PATTERNS OF GEOGRAPHIC VARIATION IN FLORIDA SNAKES

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SYNOPSIS: I analyzed geographic variation within Florida for 15 species of snakes. Contour maps were machine-produced for each of over 200 morphologic and 17 environmental variables. Factor analysis of the maps showed that seven major patterns of geographic variation account for over 60% of the total variation. Each of the patterns of geographic variation can be explained in terms of natural selection and gene-flow characteristics in 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. The geographic localities of primitive species or primitive characteristics within a species are not the centers of origin, but are merely regions in which evolution has proceeded relatively more slowly. A north-south cline on the Florida peninsula is the most obvious pattern of geographic variation, common to all species examined for at least some characters. Most species examined showed aspects of a Suwannee Straits pattern with dramatic character-state shifts occurring in the region of the present Suwannee River.

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INTRODUCTION

Darwin's theory of natural selection has as its keystone one basic re-
quirement: 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 recom-
binations of existing genes insure the continuance of this variability.
Selection acts on the differences between organisms by eliminating unfit
phenotypes (and hence their associated genotypes) from the reproductive
effort of a population. Phenotypes that are unfit in one part of a species'
geographic distribution may be suitable 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 different parts of its geographic range.
Natural selection creates different phenotypes in response to different
selective regimes. When the degree of phenotypic divergence also includes
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 is really just another form of evolution. Albert
Einstein has shown the equivalence of space and time in the physical
world, and Preston (1960, 1962) has demonstrated analogies between
space and time in ecology and species diversity. In the present study, it is
assumed that character variation through space is a form of organic evo-
lution just as character variation through time is unquestionably so.

It is presently impossible to study the environmental factors responsi-
ble 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 environmen-
tal 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 the
patterns of character variation in space are brought about and main-

tained 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, one at a time, 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 among characters of a single species. Still fewer investigators have attempted to demonstrate correlations between environmental characteristics and intraspecific geographic variation. Previous to this study, to my knowledge, no one has attempted to investigate quantitatively patterns of geographic variation common to several species, and to compare these patterns with environmental variation.

Florida is basically a peninsula with a warm temperate climate grading into that of a subtropical region. It has such diverse habitats as wooded swamps, prairies (marshes), flat pine lands, and scrubby chaparral-like deserts (Florida scrub). 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. Recent work by several authors, however, has shown that demes or micro-geographic populations can and do differentiate as they become adapted to their own unique 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 factors have been eliminated, should historical phenomena be suggested as causation in biogeography.

Leon Croizat, in a series of works spanning the last 30 years (especially 1958, 1962), has advocated a method of biogeographical analysis that begins without a priori assumptions, and lets the data speak for itself. His method is to plot the distribution of the species of a larger group (genus,

family etc.) on a map, and to connect the disjunct ranges with straight lines. When many groups are treated in this way, the lines of connection (tracks) do not form a random network over the map, but rather 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 widespread distributions.

By plotting the geographic pattern of morphologic variation of a single character of a single species on a map, and then considering many such maps together, one is, in effect, using a modification of Croizat's panbiogeographic analysis on a smaller scale. One begins 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. In this manner, patterns of organic geographic variation can be identified and compared with geographic variation in environmental factors. Patterns of morphologic variation that do not correlate with existing environmental variables may be correlated with untested environmental variables, or they may have received their present shape by past paleoclimatic or geographic factors.

ACKNOWLEDGMENTS

METHODS

THE DATA

I analyzed character variation data on 3567 specimens of 15 species of Florida snakes (Table 1). I chose the species on the basis of availability of specimens or data and, more importantly, because all are wide-ranging, rather ubiquitous species with representatives (taxonomically distinct or not) in Texas and eastern 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, and I 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.

Table 1.—Species examined, numbers and origin of data.

Species	Males	Females	Unknown	Data Source
Storeria dekayi	69	82	—	this study
Thamnophis sirtalis	74	118	—	this study
Thamnophis sauritus	101	118	60	Douglas Rossman
Coluber constrictor	238	200	2	this study
Masticophis flagellum	40	42	3	Larry D. Wilson
Opheodrys aestivus	79	97	—	this study
Elaphe guttata	267	188	—	this study
Elaphe obsoleta	—	—	370	Walter Auffenberg
Lampropeltis getulus	117	54	36	Richard Blaney
Lampropeltis triangulum	59	61	—	Kenneth Williams
Diadophis punctatus	132	162	1	this study
Cemophora coccinea	42	39	9	Kenneth Williams and Larry D. Wilson
Tantilla relicta, oolitica, coronata	97	97	4	this study and Sam Telford
Sistrurus miliarius	188	132	—	this study
Crotalus adamanteus	98	96	—	this study

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 the unpredictable color changes 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. Figure 1 shows places referred to.

I calculated Pearson Product-Moment correlation coefficients (Nie *et al*. 1970) between every character and sex and snout-vent length. Unless otherwise noted, all characters mapped and used in subsequent analyses showed no correlation with sex or body size.

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

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. Appendix B lists the environmental variables investigated. 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.

To associate data from an individual snake or weather station with the appropriate geographic locality, I developed a row and column coordinate system. Using the 1972 edition of the American Automobile Association (AAA) road map for Florida as a base map, I assigned each specimen and weather station a down and across value representing its locality on the base map. These coordinates were punched on the cards together with the data. Although the use of the AAA road map for a base 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 longitude varies in inter-line distance with the curvature of the earth, and the computational algorithms employed require that the grid system be uniform.
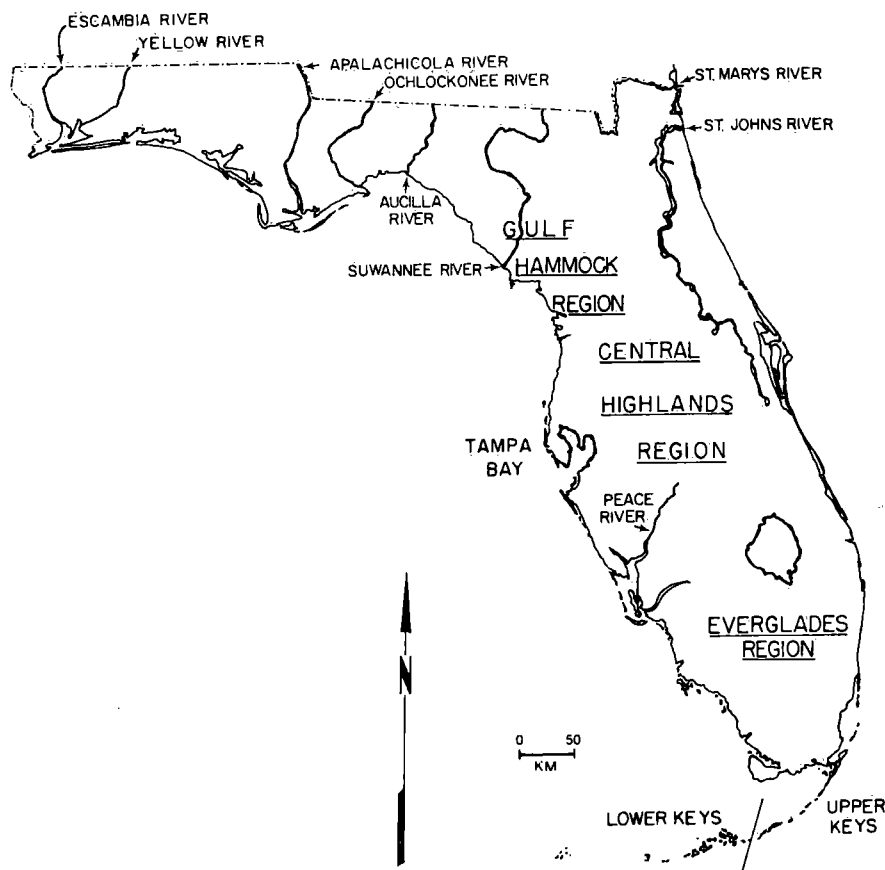
FIGURE 1.—Place names referred to in text.

THE PROBLEM OF SAMPLES AND POPULATIONS

Every previous study of geographic variation that I know of has pooled and averaged data on organisms from neighboring localities and applied the resultant average value to an arbitrary point or area representing all the individuals that live there. This seems to me an unrealistic approach to the problem. Whether the method lumps specimens by state, county, circular or square grids, or the irregular "splotch" system of Rossman (1963) and his students (Blaney 1971a, Williams 1970), it implies that the values associated with the geographic units represent values for populations. There is no reason to believe that population distributions assume regular shapes or are determined by political boundaries. Nor does there seem to be any valid reason to lump specimens with similar character states from adjacent localities— how does one define "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. For every character to be studied the character state for each specimen is plotted on a map at the exact point where the specimen was collected. If several specimens are available from the same point, they are averaged and the mean weighted accordingly; otherwise each specimen is plotted independently. The next

step involves calculating estimated data values for intermediate localities based only on the actual data values available. 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 are then constructed, and the areas of character change readily identified. Instead of the *a priori* assumptions of geographic structure that are implicit in any scheme involving the means of putative populations, this method allows the patterns of geographic variation to emerge from the consideration of individual specimens.

THE MAPPING PROCEDURE

I used the SYMAP mapping procedure, developed by the Harvard University Laboratory for Computer Graphics, to construct contour maps of character variation. This program has been used previously in studies of geographic variation by Jackson (1970) and Johnston and Sealander (1971) and is described in some detail in Peucker (1972).

Briefly the mapping procedure involves the calculation of estimated data values (EDV's) for a regular grid of points across the map surface. Each EDV is estimated by considering actual data values (ADV's) lying in its vicinity. Actual data values are weighted inversely according to the square of their distance from the EDV. Between 6 and 11 ADV's are considered in estimating each EDV. When all EDV's are calculated, there will be a value for the character at each of a regularly spaced grid of points on the map surface. Differential shading distinguishes the levels of character state variation, and contour lines are represented by the absence of shading.

This method of character mapping still suffers from the one drawback common to all cartographic procedures: 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 required to form the regular grid of estimated data values. Ideally one would like to have specimens from localities spaced evenly over the study area, which is usually impossible.

Throughout the following discussion one must remember that the mapping procedure employed does nothing more than map the data as they appear, and interpolate between data points, just as a cartographer does mentally when 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 any possible investigator bias from contour line placement.

I produced over 230 contour maps of geographic variation in Florida snakes. Some of these were linear combinations of original characters, and were not used in the multivariate analyses to follow. Others were correlated with body size, indicating a growth-related pattern, or with sex, and these were also omitted from further analyses. Publishing costs permitted printing fewer than half the contour maps produced.

COMPARISON OF MAPPED DATA

The problem of comparing mapped data is complex. If the different variables were located geographically at the same points, simple product-moment correlation analysis could be performed and any correlative tendencies readily identified. But when the maps to be compared have different data points, a preliminary step to standardize the points is required. That is, given two maps of Florida, one with X data points and the other with Y data points located at different geographic places, it is necessary to interpolate one data set so that its new data points correspond with the other's, or to interpolate both to a standard set of points. If the data are treated in this manner it should be possible to compare (for instance) climatic variables from National Weather Stations with morphological variables of snakes from wherever they were collected (usually not at weather stations).

The SYMAP mapping routine, discussed above, calculates estimated data values for a finite set of points on a map based on the points for which actual data values exist. By storing the EDV's for each map on magnetic tape, multiple sets of geographic data can be standardized to a common set of geographic points on one base map. Each of the standardized points

on the base map then will have a set of variables, one from each of the original contour maps. The standardized EDV's can then be treated as elements in a matrix for multivariate analysis.

I used the Statistical Package for the Social Sciences (SPSS) Factor Analysis procedure (Nie *et al.* 1970) to search for underlying patterns in the geographic variation represented by the entire set of snake morphology maps. If morphological characteristics of several species vary geographically in a similar manner, this suggests the presence of some underlying components or "factors" that determine how the set of contour maps are covarying. Thus factor analysis can be used to search for patterns of geographic variation that several species may share. First a matrix of product-moment correlation coefficients between the values at all points on all maps was calculated. R-type factor analysis with "varimax rotation" was employed to extract a smaller number of summarizing axes that explain the covariation in the characters (i.e. the maps). A more detailed discussion of factor analysis may be found in Harmon (1967).

I also used factor analysis to describe the covariation in environmental variables, including elevation, temperature, and precipitation in Florida. Thirteen environmental variables were contour-mapped and factor-analyzed by the same techniques used in the snake morphology analysis. The first three factors, mean annual temperature, maximum summer temperature, and average precipitation respectively, accounted for over 74% of the total variation.

At the time of this study the SPSS Factor Analysis routine was limited to 100 characters (maps, in this instance). I therefore selected 100 contour maps of snake and environmental variation for the overall factor analysis of contour maps. I was able to select 97 maps of snake variation by eliminating linear combinations, male and female redundancies, and characters that were highly correlated, such as, for example, ring width and ring position in *Diadophis punctatus*. The original contour maps of the three climatic variables (average temperature, maximum summer temperature, the average precipitation) were included in the overall factor analysis.

Factor analysis with varimax rotation of the 100 contour maps yielded two dozen factors that I call "patterns of geographic variation." By selecting those maps that contributed the most to each factor and visually comparing these to each other, I sketched in diagrammatic fashion the major patterns of geographic variation common to these 15 species of Florida snakes.

In addition to describing the important patterns of geographic variation, I have summarized all the variation of the entire set of snake morphology maps in a single contour map. This particular summary analysis was based on 166 contour maps of 14 species *(Cemophora coccinea* was inadvertently omitted). I used the principle components analysis routine of the Statistical Analysis System (Barr *et al.* 1976) without rotation to provide a summary of the variation contained in the 166 maps. That summary is, by definition, the first component (factor) extracted. Factor scores were assigned to each of 688 regularly-spaced points on the map surface (approximately 16 km between points) and these mapped with the SYMAP routine. The result was a single contour map summarizing the geographic variation observed in 166 characters of 14 species of snakes in Florida.

RESULTS

Note that the mapping procedure employed does nothing more than assign a character state value to the appropriate locality and 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. When interpreting the maps in this section, it is important to bear this in mind, and to refer to the specimen locality maps provided for each species.

Some of the contour maps showed no discernible geographic pattern. That is, the various levels of shading seemed to be interspersed at random, creating a surface that I could not describe as anything but random. I have omitted any discussion of these characters in the section to follow.

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.

THE SPECIES

Storeria dekayi (Holbrook), Brown Snake

I examined 151 S. dekayi from Florida and southern Georgia (Fig. 2) for possible geographic variation in 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 supralabials combining both sides, and 87.4% had 14 infralabials. The number of postocular scales was usually 4 (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 was only slightly correlated with sex, with the males usually having lower counts (r = 0.3559). In general the number increases southward on the peninsula and drops again on the Lower Keys. Snakes from the Everglades region have highest ventral counts, and those on the Lower Keys and in the Panhandle the lowest. A reasonable degree of concordant variation exists between the sexes.
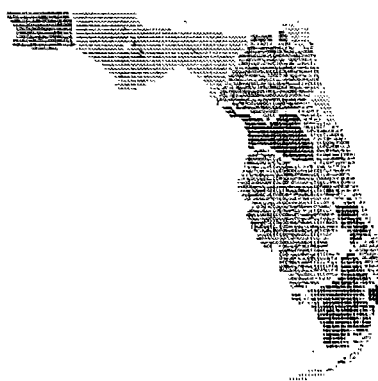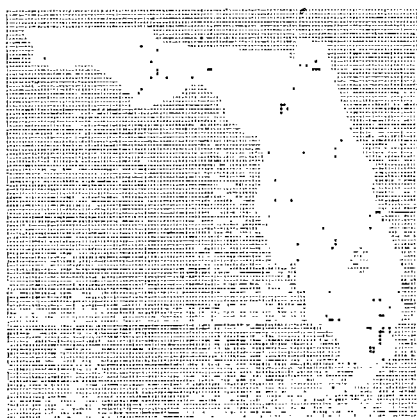

FIGURE 2.—Localities of 151 Storeria dekayi specimens examined.

FIGURE 3.—Storeria dekayi, both sexes. Sum of ventrals plus caudals. Levels by increasing shading: 169-186, 187-200, 201-215, 215-227. n = 138.

NUMBER OF SUBCAUDALS.—Males tend to have more subcaudals than females (r = 0.5167). Variation is similar to that described above for ventrals. Brown 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. Snakes from the Apalachicola Valley may be more similar to snakes from Central Florida in this character. Again concordance in the variation between 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), so the sexes are lumped to increase sample size in Figure 3. 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. (The area west of the Yellow River is represented by only a single specimen, an inadequate sample.)

PERCENT TAIL.—Males tend to have proportionately longer tails than females (r = 0.7214). Brown snakes from the southern mainland have the longest tails relative 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 (Fig. 4). Brown snakes from the Panhandle east to the vicinity of the Suwannee River have 17 scale rows around the body, whereas those from the remainder of the state have 15.

PREOCULAR SCALES.—Generally S. dekayi has a single preocular scale on each side of the head, but many individuals from the Lower Keys and

FIGURE 4.—Storeria dekayi, both sexes. Number of dorsal scale rows at mid-body. Lighter shading = 15 scale rows, darker shading, 17. n = 151.

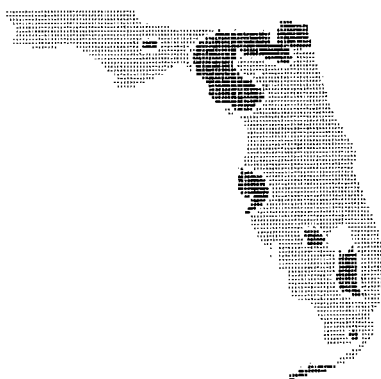FIGURE 5.—Storeria dekayi, both sexes. Number of preoculars (both sides). Lighter shading = 2, darker shading, 3 or 4. n = 149.

a high proportion of specimens from near Jacksonville and Gainesville have two preoculars on each side (Fig. 5).

VENTRAL DARK PIGMENTATION.—Generally speaking, brown snakes from the southwest coast of the peninsula have the darkest bellies and those from the Lower Keys the lightest.

TEMPORAL PIGMENT SHAPE.—Dark pigment on the temporal scale in *S. dekayi* is usually 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 peninsula specimens. 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 (Fig. 6).

SUBOCULAR PIGMENTATION.—The number of supralabial scales contained within the subocular dark blotch in Florida *S. dekayi* varies geographically as shown in Figure 7. 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 subocular spots, or none at all. Subocular spots on specimens from the Lower Keys are diffuse and faint, but cover three to five supralabials.

FIGURE 6.—*Storeria dekayi*, both sexes. Orientation of the dark temporal spot. Lighter shading = a spot with the wider end directed posteriorly, darker shading, anteriorly. n = 99.

FIGURE 7.—*Storeria dekayi*, both sexes. Number of supralabials included in the subocular dark spot. Levels by increasing shading: 0, 1-2, 3-5. n = 148.

Thamnophis sirtalis (Linnaeus), Garter Snake

Data on 192 *T. sirtalis* from Florida (Fig. 8) were analyzed for variation in 13 characters (Appendix A). Dorsal scale rows varied little throughout the study area; most specimens had 19-19-17 rows (94.7%, 95.7%, and 96.8%, respectively); 91.0% of those examined had 14 supralabials and 92.4% had 20 infralabials. None of the characters ex-
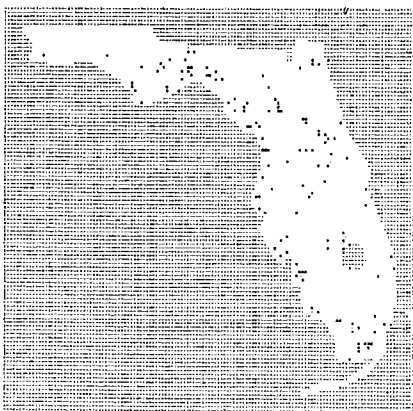
FIGURE 8.—Localities of 192 *Thamnophis sirtalis* specimens examined.

amined was size- or sex-correlated. The following characters appear to show trends of geographic variation within Florida.

NUMBER OF VENTRALS.—Although differentiation within Florida for this character is minimal, some trends are apparent. Generally, snakes from Lake Okeechobee southward have the highest ventral counts and those from the Panhandle tend to have low counts, but no well-developed cline is discernible within the state.

NUMBER OF SUBCAUDALS.—Trends in the geography of subcaudal count variation are not clear. Figures 9 and 10 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 from inadequate sample sizes (51 males, 62 females). Alternatively, the number of subcaudal scales

FIGURE 9.—*Thamnophis sirtalis*, males only. Number of subcaudal scales. Lighter shading = 58-73, darker shading, 74-98. n = 51.

FIGURE 10.—*Thamnophis sirtalis*, females only. Number of subcaudal scales. Lighter shading = 58-71, darker shading, 72-86. n = 62.

in Florida *T. sirtalis* may not correlate with anything that varies geographically.
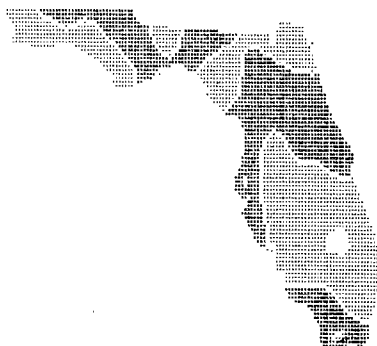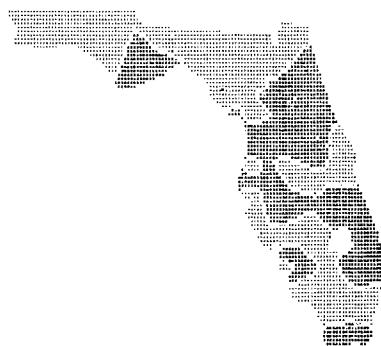
NUMBER OF VENTRALS PLUS CAUDALS.—Garter snakes tend to have the highest counts in the northern peninsula and extreme southern peninsula, with lower counts found in the intervening region and in the Panhandle.

PERCENT TAIL.—Tail length divided by total length varies as shown in Figures 11 and 12. In general, specimens from the 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.
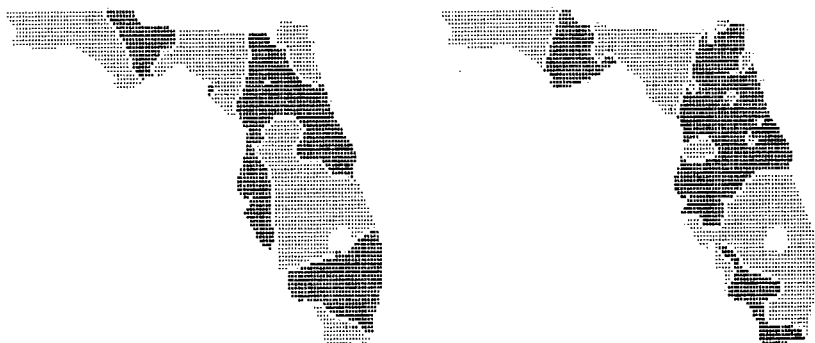
FIGURE 11.—*Thamnophis sirtalis*, males only. Tail length divided by total length. Lighter shading = 0.22-0.24, darker shading 0.25-0.33. n = 53.

FIGURE 12.—*Thamnophis sirtalis*, females only. Tail length divided by total length. Lighter shading = 0.16-0.22, dark shading, 0.23-0.33. n = 65.

DORSAL SPOTTING.—That some individual garter snakes 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). Figure 13 shows the geographic variation in this character in Florida. Snakes from the western Panhandle usually have a well-developed pattern of dorsal checks, sometimes to the complete exclusion of longitudinal stripes, and the west coast of the peninsula and parts of the Central Highlands support populations 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 in *Thamnophis* taxonomy. The geographic variation in this character is remarkably similar to that seen in the previous character, dorsal spotting. Figure 14 shows the geographic pattern as found in the present study. Again, the Panhandle, the southwest coast of the peninsula, and the southern Everglades stand out as areas

FIGURE 13.—*Thamnophis sirtalis*, both sexes. Development of dorsal checks. Increasing shading = increasing development of the dorsal checking pattern. n = 192.

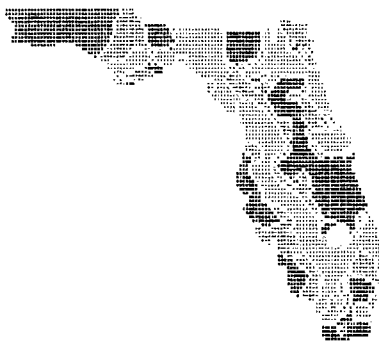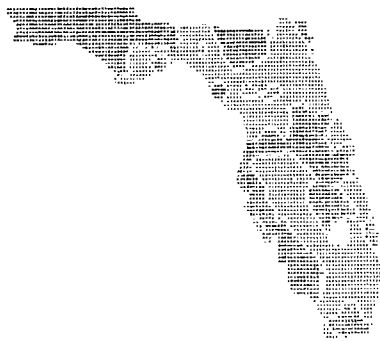FIGURE 14.—*Thamnophis sirtalis*, both sexes. Development of the parietal light spot. Lighter shading = poorly developed or absent spot, darker shading, a well-developed spot. n = 187.

with higher states for this character. Concordance between the sexes is good.

Thamnophis sauritus (Linnaeus), Ribbon Snake

I analyzed data on 279 *T. sauritus* from Florida and southern Georgia (Fig. 15) for variation in 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 10 on each side. None of the characters investigated was correlated with snout-vent length. Those characters that showed trends of geographic variation follow.

NUMBER OF VENTRALS.—Males and females do not differ significantly in ventral counts (r = 0.2910). The maps show a fairly well-defined increase in ventral counts for both sexes southward on the Florida peninsula. High counts tend to extend farther northward along the coasts, and specimens from the Gulf Hammock region on the west coast have ventral counts comparable to those from the most southerly localities. Data from Paulson (1968) and from the present study indicate that *T. sauritus* from the Lower Keys have ventral counts like those 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). Ribbon snakes from the Panhandle west of the Choctawhatchee River tend to have more subcaudals than specimens from the rest of the Panhandle and northern peninsula. Peninsula snakes usually have higher counts than those from the Panhandle, and there seems to be a weakly differentiated cline of increasing counts southward

on the peninsula. Specimens from the Lower 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 correlated with sex (r = 0.5201); males had more total ventral and subcaudal scales than females. Figures 16 and 17 show this character varies clinally, with values increasing southward. Higher values extend farther north along the coasts of the peninsula. The highest values are in Lower Key specimens. 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.
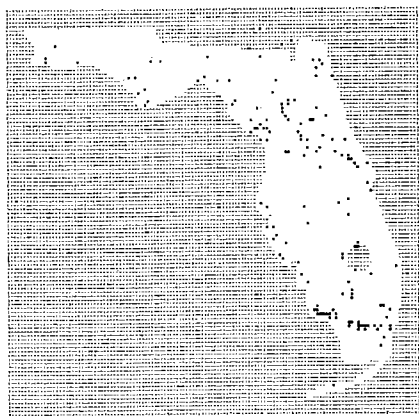
FIGURE 15.—Localities of 279 *Thamnophis sauritus* specimens examined.

FIGURE 16.—*Thamnophis sauritus*, males only (Keys specimens excluded). Number of ventrals plus caudals. Levels by increasing shading: 268-281, 282-290, 291-300. n = 58.

FIGURE 17.—*Thamnophis sauritus*, females only (Keys specimens excluded). Number of ventrals plus caudals. Levels by increasing shading: 256-271, 272-279, 280-293. n = 91.

FIGURE 18.—*Thamnophis sauritus*, both sexes (Keys specimens excluded). Number of supralabial scales. Lighter shading = 14 darker shading, 16. n = 271.

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. 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, whereas those from the peninsula have eight. Although not mapped, the ribbon snakes from the Lower Keys occasionally have seven supralabials. Figure 18 shows the geographic variation in supralabial number for both sexes.

DORSAL STRIPE EDGE.—Figures 19 and 20 show geographic variation in the width and development of the black border of the dorsal stripe. Although the pattern is complex, congruence between the sexes is good. Snakes from the Panhandle west of the Apalachicola River and from parts of the central peninsula tend to have well-developed dorsal stripe edges. Those from the Lower Keys have extremely well-developed black dorsal stripe borders. Many specimens from the northern half of the peninsula lack a stripe border altogether, and some lack even the mid-dorsal yellow stripe (Rossman 1963).

PARIETAL SPOTS.—Although Rossman (1963) stated that the nature of the paired parietal light spots of *T. sauritus* does not vary geographically, my analysis of his data indicates that it does (Fig. 21).

Most Florida *T. sauritus* lack a distinct parietal spot, but specimens from the extreme northern peninsula, the region east of Tampa Bay, and the southern tip of the peninsula have distinct parietal spots. The few
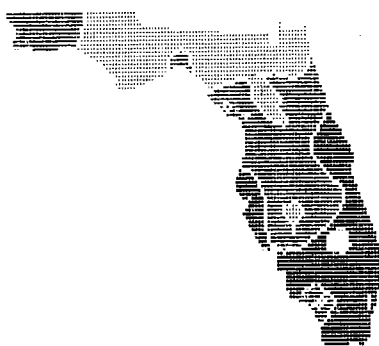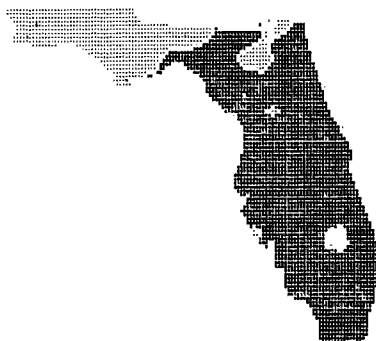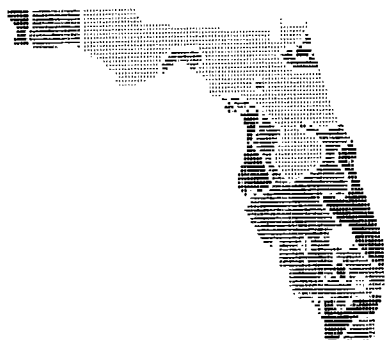

FIGURE 19.—*Thamnophis sauritus*, males only (Keys specimens excluded). Development of the black edge of the mid-dorsal stripe. Darker shading = a well-developed edge, lighter shading no black edge, or a very thin one. n = 62.
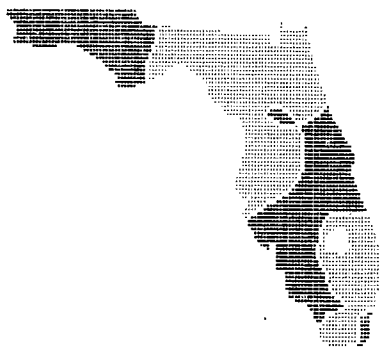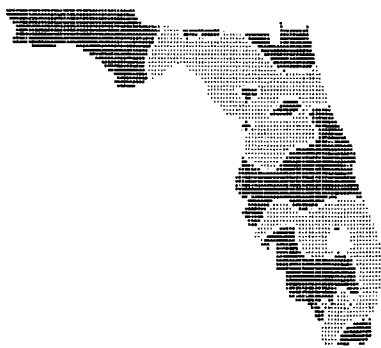
FIGURE 20.—*Thamnophis sauritus*, females only (Keys specimens excluded). Development of the black edge of the mid-dorsal stripe. Darker shading = a well-developed edge, lighter shading no such edge, or a very thin one. n = 117.
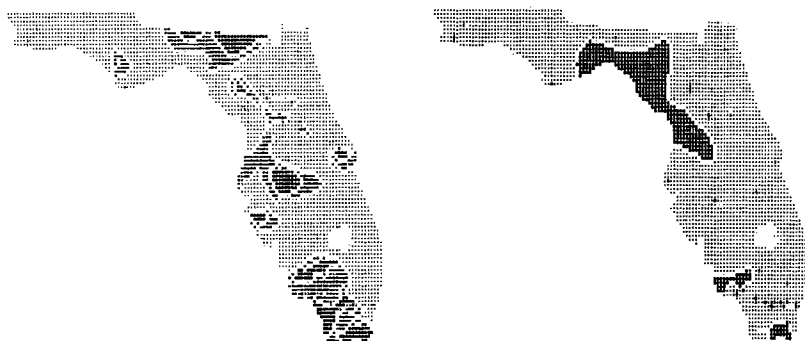
FIGURE 21.—*Thamnophis sauritus,* both sexes (Keys specimens excluded). Size of the parietal light spot. Lightest shading = no spot, darkest, a well-developed spot, and intermediate, the intermediate condition. n = 256.

FIGURE 22.—*Thamnophis sauritus,* both sexes (Keys specimens excluded). Darkness of the ground color. Lighter shading = light brown or gray ground color, and darker shading, dark brown. n = 146.

specimens available from the Lower Keys have weakly developed parietal spots.

GROUND COLOR.—The ground color of most Florida ribbon snakes is tan or light brown, but in specimens from the Gulf Hammock region it is usually a very dark brown or black. Some Everglades and southern mainland specimens also have a darker ground color, but specimens from the Lower Keys are light brown or tan (Fig. 22).

Coluber constrictor Linnaeus, Racer

I examined 440 *C. constrictor* from Florida (Fig. 23) for variation in 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 in snout-vent length). With ontogenetic change in color and pattern thus removed from consideration, none of the characters investigated correlated with snout-vent length. Those variables that showed trends of geographic variation within the study area are discussed below.

NUMBER OF VENTRALS.—Males and females show no significant difference in ventral counts (r = 0.2253), and the sexes were lumped to produce Figure 24. The degree of concordance between variation patterns in the two sexes is very good, and the number of ventrals increases in a well-developed cline as one proceeds southward down the peninsula. Specimens from the Lower Keys do not follow this trend; they have 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.
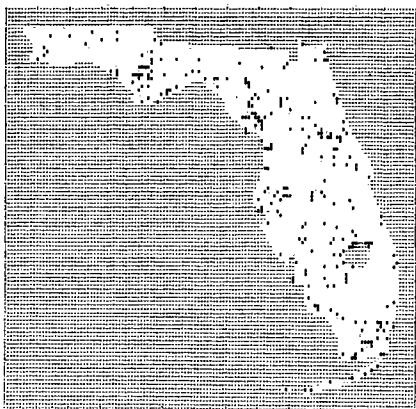
FIGURE 23.—Localities of 440 *Coluber constrictor* specimens examined.
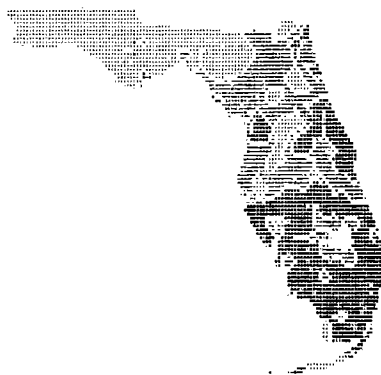
FIGURE 24.—*Coluber constrictor*, both sexes. Number of ventral scales. Levels by increasing shading: 164-176, 177-180, 181-191. n = 440.

NUMBER OF SUBCAUDALS.—Males tend to have more subcaudal scales than females (r = 0.3898), although the correlation is not strong. Panhandle specimens usually have lower counts than those from the peninsula, where a weakly defined clinal increase in subcaudal numbers for each sex is observed.

NUMBER OF VENTRALS PLUS CAUDALS.—Figure 25 shows the cline on the peninsula of increasing ventral plus subcaudal counts southward, except for a dip on the Lower Keys. The sexes are lumped in this map, for the counts are independent of sex (r = 0.1618).

SUPRALABIAL-LOREAL CONTACT.—Auffenberg (1955) first noted the variability of this character. In some specimens, especially in the southeastern United States, the first supralabial is in contact with the loreal. Although Auffenberg did not believe this character varied with any degree of geographic regularity, my analysis shows that it does. Figure 26 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.

VENTRAL WHITE.—Variation in the amount of white on the ventral surface is shown in Figure 27. Racers under 70 cm were excluded from this analysis. 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 ventrums seem to be associated with the coastal and treeless parts of the state. Upper Keys snakes are intermediate between Lower Keys and south Florida mainland specimens. The correspondence between the sexes is excellent.
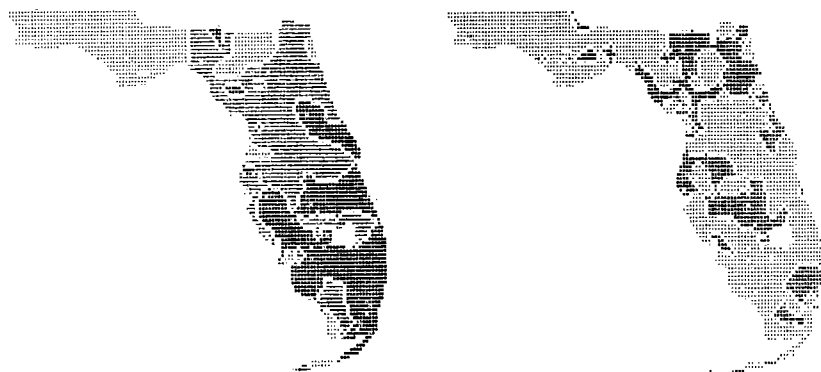
FIGURE 25.—*Coluber constrictor*, both sexes. Number of ventrals plus caudals. Levels by increasing shading: 258-280, 281-288, 289-307. n = 193.

FIGURE 26.—*Coluber constrictor*, both sexes. Contact between the first supralabial and the loreal. Lighter shading = no such contact, darker shading, contact on one or both sides of the head. n = 437.

GULAR BROWN PIGMENTATION.—The variation in the presence or absence of brown pigment on the gular scales is essentially as Auffenberg (1955) described it for the race *C. c. helvigularis*. Most racers from the Lower Apalachicola River Valley have brown pigment on the gulars. Snakes from the rest of the state seldom have such pigment. When the sexes were mapped separately, the patterns were virtually identical.

SUPRALABIAL BROWN PIGMENTATION.—See Figure 28 for the geographic variation in this character. Racers from the Apalachicola Valley have the most brown pigment on the supralabial scales. Snakes
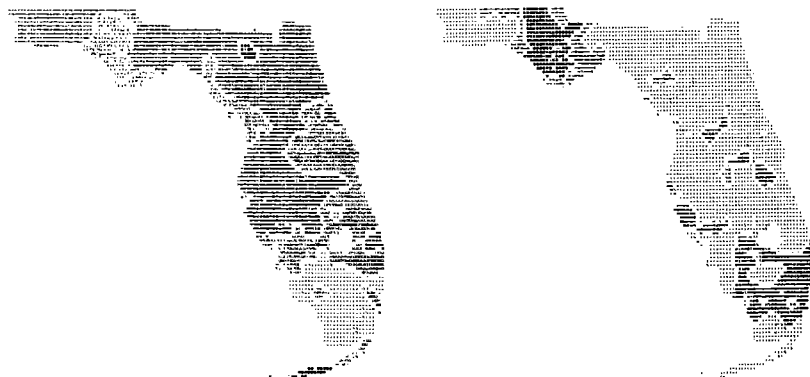
FIGURE 27.—*Coluber constrictor*, both sexes (juveniles excluded). Amount of ventral white. Increasing shading = decreasing ventral white. n = 393.

FIGURE 28.—*Coluber constrictor*, both sexes. Amount of brown pigment on the supralabials. Lightest shading = none, darkest shading, much, and intermediate shading, the intermediate condition. n = 403.
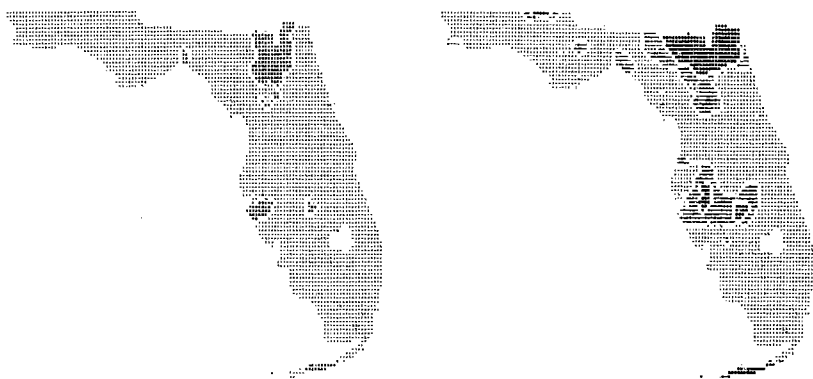
FIGURE 29.—*Coluber constrictor*, both sexes. Black pigment on the gular scales. Darker shading = snakes with black pigment on the gulars. n = 434.

FIGURE 30.—*Coluber constrictor*, both sexes. Black pigment on the supralabials. Darkest shading = essentially all black supralabials, lightest shading, no black, and intermediate shading, the intermediate condition. n = 403.

from the southern part of the Florida peninsula and the Everglades tend to have less, and those from the extreme southern tip of the peninsula and from the Lower Keys generally have none.

GULAR BLACK PIGMENTATION.—The presence or absence of black on the gular scales varies as shown in Figure 29. 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 much like the previous character (Fig. 30). Snakes from extreme northern Florida, the area east of Tampa Bay, and the Lower Florida Keys have more black on the supralabial scales than specimens from anywhere else in Florida.

Masticophis flagellum (Shaw), Coachwhip

I analyzed data on 85 *M. flagellum* from Florida, southern Alabama, and southern Georgia (Fig. 31) for variation in 9 characters (Appendix A). Over 96% of them had 16 supralabials. None of the characters was size-correlated. Those that appear to vary geographically follow.

NUMBER OF VENTRALS.—Male coachwhips usually have more ventrals than females (r = 0.4010). The highest ventral counts are generally found in snakes from the peninsula, and especially its western half. Correspondence between the sexes is weak.

NUMBER OF SUBCAUDALS.—Males and females are not significantly different in subcaudal counts (r = 0.2425). Specimens from the Panhandle and western parts of the peninsula usually have more subcaudal scales than snakes from the eastern peninsula.
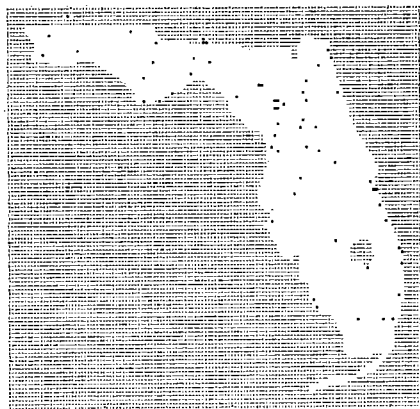
FIGURE 31.—Localities of 85 *Masticophis flagellum* specimens examined.

VENTRALS PLUS CAUDALS.—The summation of the preceding two characters is not correlated with sex (r = 0.3219). Again the Panhandle and western part of the peninsula are characterized by coachwhips with higher ventral plus subcaudal counts.

PERCENT TAIL.—Tail length divided by total length is not correlated with sex (r = 0.2422). 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, but as Figures 32 and 33 show, some individual variation occurs in this character, and snakes of the light phase are more common in two peninsular areas. This same pattern appears in both sexes, lending credence to its reality, but unfortunately the sample sizes are very small.
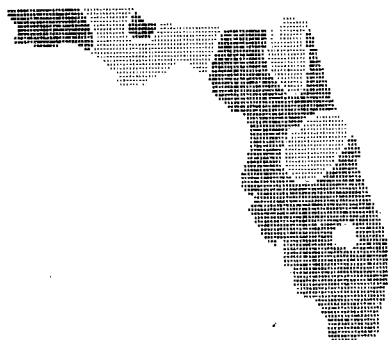
FIGURE 32.—*Masticophis flagellum*, males only. Color phase. Light shading = light phase, dark shading, the dark phase. n = 40.
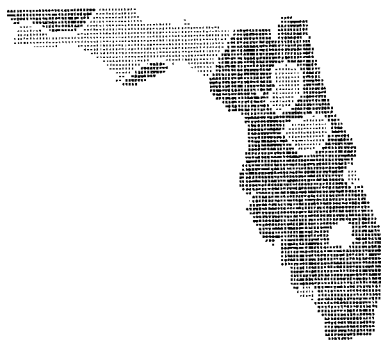
FIGURE 33.—*Masticophis flagellum*, females only. Color phase. Light shading = light phase, dark shading, the dark phase. n = 42.

Opheodrys aestivus (Linnaeus), Rough Green Snake

I examined 176 Florida *O. aestivus* (Fig. 34) for variation in 16 characters (Appendix A). Supralabial and infralabial counts remained essentially constant; 87.4% had 14 supralabials and 75.6% had 16 infralabials. Dorsal scale rows were 17-17-15 for over 95% of the specimens. Three measurements of the frontal scale were found to correlate with snout-vent length after dividing by snout-vent length. The characters that appear to show geographic variation are discussed below.
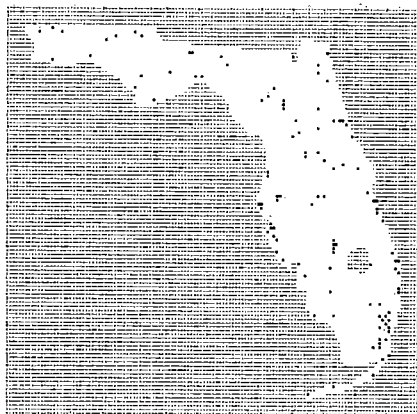
FIGURE 34.—Localities of 176 *Opheodrys aestivus* specimens examined.

NUMBER OF VENTRALS.—Females typically have more ventral scales than males (r = 0.3991). Although specimens from the southern parts of the state, and especially the southwest, usually have the highest ventral scale counts, no well-developed cline is manifest.

NUMBER OF SUBCAUDALS.—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, whereas specimens from the Everglades and southern peninsula have the fewest.

VENTRALS PLUS CAUDALS.—Although both ventrals and caudals were correlated with sex, their summation was not (r = 0.2807). Figure 35 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 ventrals plus caudals value. The variation is complex, and no simple north-south cline is discernible.

PERCENT TAIL.—Relative tail length varies with sex. Males usually have proportionately longer tails (r = 0.5211). Concordance between the sexes is poor, but generally both sexes tend to have slightly longer tails in the Panhandle and shorter tails south of Lake Okeechobee. Males show a pattern of longer tails on the Lower Keys, while the females do not.

KEELING OF THE SECOND DORSAL SCALE ROW.—Figures 36 and 37 show the 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.
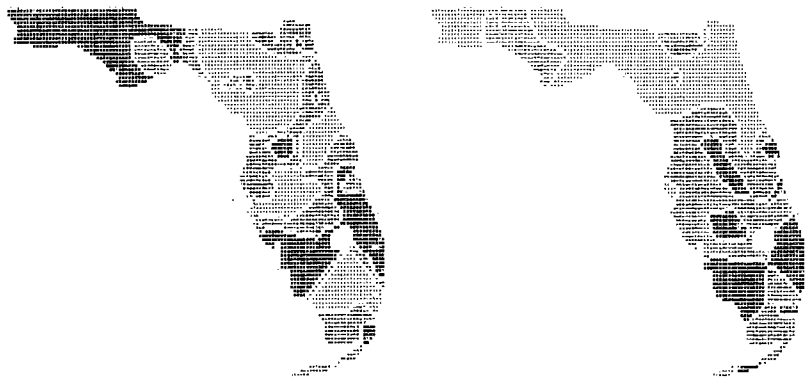
FIGURE 35.—*Opheodrys aestivus*, both sexes. Sum of ventrals plus caudals. Levels by increasing shading: 282-295, 296-303, 304-322. n = 138.

FIGURE 36.—*Opheodrys aestivus*, male only. Keel on the scales of the second dorsal row at mid-body. Lightest shading = no keel, darkest shading, a well-developed keel, and intermediate shading, the intermediate condition. n = 79.
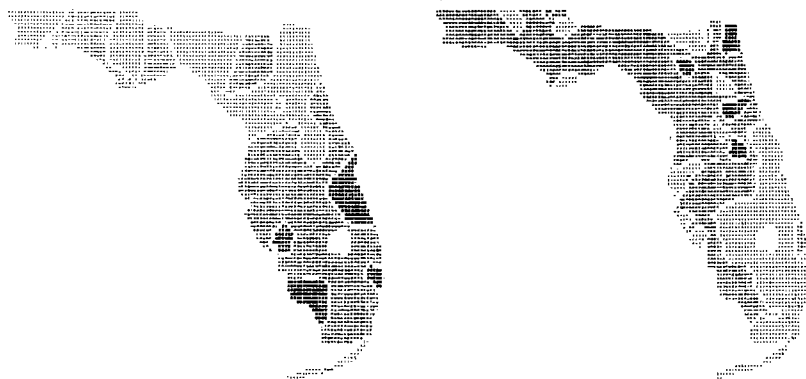
FIGURE 37.—*Opheodrys aestivus*, females only. Keel on the scales of the second dorsal row at mid-body. Lightest shading = no keel, darkest shading, a well-developed keel, and intermediate shading, the intermediate condition. n = 97.

FIGURE 38.—*Opheodrys aestivus*, both sexes. Extent of supralabial dark pigmentation. Increased shading = increased labial pigmentation. n = 175.

SUPRALABIAL PIGMENTATION.—Figure 38 shows the variation in the amount of dark pigmentation on the upper labial scales. A very strong degree of concordance between the sexes may be taken as evidence for the reality of the pattern. In general snakes with more dark pigment on the supralabials occur in the Panhandle, the northern peninsula, and southward along the west coast. Green snakes from the Keys have very light-colored upper labials.

Elaphe guttata (Linnaeus), Corn Snake

I examined 455 *E. guttata* from Florida, southern Georgia, and southern Alabama (Fig. 39) for variation in 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 still found to correlate with snout-vent length. These characters were excluded from the analysis that follows.
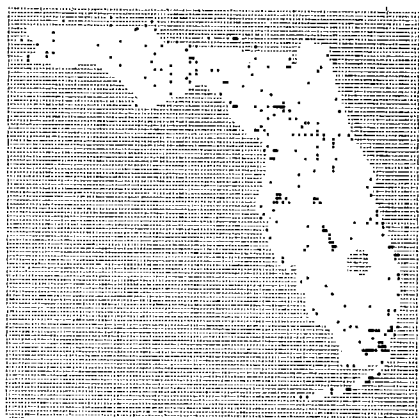

FIGURE 39.—Localities of 455 *Elaphe guttata* specimens examined.

NUMBER OF VENTRALS.—Females usually have more ventral scales than males (r = 0.5933). In both sexes ventral counts increase southward on the peninsula, with the highest values associated with snakes from the Lower Keys. Coastal areas also seem to support *E. guttata* with higher ventral counts.

NUMBER OF SUBCAUDALS.—Males tend to have more subcaudal scales than females (r = 0.5015). The number of subcaudals appears to increase southward on the peninsula, but the trend is not as clear-cut as in the preceding character.

VENTRALS PLUS CAUDALS.—As the summation of ventrals and caudals is not correlated with sex (r = 0.1118), the sexes were combined to increase sample size (Fig. 40). The highest counts occur on snakes from the Keys and adjacent mainland. Higher counts are frequently associated

with coastal areas as well; the lowest counts are on snakes from the northern peninsula and Panhandle.

NUMBER OF BODY BLOTCHES.—*E. guttata* from the Lower Keys have the highest dorsal blotch counts, specimens from the Panhandle and northern peninsula the lowest. Higher counts reach farther northward on the peninsula along both coasts. Figures 41 and 42 show the variation in number of body blotches. The rather high degree of individual variation in this character partially obscures its clinal nature.

NUMBER OF TAIL BLOTCHES.—Corn snakes from the Lower Keys and
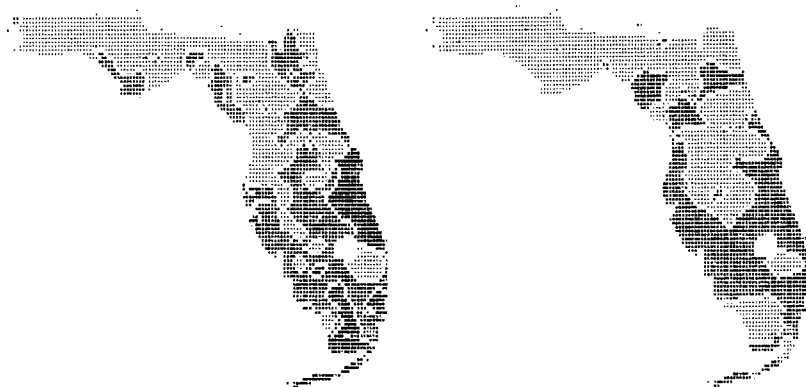
FIGURE 40.—*Elaphe guttata*, both sexes. Sum of ventrals plus caudals. Levels by increased shading: 273-292, 293-299, 300-319. n = 367.

FIGURE 41.—*Elaphe guttata*, males only. Number of body blotches. Lighter shading = 26-34, darker shading, 35-46. n = 266.
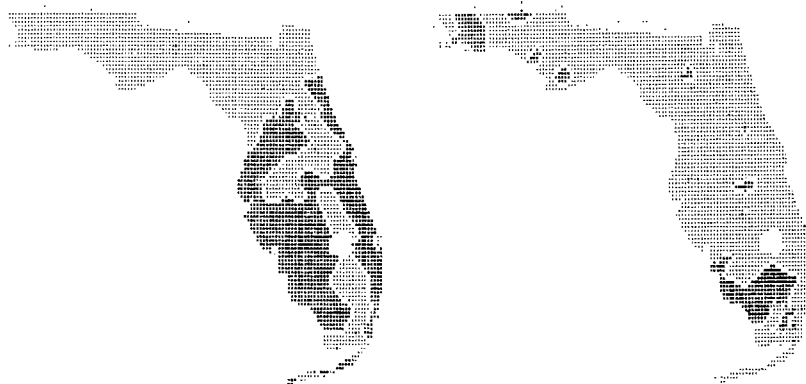
FIGURE 42.—*Elaphe guttata*, females only. Number of body blotches. Lighter shading = 26-34, darker shading, 35-50. n = 186.

FIGURE 43.—*Elaphe guttata*, both sexes. Width of the black dorsal blotch border. Lighter shading = narrow or absent, darker shading, blotch borders more than one scale in width. n = 453 specimens.

southern peninsula have the highest tail blotch counts, those from the Panhandle the lowest. The increase southward is probably clinal, although complicated by individual variation.

BLOTCH BORDER.—The red blotches on the dorsum are usually surrounded by a narrow black border, the width of which varies geographically as shown in Figure 43. Snakes from the extreme South Florida mainland and parts of the western Panhandle have much wider blotch borders.

LATERAL BLOTCH SHAPE.—Snakes from the Panhandle 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 in Panhandle specimens (Fig. 44).

VENTRAL PIGMENTATION.—Specimens from the Lower Keys have the least dark pigment ventrally. Snakes in coastal areas and offshore islands have reduced pigment, whereas most specimens from the rest of the peninsula and Panhandle tend to have much black pigment on their ventral surfaces (Fig. 45).

VENTRAL CHECK SHAPE.—The ventral dark pigmentation is generally confined to discrete rectangles. Snakes from the Lower Keys and coastal regions (especially the southwest coast) have small, often square pigment spots ventrally. Specimens from the interior, 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 spots covering entire ventral scutes.
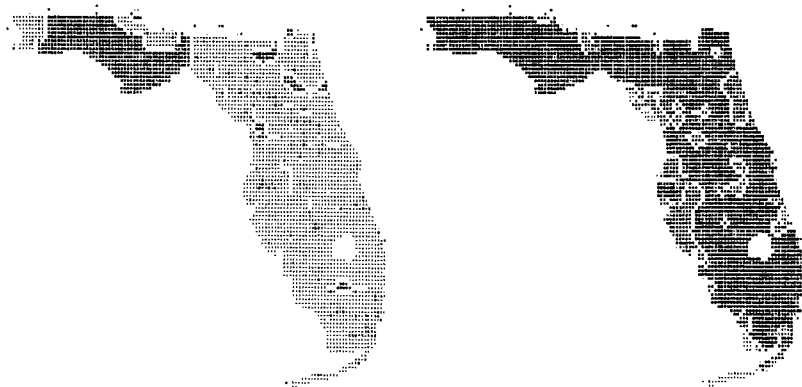
FIGURE 44.—*Elaphe guttata*, both sexes. Lateral spot shape. Lighter shading = complete lateral spots, darker shading, spots which are open on the bottom, resembling an inverted U. n = 423.

FIGURE 45.—*Elaphe guttata*, both sexes. Amount of ventral dark pigmentation. Darker shading = increased dark pigment ventrally. n = 455.

Elaphe obsoleta (Say), Rat Snake

I analyzed data on 370 Florida *E. obsoleta* (Fig. 46) for variation in six characters (Appendix A), none of which was correlated with size. The sex of the specimens was not determined, and no specimens less than 100 cm snout-vent length were examined.

NUMBER OF DORSAL BLOTCHES.—This character increases clinally southward (Fig. 47).

GROUND COLOR.—This character reflects the amount of melanin or dark pigmentation on the dorsum. Specimens from coastal areas have the lightest ground colors, those from the interior of the peninsula, the Panhandle, and the Upper Keys have darker dorsums (Fig. 48). (The species does not occur on the Lower Keys.)
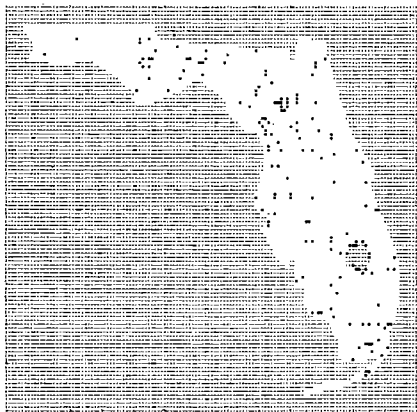
FIGURE 46.—Localities of 370 *Elaphe obsoleta* specimens examined.
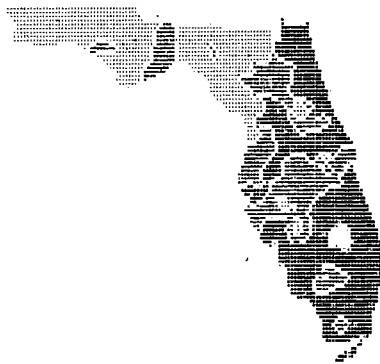
FIGURE 47.—*Elaphe obsoleta*, both sexes (excluding juveniles). Number of dorsal body blotches. Levels by increasing shading: 28-35, 36-38, 39-49. n = 222.

STRIPE DEVELOPMENT.—*E. obsoleta* from the Panhandle east to the vicinity of the Suwannee River generally lack dorsal stripes. Specimens from the northern peninsula have the most well-defined stripes; those from southern Florida usually have the stripes moderately developed (Fig. 49).

BLOTCH DEVELOPMENT.—Rat snakes from the Panhandle eastward to the Suwannee and southward along the west coast to the Withlacoochee have dorsal blotches. Specimens south of the Suwannee have dorsal stripes as well, and are recognized as the subspecies *E. o. williamsi*. Specimens from extreme southern Florida and the Upper Keys have fairly well-developed dorsal blotches and have been called *E. o. deckerti* (Fig. 50).

VENTRAL PIGMENTATION.—Figure 51 shows the variation in the amount of dark pigment in the ventral pattern of Florida rat snakes.
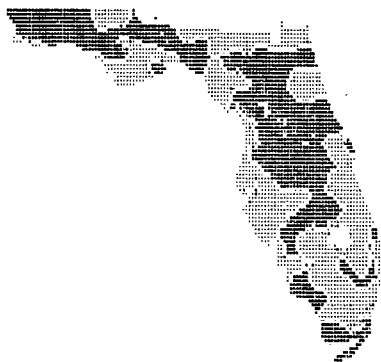
FIGURE 48.—*Elaphe obsoleta*, both sexes (excluding juveniles). Ground color. Darker shading = darker ground color. n = 370.
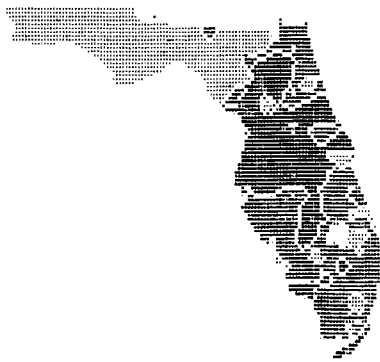
FIGURE 49.—*Elaphe obsoleta*, both sexes (excluding juveniles). Development of the dorsal stripes. Increasing shading = increasingly defined dorsal stripes. n = 322.
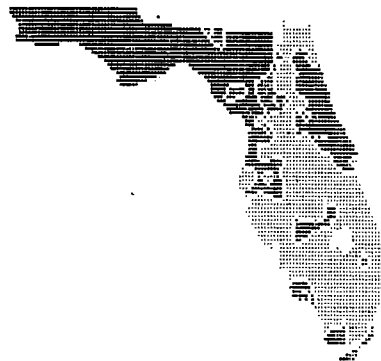
FIGURE 50.—*Elaphe obsoleta*, both sexes (excluding juveniles). Development of the dorsal blotches. Increasing shading = increasingly defined dorsal blotches. n = 323.
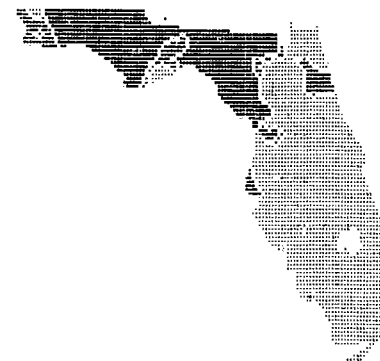
FIGURE 51.—*Elaphe obsoleta*, both sexes (excluding juveniles). Amount of dark ventral pigmentation. Darker shading = darker ventrums. n = 323.

Specimens from the Panhandle east to the Suwannee River have the darkest bellies.

SUPRALABIAL PIGMENTATION.—The variation in the amount of dark pigment on the upper labial scales varies identically to that in ventral pigmentation, except that snakes with dark supralabials occur also on the Upper Keys.

Lampropeltis getulus (Linnaeus), Kingsnake

I analyzed data on 207 *L. getulus* from Florida, southern Georgia and southern Alabama (Fig. 52) and investigated 11 characters for geographic variation (Appendix A). As head length divided by snout-vent length correlated with snout-vent length, further consideration of this character
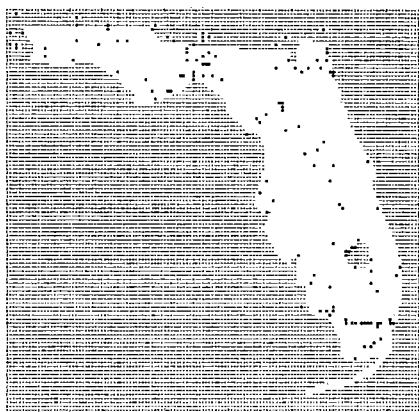
Figure 52.—Localities of 207 *Lampropeltis getulus* specimens examined.

was omitted. The characters that seem to vary geographically are discussed below.

NUMBER OF VENTRALS.—As the number of ventral scales does not correlate with sex (r = 0.1392), the sexes were 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 cline exists within the peninsula, it does not emerge from examination of the map.

NUMBER OF SUBCAUDALS.—Males usually have more subcaudals than females (r = 0.6306), but the sexes show little geographic concordance in the patterns. Subcaudal counts show a very generalized tendency to be higher in the southern peninsula.

PERCENT TAIL.—Tail length divided by total length varies as shown in
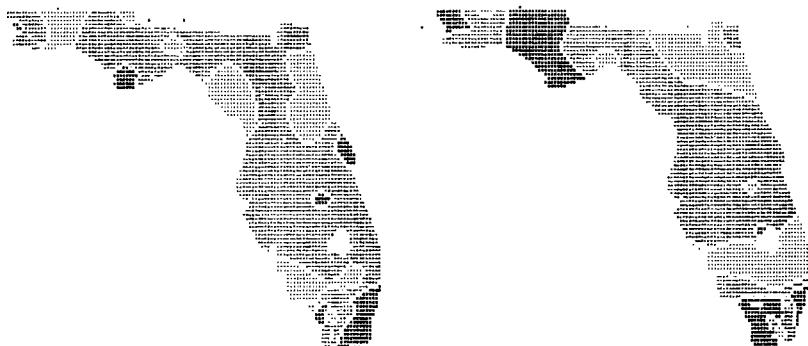
Figure 53.—*Lampropeltis getulus,* males only. Tail length divided by total length. Darker shading = proportionately longer tails. n = 63.

Figure 54.—*Lampropeltis getulus,* females only. Tail length divided by total length. Darker shading = proportionately longer tails. n = 33.

Figures 53 and 54. 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.—Kingsnakes from the Panhandle east to the
vicinity of the Aucilla River and some specimens from extreme southern
Florida have 21 midbody scale rows, whereas peninsula specimens usually
have 23 (Fig. 55).

NUMBER OF INFRALABIALS.—Most Florida kingsnakes have 18 lower
labial scales, counting both sides, but many from the extreme north have
19 or 20; those from the east coast frequently have 20.

NUMBER OF CROSS BANDS.—Figures 56 and 57 show the variation in

FIGURE 55.—*Lampropeltis getulus*, both sexes. Number of dorsal scale rows at mid-body.
Lighter shading = 21, darker shading, 23. n = 71.

FIGURE 56.—*Lampropeltis getulus*, males only. Number of body bands. Levels by increasing
shading: 15-26, 27-38, 39-50, 51-62. n = 90.
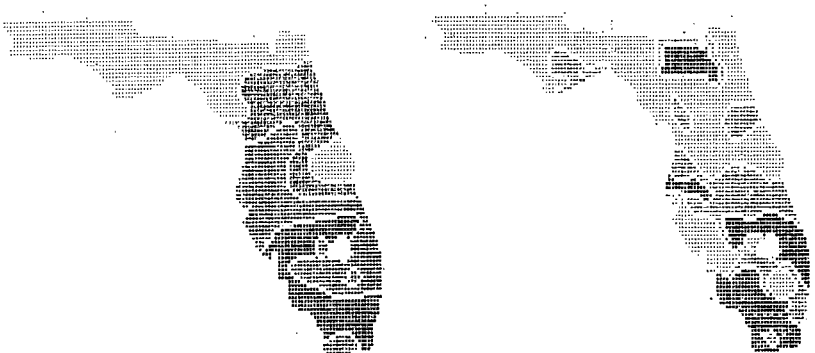
FIGURE 57.—*Lampropeltis getulus*, females only. Number of body bands. Levels by increas-
ing shading: 17-28, 29-39, 40-51, 52-63. n = 42.

FIGURE 58.—*Lampropeltis getulus*, both sexes. Amount of light pigment in the dorsal pattern.
Increased shading = increased amounts of light pigment. n = 172.

the number of dorsal precaudal cross bands in Florida *L. getulus*. The concordance between the sexes is excellent, and suggests that the sexes respond similarly to whatever environmental factor selects for cross band counts. A weak (r = 0.4038) correlation between snout-vent length and number of cross bands implies that larger snakes tend to have fewer cross bands, but no correlation is evident between snout-vent length and latitude (r = 0.1678). The number of cross bands increases in a regular cline southward on the peninsula.

DORSAL PATTERN.—The amount of light pigment in the dorsal pattern varies geographically (Fig. 58). Congruence between the sexes is good. Areas where kingsnakes tend to have more light pigment dorsally include the Everglades and southern peninsula, the Lower Apalachicola Valley, and extreme northern Florida. Frequently snakes from east of Tampa Bay are light colored as well.

Lampropeltis triangulum (Lacepede), Scarlet Kingsnake

I analyzed data on 120 *L. triangulum* from Florida, southern Georgia, and southern Alabama (Fig. 59) for variation trends in each of 15 characters (Appendix A). None of the characters investigated showed correlations with snout-vent length. Those characters that seem to vary geographically are discussed below.

FIGURE 59.—Localities of 120 *Lampropeltis triangulum* specimens examined.

NUMBER OF VENTRALS.—Males and females do not differ appreciably in number of ventral scales (r = 0.2330), but they do seem to differ in their patterns of geographic variation. Sample sizes are admittedly small, and trends uncovered by the mapping technique may be a result of sampling bias. The data available (Figs. 60 and 61) suggest that male scarlet kingsnakes have higher ventral counts in northern Florida, but females have lower counts there.

NUMBER OF SUBCAUDALS.—Males generally have more subcaudal

scales than females (r = 0.6352). Concordance between the sexes is fair. If any geographic tendency exists, 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 preceding two characters does not correlate with sex (r = 0.1106), and samples are combined for Figure 62. Snakes from the Panhandle have higher ventral plus caudal counts than specimens from most of the peninsula, but snakes from the east coast and around Lake Okeechobee also seem to have high ventral plus caudal counts.
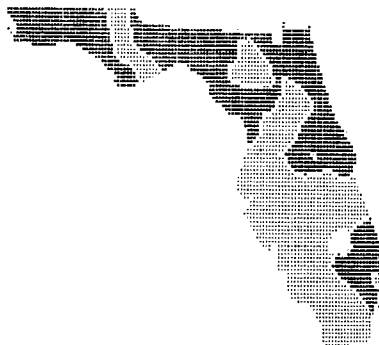
FIGURE 60.—*Lampropeltis triangulum*, males only. Number of ventral scales. Levels by increasing shading: 159-169, 170-185. n = 56.
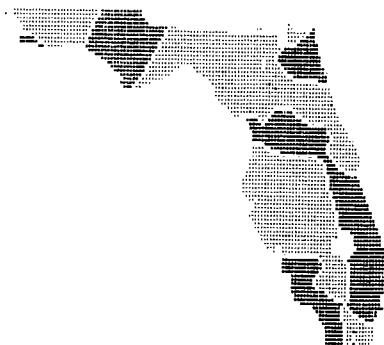
FIGURE 61.—*Lampropeltis triangulum*, females only. Number of ventral scales. Levels by increasing shading: 162-174, 175-185. n = 61.

PERCENT TAIL.—Males have proportionately longer tails (r = 0.6537). The variation is not clear-cut, but seems to show a slight tendency for relative tail length to increase clinally from north to south on the peninsula.

DORSAL SCALE ROWS.—Females usually have 19 midbody scale rows, males either 19 or 17. Figures 63 and 64 show the variation. Males from the Panhandle usually have 19 scale rows at midbody, and males from the peninsula may have either 19 or 17.

RED BODY BANDS.—High cross band counts are associated with specimens from northern Florida, including the Panhandle, the Central Highlands, and apparently the region around Miami in southern Florida.

RED TAIL BANDS.—Specimens from the Panhandle and northern peninsula generally have higher tail band counts than those from the rest of the state.

TOTAL RED BANDS.—The sum of precaudal and caudal red bands varies as shown in Figure 65. Highest counts occur in northern Florida, the area east of Tampa Bay, and the southeastern peninsula region. Scarlet kingsnakes from the southern half of the peninsula (not counting
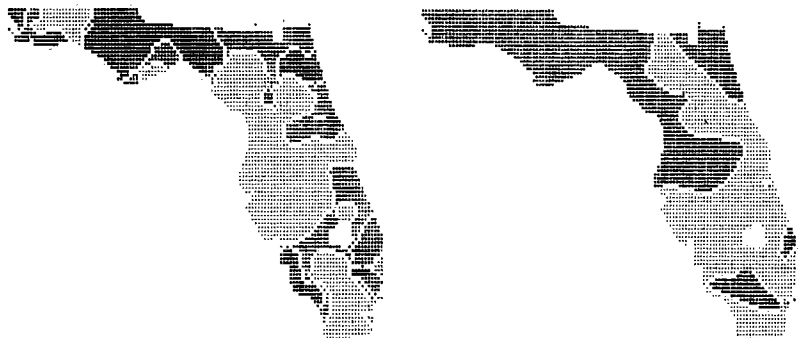
FIGURE 62.—*Lampropeltis triangulum*, both sexes. Sum of ventrals plus caudals. Levels by increasing shading: 197-211, 212-214, 215-227. n = 107.
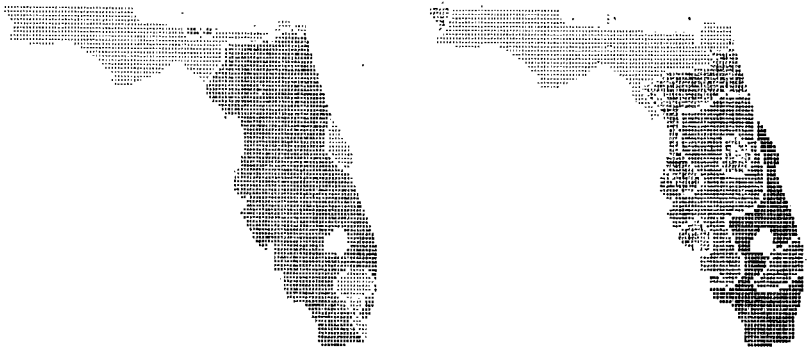
FIGURE 63.—*Lampropeltis triangulum*, males only. Number of dorsal scale rows at mid-body. Lighter shading = 17, darker shading, 19. n = 59.
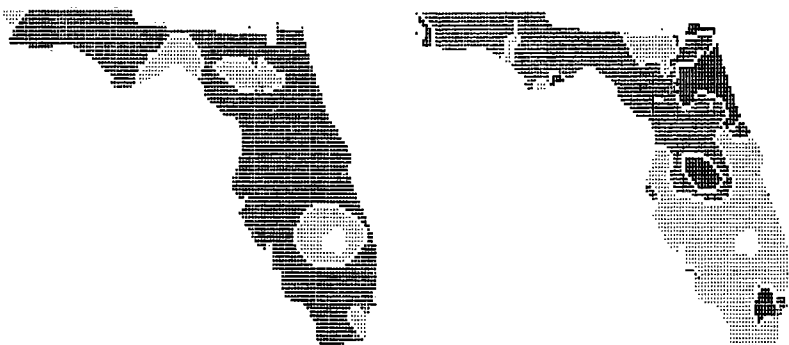
FIGURE 64.—*Lampropeltis triangulum*, females only. Number of dorsal scale rows at mid-body. Lighter shading = 17, darker shading, 19. n = 59.

FIGURE 65.—*Lampropeltis triangulum*, both sexes. Number of red bands, body and tail. Levels by increasing shading: 15-18, 19-20, 21-25. n = 80.

the Miami Rim area) have lower band counts than specimens from the Panhandle and northern half of the peninsula.

Diadophis punctatus (Linnaeus), Ringneck Snake

I examined 295 *D. punctatus* from Florida, southern Georgia, and southern Alabama (Fig. 66) for variation in 23 characters (see Appendix A). None of the characters examined was correlated with body size. Those that show apparent geographic variation are discussed below.

NUMBER OF VENTRALS.—Figures 67 and 68 show the variation in ventral numbers for male and female Florida ringneck snakes. The correlation coefficient between ventral counts and sex was 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), and the variation is more complex than that in ventral counts. Basically, ringnecks from the peninsula have lower subcaudal counts than those from the Panhandle, but many individuals from extreme southern Florida have counts like those in Panhandle specimens.

VENTRALS PLUS CAUDALS.—The summation of ventrals and subcaudals is not correlated with sex (r = 0.0624), and the samples were combined in Figure 69. Snakes from the Panhandle and northern peninsula have the highest counts. Snakes with intermediate values occupy the southern tip of the peninsula, and specimens with low counts occur on the Lower Keys and most of the central Florida peninsula.
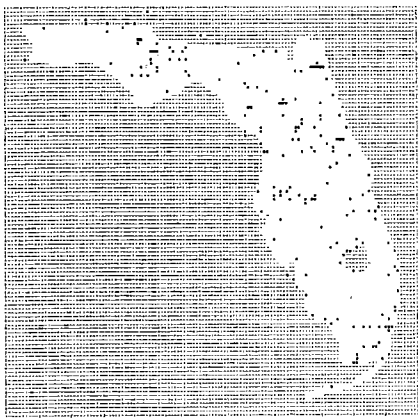
FIGURE 66.—Localities of 295 *Diadophis punctatus* specimens examined.
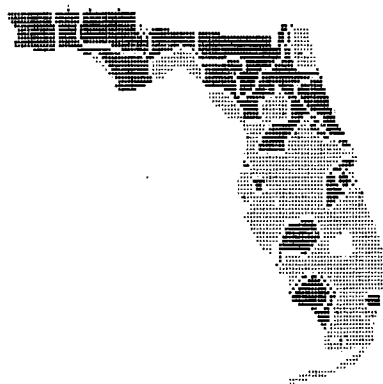
FIGURE 67.—*Diadophis punctatus*, males only. Number of ventral scales. Levels by increasing shading: 124-135, 136-138, 139-148. n = 132.
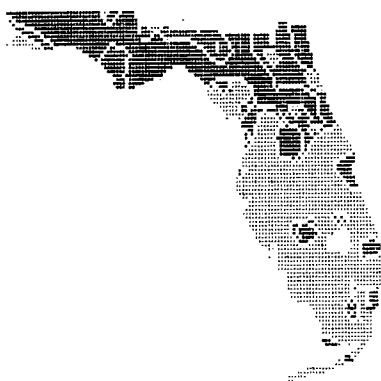
FIGURE 68.—*Diadophis punctatus*, females only. Number of ventral scales. Levels by increasing shading: 133-142, 143-144, 145-154. n = 162.
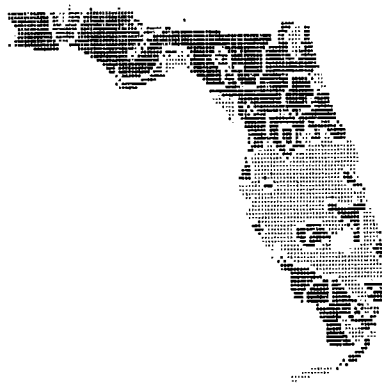
FIGURE 69.—*Diadophis punctatus*, both sexes. Sum of ventrals plus caudals. Levels by increasing shading: 171-181, 182-185, 186-198. n = 280.

PERCENT TAIL.—Relative tail length was correlated with sex (r = 0.8058), so males and females were mapped separately. Snakes from the southern half of the peninsula and the Keys have proportionately longer tails than those from the rest of the state.

NUMBER OF SUPRALABIALS.—Most southeastern ringneck snakes have 16 total supralabial scales. Occasional specimens with only 14 occur more frequently in the Panhandle and northern peninsula.

SUBCAUDAL SPOTS.—The number of small black spots on the underside of the tail varies as in Figure 70. Snakes from the Panhandle, the Gulf Hammock region, and the Lower Keys often have such spots, which are usually lacking in specimens from elsewhere.

LABIAL PIGMENTATION.—Pigment on the labials may be in discrete spots, diffuse smudges, or absent. Figure 71 shows the variation of this character for both sexes. Specimens from the Lower Keys have no such pigment or it is very diffuse, those from the southern Everglades and parts of the Gulf Hammock region usually have diffuse labial pigment. Most Florida ringneck snakes have labial pigment confined to discrete spots.
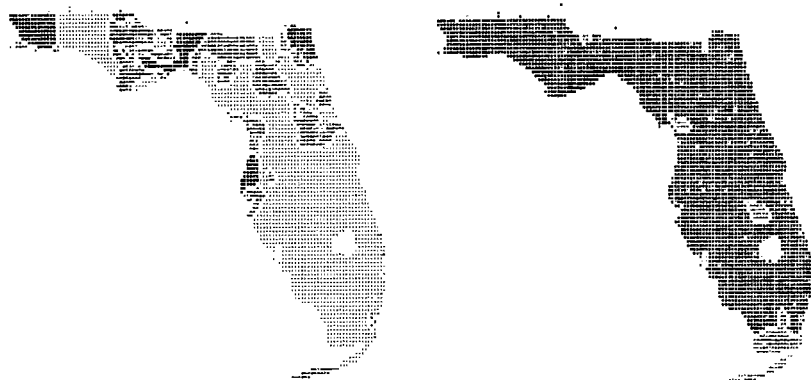
FIGURE 70.—*Diadophis punctatus*, both sexes. Number of subcaudal black spots. Lightest shading = none, intermediate shading, 1-5, and darkest shading, 6-59. n = 293.

FIGURE 71.—*Diadophis punctatus*, both sexes. Nature of the labial pigmentation. Darkest shading = labial pigment in discrete spots, lightest shading, either none or very diffuse, intermediate shading, the intermediate condition. n = 291.

PIGMENTED SUPRALABIALS.—The number of upper labial scales with black pigment varies as in Figure 72. Specimens from South Florida and the Keys as well as many from the Gulf Hammock region score high for this character, Panhandle snakes the lowest, and specimens from the rest of the state receive intermediate scores.

PIGMENTED LABIALS.—This character is the summation of labials, supra- and infra-, with black pigment. Its geography is almost identical to Figure 72. Snakes from the Gulf Hammock region and the southern tip of

the peninsula including the Keys have the most pigment, those from the Panhandle the least, and most peninsular specimens are intermediate.

RING SEPARATION.—Most ringneck snakes from Florida have a mid-dorsal break in the neck ring, but Figure 73 shows the variation in this character is complex. Lower Keys and Gulf Hammock specimens may lack a nuchal ring altogether, and many from coastal areas and the Panhandle have no middorsal ring interruption.

RING WIDTH.—The width of the nuchal ring varies as shown in Figure 74. The widest rings are in the Panhandle and northern peninsula.
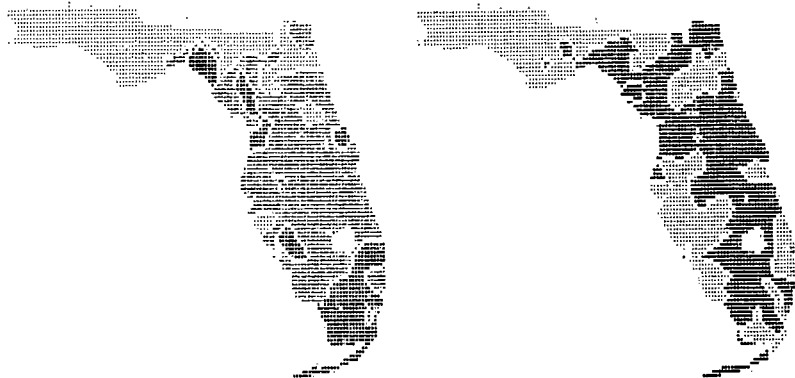
FIGURE 72.—*Diadophis punctatus*, both sexes. Number of supralabial with black spots, right side. Levels by increasing shading: 0-1, 2-4, 5-7. n = 295.

FIGURE 73.—*Diadophis punctatus*, both sexes. Width (in scale lengths) of the mid-dorsal interruption in the nuchal ring. Lightest shading = 0, intermediate shading, 1-5, and darkest shading, >5 or neck ring absent. n = 293.
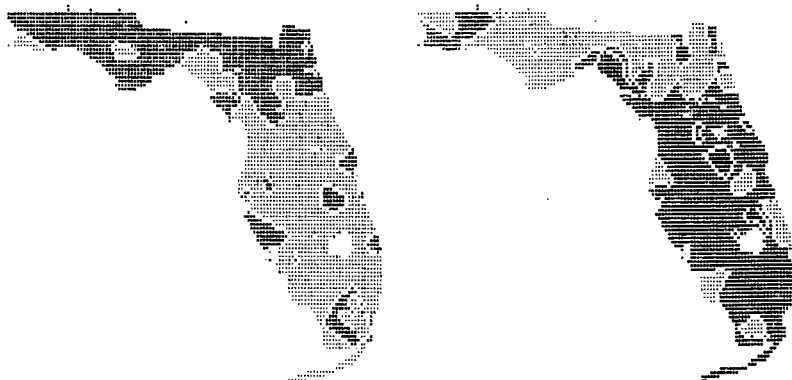
FIGURE 74.—*Diadophis punctatus*, both sexes. Width (in scale lengths) of the nuchal ring. Lighter shading = 0.5-1.5, and darker shading, 1.5-3.0. n = 291.

FIGURE 75.—*Diadophis punctatus*, both sexes. Displacement (in scale lengths) of the nuchal ring behind the parietal scales. Levels by increasing shading: 0.75-1.75, 1.75-2.5, 2.75-3.5. n = 291.

RING POSITION.—The position of the nuchal ring relative to the parietal scales varies as shown in Figure 75. In the Panhandle and northern peninsula neck rings tend to originate nearer the parietals than in southern specimens.

Cemophora coccinea (Blumenbach), Scarlet Snake

I analyzed data on 90 *C. coccinea* from Florida and southern Georgia (Fig. 76) for variation in 17 characters (Appendix A). The sample size is unfortunately small. The characters examined that show geographic variation are discussed below.

NUMBER OF VENTRALS.—As the number of ventral scales correlates with sex ($r = 0.4144$), the sexes are mapped separately (Figs. 77 and 78). Snakes from the Panhandle and the southern end of the peninsula tend to have fewer ventral scales than those from the central peninsula.
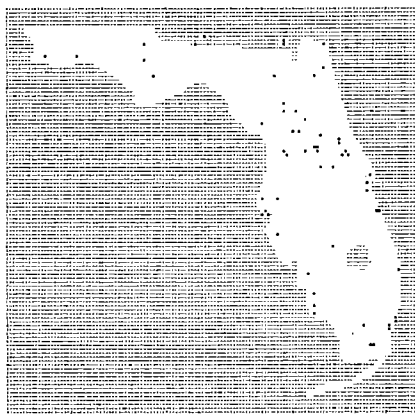
FIGURE 76.—Localities of 90 *Cemophora coccinea* specimens examined.

NUMBER OF SUBCAUDALS.—This character correlates only weakly with sex ($r = 0.3385$) with males having the higher counts. In both sexes Panhandle snakes tend to have fewer subcaudals than peninsula specimens. Specimens from the southern tip of the state also have low subcaudal counts.

VENTRALS PLUS CAUDALS.—This character summarizes the variation apparent in the two preceding counts and is not correlated with sex ($r = 0.2240$). Figure 79 shows the pattern for both sexes. Lowest counts occur in the Panhandle east to the Suwannee and in the southern peninsula south of Lake Okeechobee. Snakes from between the Suwannee and Lake Okeechobee have higher ventral scute counts.

PERCENT TAIL.—The sexes show no significant difference in relative tail lengths. Snakes from more southern sites tend to have proportionately longer tails, but the tendency is not sharply defined. In the Panhandle

females have relatively longer and males shorter tails. Thus 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 snakes may have 14, 16, or 18 lower labial scales. Specimens from the Everglades Region frequently have 14 infralabials, and many specimens from the central and northcentral peninsula have 18.

SUPRALABIALS.—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 (Fig. 80).
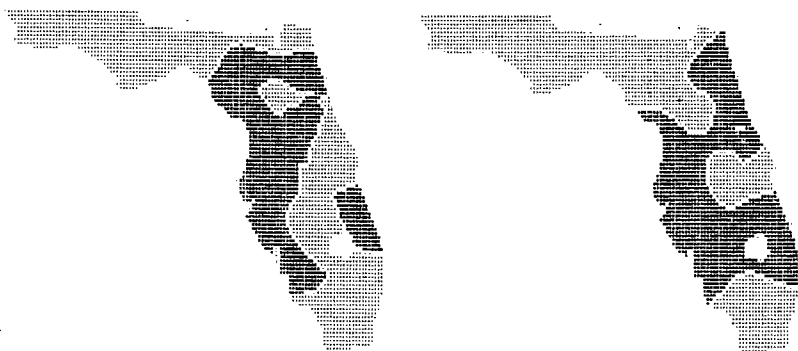
FIGURE 77.—*Cemophora coccinea*, males only. Number of ventral scales. Lighter shading = 158-170, darker shading, 171-182. n = 41.

FIGURE 78.—*Cemophora coccinea*, females only. Number of ventral scales. Lighter shading = 165-174, darker shading, 175-185. n = 37.
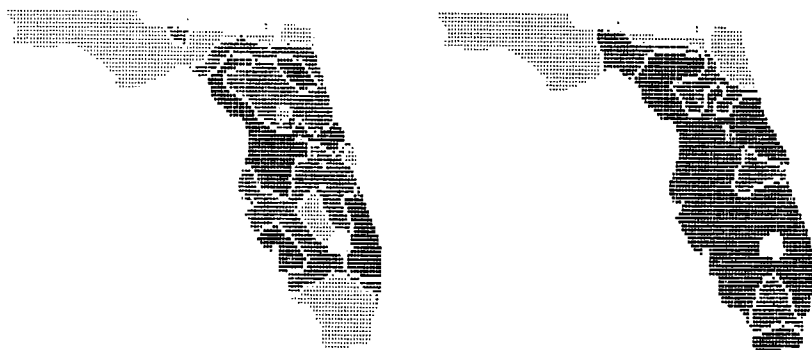
FIGURE 79.—*Cemophora coccinea*, both sexes. Sum of ventrals plus caudals. Levels by increasing shading: 197-212, 213-218, 219-228. n = 84.

FIGURE 80.—*Cemophora coccinea*, both sexes. Number of supralabial scales (both sides). Levels by increasing shading: 11-12, 13, 14-15. n = 85.

NUMBER OF RED BODY BANDS.—Snakes from northern Florida and the Osceola National Forest region, from just south of Tampa Bay, and from 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 correlates with sex ($r = 0.5179$). Although concordance between the sexes is poorly developed, a general tendency for scarlet snakes in the north to have more tail bands is apparent.

DORSAL SCALE ROWS.—Of the specimens examined 90.4% had 19 dorsal scale rows at mid body. Everglades snakes had 17 anterior scale rows, and those from extreme northern Florida usually had 21, whereas those from the rest of Florida usually had 19. All *Cemophora* examined from the Panhandle had 19 posterior scale rows, but peninsula specimens had fewer than 19.

LENGTH OF THE WHITE BANDS.—Snakes from the western Panhandle, northcentral peninsula, and the west coast of the peninsula tend to have longer white bands.

LENGTH OF RED BANDS.—Longer red bands are the rule in northern Florida, around Lake Okeechobee, and in the extreme southern Everglades.

Tantilla coronata (Baird and Girard), *Tantilla relicta* Telford, and *Tantilla oolitica* Telford, Crowned Snakes

I analyzed data on 198 *Tantilla* specimens from Florida (Fig. 81) for variation in 11 characters (Appendix A). Those characters that seem to vary geographically are discussed below.

NUMBER OF VENTRALS.—Females generally have more ventrals than
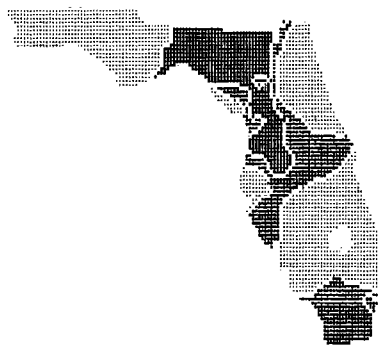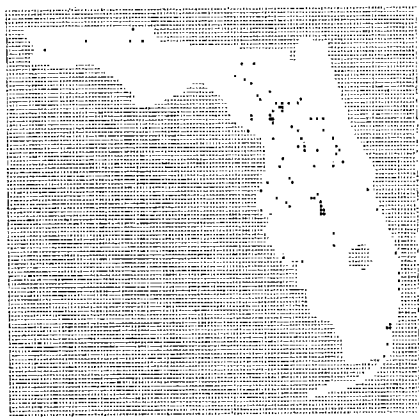
FIGURE 81.—Localities of 198 *Tantilla* sp. specimens examined.

FIGURE 82.—*Tantilla*, males only. Number of subcaudal scales. Levels by increasing shading: 45-52, 53-58, 59-67. n = 81.
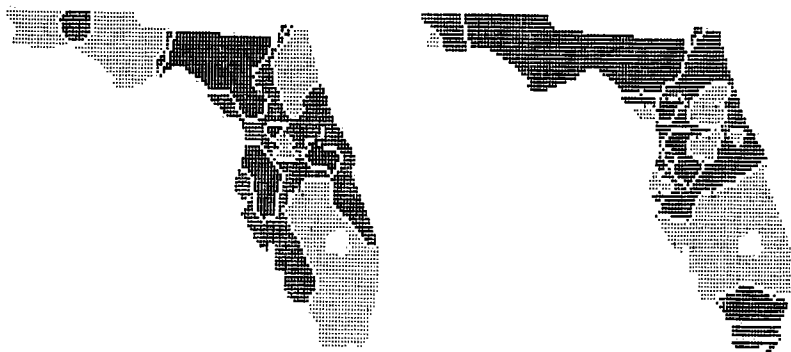
FIGURE 83.—*Tantilla*, females only. Number of subcaudal scales. Levels by increasing shading: 40-48, 49-52, 53-61. n = 68.

FIGURE 84.—*Tantilla*, both sexes. Sum of ventrals plus caudals. Levels by increasing shading: 156-180, 181-187, 188-209. n = 149.

males (r = 0.4150) and the sexes were mapped separately. In both sexes the ventral scale number decreases southward on the peninsula until southernmost Florida; Miami and Key Largo specimens 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. Figures 82 and 83 show the variation for males and females, which differ in mean subcaudal counts (r = 0.4194).

VENTRALS PLUS CAUDALS.—The sum of the preceding two counts produces a variable that does not correlate with sex (r = 0.0783). Figure 84 shows this character's pattern. Panhandle and northern peninsula snakes have the highest counts, which decrease clinally southward until in the Miami area they increase to approximate the northern counts.

PERCENT TAIL.—Males usually have proportionately longer tails than females (r = 0.6339). Both sexes vary geographically with relatively longer tails occurring in the Big Bend region and the peninsula west coast.

SUPRALABIALS.—Snakes from Highlands County often have six upper labials on each side; specimens from the rest of the state usually have seven.

PARIETAL PIGMENTATION.—Snakes from the Miami area and parts of the Big Bend region of northern Florida lack light spots on the parietal scales (Fig. 85). Specimens from the Panhandle east to the Ochlockonee River, from Highlands County, and from the lower east coast of the peninsula have extensive light parietal markings, often forming a partial nuchal ring. Snakes from the rest of the peninsula have intermediate amounts of light pigment in the parietal region.

SNOUT PIGMENTATION.—Most specimens from the lower east coast

have a large white spot on the rostral and internasal scales (Fig. 86). Highlands County snakes also have some light pigment on the snout, but most populations lack this characteristic.
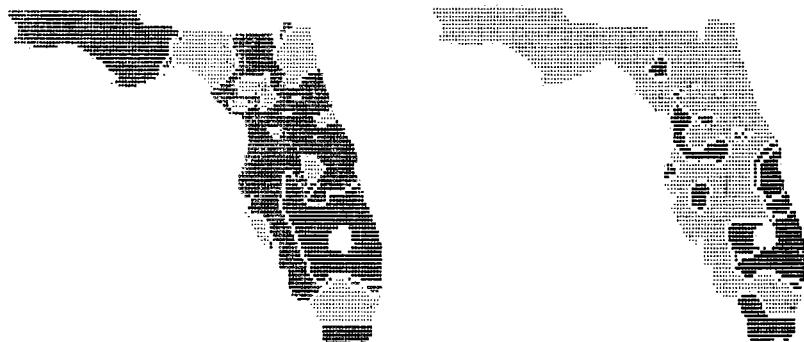
FIGURE 85.—*Tantilla*, both sexes. Light pigment on the parietal scales. Lightest shading = none, intermediate shading, some light pigment, and darkest shading, much light pigment forming a nuchal band. n = 197.

FIGURE 86.—*Tantilla*, both sexes. Size of the light spot on the snout. Lightest shading = none, darkest shading, a large spot, and intermediate shading, a small light spot. n = 197.

Sistrurus miliarius (Linnaeus), Pygmy Rattlesnake

. I examined 320 *S. miliarius* from Florida, southern Georgia, and southern Alabama (Fig. 87) for variation in 22 characters (see Appendix A). Much of the variation was irregular 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, but the mapping procedure employed here does not smooth, but plots the data exactly as they appear. Three ratios concerned with the frontal scale and snout-vent length were correlated with snout-vent
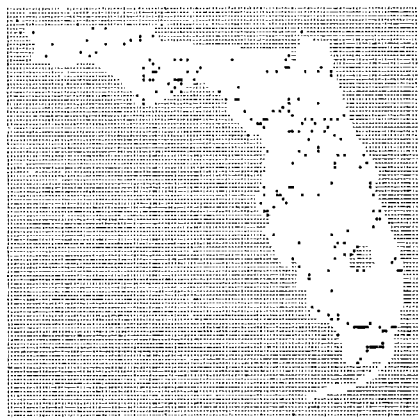
FIGURE 87.—Localities of 320 *Sistrurus miliarius* specimens examined.

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 were treated separately. The lowest ventral counts are associated with snakes from the Panhandle, the highest with those from the central peninsula.

NUMBER OF SUBCAUDALS.—Males usually have more subcaudal scales than females (r = 0.6267). The pattern is similar to that in ventral counts. Specimens from the Panhandle have the lowest counts, those from the central peninsula the highest. As with the preceding character, pygmies from the lowlands south of Lake Okeechobee tend to have lower counts than those 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). For the variation in the combined sexes see Figure 88. Snakes from the Panhandle east to the Aucilla River and in the Everglades region south of Lake Okeechobee tend to have the lowest values; those from the peninsula north of the Everglades show a clinal increase from north to south.

DORSAL SCALE ROWS.—Figures 89 and 90 show the variation in the number of dorsal scale rows at two points along the body. The lowest counts are in Panhandle specimens and the highest in specimens from both coasts. Snakes with intermediate counts occur in most of the interior peninsula. Nearly all *Sistrurus* from coastal locations in Florida have 25 scale rows at mid-body. The map doesn't show this pattern clearly because EDV's along the coast were often calculated from inland ADV's when these were nearer than coastal ADV's.

NUMBER OF DORSAL BLOTCHES.—Pygmy rattlers from the Panhandle west of the Ochlockonee and from many coastal areas on the peninsula
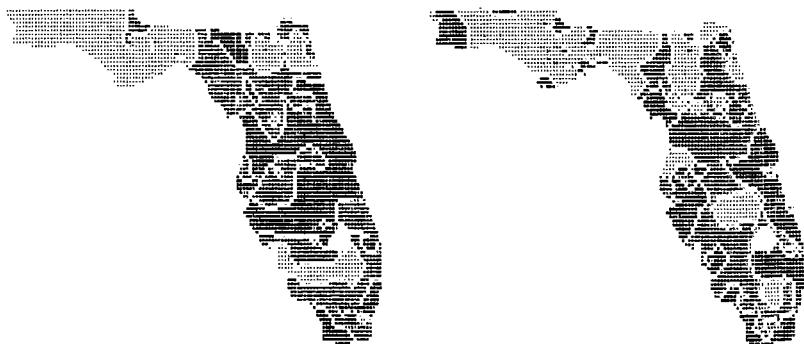
FIGURE 88.—*Sistrurus miliarius,* both sexes. Number of ventrals plus caudals. Levels by increasing shading: 156-169, 170-173, 174-186. n = 312.

FIGURE 89.—*Sistrurus miliarius,* both sexes. Number of dorsal scale rows one head length posterior to the head. Levels by increasing shading: 23, 25, and 27-29. n = 303.
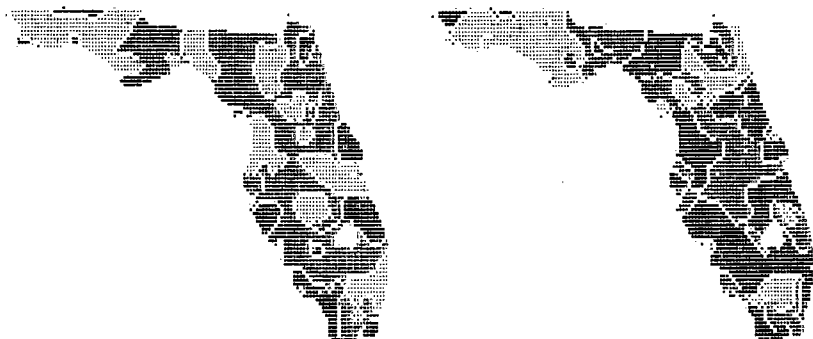
FIGURE 90.—*Sistrurus miliarius*, both sexes. Number of dorsal scale rows at mid-body. Levels by increasing shading: 21, 23, and 25. n = 316.

FIGURE 91.—*Sistrurus miliarius*, both sexes. Blotch length divided by inter-blotch space length. Levels by increasing shading: 0.33-1.00, 1.01-1.33, and 1.34-2.50. n = 318.

often have more dorsal body blotches than those from the rest of the state.

DORSAL BLOTCH/SPACE RATIO. — This character varies as shown in Figure 91. Pygmies west of the Ochlockonee River in the Panhandle and in the Everglades usually have crossband-like body blotches that are narrower than the interblotch spaces. Snakes from peninsula coastal areas tend to have larger blotches with very narrow spaces between. Many specimens from the peninsula interior have spot/space ratios intermediate between these.

DORSAL BLOTCH SHAPE.—When the length (in scales) of a typical mid-body dorsal blotch is divided by its width, the resulting ratio varies geographically as depicted in Figure 92. Panhandle and Everglades snakes have blotches more like crossbands, those from most of the peninsula more roundish blotches.

FIGURE 92.—*Sistrurus miliarius*, both sexes. Blotch shape. The darker the shading, the longer the dorsal blotches in relation to their width. n = 319.

FIGURE 93.—*Sistrurus miliarius*, both sexes. Contrast between dorsal blotches and ground color. Darker shading = greater contrast. n = 317.

DORSAL BLOTCH-GROUND COLOR CONTRAST.—Snakes 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. Coastal area snakes also tend to have higher values for this character (Fig. 93).

VENTRAL PIGMENTATION.—Pygmy rattlers from much of the Panhandle west of the Ochlockonee and from South Florida tend to be whiter ventrally than specimens from the rest of the state.

Crotalus adamanteus Beauvois, Eastern Diamondback Rattlesnake

I examined 194 *C. adamanteus* (Fig. 94) for variation in 18 characters (Appendix A). Most characters showed considerable individual variation that obscured geographic variation; consequently many of the maps appear noisy. Several characters did not vary geographically within the study area.
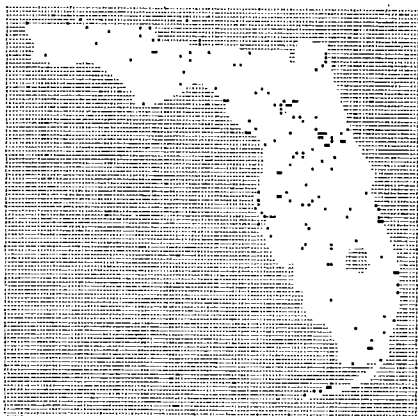
FIGURE 94.—Localities of 194 *Crotalus adamanteus* specimens examined.
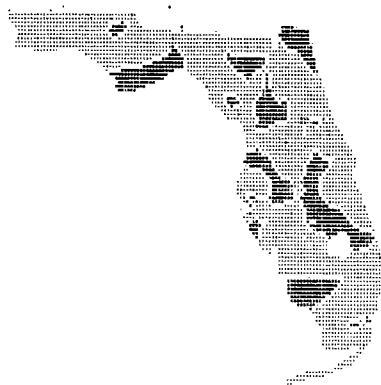
FIGURE 95.—*Crotalus adamanteus*, both sexes. Number of mid-body scale rows. Lighter shading = 25 and 27 scale rows, darker shading, 29 and 31. n = 191.

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 Florida, but no cline is manifest.

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.

DORSAL SCALE ROWS.—I can discern no geographic trend in the variation of dorsal scale row counts in Florida *C. adamanteus*. Figure 95 shows the spotty occurrence of specimens with higher scale row counts.

NUMBER OF INFRALABIALS.—The variation in this character is also complex, but some geographic trends are apparent. Snakes from northern Florida and from the Lower Keys typically have more lower labials than specimens from the central peninsula (Fig. 96).

DORSAL BLOTCHES.—The number of diamonds on Florida *C. adamanteus* varies geographically as shown in Figure 97. Specimens from the Panhandle, the Keys, and the west coast of the peninsula tend to have fewer blotches than those from the peninsula interior.

LABIAL PIGMENTATION.—The number of immaculate supralabials varies geographically as shown in Figure 98. Specimens from the western
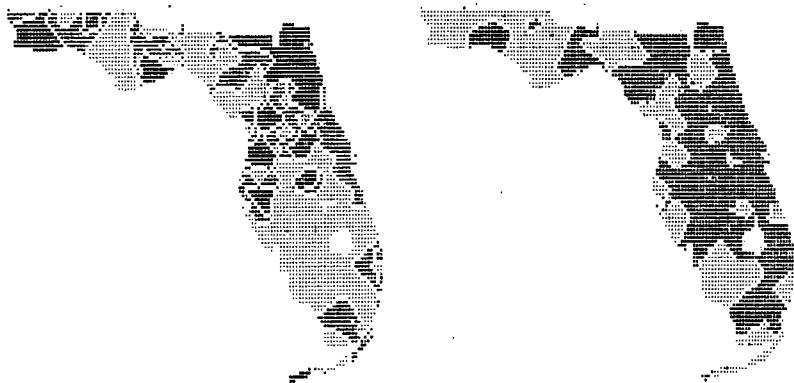
FIGURE 96.—*Crotalus adamanteus*, both sexes. Number of infralabials. Levels by increasing shading: 30-33, 34, 35-40. n = 187.

FIGURE 97.—*Crotalus adamanteus*, both sexes. Number of blotches. Lighter shading = 22-27, darker shading, 28-34. n = 190.
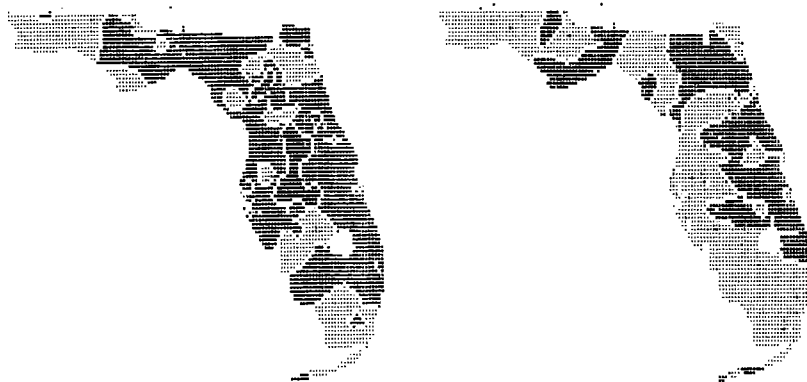
FIGURE 98.—*Crotalus adamanteus*, both sexes. Number of immaculate supralabials. Levels by increasing shading: 0-1, 2-4, 5-8. n = 192.

FIGURE 99.—*Crotalus adamanteus*, both sexes. Amount of dark pigmentation on the ventrum. Darker shading = darker venters. n = 192.

Panhandle, the Upper Keys, and the Everglades region tend to have dark pigmentation on all upper labial scales. Snakes from the Central Ridge east of Tampa Bay and from the Lower Keys frequently have the most immaculate labials.

VENTRAL PIGMENTATION.—Snakes from the Panhandle, the Everglades region, and the west coast of the peninsula tend to have lighter ventral patterns than those from the interior of the peninsula. Snakes from the Lower Keys usually have darker ventral patterns, more like specimens from north-central Florida (Fig. 99).

ENVIRONMENTAL DATA

I mapped environmental data from 196 weather stations in Florida, Georgia, and Alabama (Fig. 100). Figures 101-105 show the geographic variation of selected variables.
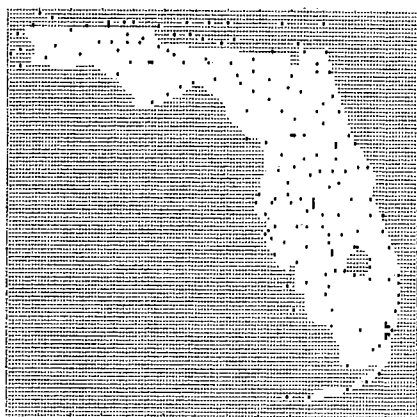
FIGURE 100.—Locations of 196 weather stations supplying data from Florida, Georgia and Alabama.
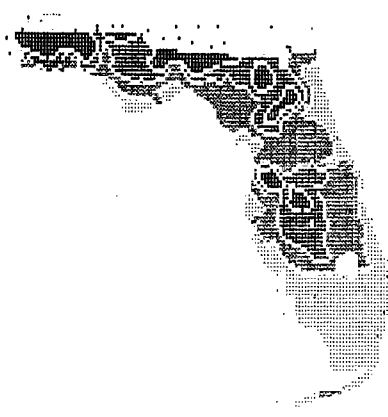
FIGURE 101.—Elevation (in meters) above mean sea level. Levels by increasing shading: 1-8, 9-26, 27-45, 46-142. n = 195.

THE PATTERNS

When an entire set of 166 contour maps of snake morphological variation was subjected to principal components analysis, the first component accounted for 17.0% of the total variation. If the original contour maps had nothing in common, we would expect each component to explain only 1/166 or 0.6% of the total variation. Thus the first component actually accounts for a very large portion of the information in the original 166 contour maps. Component 1 may be thought of as the best possible summary of the geographic variation exhibited by these 14 snake species (*C. coccinea* was omitted) in Florida. Figure 106 is a SYMAP-produced contour map of component 1. Table 2 lists the 166 characters examined,
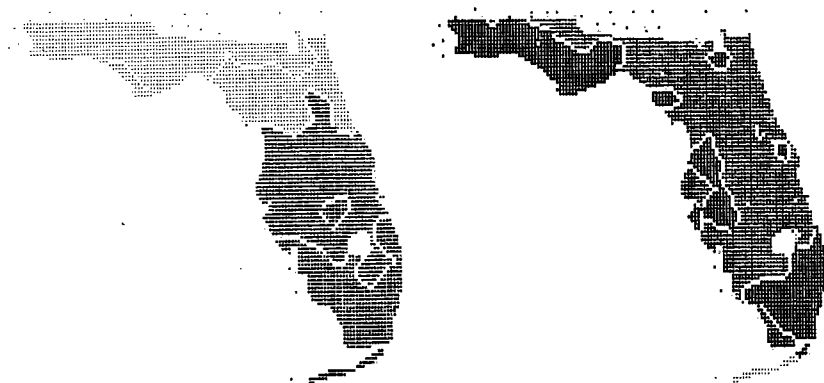
FIGURE 102.—Mean annual temperature (in °C). Levels by increasing shading: 18.9-20.1, 20.2-21.5, 21.6-22.9, 23.0-24.5, 24.6-25.7. n = 130.

FIGURE 103.—Mean annual total precipitation (in cm). Levels by increasing shading: 93-119, 120-140, 141-179. n = 196.
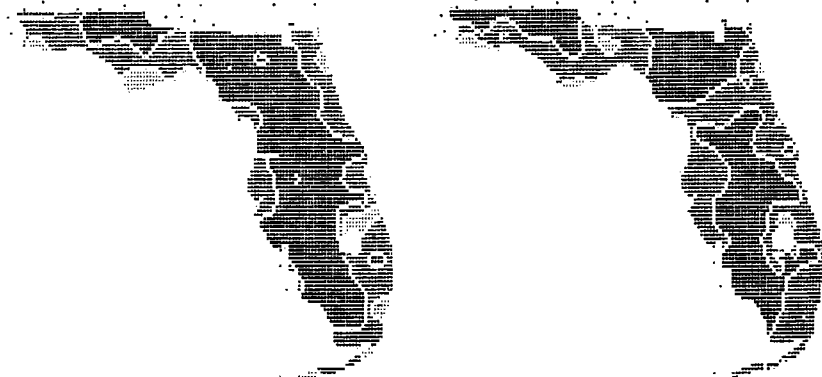
FIGURE 104.—Mean annual number of days temperature ≥ 32.2°C. Levels by increasing shading: 18-56, 57-95, 96-135. n = 130.

FIGURE 105.—Mean daily maximum August temperature (in °C). Levels by increasing shading: 29.0-30.9, 31.0-32.5, 32.6-34.2. n = 130.

their loadings on the first component, and their communalities. The component loading shows the percentage of variation explained by the first component for each character. The communality represents the proportion of variation in the character accounted for by the entire principal components solution, which actually extracted 38 components.

Figure 106 dipicts what the naturalist actually sees in the geographic variation of these fourteen species in Florida. Principal components analysis without rotation maximizes the amount of variation included in the first component. Thus Figure 106 is an artificial picture of the totality of geographic variation in fourteen species of snakes in Florida. Its basic,

underlying component is a well-developed north-south cline running the length of the Florida peninsula.
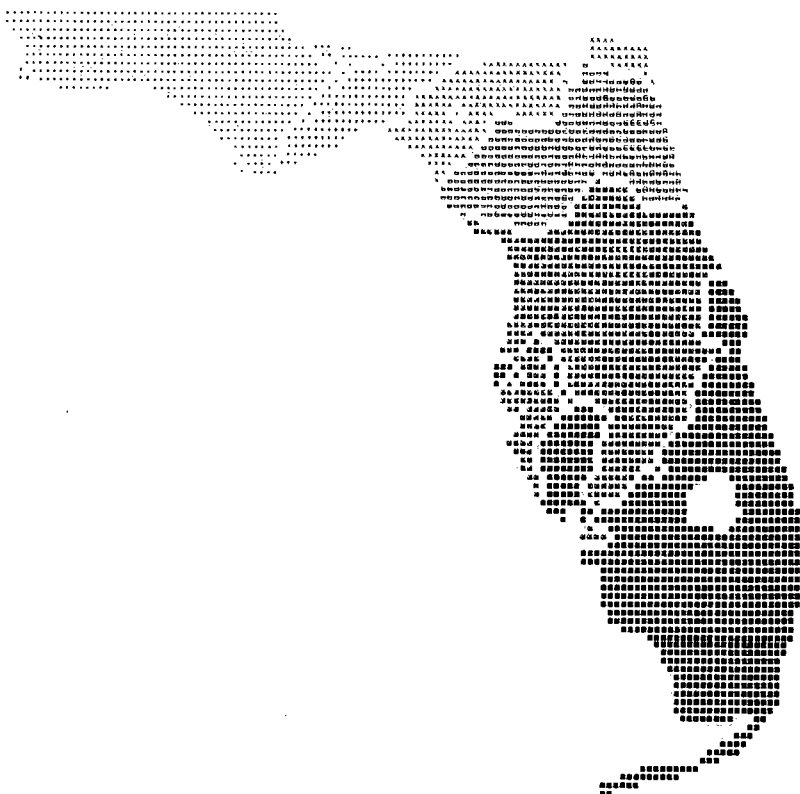
FIGURE 106.—Geographic variation in the first principal component extracted from a matrix of 166 contour maps of morphological variation in 14 species of Florida snakes. The map accounts for 17.0% of the total variation in 166 characters and summarizes the major pattern of geographic variation in these species, the North-South Cline. n = 688.

The purpose of this study, however, was to search for patterns of geographic variation that the species studied hold in common, not a single summary of all the geographic variation. To extract mutually exclusive patterns from the set of contour maps it was necessary to rotate the initial factor axes (varimax rotation) while still retaining their orthogonality. For this I used the SPSS factor analysis procedure and 100 contour maps (including characters from all 15 species and three environmental maps) as explained in the Methods section.

The factor analysis procedure extracted 24 factors (patterns of geographic variation), which accounted for 76.9% of the total information in the 100 maps. The maps (characters) analyzed and their communalities (percentage of variation accounted for) are presented in Table

Table 2.—Results of the Principal Components Analysis without rotation of 166 contour maps of morphologic variation in 14 species of Florida snakes. Provided are the variables included, their loadings on the first summarizing component, and their communalities for the entire solution.

Variable	Loading on Component 1	Communality
S. dekayi		
temporal pigment shape	0.75178	0.857320
mid-body scale rows	− 0.87844	0.959967
ventral dark pigmentation	0.59895	0.804973
temporal pigment amount	0.02760	0.779860
subocular pigmentation	0.59535	0.861935
preocular scales	− 0.03356	0.796338
postocular scales	− 0.04229	0.813917
black labial scales	0.22597	0.834405
supralabial scales	0.11204	0.829155
infralabial scales	0.06424	0.832628
ventral scales (male)	0.69085	0.917066
subcaudal scales (male)	0.73955	0.946921
percent tail (male)	0.47772	0.867071
ventral scales (female)	0.62153	0.908910
subcaudal scales (female)	0.75891	0.927840
percent tail (female)	0.56426	0.844254
T. sirtalis		
parietal spots	− 0.20325	0.821911
dorsal spotting	− 0.09702	0.811677
supralabial scales	0.28191	0.807484
ventral scales (male)	0.41559	0.878690
subcaudal scales (male)	− 0.06502	0.895418
percent tail (male)	0.27741	0.851664
ventral scales (female)	0.61143	0.759186
subcaudal scales (female)	0.59289	0.861226
percent tail (female)	− 0.09788	0.841539
T. sauritus		
parietal spot size	0.17049	0.814010
parietal spot	0.16398	0.875267
ground color	− 0.12291	0.842355
dorsal stripe edge	− 0.09702	0.805224
supralabial scales	0.83640	0.913688
ventral scales (male)	0.77527	0.884419
subcaudal scales (male)	0.47862	0.874414
percent tail (male)	− 0.27616	0.844263
ventral scales (female)	0.69939	0.809959
subcaudal scales (female)	0.33650	0.813132
percent tail (female)	− 0.02428	0.850746

Table 2 Continued

Variable	Loading on Component 1	Communality
C. constrictor		
blackness	− 0.33009	0.736223
ventral white	0.39338	0.870350
gular brown pigmentation	− 0.36636	0.783164
gular black pigmentation	− 0.01367	0.844681
supralabial brown pigmentation	− 0.32943	0.804774
supralabial black pigmentation	− 0.08446	0.860120
loreal-supralabial contact	0.12820	0.649116
ventral scales (male)	0.72032	0.806584
subcaudal scales (male)	0.56194	0.786852
ventral scales (female)	0.82968	0.842804
subcaudal scales (female)	0.75308	0.860562
M. flagellum		
color phase	0.52892	0.838177
infralabial scales	0.02678	0.872822
ventral scales (male)	0.11576	0.821633
subcaudal scales (male)	− 0.11563	0.821633
percent tail (male)	− 0.11879	0.874451
ventral scales (female)	0.13353	0.890004
subcaudal scales (female)	− 0.24867	0.892576
percent tail (female)	− 0.23883	0.865887
O. aestivus		
supralabial pigmentation	− 0.44361	0.800417
second scale row keeling	0.57483	0.829060
infralabial scales	0.13914	0.755147
ventral scales (male)	− 0.04336	0.860999
subcaudal scales (male)	− 0.58992	0.917308
percent tail (male)	− 0.35519	0.801422
ventral scales (female)	0.37148	0.812593
subcaudal scales (female)	− 0.36932	0.852755
percent tail (female)	− 0.63580	0.832181
E. guttata		
body blotches	0.57096	0.770194
tail blotches	0.40638	0.772105
mid-body scale rows	0.09533	0.714691
lateral blotch shape	− 0.33356	0.643102
ventral pigmentation	− 0.37264	0.736798
blotch border	− 0.05851	0.733278
ventral check shape	− 0.02959	0.706474
ventral scales (male)	0.49797	0.778119
subcaudal scales (male)	0.44114	0.830048
percent tail (male)	0.25626	0.758150
ventral scales (female)	0.63752	0.831445

Table 2 continued

Variable	Loading on Component 1	Communality
subcaudal scales (female)	0.30011	0.864125
percent tail (female)	−0.13015	0.744075
E. obsoleta		
dorsal blotches	0.63544	0.837826
ground color (darkness)	−0.10859	0.778195
stripe development	0.53941	0.823807
blotch development	−0.72341	0.847160
ventral pigmentation	−0.76161	0.901291
supralabial pigmentation	−0.75117	0.877764
L. getulus		
dorsal cross bands	0.88325	0.935943
mid-body scale row	0.77041	0.906259
dorsal pattern	0.50862	0.813884
infralabial scales	−0.03700	0.784680
ventral scales (male)	0.36681	0.794619
subcaudal scales (male)	−0.06543	0.738864
percent tail (male)	0.03785	0.730315
ventral scales (female)	0.22155	0.888972
subcaudal scales (female)	0.28291	0.866032
percent tail (female)	−0.22312	0.829679
L. triangulum		
mid-body scale rows	−0.38625	0.837915
red body bands	−0.46686	0.838038
red tail bands	−0.43715	0.857626
infralabial scales	0.23095	0.857427
loreal scales	−0.11961	0.814579
ventral scales (male)	−0.51637	0.869459
subcaudal scales (male)	−0.02223	0.876373
percent tail (male)	0.14400	0.812309
mid-body scale rows (male)	−0.65058	0.862233
ventral scales (female)	−0.04569	0.832411
subcaudal scales (female)	−0.77806	0.879400
percent tail (female)	−0.33692	0.810978
mid-body scale rows (female)	0.01500	0.833400
D. punctatus		
paired gular scales	−0.28419	0.764453
ventral pigmentation	−0.02896	0.800611
ventral spot shape	−0.28664	0.804063
ring separation	0.33222	0.790843
ring position	0.44038	0.812375
ring width	−0.55495	0.723710
labial pigmentation	−0.26576	0.792337

Table 2 continued

Variable	Loading on Component 1	Communality
subcaudal spots	− 0.26160	0.764708
immaculate ventral scales	0.02396	0.738373
supralabial scales	0.38404	0.717300
pigmented labials	0.51803	0.806656
ventral scales (male)	− 0.49355	0.822025
subcaudal scales (male)	− 0.06949	0.835554
percent tail (male)	0.40379	0.879478
ventral scales (female)	− 0.64135	0.818082
subcaudal scales (female)	− 0.29922	0.816859
percent tail (female)	0.03604	0.806662
T. relicta, oolitica, coronata		
infralabial—chin shield	− 0.24407	0.716007
parietal pigmentation	− 0.40639	0.901413
snout pigmentation	0.50772	0.783422
nuchal collar width	− 0.26084	0.800727
mental—chin shield contact	0.08308	0.805688
supralabial scales	− 0.03638	0.809969
ventral scales (male)	− 0.70326	0.936221
subcaudal scales (male)	0.14401	0.933545
percent tail (male)	0.45205	0.907943
ventral scales (female)	− 0.73648	0.965518
subcaudal scales (female)	− 0.01988	0.917414
percent tail (female)	0.24749	0.870040
S. miliarius		
dorsal blotches	− 0.09613	0.783995
tail bands	− 0.19109	0.731414
divided subcaudal scales	0.05648	0.692906
anterior scale rows	0.61645	0.831487
mid-body scale rows	0.41786	0.786220
posterior scale rows	0.35181	0.657073
dorsal blotch—ground color contrast	− 0.26618	0.695940
ventral pigmentation	0.00091	0.666744
supralabial scales	0.22321	0.699299
infralabial scales	0.18836	0.665685
dorsal blotch shape	0.44574	0.801361
inter-blotch distance	0.50330	0.726141
ventral scales (male)	0.63696	0.812932
subcaudal scales (male)	0.57465	0.820075
percent tail (male)	0.19769	0.762859
ventral scales (female)	0.59573	0.870476
subcaudal scales (female)	0.52361	0.828918
percent tail (female)	0.21109	0.806835
C. adamanteus		
divided subcaudal scales	− 0.01062	0.757572

Table 2 continued

Variable	Loading on Component 1	Communality
dorsal blotches	0.15805	0.768355
mid-body scale rows	− 0.03543	0.714004
black subcaudal scales	− 0.21744	0.651669
ventral pigmentation	− 0.10999	0.771955
labial pigmentation	0.03727	0.809250
immaculate supralabials	0.12439	0.777874
supralabial scales	0.11801	0.756410
infralabial scales	− 0.25936	0.795670
ventral scales (male)	0.30361	0.848964
subcaudal scales (male)	− 0.00287	0.799858
ventral scales (female)	0.24668	0.801790
subcaudal scales (female)	− 0.05363	0.742912

3. Table 3 also gives the principal pattern of geographic variation with which each character is most closely associated, and the factor loading on the first factor extracted.

Much of the geographic variation observed in Florida snakes is oriented 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 that showed distinct north-south changes. Of the 100 maps analyzed, 38 had Factor 1 as their principal factor and 10 had over 50% of their variation explained by Factor 1 (Table 3). For all of the maps Factor 1 accounts for that part of the variation that is north-south oriented.

Factor 1 actually identifies two important patterns of geographic variation. Unfortunately, the statistics available (factor analysis) do not have the power to separate a cline from a simple one step character state shift. It was therefore necessary to examine the original contour maps loading highest on Factor 1 and visually select those that had a single one-step character state shift. The North-South Cline Pattern describes the geographic variation for those characters that vary in a cline southward on the peninsula. The Suwannee Straits Pattern is shared by those species that demonstrate abrupt character state changes in the region of the present Suwannee River.

Table 3 presents the characters (maps) and their factor loadings on Factor 1. The 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 the character's variation accounted for by the factor. The important observation to be made here is that nearly all of the characters analyzed have a major portion of their variation that can

Table 3.—Results of the Factor Analysis with Varimax Rotation of 100 Contour Maps of Snake Morphologic and Environmental Variation. Note that many variables exhibit aspects of more than one pattern, but only the principal pattern is included here, except where two patterns were relatively equal in importance.

Variable	Communality	Loading on Factor 1	Principal Pattern of Geographic Variation
S. dekayi			
mid-body scale rows	.95369	− 0.88912	Suwannee Straits
ventral dark pigmentation	.68403	.58711	Suwannee Straits
temporal pigment shape	.80744	.73400	Suwannee Straits
temporal pigment amount	.58571	.03903	Factor 20
subocular pigmentation	.83800	.59878	Suwannee Straits
ventrals plus caudals	.82341	.68715	North-South Cline
preocular scales	.54303	− .09941	Lower Keys-N. Florida
postocular scales	.71416	− .02662	Factor 13
black labial scales	.73975	.15218	Factor 18
T. sirtalis			
parietal spots	.62678	− .17929	Factor 9
dorsal spotting	.73091	− .02442	Factor 9
ventrals plus caudals	.54009	.50298	North-South Cline
supralabial scales	.95685	.23957	Factor 13
T. sauritus			
parietal spot size	.57189	.02563	Factor 22
dorsal stripe edge	.66962	.03231	Factor 19
ventrals plus caudals	.63856	.30364	Factor 22
supralabial scales	.91204	.77160	Suwannee Straits
C. constrictor			
ventral white	.76578	.29000	Everglades, Lower Keys-N. Florida
gular brown pigmentation	.46922	− .36889	none
gular black pigmentation	.80162	.01574	Lower Keys-N. Florida
supralabial brown pig- mentation	.79836	− .34031	none
supralabial black pigmen- tation	.84235	− .03129	Lower Keys-N. Florida
loreal-supralabial contact	.42071	.13485	Factor 19
ventrals plus caudals	.78969	.73851	North-South Cline
M. flagellum			
color phase	.75184	.39039	Suwannee Straits
ventrals plus caudals	.77890	− .31311	Factor 15
infralabial scales	.69603	.01632	Panhandle-Everglades
O. aestivus			
supralabial pigmentation	.51104	− .26689	Factor 7

Table 3 continued

Variable	Communality	Loading on Factor 1	Principal Pattern of Geographic Variation
second scale row keeling	.76185	.48867	North-South Cline, Factor 7
ventrals plus caudals	.75063	− .31820	none
infralabials scales	.54415	.08321	Factor 24
E. guttata			
body blotches	.62129	.51736	North-South Cline
tail blotches	.58125	.38104	North-South Cline
mid-body scale rows	.40211	.06079	Factor 16
ventral pigmentation	.54088	− .35622	Coastal
blotch border	.62571	− .03501	Everglades
ventral check shape	.39840	− .01880	Coastal
ventrals plus caudals	.59094	.45058	North-South Cline
E. obsoleta			
dorsal blotches	.73191	.70040	North-South Cline
stripe development	.70248	.68599	Suwannee Straits
blotch development	.81187	− .81544	Suwannee Straits
ventral pigmentation	.87962	− .84751	Suwannee Straits
supralabial pigmentation	.84859	− .84396	Suwannee Straits
L. getulus			
dorsal cross bands	.92423	.77272	North-South Cline
mid-body scale rows	.86965	.78203	Suwannee Straits
dorsal pattern	.70095	.38190	North-South Cline, Everglades
ventrals plus caudals	.66946	.47711	North-South Cline
infralabial scales	.68396	-.00146	Factor 10
L. triangulum			
mid-body scale rows	.58845	− .30452	Central Highlands
red body bands	.74186	− .23409	Factor 7
red tail bands	.74450	− .28188	Factor 7
ventrals plus caudals	.77099	− .43181	North-South Cline
infralabial scales	.76916	.29109	Panhandle-Everglades
loreal scales	.65063	− .14573	Factor 11
C. coccinea			
anterior scale rows	.65221	− .16574	Factor 20
posterior scale rows	.86221	− .45041	Suwannee Straits, Everglades
red body bands	.88621	− .08845	Everglades
red tail bands	.77072	− .31636	Factor 11
width fifth red band	.77706	− .25570	Everglades
width fifth white band	.86478	.49117	Suwannee Straits
supralabial scales	.92083	.72762	Suwannee Straits

Table 3 continued

Variable	Communality	Loading on Factor 1	Principal Pattern of Geographic Variation
infralabial scales	.86708	.05655	Everglades
ventrals plus caudals	.85531	.53298	North-South Cline, Everglades
D. punctatus			
ventral pigmentation	.68257	.00094	Factor 8
ventral spot shape	.58628	− .20558	Factor 8
ring separation	.51227	.30422	Suwannee Straits, Panhandle-Everglades
ring width	.52656	− .53219	Suwannee Straits
labial pigmentation	.59992	− .15822	Coastal
immaculate ventral scales	.55130	− .05158	Factor 8
ventrals plus caudals	.57328	− .58642	North-South Cline
supralabial scales	.30275	.31443	Suwannee Straits
pigmented labials	.64861	.41560	North-South Cline, Suwannee Straits
T. relicta, oolitica, coronata			
infralabial-chin shield	.65249	− .17786	Factor 23
parietal pigmentation	.77002	− .40090	North-South Cline
snout pigmentation	.65309	.35250	Factor 7
nuchal collar width	.71403	− .20308	Central Highlands
ventrals plus caudals	.80101	− .55866	North-South Cline
supralabial scales	.77949	− .03635	Central Highlands
S. miliarius			
body blotches	.53895	− .07901	Factor 19
tail bands	.44302	− .15767	Factor 19
anterior scale rows	.71182	− .48877	North-South Cline, Coastal
mid-body scale rows	.46439	.28273	Factor 18, Coastal
blotch-ground color contrast	.40396	− .30038	Factor 21
ventral pigmentation	.46360	− .01047	Panhandle-Everglades
ventrals plus caudals	.75488	.58551	North-South Cline
supralabial scales	.50758	.16292	Factor 17
infralabial scales	.49931	.15802	Factor 17
dorsal blotch shape	.56716	.42178	North-South Cline, Panhandle-Everglades
inter-blotch space	.52296	.41702	North-South Cline
C. adamanteus			
dorsal blotches	.55132	.14065	Factor 14
black subcaudal scales	.41927	− .18888	none
ventral pigmentation	.51970	− .05206	Factor 22

Table 3 continued

Variable	Communality	Loading on Factor 1	Principal Pattern of Geographic Variation
immaculate supralabials	.44236	.17053	Everglades, Panhandle-Everglades
ventrals plus caudals	.48915	.14411	Factor 23
supralabial scales	.70976	.10392	Factor 12
infralabial scales	.61233	− .20077	Factor 12
Florida environment			
mean annual temperature	.76211	.82022	North-South Cline
mean annual precipitation	.59495	− .35357	Panhandle-Everglades
mean annual number of days temperature exceeds 32.2°C	.67363	.23942	Coastal

be described as either a north-south gradient or a character shift along north-south lines, or both.

The North-South Cline Pattern (Factor 1, in part) is the most important pattern of geographic variation observed in Florida snakes. Even characters that vary primarily in some other pattern usually have some component of their variation that can be described as a north-south cline. 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 Cline Pattern.

The Suwannee Straits Pattern (Factor 1, in part) is presented in Figure 107, and is best exemplified by the variation in such characters as midbody scale rows in *Storeria dekayi,* number of supralabials in *Thamnophis sauritus,* midbody scale rows in *Lampropeltis getulus,* and dorsal blotch development in adult *Elaphe obsoleta.* Like the North-South Cline Pattern, this pattern is frequently superimposed on other patterns of geographic variation (see, for example, 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 4 presents factor loadings on Factor 2 for the variables that were important in its construction. This pattern may be called the Everglades Pattern (Fig. 108) and is the principal pattern of variation for such characters as the number of immaculate labials in *Crotalus adamanteus,* development of the dorsal
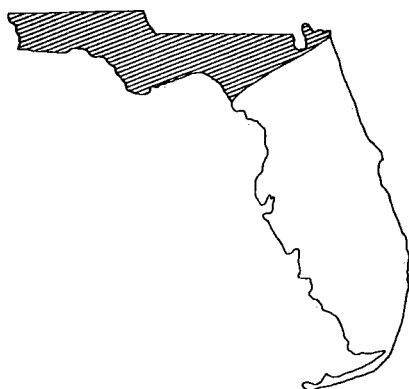
FIGURE 107.—Suwannee Straits Pattern of Geographic Variation (Factor 1, in part).

FIGURE 108.—Everglades Pattern of Geographic Variation (Factor 2).

Table 4.—Everglades pattern of geographic variation (Factor 2). Variables followed by an asterisk have Factor 2 as their principal pattern.

Variable	Factor Loading
C. constrictor	
ventral white	−0.42099
E. guttata	
blotch border*	− 0.45133
ventrals plus caudals	− 0.29934
L. getulus	
dorsal pattern	− 0.28488
C. coccinea	
posterior scale rows	0.37496
red body bands*	0.74285
width fifth red band*	− 0.56371
infralabial scales*	0.84919
ventrals plus caudals	0.45206
C. adamanteus	
immaculate supralabials*	0.36125

blotch border in *Elaphe guttata,* and number of crossbands, number of infralabials, and length of the red bands in *Cemophora coccinea.*

Factor 3 describes a Lower Keys-North Florida Pattern (Table 5, Fig. 109) and is best illustrated by the variation seen in supralabial and gular black pigmentation in *Coluber constrictor* and number of preocular scales

Table 5.—Lower Keys-North Florida pattern (Factor 3). Variables followed by an asterisk have Factor 3 as their principal pattern.

Variable	Factor Loading
S. dekayi	
ventrals plus caudals	− .0.23989
preocular scales*	0.40677
black labial scales	0.23295
C. constrictor	
ventral white	0.45636
gular black pigmentation*	0.85700
supralabial black pigmentation*	0.88389
supralabial brown pigmentation	− 0.32688
loreal-supralabial contact	0.28467
O. aestivus	
ventrals plus caudals	0.27052

in *Storeria dekayi*. This pattern summarizes the geography of a phenetic resemblance between populations in northern Florida, the region east of Tampa Bay and the Lower Keys. Ventral white in *Coluber constrictor*, ventral plus caudals in *Storeria dekayi*, and supralabial-loreal contact in *Coluber constrictor* also have elements of this pattern.

The fourth factor is the Panhandle-Everglades Pattern, (Table 6, Fig. 110) 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. The number of infralabials in *Masticophis flagellum* and *Lampropeltis triangulum*, and the amount of
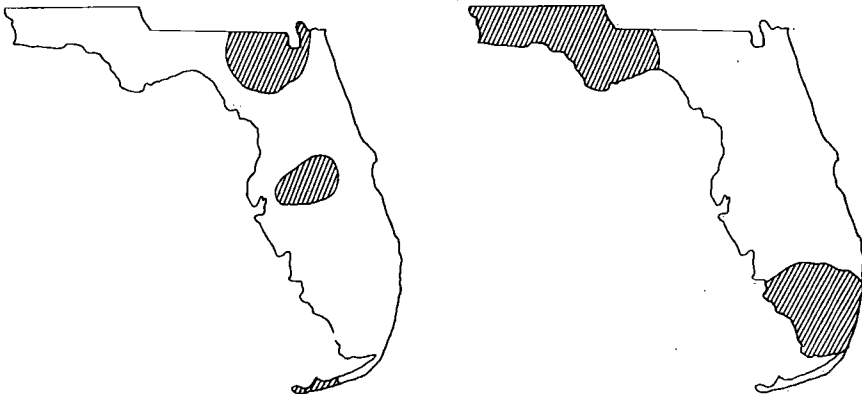
FIGURE 109.—Lower Keys-North Florida Pattern of Geographic Variation (Factor 3).

FIGURE 110.—Panhandle-Everglades Pattern of Geographic Variation (Factor 4).

Table 6.—Panhandle-Everglades pattern (Factor 4). Variables followed by an asterisk have Factor 4 as their principal pattern.

Variable	Factor Leading
M. flagellum	
color phase	– 0.31427
infralabial scales*	0.72896
O. aestivus	
ventrals plus caudals	– 0.28898
second scale row keeling	– 0.24849
E. guttata	
body blotches	– 0.27224
L. triangulum	
infralabial scales*	– 0.46470
ventrals plus caudals	0.27908
D. punctatus	
ring separation	0.30168
T. relicta	
supralabial scales	0.28222
S. miliarius	
ventral pigmentation*	– 0.44881
dorsal blotch shape	0.31826
C. adamanteus	
black subcaudal scales	0.26556
immaculate supralabials	0.30508
Florida environment	
mean annual precipitation	– 0.37981

white in the ventral pattern of *Sistrurus miliarius* illustrate this pattern. Spot shape in *Sistrurus miliarius*, supralabial brown pigment in *Coluber constrictor*, and ring separation in *Diadophis punctatus* also have elements of the Panhandle-Everglades Pattern.

The Coastal Pattern is defined by Factor 5 (Table 7, Fig. 111). Such characters as ventral pigmentation and dorsal blotch border in *Elaphe guttata*, labial pigmentation in *Diadophis punctatus*, and dorsal scale rows and body blotches in *Sistrurus miliarius* load highly on Factor 5. In this pattern populations from coastal regions and the Florida Keys (when the species occurs there) tend to form a phenetic entity distinct from populations farther inland.

Factor 6 represents the Central Highlands Pattern (Table 8, Fig. 112)

FIGURE 111.—Coastal Pattern of Geographic Variation (Factor 5).

FIGURE 112.—Central Highlands Pattern of Geographic Variation (Factor 6).

Table 7.—Coastal pattern (Factor 5). Variables followed by an asterisk have Factor 6 as their principal pattern.

Variable	Factor Loading
M. flagellum	
color phase	0.28903
E. guttata	
ventral pigmentation*	− 0.46907
blotch border	− 0.34480
ventral check shape	− 0.61322
L. triangulum	
mid-body scale rows	− 0.23046
S. miliarius	
body blotches	0.25744
anterior scale rows	0.34333
mid-body scale rows	0.22124
C. adamanteus	
immaculate supralabials	− 0.24009
Florida environment	
mean annual number of days temperature exceeds 32.2°C	− 0.40011

seen in the number of midbody scale rows in *Lampropeltis triangulum*, number of supralabial scales in *Tantilla*, and nuchal collar width in *Tantilla*. The Central Highlands Pattern is characterized by geographic variation in which the region around Lake Okeechobee, and especially the

Table 8.—Central Highlands pattern (Factor 6). Variables followed by asterisk have Factor 6 as their principal pattern.

Variable	Factor Loading
S. dekayi	
temporal pigment amount	0.28584
T. sauritus	
dorsal stripe edge	0.25478
O. aestivus	
infralabial scales	0.23024
E. guttata	
ventral pigmentation	− 0.23154
L. getulus	
ventrals plus caudals	0.25687
L. triangulum	
mid-body scale rows*	0.41243
T. relicta	
nuchal collar width*	0.71364
ventral plus caudals	0.41977
supralabial scales*	0.65938
infralabial-chin shield	0.23273

high ridge immediately to the west, is inhabited by snakes phenetically different from conspecifics to the north and to the south.

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 the contour maps has shown that the variation can be reduced to seven major patterns (North-South Cline Pattern, Suwannee Straits Pattern, Everglades Pattern, Lower Keys-North Florida Pattern, Panhandle-Everglades Pattern, Coastal Pattern, and Central Highlands Pattern). There are other patterns, but these are of lesser 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 small 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.

The seven major patterns of geographic variation in Florida snakes account for 60.4% of the information contained in the original 100 contour

maps. The remaining information is partitioned into lesser patterns, some of them unique to a particular species or character.

THE CORRELATIONS

To search for correlations between the patterns of geographic variation and environmental factors, I analyzed 13 parameters of environmental variation. When these variables were factor-analyzed, three factors were extracted that accounted for 74.4 % of the variation: (1) average annual temperature, (2) maximum summer temperatures, and (3) average annual rainfall. These factors were included in the factor analysis of the snake morphological data.

Average annual temperature loads very highly on Factor 1 (Table 3). Inspection of Figure 102 reveals that average annual temperature belongs in the North-South Cline Pattern. Thus the North-South Cline Pattern of geographic variation is correlated with mean annual temperature. Similarly, the Panhandle-Everglades Pattern is correlated with mean annual rainfall (Fig. 103), and the Coastal Pattern is correlated negatively with maximum summer temperatures (Figs. 104 and 105).

Although correlation does not prove cause and effect, its existence suggests the possibility of such a relationship. Until experimental disproof is at hand, I would hypothesize that mean annual temperature has an important influence on morphological variation in Florida snakes. Using the same line of reasoning, moderate temperature extremes may be responsible for the Coastal Pattern, 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 be true, we must acknowledge that present selective regimes have been insufficient to change phenotypes to adapt to present conditions. For example, the Suwannee Straits Pattern does not seem to correlate with any known environmental variable, and may reflect past adaptations to an insular environment during former periods of high sea level. 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 after they became geographically rejoined. Such a pattern would not necessarily be expected to correlate with any present environmental measurement, and would have to be interpreted as

a remnant of some past selective influence, the exact nature of which remains unknown.

DISCUSSION

PATTERNS OF GEOGRAPHIC VARIATION

Analysis of geographic variation in 15 species of Florida snakes makes obvious a small 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, whereas others seem not to be.

The most important pattern of variation observed in Florida snakes is a north-south cline with increasing or decreasing character states southward on the peninsula. As all snake species examined have some (and frequently many) characters that vary in the North-South Cline Pattern, this probably 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 contributor to the maintenance of the North-South Cline Pattern in Florida snakes.

Previous workers (e.g. Edgren 1961, Smith 1956, Duellman and Schwartz 1958, and others) have pointed out the existence of north-south clines in snake variation, and Fox *et al.* (1961) showed a correlation 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, but the adaptive significance of such a pattern remains to be discovered.

Most of the characters that vary according to the North-South Cline Pattern of geographic variation are meristic (Table 2). Ventral and subcaudal counts usually increase southward, as do cross-band and blotch counts, but 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 Florida 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 probably have relatively less surface area per unit of volume. These

snakes would be expected to retain body heat longer after initial warming than more slender snakes from warmer regions. I hypothesize that snakes with more vertebrae and relatively longer tails 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 crossband counts in *Lampropeltis getulus* southward on the Florida peninsula results in a lighter-colored phenotype in the southernmost parts of its range. A lighter dorsal color presumably reflects more solar energy in low latitudes. Similarly ventral and dorsal color in *Coluber constrictor* generally lighten southward in Florida.

The discussion thus far has assumed that the well-developed clines seen in the geographic variation of Florida snakes are ecoclines (*sensu* Auffenberg 1955), maintained by adaptation to environmental conditions that also vary clinally. Although the North-South Cline Pattern correlates well with various measures of average temperature, possibly the pattern is really a geocline, maintained by reduced gene flow from the central portions of the various species' distributions. Brown (1957) defined centrifugal speciation as the process by which peripheral populations of a species may come to be divergent from more centrally-located populations. This happens when the central populations diverge from some ancestral condition while the peripheral populations remain unchanged. He argued effectively on theoretical grounds that the central part of a species' range should be the principal area of evolutionary change, with adaptive changes then spreading to the periphery at a rate determined by gene flow. The more distant or isolated a peripheral population, the longer it will take for an evolutionary change to reach it. Populations completely isolated (such as on islands) may never acquire the new adaptation, and thus remain "primitive" with respect to that adaptation.

It follows that populations of a species occurring near the end of a peninsula (which is directed away from the central parts of the total range) may retain primitive characteristics long since lost by populations near the center of the range. Even peninsulas that are oriented east-west should show clinal variation for those species whose main distribution is on the mainland. Probably both types of clines are operating in Florida. It is interesting to compare Figures 102 (mean annual temperature) and 106 (North-South Cline Pattern for Florida snakes). The isophenes of the temperature cline are roughly parallel to latitude, whereas the isophenes of the snake morphology cline seem to be perpendicular to the axis of the peninsula, favoring a geoclinal interpretation.

The Suwannee Straits Pattern (Fig. 107) appears in many of the snake species studied. I could find no component of present climate correlating with this pattern. Brooks (1968, 1973) and others before him have shown that Plio-Pleistocene fluctuations in world wide sea level have period-ically inundated much of peninsular Florida. When the sea stood at 46 m above present mean sea level (Okeefenokee 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 standing some 27 to 30 m above the present separated Florida from the mainland by a low-lying, presumably brackish water barrier, the Suwannee Straits (Neill 1957). Snake popula-tions thus isolated may well have acquired divergent characteristics, or remained relatively unchanged while populations to the north were changing.

On the other hand Remington (1968) suggested that this pattern (his "Northern Florida Suture Zone") owes its shape to a habitat barrier as op-posed 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.

For one reason or another, populations of snakes in peninsular Florida demonstrate different phenotypes than conspecific populations on the mainland. Whatever isolating barrier effected this divergence is no longer visible, but the remnants of its reality are retained in a series of dramatic character-state shifts occurring today in populations in the Suwannee River region. Such seemingly unrelated characters as number of supra-labials 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 and thence spread northward as Ross (1974) or Brundin (1975) might have us believe? Croizat (1958, 1962), and Croizat *et al.* (1974) have shown that the "center of origin" concept is an unrealistic approach in evolutionary studies. New species are spawned when former species are split by physical or biotic barriers. Species do nor originate at a point in space and then spread to their pre-sent distribution as Darwin (1859:353) 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 pre-sent 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.* 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 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 or character states will be preserved in that area. Thus islands often harbor the most primitive members of a taxonomic group. This does not suggest 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 places 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 wide-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

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* Vicariance may be defined as the historical process giving rise to geminate (= vicariant) taxa. Speciation is typically a process of vicariance, whereas sympatry and distribution are functions of dispersal (See Croizat et al. 1974).

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) explained this situation by postulating a now submerged land bridge connecting the Florida peninsula with the west including, supposedly, the Mexican Plateau area when lower Pleistocene sea levels exposed a portion of the Gulf Coast continental shelf. Organisms supposedly migrated eastward along this corridor to occupy the Florida peninsula, thus giving rise to the situation seen today with phenotypic resemblances between Floridian and Mexican populations while geographically intermediate populations remain divergent.

This model assumes that the newly exposed Gulf Coast Corridor was colonized by populations from the west that subsequently migrated eastward, while adjacent 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 was not colonized by populations immediately adjacent to it. No evidence suggests 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 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 force in the differentiation process.

When disjunct populations of a species are more similar to each other than either is to intermediate populations, the simplest explanation suggests 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 geographically 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) proceeded relatively more rapidly in the continental region between the Suwannee Straits and the Mississippi Embayment. The question for biogeographers is not "why are Floridian and Mexican popula-

tions similar?," but rather "why are geographically intermediate populations different from Floridian and Mexican populations?"

Two explanations are possible for lower evolutionary rates in Florida and Mexico, and both probably are 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. Populations west of the Mississippi Embayment, including the Mexican and Guatemalan Plateaus are also relatively isolated from populations on the main continent. When a new adaptive character state occurs in a population of sexually reproducing organisms, it will spread throughout the population everywhere that it remains adaptive, but if gene communication with outlying populations is reduced, the new adaptation may simply not reach these peripheral populations. Brown (1957) showed 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 populations in the main body of the species' range. This is why islands frequently harbor the most primitive members of many groups. Thus snake species occurring across the southern North American continent changed more in the central region than they did in the peripheries.

The second explanation contributing to this pattern of geographic variation is concerned with the selective pressures responsible for evolutionary change. Analysis of Pleistocene pollen deposits (Watts 1969) showed that climatic changes 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, whereas those in Florida changed less dramatically (Watts 1970). Under the influence of dramatically changing climates and vegetation, phenotypes would 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.

The Everglades Pattern of geographic variation (Fig. 108) is shared by several snake species. The selective pressures responsible for maintaining distinctive phenotypes in snake species occurring in the Everglades are probably related to the unique habitat there. A lighter dorsal and ventral color in both *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 in the treeless Great Plains region.

Most interesting is the Lower Keys-North Florida Pattern (Fig. 109) in which several species have similar phenotypes in extreme northern Florida, the Lower Keys, and the high ridge east of Tampa Bay. This pattern has been recognized by previous authors (e.g. Neill 1957; Duellman and Schwartz 1958), though they failed to note the apparent inclusion of the area east of Tampa Bay. Several species have been reported to vary in the Lower Keys-North Florida 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 67 and 68, based on larger samples, fail to show this pattern..

Nevertheless enough species show aspects of the Lower Keys-North Florida Pattern in their geographic variation to suggest that the phenomenon must be real. The simplest explanation 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 has permitted 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 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 than either the sediment-filled Everglades or the coral reef formation that is now the Upper Keys. Snake species established on the Lower Keys before the Upper Keys emerged were probably phenotypically similar to peninsular populations. As southern Florida and the Upper Keys emerged, these areas were colonized by populations from the north that adapted to conditions there. The isolation of the Lower Keys has allowed populations 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 (Fig. 101). Conceivably 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 its present elevation suggests. That is, although the maximum elevation of the Lower Keys is today only about 6 m above present mean sea level, the islands may have been emergent even when sea level stood 27-30 m above present.

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.

Mean annual precipitation (Fig. 103) is highest in the Florida Panhandle and Everglades regions. Snake species showing the Panhandle-Everglades Pattern of geographic variation (Fig. 110) may be responding to similar selective regimes created by rainfall patterns.

Populations of snakes along the coast and on offshore islands of Florida are frequently distinct from populations farther inland. The Coastal Pattern (Fig. 111) is probably maintained by something in the ecology of the coastal environment. Elevations are lower and temperatures are less extreme, either or both of which may help maintain the Coastal Pattern.

Several of the species examined show major character state shifts in the region west and northwest of Lake Okeechobee. The Central Highlands Pattern (Fig. 112) is probably maintained by conditions unique to the high elevation scrub and sandhill habitats of the area.

PHYLOGENETIC CONSIDERATIONS

Storeria dekayi. —Ventrals and subcaudals increase clinally to the south on the peninsula. *S. 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 mid-body scale rows and the shape of the temporal spot (Figs. 4 and 6).

Current taxonomy (Neill 1950a, Conant 1975) recognizes these as the subspecies *S. d. wrightorum* in the north and west and *S. d. victa* on the peninsula. Apparently no specimens are available from the region between the two morphotypes, where snakes with intermediate characteristics might be sought. Thus, no evidence exists for intergrada-

tion between *S. d. victa* and *S. d. wrightorum* in Florida and the two may
be entirely allopatric. Neill (1950a) made a weak case for the apparent
conspecificity of the two forms by suggesting intergradation in the
Coastal Plain of eastern Georgia, but he failed to list any specimens.
Whether or not the two forms are reproductively isolated (i.e. distinct
species) is of little consequence to a discussion of their origin.

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

Besides having characteristics reminiscent of more northern popula-
tions, 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 usually have two preoculars on each side, a
character shared in the genus only with *S. storerioides* and *S. oc-
cipitomaculatum*. Trapido (1944) postulated that *S. storerioides* was
closest to the ancestor of *S. dekayi*, which in turn gave rise to *victa*. He
wrestled with the difficulty of assuming an increase in dorsal scale rows
from *storerioides* to *dekayi* and a subsequent decrease again in *victa*, but
finally concluded that *dekayi* must have given rise to *victa* (*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 victa* 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 be-
tween Lower Keys *victa* and *S. storerioides*.

The immediate common ancestor of the taxa in question was a snake
much like *S. storerioides* and occurred in what is today Mexico and
southern United States including Florida, although not necessarily at any
one point in time. 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. oc-
cipitomaculatum hidalgoensis* and *S. storerioides*). The former differen-
tiated into *S. o. occipitomaculatum* in the eastern United States, and *S. o.
obscura* on the Florida peninsula. *Storeria storerioides* meanwhile con-
tinued to differentiate on the American continent. Differentiation pro-
ceeded relatively more slowly on the Florida peninsula owing to reduced
gene flow with continental populations (peninsular effect), a likely re-
duced population size resulting in slower rates of recombination and
mutation, and also a weaker selective 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 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) called this type of evolution, "centrifugal speciation."

The differentiation between mainland *dekayi* and Florida *victa* was probably speeded by further reduction in gene flow brought about by the periodic insulation of Florida caused by rising sea levels.

S. d. victa is considered autochthonous in Florida and descended from the same ancestor as *S. d. wrightorum* but with less differentiation. No evidence suggests that *S. d. wrightorum* and *S. d. victa* are members of the same biological species. *Storeria* on the Lower Florida Keys are differentiated even less than peninsular *victa* and could realistically be assigned subspecific status.

Thamnophis sirtalis.—Ventral and subcaudal counts are generally higher in the south. A general pattern involving the characters, dorsal spotting and parietal spots 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 is 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 instead 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.

On the other hand, Blaney (1971b) suggested that the spotted phase in this species may once have been continuous along the coast, and the present disjunct nature of the phenotype a result of more recent fragmentation. This may be true. The pattern of geographic variation in this character (Fig. 13) suggests a coastal distribution. When much of the Gulf continental shelf 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 garter snakes in coastal regions and

throughout most of the Everglades. If this interpretation is correct, it offers a clue 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 that has not been investigated since Ruthven (1908). Based on patterns in other species, I 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.—Ventral and subcaudals increase clinally to the south on the Florida peninsula, although the patterns are not especially well-developed. *T. sauritus* from the Florida peninsula differ markedly in the number of supralabials from snakes inhabiting the Panhandle and regions north of Florida. The nature of the paired parietal light spots varies in a pattern like that noted 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 subspecies, *T. s. nitae* of the Gulf Hammock region is identified 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 ancestral ribbon snake, very much like present day *T. proximus*, became widespread 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 (Rossman 1962). Phenotypically the snakes on the east side of the Mississippi were probably still a lot like *proximus* characterized by eight supralabials. Another vicariation occurred when snakes on the Florida peninsula became relatively isolated owing either to 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 eight supralabials.

We have no reason to believe that reproductive isolation between *proximus* and *sauritus* occurred before the evolution of a reduced supralabial count in *sauritus*. Thus the development of the present *sauritus* phenotype in eastern North America may have occurred before, during, or after the events that 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. The species concept relies only on reproductive incompatibility, not on degree of divergence nor time since divergence.

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 geographically intermediate eastern North America. Superficially (i.e. in color and pattern), *sackeni* from the Lower Florida Keys are even more like western *proximus*, indicating that evolution has proceeded even more slowly on the isolated Lower Keys than on the peninsula.

The Gulf Hammock subspecies, *nitae*, is presumed antochthonous in that region, having vicariated with *sackeni*.

Coluber constrictor. —Ventral and subcaudal numbers increase in a cline southward on the Florida peninsula, although the subcaudal cline is poorly defined. *Coluber* tend to have lighter colored venters in the southern peninsula and northward along both coasts, but the darkest venters are seen in the Lower Keys. Gular brown is the best single character for differentiation of the subspecies *C. c. 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: Racers 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.

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 possible evolutionary scheme. The original ancestor of *Coluber constrictor* probably looked much like present day *C. c. flaviventris* or *oaxaca*. Geographic variation is the rule in natural systems, and such variation in a wide-ranging species such as the racers must have led to the geographic differentiation we see today. The Mississippi Embayment may have helped reduce gene flow between populations on either side as these differentiated. *Coluber* east of this barrier became dark black in color, and with black gulars and supralabials. This is the condition in 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 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 of the black supralabials and gulars in most populations, but 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 gular and supralabial pigmentation. Evolution in these characteristics apparently has proceeded more slowly in these three regions.

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 *C. c. priapus* with white supralabials and southern Florida *C. c. 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 (= adaptation to similar environments) or of more recent gene flow with western forms via some past land connection (e.g. the Gulf Coast Corridor).

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. c. helvigularis)*. This condition is also approached 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-chined racers along the west coast of Florida. As 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 *Coluber* stock in Florida characterized by black supralabials and gular scales. Geographic variation led to lighter colored snakes in southern and coastal Florida 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 levels dropped as much as 100 meters (Fairbridge 1960), additional habitat 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.

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

Both Auffenberg (1955) and Wilson (1970a) implied that southern Florida *paludicola* may be closely related to western *flaviventris*. This could be true because the emergent Gulf Coast Corridor would have provided the opportunity for gene flow between coastal western populations *(flaviventris)* and coastal Florida populations *(paludicola* and *helvigularis)*, but the important point is that the Gulf Coast Corridor was inhabited by *Coluber* adapted to the conditions present at that time. If south Florida *paludicola* and western U.S. *flaviventris* have experienced more recent contact along the Gulf Coast, it would imply that the habitat there at the time of contact was treeless, probably similar to the present Everglades. 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 *paludicola* and *helvigularis*. If this were true, recourse to the Gulf Coast

Corridor hypothesis would be unnecessary, but for the present all available evidence points to the development through differential selection acting on coastal populations of a phenotype of *Coluber constrictor* characterized by light dorsal and ventral colors and brown-pigmented supralabials. Snakes sharing these characters occur today in the Everglades, coastal situations, islands, and (without the lighter dorsal color) 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, but 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) cannot be defended with available data.

Masticophis flagellum.—Ventral and subcaudal counts tend to be higher in the Panhandle and western penninsula, but no cline is evident. Relative tail length also varies in this manner.

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

The ancestral *Masticophis flagellum* was a light-colored snake, phenotypically 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 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. Nothing suggests that *testaceus*-like coachwhips invaded Florida along a now-submerged land bridge while darker coachwhips were already present north of Florida. The pattern of geographic variation in this character suggests merely that differentiation 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 Floridian and western populations with respect to color pattern.

Opheodrys aestivus.—Although no well-developed cline is evident, green snakes do tend to have more ventral scales in the southern parts of Florida, and caudal scale counts are highest in Panhandle specimens. Snakes from the Panhandle and west coast of the peninsula have darker supralabial scales than those from the rest of the state. The lightest supralabials are on snakes from the Florida Keys and the peninsula, ex-

clusive of the west coast. *Opheodrys* 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.

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, following post-Wisconsin extirpation in southern regions in the wake of a warming climate, but the distribution of *Opheodrys 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 rest of the range have white bellies. 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). 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 to the south in Florida, as do blotches on the body and the tail. A coastal pattern is evident in the geography of several characters. Corn snakes from coastal parts of the peninsula including offshore 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 are also noteworthy for their lighter dorsal color, absent or very narrow dorsal blotch borders, very high ventral and subcaudal counts, and a more slender body.

Geographic variation in the corn snake has not been studied in detail until very recently (Mitchell 1977; Thomas 1974). The distinctive Lower Keys population, which display characteristics not shared by any other population, was once recognized subspecifically, but was synomized by

Duellman and Schwartz (1958). 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. These snakes very likely retain ancestral states for these characters, while populations on peninsular Florida and elsewhere in the east have developed more ventral pigment, fewer blotches, and wider dorsal blotch borders. The evolutionary history of this species probably involved a differentiating sequence 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. The reduction of ventral pigment may be an adaptation to coastal climates, the epitome of which would be in off-shore insular situations.

Where *E. guttata* occurs in the absence of its congener, *E. obsoleta*, as on the Lower Keys and Gulf Coast islands, the former demonstrates a phenotype more closely approaching that of *E. obsoleta* than anywhere else within its range. Such "ecological release" has been suggested for many species (see for example, Ricklefs 1973) and may help explain the reduced ventral pigment, paler dorsal pattern, more slender and elongate body form, and increased arboreal tendencies (personal observations) of corn snakes from the Lower Keys and Florida Gulf Coast islands. Where it occurs syntopically with *E. obsoleta*, *E. guttata* is stockier, more boldly marked both ventrally and dorsally, and more confined to a terrestrial or fossorial existence.

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

Elaphe obsoleta.—The currently recognized subspecies *E. o. spiloides* is clearly defined by the geographic variation in stripe development, blotch development, ventral pigmentation, and supralabial pigmentation. The subspecies *williamsi* appears in an area where both spots and stripes are fairly well-developed. Specimens from the Gulf Hammock region also have darker labials and venters, more like northern *spiloides* than *quadrivittata*. Another subspecies, *rossalleni* (Neill 1949) 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 rat 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 *E. 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 eastern parts of the United States to the solid-colored snake known as *E. o. obsoleta*. Populations from extreme southern Florida have probably diverged less from the ancestral condition, and still retain the darker pigmentation and blotched phenotype. 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 (*E. o. williamsi*) in the Gulf Hammock region 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 region today suggests a pattern of recombinants such as would be observed when isolated populations come secondarily into contact. Rat snakes with both stripes and blotches occur along a narrow band from the Gulf Hammock region to coastal South Carolina (W. Auffenberg, pers. comm.) providing additional evidence for the hybrid origin of the phenotype.

Lampropeltis getulus.—Kingsnakes from the southern regions have a weakly developed tendency to more ventrals and subcaudals, as in most snake species studied. The Suwannee Valley shows up again as a major transition zone in kingsnakes, this time for a rapid 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) 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 a Gulf Coast migration route appeared overnight to allow dispersal into unoccupied habitats. On the contrary, the accumulation of continental ice and resulting sea level drop occurred slowly, allowing the gradual establishment of continental organisms seaward as suitable terrestrial habitats became available.

Blaney (1971a) suggested that the higher scale row counts 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 remained to the north. I believe that kingsnakes in peninsular Florida have retained the ancestral condition for scale row numbers (as has *splendida*) while populations to the north diverged by reduction of scale rows. I agree that the higher counts in *splendida* and peninsular Florida kingsnakes represent an ancestral condition. The northern populations of *getulus* evolved a reduction in scale rows while populations to the west *(splendida)* and south (Florida forms) remained unchanged in this character. Peninsular Florida thus emerges once again as a place where evolutionary change in some characters proceeds more slowly than in continental areas to the north.

The presence of light-colored 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, with relict populations remaining disjunct in these two regions. 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. Scarlet kingsnakes 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 widest distribution of any terrestrial snake species in the world, and one recent authority recognized 23 distinct subspecies (Williams 1970). Williams' evolutionary speculations are based on the premise that the group has had a center of origin and each of the subspecies has developed from another 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 of *L. triangulum*. I view the 23 distinguishable phenotypes of *L. triangulum* as localized populations adapted to environmental conditions where they exist. Their differentiation can be accounted for by responses to 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) believed to be the ancestral phenotype than are those 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 southeastern 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 to 17 dorsal scale rows at midbody.

Cemophora coccinea.—The patterns of variation of *C. coccinea* in Florida are apparently more complex than previous workers have recognized. Correlation analyses (Christman, unpubl.) seem to show two rather distinctive morphotypes in Florida characterized by a combination of features. Generally speaking, *Cemophora* with high ventral counts are frequently larger, have more infralabials, more dorsal scale rows both anteriorly and posteriorly and more subcaudals. Without additional material it is difficult to determine the significance of this variation, but apparently *Cemophora* that tend to be larger and have more ventrals and subcaudals, more infralabials, and more dorsal scale rows, occur most frequently in the central part of the peninsula; snakes of a contrasting phenotype occur in North Florida, the Panhandle, and to the south in the Everglades regions. Additionally, the central peninsular snakes usually have 14 supralabials, while *Cemophora* to the north and south have 12. Previous studies (Neill 1950b, Duellman and Schwartz 1958, Williams

and Wilson 1967) 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 assigns all *C. coccinea* from the peninsula south of Marion County to the nominate race.

The scarlet snakes may represent another example of the morphological similarity between North and South Florida populations with divergent populations in the geographically intermediate region.

Diadophis punctatus.—Unlike most snake species investigated, *D. punctatus* tend to have lower ventral counts southward. Variation of subcaudal numbers shows no obvious trend. 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 number of supralabials, labial spots, and ring width.

Most of the previous work on variation in *Diadophis* has concerned the validity and distribution of the various taxonomic entities within the genus (Conant 1946, Paul 1967, and others). A recent study by Gehlbach (1974) speculated on the evolutionary history within the species. Gehlbach believes that the smaller body size in populations called *arnyi* 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 *arnyi* is ancestral, and that more northeastern populations have lost these characteristics. I agree with these speculations and add the following comments on the species' color pattern.

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. The fact that some populations of ringnecks in the southwestern U.S. also lack a neck ring (Stebbins 1966) lends credence to this hypothesis. 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.

Ringneck snakes from the peninsula generally differ from their mainland relatives in the nature of the nuchal ring. Snakes from south of the Suwannee River frequently have a narrower neck ring that is interrupted middorsally and displaced farther posteriorly than specimens to

the north and west. This phenotype may represent an intermediate condition between the virtually ringless populations on the Keys and the typical ringed *Diadophis* north and west of Florida.

Alternatively, the Keys populations 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.

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

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 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" (*op. cit.*: 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 disjunct regions.

Geographic variation in crowned snakes on the peninsula has led to the complex picture Telford treated taxonomically in 1966. The different phenotypes are probably restricted to particular ecological situations, as suggested by Telford. Whether the phenotypes have or have not achieved reproductive isolation cannot be determined by a phenetic study.

Sistrurus miliarius.—Ventrals and caudals appear to increase clinally

to the south. The Coastal Pattern describes the variation in several characters: Coastal populations have 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 phylogenetic relationships in the genus *Sistrurus*. He pointed out that the Florida subspecies *barbouri* has more primitive character states than either of the other two subspecies. He went on to speculate that *barbouri* must therefore have given rise to the other two following its isolation in Pleistocene Florida. If *barbouri* does 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. 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.

Just as Florida appears to be acting as a refuge for ancestral character states with respect to the remainder of North America, parts of Florida seem to preserve primitive characters with respect to the rest of the state. The morphological similarities 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 to any other Florida populations. This phenotype is probably ancestral, with populations in other parts of the range having differentiated more from this condition. The alternative hypothesis suggests that this phenotype has arisen independently in the several remote regions where it occurs today.

Crotalus adamanteus.—Variation in ventral and subcaudal counts for Florida *Crotalus* show no obvious trends except that Keys specimens have higher ventral counts. The number of infralabial scales varies in such a way that Keys rattlesnakes are closer to more northern specimens than to those from the adjacent mainland. Pigmentation of the labials and ventral surface shows a similarity between specimens from the Lower Keys and the Central Ridge.

Gloyd (1940) believed that *Crotalus adamanteus* was derived from 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 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 where rattlesnakes have evolved more slowly. There is no reason to suppose that *adamanteus* arose on the Mexican Plateau and dispersed into Florida.

Within Florida *Crotalus adamanteus* has differentiated 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 suggests that these forms share a common history. Evolution in the intermediate parts of the peninsula has produced a phenotype somewhat distinct from that still persisting both northward and southward.

SUMMARY

Much of the morphological variation in 15 species of snakes occurring in Florida can be summarized by seven major patterns of geographic variation. Totally unrelated characters of unrelated species often vary geographically in remarkably similar ways. Such patterns of geographic variation must reflect the history of these species in Florida including the present as well as past selective regimes.

Peninsular Florida has been widely cited as the center of origin for a number of plant and animal species, largely because the most primitive members of the various groups now occur there. As pointed out by Croizat *et al.* (1974) the concept of a center of origin is of little theoretical value. A new species forms when another species splits into isolated populations that receive different selective pressures and have reduced genetic mixing with each other. The center of origin is thus the entire range of each isolated population.

The reason so many primitive species and primitive character states occur in Florida is simply that these populations have diverged less from their ancestral stocks than have populations elsewhere. The geographic location of the most primitive species of a group or the most primitive character state for a species tells us nothing about the origin of that group or species, but it does tell us that, for some reason, evolution has been proceeding more slowly in these areas.

Evolution has proceeded more slowly on the Florida Peninsula than elsewhere in the eastern United States for two important reasons. The first involves a consideration of gene flow. Because Florida is a peninsula (and from time to time in the past was an archipelago), gene flow between continental populations and Florida populations has been reduced below that for other areas of similar size. This means simply that evolutionary changes that occurred in the central continental parts of a species' range (where they are most likely to occur anyway) were not always as fully incorporated into the genotypes of the partially isolated peninsular populations. The phenomenon of centrifugal speciation, discussed theoretically by Brown (1957), is demonstrated clearly in Florida where many species retain more primitive characteristics at the periphery of their distributions.

The second reason that evolution has proceeded relatively more slowly in Florida involves natural selection. Paleoecologic data suggest that Florida has been climatically more stable since the Pliocene than have areas to the north. Obviously organisms living in a more stable climatic region will be under less selective pressure to change their morphology. Species inhabiting the continent north of Florida during the Pleistocene were faced with changing climatic regimes to which they responded with extinction or adaptation. Thus there are today fewer species in the north, and those that are still present are often quite divergent from ancestral stocks.

Although little is to be gained from speculating on centers of origin, the position of the barrier that somehow reduced gene flow and allowed the differentiation process to proceed is of interest. In Florida the most important vicariating barrier was certainly the base of the peninsula or Suwannee Straits region. Species that today range across the region of the present Suwannee River often demonstrate abrupt shifts in character states on either side of this region. I can think of no selective pressure now operating that might maintain such well defined phenotypes on opposite sides of the Suwannee Valley, and must conclude that the pattern is a remnant of past genetic barriers and selective pressures no longer visible. The present Suwannee Valley is, of course, the very region where Florida becomes a peninsula, and the region that was at least partially inundated during higher sea levels, even while parts of the peninsula were still emergent. Thus populations on opposite sides of the Suwannee Straits have had a history of at least partial isolation and therefore independent evolution.

Even within Florida evolutionary rates have varied geographically in response to varying degrees of isolation. Lower Keys populations have been relatively isolated from peninsula populations and today usually retain more primitive characteristics.

One of the most interesting patterns of geographic variation in Florida organisms is the Lower Keys—North Florida Pattern. In this pattern, species that range throughout Florida frequently demonstrate morphological similarities in three disjunct regions: the extreme northern peninsula, the Lower Keys, and the Central Highlands just east of Tampa Bay. Conspecific individuals from these three widely separated regions are often more similar to each other than they are to individuals living between them. The three regions probably represent islands of slower evolutionary rates. The northernmost peninsula, the Central Highlands and the Lower Keys may have been islands of terrestrial habitat when much of the remainder of the peninsula was submerged (see Fig. 101 for elevations in Florida), and their populations probably shared common ancestors. When the rest of the peninsula became available for colonization, the stocks moving in from the three islands were plastic enough in their genotypes to respond differentially to selective pressures in the lower elevations.

Variations in present day selective pressures have also contributed to the patterns of morphologic variation in Florida snakes. Many populations living in open, largely treeless environments differ phenotypically from conspecifics in more forested habitats, even when the treeless habitats are disjunct. Similarly the two regions of highest annual precipitation (the Everglades and the Panhandle), although widely disjunct, support populations of some species that are more similar to each other than either is to geographically intermediate populations. The unique habitat afforded by the Central Highlands ridge of scrub and sandhills often supports populations somewhat divergent from other Florida populations, and the same can be said for the Gulf Hammock Region.

The striking north-south clines running the length of the peninsula in nearly all species examined parallel mean annual temperature and most other temperature-related climatic measurements, which also vary clinally down the peninsula. This suggests a cause and effect relationship, although its adaptive significance is not clear.

A cline would also be maintained by the peninsula or gene-flow effect. The base of the peninsula is a partial barrier to most species' gene flow. Adaptations occurring north of Florida would spread (if they remained adaptive) southward onto the peninsula. A picture of such dynamic variation at one point in time (i.e. this study) would be a cline.

Some of the variation in Florida snakes may be explained in terms of release from competition with ecologically related species. Where *Elaphe guttata* occurs in the absence of *E. obsoleta* (the Lower Keys and several Gulf Coast islands), the former is generally more slender, less distinctly patterned ventrally and dorsally and more arboreal in habits, all characteristics of *E. obsoleta*. Many authors (Carr 1940, Duellman and

Schwartz 1958) have noted that *Storeria dekayi victa* is essentially an aquatic snake, but this species is terrestrial on the Lower Keys where such potential competitors and predators as *Tantilla, Rhadinaea flavilata*, and *Lampropeltis triangulum* are absent. It seems possible that the distinctive morphology of Lower Keys *Storeria* might reflect its use of habitats not used on the mainland.

In several instances a coastal pattern of geographic variation is manifest where populations demonstrate a unique phenotype typical only of coastal localities. These snakes may be better adapted to coastal environments, which are often more open (i.e. less forested) and subject to less extreme temperature fluctuations.

For several of the species examined, the analysis of geographic variation revealed patterns of potential taxonomic significance. Although I withhold formal taxonomic judgments, the data suggest the following conclusions:

(1) *Storeria dekayi wrightorum* and *S. d. victa* are apparently allopatric, are morphologically and behaviorally distinct, and are probably evolving independently. The population on the Lower Keys is distinctive and could probably be considered a subspecies of the peninsular form, *victa*.

(2) The population of *Coluber constrictor* on the Lower Keys is as distinctive as any of the currently recognized subspecies.

(3) *Elaphe guttata* on the Lower Keys is distinctive and could also be recognized taxonomically.

(4) *Cemophora coccinea* may consist of two rather distinctive morphotypes on the Florida peninsula.

(5) The validity of *Tantilla relicta* or *T. oolitica* is not supported (or denied) by any of the data used in this study.

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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 a 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 only for specimens with complete tails.

SEX. In snakes without everted hemipenes, sex was determined by dissecting the base of the tail.

QUALITATIVE CHARACTERS. Aspects of carination, pattern, and pigmentation were ranked on qualitative scales and assigned numerical character states. For pattern analysis line drawings

on the data-collection forms were filled in, and numerical scores assigned only after all the material had been examined. For 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 DARK PIGMENTATION. 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 when the entire temporal is pigmented.

TEMPORAL PIGMENT SHAPE. The orientation of the tear-drop-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. Noting merely in which direction the blotch seems to point provides a more manageable character. 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. Specimens whose temporal pigment was entirely confined within the scale and specimens without temporal pigment were given missing values for this character.

SUBOCULAR PIGMENTATION. 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 SPOTS. The distinctiveness and size of the parietal spots were 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. The spots were scored zero for absent, one for faint or indistinct, and two for distinct.

GROUND COLOR. 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 was scored one, its absence zero.

DORSAL STRIPE EDGE. The black border of the dorsal stripe may be absent, weak and irregular, present but narrow, or up to 1½ scales wide. 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. Adult specimens (> 70 cm) were scored one, two, or three, based on how dark they appeared in preservative.

VENTRAL WHITE. The amount of white pigment on the ventral surface was assigned values ranging from zero (no white on any part of the venter) to five (venter completely white).

GULAR BROWN PIGMENTATION. The amount of brown pigment in the gular region was assigned values ranging from zero for no pigment to five for much pigment.

GULAR BLACK PIGMENTATION. Like gular brown, the values for this character ranged from zero to five.

SUPRALABIAL BROWN PIGMENTATION. The amount of brown pigment on the supralabial scales was assigned values from zero for no pigment to five for much pigment.

SUPRALABIAL BLACK PIGMENTATION. The amount of black pigment on the supralabial scales was scored with values from zero to five.

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. Linear measurements were made on three aspects of the frontal plate. The anterior width is the straight line distance between 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.

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 by the method proposed by Dowling (1951).
Number of subcaudals.
Number of supralabials.
Number of infralabials.
Color phase. On the basis of overall color and pattern, the specimens were assigned to either a light phase (1), intermediates (2), or dark (3).
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 (immaculate) to five (completely pigmented).
Keeling of the second dorsal scale row. A value of zero was assigned to specimens showing no keel on this scale row and a maximum of three when the keel was developed to the same extent as the adjacent third row; intermediate conditions were scored as one or two. This charcter was introduced by Cope (1900).
Frontal measurements. Three dimensions of the frontal plate were recorded as in *C. constrictor.*
Snout-vent length.
Tail length.
Sex.

Elaphe guttata

Number of ventrals.
Number of subcaudals.
Number of body 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, as in *C. constrictor.*
Lateral blotch shape. The lateral series of spots was examined and scored for presence or absence, and (when present) whether the surrounding border was complete or incomplete.
Blotch 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 on a scale of zero (venter immaculate) to five (venter with black pigment over more than ¾ of surface).
Ventral check shape. The general shape of the ventral checks in a typical midbody section 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 qualitative assessment of the degree to which the dorsal stripes are evident ranged from zero for no stripes to five for very well-developed stripes.
BLOTCH DEVELOPMENT. The degree of development of the dorsal blotches was ranked on a scale like that for stripe development.
GROUND COLOR. The dorsal ground color was compared with a series of color chips showing increasing melanism scaled from zero to 3.5.
VENTRAL PIGMENTATION. The totality of dark pigment on the ventral surface was scored from one to four with increasing darkness.
SUPRALABIAL PIGMENTATION. The values for supralabial pigmentation ranged from one to four with increasing darkness.
SIZE. The head length was recorded to obtain rough size correlations and for grouping the specimens.

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 CROSS BANDS. This includes only the precaudal bands.
NUMBER OF INFRALABIALS.
DORSAL SCALE ROWS AT MIDBODY.
DORSAL PATTERN. This character attempts to describe the relative amount of light pigment in the dorsal pattern. The three states for this character (1-3) correspond in part to Blaney's (1971a) 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.
RED BODY BANDS. This is a count of precaudal red bands.
RED 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 RED BODY BANDS. This is the number of precaudal red saddles.

NUMBER OF RED TAIL BANDS.

LENGTH OF FIRST RED BAND. This is the number of scale lengths in the first red dorsal saddle.

LENGTH OF FIFTH RED BAND.

LENGTH OF FIRST WHITE BAND.

LENGTH OF FIFTH WHITE BAND.

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. Of the specimens examined, 23% 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.

SUBCAUDAL SPOTS. The number of black spots on the underside of the tail was recorded for each specimen.

VENTRAL PIGMENTATION. The amount of black pigment at a typical midbody section 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 assigned values from zero (slightly higher than wide) to five (as wide as the whole ventral scale). This character measures the degree to which the ventral spot is elongated into a bar.

CONNECTED SPOTS. The state for this character is three if most 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. The width of the break in the nuchal ring was scored using a scale of zero for no break to five for a break more than one scale wide. 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 measured in number of scales at its widest dorsal part.

LABIAL PIGMENTATION. Specimens with diffuse labial pigment were assigned a value of zero, those with clear, distinct labial spots or with no pigment were given three, intermediate specimens one or two.

PIGMENTED SUPRALABIALS. The number of supralabial scales with black spots was recorded for the right side.

PIGMENTED INFRALABIALS. The number of infralabial scales with black spots was recorded for the right side.

SNOUT-VENT LENGTH.

TAIL LENGTH.

SEX.

Tantilla sp.

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

NUMBER OF VENTRALS. Dowling's (1951) method was used.

NUMBER OF SUPRALABIALS.

NUMBER OF SUBCAUDALS. The terminal spine was not counted.

INFRALABIALS-CHIN SHIELDS. The first four infralabials generally contact the anterior chin shields. In some snakes only the first three infralabials make contact with the anterior chin shields. The condition for this character was noted on both sides.

PARIETAL PIGMENTATION. Specimens with totally black parietals were scored zero 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).

SNOUTH 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 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-CHIN SHIELD CONTACT. Whether or not the mental scale was in contact with the anterior chin shields was noted.

SNOUT-VENT LENGTH.

TAIL LENGTH.

SEX.

Sistrurus miliarius

NUMBER OF VENTRALS.

NUMBER OF SUBCAUDALS.

NUMBER OF DIVIDED SUBCAUDALS.

NUMBER OF DORSAL BLOTCHES. This includes only blotches anterior to the tail.

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 PIGMENTATION. The amount of white in the ventral pattern was given a subjective ranking of one for almost no white to three for much white.

DORSAL BLOTCH SHAPE. The dimensions of a typical dorsal blotch at midbody were recorded in scales wide, scales long, and the number of scales included in the interblotch space. These three values describe the shape and spacing of the blotches.

FRONTAL MEASUREMENTS. Three measurements were taken on the frontal plate as in *C. constrictor*.

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 ¾ black were counted.

VENTRAL PIGMENTATION. The amount of dark pigment was ranked from zero for no pigment to three for 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. The number of supralabials at least ¾ immaculate were counted 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. In meters above mean sea level.

Mean annual temperature.

Mean January temperature.

Mean August temperature.

Mean annual rainfall.

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

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

Mean August maximum temperature.

Mean January minimum temperature.

Mean number of days with over 0.254 cm precipitation.

Mean temperature range. Average difference between mean August and mean January temperatures.

Mean extreme temperature range. Average difference between mean August maximum and the mean January minimum temperature.

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

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