represents generally higher counts for all of these. Total variation accounted for by Factor 3: 13.5% (14 characters). Based on 90 specimens.



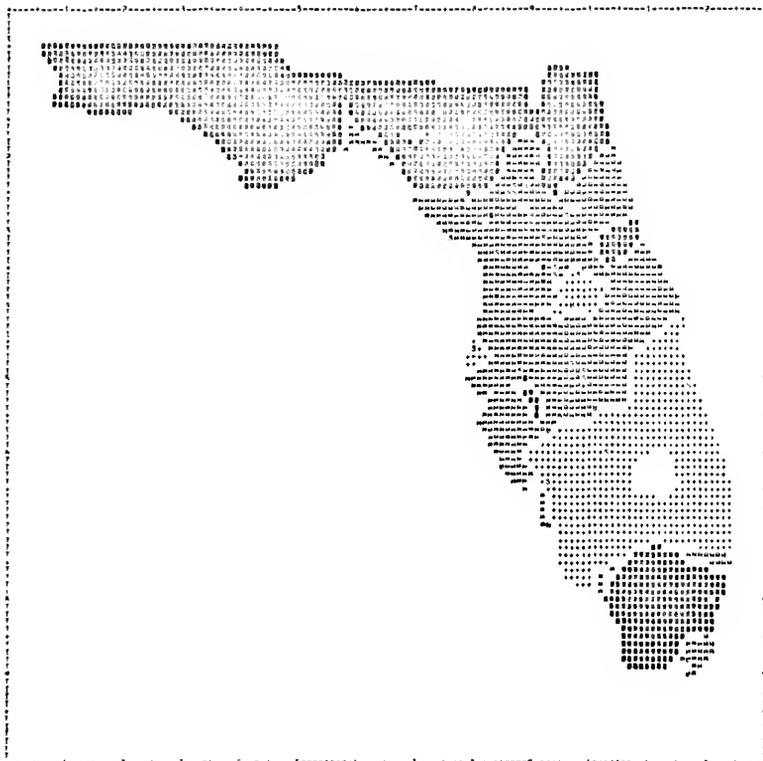
MAP 187. Geographic variation in Factor 4 for Cemophora coccinea, both sexes. Factor 4 accounts for much of the variation in the three dorsal scale row counts. Darker shading represents higher dorsal scale row counts. Total variation accounted for by Factor 4: 10.3% (14 characters). Based on 90 specimens.



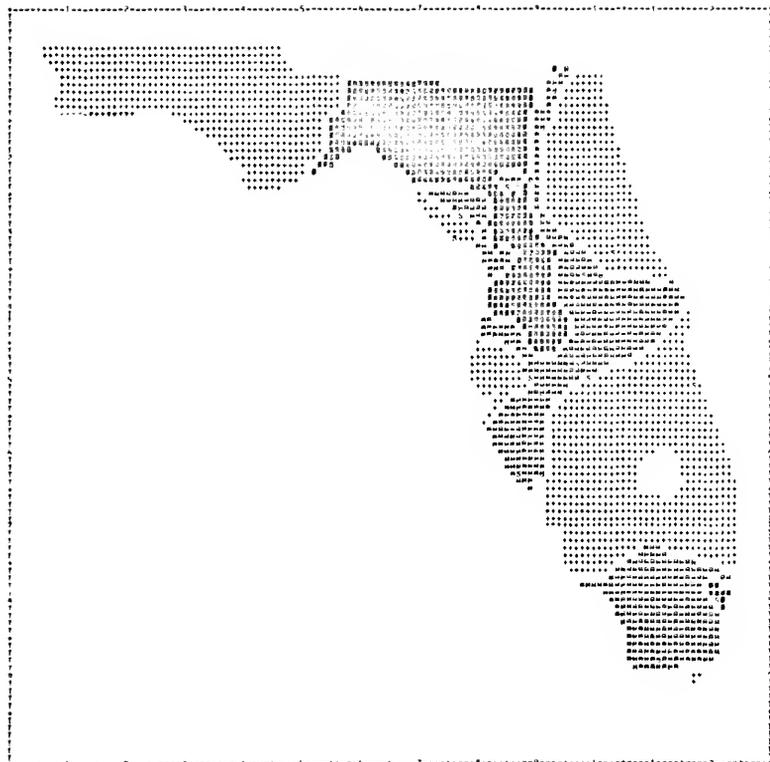
MAP 188. Localities of 198 *Tantilla* sp. specimens examined. An asterisk represents one specimen; an S represents more than one.



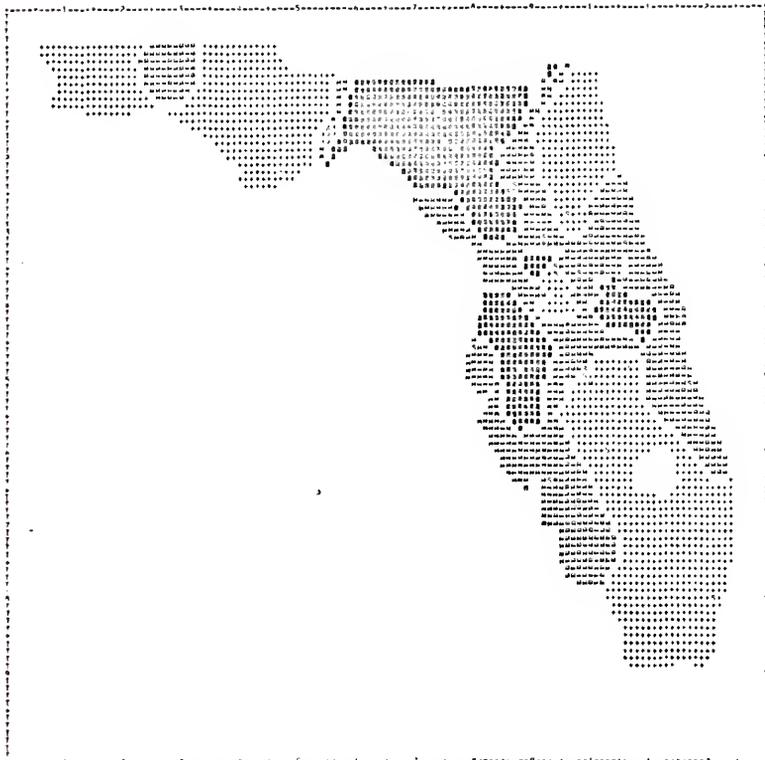
MAP 189. Geographic variation in number of ventral scales in *Tantilla*, males only. Levels by increasing shading are: 110-124; 125-128; 129-144. Based on 97 specimens.



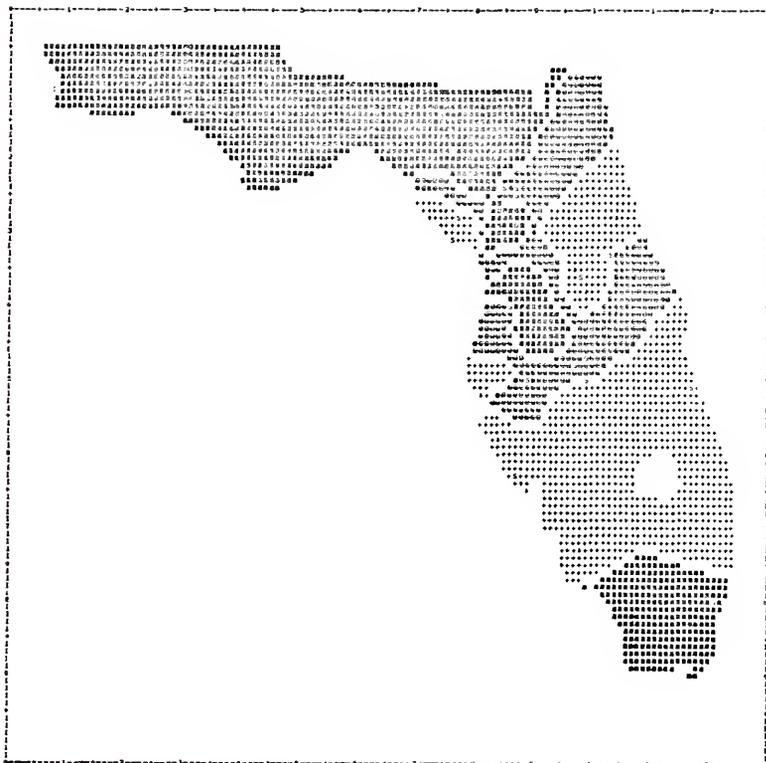
MAP 190. Geographic variation in the number of ventral scales in *Tantilla*, females only. Levels by increasing shading: 113-129; 130-135; 136-148. Based on 97 specimens.



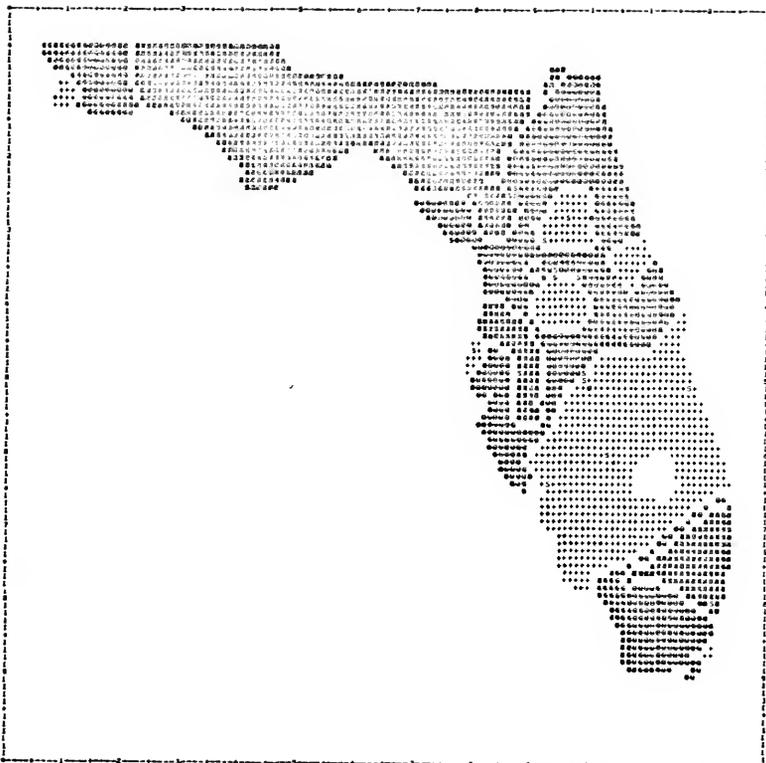
MAP 191. Geographic variation in number of subcaudal scales in *Tantilla*, males only. Levels by increasing shading are: 45-52; 53-58; 59-67. Based on 81 specimens.



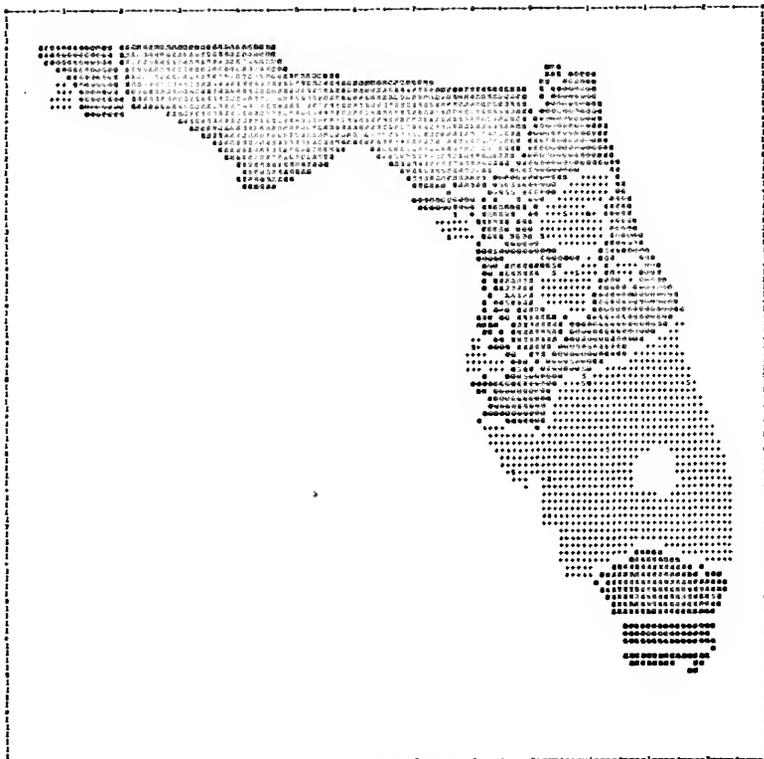
MAP 192. Geographic variation in number of subcaudal scales in *Tantilla*, females only. Levels by increasing shading are: 40-48; 49-52; 53-61. Based on 68 specimens.



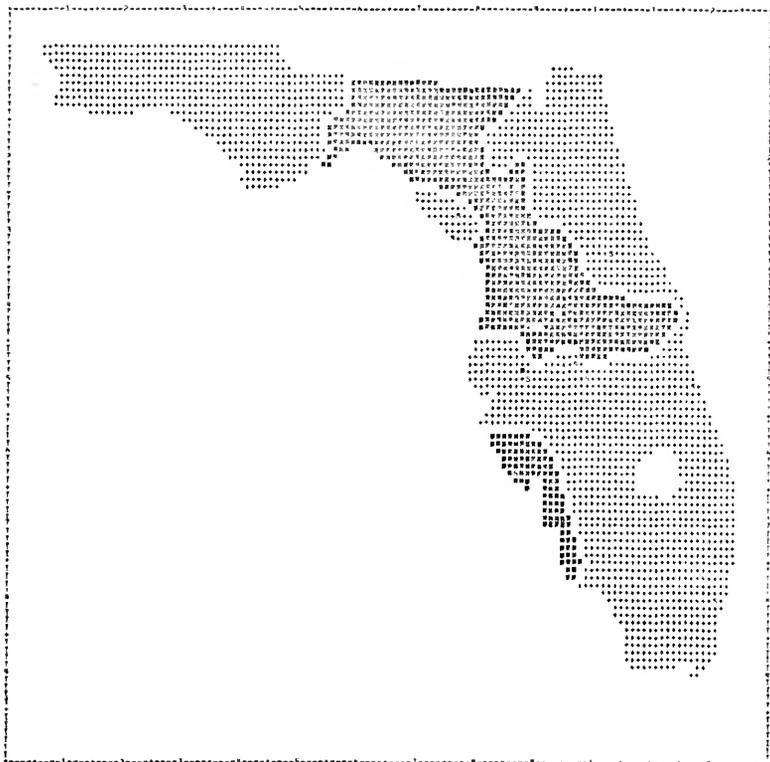
MAP 193. Geographic variation in the sum of ventrals plus caudals in *Tantilla*, males only. Levels by increasing shading are: 157-180; 181-187; 188-200. Based on 68 specimens.



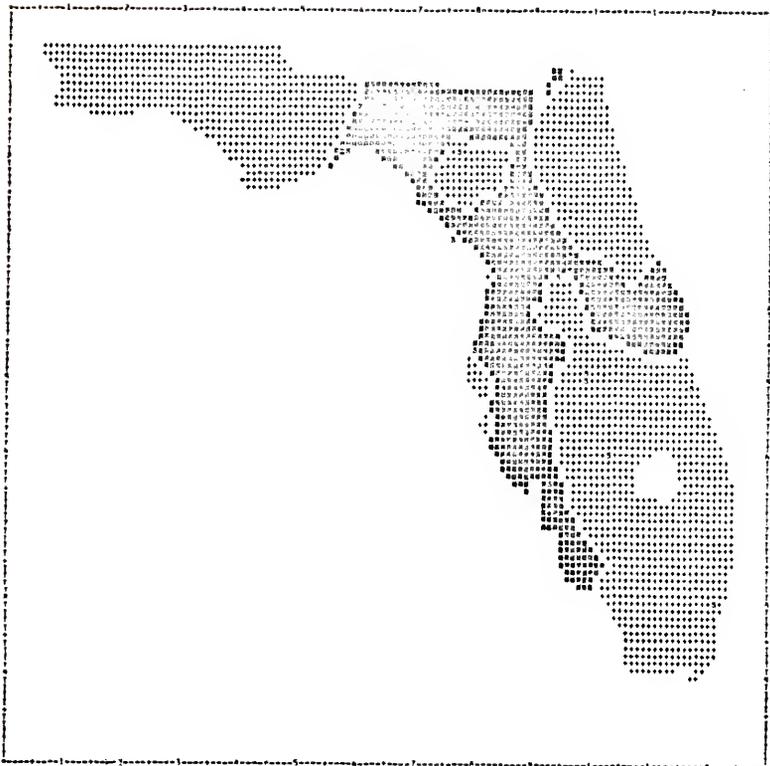
MAP 194. Geographic variation in the sum of ventrals plus subcaudals in *Tantilla*, females only. Levels by increasing shading are: 156-180; 181-188; 180-209. Based on 81 specimens.



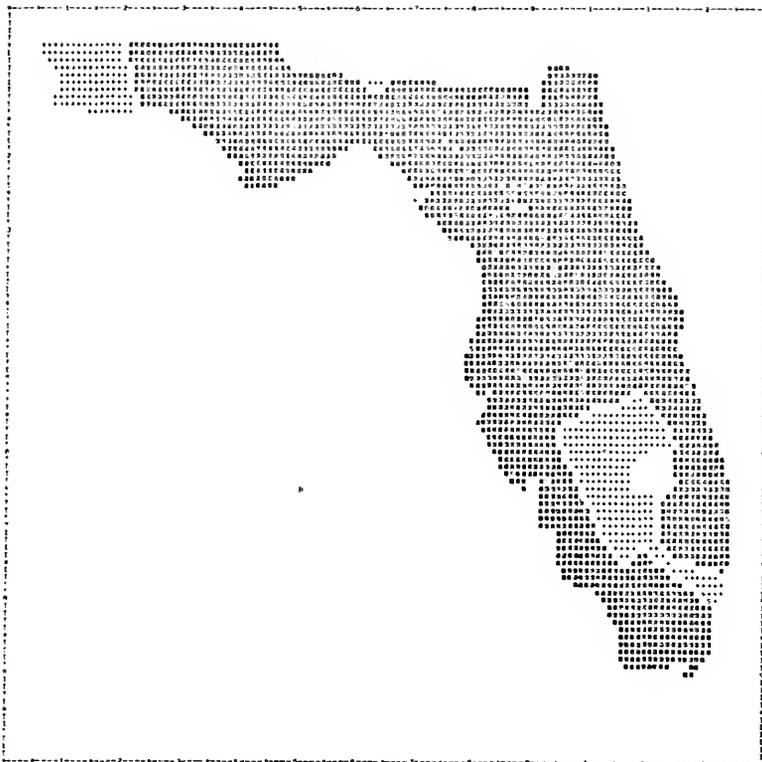
MAP 195. Geographic variation in sum of ventrals plus caudals in *Tantilla*, both sexes. Levels by increasing shading are: 156-180; 181-187; 188-209. Based on 149 specimens.



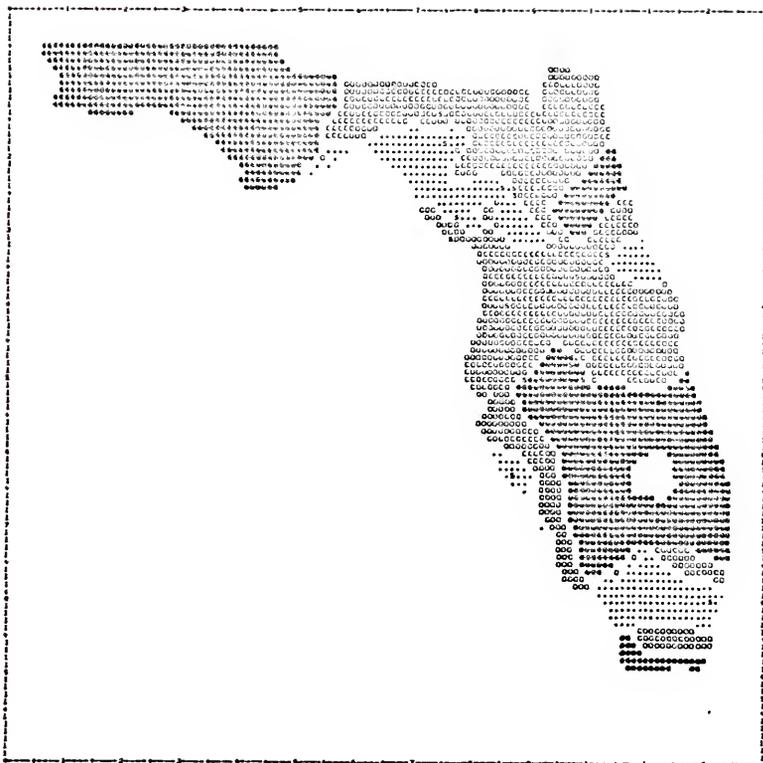
MAP 196. Geographic variation in tail length divided by total length in *Tantilla*, males only. Levels by increasing shading are: 0.19-0.23; 0.24-0.28. Based on 84 specimens.



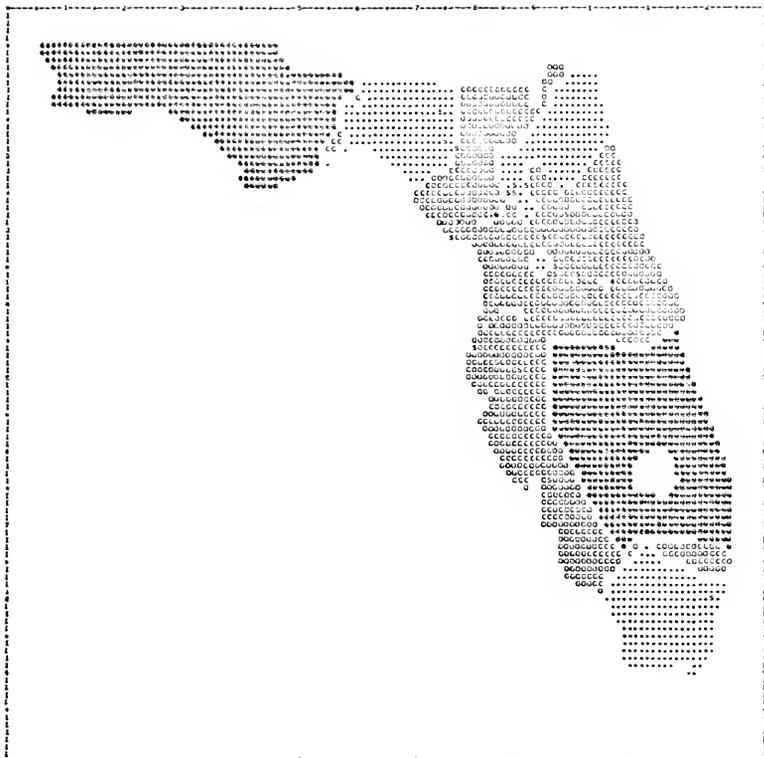
MAP 197. Geographic variation in tail length divided by total length for *Iantilla*, females only. Lighter shading represents 0.16-0.20; darker shading, 0.21-0.25. Based on 70 specimens.



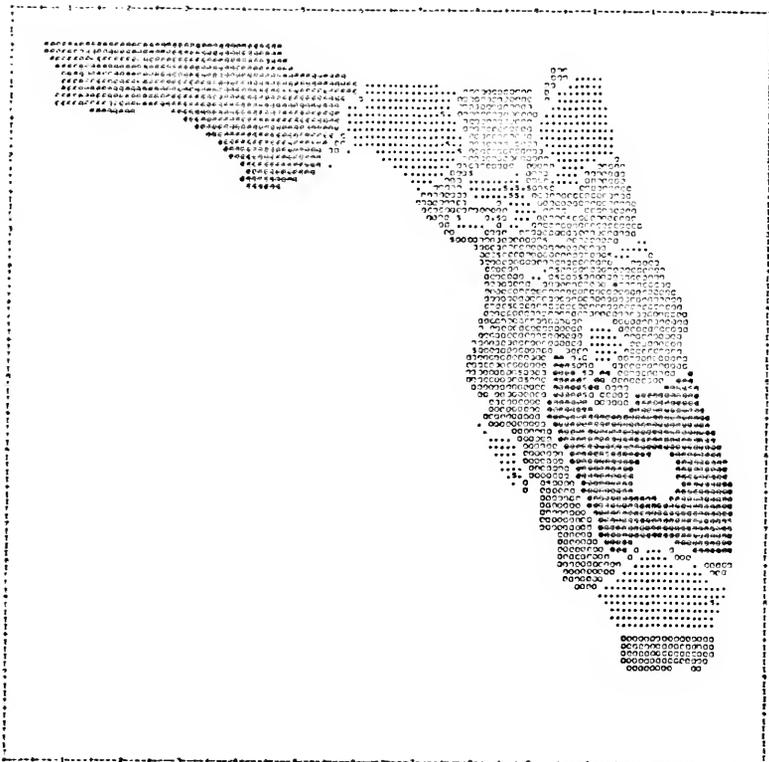
MAP 198. Geographic variation in number of supralabial scales in *Tantilla*, both sexes. Lighter shading represents snakes with 12 supralabials, and darker shading, 14 supralabials. Based on 195 specimens.



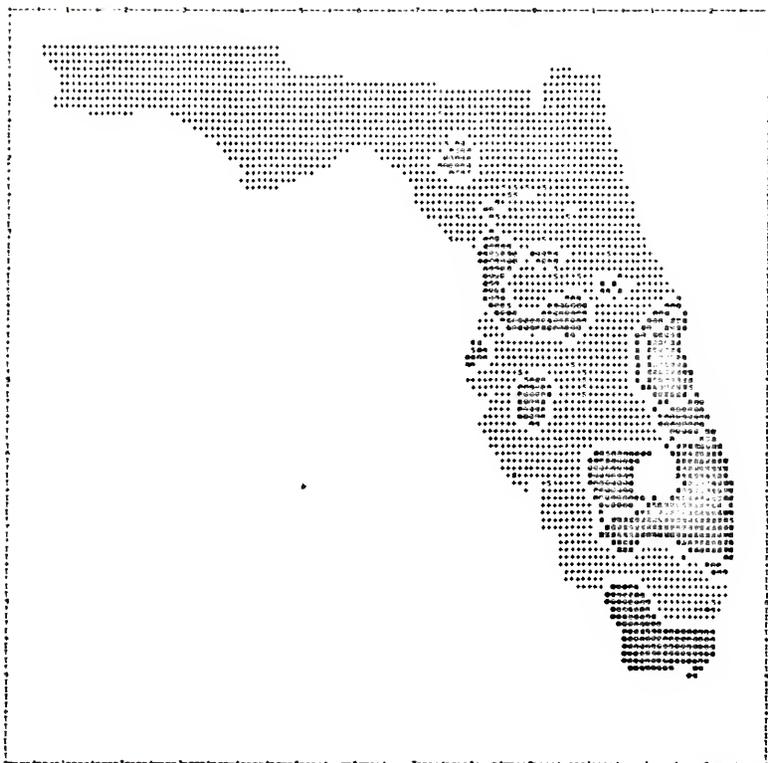
MAP 199. Geographic variation in the amount of light pigment on the parietal scales in *Tantilla*, males only. Lightest shading represents snakes with black parietals and no nuchal light band; intermediate shading represents specimens with some light pigment on the parietal scales; darkest shading represents snakes with much light pigment on the parietals and a light nuchal band. Based on 97 specimens.



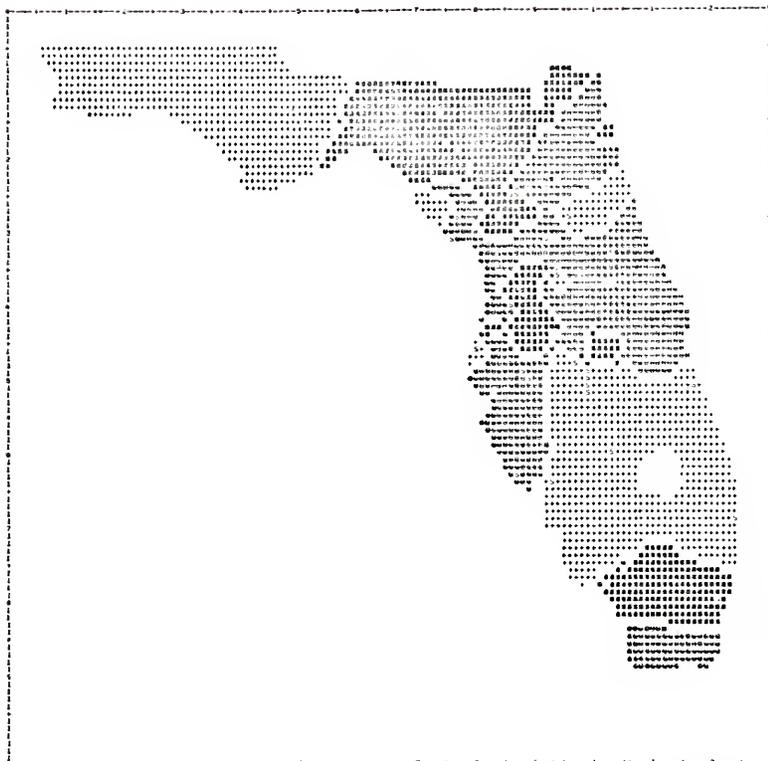
MAP 200. Geographic variation in the amount of light pigment on the parietal scales in *Tantilla*, females only. Lightest shading represents specimens with black parietals, and no nuchal light band; intermediate shading, specimens with some light pigment on the parietal scales; the darkest shading represents snakes with much light pigment on the parietals, and a nuchal light band. Based on 96 specimens.



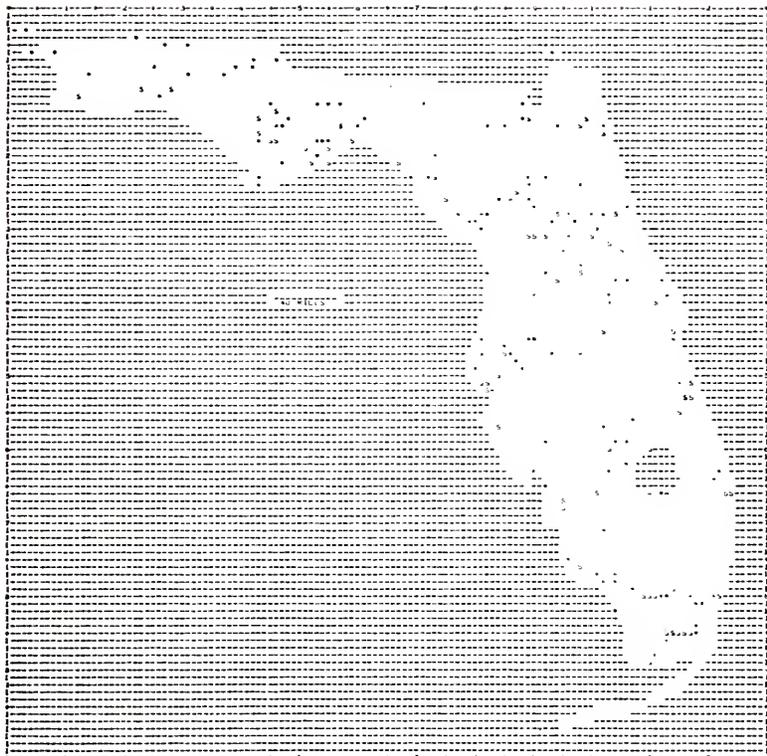
MAP 201. Geographic variation in the amount of light pigment on the parietal scales in *Tantilla*, both sexes. Lightest shading represents snakes with black parietals and no nuchal light band; intermediate shading represents specimens with some light pigment on the parietals; darkest shading, snakes with much light pigment on the parietals, and a nuchal light band. Based on 197 specimens.



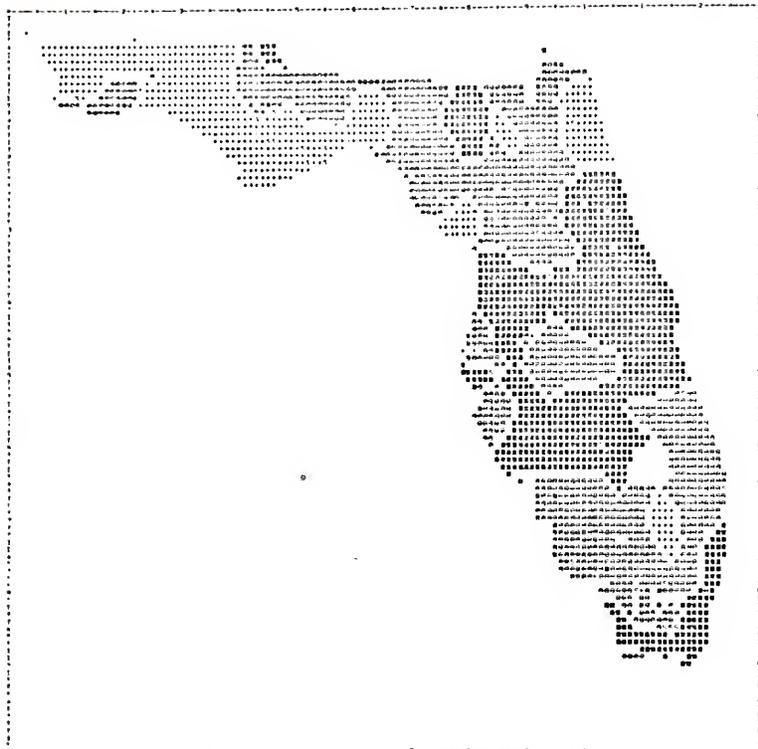
MAP 202. Geographic variation in size of the light spot on the snout in *Tantilla*, both sexes. Lightest shading represents snakes with no light spot on the snout; darkest shading represents a large spot; an intermediate shading, a small light spot. Based on 197 specimens.



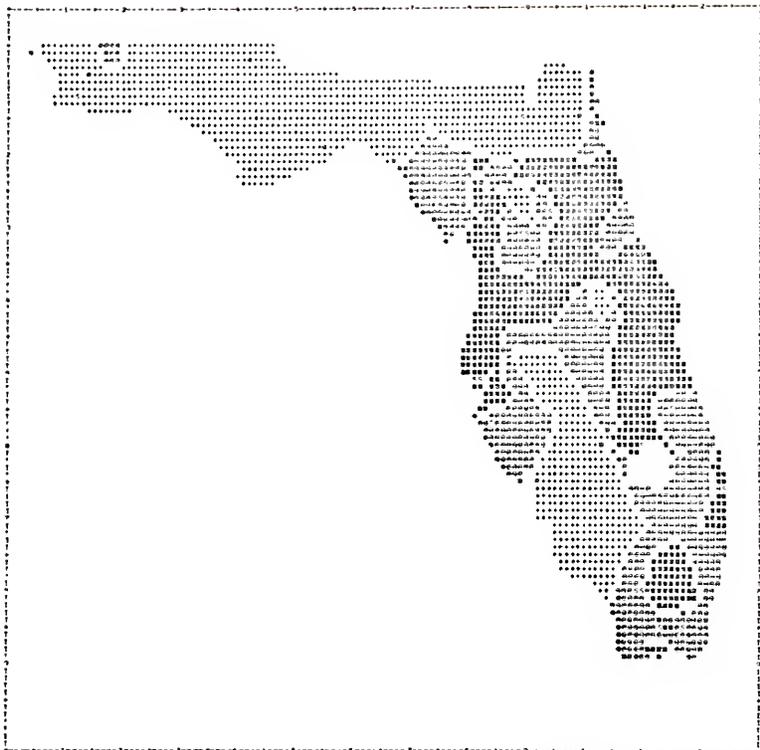
MAP 203. Geographic variation in Factor 2 for *Tantilla* from Florida, both sexes. Factor 2 accounts for most of the variation in snout and parietal pigmentation, and much of the variation in ventrals plus caudals. Darker shading represents less pigment on the head, and more ventrals plus caudals. This factor accounts for a total of 12.1% of the variation in 8 characters. Based on 198 specimens.



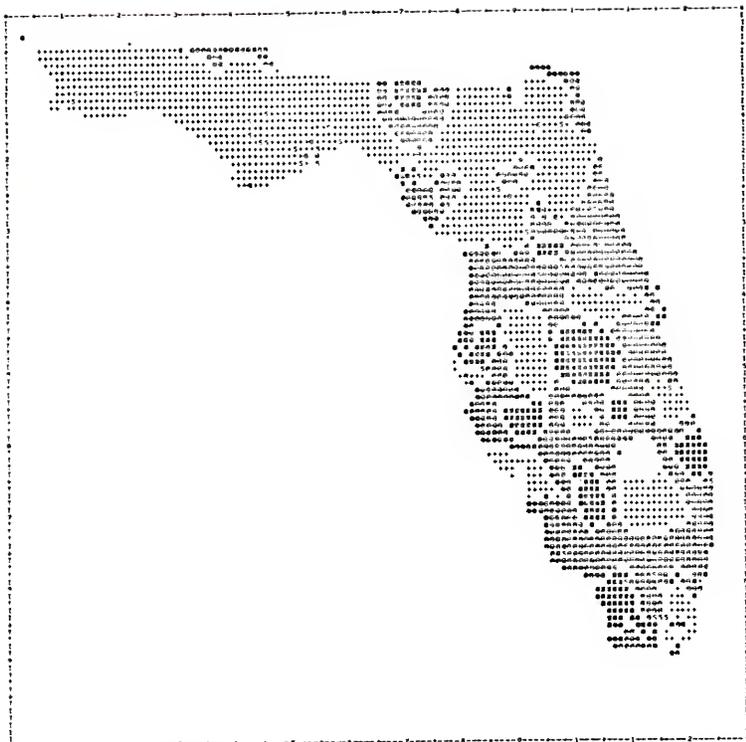
MAP 204. Localities of 320 *Sistrurus miliarius* specimens examined. An asterisk represents one specimen; an S represents more than one.



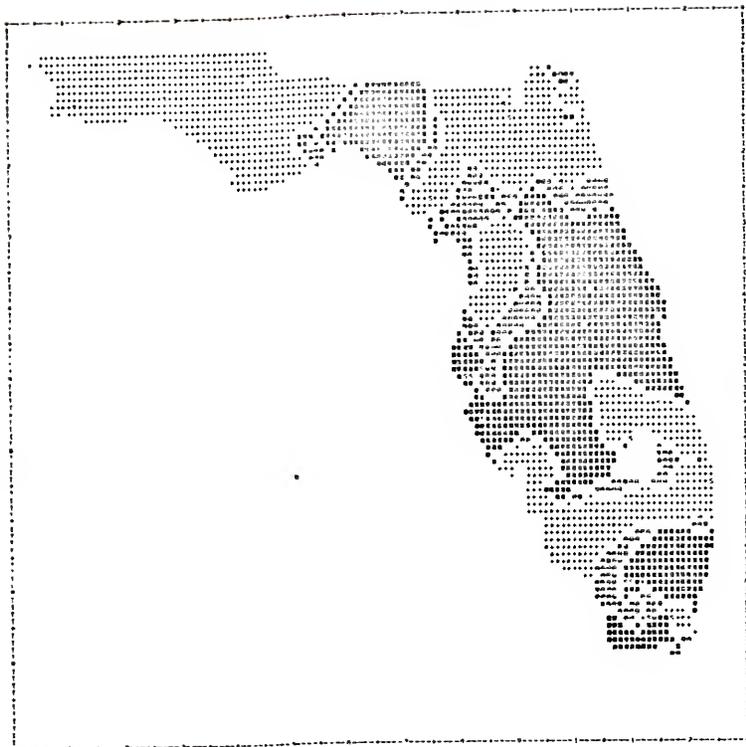
MAP 205. Geographic variation in number of ventral scales in *Sistrurus miliaris*, males only. Levels by increasing shading are: 125-134; 135-137; 138-144. Based on 186 specimens.



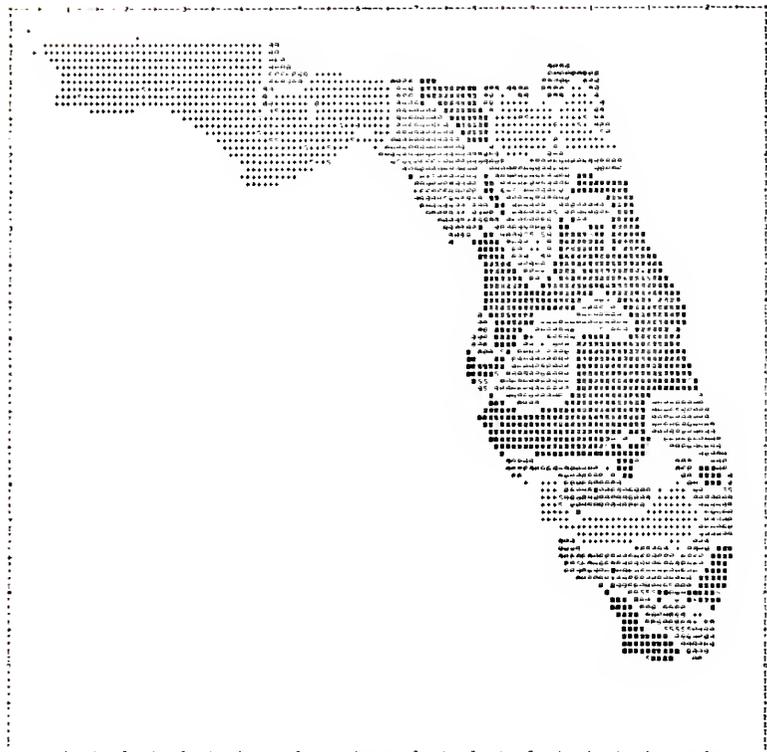
MAP 206. Geographic variation in number of ventral scales in *Sistrurus miliarius*, females only. Levels by increasing shading are: 128-138; 139-141; 142-150. Based on 130 specimens.



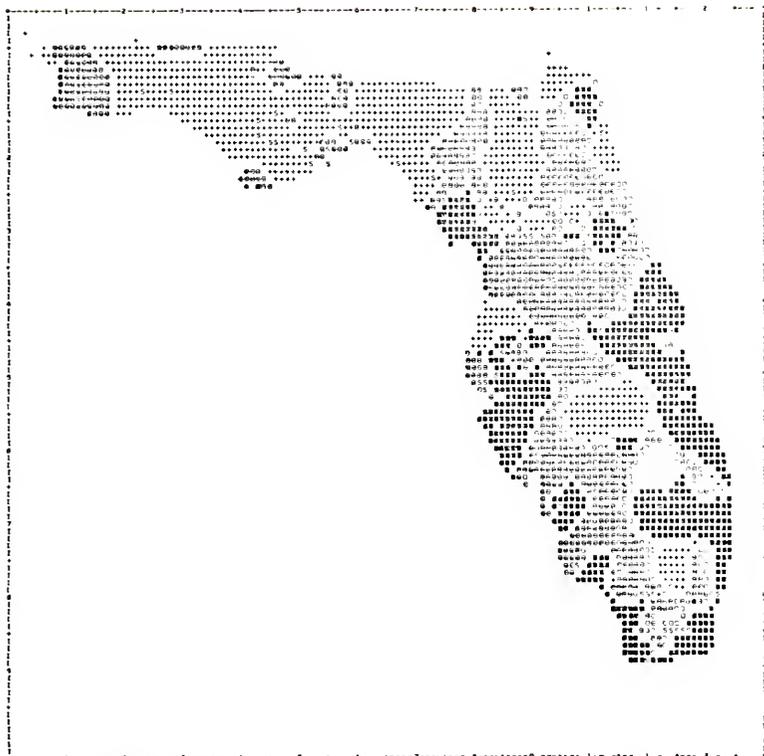
MAP 207. Geographic variation in number of subcaudal scales in *Sistrurus miliarius*, males only. Levels by increasing shading are: 29-34; 35-36; 37-41. Based on 185 specimens.



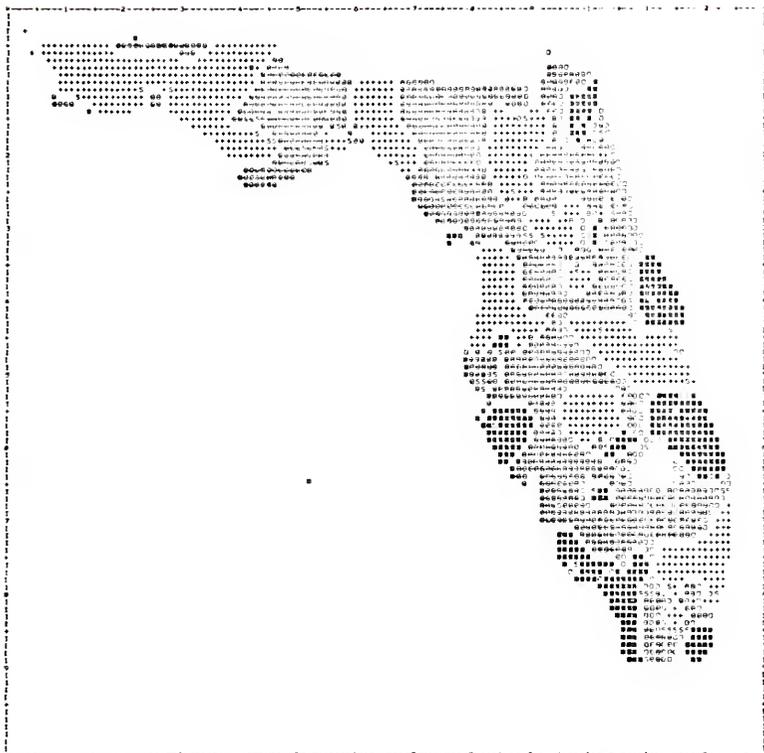
MAP 208. Geographic variation in number of subcaudal scales in *Sistrurus miliarius*, females only. Levels by increasing shading are: 25-30; 31; 32-29. Based on 130 specimens.



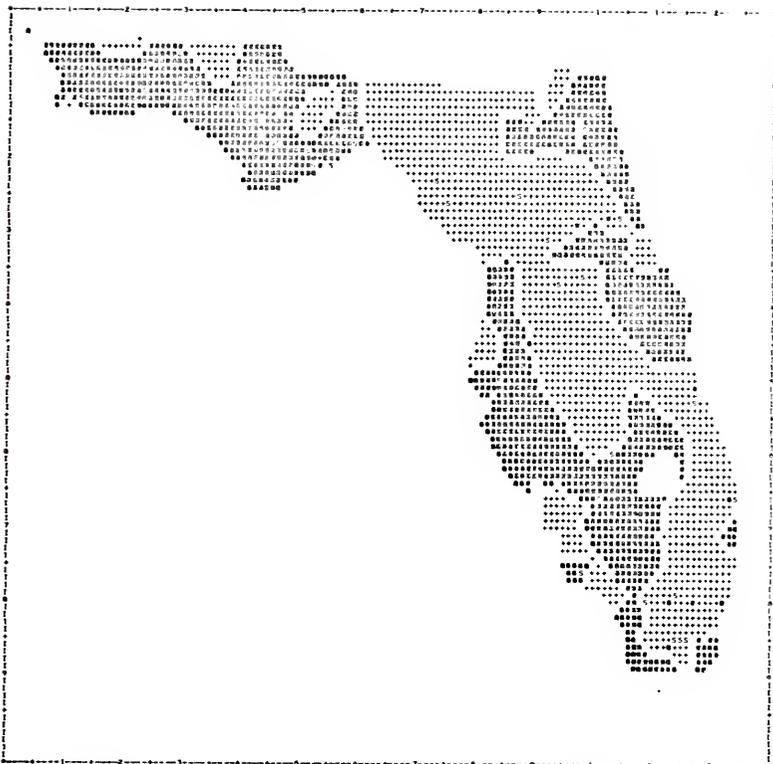
MAP 209. Geographic variation in number of ventrals plus caudals in *Sistrurus miliarius*, both sexes. Levels by increasing shading are: 156-169; 170-173; 174-186. Based on 312 specimens.



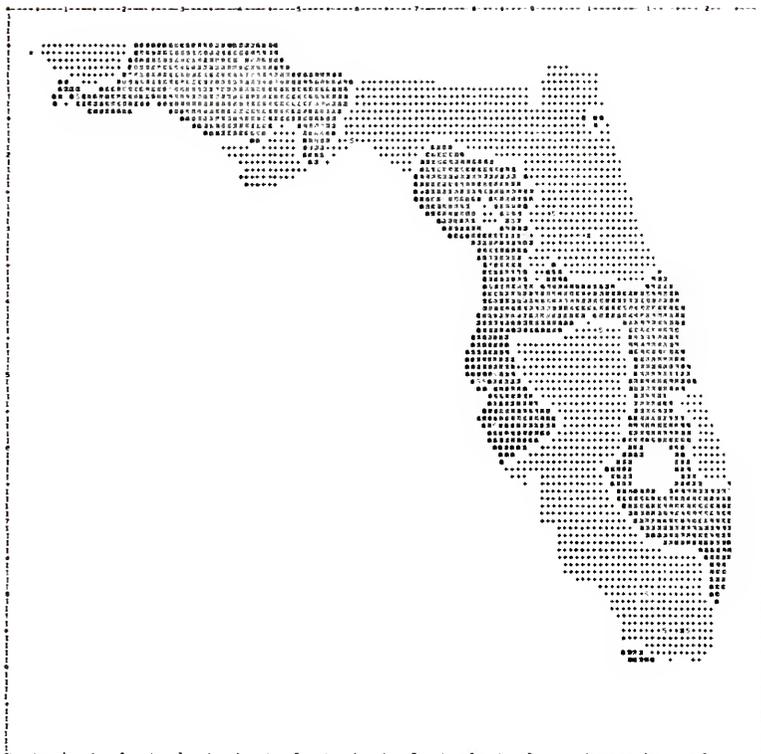
MAP 210. Geographic variation in number of dorsal scale rows one head length posterior to the head in *Sistrurus miliarius*, both sexes. Lightest shading represents 23 scale rows, intermediate shading 25 and darkest shading 27 and 29. Based on 303 specimens.



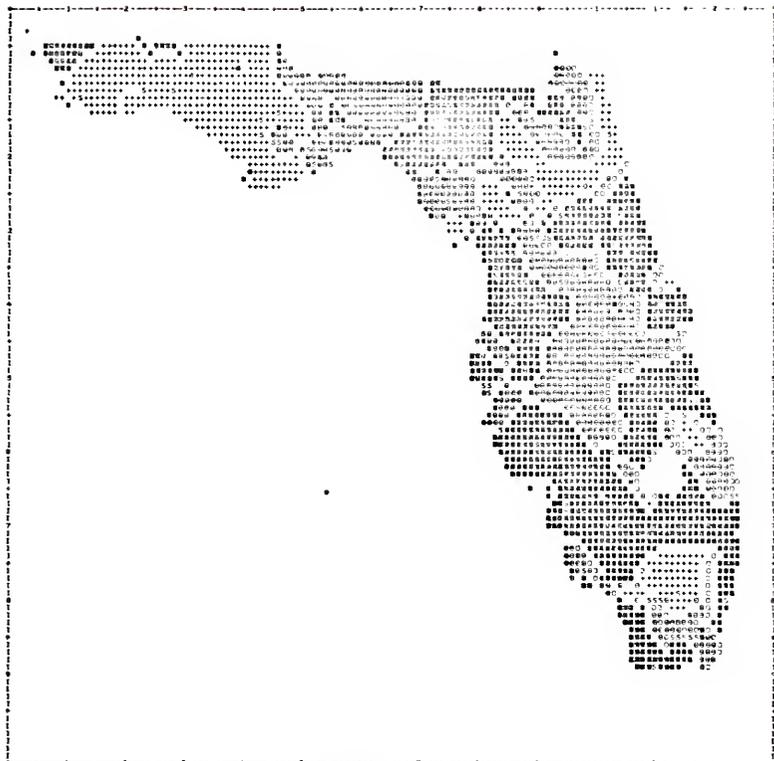
MAP 211. Geographic variation in number of dorsal scale rows at mid-body in *Sistrurus miliarius*, both sexes. Levels by increasing shading are: 21; 23; 25. Based on 316 specimens.



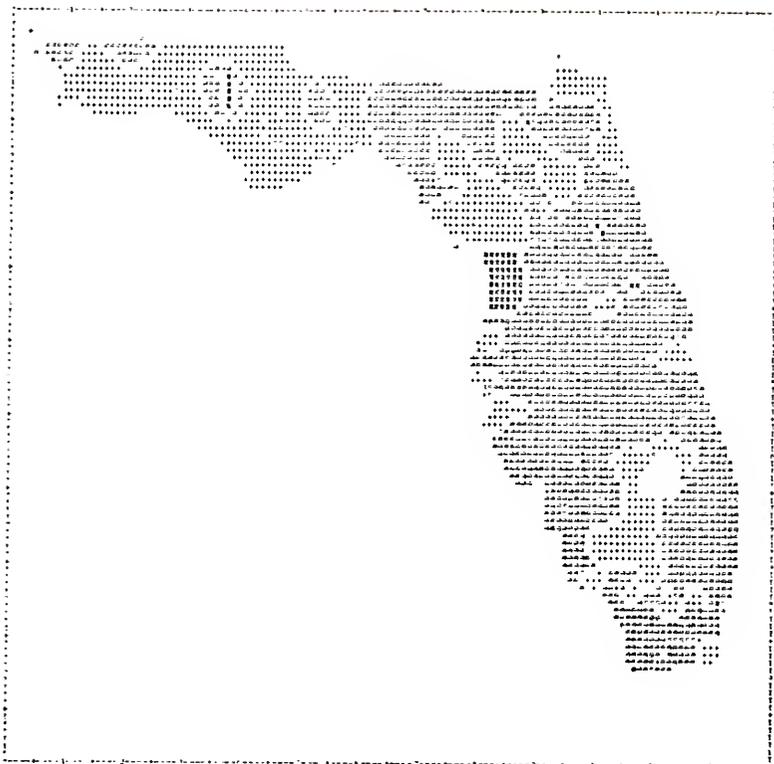
MAP 212. Geographic variation in total number of dorsal blotches, body and tail, in *Sistrurus miliaris*, males only. Levels by increasing shading are: 35-43 and 44-54. Based on 171 specimens.



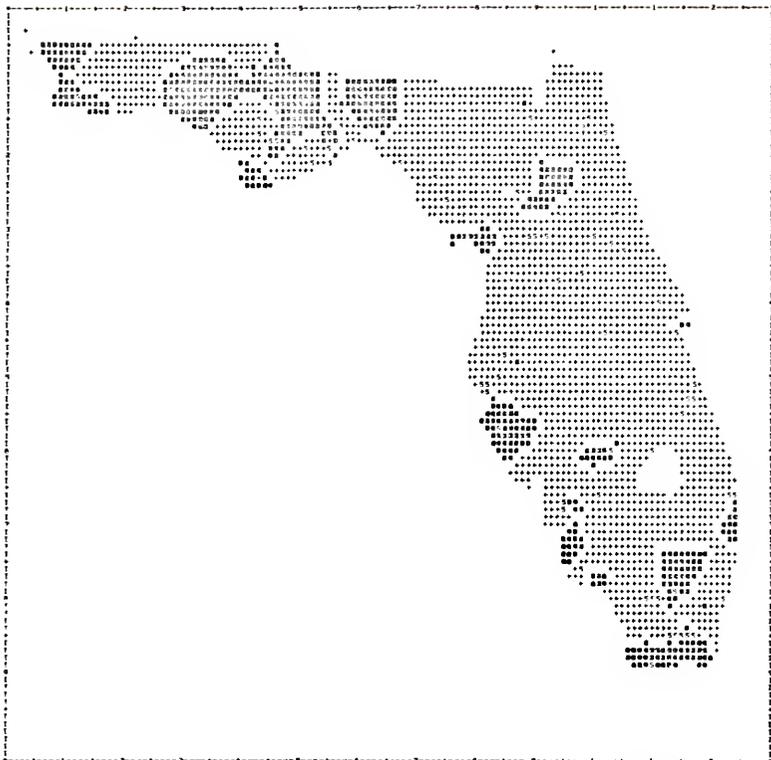
MAP 213. Geographic variation in total number of dorsal blotches for *Sistrurus miliaris*, females only. Levels by increasing shading are: 38-45; 46-58. Based on 108 specimens.



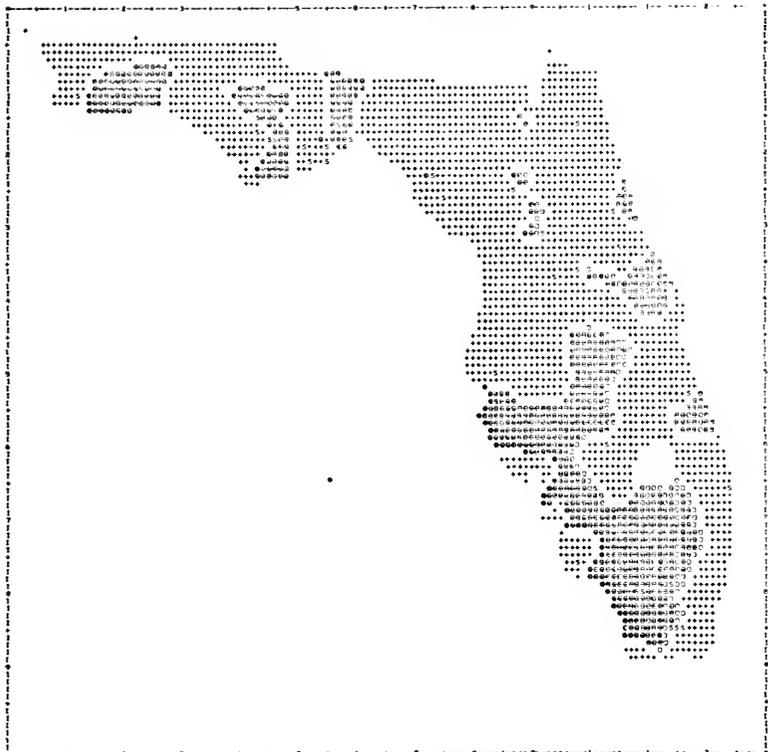
MAP 214. Geographic variation in spot length divided by inter-spot space length in *Sistrurus miliarius*, both sexes. Lightest shading represents spots that are shorter than the inter-spot space; darker shading represents increasing values for this ratio. Based on 318 specimens.



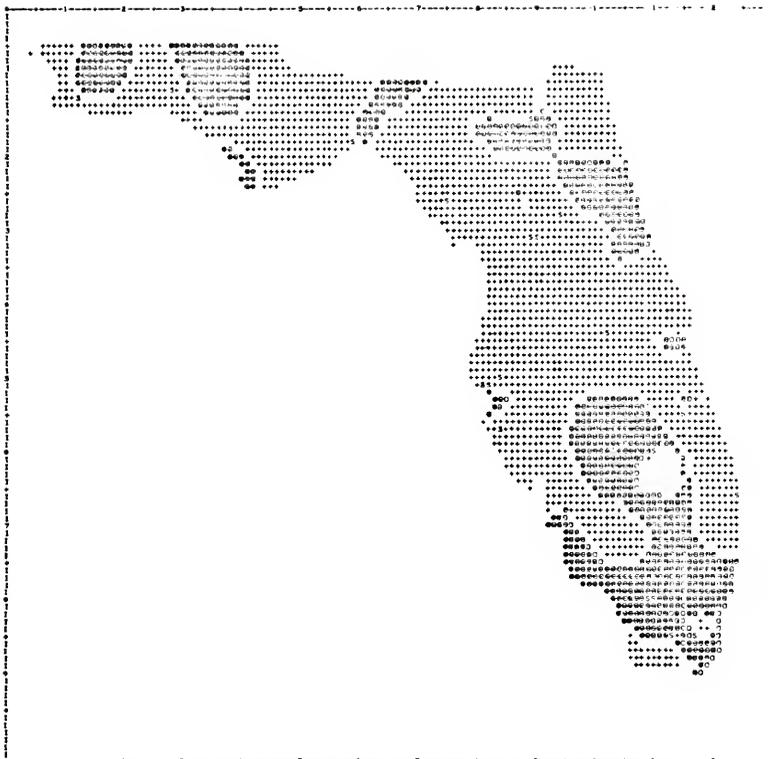
MAP 215. Geographic variation in spot shape in Sistrurus miliarius, both sexes. The darker the shading, the longer the dorsal spots in relation to their width. Based on 319 specimens.



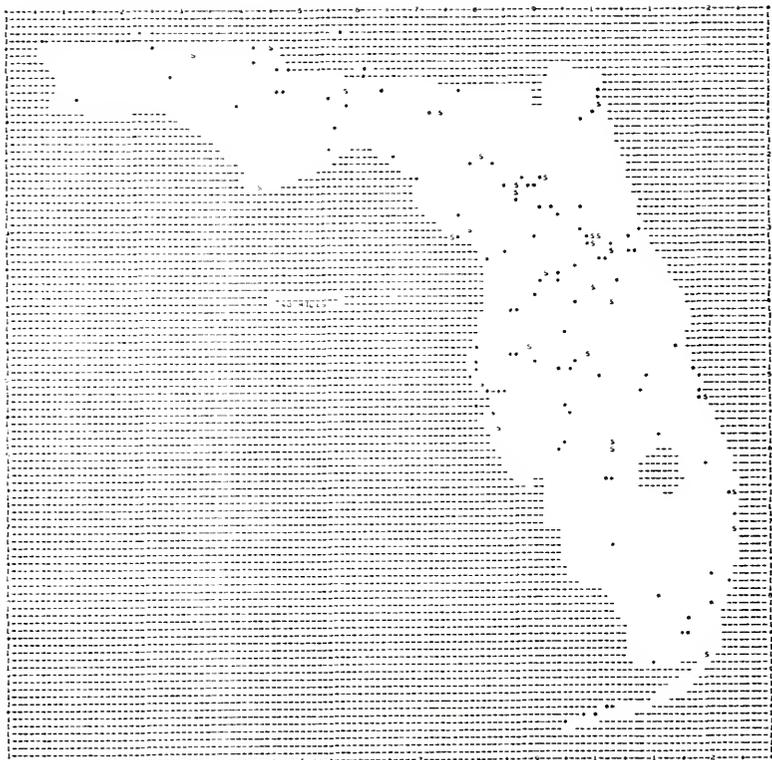
MAP 216. Geographic variation in level of contrast between dorsal spots and ground color in Sistrurus miliarius, both sexes. Darker shading represents greater contrast. Based on 317 specimens.



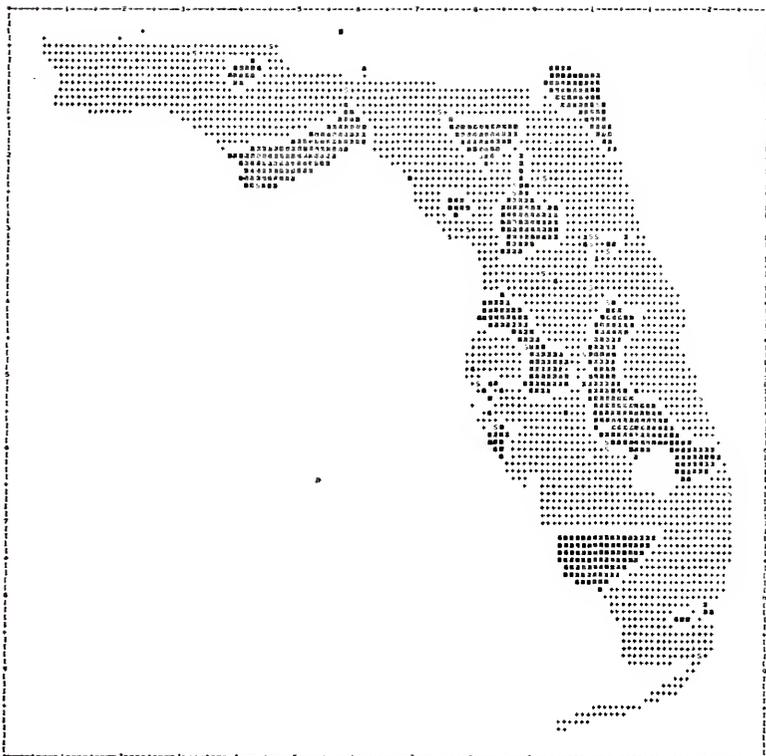
MAP 217. Geographic variation in the amount of white in the ventral pattern in *Sistrurus miliaris*, males only. The darker the shading, the more white ventrally. Based on 186 specimens.



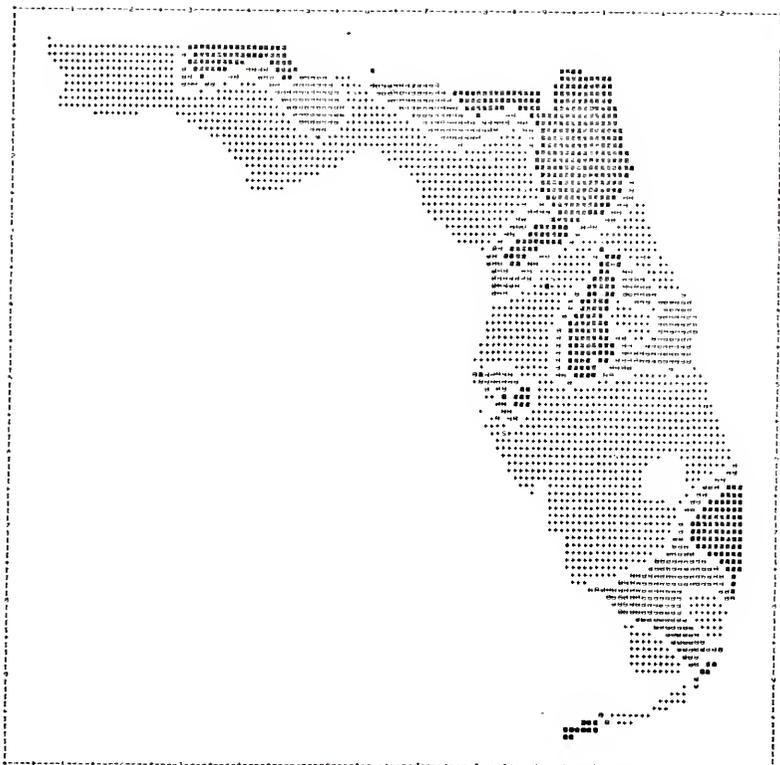
MAP 213. Geographic variation in the amount of white in the ventral pattern of *Sistrurus miliaris*, females only. The darker the shading, the more white on the ventral surface. Based on 132 specimens.



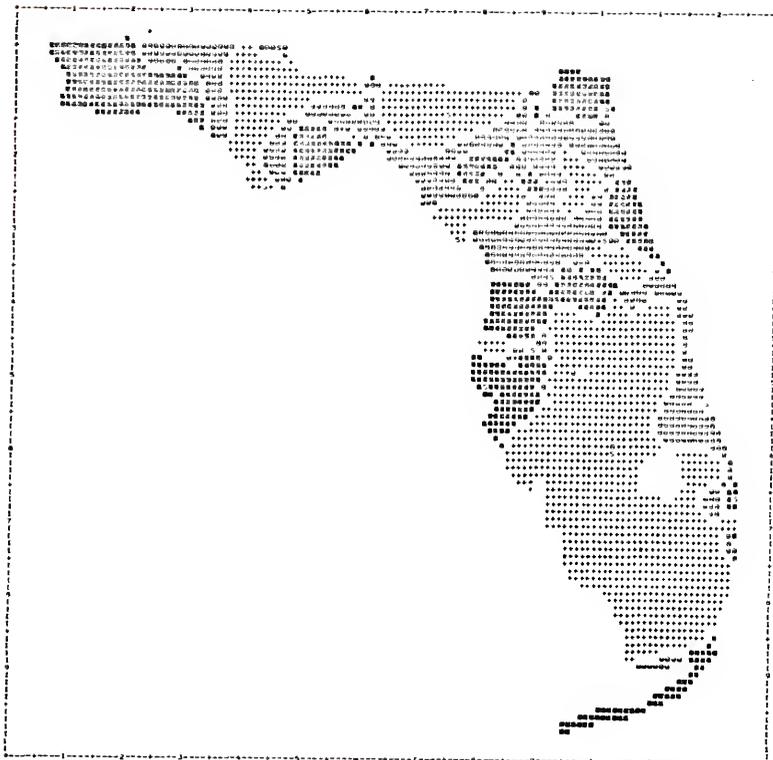
MAP 219. Localities of 194 *Crocalus adamanteus* specimens examined. An asterisk represents one specimen; an S represents more than one.



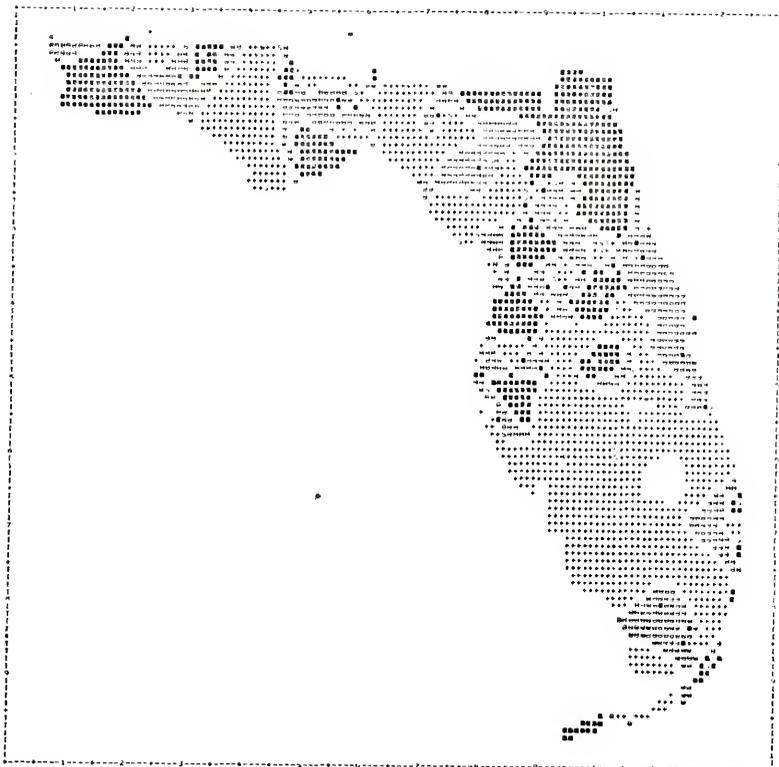
MAP 220. Geographic variation in number of midbody scale rows in *Crotalus adamanteus*, both sexes. Lighter shading represents 25 and 27 scale rows; darker shading represents 29 and 31. Based on 191 specimens.



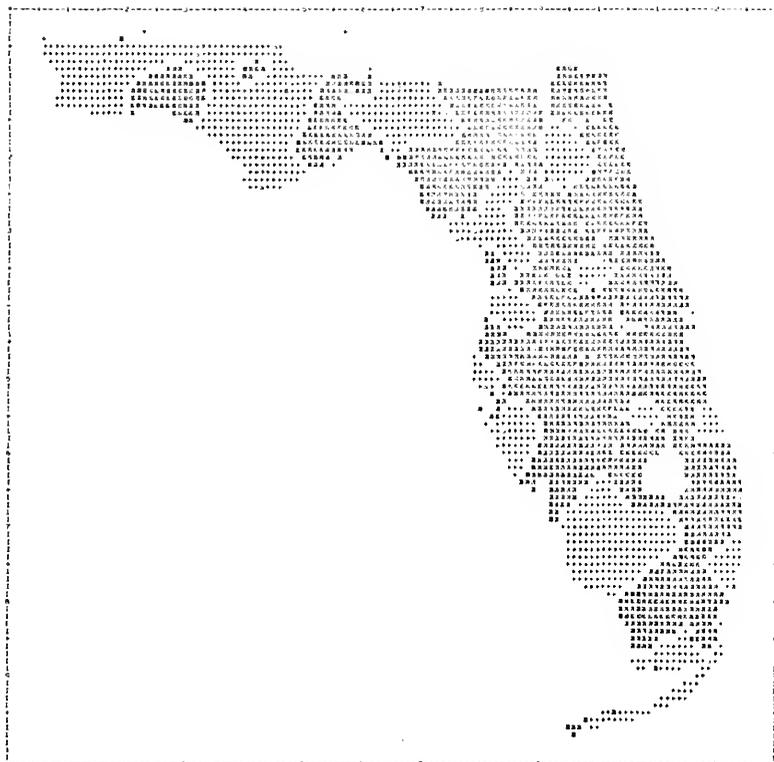
MAP 221. Geographic variation in the number of infralabial scales in Crotalus adamanteus, males only. Levels by increasing shading are: 31-34; 35; 36-40. Based on 93 specimens.



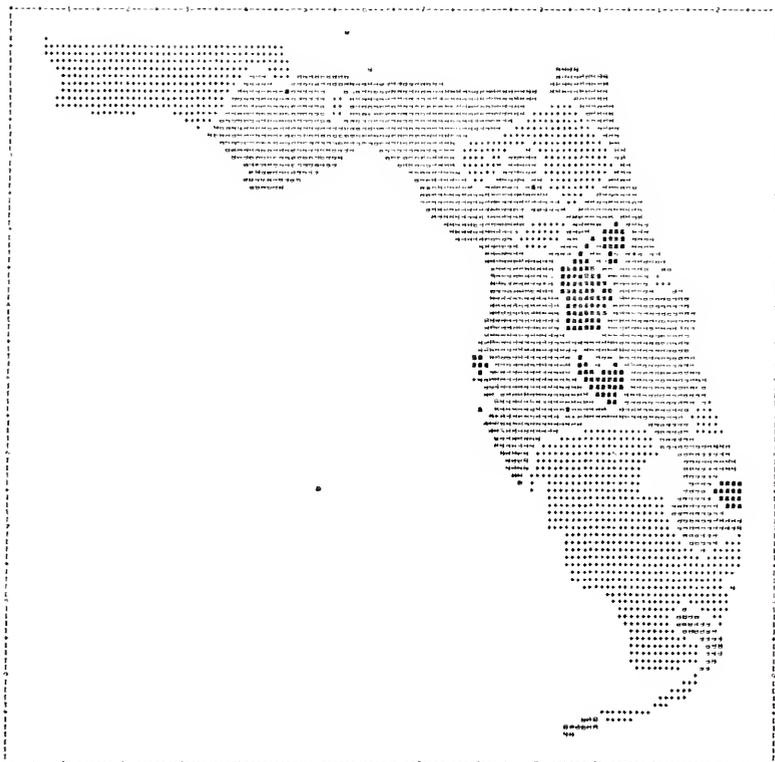
MAP 222. Geographic variation in number of infralabials in *Crotalus adamanteus*, females only. Levels by increasing shading are: 30-33; 34; 35-39. Based on 94 specimens.



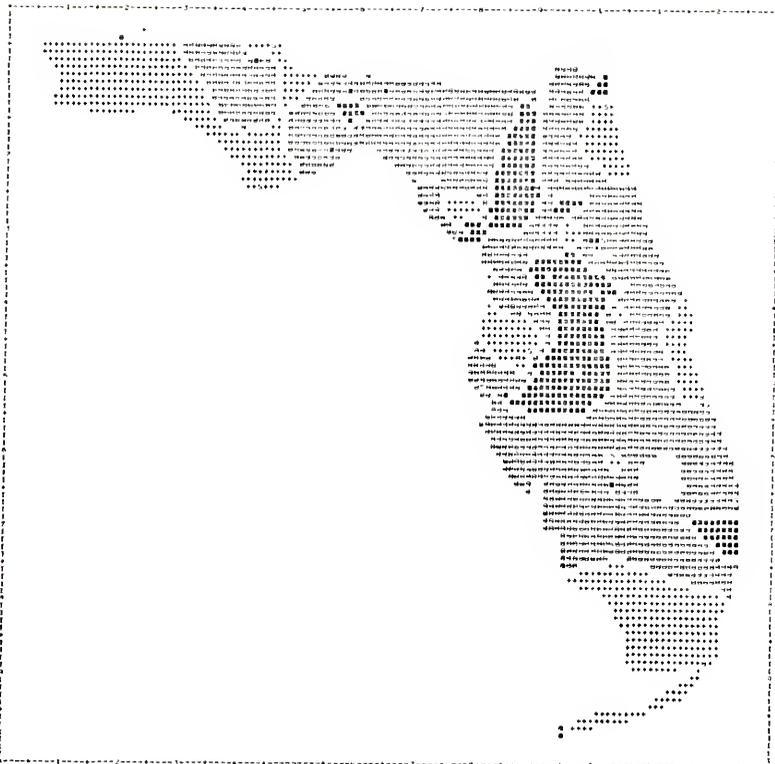
MAP 223. Geographic variation in number of infralabials for *Crotalus adamanteus*, both sexes. Levels by increasing shading are: 30-33; 34; 35-40. Based on 187 specimens.



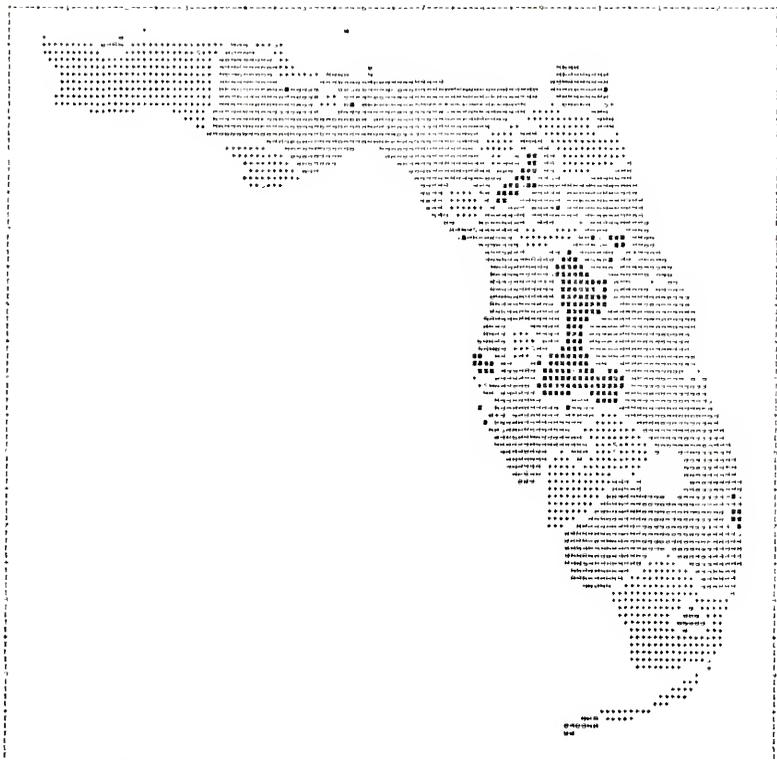
MAP 224. Geographic variation in the number of diamonds in *Crotalus adamanteus*, both sexes. Lighter shading represents 22-27 diamonds; darker shading, 28-34. Based on 190 specimens.



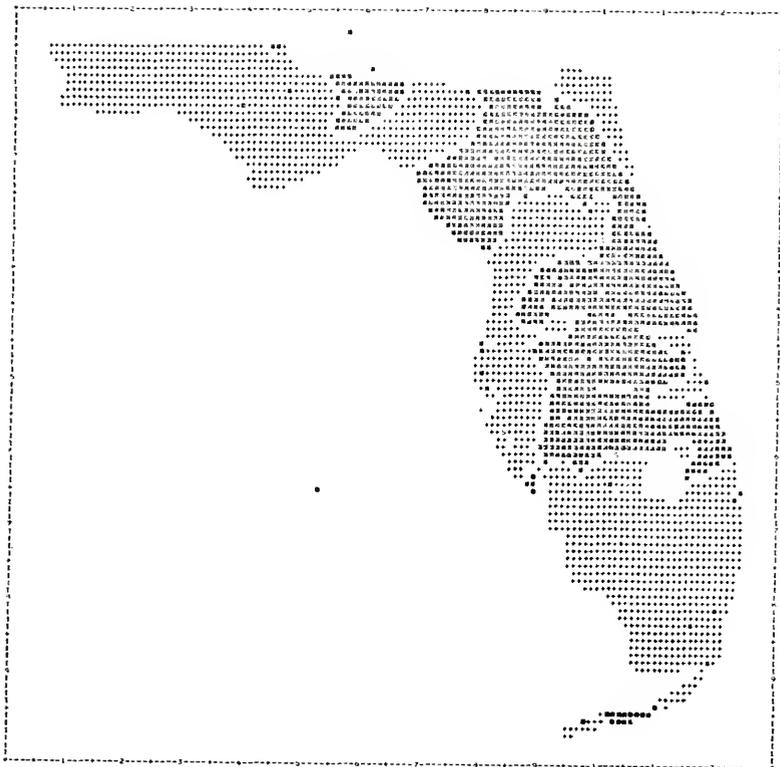
MAP 225. Geographic variation in the number of immaculate labial scales in *Crotalus adamanteus*, males only. Levels by increasing shading are: 0-1; 2-4; 5-8. Based on 97 specimens.



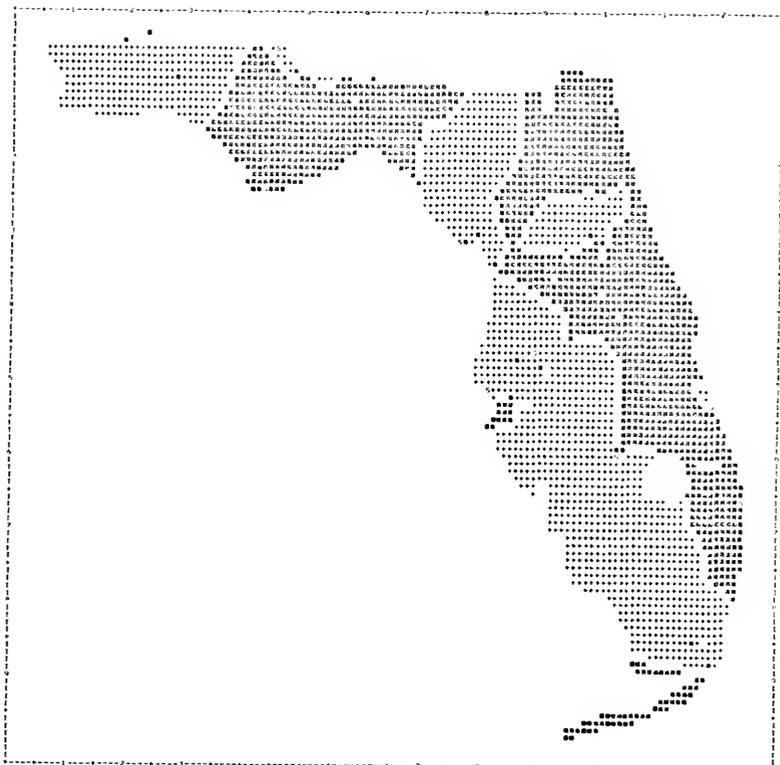
MAP 226. Geographic variation in the number of immaculate labial scales in *Crotalus adamanteus*, females only. Levels by increasing shading are: 0-2; 3-4; 5-8. Based on 95 specimens.



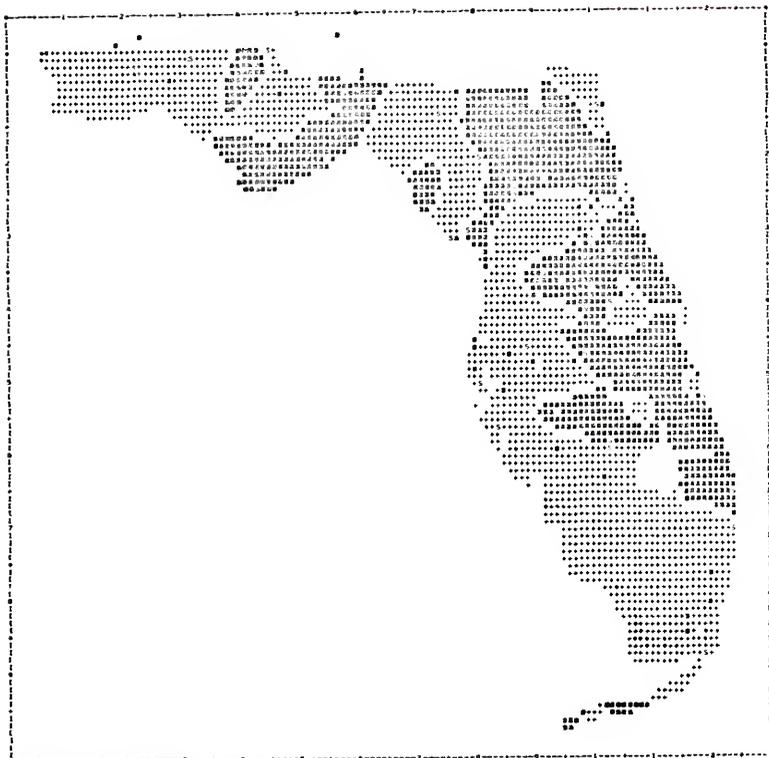
MAP 227. Geographic variation in the number of immaculate labial scales in *Crotalus adamanteus*, both sexes. Levels by increasing shading are: 0-1; 2-4; 5-8. Based on 192 specimens.



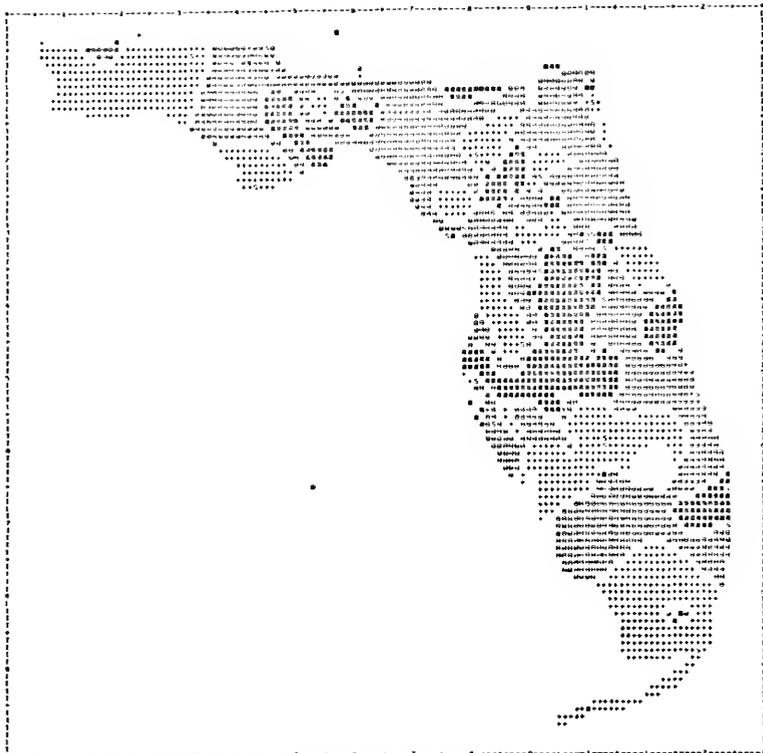
MAP 228. Geographic variation in the amount of dark pigmentation on the ventral surface in Crotalus adamanteus, males only. Darker shading represents snakes with darker venters. Based on 97 specimens.



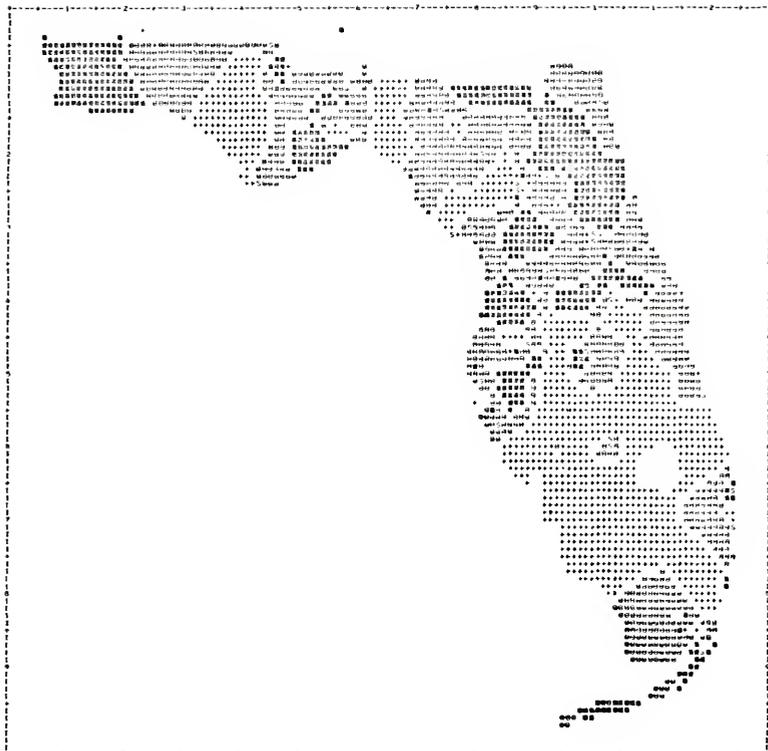
MAP 229. Geographic variation in amount of dark pigmentation on the ventral surface in *Crotalus adamanteus*, females only. Darker shading represents snakes with increased dark pigmentation ventrally. Based on 95 specimens.



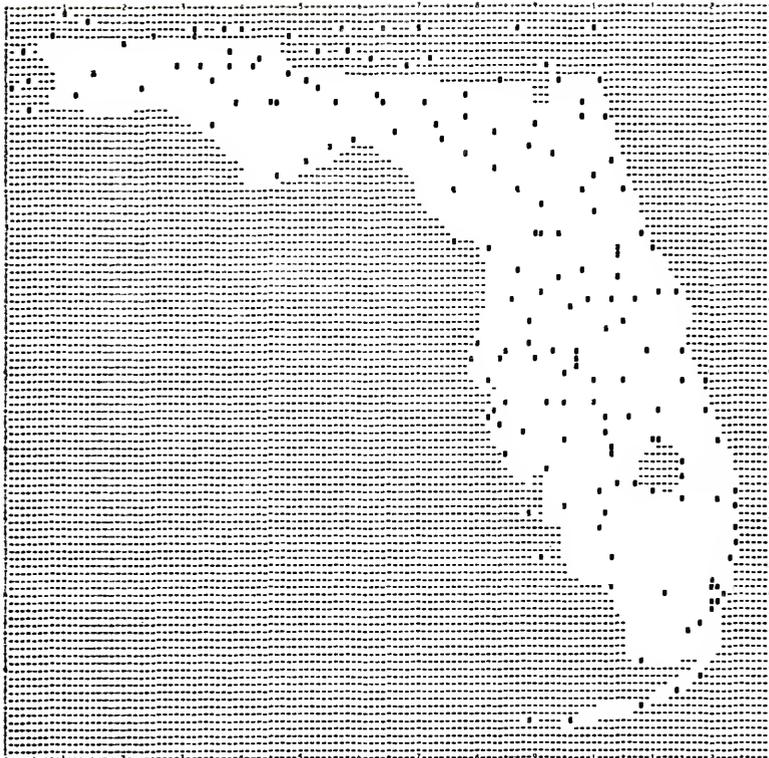
MAP 230. Geographic variation in the amount of dark pigmentation on the ventral surface in *Crotalus adamanteus*, both sexes. Darker shading represents darker venters. Based on 192 specimens.



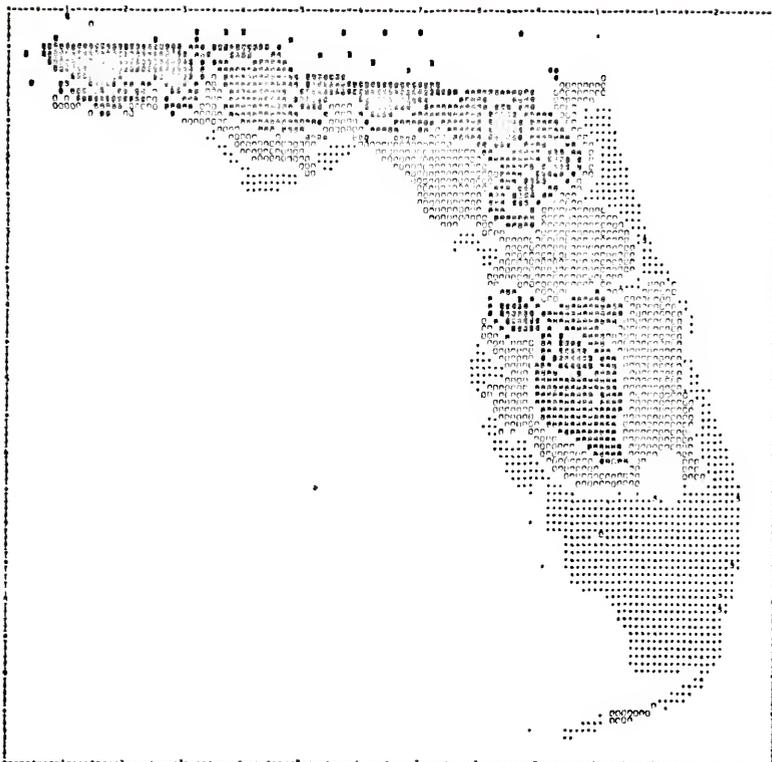
MAP 231. Geographic variation in Factor 1 for *Crotalus adamanteus*, both sexes. This factor accounts for 16.7% of the total variation in 14 characters, and most of the variation in labial pigmentation and number of immaculate labials. The darker the shading, the darker the labials. Based on 194 specimens.



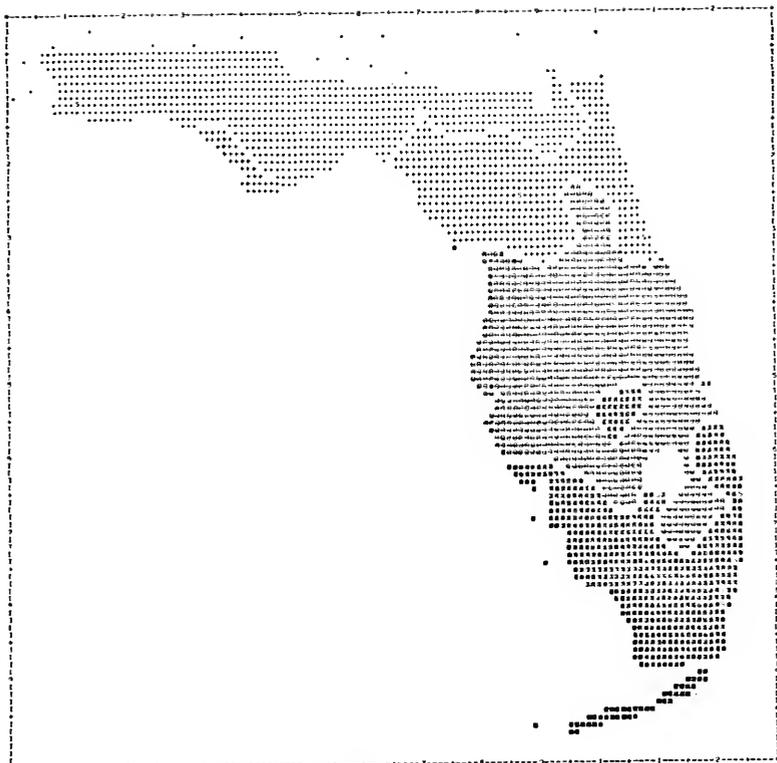
MAP 232. Geographic variation in Factor 2 for *Crotalus adamanteus*, both sexes. The second factor extracted from a matrix of 14 characters accounts for 12.8% of the total variation, and most of the variation in infralabial counts, with a contribution from supralabial counts. The darker the shading, the higher the labial counts. Based on 194 specimens.



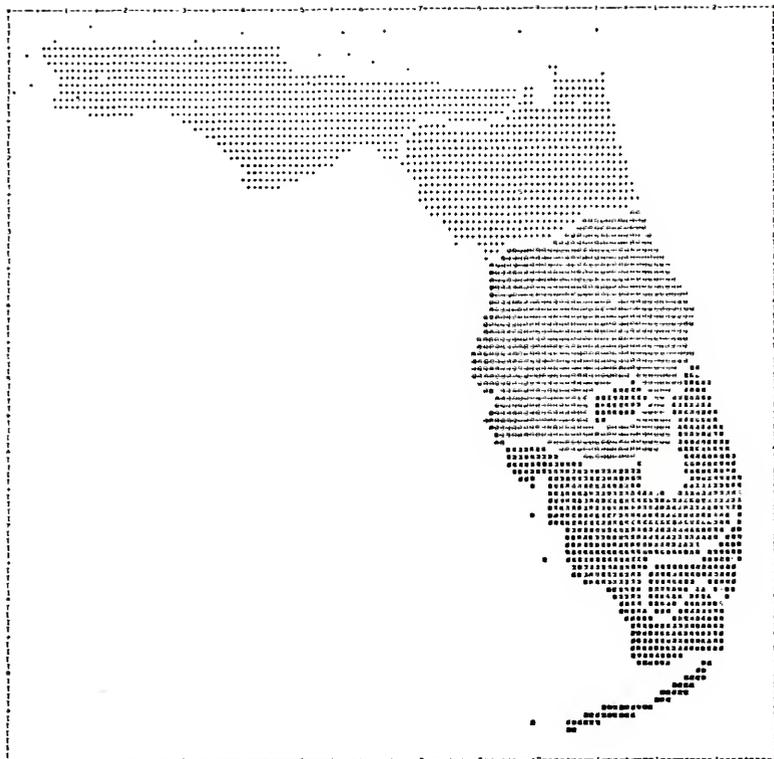
MAP 233. Locations of 196 weather stations supplying data from Florida, Georgia and Alabama.



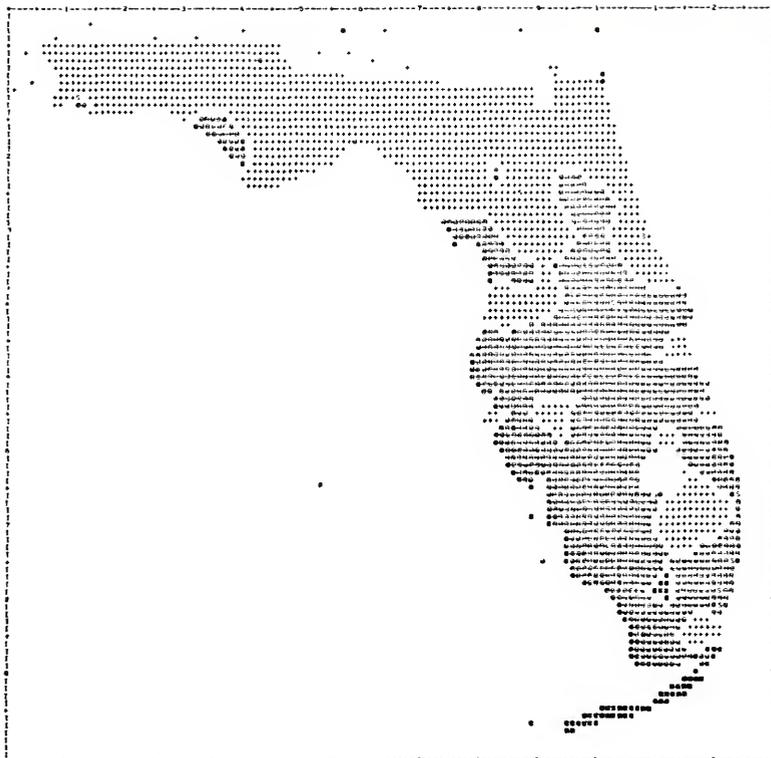
MAP 234. Geographic variation in elevation above mean sea level for Florida. Levels by increasing shading are (in meters): 1-8; 9-26; 27-45; 46-142. Based on 195 recorded points.



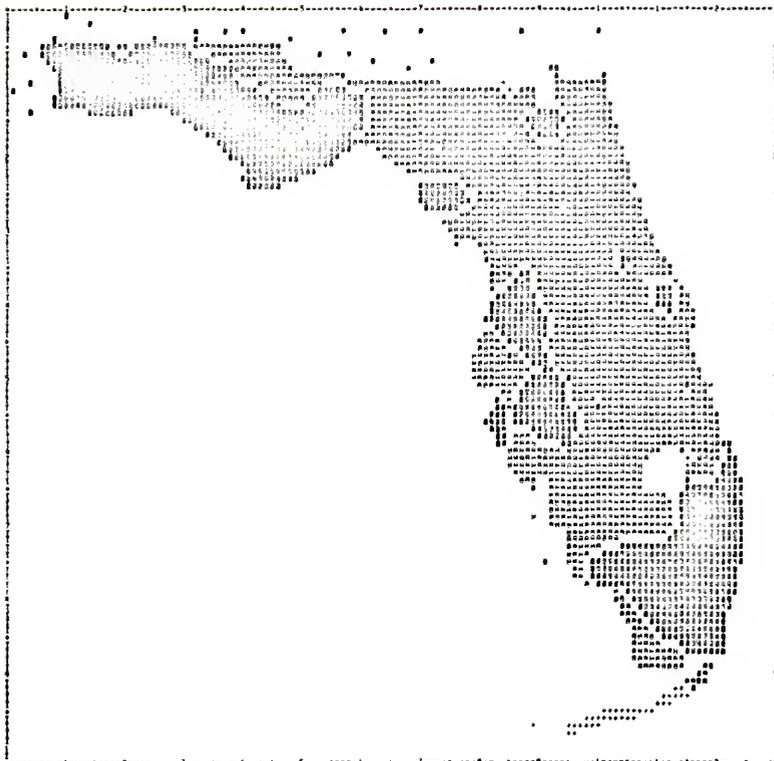
MAP 235. Geographic variation in mean annual temperature for Florida. Levels by increasing shading are (in °C): 18.9-20.1; 20.2-21.5; 21.6-22.9; 23.0-24.5; 24.6-25.7. Based on 130 weather stations.



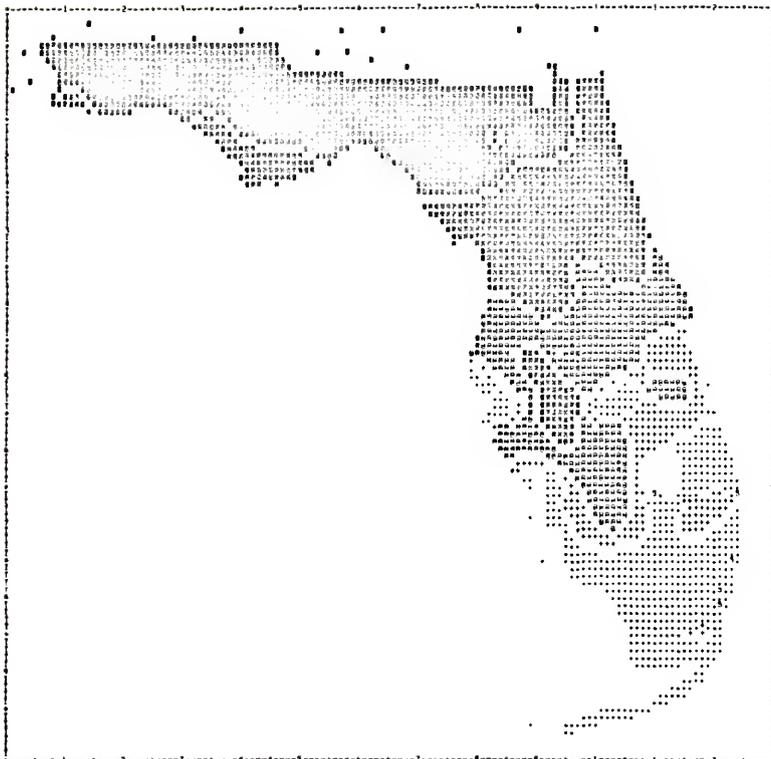
MAP 236. Geographic variation in mean January temperature for Florida. Levels by increasing shading are (in °C): 10.0-12.3; 12.4-14.6; 14.7-16.8; 16.9-19.1; 19.2-21.5. Based on 130 weather stations.



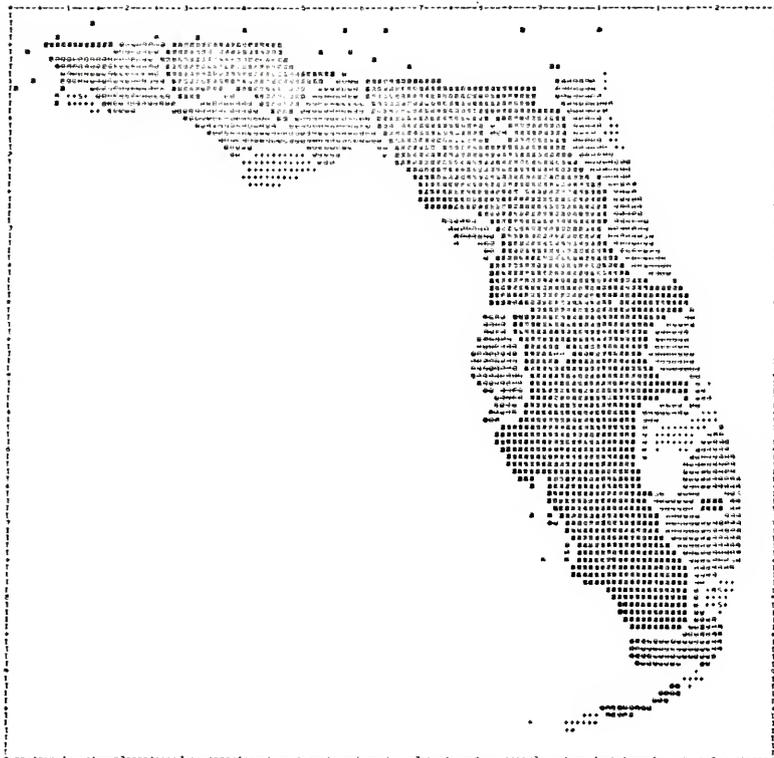
MAP 237. Geographic variation in mean August temperature for Florida. Levels by increasing shading are (in °C): 26.8-27.5; 27.6-28.4; 28.5-29.3. Based on 130 weather stations.



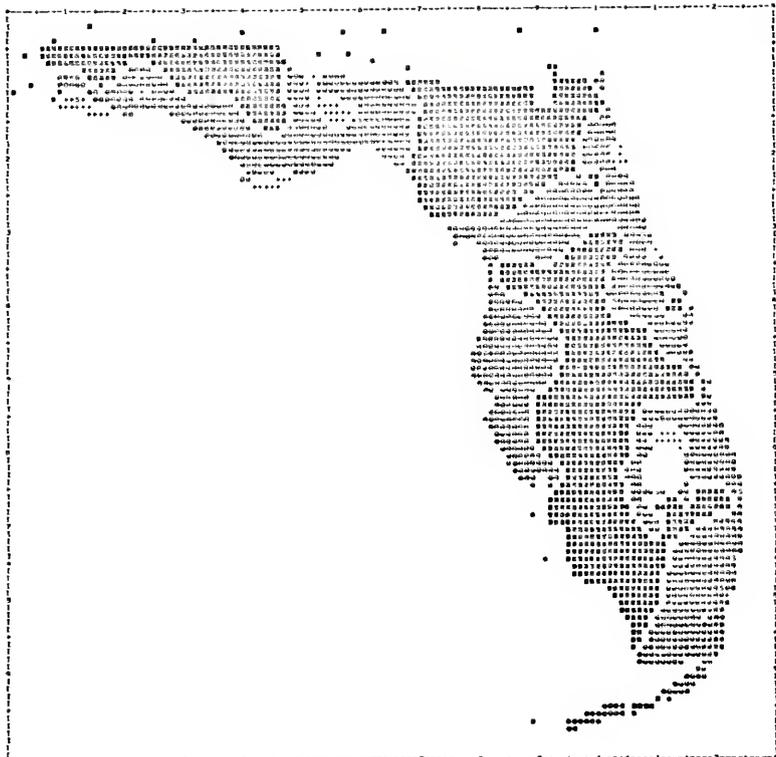
MAP 238. Geographic variation in mean annual total precipitation for Florida. Levels by increasing shading are (in cm): 93-119; 120-140; 141-179. Based on 196 weather stations.



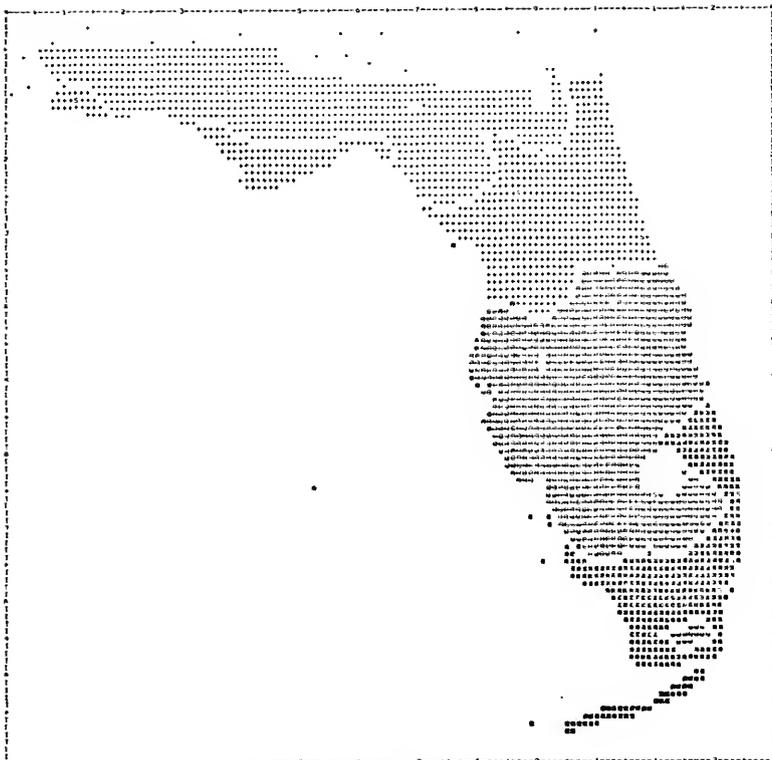
MAP 239. Geographic variation in the mean annual number of days the temperature was equal to or below  $0^{\circ}\text{C}$ , for Florida. Levels by increased shading are (in days): 0; 1-2; 3-4; 5-16; 17-47. Based on 130 weather stations.



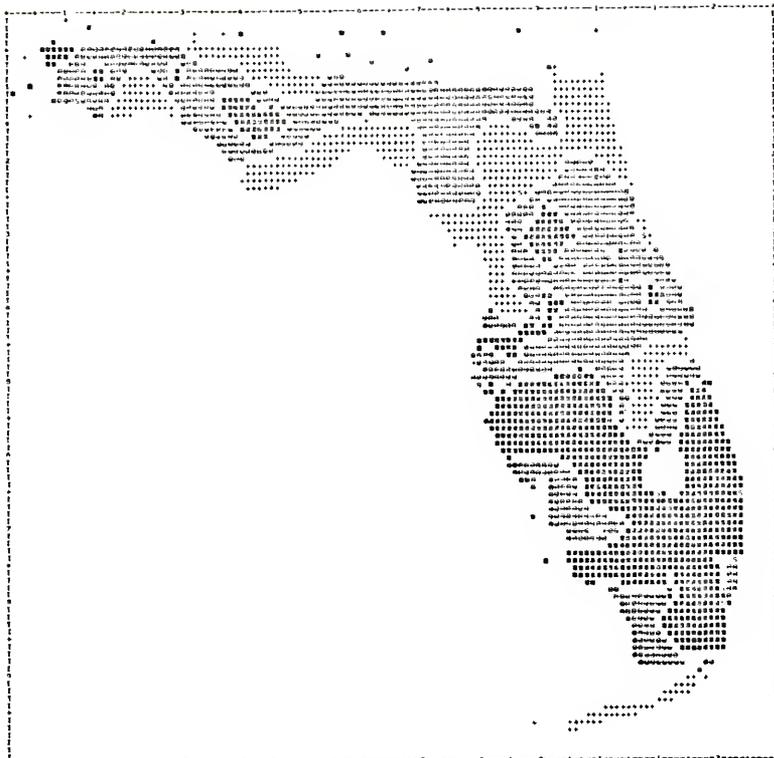
MAP 240. Geographic variation in the mean annual number of days the temperature was equal to or above 32.2°C, for Florida. Levels by increasing shading are (in days): 18-56; 57-95; 96-135. Based on 130 weather stations.



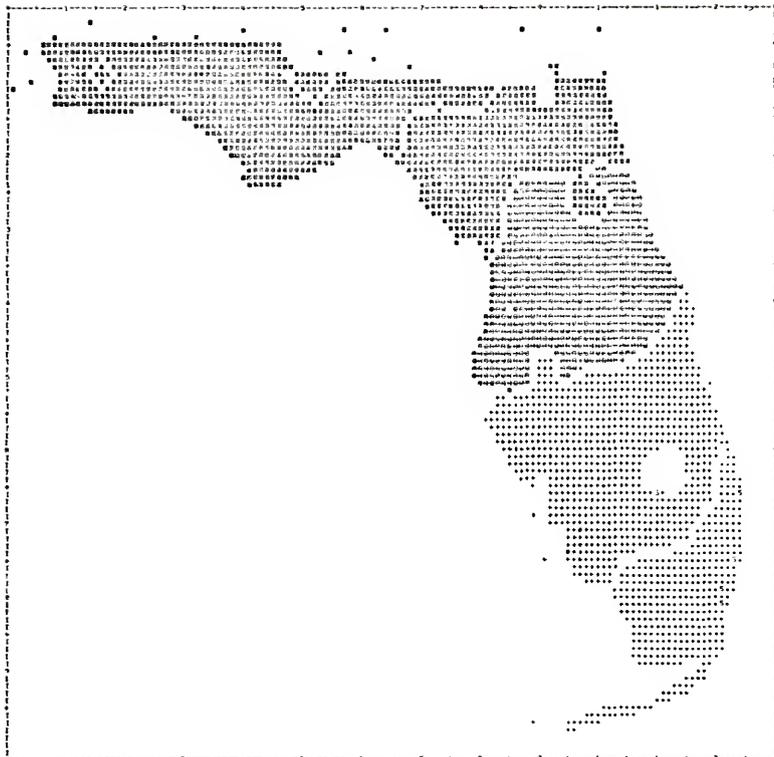
MAP 241. Geographic variation in mean daily maximum August temperature for Florida. Levels by increasing shading are (in °C): 29.0-30.9; 31.0-32.5; 32.6-34.2 Based on 130 weather stations.



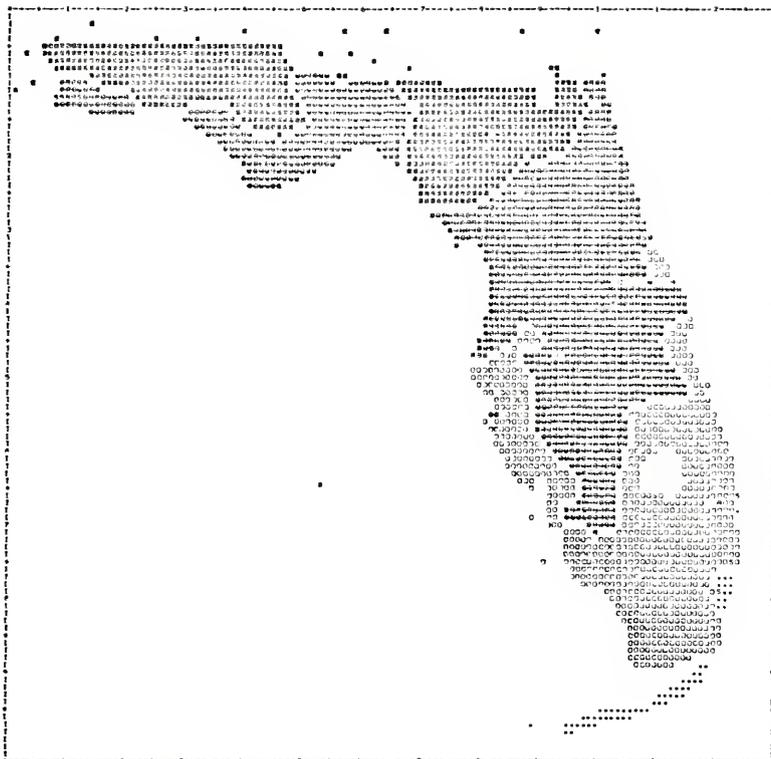
MAP 242. Geographic variation in mean daily January minimum temperature for Florida. Levels by increasing shading are (in °C): 3.4-6.3; 6.4-9.4; 9.5-12.3; 12.4-15.3; 15.4-18.4. Based on 126 weather stations.



MAP 243. Geographic variation in the mean annual number of days the total precipitation exceeded 0.254 cm for Florida. Levels by increasing shading are (in days): 55-74; 75-81; 82-101. Based on 168 weather stations.



MAP 244. Geographic variation in the difference between mean August temperature and mean January temperature for Florida. Levels by increasing shading are (in °C): 7.8-9.6; 9.7-11.4; 11.5-13.3; 13.4-15.1; 15.2-17.1. Based on 130 weather stations.



MAP 245. Geographic variation in the difference between the mean daily August maximum temperature and the mean daily minimum January temperature for Florida. Levels by increasing shading are (in °C): 13.4-17.6; 17.7-21.8; 21.9-26.1; 26.2-30.4. Based on 126 weather stations.

## DISCUSSION

### Patterns of Variation

From an analysis of geographic variation in over 200 characters in 15 species of Florida snakes, it has become obvious that there are a smaller number of underlying patterns of variation. That is, most of the geographic variation examined can be described with recourse to no more than seven main patterns of spatial evolution. Some of these patterns are related to present environmental conditions, while others seem not to be.

The most important pattern of variation observed in Florida snakes is one described as a north-south cline with increasing or decreasing character states southward on the peninsula. Since all snake species examined have some (and frequently many) characters which vary in the North-South Pattern, it is likely that this represents an adaptive response to present environmental conditions. Measurements of mean annual temperature load vary highly on factor 1, with increasing temperatures southward on the peninsula. Thus average temperature may be an important factor contributing to the maintenance of the North-South Pattern in Florida snakes.

Previous workers (*e.g.* Edgren, 1961; Smith, 1956; Duellman and Schwartz, 1953; and others) have pointed out the existence of north-south clines in snake variation. Fox *et al.* (1961) have shown that a correlation exists between developmental temperature and snake meristic

counts. Thus the developmental temperature of embryonic snakes may be the mechanism maintaining north-south clines in snake meristics. However, the adaptive significance of such a pattern remains to be discovered.

Most of the characters which vary according to the North-South Pattern of geographic variation are meristic ones (Table 1). Ventral and subcaudal counts usually increase southward, as do cross band and blotch counts. However, some species reverse this trend and show decreasing counts to the south (e.g. *Diadophis punctatus* scale counts). In most species studied, relative tail length also increases southward. The end result of this variation is that most snake species tend to have relatively longer tails and more ventral and subcaudal scales in warmer parts of their ranges. Many species also have more crossbands or body blotches in warmer regions.

Ventral and subcaudal counts reflect the number of vertebrae (Ruthven and Thompson, 1913). If a correlation exists between vertebral number and body shape (this has not been tested), perhaps the lower heating and cooling rates of more heavily-bodied snakes in cooler regions might be adaptive. Thus snakes from cooler regions have fewer vertebrae and may have relatively less surface area per unit volume. These snakes would be expected to retain body heat longer after initial warming than more slender snakes from warmer regions. I would hypothesize that snakes with more vertebrae and relatively longer tails would tend to have more slender bodies resulting in more surface area per unit of body volume. This body shape would tend to lose heat more rapidly than a stockier shape. In cooler regions, a slower cooling rate might allow snakes more foraging time after achieving optimal body temperature.

North-south clines in crossband and blotch counts may also be related to mean annual temperature. The increasing light cross-band

counts in *Lampropetis getulus* as one proceeds southward on the Florida peninsula results in a lighter-colored phenotype in the southernmost portions of the range. A lighter dorsal color would presumably reflect more solar energy in low latitudes. Similarly, ventral and dorsal color in *Coluber constrictor* generally lightens southward in Florida.

The Suwannee River Pattern of geographic variation shows up in many of the snake species studied. I could find no component of present climate correlating with this pattern. However, Brooks (1968, 1973) and others before him have shown that Plio-Pleistocene fluctuations in world wide sea level have periodically inundated much of peninsular Florida. According to these authors, when the sea stood at 150 feet above present mean sea level (Okefenokee Terrace), Florida was reduced to an archipelago of small islands separated from the mainland in the region of the present Suwannee River. More recently, during the Aftonian Interglacial, sea levels stood some 90 to 100 feet above present. This caused peninsular Florida to be separated from the mainland by a low-lying, presumably brackish water barrier, the Suwannee Straits (Neill, 1957).

On the other hand, Remington (1968) has suggested that this pattern (his "Northern Florida Suture Zone") owes its shape to a habitat barrier as opposed to a physical one, and is younger in age than eustatic sea level rises would dictate. He cites evidence that northern Florida went through a period of moist, dense forestation about 3000 to 4000 years ago (see also Watts, 1971). This band of forest may have acted as a barrier for non-forest species, resulting in partial isolation for peninsular populations.

One way or another, populations of snakes in peninsular Florida have achieved slightly different phenotypes than conspecific populations

on the mainland. Whatever isolating barrier effected this divergence is no longer visible. However, the remnants of its reality are retained in a series of dramatic character state shifts occurring today in populations in the region of the Suwannee River in northern Florida. Such seemingly unrelated characters as number of supralabials in *Thamnophis sauritus*, number of dorsal scale rows in *Storeria dekayi*, and stripe development in *Elaphe obsoleta* show major changes as one crosses the region of the former "Suwannee Straits."

More often than not, the phenotypes associated with peninsular populations are considered the more primitive. Does this mean that these species "originated" on the Florida peninsula (= island) and thence spread northward as Ross (1974) or Darlington (1957) might have us believe? Croizat (1958, 1962), and Croizat *et al.* (1974) have shown that the concept of "center of origin" is an unrealistic approach in evolutionary studies. New species are spawned when former species are split by physical or biotic barriers. Species do not originate at a point in space and then spread to their present distribution as Darwin (1859:353) has stated:

Hence it seems to me, as it has to many other naturalists, that the view of each species having been produced in one area alone, and having subsequently migrated from that area as far as its powers of migration and subsistence under past and present conditions permitted, is the most probable.

Udvardy (1969:7) put it even more bluntly:

Every animal species originated from a few ancestors in a limited area; if a particular species is now found to be widespread, it must of necessity have reached parts of its present range at an earlier period.

Speciation is a process of vicariance (Croizat *et al.*, 1974).

New species form within the ranges of preexisting species. This process proceeds with the impetus provided by natural selection and the mechanism provided by a reduced gene flow between populations. All species pairs (cognates) were originally parapatric. If they are now sympatric, then dispersal is indicated, and we may rightfully ask where the original vicariating barrier was positioned. The center of origin for a species is its present distribution unless dispersal has occurred. The center of origin for a group (*e.g.*, a genus) is a meaningless concept, because we must look back in time to when the group was but one of a pair of vicariating populations. When we do this, we again find that the center of origin is the original range of that individual population.

In their efforts to locate "centers of origin," biogeographers have formulated rules, a summary of which may be found in Cain (1944). One of the most often used rules states that the area occupied by the most primitive members of a group must be the area of origin for the group (Ross, 1974). When a systematist determines the distribution of the most primitive character states for a wide-ranging species, or the location of the most primitive species of a genus, he is not locating the center of origin of that group. Rather, he is defining the area where differentiation (= evolution) has proceeded relatively more slowly. Indeed, this area may actually be one of the latest regions colonized by the group in question. If for some reason differentiation proceeds more slowly in one area relative to another, primitive species and/or character states will be retained in that area. Thus islands often harbor the most primitive members of a taxonomic group. This doesn't imply that the

group originated there, but that once it got there, it changed less than populations elsewhere. The biogeographer should ask why evolution proceeds slowly in some areas and faster in others.

Peninsular Florida has been cited as the center of origin for a number of plant and animal groups, chiefly because representatives there retain more primitive characters than representatives to the north. In other groups, the Mexican Plateau region has been called the center of origin, because primitive members occur there. In many vertebrate species studied, and several of the snake species reported on here, peninsular Florida and the Mexican Plateau region harbor primitive populations of wider ranging groups. Biogeographers have explained this by suggesting an origin on the Mexican Plateau, dispersal into eastern North America accompanied with differentiation, and subsequent dispersal onto the Florida peninsula accompanied this time with regressive differentiation back to the original phenotype (*e.g.*, Trapido, 1944). More recently Auffenberg and Milstead (1965), and Blaney (1971b) have explained this situation by making recourse to a now submerged land bridge connecting the Florida peninsula with western areas including, supposedly, the Mexican Plateau areas. In this model, it is pointed out that Pleistocene lowered sea levels exposed a portion of the Gulf Coast continental shelf thus creating a bridge connecting Florida with the west. Organisms are said to have migrated eastward along this corridor to occupy the Florida peninsula, thus giving rise to the situation seen today with phenotypic resemblances between Floridan and Mexican populations while geographically intermediate populations remain divergent. This model assumes that the newly exposed Gulf Coast Corridor would have been colonized by popula-

tions from the west, which would have subsequently migrated eastward, while nearby populations to the north of the corridor failed to take advantage of the new habitat. It is difficult, at best, to see why Florida would not have been colonized by populations to the north, or why the newly exposed continental shelf would not have been colonized by populations immediately adjacent to it. There is no evidence that the Gulf Coast Corridor appeared "overnight;" on the contrary, the sea levels are thought to have dropped gradually as water became tied up in northern latitude glaciers (Flint, 1971). Furthermore, the Gulf Coast Corridor Land Bridge theory requires that the species in question were not already present in Florida, or if they were, their phenotypes were swamped by the immigrating populations from the west. The phenetic similarity between species occurring on the Florida peninsula and the Mexican Plateau, while populations occurring in between remain divergent, can be explained without recourse to a land bridge or to retrogressive evolution. An evolutionary (*sensu* Croizat, 1962) explanation requires fewer assumptions and does not rely on dispersal as a major factor in the differentiation process.

Geographic variation is probably the rule in living systems. Populations of organisms become adapted to their physical and biotic environments. If these environments vary from place to place, so too will the adaptations of the organisms living there. I call this process spatial evolution. (If environments vary through time, the organisms living there will also vary through time. This is temporal evolution.)

When disjunct populations of a species are more similar to each other than either is to intermediate populations, the principal of

parismony dictates that the disjunct populations probably represent the primitive (= ancestral) condition. To believe otherwise requires that the populations in the disjunct regions have developed independently to achieve similar phenotypes. It requires fewer assumptions to believe that the intermediate populations have diverged while the disjunct populations have remained relatively unchanged. Thus something in the environment of both the Florida peninsula and the Mexican Plateau has allowed species there to remain unchanged relative to conspecific populations in the South-Central United States. In other words, evolution (= differentiation) has proceeded relatively more rapidly in the continental region between the Suwannee Straits and the Mississippi Embayment. The question for biogeographers is not "why are Florida and Mexican populations similar?," but rather, "Why are intermediate populations different from Florida and Mexican populations?"

There are two possible explanations for lower evolutionary rates in Florida and Mexico, and both have probably been responsible for the patterns seen today. The first involves gene flow. Florida is a peninsula (and has from time to time been an island) and as such is partially isolated from continental populations to the north. Populations to the west of the Mississippi Embayment including the Mexican and Guatemalan Plateau are also relatively isolated from populations on the main continent. When a new character state occurs in a population of sexually reproducing organisms, and if it proves to be adaptive, it will spread throughout the population everywhere that it remains adaptive. However, if gene communication with out-lying populations is reduced, the new adaptation may simply not reach these peripheral populations. Further-

more, Brown (1957) has shown on theoretical grounds that new phenotypes are most likely to occur near the center of a species' geographic distribution. Thus it is not surprising that peripheral populations tend to retain more primitive character states than the main body of the species' range. This is why islands tend to harbor the most primitive members of many groups. Thus snake species occurring across the southern North American continent have evolved (changed) more in the central region than they have in the peripheral regions.

The second factor contributing to this pattern of geographic variation is concerned with the selective pressures responsible for evolutionary change. Analysis of Pleistocene pollen deposits (Watts, 1969) has indicated that climatic changes have occurred during the glacial ages in Florida. However, these fluctuations were apparently of a lesser magnitude than simultaneous fluctuations occurring to the north on the North American continent (Whitehead, 1965). Climatic fluctuations including wind and rain patterns as well as temperature were felt more strongly on the main North American continent than on the Florida peninsula and, presumably, the Mexican Plateau (and southward). Plant communities in North Carolina and Virginia underwent radical changes during the Pleistocene, while those in Florida changed less dramatically (Watts, 1970). Under the influence of dramatically changing climates and vegetation, snake species would be expected to change as well. Populations of these same species on the Florida peninsula and southwestern United States and Mexico where climates remained more stable, would be expected to change less.

It should come as no surprise that primitive members of phylogenetic groups frequently occur in the tropics, where selective pressures

dictated by climate have been less severe. This model may also have some bearing on the problem of species diversity patterns on a world-wide basis. In regions with a history of climatic fluctuation, species are required to change their own phenotypes with the changing environment. When necessary adaptations are not forthcoming, extinctions occur. In the tropics, however, climatic fluctuations have been less severe and species there have not been as susceptible to climatically-induced extinctions. Thus species tend to retain more primitive characteristics, and there tends to be more species in climatically stable regions, such as the tropics.

The Everglades Pattern of geographic variation is shared by several of the snake species studied. This pattern correlates well with the unique habitat of the Florida Everglades. It is likely that the selective pressures responsible for maintaining distinctive phenotypes in snake species occurring in the Everglades are related to the habitat there. A lighter dorsal and ventral color in *Lampropeltis getulus* and *Coluber constrictor* may be adaptive in the open treeless environment of the marshlands. It is noteworthy that these species also have reduced dark pigment when they occur in the Great Plains region of North America.

Perhaps the most interesting pattern of geographic variation in Florida snakes is the North Florida-Lower Keys Pattern. Several species examined have similar phenotypes when they occur in extreme northern Florida, the Lower Florida Keys and the high ridge to the east of Tampa Bay. This pattern has been recognized by previous authors (e.g., Neill, 1957 and Duellman and Schwartz, 1958), although they failed to note the apparent inclusion of the area east of Tampa Bay. Other species have also

been observed to vary in the North Florida-Lower Keys Pattern. McConkey (1957) noted the similarity between Lower Keys and north Florida populations of the lizard *Eumeces egregius*, and Duellman and Schwartz (1958) discuss this situation with regard to five species (*Scincella laterale*, *Eumeces egregius*, *Coluber constrictor*, *Diadophis punctatus*, and *Storeria dekayi*). The inclusion of *Diadophis* in this list is apparently not warranted. Duellman and Schwartz (1958), using a very small sample size, stated that ventral counts for Lower Keys ringneck snakes were similar to northern Florida counts, and distinct from southern mainland counts. Maps 145 and 146, based on larger samples, do not show this pattern.

Nevertheless, enough species show aspects of the North Florida-Lower Keys Pattern in their geographic variation, that the phenomenon must be real. The principal of parsimony suggests that the distinctive phenotypes, distributed as they are in three disjunct regions, have arisen only once. This implies that snake populations in the remainder of Florida have diverged since the establishment of the species in extreme northern Florida, the area east of Tampa Bay and the Lower Florida Keys. The problem is to discover what these regions have in common that might allow for slower divergence from the ancestral condition.

Geological and biological evidence summarized by Duellman and Schwartz (1958) support the contention that the Lower Keys were connected to the central Florida mainland at a time when the Upper Keys were still submerged. The eastern rim of the southern Florida mainland and the Lower Keys are composed of Miami oolite, a formation apparently older in age than either the sediment-filled Everglades or the coral reef formation that is now the Upper Keys. Snake species established on the

Lower Keys at a time before the Upper Keys were emergent were probably phenotypically similar to peninsular populations. As southern Florida and the Upper Keys emerged, these areas were colonized by populations from the north, adapting to conditions there. The isolation of the Lower Keys has allowed populations existing there to remain more like the original stock. Further evidence is provided by the fact that extreme northern Florida and the area east of Tampa Bay have the highest elevations in the peninsula (Map 234). It is conceivable that the Lower Keys and eastern rim of the southern mainland have also been much higher with respect to present sea levels. The limestone formation on the Lower Keys shows all the signs of extensive erosion and solution (Duellman and Schwartz, 1958) and may have had a history of emergence much longer than present elevation would suggest.

I believe that the snake species under scrutiny were already present on the Lower Keys, the area east of Tampa Bay and extreme northern Florida before the Everglades and Upper Keys were available for colonization. When these latter regions were finally inhabited, selection effected evolutionary divergence without altering phenotypes on the Lower Keys. The high elevations of northern Florida, the area east of Tampa Bay and (perhaps) the Lower Keys may have supported similar habitats. Snakes adapting to habitats on lower elevations in Florida have diverged more from the ancestral phenotypes.

Mean annual precipitation (Map 238) is highest in the Florida Panhandle and Everglades regions. Snake species showing the Panhandle-Everglades Pattern of geographic variation may be responding to similar selective regimes created by rainfall patterns.

Populations of snakes occurring along the coastline and on offshore islands of Florida are frequently distinct from populations farther inland. The Coastal Pattern is probably maintained by something in the ecology of the coastal environment. Elevations are lower, temperatures are less extreme, and vegetation is more sparse in coastal regions. Any or all of these factors may help maintain the Coastal Pattern.

Several of the species examined in the present study show major character state shifts in the region of Lake Okeechobee and the high ridge to the west. The Okeechobee Pattern is probably maintained by conditions unique to the high elevation scrub forest of the area.

#### Phylogenetic Considerations

*Storeria dekayi*. Ventrals and subcaudals increase clinally to the south on the peninsula. *Storeria dekayi* from the southern parts of the state have proportionately longer tails. Duellman and Schwartz (1958) noted the phenotypic resemblance in ventral and subcaudal counts between Lower Keys and northern Florida brown snakes, separated by divergent peninsular snakes. This study shows that the phenomenon is also well-developed in preocular counts and ventral dark pigmentation. Another major geographic pattern of character variation in this snake is the existence of two well-differentiated morphotypes, exemplified by factor 1 (Map 14). Current taxonomy (Neill, 1950a; Conant, 1975) recognizes these as the subspecies *S. dekayi wrightorum* in the Panhandle and *S. dekayi vieta* in the peninsula. There are apparently no specimens available from the region in Florida between the two morphotypes, where intermediate characteristics might be looked for. Thus, there is no evidence for intergradation between *S. dekayi vieta* and *S. dekayi wrightorum* in

Florida; indeed, the two may be entirely allopatric, at least in Florida. Neill (1950a) makes a case for the apparent conspecificity of the two forms by citing evidence of intergradation in the Coastal Plain of eastern Georgia. Whether or not the two forms are reproductively isolated (*i.e.* distinct species) is of little consequence to a discussion of their origin, however.

*Storeria* occurs on the Lower Keys but apparently not on the Upper Keys (Duellman and Schwartz, 1958). The population on the Lower Keys is phenetically more closely related to populations from northern Florida than to populations from the southern mainland. This is a common pattern, and was discussed in the last section.

Besides having characteristics reminiscent of more northern populations, the snakes on the Lower Keys are noteworthy also for their reduced pigmentation dorsally, ventrally and on the head. In addition, brown snakes from the Lower Keys have two preoculars on each side, a character shared in the genus only with *S. storerioides* and *S. occipitomaiculatum*. Trapido (1944) postulated that *S. storerioides* was closest to the ancestor of *S. dekayi*, which in turn gave rise to *vieta*. He wrestled with the difficulty of assuming an increase in dorsal scale rows from *storerioides* to *dekayi* and a subsequent decrease again in *vieta*, but finally concluded that *dekayi* must have given rise to *vieta* (*op. cit.*: 44). I believe his conclusions were largely correct, but the assumption of a reversal in scale row evolution is unnecessary. Fifteen scale rows in *S. dekayi* *vieta* on the Florida peninsula is primitive, not derived. *Storeria dekayi* with 17 scale rows represents the derived condition. My scheme takes this into account, as well as the similarity in preocular counts between Lower Keys *vieta* and *S. storerioides*.

The immediate common ancestor of the taxa in question was a snake very much like *S. storerioides* and occurred in what is today Mexico and the south-eastern United States including Florida. This snake was characterized by 15 scale rows and 2 preoculars. Geographic variation coupled with geographic isolation led ultimately to genetically isolated populations in Mexico (*S. occipitamaculatum hidalgoensis* and *S. storerioides*). The former increased its range north and east in the United States as it differentiated into *S. o. occipitamaculatum*, and ultimately *S. o. obscura* on the Florida peninsula. *Storeria storerioides*, meanwhile continued to differentiate on the American continent. Differentiation proceeded, however, relatively more slowly on the Florida peninsula owing to reduced gene flow with continental populations (peninsular effect), a likely reduced population size resulting in slower rates of mutation, and possibly a weaker selection pressure in the climatically more stable Florida peninsula. Consequently, *Storeria* on the Florida peninsula retain more primitive characters than do populations from the mainland where evolution has proceeded more rapidly. Populations on the Lower Keys retain still more primitive characters, being isolated from the center of the range even more. Brown (1957) calls this type of evolution, "centrifugal speciation."

The differentiation between mainland *dekayi* and Florida *vieta* was probably speeded by further reduction in gene flow brought about by the periodic insulation of Florida caused by rising sea levels. This model accounts for the evolution of *Storeria dekayi vieta* with or without recourse to fluctuating sea levels, however.

*Storeria dekayi viota* is considered autochthonous in Florida and descended from the same ancestor as *S. d. wrightorum* but with less differentiation. Populations on the Lower Florida Keys are differentiated even less than peninsular *viota* and could realistically be assigned sub-specific status.

*Thamnophis sirtalis*. Ventral and subcaudal counts are generally higher in the south. The tendency is for snakes from the peninsula and Apalachicola Valley to have more ventrals and subcaudals than specimens from the remainder of the state. There is a general pattern involving the characters, dorsal spotting and parietal spots which sees higher character states in the geographically disjunct regions of the western Panhandle, Central Highlands, southern Everglades, and southwestern coast of the peninsula.

Very little previous work has been done on geographic variation in this species beyond the naming and delimitation of subspecies. Rossman (1965) described the race *T. sirtalis similis* from the Gulf Hammock region of peninsular Florida. None of the characters investigated in the present study is diagnostic of *similis* which was characterized by its distinctive color in life. Pattern and meristic variation reported here vary discordantly with color; thus it is not possible to discern the range of *similis* in any of my maps.

Garter snakes with dorsal checks (*ordinatus* phase) apparently occur in several areas within the range of *T. sirtalis*. Many individuals from the Panhandle have no stripes, with a dorsal pattern of small black checks. Snakes from the Everglades have the checks, but still retain the longitudinal stripes. The color phase is also known from the

Carolinas. In view of the scattered geography of the spotted phenotype, it seems unlikely that it represents a monophyletic stock. In all likelihood, spotting in *T. sirtalis* has arisen several times, perhaps in response to similar environmental selective pressures.

Blaney (1971b) has suggested that the spotted phase in this species may once have been continuous in coastal areas and the present disjunct nature of the phenotype a result of more recent fragmentation. This may be the case. The pattern of geographic variation in this character (Map 25) suggests a coastal distribution. When much of the Gulf Coastal Plain was exposed during former periods of lower sea level, a spotted *sirtalis* may have occupied this region. Subsequent rise in sea level has left scattered colonies of spotted gartersnakes in coastal regions, and throughout most of the Everglades. If this interpretation is correct, it offers a clue as to the nature of the habitat on the now submerged coastal plain: It was probably treeless, and similar to the present Everglades, where the spotted phenotype is common today.

The evolutionary history of the garter snakes is certainly a subject of interest, but one which has not been investigated since Ruthven (1908). Based on patterns in other species, I would predict that the populations of *T. sirtalis* in Florida will be found to share conservative characteristics with populations considered closest to the ancestral stock. Like other species for which we have better information, garter snakes have probably evolved more slowly in Florida, and also in Mexico. Indeed, Ruthven (1908) considered Mexico to be the "center of origin" of the entire genus. Although the concept of center of origin is of little theoretical value (Croizat *et al.*, 1974), the fact that the

most primitive garter snakes occur there today implies that evolution has proceeded more slowly there than in the rest of North America. It is anticipated that future studies will show that divergence has also proceeded relatively more slowly in Florida garter snakes.

*Thamnophis sauritus*. Ventrals and subcaudals increase clinally to the south on the Florida peninsula, although the patterns are not especially well-developed. *Thamnophis sauritus* from the Florida peninsula differ markedly in the number of supralabials from snakes inhabiting the Panhandle and regions to the north of Florida. The nature of the paired parietal light spots varies in a manner like that observed in several other species with specimens from the southern edge of the Okefenokee Swamp, the area east of Tampa Bay, and the southern tip of the peninsula forming a phenetic entity. Finally, the Gulf Hammock region and subspecies, *T. sauritus nitae* are depicted in the geographic variation of dorsal ground color.

The evolutionary history of the ribbon snake complex as envisioned here is largely in agreement with that proposed by Rossman (1963).

The ancestor ribbon snake, very much like present day *T. proximus*, became wide-spread across the North American continent including Mexico and Florida. The Mississippi embayment provided a barrier to gene flow, and differentiation occurred between the snake populations on either side, resulting in, among other things, reproductive isolation. Phenotypically, the snakes on the east side of the Mississippi were probably still a lot like *proximus* with eight supralabials. Another vicariation occurred when snakes on the Florida peninsula became relatively isolated owing to either the peninsula effect or actual insulation during high sea level

periods. Because of presumed climatic stability, smaller population sizes, and decreased gene flow with the mainland populations, the Florida snakes changed less and more slowly than their mainland relatives. As eastern mainland ribbon snakes differentiated into the *sauritus* phenotype with seven supralabials, the Florida populations remained like the original stock, including the retention of the ancestral number of eight supralabials. The order of these events is not known. There is no reason to believe that reproductive isolation between *proximus* and *sauritus* occurred before the evolution of a reduced supralabial count in *sauritus*. I believe that the ribbon snakes have always been adapted to their environmental surroundings. Thus the development of the present *sauritus* phenotype in eastern North America may have occurred before, during, or after the events which led to reproductive isolation between *proximus* and *sauritus*. Furthermore, the differences between Florida *sackeni* and eastern North American *sauritus*, although not including reproductive isolation (Rossman, 1963), may predate the divergence of the eastern from the western species.

Thus the phenotypic resemblance between western *proximus* (presumed primitive) and Florida *sackeni* is due to the fact that they have each differentiated less from their common ancestor than has the *sauritus* stock in eastern North America. Superficially (*i.e.* in color and pattern), *sackeni* from the Lower Florida Keys are even more like western *proximus*. This may indicate that evolution has proceeded even less on the isolated Lower Keys than on the peninsula. This is certainly the case for the Lower Keys populations of *Storeria dekayi* (see above).

The Gulf Hammock subspecies, *nitae*, is presumed autochthonous in that region, having vicariated with *sackeni* in the not-too-remote past.

*Coluber constrictor*. Ventral and subcaudal numbers increase in a cline southward on the Florida peninsula, although the cline is poorly defined for subcaudal counts. *Coluber* tend to have lighter colored venters in the southern peninsula and northward along both coasts, except that the darkest venters are seen in specimens from the Lower Keys. Gular brown is the best single character for differentiation of the subspecies, *C. constrictor helvigularis*, found only in the Apalachicola River Valley, especially the lower valley (Auffenberg, 1955). Snakes from that area also have the most brown pigment on their supralabial scales, but specimens from the Everglades and parts of the southern peninsula also have brown supralabials. Gular black, supralabial black pigment and supralabial-loreal contact vary in a manner observed in several other species. Snakes from extreme northern Florida, the area east of Tampa Bay and the Lower Keys share a common state for these characters. Because this pattern of geographic variation occurs so frequently, the hypothesis of an independent origin of these characteristics in each of the three regions must be rejected in favor of a monophyletic origin followed by change in the intervening populations. Thus at the level of infraspecific variation, black supralabials and little or no white ventrally are considered primitive to the condition in which snakes have more white pigment. However, Ortenburger (1928) believed that light dorsal coloration was primitive, and the darker black dorsum and labials of eastern and Florida *C. constrictor* was derived. This difference can be resolved in the following hypothetical evolutionary scheme.

The original ancestor of the *Coluber constrictor* probably looked a lot like present day *C. constrictor falviventris* or *oaxaca*. Geographic variation is probably the rule in natural systems, and such variation in a wide-ranging species such as the black snakes must have led to the geographic differentiation we see today. The Mississippi River may have helped to reduce gene flow between populations on either side as these vicariated. *Coluber* east of this barrier became dark black in color, and with black gulars and supralabials. This is the condition of most *C. c. constrictor* today. Differentiation in the northeastern parts of its range (east of the Mississippi and north of Florida) included the loss of the enlarged hemipenial basal spines (hooks), as well. *Coluber* from the remainder of the range retain the enlarged basal spines (Auffenberg, 1955). Evidence based on present hybridization between adjacent phenotypes (subspecies) suggests that reproductive isolation has never been achieved. Nevertheless, we can attempt to reconstruct the subsequent history of eastern populations alone if evolution there proceeded relatively independent of evolution in western populations. The effect of distance on gene flow (Huxley, 1942) probably has insured that evolution in (for example) Florida populations has proceeded independent of any differentiation in populations west of the Mississippi River.

Geographic variation in Florida led eventually to the loss in most populations of the black supralabials and gulars. However, for some reason *Coluber* from three separate regions in Florida failed to change in this direction, and today still retain black supralabial and gular scales. Black snakes from extreme northern Florida, the area east of Tampa Bay, and the Lower Florida Keys retain the primitive condition

regarding gular and supralabial pigmentation. It may be said that evolution has proceeded more slowly in these three regions with regard to the characteristic in question.

The difference between Ortenburger's (1928) and my own conclusion regarding black supralabials and dorsal color now disappears: a light dorsum and labials are primitive for the group as a whole, but a darker dorsal and labial pattern is primitive if we consider only populations east of the original vicariating border (Mississippi River). Therefore most Florida *priapus* with white supralabials and southern Florida *paludicola* with much white ventrally and lighter dorsal color are considered derived with respect to these characters, and the latter's similarity with western *flaviventris* a result of either convergent evolution in south Florida or of more recent gene flow with western forms via some past land connection (e.g. the Gulf Coast Corridor of Auffenberg and Milstead, 1965).

Another pattern of geographic variation in this species offers a clue as to which alternative seems more likely. Snakes from the Apalachicola region have brown or tan supralabials and gulars (*C. constrictor helvigularis*). This condition is also noted in most specimens of southern Florida *paludicola*. The two forms are readily distinguishable on the basis of ground color, but the similarity in supralabial pigmentation suggests a common ancestry. The occurrence of this phenotype in the Everglades and the Apalachicola River Valley suggests a once continuous distribution of brown-chinned racers along the now-submerged Gulf Coast Corridor. Since the occurrence of three disjunct populations of black-chinned racers on the Florida peninsula and Keys necessitates calling

that phenotype ancestral in Florida, the brown-chinned form must be of more recent derivation. The most reasonable interpretation of the data has a black snake stock in Florida characterized by black supralabials and gular scales. Geographic variation led to lighter colored snakes in south Florida and coastal regions and to a loss of the black throat and labial pigmentation in all populations save the three already mentioned. The lighter dorsal and ventral color may be more adaptive near the coasts and in prairie situations such as the Everglades. Thus during the Wisconsin, when sea level dropped as much as 100 meters (Fairbridge, 1960), additional real estate along the Gulf Coast of Florida was inhabited by *Coluber* with light-colored dorsums and ventrums, and probably brown supralabials as well. Today all that remains of this once-continuous population are remnants in the Everglades and the lower Apalachicola Valley, and certain coastal areas of Florida.

It is likely that the similarity in dorsal and ventral color between south Florida *paludicolus* and western *flaviventris* results from similar responses to similar selective pressures. On the other hand, it may be that the similarity in labial coloration between Panhandle *helvigularis* and south Florida *paludicolus* is a remnant of a once continuous, interbreeding stock that has since gone extinct leaving relicts in disjunct regions.

Both Auffenberg (1955) and Wilson (1970a) implied that southern Florida *paludicolus* may be closely related to western *flaviventris*. This may be the case, because the emergent Gulf Coast Corridor would have provided the opportunity for gene flow between coastal western populations (*flaviventris*) and coastal Florida populations (*paludicolus* and

*helvigularis*). The important point, however, is that the Gulf Coast Corridor was inhabited by *Coluber* that were adapted to the conditions at that time. If south Florida *paludicolus* and western U.S. *flaviventris* have experienced more recent contact along the Gulf Coast, it would imply that the habitat there was treeless, probably similar to the present Everglades, at the time of contact. A more detailed study of variation, perhaps at the biochemical level might establish a closer relationship between these taxa but evidence available at this time does not.

Brown pigment on the supralabials may have originated separately in *paludicolus* and *helvigularis*. (If this were the case, recourse to the Gulf Coast Corridor hypothesis would be unnecessary.) For the present, however, all available evidence points to the development through differential selection acting on coastal populations of a phenotype of *Coluber constrictor* characterized by a lighter dorsal color, lighter ventral color and brown pigmented supralabials. Snakes sharing these characters occur today in the Everglades, coastal situations, islands and (without the reduced body pigment) the lower Apalachicola River Valley. Blaney (1971b) was correct in interpreting his light-colored *Coluber* from islands off the Apalachicola River mouth as representatives of this coastal phenotype. However, his statement that they represent relicts of an ancestral population "which dispersed eastward along the Gulf Coast migration route during a period of lower sea level, ultimately giving rise to *C. c. paludicola*" (Blaney, 1971b: 422) is untenable.

*Masticophis flagellum*. Ventral and subcaudal counts tend to be higher in the Panhandle and western peninsula. No cline is evident. Relative tail length also varies in this manner. There may be a north-

south disjunction pattern, observed when ventrals, caudals and infra-labials are considered together (factor 1).

Wilson (1970) noted the disjunct nature of the color phase variation in Florida *Masticophis*. Blaney (1971) suggested that the light phase might indicate a closer relationship with the western *M. flagellum testaceus*. I am in agreement with Blaney's thesis and envision an evolutionary history of the Florida subspecies as follows.

The ancestral *Masticophis flagellum* was a light colored snake, similar to present day *testaceus* in the west and hatchling and juvenile *flagellum* in the east. Evolution east of the Mississippi River in the form of geographic variation led to a phenotype of coachwhip characterized by increased dark pigment, especially anteriorly. In some areas, this differentiation has proceeded more slowly, and light colored coachwhips are still the common phenotype. It is noteworthy that the center of this region of "slower" differentiation is again located in Florida. There is no reason to believe that *testaceus*-like coachwhips invaded Florida along a now submerged land bridge (Gulf Coast migration route) while darker coachwhips were already present north of Florida. The pattern of geographic variation in this character suggests merely that evolution (differentiation) has proceeded relatively more slowly in parts of Florida than in other parts of the species' distribution. Thus the darker individuals in the northeastern parts of the range represent populations more derived than Florida and western populations with respect to color pattern.

*Ophedrys aestivus*. Although there is not a well-developed cline, green snakes do tend to have more ventral scales in the southern parts of

Florida. Caudal scales, however, are highest in Panhandle specimens. Snakes from the Panhandle and west coast of the peninsula have darker supralabial scales than specimens from the remainder of the state. The lightest supralabials are found on snakes from the Florida Keys and the peninsula, exclusive of the west coast. *Ophedryx* from northern Florida and the Panhandle tend to have little or no keeling on the scales of the second dorsal scale row. Specimens from the southern half of the peninsula have well-developed keels on these scales. Green snakes from the Lower Keys may be sexually dimorphic for this trait, but more specimens should be examined to be sure.

Little previous variational work has been done on this species. It is a wide-ranging form with a distribution fragmented in the north and west, suggesting a shrinking range to the southeast, with relictual colonies remaining in scattered areas to the north and west of the main range (see Conant, 1975 for range maps). This is an unusual pattern in North America where most species with disjunct distributions appear to be shrinking to the north. This latter pattern is explicable in terms of a post-Wisconsin extirpation in southern regions in the wake of a warming climate. However, the distribution of *Ophedryx aestivus* cannot be explained in these terms. The disjunct colonies to the north and west of the main range may be remnants of a former distribution during the post-Wisconsin Xerothermic Interval (Deevey, 1949).

A study currently in progress by Grobman and Markezich (pers. comm.) shows that the keeling character of the second dorsal scale row is highly developed only in central and southern Florida. Furthermore, Carr (1940) and I have noticed that green snakes from central and

southern Florida have yellow venters, while specimens from the remainder of the range have white ventral patterns. I believe that green snakes from the southern half of the Florida peninsula are more highly evolved with respect to these two characters, and probably represent fairly recent adaptations to something in the south Florida environment. Specimens from the Lower Keys have white venters (Carr, 1940) and may be dimorphic for the keeling character. The Lower Keys thus stand out as refugia for ancestral character states, as in other species of snakes studied.

*Elaphe guttata*. Both ventrals and subcaudals increase clinally southward in Florida. Blotches on the body and the tail also seem to increase southward. A coastal pattern is evident in the geography of several characters. Corn snakes from coastal parts of the peninsula including off shore islands tend to have less dark pigment ventrally, and that pigment confined to smaller, square blotches. In addition, coastal corn snakes have higher ventral counts than their inland relatives. These trends find their maximum expression on the Lower Florida Keys, where the populations there are also noteworthy for their lighter dorsal color, absent or very narrow dorsal blotch borders, and very high ventral and subcaudal counts.

Geographic variation in the corn snake has not been studied in detail until very recently (two studies, currently in progress that I know of). The distinctive Lower Keys population was once recognized subspecifically, but synonymized by Duellman and Schwartz (1958). The Lower Keys corn snakes share characteristics not shared by any other populations.

It is noteworthy that the corn snakes from the Lower Florida Keys are more like specimens from west of the Mississippi River in ventral

pigment amount and shape, as well as dorsal blotch counts. It is possible these snakes have retained ancestral states for these characters, while populations on peninsular Florida and elsewhere in the east have developed darker ventral pigment and dorsal blotch borders. The evolutionary history of this species probably involved a vicariating event on opposite sides of the Mississippi which included a change to red dorsal blotches from the original brown. Further evolution in the east and north involved a reduction in number of blotches and an increase in darker pigmentation. Alternatively, the reduction of pigment ventrally may be an adaptation to coastal climates, the epitome of which would be off shore insular situations.

Occasional specimens of *Elaphe guttata* from southwestern Florida have brown dorsal blotches, and ventral patterns very much reminiscent of *E. guttata emoryi* in western United States, suggesting retention of ancestral characteristics in these specimens.

*Elaphe obsoleta*. The currently recognized subspecies *Elaphe obsoleta spiloides* is clearly defined by the geographic variation in stripe development, blotch development, ventral pigmentation, and supra-labial pigmentation. The subspecies *williamsi* shows up as the area where both spots and stripes are fairly well-developed. In addition, specimens from the Gulf Hammock region have darker labials and venters, more like northern *spiloides* than *quadrivittata*. Another subspecies, *rossalleni*, is not defined by any of the characters investigated in the present study. The subspecies *E. o. deckerti* (synonymized by Duellman and Schwartz, 1958) shows up as a disjunct population with stripes and blotches, and dark supralabial pigmentation on the extreme south Florida mainland and Upper Keys.

The evolutionary history of the chicken snakes is currently under investigation by Richard Blaney (pers. comm.), but some preliminary speculations can be made here. The juveniles of all subspecies, and the adults of the western forms are blotched. Thus I believe this to be the ancestral condition, most clearly matched by present-day *Elaphe o. lindheimeri*. Geographic variation in most of Florida has led to the development of the striped pattern seen in *quadrivittata* and *rossalleni*, and in the northeastern parts of the United States to the solid-colored snake known as *Elaphe o. obsoleta*. It is no surprise that populations in the insular situation of the Upper Keys have changed less from the ancestral condition, and still retain the darker pigmentation and blotched phenotype. This pattern recurs frequently in the snake species studied to date. More recent geographic variation on the Florida peninsula has led to the reduction in ground color dark pigment along the coasts and in the Everglades region.

The development of the striped phenotype in peninsular Florida was probably expedited by a reduction in gene flow brought about by the insulation of parts of Florida during periods of higher sea level. Populations in the Gulf Hammock region of northern Florida probably represent hybrids from a subsequent contact between mainland blotched and peninsular striped forms. The fact that all combinations of striped and blotched phenotypes can be found in the Gulf Hammock regions suggests a pattern of recombinants such as would be observed when isolated populations come secondarily into contact.

*Lampropeltis getulus*. There is a weakly developed tendency for kingsnakes from the southern regions to have more ventrals and sub-

caudals, as in most snake species studied. The region of the Suwannee Valley shows up again as a major transition zone in kingsnakes, this time for a steep change in number of dorsal scale rows. Kingsnakes from the extreme southern peninsula have the longest tails, relative to their body length. An extremely well-developed clinal increase in cross band counts is evident for both sexes. Dorsal color pattern reflects the taxonomy as recognized by Blaney (1971a) with lighter colored individuals (Blaney's *floridana*) occurring in southern Florida, the extreme northern peninsula and the Apalachicola River Valley.

Blaney (1971a) has discussed the evolutionary history of the North American *Lampropeltis getulus* complex. His speculations, relying chiefly on an eastward migration of early *getulus* stock from the west into an unoccupied Florida peninsula during the Pleistocene seem unduly complex.

Sea levels change gradually. There is no evidence that the Gulf Coast migration route appeared "over night" to allow dispersal into unoccupied territories. On the contrary, we believe that the accumulation of continental ice occurred slowly, with the resulting sea level drop taking place at a corresponding rate. I envision the Pleistocene glacial stages with a gradually receding sea allowing the gradual establishment of continental organisms seaward as suitable terrestrial habitat became available.

Blaney (1971a) suggested that the higher scale row counts as seen in the subspecies *splendida* are probably ancestral. He attributes the same high counts in peninsular Florida kingsnakes to invasion of Florida from the west by *splendida*-like snakes while *getulus*-like kingsnakes with

fewer scale rows occurred to the north. This is unlikely. I believe that kingsnakes in peninsular Florida have retained the ancestral condition for scale row numbers while populations to the north have diverged by reduction of scale rows. I agree that the higher counts as seen in *splendida* and peninsular Florida kingsnakes represent an ancestral condition. The northern populations of *getulus* have evolved a reduction in scale rows while populations to the west (*splendida*) and south (Florida forms) have remained unchanged regarding this character. Peninsular Florida thus emerges once again as an area where evolutionary change in some characters proceeds more slowly than in continental areas to the north.

The presence of lightcolored kingsnakes reminiscent of south Florida *brooksi* (Blaney's *floridana*) in extreme northern Florida and the Apalachicola Valley suggest that this phenotype was once more widespread in Florida. Evolution elsewhere has led to an increase in dark pigment dorsally, while relict populations remain disjunct in these two regions. It is noteworthy that the extreme northern peninsular region and the Apalachicola Valley seem to be refugia for ancestral character states in other species as well (e.g., *Coluber constrictor*, *Thamnophis sauritus*).

Contrary to Blaney's (1971a) interpretation, I view the very wide intergrade zone between light-colored south Florida kingsnakes and darker northern snakes as evidence of recent differentiation in the northern populations, and not of secondary hybridization following differentiation in isolation.

Whether or not complete geographic isolation accompanied the differentiation of *getulus* is not important. What is important is that the kingsnakes in peninsular Florida, and especially southern peninsular

Florida have remained relatively unchanged with respect to dorsal color pattern and number of midbody scale rows while populations to the north have differentiated.

*Lampropeltis triangulum*. Ventrals and caudals appear to decrease southward on the peninsula, but the trend is probably more complex than that. Milk snakes tend to have proportionately longer tails in the southern parts of the peninsula. The area east of Tampa Bay, northern Florida and a small region in southeastern Florida are set off with similar character states for red cross band counts.

This species may have the largest geographic distribution of any terrestrial snake species in the world, and one recent authority recognizes 23 distinct subspecies in different parts of that distribution (Williams, 1970). His evolutionary speculations are based on the premise that the group has had a center of origin and each of the subspecies has been derived from other of the subspecies and dispersed into its present range. He decided that the area of greatest subspecific diversity represents the "point of origin," and identified central Mexico as the ancestral home for *L. triangulum*. Evolution does not proceed in the manner envisioned by Williams (1970) (see Croizat *et al.*, 1974). I view the 23 distinguishable phenotypes of milk snakes as examples of localized populations adapted to environmental conditions where they exist. Their differentiation can be accounted for by differential selection under differential selective pressures brought about by different environments. If central Mexico has more subspecies than other areas of comparable size, the reason must lie in the environmental heterogeneity of that part of Mexico, coupled to an unknown extent with a tendency for reduced gene

flow between the populations. If central Mexico is the present home of the subspecies retaining the most primitive character states, we can definitely state that evolution (= change) has proceeded relatively more slowly in that part of Mexico than in other regions for the characters in question.

The milk snakes in peninsular Florida are closer to what Williams (1970) believes to be the ancestral phenotype than are milk snakes from north of Florida. Thus Florida has been acting as a refugium for preservation of certain ancestral character states.

Within Florida, the pattern of geographic variation suggests that differentiation in the southern half of the peninsula has led to a reduction in number of cross bands in all areas except the Central Highlands and the south-eastern part of the peninsula. Alternatively, cross bands could have increased in these two regions while remaining lower in the rest of the southern peninsula.

According to Williams (1970), the ancestral midbody scale row number was probably 21. Southwestern milk snakes typically have 19 scale rows. Many Florida specimens have reduced this still further and are characterized by 17 dorsal scale rows at midbody.

*Cemophora coccinea*. The patterns of variation of *C. coccinea* in Florida are apparently more complex than previous authors have recognized. On the basis of correlation analyses, there seem to be two rather distinctive morphotypes in Florida characterized by a combination of features. Generally speaking, *Cemophora* with high ventral counts are also larger, have more infralabials, more dorsal scale rows both anteriorly and posteriorly and more subcaudals. Without additional material, it would

be difficult to analyze the geography of this variation. However, it appears that *Cemophora* which tend to be larger, have more ventrals and subcaudals, more infralabials, and more dorsal scale rows, occur most frequently in the central part of the Florida peninsula, with snakes of a contrasting phenotype occurring in north Florida, the Panhandle, and to the south in the Everglades regions. Additionally, these central snakes usually have 14 supralabials, while *Cemophora* to the north and south have 12. Factor 3, figured in Map 186, most closely approximates the distribution of the two phenotypes. Previous studies (Williams and Wilson, 1967; Duellman and Schwartz, 1958; Neill, 1950a) have failed to notice this pattern. Current taxonomy (Williams and Wilson, 1967) recognizes the snakes from the northern peninsula and Panhandle as *C. coccinea copei*, and includes all *Cemophora* from the peninsula south of Marion County in the nominate race.

The scarlet snakes may represent another example of the phenetic similarity between north and south Florida populations with divergent populations in the geographically intermediate region.

*Diadophis punctatus*. Unlike most snake species investigated, *Diadophis punctatus* tend to have lower ventral counts southward. There is no obvious trend in the variation of subcaudal numbers. Like other species, ringnecks usually have proportionately longer tails in the south. Many of the characters concerned with the nuchal ring and labial pigmentation show a relationship between the Gulf Hammock region and the extreme southern peninsula including the Lower Keys. Superimposed upon this pattern is frequently the Suwannee Straits break in phenotype as seen in other species and evident in *Diadophis* in the variation of number of supralabials, labial spots, and ring width.

Most of the previous work on variation in *Diadophis* has been concerned with the validity and distribution of the various taxonomic entities within the genus (Conant, 1946; Paul, 1967; etc.). A recent study by Gehlbach (1974) has included some speculations on evolutionary history within the species. Gehlbach believes that the smaller body size seen today in populations called *armyi* is probably ancestral. The larger *Diadophis* in the southwestern United States reflect adaptation to present conditions there. He further speculates that the tail-coiling habit and distinctive subcaudal coloration (Myers, 1965), seen in Florida populations and in *armyi* is ancestral, and that more northeastern populations have lost these characteristics. I agree with these speculations, and would add these comments concerning color pattern in this species.

The lack of a nuchal ring in Lower Keys populations may be ancestral and imply that *Diadophis* there have failed to evolve a complete neck ring while populations to the north have changed in the direction indicated. The fact that some populations of ringnecks in the southwestern U.S. also lack a neck ring (Stebbins, 1966) lends credence to this hypothesis. In addition, the development of discrete pigment spots on the labial scales in northern populations has proceeded relatively more thoroughly there than in Keys populations. The Lower Florida Keys may be acting as a refugium for such ancestral character states as presence of subcaudal black spots, a reduced labial pigmentation pattern, and a reduced neck ring.

In general, ringneck snakes from the peninsula of Florida differ from their mainland relatives in the nature of the nuchal ring. Snakes from south of the Suwanee River frequently have a neck ring interrupted

middorsally, and one that is both narrower and displaced farther posteriorly than specimens to the north and west. This phenotype may represent an intermediate condition between the virtually ring-less populations on the Keys and the typical ringed *Diadophis* north and west of Florida.

Alternatively the populations on the Keys may be more derived with respect to the nuchal ring and labial pigmentation, perhaps a relatively recent adaptation to conditions there. The disjunct nature of the variation seen in number of subcaudal black spots suggests that these spots have been lost in peninsular populations while they were retained by both northern Florida and Lower Keys populations. This pattern has been observed in several other species (Duellman and Schwartz, 1958; this study), and does not support the suggestion that the Keys might harbor more advanced phenotypes.

On the basis of number of subcaudal black spots, labial pigmentation and absence of the nuchal ring, a relationship between *Diadophis* populations in the Gulf Hammock Region and the Lower Keys is suggested. Again, these areas may be refugia for ancestral character states, while evolutionary change has proceeded in areas geographically intermediate.

*Tantilla* sp. Ventral and subcaudal counts tend to decrease clinally to the south on the Florida peninsula. Specimens from the Miami and Key Largo populations are an exception to this, having generally high ventral and caudal counts. *Tantilla* from the west coast of the peninsula and the Suwannee River Valley usually have proportionately longer tails than specimens from elsewhere in the state.

Geographic variation in most of the characters examined is complex. Populations from Miami and the Suwannee River Valley are more closely

related phenetically than geographically intermediate populations. Telford (1966) noted this when he described *T. oolitica* from Miami. The disjunct nature of this pattern suggests a retention of ancestral character states in these regions while adaptation in geographically intermediate regions has led to partial differentiation. I cannot agree with Telford (1966) that this disjunct pattern implies the existence of a former gene corridor connecting the two regions while "strongly dissimilar, evolutionary older populations" (Telford, 1966: 300) existed alongside the corridor. Rather, I believe the similarity between northern and extreme southern populations is more easily explained by assuming moderate differentiation in intermediate populations and less differentiation in the two regions under discussion.

Geographic variation in crowned snakes on the Florida peninsula has led to the complex picture treated taxonomically by Telford in 1966. The different phenotypes are probably restricted to particular ecological situations, as suggested by Telford. Whether the phenotypes have achieved reproductive isolation or not, cannot be determined by a phenetic study. Thus confirmation of the validity of *Tantilla relicta* must await experimental investigation.

*Sistrurus miliaris*. Ventrals and caudals appear to increase clinally to the south. In several characters, I note a weakly defined coastal effect with populations from coastal areas on the peninsula having higher dorsal scale row counts, higher dorsal blotch counts, and larger, rounder dorsal blotches. The Panhandle west of the Ochlockonee River and the Everglades seem to be set apart phenetically from geographically intermediate regions. *Sistrurus* from these two disjunct

regions share character states for ventral pigmentation, dorsal contrast, spot shape, spot-space ratio, and ventrals and caudals.

Gloyd (1940) commented on the phylogenetic relationships in the genus *Sistrurus*. He pointed out that the Florida subspecies *barbourni* has more primitive character states than either of the other two subspecies. He went on to speculate that *barbourni* must therefore have given rise to the other two following its isolation in Pleistocene Florida. I do not follow this speculation. If *barbourni* does indeed retain more primitive characteristics (and I agree that it probably does) the implication is that it has changed less than the others, not that it is ancestral to them. I believe that geographic variation (*i.e.* adaptation to the local environments) is the rule in living systems, and there is no reason to suppose that the pigmy rattlers are an exception. Populations of *Sistrurus miliarius* are adapted to local conditions wherever they exist. If the populations on peninsular Florida retain presumed ancestral states for some characters, while populations to the north and west demonstrate character states believed to be derived, it follows that something about the Florida environment has allowed populations there to remain unchanged, while populations elsewhere have been forced to differentiate. The location of the area of least evolutionary change is not the center of origin, center of dispersal or anything but the area where evolution has proceeded more slowly. It is for the biogeographer to determine why evolutionary rates are not the same everywhere.

Just as Florida appears to be acting as a refuge for ancestral character states with respect to the remainder of North America, there are areas within Florida that seem to preserve primitive characters

with respect to the rest of the peninsula. The phenetic affinities between *Sistrurus* from the Everglades and the widely disjunct western Panhandle cannot be denied. These snakes with their narrow, crossband-like dorsal blotches, increased dorsal contrast and increased ventral white, are more similar to the western subspecies, *streckeri*, than are any other Florida populations. This phenotype may be ancestral, with populations in other parts of the range having differentiated more from this condition. An alternative hypothesis would be to suggest that this phenotype has arisen independently in the several remote regions where it occurs today.

*Crotalus adamanteus*. There are no obvious trends of geographic variation in ventral and subcaudal counts for Florida *Crotalus*, except that Keys specimens have higher ventral counts than other specimens. The number of infralabial scales varies in such a way that rattlers from the Florida Keys are more like more northern specimens than those from the adjacent mainland. Pigmentation of the labials and ventral surface show a phenetic affinity between specimens from the Lower Keys and the Central Ridge.

Gloyd (1940) believed that *Crotalus adamanteus* was derived from the western *atrox*, which he suggested was closest to the ancestral type for the *atrox* group of rattlesnakes. The implication, although not noticed by Gloyd, is that *adamanteus* in Florida has diverged less from the ancestral phenotype than have other members of the group. The fact that *atrox* is the most primitive (= generalized) and occurs today in the southwestern United States implies not that it arose there as Gloyd believed, but that it has changed less there. The southwestern United

States has acted as a refuge, preserving ancestral character states while other regions have dictated evolutionary change in their rattlesnake populations. Similarly, Florida has been a refuge for rattlesnake evolution, although not as strongly as has the southwestern United States. There is no reason to suppose that *adamanteus* arose on the Mexican Plateau and dispersed into Florida.

Within Florida, *Crotalus adamanteus* has experienced differentiation in response to different selective regimes, with this differentiation no doubt effected by variations in gene flow. The phenotypic resemblance between disjunct populations on the Keys and in northern Florida suggest that these phenotypes share a common history. Evolution in the geographically intermediate region of the Florida peninsula has produced a phenotype in populations there that is somewhat distinct from that persisting both northward and southward.

## SUMMARY

Fifteen species of Florida snakes have been shown to vary geographically in seven major patterns. These patterns correlate with present and past environments.

A North-South Pattern describes the situation in which clinal changes in character states occur southward on the Florida peninsula. This pattern correlates well with measurements of mean annual temperature. A Suwannee River Pattern which correlates with the geologic history of Florida, involves abrupt changes in character states as one crosses the region of the former "Suwannee Straits." Several snake species investigated show phenotypic uniqueness in the Everglades of southern Florida. This pattern correlates with the unique habitat of the region. The North Florida-Lower Keys Pattern seems to correlate with the geologic history of the state. The Okeechobee and Coastal Patterns correlate with the unique environments with which they are associated. The Panhandle-Everglades Pattern of geographic variation seems to correlate with rainfall patterns.

Geographic variation in Florida snakes can be explained on the basis of natural selection without recourse to dispersal as an important factor in evolution. Thus phenotypic similarities between disjunct populations are the result of adaptation to similar environments and/or differentiation in intermediate populations.

APPENDICES

APPENDIX A  
CHARACTERS EXAMINED

All Species

Number of Ventrals. Unless otherwise noted, this count includes the first anterior ventral scute that is wider than long, through the last scute anterior to the anal plate. This method, recommended by Schmidt and Davis (1941), is less time-consuming to determine, and thus more efficient in terms of information gathered than the more complicated method advocated by Dowling (1951).

Number of Subcaudals. Only those specimens with terminal spine were counted. Unless otherwise stated, the spine was included, and the anal plate was not.

Number of Supralabials. Counts were made on both sides.

Number of Infralabials. Counts were made on both sides.

Dorsal Scale Rows. Scale rows around the body were counted in three places: one head length posterior to the head; at midbody; and one head length anterior to the anal plate.

Snout-Vent Length. This was measured from the tip of the snout to the posterior margin of the anal plate.

Tail Length. The length of the tail from the posterior margin of the anal plate to the tip of the terminal spine was recorded for specimens with complete tails only.

Sex. In snakes without everted hemipenes, sex was determined by dissection of the base of the tail.

Qualitative Characters. Several qualitative characters have been used in the present study. Aspects of carination, pattern, and pigmentation were ranked on qualitative scales and assigned numerical character states. In most cases of pattern analysis, line drawings on the data-collection forms were filled in, and numerical scores assigned only after all the material had been examined. In cases involving carination or pigmentation characters, a preliminary investigation determined the range of variation, and a scale was constructed beforehand. "Voucher" specimens were used as models for the character states while the scoring was in process. In this manner, the specimens could be compared with the models, and assigned the appropriate character state value.

*Storeria dekayi*

Number of Ventrals.

Number of Subcaudals.

Number of Supralabials.

Number of Infralabials.

Dorsal Scale Rows.

Number of Preoculars. The preocular scales were counted on each side of the head. Scales divided incompletely were counted as half scales.

Number of Postoculars. These scales were counted in the same manner as the preoculars.

Ventral Pigment. The general extent of ventral dark pigment was ranked on a scale of zero (venter immaculate) to five (venter with much dark pigment).

Temporal Pigment Amount. The amount of black pigment on the temporal scale was noted and assigned values from zero for no such pigment to five for the condition when the entire temporal is pigmented.

Temporal Pigment Shape. The orientation of the tear-shaped temporal blotch (when present) was noted. This blotch has been used by previous workers (Anderson, 1961 and Sabath and Sabath, 1969) but has always been confusing. By noting merely in which direction the blotch seems to point, a more manageable character is at hand. Specimens in which temporal pigment appeared to enter the temporal at its posterior margin were given values of one; those in which pigment entered at the anterior margin were scored as two, and those whose temporal pigment was entirely confined to within the scale were scored as three. Specimens without temporal pigment were given missing values for this character.

Subocular Spot. This is the number of supralabial scales covered by the large subocular spot. If pigment covered more than half a supralabial it was counted. Only the right side was examined.

Black Supralabials. The number of supralabial scales with black pigment was recorded for the right side.

Black Infralabials. The number of infralabial scales with black pigment was recorded for the right side.

Snout-Vent Length.

Tail Length.

Sex.

*Thamnophis sirtalis*

Number of Ventrals.

Number of Subcaudals.

Dorsal Scale Rows.

Number of Supralabials.

Number of Infralabials.

Parietal Spot. The distinctiveness and size of the parietal spot was ranked on a scale of one to three.

Dorsal Spotting. The degree of dorsal spotting ("ordinatus" phase, discussed by Rossman, 1965) was ranked on a scale of one to three.

Snout-Vent Length.

Tail Length.

Sex.

*Thamnophis sauritus*

The data for this species were supplied by Douglas A. Rossman.

Number of Ventrals.

Number of Subcaudals.

Number of Supralabials.

Number of Infralabials.

Parietal Spot Size. The small paired light spots near the medial margin of the parietal scales were scored for presence or absence as well as size when present. The smallest spots were assigned values of one; the largest, values of 2. Specimens lacking the parietal spot received scores of zero for this character.

Parietal Spot Distinctiveness. The spots were scored one for faint or indistinct and two for distinct. Specimens lacking parietal spots were assigned values of zero for this character.

Dorsal Brown. Rossman described the brown in the dorsal ground color as light, medium, dark, very dark, or black. I assigned numbers from one to five to these qualitative assessments.

Dorsal Gray. The presence of gray in the dorsal ground color caused this character to be scored one; its absence was scored as zero.

Dorsal Stripe Edge. The black border of the dorsal stripe may be absent, weak and irregular, present but narrow, or at least 1 1/2 scales wide. Numerical values of zero to three were assigned for these conditions.

Snout-Vent Length.

Tail Length.

Sex.

*Coluber constrictor*

Number of Ventrals.

Number of Subcaudals.

Blackness. Specimens were scored one, two or three, based on how dark black they appeared in preservative.

Ventral White. The amount of white pigment on the ventral surface was assessed and values ranging from zero (no white on any part of the venter) to five (venter completely white) were assigned.

Gular Brown. The amount of brown pigment in the gular region was examined, and values ranging from zero for no such pigment to five for much brown pigment were assigned.

Gular Black. Like Gular Brown, the values for this character ranged from zero to five.

Supralabial Brown. The amount of brown pigment on the supralabial scales was examined, and values from zero for no brown pigment to five for much brown pigment were assigned.

Supralabial Black. The amount of black pigment on the supralabial scales was scored with values from zero to five, as in the previous characters.

Supralabial-Loreal Contact. This character, introduced by Auffenberg (1955), was examined on both sides of the head. The first supralabial is either in contact with the loreal, or it is not.

Number of Supralabials.

Number of Infralabials.

Frontal Measurements. Three measurements were taken, as in *E. guttata*.

Size. Specimens were categorized as either large, medium, small or hatchling.

Sex.

*Masticophis flagellum*

Data for this species were supplied by Larry David Wilson.

Number of Ventrals. Ventrals were counted using the method proposed by Dowling (1951).

Number of Subcaudals.

Number of Supralabials.

Number of Infralabials.

Phase. On the basis of overall color and pattern, the specimens were assigned to either a light phase (1), or a dark phase (3). There were some intermediates (2).

Snout-Vent Length.

Tail Length.

Sex.

*Opheodrys aestivus*

Number of Ventrals.

Number of Subcaudals.

Dorsal Scale Rows.

Number of Supralabials.

Number of Infralabials.

Supralabial Pigmentation. The amount of dark pigment on the supralabials was scored from zero (supralabials immaculate) to five (supralabials completely pigmented).

Keeling of the Second Dorsal Scale Row. The extent of carination of the scales in the second dorsal scale row at midbody was evaluated. A value of zero was assigned to specimens showing no keel on this scale row, and a maximum value of three was assigned when the keel was developed to the same extent as the adjacent third row. Values of one and two were given to specimens with intermediate conditions. This character was first used by Cope (1900).

Frontal Measurements. Three dimensions of the frontal plate were recorded as in *E. guttata*.

Snout-Vent Length.

Tail Length.

Sex.

*Elaphe guttata*

Number of Ventrals.

Number of Subcaudals.

Number of Dorsal Blotches. This includes only the precaudal blotches.

Number of Tail Blotches.

Dorsal Scale Rows.

Frontal Measurements. Linear measurements were made on three aspects of the frontal plate. The anterior width is the straight line distance be-

tween the junction of the left prefrontal, the left supraocular, and the frontal, and the junction of the right prefrontal, the right supraocular and the frontal. The posterior width is the straight line distance between the junction of the left supraocular, the left parietal and the frontal and the junction of the right supraocular, the right parietal and the frontal. The frontal length is the straight line distance from the junction of the two prefrontals and the frontal to the junction of the two parietals and the frontal.

Nature of the Lateral Spot. The lateral series of spots was examined and scored for presence or absence, and (when present) whether the surrounding border was complete or incomplete.

Dorsal Spot Border. The black border surrounding a typical midbody dorsal blotch was scored for width and distinctiveness on a scale of zero (no border) to four (border very well developed and more than two scales in width).

Ventral Pigmentation. The general totality of dark pigment in a typical midbody ventral section was scored for each specimen on a scale of zero (venter immaculate) to five (venter with black pigment over more than 3/4 of surface).

Ventral Pigment Shape. This character attempts to formalize the general shape of the ventral checks in a typical midbody section. It was scored on a scale of one (ventral pigment consisting mainly of small spots) to five (ventral pigment usually covering entire ventral scales).

Snout-Vent Length.

Tail Length.

Sex.

*Elaphe obsoleta*

The data for this species were supplied by Walter Auffenberg.

Number of Dorsal Blotches. This includes only the precaudal blotches.

Stripe Development. This variable is a qualitative assessment of the degree to which the dorsal stripes are evident. The values ranged from zero for no stripes to five for very well-developed stripes.

Blotch Development. Ranked on a scale like that for Stripe Development, this character attempts to describe the degree to which the dorsal blotches are developed.

Ground Color. The dorsal ground color of each specimen was compared with a series of color chips, and assigned a value corresponding to the chip. The numerical representation of those values represents increasing melanism, scaled from zero to 3.5.

Ventral Pigment. The totality of dark pigment on the ventral surface was scored values from one to four with increasing darkness.

Supralabial Pigment. The values for Supralabial Pigment ranged from one to four with increasing darkness.

Size. To obtain rough size correlations, and for grouping the specimens, the head length was recorded.

*Lampropeltis getulus*

Data for this species were supplied by Richard M. Blaney.

Number of Ventrals. These were counted by Dowling's (1951) method.

Number of Subcaudals.

Number of Dorsal Bands. This includes only the precaudal bands.

Number of Infralabials.

Dorsal Scale Rows at Midbody.

Pattern. This character attempts to describe the relative amount of light pigment in the dorsal pattern. The three states of this character (1-3) correspond to parts of Blaney's (1971) Figure 13.

Snout-Vent Length.

Tail Length.

Sex.

*Lampropeltis triangulum*

Data for this species were supplied by Kenneth Williams.

Number of Ventrals.

Number of Subcaudals.

Dorsal Scale Rows.

Number of Supralabials.

Number of Infralabials.

Number of Loreals. These were counted on each side.

Number of Body Bands. This is a count of precaudal red bands.

Number of Tail Bands.

Total Length.

Tail Length.

Sex.

*Cemophora coccinea*

Data for this species were provided by Kenneth Williams and Larry David Wilson.

Number of Ventrals.

Number of Subcaudals.

Number of Supralabials.

Number of Infralabials.

Dorsal Scale Rows.

Number of Body Blotches. This is the number of precaudal red saddles.

Number of Tail Blotches.

Length of First Red Blotch. This is the number of scale lengths in the first red dorsal blotch.

Length of Fifth Red Blotch.

Length of First White Blotch.

Length of Fifth White Blotch.

Total Length.

Tail Length.

Sex.

*Diadophis punctatus*

Number of Ventrals.

Number of Subcaudals.

Number of Paired Gulars. This is the number of paired scales in the throat region between the posterior chin shields and the first ventral scales.

Number of Anal Plates. 23% of the specimens examined had the last ventral scale enlarged and patterned like the adjacent anal plate, giving the appearance of two anal plates.

Number of Supralabials.

Number of Infralabials.

Number of Tail Spots. The number of black spots on the underside of the tail was recorded for each specimen.

Ventral Pigmentation. At a typical midbody section, the general amount of black pigment was ranked on a scale of zero (venter immaculate) to five (venter very heavily pigmented).

Ventral Spot Shape. The shape of the ventral spot was recorded, and assigned values from zero (slightly higher than wide) to five (as wide as the whole ventral scale). This character thus measures the degree to which the ventral spot is elongated, and not a spot at all, but a ventral "bar."

Connected Spots. The state for this character is three if the majority of the ventral spots are connected anterior-posteriorly, one if none is, and two if some are.

Ventral Spot Distinctiveness. The snakes were given values of one, two or three depending on how clear-cut and distinct the ventral spots were.

Number of Immaculate Ventrals. The number of ventral scales lacking black spots was recorded.

Ring Separation. Using a scale of zero (for no break) to five (break more than one scale wide), the width of the break in the nuchal ring was scored. A value of six was assigned to those specimens in which the ring was reduced to a pair of dorso-lateral dots or lacking altogether.

Ring Position. This is the number of scales between the parietal and the anterior margin of the nuchal ring.

Ring Width. The width of the nuchal ring was determined at its widest dorsal part in number of scales.

Labial Pigment Distinctiveness. Specimens with diffuse labial pigment were assigned a value of zero for this character. Those with clear, distinct labial spots, or with no pigment, were given values of three. Intermediate specimens were scored one or two.

Supralabial Spots. The number of supralabial scales with black spots was recorded for the right side.

Infralabial Spots. The number of infralabial scales with black spots was recorded for the right side.

Snout-Vent Length.

Tail Length.

Sex.

*Florida tantilla*

Some of the data used in this analysis were supplied by Sam R. Telford.

Number of Ventrals. These were counted using the method proposed by Dowling (1951).

Number of Subcaudals. The terminal spine was not counted.

Infralabials Contact Anterior Chin Shields. The first four infralabials generally contact the anterior chin shields. In some cases, only the first three infralabials make contact with the Anterior Chin Shields. The condition for this character was noted on both sides.

Parietal Pattern. The extent of light pigment in the nuchal area was noted. Specimens with totally black parietals were scored zero for this character, while the highest score assigned was six for specimens with much white pigment in the form of a wide neck band. The numerical designations correspond partially with Telford's (1966) alphabetic pattern analysis (his figure 5).

Snout Pigmentation. The extent of light pigment on the internasals, prefrontals, and rostral was ranked on a scale of zero for completely black, to three for the condition exhibiting a large light spot on the snout.

Nuchal Collar Width. The width of the light neck ring was expressed in number of scale-lengths at the dorsal midline.

Mental Contacts Anterior Chin Shields. Whether or not the mental scale was in contact with the anterior chin shields was noted.

Snout-Vent Length.

Tail Length.

Sex.

*Sistrurus miliaris*

Number of Ventrals.

Number of Subcaudals.

Number of Divided Subcaudals.

Number of Dorsal Blotches. This includes blotches anterior to the tail only.

Number of Tail Bands.

Dorsal Scale Rows.

Number of Supralabials.

Number of Infralabials.

Dorsal Blotch-Ground Color Contrast. The contrast between the ground color and the dorsal blotches at a typical midbody section was ranked on a scale of zero (blotches not discernible) to three (blotches very distinct from ground color).

Ventral White Pigment. The amount of white in the ventral pattern was given a subjective ranking of one for almost no white, to three for much white included on the ventrum.

Dorsal Spot Shape. The dimensions of a typical dorsal blotch at midbody were recorded in scales wide and scales long. In addition, the number of scales included in the interblotch space was recorded. These three values describe the shape and spacing of the dorsal blotches.

Frontal Measurements. Three measurements were taken on the frontal plate, as in *E. guttata*.

Snout-Vent Length.

Tail Length.

Sex.

*Crotalus adamanteus*

Number of Ventrals.

Number of Subcaudals.

Number of Divided Subcaudals.

Number of Dorsal Blotches. This is the number of diamonds not including the tail.

Number of Supralabials.

Number of Infralabials.

Dorsal Scale Rows.

Number of Black Subcaudals. Subcaudals more than 3/4 black were counted.

Ventral Pigment. The amount of dark pigment on the ventral surface was ranked from zero for no pigment to three for quite heavy dark pigmentation.

Labial Pigmentation. A general subjective interpretation of labial dark pigment was scored from one to three, with one being very little such pigment, and three much pigment.

Immaculate Supralabials. A count of the number of supralabials at least 3/4 immaculate was made on the right side.

Size. Specimens were assigned values meaning small, medium, large or extra large.

Sex.

APPENDIX B  
ENVIRONMENTAL VARIABLES EXAMINED

I analyzed summary data for the period of record for each of 196 weather stations in Florida, Georgia and Alabama. A list of the stations and their localities may be obtained from the author.

Elevation. The elevation in meters above mean sea level was recorded for each weather station.

Annual temperature. This is the average annual temperature at a station.

January temperature. This is the average temperature for the month of January.

August temperature.

Annual rainfall. This is the average total rainfall received during a calendar year.

Number of days per year having a low temperature of 0°C or less.

Number of days per year having a high temperature of 32.2°C or more.

August maximum temperature. This is the average highest temperature per day for the month of August.

January minimum temperature.

Number of days with over 0.254 cm precipitation.

Temperature range. This is the average difference between the average August and average January temperatures.

Extreme temperature range. This is the average difference between the daily August maximum temperature and the daily January minimum temperature.

Number of days per year with average temperature between 0° and 32.2°C.

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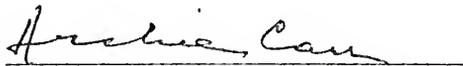
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Steven P. Christman, the son of Raymond J. and Dorothy D. Christman, was born 21 May 1945 in Grass Valley, California. He graduated from Whitesboro Central High School, Whitesboro, New York in 1963. Mr. Christman attended the State University of New York at Oswego, New York from 1963 to 1964. After serving three years in the United States Army Special Forces, he enrolled at the University of Florida where he received the Bachelor of Science degree with a major in zoology in 1971. During graduate training at the University of Florida, Mr. Christman held assistantships in the Zoology Department and the Florida State Museum. In 1974 he received the Florida State Museum Curator's Austin Award.

Steven P. Christman is married to the former Sheila Anne Lee of Oswego, New York.

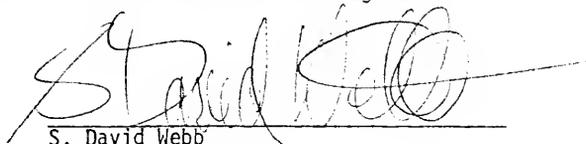
I certify that I have read this study and that in my opinion it conforms to acceptable standards of scholarly presentation and is fully adequate, in scope and quality, as a dissertation for the degree of Doctor of Philosophy.

  
Archie Carr, Chairman  
Graduate Research Professor of Zoology

I certify that I have read this study and that in my opinion it conforms to acceptable standards of scholarly presentation and is fully adequate, in scope and quality, as a dissertation for the degree of Doctor of Philosophy.

  
Frank G. Nordlie  
Associate Professor of Zoology

I certify that I have read this study and that in my opinion it conforms to acceptable standards of scholarly presentation and is fully adequate, in scope and quality, as a dissertation for the degree of Doctor of Philosophy.

  
S. David Webb  
Professor of Geology

This dissertation was submitted to the Graduate Faculty of the Department of Zoology in the College of Arts and Sciences and to the Graduate Council, and was accepted as partial fulfillment of the requirements for the degree of Doctor of Philosophy.

December, 1975

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Dean, Graduate School



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