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CHARACTER NUMBER AND THE MULTIVARIATE ANALYSIS OF SIMPLE PATTERNS OF GEOGRAPHIC VARIATION: CATEGORICAL OR "STEPPED CLINAL" VARIATION

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Abstract.—Computer selection of random sets of real characters was used to elucidate the relationship between character number and the reliability of multivariate patterns of geographic variation. The simple pattern of geographic variation was a distinct pair of parapatric races (categorical or "stepped clinal" variation) in the grass snake (*Natrix natrix*) in Europe. The characters used were 71 significant characters of low within-group correlation drawn from six different character systems (e.g., scalation, color pattern and internal morphology). The pattern was assessed by principal coordinate analysis, and the congruence was taken as the absolute correlation between the "first" principal coordinates.

The investigation was based on two procedural models: (A) the congruence between completely independent character sets using from 1 to 35 characters; and (B) the congruence between the analysis based on the total 71 characters and analyses based on from 1 to 65 characters. The relationship between congruence and character number is expressed by one of two mathematical models depending on the procedural model employed. Congruence is clearly asymptotic with respect to character number. This indicates the existence of a stable, overall pattern of racial variation that, once established, is unlikely to be influenced by the addition of further characters. The asymptotes are reached at an early stage and, between 8 to 10 characters, reveal the distinct patterns of racial variation with at least 90% confidence, depending upon whether one is characterizing patterns on the basis of a geographic transect or a scatter on the first two principal coordinates. It does not appear to be cost effective to use more than 18 significant characters, because each additional character increases the minimum congruence by very little beyond this point. Univariate characters, and those patterns based on too few characters, can misrepresent this stable pattern. The observed failure of univariate/conventional studies to reveal this pattern, or to agree with one another, is related to the low probability of selecting the appropriate individual characters, even though they occur. [Geographic variation; races; character number; congruence; predictivity; multivariate morphometrics; stepped cline.]

Multivariate analysis is frequently used to investigate patterns of geographic variation (reviewed by Thorpe, 1976, 1983). Two techniques, canonical analysis and principal coordinate/component analysis, are most frequently applied to summarize the geographic variation of many characters in fewer axes. Population affinities can then be investigated by plotting a scatter diagram of the most important axes or by considering the axes separately (e.g., by mapping the scores of an axis and then taking a geographical transect).

Multivariate ordination analysis is not restricted to morphological data but can be appropriate for biochemical and other information (Menozzi et al., 1978; Piazza et al., 1981). Nevertheless, multivariate analysis is most frequently based on phenotypic characters and referred to as multivariate morphometrics (Blackith and Reyment, 1971). This term should not be restricted to the analysis of linear proportions, even though they are frequently used, but should pertain to all morphological features, such as scalation, internal organs and color pattern.

The specific aims of studies involving the multivariate morphometric analysis of geographic variation vary widely. However, many such studies have, at least the implicit aim, of revealing "general" (i.e., predictive) patterns of racial differentiation. How many characters are needed to achieve this aim? Although I (Thorpe, 1976) and others have loosely suggested that many characters should be used, little precise work has been done on this problem. The number of characters needed may well depend on the complexity of the pat-

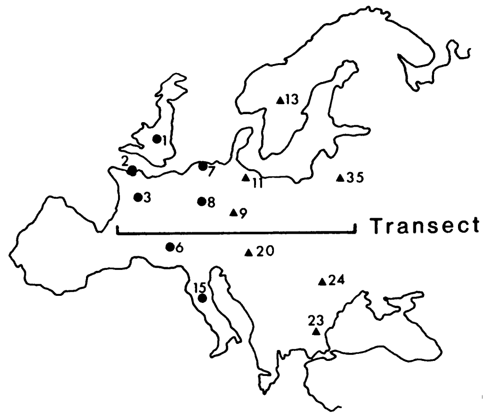

FIG. 1. Map of Europe showing the locality of populations 1, 2, 3, 6, 7, 8 and 15 (circles) of the western race and of populations 9, 11, 13, 20, 23, 24 and 35 (triangles) of the eastern race. The transect line used in Figure 7 is illustrated.

tern of geographic variation. Therefore, in this first paper of a series, I attempt to take a simple case and investigate the influence of character number on the portrayal of a simple pair of distinct parapatric races.

My primary questions are: (1) Is the congruence between multivariate studies asymptotic in relation to character number such that addition of further characters does not alter the pattern of geographic variation (i.e., does a stable "overall" pattern of geographic variation exist)? (2) If such a stable pattern exists, how many characters are necessary to reveal it and achieve congruence between different sets? At what point is it no longer cost effective to use more characters? I also attempt to explain the poor congruence of conventional (univariate) studies and the unreliability of conventional subspecies.

While the methods used in this study could be adapted to study the more general problem of taxonomic congruence (see Mickevich, 1978, 1980; Colless, 1980, 1981; Rohlf and Sokal, 1981; Schuh and Farris, 1981; Sokal and Rohlf, 1981; and other recent papers in *Systematic Zoology*), this study differs from those listed in two respects. First, the pattern of geographic variation is simple (i.e., essentially unidimensional), rather than a complex multidimensional or hierarchical pattern. Second, the geographic position of the population is directly pertinent since it is the pattern of geographic variation that is of interest.

METHODS

I have selected for analysis a distinct pair of parapatric races of grass snake, *Natrix natrix*, in Europe (Fig. 1). An east-west transect (Fig. 1) across this geographic region shows two distinct races such that a flat valley in the west abuts a flat plateau in the east (Thorpe, 1979, 1980a). I refer to this as categorical (i.e., distinct from clinal) geographic variation. Sometimes this pattern is referred to as a "stepped cline," but I believe that this term is best limited to the case where there is a step in an otherwise smooth cline (i.e., a smooth unidirectional change of character score in space interrupted by a step). There is a very narrow zone of intergradation (Thorpe, 1979, 1980a) which is not represented in this study. If portrayed using a scatter diagram, eastern and western races appear as distinct aggregations (Thorpe, 1979, 1980b).

There is substantial geographic variation within the complete range of the eastern and western races, but seven populations from each race have been selected so that a simple pair of categories can be analyzed. The inclusion of the small island population of Jersey gives the western category a less compact appearance. Even though the Jersey population is something of a western outlier, it is nevertheless clearly part of the western race (Thorpe, 1979, 1984b). This east-west categorical pattern of geographic variation reflects a fundamental phylogenetic division within the species which can be related to geological events (Thorpe, 1979, 1984a). I have recognized these two races as separate subspecies.

This paper is based on the analysis of data recorded from male specimens, the only computer simulation being in the selection of data sets. Initially, over 160 characters were recorded, but these included characters (i.e., characters, not character states) derived from others. For example, the somite length of the liver is derived from the somite position of the anterior and posterior tips. To avoid difficulty in interpreting the percentage of significant characters this study was restricted to the "underived" characters that could be recorded from all 14 populations.

Ninety-three such characters were found, of which 71 showed statistically significant between-group variation by one-way analysis of variance. Only these 71 characters were used (Appendix). They encompass a wide range of morphological character types, including scalation, color pattern, internal morphology, dermal sense organs, dentition, and a few linear body proportions that have been adjusted for growth-independence by regression (Thorpe, 1975).

The multivariate pattern of geographic variation was assessed by principal coordinate/component analysis on the normalized population means. Since the characters reflect independent facets of the phenotype and generally have low within-population correlation with one another (Thorpe, 1976), principal coordinate analysis gives the same results (Thorpe, 1980b) as canonical analysis (which considers the within-group covariance).

The primary pattern of geographic variation between the 14 populations is simple; that is, it is essentially unidimensional because there are just two categories. Consequently, a quantitative measure of the congruence between the patterns of variation portrayed by two analyses is obtained by the absolute value of the product-moment correlation between the "first" principal coordinate of each (the term "first" or "first two" is used throughout this paper to refer to the principal coordinates associated with the largest eigenvalues).

I used two models for the selection and comparison of character sets. These are explained below.

Model A.—To investigate the influence of character number on congruence of geographic variation patterns, independent character sets were compared. This is achieved as follows. (1) $2n$ characters (where n is the number of characters in the set) were randomly selected from the total set of 71 characters; (2) this set of $2n$ characters was divided into two mutually exclusive sets of n characters each; (3) principal coordinate/component analyses were run on these two sets of n characters; (4) the congruence of these sets was computed as the absolute correlation of their first coordinates; (5) steps 1 to 4 were repeated 10 times for a given level of n; (6) the mean, maximum and minimum congruence of these 10 runs were then compared for a given level of n.

The maximum size of n is the integer value of half the total character set (i.e., 35 in this case). The number of characters, n, was varied from 1 to 35 (through progressions 2, 3, 4, 5, 6, 8, 10, 12, 15, 20, 25 and 30). Ten pairs of analyses were run for each level of n, thus requiring 280 principal coordinate/component analyses in all.

In the unique case of n equals 1, the absolute correlation between coordinates is the same as that between the individual characters. In addition to the 10 pairs of randomly selected characters used for Model A, the equivalent (between-group) correlation was also computed for all independent pairs of characters (i.e., $[71^2 - n]/2 = 2{,}485$ character pairs). These univariate correlations, commensurate with the other correlations in Model A, are presented as a histogram in Figure 2.

Model B.—If one considers the best available estimate of the pattern of geographic variation to be given by the analysis based on the maximum number of significant characters, this can be used as an end point against which to judge an analysis based on fewer characters. The procedure in this model was as follows: (1) n characters were randomly selected by computer from the total set of 71; (2) a principal coordinate/component analysis was run on this set of n characters; (3) the congruence between this analysis and the principal coordinate/component analyses based on the total 71 characters was computed as the absolute correlation between the first coordinates; (4) steps 1 to 3 were repeated 10 times for a given level of n;

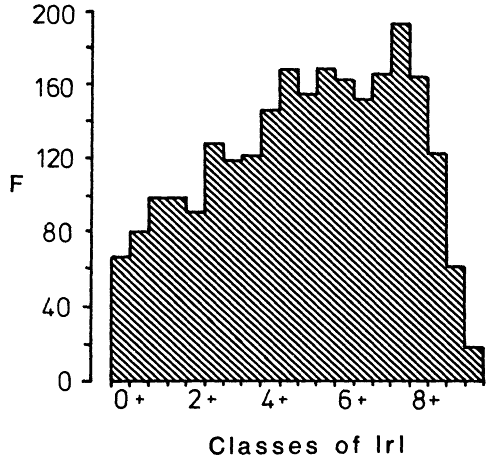

FIG. 2. Frequency histogram of absolute (between-population) correlations between independent pairs of characters. From 0 to 1, there are 20 classes of 0.05r width.

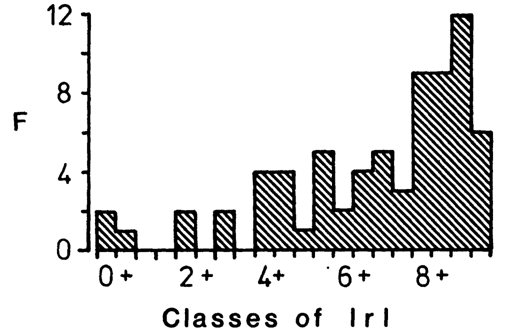

FIG. 3. Frequency histogram of absolute correlations between each of the 71 individual characters and the first principal coordinate of the analysis based on the total 71 characters. From 0 to 1, there are 20 classes of 0.05r width.

(5) the mean, maximum and minimum congruence of these 10 runs were then computed for a given level of n.

The number of characters, n, was varied from 1 to 65 (through progressions 2, 3, 4, 5, 6, 8, 10, 12, 15, 20, 25, 30, 35, 45 and 55). The process was repeated 10 times for each level of n thus generating 171 principal coordinate/component analyses when the total analysis was included.

In the unique case of n equals 1 the absolute correlation between the first coordinates of the n set, and total set, is the same as the absolute correlation between the individual character and the first coordinate of the total set analysis. In addition to the 10 randomly selected characters used for Model B, the equivalent correlations were also computed for the remaining 61 characters, and the histogram of the total 71 correlations is given in Figure 3. These "univariate" correlations are commensurate with the other correlations in Model B.

While it is evident that $|r|$ (absolute correlation between coordinates) must tend to unity as n tends to 71 (i.e., n_{max}), this does not determine the shape of the relationship between $|r|$ and n. Indeed one may use the shape of the relationship between $|r|$ and n to evaluate the use of the total character set as an end point against which to judge other analyses.

If the relationship between $|r|$ and n is linear, or if $|r|$ is still substantially increasing as n approaches n_{max}, then it is reasonable to suppose that the addition of characters beyond n_{max} would alter the results of a principal coordinate/component analysis. Under these circumstances one could have little confidence in the use of n_{max} as a basis for judging other studies where n is lower.

If, on the other hand, $|r|$ approaches unity in an asymptotic curve long before n approaches n_{max}, then it is reasonable to suppose that the pattern of geographic variation would not alter even if the number of characters were increased beyond n_{max}. In this situation, one could have confidence in n_{max} as a basis for comparing analyses using fewer characters.

Scatter diagrams of the first two principal coordinates from selected analyses are presented. These can be visually inspected to see if distinct aggregations exist that reflect the two races. The first coordinate scores are also plotted against the geographical transect in Figure 1. These transects are visually inspected for the existence of distinct categorical geographic variation. The figured scatter diagrams and transects are from those analyses (Model B) which have closest to the mean congruence for a given number of characters.

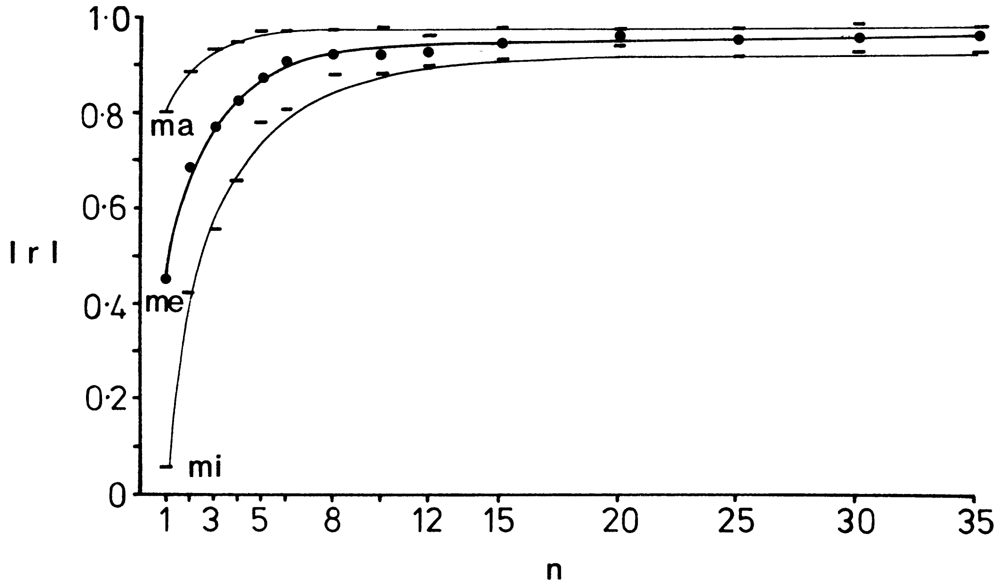

FIG. 4. Model A. Congruence between completely independent character sets. Vertical axis indicates the absolute correlation, $|r|$, between the first coordinates of pairs of analyses, while the horizontal axis indicates the number of characters (n) in the analyses. For a given level of characters, the mean (me) is indicated by a circle, and the maximum (ma) and minimum (mi) by bars. The asymptotic curves for the three parameters are fitted by formula 1.

However, all scatter diagrams and transects were visually inspected even though they are not all illustrated herein.

RESULTS

Model A.—The relationship between the congruence, $|r|$, of entirely independent character sets and the number of characters, n, clearly indicates that the maximum, mean and minimum congruence are all asymptotic in relation to character number (Fig. 4). The asymptotic curves of Figure 4 are all fitted by the formulas below for the linear and asymptotic forms, respectively:

$$|r| = a + b[1 - 1/e^{(n^c)}] \tag{1a}$$

and

$$|r| = \hat{a} + \hat{b}e^{(-n^c)}, \tag{1b}$$

where a is the intercept, b is the slope, $\hat{a}$ is the asymptote ($a + b$) and $\hat{b}$ is $-b$.

The mean congruence between univariate studies (Fig. 4) is poor, with a correlation of 0.45 between patterns of geographic variation when n is 1. This is what one would expect, when the histogram of all possible correlations of independent pairs of characters is evaluated (Fig. 2). The relationship between mean, $|r|$ and the number of characters is expressed by formula 1b, where the asymptote ($\hat{a}$) = 0.96, $\hat{b} = -1.38$, $c = 0.63$, and the residual sum of squares is 0.0015. Consequently, the mean congruence rises rapidly from 0.45 when 1 character is used, to 0.9 when only 6 characters are used, and approaches (within 0.01 of) the asymptote when as few as 13 characters are used.

The minimum congruence between analyses based on single characters (Fig. 4) is extremely poor with a correlation of 0.06. This is commensurate with the histogram of all possible correlations of independent pairs of characters (Fig. 2). The relationship between the minimum $|r|$ for the 10 pairs of analyses and the number of characters is expressed by formula 1b, where the asymptote ($\hat{a}$) = 0.93, $\hat{b} = -2.37$, $c = 0.59$, and the residual sum of squares is 0.0098. Consequently, the minimum congruence rises rapidly from $r = 0.06$ for

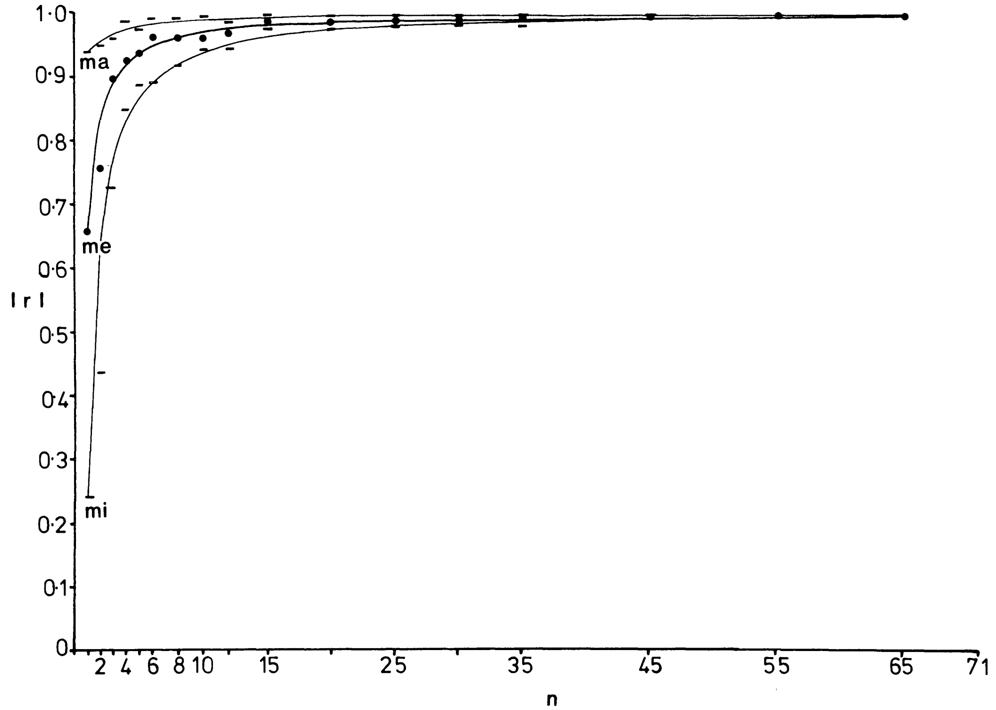

FIG. 5. Model B. Congruence between the analysis based on the total number of characters and analyses based on fewer characters. Vertical and horizontal axes and symbols as Figure 2. The asymptotic curves for the three parameters are fitted by formula 2.

1 character to $r = 0.8$ for 6 characters, and to $r = 0.9$ for 12 characters. At 18 characters, it approaches (within 0.01 of) the asymptote.

The maximum congruence between univariate studies is moderately high at 0.8 (Fig. 4). Some univariate correlations are greater than this, but selecting them with only 10 runs is improbable. The relationship between the maximum $|r|$ for the 10 pairs of analyses and the number of characters is expressed by formula 1b, where the asymptote $(\hat{a}) = 0.98$, $\hat{b} = -0.50$, $c = 0.76$, and the residual sum of squares is 0.0006. Consequently, the maximum congruence rises steadily from $|r| = 0.80$ at one character to $|r| = 0.95$ at four characters to approach (within 0.01 of) the asymptote at six characters.

Model B.—In model B, it is evident (Fig. 4) that the congruence parameters—whether maximum, mean or minimum—are all asymptotic in relation to the number of characters. The asymptotic curves of Figure 5 are all fitted by the formulas below for the linear and asymptotic forms respectively:

$$|r| = a + b(1 - 1/n^c) \quad (2a)$$

and

$$|r| = \hat{a} + \hat{b}n^{-c}, \quad (2b)$$

where a is the intercept, b is the slope, $\hat{a}$ is the asymptote $(a + b)$ and $\hat{b}$ is $-b$. Since the spread of the congruence varies very substantially with character number, the minimum and mean curves are fitted by weighting with the reciprocal of the standard deviation of the congruence for a given number of characters. Little difference between the goodness of fit of the various formulae was found for the maximum values, so formula 2 was used for the sake of consistency.

The average congruence between the 10 univariate studies and the "total" study was only moderate at $|r| = 0.65$, but this is commensurate with the histogram of all such correlations (Fig. 3). The relationship between the number of characters and the mean congruence is expressed as formula 2b where the asymptote ($\hat{a}$) = 1.0, $\hat{b}$ = −0.37, c = 1.0, and the residual sum of squares = 0.056. Consequently, in this near hyperbolic curve ($c \simeq$ unity), the mean congruence rises very sharply from 0.65 when one character is used, to almost 0.9 when three characters are used, and to over 0.96 when eight characters are used. The curve then gently flattens to its asymptote.

The minimum congruence between the 10 analyses based on a randomly selected single character and the "total study" was very poor at $|r| = 0.24$. Once again, this is commensurate with the histogram depicting the complete set of these correlations (Fig. 3). The relationship between the number of characters and the minimum congruence is expressed as formula 2b where the asymptote ($\hat{a}$) = 1.0, $\hat{b}$ = −0.84, c = 1.1, and the residual sum of squares = 0.296. Once again this curve is close to hyperbolic so the congruence rises sharply from 0.24 when 1 character is used, to r = 0.9 when 7 characters are used, and to 0.96 when 15 characters are used. The curve then gently flattens to its asymptote.

The maximum congruence is fairly high even for the univariate studies ($|r| = 0.93$) which is generally commensurate with the distribution of all such correlations (Fig. 3). The relationship between the number of characters and the maximum congruence is expressed by formula 2b, where the asymptote ($\hat{a}$) = 1.0, $\hat{b}$ = −7.37, c = 0.61, and the residual sum of squares is 0.0005. Consequently, the maximum congruence rises slowly from 0.93 at one character to 0.98 at four characters, and gently flattens to its asymptote.

Scatter diagrams and geographical transects.—Figures 6 and 7 portray the principal coordinate analyses of Model B that are closest to mean congruence for a given number of characters. These give a visual portrayal of the patterns of geographic variation, and indicate the close relationship between the correlation of the first coordinates and visual interpretation of the existence of racial categories. There is a close relationship between the two; consequently, the scatters and transects from every run for each level of n were plotted and visually inspected to see if the existence of the two racial categories was apparent. This, of course, has an element of subjectivity in it, but is useful nonetheless.

When the total number of characters are used and the results are portrayed in a scatter diagram (Fig. 6; $n = 71$), clear aggregations corresponding to the two racial categories are indicated. Even though the "tightness" of these aggregations may decrease slightly as the number of characters decreases, it is not until the number of characters are reduced to below 10 that these distinct aggregations may begin to disintegrate. For example, in Figure 6 (n = 8) one of the populations from the west has an "eastern" population as its nearest neighbor. A complete analysis of the scatter diagrams indicates that when one character is used, none of the 10 runs indicates the racial categories. When 10 or more characters are used, all of the runs indicate the racial categories (albeit loosely in some cases). Hence, when scatter diagrams are used, the frequency of analyses showing the racial categories increases from f = 0% (n = 1), to f = 30% (n = 2), f = 40% (n = 3), f = 50% (n = 4), f = 50% (n = 5), f = 80% (n = 6), f = 90% (n = 8), and f = 100% ($n \geq$ 10).

The geographical transect from the analysis based on the total 71 characters (Fig. 7; $n = 71$) shows distinct parapatric racial categories. The distinctiveness of the categorical or "stepped cline" pattern may decrease as the number of characters decreases, but it is not lost until the number of characters is reduced to below eight (Fig. 7; $n = 4$). A complete analysis of the geographical transects reveals that for the 10 runs for each level of n, the frequency of analyses revealing the racial categories increases from f = 0% (n = 1), f = 20% (n = 2), f = 70% (n = 3), f = 70% (n = 4), f = 80% (n = 5), f = 90% (n = 6) and f = 100% ($n \geq$ 8).

When too few characters are used, the

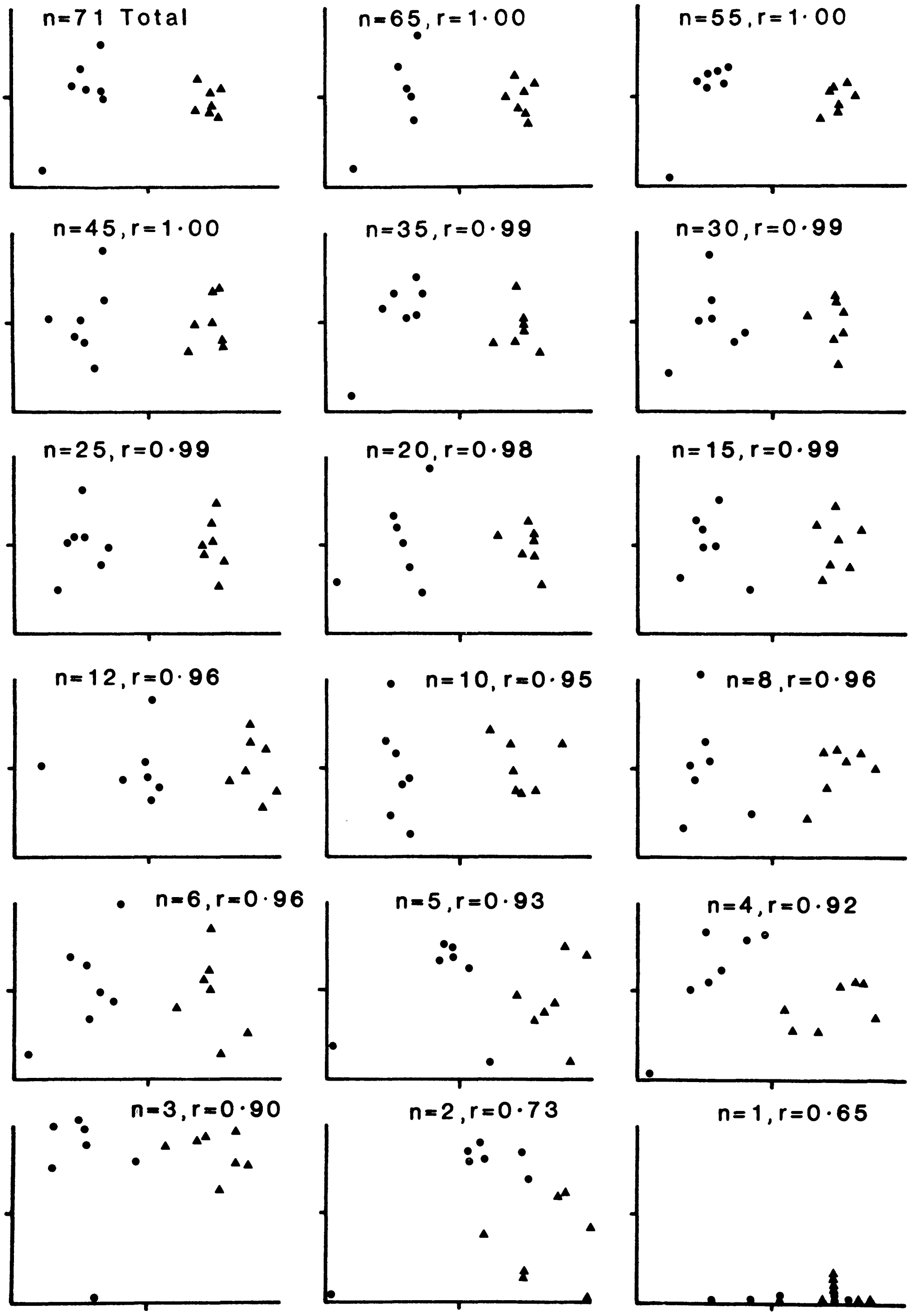

FIG. 6. Scatter diagrams of first (horizontal) and second (vertical) principal coordinates based on various numbers of characters. Circles = western race; triangles = eastern race; n = number of characters; r = absolute correlation between the first principal coordinate of that analysis and the first principal coordinate of total, 71-character analysis (i.e., Model B). The analyses selected to represent a given value of n are those that have an $|r|$ closest to the mean for that given number of characters.

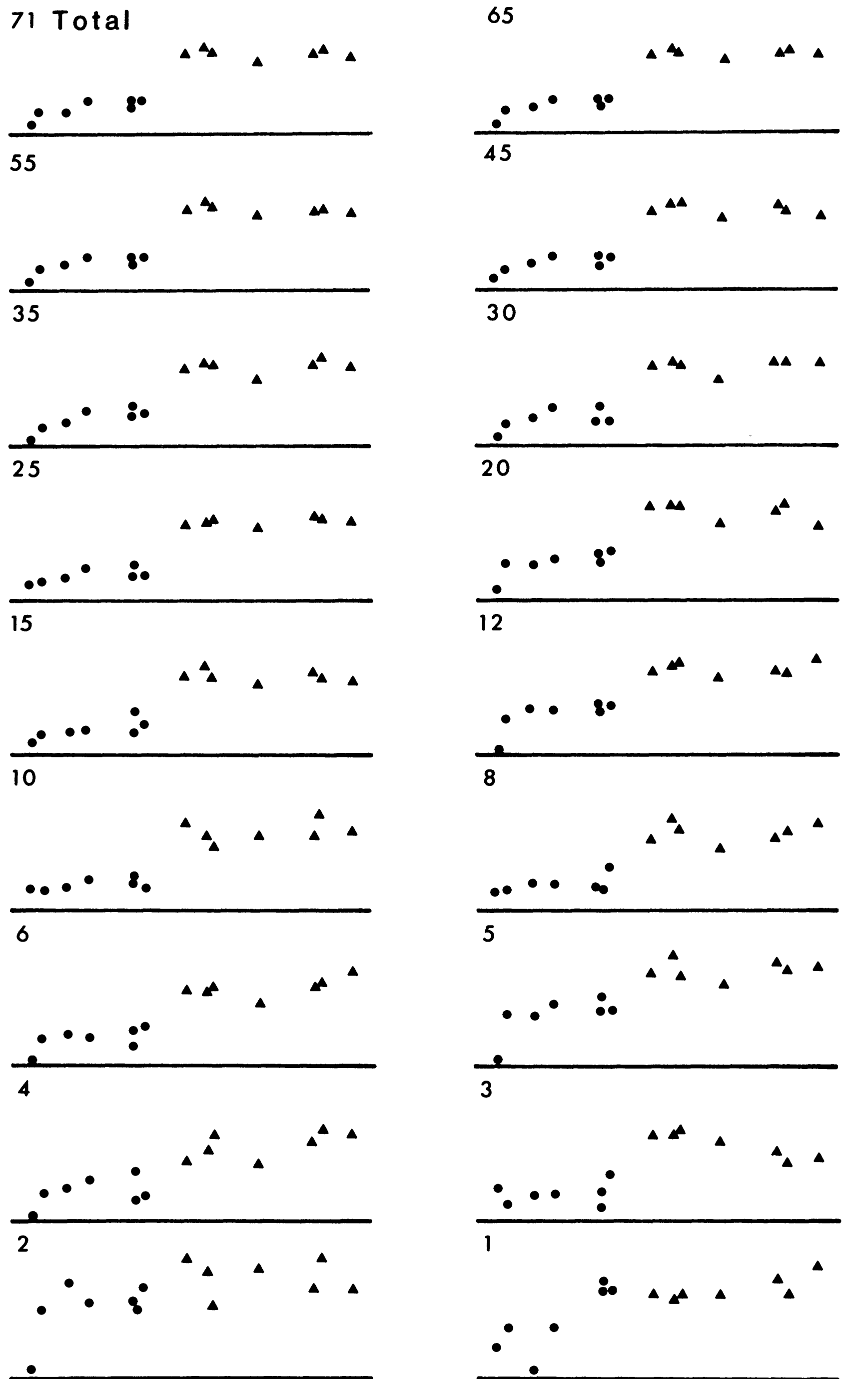

FIG. 7. Geographical transects (horizontal) of first coordinate scores (vertical) of the analyses in Figure 6. The number of characters on which the analysis was based is indicated, and the Model B correlation can be obtained from Figure 6. The circles are from the western race and triangles from the eastern race. The order of the localities along the transect (Fig. 1) is as follows: 2, 3, 1, 6, (15, 8), 7, 9, 11, 20, 13, 23, 24 and 35.

pattern may be "misrepresented" as clinal, rather than categorical. However, if a categorical pattern is revealed, it may contradict the real eastern and western categories (e.g., Fig. 7; $n = 1$). Consequently, the univariate analysis would be completely misleading if interpreted as indicating the general pattern of racial differentiation.

DISCUSSION

Based on these analyses, it is quite clear that the congruence between patterns of geographic variation is asymptotic in relation to character number. The evidence unambiguously indicates that the addition of other statistically significant characters drawn from the wide range of features utilized would not alter this overall pattern. Consequently, for the populations under consideration the concept of a stable, "overall" pattern of geographic variation is strongly supported.

The results of both Model A and Model B support the above contention, but the rigorous condition of completely independent sets required by the former model makes the results particularly convincing. Again, the characters are generally independent within groups, so that high between-group correlation is not determined by high within-group correlation (Thorpe, 1976); that is, generally the same feature (e.g., size or increase in growth) is not measured in a variety of different ways to produce characters correlated highly within-group and therefore between-group (i.e., similar patterns of geographic variation).

How many characters are required to elucidate this simple categorical pattern of geographic variation? It is evident that the number of characters required for high congruence between independent sets and high congruence with the analysis based on the total number of characters is noticably low (i.e., the congruence asymptotes are reached at an early stage; Figs. 4 and 5). However, to answer this question specifically one must first consider how the pattern is to be elucidated (scatter and transect) and what parameters (e.g., mean, minimum congruence) are to be used, because the answer varies according to these contingencies.

The maximum is the least useful of the three parameters for answering this question. Inspection of the histograms corresponding to both Model A (Fig. 2) and Model B (Fig. 3) indicates that, even for univariate studies, the potential maximum congruence is high. This is to be expected if there is a deep-seated, stable pattern of geographic variation. One would expect some individual characters to correspond closely to this stable pattern (Model B; Fig. 3), and be highly (between-group) correlated to other such characters (Model A; Fig. 2). The probability of revealing this pattern or obtaining this high congruence with univariate, as compared to multivariate, studies is an entirely separate question.

The mean congruence is a useful parameter insofar as its position is not biased by the number of runs (10) upon which it is based. However, the minimum congruence from a given number of characters (n) is also of value, even though one can expect the minimum to be depressed as the number of repeated runs is increased. Since there are 10 runs for each level of n, the probability of obtaining equal or better congruence than that indicated by the curve fitting the minimum congruence of Figures 4 and 5 is 90%.

Inspection of the transects (Fig. 7) indicated that one can use as few as eight characters to be at least 90% confident of revealing the racial categories. Similarly, inspection of the scatter diagrams (Fig. 6) indicates that as few as 10 characters will do the same. A greater degree of confidence would of course require a higher number of characters.

Therefore, around 10 characters is the minimum required for 90% confidence, with the transects needing slightly fewer characters than scatter diagrams for a given level of confidence. While one may reveal these categories with even fewer than 10 characters, the probability of doing so decreases. Moreover, up to a point, the clarity of the pattern generally improves as the number of characters increases.

However, this begs the ancillary question, "At what point is it no longer cost effective to use more characters?" In Model A the asymptote for the minimum is approached (i.e., within 0.01) when 18 characters are used. Beyond this point, it may not be cost effective to add more characters, as each additional character only raises the congruence by $0.0005r$. Similarly, for Model B the minimum curve indicates a congruence of $|r| = 0.97$ using 18 characters, which is sufficient to reveal the pattern of distinct racial categories regardless of whether transects or scatter diagrams are used. Increasing the number of characters beyond this point gives approximately the same increase in congruence per unit character (i.e., $0.0006r$) as in Model A. Of course, increasing the confidence by increasing the number of runs should slightly alter the shape of the minimum curve, such that a greater number of characters are indicated.

Not all of the recorded characters showed significant differences between geographic populations. Since 71 out of 93 characters showed significant geographic variation, a given number of characters in the above discussion should be multiplied by 93/71 (1.31) to indicate the appropriate number of characters that had to be recorded to obtain that number of significant characters. This ratio of significant to insignificant characters has little comparative meaning for other species but does indicate the deep-seated nature of the pattern of variation.

Given that some individual characters have a high correlation to the analysis based on the total number of characters (Model B; Fig. 3) and that some pairs of single characters are highly correlated (Model A; Fig. 2), why do conventional univariate studies have poor congruence with other such studies (e.g., the disagreement of univariate subspecies; Thorpe, 1980a, 1984b) and why do conventional univariate studies generally disagree with their multivariate counterparts (Clover, 1979; Thorpe, 1979, 1980a, 1984b)? Although the methodology of these "conventional" studies is generally flawed (Thorpe, 1980a, 1984b), the current study reveals that the answer partly lies in the relative probability of obtaining the high congruence with univariate as compared to multivariate studies.

With univariate studies (Fig. 2) the probability of obtaining congruence between independent characters equal or greater than the asymptotic maximum congruence of Model A ($|r| = 0.98$) is only 2,485/2 ($P = 0.0008$). The probabilities of obtaining the asymptotic mean congruence and asymptotic minimum congruence of Model A are 0.005 and 0.0165, respectively. Therefore, it is most improbable that univariate studies can match the congruence of multivariate studies based on an adequate number of characters. Indeed, between univariate studies, the probability of obtaining a correlation of even $|r| = 0.9$ is only 0.03.

Similarly, with Model B, even though the frequency distribution of correlations between all individual characters and the "total analysis" has a strong right-hand skew with a mode at the 0.900/0.949 category, the probabilities of obtaining a single character with a correlation of at least 0.93, 0.95, 0.96, and 0.97 are 0.15, 0.08, 0.03, and 0.0, respectively. Consequently, even though a few individual characters have a high congruence with the "total analysis" and could show the races (categorical variation) in transect or scatter, they were not included among the 10 randomly selected characters because they occurred too infrequently.

It is evident that, even where the simple pattern of geographic variation is deep-seated (Thorpe, 1984a), widespread among characters, and stable, it is unlikely that a single character can adequately depict this general pattern of geographic variation. Moreover, the transects show that analyses based on too few characters can be misleading if taken as being predictive (i.e., as representing a reliable pattern that can be used in the erection of subspecies or reconstructing vicariant events, etc.). For example, the transect based on four characters (Fig. 7; $n = 4$) indicates a rather clinal pattern, while the transect based on one character (Fig. 7; $n = 1$) shows an east-west categorical pattern but with the boundary between parapatric forms entirely different from the stable pattern. It is relevant that the major conventional study of this species complex (Mertens, 1947) indicates subspecies (implied categorical variation) in this region, but with the boundary between subspecies in the "wrong position" (i.e., in disagreement with the stable categories as was the univariate transect; Fig. 7; $n = 1$).

Congruence curves based on characters randomly selected from a multiplicity of character types, such as the curves in Figures 4 and 5, may provide a suitable baseline against which to judge studies based on single types of character. This may indicate whether or not a stable pattern exists and whether or not it is advisable to use more than one character type to elucidate a stable pattern.

This paper establishes a procedure to test for the existence of a stable (i.e., predictive) pattern of geographic variation and shows that the categorical pattern under consideration is stable. How general this is among various species and patterns of geographic variation can only be established by carrying out these procedures on different patterns (Thorpe, 1985a, b) and species.

All patterns of geographic variation cannot be expected to be as stable as the one in this study, which was caused by fundamental historical processes (i.e., phylogenesis; Thorpe, 1984a). For example, if a type of character responds to a current selection gradient (e.g., linear proportions in small endotherms responding to climatic conditions), one would not necessarily expect other types of character to show congruent patterns of geographic variation. Given a sufficient number of studies, it may be possible to show a relationship between the existence of stable patterns across several character types and whether phylogenesis or current ecological conditions (Thorpe, 1984a; Endler, 1983) are the causative factor for the geographic variation.

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APPENDIX

Characters

Scalation.—Number of ventral, subcaudal, posterior temporal and gular scales; lateral position of the reduction from 23–21, 19–17, 12–10, 10–8 and 4–2 dorsal scale rows; dorsoventral position of the reduction from 21–19, 19–17, 14–12, 12–10 and 8–6 dorsal scale rows.

Color pattern.—Extent of postocular streaking, light edges to dorsal scales, occipital line, parietal-occipital and temporo-labial marking; number of supralabial streaks, lateral blotches, dispersed lateral blotches, ventrolateral blotches, scale coverage of lateral blotches, dorsal blotches, ventrolateral blotches and nuchal marking; presence of longitudinal streaks; position of the upper and lower edge of the lateral blotches, lower edge of the dorsal blotch, anterior edge of the upper and lower lunar marking and anterior edge of the nuchal markings; the separation, length, streaking and upper and lower curvature of the nuchal markings; and the erosion of the lunar and nuchal markings.

Internal morphology.—Somite position of the thyroid, heart, bronchus, systemic junction, pancreas, posterior tip of the right lung, anterior and posterior tips of the liver and right and left testes and kidneys; size of the hemipenes, vestigial lung, cloacal gland and cystic duct.

Dentition.—Number of maxillary, palatine, pterygoid and dentary teeth.

Body proportions.—Head width, head length, head depth and body width regressed against snout-vent length.

Dermal sense organs.—Number of sensory pits on the temporal and postocular scales.