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BODY SHAPE METRICS AND ORGANISMAL EVOLUTION

LORRAINE M. CHERRY,[1,5] SUSAN M. CASE,[2] JOSEPH G. KUNKEL,[3]
JEFF S. WYLES[1,4] AND ALLAN C. WILSON[1]
[1]*Department of Biochemistry, University of California, Berkeley, California 94720*
[2]*Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts 02138*
[3]*Department of Zoology, University of Massachusetts, Amherst, Massachusetts 01003*
and [4]*Department of Biology, University of Houston, Houston, Texas 77004*

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It is becoming increasingly desirable to study organismal evolution in a quantitative way. The last decade witnessed the development and application of methods for quantifying molecular evolution (Lewontin, 1974; Nei, 1975; Wilson et al., 1977*a*), karyotypic evolution (Wilson et al., 1974, 1975, 1977*b*; Bengtsson, 1980; Maruyama and Imai, 1981) and speciation (Stanley, 1975, 1979; Levin and Wilson, 1976; Bush et al., 1977). A quantitative examination of the relation between these types of evolution and organismal evolution will thus become possible when a convenient method for measuring degree of difference at the organismal level has been developed. Such a method will permit more rigorous testing of hypotheses about the mechanism of organismal evolution than was possible with the more qualitative approaches of earlier workers (e.g., Mayr, 1963; Dobzhansky, 1970; Wilson et al., 1974; Stanley, 1979).

Two basic methods—quantal and quantitative—are available for the numerical comparison of whole organisms. Quantal (i.e., discrete) traits seem unsuitable for estimating overall degree of difference at the organismal level for the reasons given by Cherry et al. (1979). Furthermore, numerical taxonomists, the chief users of quantal methods, are more concerned with delineating and discriminating among closely related taxa (Sneath and Sokal, 1973) and with cladistic analysis (Hennig, 1966) than with the measurement of overall morphological difference.

Quantitative traits seem more appropriate for the study of morphological distance (Cherry et al., 1979). Such traits fall in the domain of morphometrics (Blackith and Reyment, 1971). Quantitative geneticists have developed the most explicit approaches to explaining the genetic and environmental sources of quantitative variation within species (Mather and Jinks, 1971). Morphometrics has also been applied to the interpretation of differences between species, forming a bridge between the study of physiological function, development and the evolutionary forces that have been involved in anatomical change (Oxnard, 1973; Gould, 1977; Bookstein, 1978). Although this approach has often concentrated on a particular body part such as the hominoid skull (e.g., Howells, 1973), there has been a growing interest in the morphometric comparison of whole organisms (Cherry et al., 1978; Oxnard, 1979; Douglas and Avise, 1982).

Our approach makes use of quantitative linear traits that enabled previous workers to compare the body shapes of frogs (Jameson et al., 1966; Jameson and Richmond, 1971; Cherry et al., 1978). The shape metric introduced by Cherry et al. (1978) has been termed the M statistic (Atchley, 1980). This metric was evaluated by comparison with the classical taxonomic hierarchy, which was assumed to summarize the intuitive judgements of classical taxonomists about overall degree of morphological difference among organisms. The striking result was a strong correlation between M (i.e., degree of differ-

[5] Present address: Department of Cell Biology, University of Texas System Cancer Center, M.D. Anderson Hospital and Tumor Institute, Texas Medical Center, Houston, Texas 77030.

ence in body shape) and distance in the taxonomic hierarchy (Cherry et al., 1978). The implication was that M may be a measure related to degree of difference at the organismal level.

In the present article the same approach is applied to a broader selection of tetrapod vertebrates. Furthermore, since public debate (Cherry et al., 1979; Findley, 1979; Atchley, 1980; Kunkel et al., 1980) has called into question the adequacy of M and suggested that Mahalanobis distance is a more appropriate metric, we now compare the M statistic to three other metrics (including Mahalanobis distance) for estimating body shape difference. These comparisons are based on more than 20,000 measurements taken on 184 taxa of mammals, lizards and frogs. The metrics differ from one another according to the amount of information and expense required for their computation. We present empirical evidence that simple metrics, which do not correct mathematically for trait correlation, currently provide the better estimates of morphological distance.

We also illustrate the potential value of simple metrics for examining the mechanism of organismal evolution, by employing the proportional distance (Δ) to conduct a preliminary test of the hypothesis that morphological change is concentrated in speciation events.

Materials and Methods

Specimens.—Mammalian measurements were taken on skeletons located at the Museum of Vertebrate Zoology (Berkeley), the American Museum of Natural History (New York), Harvard Medical School (Boston), the University of California at San Diego (La Jolla), and the University of California at Davis. Frog measurements were taken on whole specimens located at the American Museum of Natural History, the Museum of Vertebrate Zoology, the Museum of Comparative Zoology (Cambridge), University of Michigan Museum of Zoology (Ann Arbor), and the United States National Museum (Washington, D.C.). Lizard measurements were taken on whole specimens located at the Museum of Vertebrate Zoology.

The taxa used in this study are listed in the Appendix, Table 1. Because of space limitations, we do not list the museum numbers, sex or age of any specimen. For each taxon, the specimens examined were adult and the two sexes were represented about equally. (Sexual dimorphism will be the subject of a separate publication.)

Measurements.—Eight linear traits measured on each specimen were head width, head length, eye to nostril, nostril to lip, shank length, forearm length, toe length, and length of the vertebral column. These traits, as measured on mammalian skeletons, are described in Cherry et al. (1978). The frog traits are described in Jameson et al. (1966). The traits measured on lizards are similar to those used in frogs, with the exceptions mentioned below.

While we aimed at measuring homologous traits, this criterion was not always strictly met. Practical considerations dictated that closely related, but not strictly homologous, measurements be taken in some cases. Thus, toe length is defined as the maximum length of the fourth toe measured from the proximal side of the metatarsal tubercle in frogs; as the length of the third metatarsal in mammals; and as the length of the foot, measured from the distal end of the tibia to the distal end of the longest toe in lizards.

Calculation of Relative Trait Lengths.—In order to concentrate on shape changes alone and ignore size changes, the trait lengths from each individual were normalized. For each individual, j, a given trait length, a_{ij}, was divided by the sum of all p trait lengths in that individual. The resulting value, x_{ij}, is termed the relative trait length:

$$x_{ij} = a_{ij}\left(\sum_{i=1}^{p} a_{ij}\right)^{-1}. \qquad (1)$$

To calculate for a group of n individuals the mean value of the relative trait length, x_i, one sums the x_{ij} values over all n individuals and divides the sum by n:

$$x_i = n^{-1} \sum_{j=1}^{n} x_{ij}. \quad (2)$$

The units in which the x_i values are expressed are parts per ten thousand, eliminating any decimal remainder by rounding off (see Appendix, Table 1). All further manipulation is of these transformed data.

Description of the Metrics.—One statistic which figures heavily in many of the metrics used is the mean difference, d_i, between trait i in species X and Y, for traits $i = 1, 2, \ldots, p$:

$$d_i = x_i - y_i \quad (3)$$

where x and y are the respective means of the ith relative trait length in species X and Y, respectively.

The four distance metrics considered here differ from one another in the amount of information which must be retained from the original data set. Manhattan distance (Farris, 1972), H, is computed from the d_i values with equation 4:

$$H = 100 \sum_{i=1}^{p} |d_i|. \quad (4)$$

The proportional distance, Δ, is related to the Canberra metric (Sneath and Sokal, 1973):

$$\Delta = 200p^{-1} \sum_{i=1}^{p} |d_i|(x_i + y_i)^{-1}. \quad (5)$$

Both means and variances of the relative traits are required for the computation of the previously described M statistic (Cherry et al., 1978):

$$M = p^{-1} \sum_{i=1}^{p} |d_i|\sigma_i^{-1}. \quad (6)$$

Mahalanobis distance (D), a multivariate measure of distance, requires estimation of means, variances and covariances (Mahalanobis, 1936). It is most conveniently described in terms of matrix algebra. If d is a $p \times 1$ column vector of the trait differences, d_i, defined in equation 3, and S is a $p \times p$ residual covariance matrix for traits in the two species, X and Y, then the Mahalanobis distance for the two species is given by the matrix algebraic equation:

$$D = \sqrt{d'S^{-1}d}. \quad (7)$$

Since the relative trait lengths sum to ten thousand, by definition, a full $p \times p$ covariance matrix would be algebraically singular and not allow an inverse to be calculated. For this reason, in the calculation of D it was necessary to drop the last trait, vertebral column length, after having used it to calculate the relative trait lengths.

Application of the Metrics to the Data.—From a biometrical point of view, one might like to have all comparisons independent of each other, but this is practically impossible since it would not allow many comparisons of interest to be done. Alternatively, one could compare every taxonomic unit to every other one but this would be time-consuming and expensive, since the number of possible pairwise comparisons increases as the square of the available number of taxonomic units. A representative selection of species with which to make pairwise comparisons was made as follows: for any comparison of one taxonomic group of rank R with another, we used at least one species from each subordinate taxon of rank $R-1$ (see Appendix, Table 2).

Choice of Taxonomic Classification.—The taxonomic relationships of the animals used in this study are illustrated in the branching diagram in Figure 1. This diagram is based on the following sources: Simpson (1945), Goin and Goin (1962), Griffiths (1963), Romer (1966) and Liem (1970).

For comparison with morphological distance estimates, ordinal values were assigned to taxonomic ranks as follows: population (0.5), subspecies (1), species (2), genus (3), subfamily (4), family (5), superfamily (6), suborder (7), order (8), cohort (9), subclass (10), and class (11).

Results

Trait Lengths

This study is based on 21,936 measurements made on 184 vertebrate taxa. A summary of these measurements appears

in Table 1 of the Appendix. For each taxon, the Appendix gives the number of individuals measured, the mean value of the relative trait length (x) for each of the eight traits, the mean value of the total length of the eight traits per individual, and a code number. A traditional classification for these taxa appears in Figure 1.

Empirical Evaluation of Metrics

From the measurements we estimated the morphological distances between many pairs of taxa. To choose the most appropriate metric for estimating morphological distance, we evaluated some statistical properties of each metric and compared the distance values with an independent assessment of the degrees of morphological similarity. The results of four such empirical tests appear below.

1. Metric Stability.—A factor of both theoretical and practical importance in estimating morphological distance is the stability of the estimate. A good metric will consistently give the same distance value when independent samples of the same size are used. One effect of a small sample size is to increase the variability of a distance estimate. We sought that metric which would behave most consistently with small independent samples. The test described below shows major differences in the stability of the four morphological distance metrics.

This test used eight taxa with sample sizes greater than or equal to 36. These eight taxa were grouped into four discrete pairs. We randomly divided each taxon into six subgroups of six individuals each. For the four pairs, six independent distance estimates, based on sample sizes of six for each taxon, were compared by computing the coefficient of variation for each group of estimates (Table 1).

The proportional distance metric, Δ, had the smallest coefficient of variation (14%). For Manhattan distance and the M statistic, the coefficients were slightly larger (16% and 20%, respectively). The coefficients of variation for Mahalanobis D varied widely. They ranged from 31% to 55%, with an average of 38%, suggesting that estimates of D are unreliable for small samples.

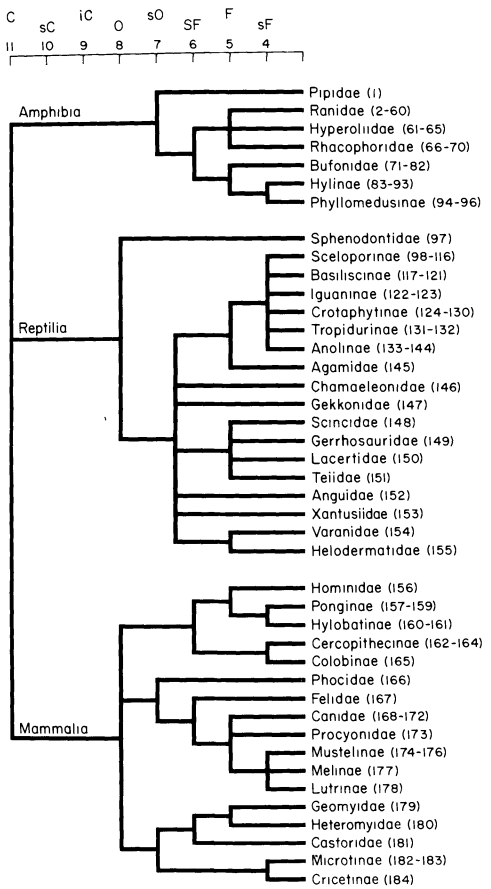

FIG. 1. Branching diagram representing taxonomic relationships of the frogs, lizards and mammals measured for this study. This is not a phylogenetic tree, rather it is a diagrammatic representation of the taxonomic classifications proposed by Simpson (1945), Goin and Goin (1962), Griffiths (1963), Romer (1966) and Liem (1970). The abbreviations and numbers at the top of the diagram refer to taxonomic ranks: class (C, 11), subclass (sC, 10), cohort (iC, 9), order (O, 8), suborder (sO, 7), superfamily (SF, 6), family (F, 5), subfamily (sF, 4). The code numbers in parentheses refer to the taxa listed in Table 1 of the appendix.

2. Statistical Bias and Sample Size.—A different error in distance estimates results when a metric systematically under- or overestimates the distance, leading to statistical bias. To evaluate this possible source of error, we compared the mean

TABLE 1. *Variability of morphological distances estimated from small samples.*

Taxa compared[2]	Coefficient of variation[1]			
	Manhattan distance (H)	Proportional distance (Δ)	M statistic	Mahalanobis distance (D)
Rana cascadae a and *R. cascadae* c (14–16)	19	14	17	28
R. sylvatica a and *R. aurora* a (7–53)	21	18	20	39
R. clamitans 2 and *R. utricularia* (21–57)	14	13	14	31
R. montezumae and *Bufo compactilis* (28–76)	10	10	28	55
Mean	16	14	20	38

[1] Defined as one hundred times the standard deviation divided by the mean.
[2] Code numbers, in parentheses, for the pairs of taxa are taken from Table 1 of the Appendix.

value computed from the same small samples of each pair with the value obtained for the corresponding large sample ($n \geq 36$ for each taxon). At these large sample sizes, all metrics should be accurate and unbiased. As shown in Table 2, small samples gave slightly biased estimates of the Manhattan and proportional distances. The M statistic overestimated the distances by a little more (16%). Mahalanobis distance, however, overestimated morphological distance seriously and systematically by about 120% with small sample sizes. This overestimation was as severe in intraspecific comparisons as in interfamilial ones.

3. Triangle Inequality.—The most desirable metrics are those which obey the triangle inequality (Shepard, 1980). When all pairwise comparisons are made among three species, the distances between each pair of species can be represented as the sides of a triangle. The triangle inequality states that the length of a single side (i.e., one distance) cannot be greater than the sum of the other two. Failure to meet this a priori criterion makes results difficult to interpret geometrically, and invalidates the

TABLE 2. *Small samples and statistical bias in morphological estimates.*

Metric	Morphological distance[1]				Mean ratio
	14–16	7–53	21–57	28–76	
Manhattan distance					
Mean for small[2] samples	3.31	4.02	7.05	16.55	
Large[2] sample	3.16	3.67	7.19	16.41	
Ratio	1.05	1.10	0.98	1.01	1.04
Proportional distance					
Mean for small samples	4.61	5.90	7.65	14.82	
Large sample	4.44	5.31	7.74	14.44	
Ratio	1.04	1.11	0.99	1.03	1.04
M statistic					
Mean for small samples	0.96	1.26	1.84	3.24	
Large sample	0.86	1.02	1.71	2.68	
Ratio	1.12	1.24	1.08	1.21	1.16
Mahalanobis distance					
Mean for small samples	6.96	8.07	8.60	22.15	
Large sample	3.27	3.46	5.04	8.75	
Ratio	2.13	2.33	1.71	2.53	2.18

[1] The taxa compared are those listed in Table 1; here, they are designated by code numbers (see Table 1, or Table 1 of the Appendix for the code).
[2] Small ($n = 6$); large ($n \geq 36$)

TABLE 3. *Morphological distance and the triangle inequality.*

Metric	Number of violations
Manhattan distance (H)	0
Proportional distance (Δ)	0
M statistic	76
Mahalanobis distance (D)	121
Violations common to M and D	39

technique as an accurate measure of shape differences.

For the triangle inequality test, we examined 1448 trios of taxa drawn from a wide variety of frogs, lizards and mammals. As shown in Table 3, both Manhattan distance and the proportional distance satisfied the triangle inequality in all cases. Mahalanobis distance (D) had the highest number of violations (8%), significantly greater than the M statistic had (5%).

Violations of the triangle inequality by M and D were not independent. Of the 76 triplets which produced a violation by M, 39 also had a violation by D. In contrast, the expected number of violations in common is only 6, if the M and D violations are independent. This six-fold excess of shared violations is very highly significant ($P < .005$) and implies that both M and D are heavily influenced by a common factor.

From the results of sections 1 and 2 above, one might expect that violations in the triangle inequality would stem solely from small sample size. However, two factors seem to contribute to violations of the triangle inequality: sample size and another factor. There are 158 triplets in which the triangle inequality is violated. Of these, 63% involved at least one taxon with a sample size less than ten. In contrast, only 31% of the 39 triplets which had a violation by both M and D involve such a small sample size. Therefore, the excess of shared triplet violations is probably caused by a factor other than small sample size. This factor is probably the variance, which enters the calculation of both M and D.

4. Correlation with Taxonomic Distance.—The fourth test examined the correlation between morphological distance and taxonomic distance, i.e., distance in the traditional taxonomic hierarchy. We assume that this latter distance represents the collective judgement of past generations of taxonomists concerning the degree to which taxa differ at the organismal level (see Discussion).

A significant correlation exists for all metrics between metric value and taxonomic distance for all vertebrates tested (Table 4). A similar picture emerges when the analysis is confined to a single class of vertebrates, such as frogs, lizards or mammals (Table 4). The highest correlations are for Manhattan distance and the proportional distance. In contrast, Mahalanobis distance generally gives the weakest correlation.

Figure 2 illustrates the approximately linear relation of both D and Δ to taxonomic distance. It also shows that the variability in Δ value increases with taxonomic rank. A comparable effect (termed heteroscedasticity) is also observed for H, M and D values.

TABLE 4. *Correlation between morphological distance and taxonomic rank.*

Group	Correlation coefficient			
	Manhattan distance	Proportional distance	M statistic	Mahalanobis distance
Frogs	0.78	0.79	0.76	0.69
Lizards	0.81	0.87	0.71	0.68
Mammals	0.68	0.69	0.73	0.71
All vertebrates[1]	0.78	0.79	0.74	0.70

[1] Interclass comparisons included (see Fig. 2)

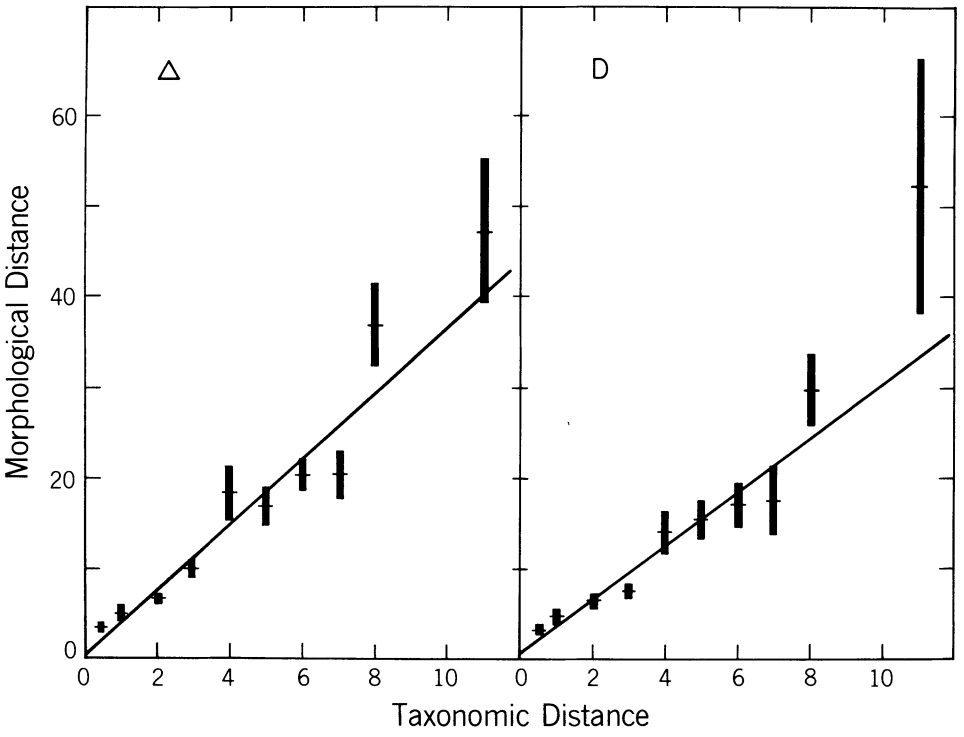

FIG. 2. Dependence of two measures of morphological distance (Δ and D) on distance in the traditional taxonomic hierarchy for frogs, lizards and mammals combined. Each number on the abscissa refers to the taxonomic rank at which morphological comparisons are made. See Figure 1 and Table 6 for the correspondence between number and rank. See Table 2 of the appendix for a list of the taxa compared at each level. The vertical bar around each mean shows the standard error.

A more quantitative analysis of the data allows us to calculate how much of the variability in morphological distance is explained by linear relationships with taxonomic distance. Total variability within each metric for all taxonomic comparisons from rank 0.5 to rank 8 was partitioned into four independent components: (1) a linear component assuming a single regression line for the combined frogs, lizards and mammals; (2) a linear component comprising the additional variability explained by using three separate regression lines for the three groups; (3) a component representing departures from linearity; and (4) an unexplained residual component. As seen in the first row of Table 5, most of the variability in H, Δ, M, and D is explained by assuming a single regression line for all vertebrates. In calculating the significance of these proportions of variability a reduction of the residual degrees of freedom was used to compensate for species used more than once in a comparison. By considering separate regression lines for frogs, lizards and mammals, as opposed to a single line, a small but significant additional component of variability is accounted for in all metrics (see Row 2). All of the metrics have small but significant nonlinear components of variability. In this connection we note the mean Δ value for subordinal comparisons (see Fig. 2, taxonomic distance 7); the 95% confidence interval for this mean is below the regression line. This example of a departure from linearity contributes to the small nonlinear component of variability estimated in Row 3 of Table 5. Next, we consider the category of variability unex-

TABLE 5. *Partition of variability in metric value as a function of taxonomic distance.*

Sources of variability	Degrees of freedom	Percent of variance explained: Manhattan distance	Proportional distance	*M* statistic	Mahalanobis *D*
Taxonomic distance					
Combined regression[1]	1	56.9	57.3	52.6	48.9
Separate regression[2]	4	6.9	13.4	11.6	14.4
Departures from linearity	18	6.4	8.9	10.1	6.8
Unexplained sources	70	29.8	20.4	25.6	30.0

[1] Variability explained by one linear regression for all vertebrates tested, excluding interclass comparison (rank 11).
[2] Additional variability explained by going from one to three linear regression lines for frogs, lizards and mammals (cf. Table 4).

plained by taxonomic rank (see Row 4). It is the variability about the means for each taxonomic rank, considering frogs, lizards and mammals separately. These means appear for Δ in Table 6. A high value for this component of variability indicates that the metric does not accurately measure morphological distance as predicted by the taxonomic hierarchy. Δ exhibits the lowest value for this component, as shown in Row 4 of Table 5.

Equivalence of Taxa

Since the eight traits were chosen originally by Jameson et al. (1966) for their ability to discriminate among frogs, it might be expected that morphological distance based on these traits would be greater for frog taxa than for mammal or lizard taxa of comparable rank. This expectation is not fulfilled. Rather, the slope of the line relating morphological distance (Δ) to taxonomic distance is significantly lower ($P < .01$) for frogs (2.0) than for lizards (3.5) or mammals (3.9).

As a general rule, in terms of metric value, lizards of a given taxonomic rank are roughly equivalent to mammalian taxa of comparable rank. In contrast, frog taxa of the same rank usually differ slightly less in body proportions than comparable lizard or mammal taxa. The greatest discrepancies occur at the subfamily and family levels (see Table 6), where there is a strong tendency for mammals to differ more in body shape than do frogs or lizards. The most striking cases of equivalence of taxa occur at the subspecies and species levels. Species within a genus, for instance, generally differ in proportional distance to about the same extent in all three major groups.[6]

DISCUSSION

The above results help us to choose an efficient and economical way to study evolution at the organismal level. They focus attention on the utility of simple metrics and small numbers of linear traits. We have examined four metrics, each with different attractive features. The Manhattan distance, H, is the simplest metric examined. However, because it is unweighted, it inadvertently emphasizes changes in large traits. The proportional distance, Δ, attempts to weight smaller traits more equitably but has the disadvantage of being more affected by the error of measuring small traits. Both H and Δ are simple to compute, requiring only a table of mean traits (Appendix, Table 1) for calculation. They ignore the variability of traits within a taxon.

By contrast, the M statistic and Mahalanobis distance (D) use the intrataxon variability of traits in their computation. Mahalanobis distance satisfies demands for corrections for correlations between traits

[6] Care must be taken in using the porportional distance as the basis for taxonomic judgements. Although the current work indicates that taxonomic categories of comparable rank in different groups may be roughly equivalent, there is nonetheless a considerable amount of overlap among the Δ values found at contiguous taxonomic levels within a group (see Fig. 2 and Table 6).

but M, being similar to the Coefficient of Racial Likeness (Pearson, 1926), does not estimate intertrait correlations.

Reliability of Metrics

Of the four types of metrics examined here, Manhattan distance and proportional distance proved the most reliable. Both always satisfied a minimum requirement of reliability, the triangle inequality (Shepard, 1980), and produced consistent, unbiased estimates of morphological distance, even with small samples.

The Manhattan distance, H, is constrained to obey the triangle inequality by its algebraic definition (seen clearly by geometric analogy). The proportional distance, Δ, is not so constrained. Conditions were observed in preliminary calculations in which Δ did violate the triangle inequality. These violations occurred whenever a trait length was zero for one taxon. When a trait length was zero, it inflated the contribution of that particular trait to the overall distance for two of the pairs involved in the triangle inequality test. This often led to a violation. Thus, it is important to use traits that do not vanish in any of the taxa to be compared. This consideration led us to exclude the eye-tympanum measurement used by Cherry et al. (1978), because it could not be made in all taxa considered here.

Both M and D violated the triangle inequality often enough to question their routine use as metrics. Many of their violations involved comparisons with small sample sizes but another factor was implicated. This other factor is likely to be the variances which are shared by the calculating of both M and D. Furthermore, it was shown that small sample sizes led to systematic overestimates of M and D.

Mahalanobis D was widely recommended to us as a measure of organismal difference but it did not perform as well as the other metrics in this study. There are important theoretical reasons for this result, discussed elsewhere by Kunkel et al. (1980) and Rao (1980), concerning the mathematical assumptions on which the metric is based. Briefly, the calculation of Mahalanobis D requires the accurate estimation of covariance matrices, and these covariance matrices must be homogeneous among the species compared. These requirements can generally be met only when large samples are available and closely related species are compared. Many comparisons made in the current study necessarily involve distantly related species represented by small samples. In such cases the morphological distance estimates obtained from Mahalanobis D would be expected to be unstable and unreliable. We observed this to be the case. A reevaluation of the role of Mahalanobis D in systematic and evolutionary biology may thus be in order. As a reviewer commented, "It is no doubt true that simple distance measures are often the best and should be used more frequently than they are."

Trait Selection and Trait Number

Taxonomists advocate the use of large numbers of traits in order to discriminate among closely related taxa (Mayr, 1969; Sneath and Sokal, 1973). Our goal, however, is to produce a morphological distance scale applicable to higher as well as lower taxonomic categories. We have found that a small number of quantitative traits is sufficient for this purpose, if they represent all major parts of the body. Our original study of frogs, humans and chimpanzees was based on nine such traits (Cherry et al., 1978). Here we have eliminated one of them (see above) and further studies indicate that as few as five quantitative traits can be used to estimate morphological distance accurately (Kunkel et al., unpubl.), thereby raising the hope of applying this approach to incomplete fossil specimens.

Trait Correlations

Our study suggests that, in research with small samples and few traits from all major parts of the body, intertrait correlations can be ignored. This suggestion is in contrast to prevailing views, which are critical of metrics that do not correct for correlations between traits (e.g., Atchley, 1980). The critics have been concerned

with demonstrating significant differences between closely related taxa. Although a significance test requires that correlations be corrected for, the need for a correction disappears when such a test is not an objective.

Covariance correction is essential to remove the inordinate weighting of a particular part of the body when many traits from that part are measured. Since a crucial element in our approach is the use of only a few traits from all parts of the body, such corrections are of limited value. These few traits are sufficient to capture the shape difference between taxa. It is notable, also, that the correlations of traits differ substantially among higher taxonomic categories (Kunkel et al., 1980), so that conventional correction for correlations lacks theoretical justification (Rao, 1980).

Practical Implications

Important practical results are realized if one accepts that correcting for intertrait correlations is inappropriate for comparisons of shape. The best linear and unbiased metrics in our analysis, Δ and H, require only trait means for each taxon. These are extremely simple to calculate and do not necessitate extensive sampling. A sample size greater than five produces only modest gains in accuracy for each equivalent effort of data collection. Variance and covariances, however, require large sample sizes for precise estimation.

When means are a sufficient statistic for calculating a distance metric (i.e., H and Δ), benefits other than small sample size requirements accrue. To calculate D one must know the means, sample size and covariance matrix for each taxon. The sheer bulk of the data precludes their publication, even for modest lists of taxa. If means of a small number of common traits are adequate to compare shape, a comprehensive treatment of shape change becomes realizable and publication of the data on which it is based becomes feasible. Accordingly, Table 1 of our appendix, which occupies four pages, contains all the data needed to calculate H and Δ for every possible pairwise comparison of 184 taxa. By contrast, the information needed to calculate M and D as well would require 14 additional pages. In addition to enabling workers to verify the assertions of a study without enormous expenditures of computer and human time, this approach will renew interest in trait lengths published in current as well as older works.

Relation to Taxonomic Distance

Our examination of the relation between morphological distance and distance in the taxonomic hierarchy is based on the assumption that the chief role of taxonomy in past decades was to summarize information concerning the degree of phenotypic similarity among species. We are aware that taxonomists also strive to incorporate into classifications information about the branching order and times of divergence of the lineages leading to modern species. There is much debate about the relative importance that degree of phenotypic difference and time of divergence should have in taxonomic classifications (Mayr, 1974; Mickevich, 1978). However, it is widely agreed that until the last decade, most classifications were mainly phenetic. For our study it was important to use such classifications since taxonomic distance would then be predominantly a measure of phenotypic difference.

Cain and Harrison (1958), in an early discussion of some of the problems associated with doing this type of study, emphasized the need to separate the estimation of similarity from phylogenetic considerations. The objective of evaluating our metrics and ultimately examining the relation between morphological change and time[7] could not have been achieved if we had simply examined the correlation

[7] Preliminary tests indicate that morphological distance is not related in a simple way to time of divergence, except at very low taxonomic levels. We therefore stress that one must be cautious about using these distances for the construction of evolutionary trees or quantitative analysis of rates of evolution (Cherry, 1980).

between metric value and taxonomic distance in a phylogenetic classification. Had we used phylogenetic classifications, distance in the taxonomic hierarchy would have been more seriously confounded with time of divergence.

Overall Difference at the Organismal Level

The correspondence that we observed between morphological distance and the classical taxonomic hierarchy is paralleled by the results obtained in Oxnard's (1979) study of body proportions in 36 taxa of primates. As he points out, classical taxonomists did not usually consider body proportions when ranking taxa. Rather, such judgements were made intuitively, based on a thorough knowledge of the detailed anatomy of particular organs and functional complexes. Since body shape differences correlate with these intuitive estimates, anatomical changes may frequently entail changes in body proportions and vice versa. Thus, estimates of body shape difference may provide an approximation of overall difference at the organismal level.

Body shape comparison will not always be a reliable guide to overall degree of difference. This is most evident from our unpublished studies of dog breeds. The proportional distance between the German shepherd and bulldog ($\Delta = 16$), for instance, is comparable to that between taxonomic subfamilies although these two breeds belong to the same species. The proportional distance value correctly shows that they are very different in body shape. This is the result of artificial selection on body shape. In internal anatomy, physiology and behavior, these breeds have presumably not diverged as much as have vertebrates in different subfamilies. This is a case in which body shape and total organismal biology have not changed in unison. In general, however, as noted in the previous paragraph, the two types of change, i.e., change in body shape and overall organismal biology, appear to be highly correlated in non-domesticated species. Consequently, body shape metrics may usually reflect overall degree of difference at the organismal level and thus permit the testing of hypotheses about evolutionary mechanisms.

Rates of Morphological Evolution and Speciation

The present work sets the stage for using H or Δ as a measure of morphological distance in research on evolution at the organismal level for a wide range of land vertebrates. In the future, we intend to study the relation between morphological distance and time of divergence.[8] To illustrate the potential value of such studies, we present below the result of using one simple method to obtain rates of morphological evolution for frogs, lizards and mammals.

Consider first the mean morphological distance (Δ) among species within a genus (see Table 6). The Δ values are rather similar for frogs, lizards and mammals, viz. 6.7, 6.7 and 5.9, respectively. Next, consider the estimates of mean generic age (t) published by Bush et al. (1977) on the basis of fossil evidence, viz. 26.4 million years for frogs, 20.1 million years for lizards and 6.5 million years for mammals. Hence, the mean rate of morphological evolution (Δ/t) within extant genera appears higher for mammals (0.88) than for lizards (0.36) or frogs (0.25). This quantitative approach confirms the qualitative impression of many biologists that the tempo of organismal evolution in mammals has been higher than in lizards or frogs.

In Figure 3 the above estimates of mean rates of morphological evolution are plotted against the mean rates of speciation estimated for extant genera of frogs, lizards and mammals by Bush et al. (1977). A straight line with a positive slope can be drawn through the three points and this is consistent with the view that speciation can accelerate morphological evolution (Mayr, 1963; Wilson et al., 1977*b*; Gould, 1977; Stanley, 1979). Further, from the

[8] See footnote number 2.

TABLE 6. *Morphological distance and the equivalence of taxa.*

Taxonomic rank of comparison	Mean morphological distance (Δ)			Equivalent taxa[2]
	Frogs	Lizards[1]	Mammals	
0.5, populations	2.9	5.0	—	
1, subspecies	4.9	4.8	5.5	FLM
2, species	6.7	6.7	5.9	FLM
3, genera	9.1	8.2	12.8	FL
4, subfamilies	10.8	13.3	25.6	
5, families	10.8	14.8	25.5	
6, superfamilies	15.3	22.0	22.1	LM
7, suborders	17.3	—	22.7	
8, orders	—	30.6	39.5	

[1] The term lizards, as used here, includes both the order Rhynchocephalia and conventional lizards (order Squamata).
[2] F = frogs, L = lizards, M = mammals. Equivalent taxa do not differ in Δ value at the .05 level, using the Students *t* test.

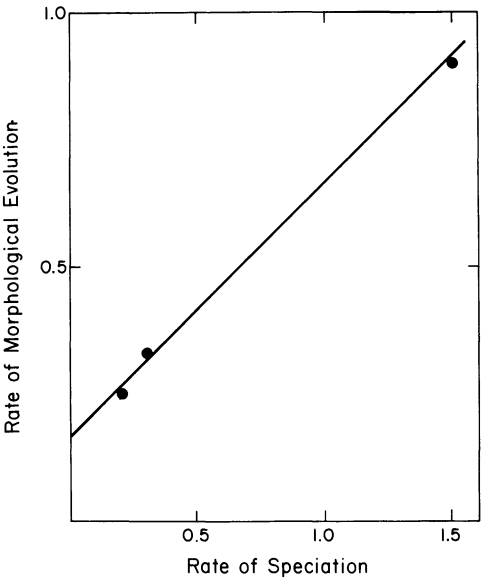

FIG. 3. Dependence of morphological evolution on speciation for three groups of extant genera, namely frogs, lizards and mammals. The ordinate gives, for each group of genera, the mean interspecific Δ value for species within a genus divided by the mean generic age in millions of years. The mean Δ values are from Table 6 and the mean generic ages are from Bush et al. (1977). The abscissa gives, for each group of genera, the mean number of speciation events per million years within a lineage (from Bush et al., 1977). The point nearest the origin is for frogs, the next point is for lizards and the point farthest from the origin is for mammals.

line's intercept on the ordinate, one could infer that morphological evolution usually takes place slowly in the absence of speciation.

The result shown in Figure 3, and based on 17 genera, might seem to contrast with that obtained in a recent study of two fish genera. According to Douglas and Avise (1982), the mean interspecific morphological distance is equivalent for *Notropis,* a speciose genus, and *Lepomis,* a species-poor genus. Although these two genera differ by a factor of two as regards net speciation rate (R), it is important to recognize that the true rate of speciation (S) is defined by equation 8,

$$S = R + E, \tag{8}$$

where E is the extinction rate (Stanley, 1975; Bush et al., 1977). Since no estimate is available for E in the fish case, the possibility exists that *Notropis* and *Lepomis* do not differ in speciation rate and, therefore, do not provide an opportunity to test the hypothesis of a relationship between morphological change and speciation.

Our study illustrates the potential value of using an approach that allows morphological evolution to be compared in representatives of different taxonomic Classes, like mammals and frogs. By comparing morphological evolution between Classes, which differ greatly in biological properties, one raises the probability of encountering large differences in rates of evolution. Mammals differ from frogs by about five-fold as regards the true rate of speciation (Fig. 3). Such large differences in rate may be a prerequisite for adequate testing of hypotheses concerning the relationship of morphological evolution to speciation.

We do not suggest that the results shown in Figure 3 suffice to establish the relationship implied by the straight line. Proof for such a relationship will require more evidence and a deeper analysis[9] of the dependence of Δ on t. Our aim in this final section of the paper has merely been to point out briefly how the quantitative study

[9] See footnote number[7].

of morphological evolution may provide a new way of testing theories about the mechanism of evolution.

Summary

Quantitative methods of comparing body shapes were applied to 184 taxa of frogs, lizards and mammals. The shape comparisons were based on measurement of eight linear traits from all major parts of the body.

Four metrics were tested for their usefulness in quantifying overall shape difference. The metrics vary in the amount of information required for their calculation. Two of them (H and Δ) require only mean trait lengths, the third (M) requires means and variances of trait lengths and the fourth (D) requires means, variances and covariances of trait lengths to be calculated.

The most stable and unbiased estimates of distance were given by the simplest metrics, H and Δ. In addition, these two metrics satisfied the triangle inequality, whereas M and D frequently violated this relationship. All four metrics proved to be highly correlated with distance in the classical taxonomic hierarchy. Mahalanobis D, the most widely recommended multivariate distance metric, was the least adequate in these empirical tests. The superiority of H and Δ as distance metrics arises because they are not subject to the errors introduced in estimating variances and covariances.

According to the Δ metric, species within frog genera differ in body proportions to about the same extent as do species within genera of lizards or mammals. Analogous findings were made at the subspecies level. At other levels of the taxonomic hierarchy, however, equivalence of frog, lizard and mammal taxa with regard to body shape difference was not observed; rather, frogs tend to be more alike in body shape than is the case for lizards or mammals at a given level in the taxonomic hierarchy.

The strong correlation between metric value and distance in the taxonomic hierarchy could imply that body shape difference is an indicator of degree of overall morphological difference. Oxnard (1979) reached a similar conclusion from an analogous study of 36 primate taxa.

From the average value of Δ for interspecific comparisons within genera as well as mean generic age (t) for each group, we calculated that the mean rate of morphological divergence (Δ/t) has been higher for mammalian genera than for genera of lizards or frogs. These rates appear to be linearly related to published values for the average rates of speciation within groups of extant genera. This finding is consistent with the view that morphological evolution is concentrated in speciation events.

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Corresponding Editor: S. J. Gould

APPENDIX

Table 1. Mean trait lengths for 184 taxa.

TAXONOMIC GROUP[a] and CODE NUMBER	SAMPLE SIZE (n)	MEAN RELATIVE TRAIT LENGTHS[b], (x_i)								MEAN SUM OF TRAIT LENGTHS[c]
		HW	HL	E-N	N-L	SL	FA	TL	VL	
CLASS AMPHIBIA										
Pipidae										
1 Xenopus laevis	8	1153	813	184	241	1767	762	1837	3244	159
Ranidae										
2 Dicroglossus occipitalis	20	1397	1273	291	330	1732	735	1889	2352	214
3 Hylarana temporalis	10	1258	1284	323	248	2028	779	1849	2231	159
4 Rana areolata 1	19	1563	1324	334	289	1724	719	1797	2249	201
5 R. areolata 2	20	1314	1099	274	302	1845	718	1845	2603	241
6 R. areolata 3	16	1514	1273	264	310	1709	755	1885	2290	214
7 R. aurora 1a	50	1257	1113	252	290	1957	785	2015	2331	216
8 R. aurora 1b	12	1261	1132	259	304	1963	778	1997	2306	180
9 R. aurora 1c	16	1254	1058	251	283	1998	759	2063	2333	225
10 R. aurora 2	21	1191	1086	239	291	2015	799	2076	2303	166
11 R. berlandieri	21	1180	1078	259	285	2044	752	1978	2425	206
12 R. blairi	26	1126	1061	258	309	2130	719	1993	2404	183
13 R. boylii	14	1308	1058	278	291	2067	776	1905	2316	150
14 R. cascadae a	41	1210	1125	257	277	1953	802	2012	2366	147
15 R. cascadae b	19	1226	1043	245	286	2054	788	1981	2377	161
16 R. cascadae c	36	1230	1036	236	300	2002	781	1984	2431	165
17 R. cascadae d	15	1237	1058	239	300	1987	780	1999	2399	156
18 R. cascadae e	26	1213	1068	249	292	2012	781	1977	2407	160
19 R. catesbeiana	17	1435	1259	233	326	1761	734	1939	2313	238
20 R. clamitans 1	16	1284	1234	268	270	1875	737	1945	2388	181
21 R. clamitans 2	49	1234	1193	288	305	1867	637	1994	2482	150
22 R. dunni	29	1327	1170	225	311	1767	732	2034	2434	213
23 R. grylio	27	1284	1345	271	260	1762	718	2029	2330	206
24 R. japonica	11	1109	1047	240	246	2000	797	2134	2427	148
25 R. johni	14	1292	1304	274	263	1854	809	1904	2300	148
26 R. maculata	22	1220	1151	272	284	2063	792	1931	2286	167
27 R. megapoda	21	1322	1121	233	283	1818	799	2030	2395	232
28 R. montezumae	43	1290	1133	245	325	1783	740	2060	2425	183
29 R. muscosa	23	1272	1083	244	288	1991	757	1965	2401	151
30 R. onca	18	1345	1226	240	344	1806	752	1895	2393	129
31 R. palmipes	35	1321	1283	313	284	1911	746	1891	2251	166
32 R. palustris	29	1151	1121	250	299	2064	742	2014	2358	146
33 R. pipiens	20	1159	1054	237	300	2031	727	2068	2423	185
34 R. pretiosa a	38	1237	1056	221	303	1892	742	2036	2512	165
35 R. pretiosa b	16	1247	1069	234	281	1904	780	1995	2490	178
36 R. pretiosa d	17	1188	1092	249	309	1977	802	2029	2354	135
37 R. pretiosa e	11	1207	1056	250	303	1868	754	2007	2555	172
38 R. pretiosa f	25	1209	1041	239	287	1904	776	2046	2498	135
39 R. pretiosa g	10	1205	1062	243	274	1895	797	2064	2460	159
40 R. pretiosa h	10	1213	1054	229	286	1865	786	2005	2563	151
41 R. pretiosa i	13	1244	1042	223	299	1873	785	2029	2506	180
42 R. pretiosa j	10	1209	1108	244	307	1968	738	1964	2462	138
43 R. pretiosa k	10	1238	1074	226	301	1853	735	2048	2526	164
44 R. pretiosa l	10	1250	1074	233	297	1878	717	2016	2534	154
45 R. pretiosa m	18	1208	1060	226	292	1874	793	1963	2584	168
46 R. pretiosa n	11	1182	1038	222	284	1899	813	1969	2594	172
47 R. pretiosa o	10	1190	1085	239	314	1903	779	2079	2410	138
48 R. pretiosa p	10	1198	1056	252	301	1866	769	2014	2544	172
49 R. pretiosa q	10	1204	1088	252	303	1746	793	1981	2632	138
50 R. pretiosa s	18	1226	1060	242	304	1834	752	2045	2538	165
51 R. pustulosa	17	1339	1227	255	333	1964	768	1827	2286	192
52 R. septentrionalis	27	1258	1163	221	304	1804	702	2054	2494	141
53 R. sylvatica a	38	1221	1082	220	259	2050	775	1971	2422	126
54 R. sylvatica b	18	1276	1093	209	297	1769	763	1976	2617	112
55 R. tarahumarae	25	1305	1161	267	336	1937	746	1896	2350	176
56 R. temporaria	18	1160	978	193	277	1894	794	2062	2642	168

[a] The classification parallels that in Figure 1.

[b] The abbreviations for traits are: HW (head width), HL (head length), E-N (eye to nostril), N-L (nostril to lip), SL (shank length), FA (forearm), TL (toe length), VL (length of the vertebral column excluding the tail). Relative trait lengths (see equation 1) are given in parts per ten thousand.

[c] Given in millimeters. This corresponds to the term $\sum_{i=1}^{p} a_{ij}$ from equation 1.

APPENDIX

Table 1. Mean trait lengths for 184 taxa.

TAXONOMIC GROUP[a] and CODE NUMBER	SAMPLE SIZE (n)	MEAN RELATIVE TRAIT LENGTHS[b], (x_i)								MEAN SUM OF TRAIT LENGTHS[c]
		HW	HL	E-N	N-L	SL	FA	TL	VL	
57 R. utricularia	39	1132	1139	257	292	2023	722	2113	2322	170
58 R. vibicaria	22	1215	1195	268	285	1805	843	1954	2436	175
59 R. virgatipes	30	1318	1273	264	279	1712	703	2030	2422	134
60 R. warschewitschii	11	1145	1396	327	235	2000	798	1807	2292	121
Hyperoliidae										
61 Afrixalus fornasinsi	19	1235	1076	402	232	1849	725	1684	2797	79
62 Hyperolius ahli	19	1319	1094	349	241	1983	725	1649	2640	84
63 H.puncticulatus	20	1290	1033	344	238	1820	830	1526	2920	82
64 H. viridiflavus	15	1142	917	305	237	1980	801	1697	2921	79
65 Leptopeltis christyi	19	1470	1239	323	288	1791	756	1642	2491	104
Rhacophoridae										
66 Chiromantis petersi	19	1214	1090	336	234	2038	728	1542	2818	135
67 C. rufescens	16	1177	1149	395	233	1971	712	1550	2813	125
68 C. xerampelina	14	1234	1059	317	241	1883	785	1509	2972	158
69 Rhacophorus gondoti	13	1368	1164	240	294	2083	764	1847	2240	220
70 R. leucomystax	16	1270	1271	421	216	2137	729	1598	2360	159
Bufonidae										
71 Bufo alvarius	11	1557	1195	280	354	1463	897	1500	2753	226
72 B. americanus	17	1529	1090	245	278	1521	1013	1655	2669	151
73 B. boreas	19	1411	1034	235	301	1461	929	1842	2786	211
74 B. bufo	20	1529	1092	229	298	1431	930	1752	2739	218
75 B. cognatus	19	1543	1051	271	303	1488	867	1610	2867	179
76 B. compactilis	40	1493	1055	288	310	1522	853	1593	2887	133
77 B. debilis	34	1448	1083	331	290	1573	801	1502	2971	93
78 B. marinus	15	1485	1133	272	327	1527	930	1574	2752	229
79 B. melanostictus	20	1526	1145	260	306	1520	1021	1545	2677	208
80 B. regularis	19	1460	1031	262	315	1547	848	1555	2983	202
81 B. viridis	17	1423	1015	244	297	1474	915	1747	2886	180
82 B. woodhousei	16	1500	1027	243	295	1611	864	1727	2732	190
Hylinae										
83 Hyla crucifer	20	1328	1292	340	284	1868	884	1432	2573	65
84 H. chrysoscelis	15	1400	1211	303	307	1778	899	1470	2631	103
85 H. eximia	19	1261	1170	291	296	1799	861	1591	2731	78
86 H. femoralis	20	1357	1297	327	301	1866	866	1405	2582	76
87 H. regilla 1	20	1332	1196	322	309	1817	888	1526	2610	91
88 H. regilla 2	20	1344	1205	308	311	1829	881	1520	2600	101
89 H. regilla 3	20	1288	1207	298	310	1806	903	1568	2619	84
90 H. regilla 4	20	1212	1138	285	295	1839	915	1696	2620	98
91 H. squirella	20	1301	1234	315	282	1921	831	1389	2726	78
92 Phrynohyas venulosa	24	1276	1086	320	245	1957	771	1594	2752	172
93 Pternohyla fodiens	23	1363	1157	318	291	1598	724	1682	2867	125
Phyllomedusinae										
94 Agalychnis callidryas	9	1289	1155	365	210	2085	927	1330	2638	152
95 Pachymedusa dachnicolor	16	1327	1151	312	262	1624	939	1441	2944	173
96 Phyllomedusa tarsius	12	1331	1113	308	223	1875	1128	1225	2797	206
CLASS REPTILIA										
Sphenodontidae										
97 Sphenodon punctatus	2	1201	1698	331	237	856	721	1164	3793	448
Sceloporinae										
98 Callisaurus draconoides	12	785	1099	312	116	1353	802	1987	3546	139
99 Cophosaurus texanus	12	831	1111	322	139	1333	796	1953	3516	129
100 Holbrookia maculata	12	881	1155	312	130	1220	820	1770	3711	110
101 Petrosaurus thalassinus	12	977	1397	397	132	1181	826	1453	3636	223
102 Phrynosoma m'calli	6	1013	1166	291	254	1295	892	1287	3802	129
103 P. platyrhinos	12	1015	1159	300	209	1196	862	1386	3873	148
104 Sator angustus	12	862	1391	409	113	1237	799	1606	3584	153
105 Sceloporus graciosus	6	938	1308	376	128	1145	730	1546	3828	99
106 S. jarrovi	6	1096	1358	352	121	1098	793	1380	3802	155

[a] The classification parallels that in Figure 1.

[b] The abbreviations for traits are: HW (head width), HL (head length), E-N (eye to nostril), N-L (nostril to lip), SL (shank length), FA (forearm), TL (toe length), VL (length of the vertebral column excluding the tail). Relative trait lengths (see equation 1) are given in parts per ten thousand.

[c] Given in millimeters. This corresponds to the term $\sum_{i=1}^{p} a_{ij}$ from equation 1.

APPENDIX

Table 1. Mean trait lengths for 184 taxa.

TAXONOMIC GROUP[a] and CODE NUMBER	SAMPLE SIZE (n)	MEAN RELATIVE TRAIT LENGTHS[b], (x_i)								MEAN SUM OF TRAIT LENGTHS[c]
		HW	HL	E-N	N-L	SL	FA	TL	VL	
107 S. magister	12	1023	1294	356	129	1166	837	1456	3739	188
108 S. occidentalis 1	6	983	1287	333	104	1243	777	1605	3668	158
109 S. occidentalis 2	6	983	1284	379	130	1184	781	1527	3733	122
110 Streptosaurus mearnsi	12	943	1344	417	96	1277	892	1440	3592	153
111 Uma inornata	12	887	1215	338	139	1314	826	1499	3782	169
112 Urosaurus graciosus	12	866	1369	410	125	1108	734	1595	3791	93
113 U. microscutatus	6	960	1406	371	143	1201	810	1494	3615	80
114 U. ornatus	6	912	1284	404	114	1159	769	1459	3898	107
115 Uta palmeri	4	891	1360	383	102	1273	829	1553	3609	121
116 U. stansburiana	12	934	1337	381	123	1245	748	1615	3617	90
Basiliscinae										
117 Basiliscus plumbifrons	1	754	1391	385	131	1642	751	2131	2815	298
118 B. vittatus	12	727	1284	396	115	1467	669	2110	3232	242
119 Corythophanes cristatus	1	919	1326	341	160	1458	897	1980	2921	182
120 C. percarinatus	2	879	1272	364	145	1371	758	1780	3430	159
121 Laemanctus serratus	1	864	1382	363	143	1482	816	1797	3153	231
Iguaninae										
122 Dipsosaurus dorsalis	6	808	1162	334	115	1257	692	1813	3817	219
123 Iguana iguana	6	651	1290	412	117	1237	876	1870	3547	359
Crotaphytinae										
124 Crotophytus collaris	16	1016	1406	374	141	1330	721	1714	3299	198
125 Gambelia silus a	24	999	1284	355	129	1235	718	1641	3638	210
126 G. silus b	10	969	1281	357	120	1311	731	1696	3534	199
127 G. wislizenii a	19	908	1320	397	116	1196	692	1659	3712	222
128 G. wislizenii b	4	879	1342	425	121	1219	663	1887	3465	228
129 G. wislizenii c	6	890	1344	428	116	1243	706	1755	3518	212
130 G. wislizenii d	4	966	1332	357	133	1226	672	1603	3711	203
Tropidurinae										
131 Tropidurus peruviensis	6	891	1291	351	131	1366	753	1733	3486	160
132 T. torquatus	6	912	1405	414	120	1264	776	1596	3512	145
Anolinae										
133 Anolis carolinensis	6	931	1757	627	145	1114	721	1342	3363	114
134 A. cybotes 1	11	1056	1485	431	133	1178	761	1702	3254	110
135 A. cybotes a	14	1014	1478	440	138	1279	784	1700	3167	130
136 A. cybotes b	20	951	1488	472	113	1254	761	1688	3274	114
137 A. evermanni	6	822	1552	563	93	1251	812	1554	3353	121
138 A. grahami	15	938	1505	565	102	1179	715	1579	3417	119
139 A. krugi	23	827	1446	517	115	1245	645	1768	3438	94
140 A. marcanoi	18	957	1462	450	131	1271	829	1685	3216	115
141 A. pulchellus	21	796	1596	577	95	1163	586	1659	3527	87
142 A. sagrei a	6	841	1502	526	100	1237	752	1596	3446	123
143 A. sagrei b	17	836	1354	399	98	1207	679	1761	3667	93
144 A. shrevei	17	961	1448	404	138	1174	731	1645	3499	93
Agamidae										
145 Agama stellio	6	1172	1523	314	130	1267	843	1520	3231	170
Chamaeleonidae										
146 Chamaeleo dilepis	6	919	1502	204	117	1134	1156	706	4261	191
Gekkonidae										
147 Coleonyx variegatus	6	913	1532	407	95	1067	840	879	4266	107
Scincidae										
148 Eumeces skiltonianus	6	898	1446	394	116	712	543	1194	4698	102
Gerrhosauridae										
149 Gerrhosaurus flavigularis	6	753	1310	390	85	843	528	1354	4736	129
Lacertidae										
150 Lacerta mellisellensis	6	787	1454	412	96	880	546	1486	4339	105
Teiidae										
151 Ameiva undulatus	6	819	1487	497	85	1098	690	1845	3478	195
Anguidae										
152 Gerrhonotus coeruleus	6	935	1527	365	101	711	576	939	4845	154

[a] The classification parallels that in Figure 1.

[b] The abbreviations for traits are: HW (head width), HL (head length), E-N (eye to nostril), N-L (nostril to lip), SL (shank length), FA (forearm), TL (toe length), VL (length of the vertebral column excluding the tail). Relative trait lengths (see equation 1) are given in parts per ten thousand.

[c] Given in millimeters. This corresponds to the term $\sum_{i=1}^{p} a_{ij}$ from equation 1.

APPENDIX

Table 1. Mean trait lengths for 184 taxa.

TAXONOMIC GROUP[a] and CODE NUMBER	SAMPLE SIZE (n)	MEAN RELATIVE TRAIT LENGTHS[b], (x_i)								MEAN SUM OF TRAIT LENGTHS[c]
		HW	HL	E-N	N-L	SL	FA	TL	VL	
Xantusiidae										
153 Xantusia henshawi	6	1032	1497	396	258	901	688	1041	4185	92
Varanidae										
154 Varanus niloticus	4	619	1411	348	148	868	687	1276	4644	328
Helodermatidae										
155 Heloderma suspectum	6	1049	1327	324	139	716	667	846	4932	385
CLASS MAMMALIA										
Hominidae										
156 Homo sapiens	16	590	703	149	116	2359	1673	481	3929	1578
Ponginae										
157 Gorilla gorilla	11	688	1134	247	215	1656	1971	446	3643	1791
158 Pan troglodytes	13	634	1083	174	247	1736	2011	507	3607	1458
159 Pongo pygmaeus	6	711	1123	201	273	1518	2361	639	3174	1431
Hylobatinae										
160 Hylobates hoolock	12	515	941	123	88	1759	2723	476	3375	936
161 H. lar	3	527	907	133	81	1857	2779	489	3228	838
Cercopithecinae										
162 Cercopithecus aethiops	9	556	949	173	101	1692	1592	517	4420	794
163 Macaca arctoides	5	624	1046	293	118	1555	1817	497	4050	845
164 M. nemestrina	13	615	1052	320	121	1712	1891	487	3802	931
Colobinae										
165 Presbytis entellus	4	540	816	138	74	1872	1798	559	4205	1090
Phocidae										
166 Phoca vitulina	5	637	1391	226	48	1135	796	478	5290	1306
Felidae										
167 Lynx rufus	8	515	1000	214	36	1468	1405	626	4737	1092
Canidae										
168 Canis latrans 1	6	413	1258	471	25	1341	1332	564	4596	1389
169 C. latrans 2	5	419	1294	484	30	1350	1424	571	4428	1356
170 C. lupus	6	470	1248	428	35	1316	1434	589	4480	1809
171 Urocyon cenereoargenteus 1	3	453	1348	410	21	1323	1203	417	4826	828
172 U. cenereoargenteus 2	10	463	1298	422	20	1327	1200	593	4675	904
Procyonidae										
173 Procyon lotor	10	646	1357	372	37	1539	1465	485	4100	783
Mustelinae										
174 Martes americana	13	532	1325	296	30	1258	992	527	5039	582
175 Mustela vison 1	8	520	1279	255	44	1066	847	464	5526	490
176 M. vison 2	6	540	1295	263	42	1058	831	451	5519	512
Melinae										
177 Taxidea taxus	6	681	1584	384	46	1024	1346	373	4561	762
Lutrinae										
178 Enhydra lutris	10	547	1068	200	83	1152	922	667	5362	1193
Geomyidae										
179 Thomomys bottae	9	530	1477	646	41	1002	1019	374	4912	256
Heteromyidae										
180 Dipodomys merriami	20	525	1386	973	98	1653	952	807	3606	199
Castoridae										
181 Castor canadensis	11	783	1340	500	71	1373	1179	595	4159	958
Microtinae										
182 Microtus californicus 1	10	537	1498	518	78	1110	932	453	4873	178
183 M. californicus 2	11	483	1379	457	80	1045	893	405	5259	217
Cricetinae										
184 Peromyscus mexicanus	20	560	1423	657	112	1274	952	582	4442	192

[a] The classification parallels that in Figure 1.

[b] The abbreviations for traits are: HW (head width), HL (head length), E-N (eye to nostril), N-L (nostril to lip), SL (shank length), FA (forearm), TL (toe length), VL (length of the vertebral column excluding the tail). Relative trait lengths (see equation 1) are given in parts per ten thousand.

[c] Given in millimeters. This corresponds to the term $\sum_{i=1}^{p} a_{ij}$ from equation 1.

APPENDIX

Table 2. Pairwise comparisons used to examine the relationship between taxonomic distance and metric value

TAXONOMIC LEVEL OF COMPARISON	PAIRS OF TAXA* (referred to by code numbers)						
0.5 (populations)	7-8	14-15	16-17	34-35	36-37	38-39	40-41
	42-43	44-49	45-46	47-48	53-54	125-126	128-129
	135-136	142-143					
1.0 (subspecies)	4-5	9-10	20-21	87-88	89-90	108-109	134-136
	134-135	168-169	171-172	175-176	182-183		
2.0 (species)	6-11	12-13	18-50	23-24	25-26	27-28	62-63
	66-67	69-70	71-72	73-74	75-76	83-85	84-86
	102-103	105-107	106-109	112-114	115-116	117-118	125-127
	131-132	134-138	138-141	140-144	160-161	163-164	168-170
3.0 (genera)	2-29	2-59	3-30	3-60	61-64	62-65	68-69
	91-92	92-93	95-96	98-99	101-104	108-111	110-113
	118-121	124-129	157-158	157-159	158-159	162-164	168-172
	170-172	174-175					
4.0 (subfamilies)	85-96	87-95	92-95	92-96	93-95	93-96	99-127
	100-134	108-118	117-125	122-138	123-129	124-132	157-160
	158-160	159-160	162-165	164-165	174-177	174-178	175-177
	175-178	177-178	183-184				
5.0 (families)	31-69	32-65	57-61	58-66	61-66	63-67	64-70
	65-68	77-95	78-93	82-88	100-145	123-145	124-145
	131-145	143-145	148-150	148-151	149-150	150-151	154-155
	156-157	156-158	156-159	156-160	168-173	170-175	172-173
	173-174	173-177	179-180				
6.0 (superfamilies)	2-80	22-94	51-79	52-95	55-92	61-83	66-96
	104-146	113-148	145-153	146-147	146-152	146-155	147-148
	147-153	148-155	150-152	152-153	153-155	156-164	158-162
	160-165	167-168	167-173	167-174	179-181	180-181	
7.0 (suborders)	1-56	1-63	1-67	1-81	1-92	1-95	166-167
	166-173	166-172	166-177	179-182	180-184	181-183	181-184
8.0 (orders)	97-99	97-118	97-124	97-143	156-170	157-166	159-179
	162-181	164-182	165-167	166-180	167-184	175-179	
11.0 (classes)	1-172	33-162	72-140	95-101	97-173	149-183	

* Each hyphenated pair of code numbers refers to a pair of taxa. The code numbers for taxa appear in Table 1 of the Appendix.