

ANNALS of CARNEGIE MUSEUM

CARNEGIE MUSEUM OF NATURAL HISTORY

4400 FORBES AVENUE • PITTSBURGH, PENNSYLVANIA 15213

VOLUME 54

6 DECEMBER 1985

ARTICLE 13

UTILITY OF MORPHOLOGICAL DISTANCE MEASURES AND CLUSTERING ALGORITHMS: A TEST USING PHYLLOSTOMID BATS

KAREN MCBEE

Rea Postdoctoral Fellow, Section of Mammals

ROBERT J. BAKER¹

Research Associate, Section of Mammals

STUART L. PIMM²

ABSTRACT

Results of three measures of morphological distance (M-statistic, Mahalanobis' D^2 , and Euclidean distance) are calibrated on the basis of three simple test criteria against nine taxa of phyllostomid bats whose morphological (phenetic) relationships are unequivocal. Eighteen different permutations of distance algorithm, data transformation, morphological measurement, and clustering algorithm were used to evaluate major criticisms that have been directed against morphological distance measures. The M-statistic is shown to be no less successful at meeting the test criteria than are the other two measures. However, the type of clustering algorithm used has a very definite effect on the representation of the measure of morphological distance on a one dimensional scale.

INTRODUCTION

Man's attempts to quantify his level of morphological distinctness from his nearest living relatives have been controversial. This contro-

¹ Address: Department of Biological Sciences and The Museum, Texas Tech University, Lubbock, TX 79409.

² Address: Graduate Program in Ecology, University of Tennessee, Knoxville, TN 37916. Submitted 8 April 1985.

versy stems, in part, from disagreement about which morphological characteristics should be used, how they should be transformed, and what distance metrics should be calculated from them. Cherry et al. (1978) described a measure of morphological difference, the distance statistic M , to compare the morphological relationships of frogs, chimpanzees, and humans. The M -statistic has been cited as more valuable than other similar statistics for "broad comparative studies of evolution at the organismal level" (Kunkel et al., 1980:1061), but has also received criticism on several points (Findley, 1979; Atchley, 1980; Cherry et al., 1982). More recently, Cherry et al. (1982) compared the facility of the M -statistic with three other distance metrics in accurately portraying morphological relationships of a broad selection of tetrapod vertebrates. They found all four distance metrics to be highly correlated with distance in a taxonomic hierarchy based primarily on a phenetic classification. They used such a wide variety of taxa, including many groups for which relationships are poorly understood, that the accuracy of the distance metrics may not be well represented in their tests. This study describes tests to evaluate the M -statistic and two more conventional methods (Mahalanobis' D^2 , Mahalanobis, 1936; and Euclidean Distance, Sneath and Sokal, 1973) by examining nine species of bats whose morphological features are so obvious that certain phenetic relationships should result from any valid measure of morphological distinctness. Additionally, we investigated the efficacy of type of measurement, transformation, and clustering algorithm in achieving a satisfactory classification. Two different sets of measurements were used. The first, labelled "bats" are those frequently used by bat taxonomists; the second, labelled "frogs" are ones considered applicable to all vertebrates, including those as specialized as frogs or apes (Cherry et al., 1978). A comparison of results from the two sets of measurements allows estimation of the extent to which choice of measurements affects results (Findley, 1979). Cherry et al. (1978) used a ratio transformation of their data to eliminate size as a factor *per se*. Our measurements were ratio and log transformed as well as untransformed in order to evaluate Atchley's (1980) criticism of the instability of ratio transformations. Combinations of measurements and transformations were then used in each of the distance statistics. Finally, taxonomists conveniently use cluster analysis as a primary technique for portraying morphological relatedness in one dimension, so we applied three clustering algorithms to each combination of measurements, transformations, and distance algorithms—Unweighted Pair Group Method using Arithmetic Averages (UPGMA, Sneath and Sokal, 1973); minimum distance (single linkage, Sokal and Sneath, 1963), and maximum distance (complete linkage, Johnson, 1967).

The basis for the calibration was to choose species whose morpho-

logical relationships were sufficiently obvious that the relative nature of the distance values and expected patterns of phenetic clustering would be predictable. Inaccuracies could be identified when calculations misrepresented the morphological relationships of these species.

In order to test the power of morphological distance metrics in accurately portraying the phenetic relationships of a group of organisms, those relationships must already be well understood. Furthermore, the probability of choosing a group of organisms that would provide a rigorous test would be increased if other aspects of their relatedness were also well known. Therefore, we chose nine species of New World leaf nosed bats of the family Phyllostomidae for which extensive karyological (Baker and Bass, 1979; Baker, 1979; Haiduk and Baker, 1982) molecular (Honeycutt et al., 1981; Baker et al., 1981), and morphological (Griffiths, 1982; Hood and Smith, 1982, 1983; Smith and Starrett, 1979) data are available.

The morphological relationships of the bat species chosen for this study can be grouped into two major categories reflective of their feeding habits. One group is the three species of vampire bats (recognized as three monotypic genera, *Desmodus*, *Diphylla*, and *Diaemus*). The other group is composed of five species of nectar and fruit eaters, which have elongated rostra (taxa examined were *Phyllonycteris aphylla*, *Erophylla sezekorni*, *Glossophaga soricina*, *Monophyllus redmani*, and *M. plethodon*). It is a critical assumption of this study that the three species of vampires more closely resemble each other than any nectar-feeding species and that the five nectar-feeders more closely resemble each other than any vampire. The first test is that any combination of measurements, transformations, distance computations, and clustering algorithms which does not distinguish the two major groupings will be judged an invalid measure of morphological distinctiveness.

The second test involves the ninth taxon examined in the study (*Brachyphylla cavernarum*). *Brachyphylla* is also a nectar and fruit eater but is so morphologically distinct that bat systematists have encountered considerable problems in determining its evolutionary origin (Baker and Bass, 1979; Griffiths, 1982, 1985). Only one point concerning *Brachyphylla* is critical, however. Because of its robust size, stocky build, and shortened snout, *Brachyphylla* is sufficiently morphologically distinct, from both the long-rostra nectar feeders and vampires, that it should not be classified within either group. Relative to the two groups, its position should be that of an outlier. Failure to place *Brachyphylla* as an outlier to the vampires and long-rostra nectar feeders would result in rejection of that method as a valid one.

The third test is within the long-rostra group. We chose two sibling species (*Monophyllus redmani* and *M. plethodon*) which are morphologically so similar that it is necessary to have detailed cranial mea-

surements for species identification (Schwartz and Jones, 1967). The final criterion for a valid measure of morphological distinctiveness is that the method places each of the two species of *Monophyllus* closer to each other than to any of the other taxa examined.

METHODS AND MATERIALS

In all but one case (*Diaemus youngi*, $n = 9$) 10 adult individuals of each species were measured from the collections of The Museum of Texas Tech University and The Texas Cooperative Wildlife Collection at Texas A&M University. Specimens examined are listed in Appendix I.

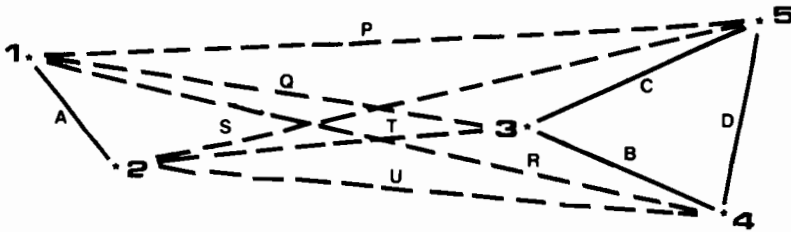
Two sets of measurements were chosen. For their study, Cherry et al. (1978) chose a set of nine morphological measurements previously used to assess shape changes in frogs (Jameson et al., 1966; Jameson and Richmond, 1971) to avoid bias toward humans and against frogs. We used these nine measurements, taken from all major parts of the body, in the attempt to evaluate Cherry et al.'s statement that "almost any evolutionary change in body shape would be reflected in at least one of these measurements" (Cherry et al., 1978:210). Whereas, the morphological uniqueness of bats in comparison with either higher primates or frogs made it somewhat difficult to modify these measurements they are: 1) tibia length; 2) forearm length; 3) hindfoot length; 4) greatest length of skull; 5) width of maxilla at first incisors; 6) vertebral length; 7) distance from anterior margin of auditory meatus to lacrimal canal; 8) distance from lacrimal canal to anterior margin of nasals; and 9) mastoidal breadth.

We also chose nine highly repeatable measurements from bats, some of which obviously reflect much of the evolutionary change within the order and others which are general mammalian measurements. These are: 1) total length; 2) tail length; 3) hindfoot length; 4) ear length; 5) forearm length; 6) length of metacarpal of digit five; 7) length of extended calcar and leg; 8) greatest length of skull; and 9) mastoidal breadth. All measurements except total, tail, hind foot, and ear lengths were measured on museum study skins and skulls to the nearest 0.1 millimeter with dial calipers. The four remaining measurements were taken directly from museum specimen labels. All measurements are given in Appendix II. A comparison of the results from the nine measurements of Cherry et al. (1978) with the results from the nine measurements selected especially for bats allows the opportunity to estimate the extent to which choice of measurements affects results (Findley's, 1979, criticism).

Both sets of measurements were ratio and log transformed and utilized in each of the three distance statistics. Comparison of the three types of distance matrices (Appendix III) allows the opportunity to evaluate the role correlation of characters plays in distance measures (Atchley's, 1980, criticism).

In this study, M-statistics were calculated using a FORTRAN program and Mahalanobis' D^2 and Euclidean distances were generated from SAS programs (Barr et al., 1979). Clustering analyses were performed on each of the distance matrices using the Unweighted Pair Group Method using Arithmetic Averages (UPGMA) with TAXON from the Numerical Taxonomy System (NT-SYS) package (Rohlf et al., 1974; Sneath and Sokal, 1973), and minimum distance (Johnson, 1967) and maximum distance method (Johnson, 1967) using the FACTOR, SCORE, and CLUSTER procedures of SAS (Sneath and Sokal, 1973; Barr et al., 1979). Fig. 1 demonstrates how candidates are merged with existing clusters in each of the three clustering methods.

The average distance method is the most widely used on taxonomic data. It selects clusters so that the average distance between members in the same cluster is less than the average distance between members of different clusters. A candidate will join a cluster if the average distance between it and the center of the cluster is less than the average distance to the center of any other cluster. The corresponding criterion for the maximum



TAXA 1 & 2 WILL BE PLACED IN A SEPARATE CLUSTER FROM TAXA 3,4 & 5 IF:

AVERAGE DISTANCE $\frac{A+B+C+D}{4} < \frac{P+Q+R+S+T+U}{6}$

MAXIMUM DISTANCE $MAX (B, C, D) < MIN (P, Q, R, S, T, U)$
 $A < MIN (P, Q, R, S, T, U)$

MINIMUM DISTANCE $A < MIN (P, Q, R, S, T, U)$
 $MIN (B, D) < MIN (Q, T)$
 $MIN (B, C) < MIN (P, S)$
 $MIN (C, D) < MIN (R, U)$

Fig. 1.—Criteria by which Average Distance, Minimum Distance, and Maximum Distance clustering algorithms form clusters; further details in text.

Taxa	Distance value between taxa
1,2	A
3,4	B
3,5	C
4,5	D
1,3	P
1,4	Q
1,5	R
2,3	S
2,4	T
2,5	U

distance method is that no species within a cluster can be further away from any species in the cluster than from a species outside its cluster. In the minimum distance method a species will be placed according to the cluster membership of the species closest to it. Essentially, maximum and minimum clustering methods merge two clusters on the basis of a single value; the greatest distance or least distance value, respectively, between

Table 1.—Results of test of resolution of different combinations of measurements, distance statistics and transformation of data from nine taxa of bats. OK = taxa correctly classified; F = taxa incorrectly classified. Test 1 was correct separation of vampires and long-rostra nectar feeders into distinct groups. Test 2 was distinguishing *Brachyphylla* as an outlier from both vampires and long-rostra bats and Test 3 was the association of two sibling species nearer to each other than to any other taxon. *M* = *M*-statistic; *D*² = Mahalanobis distance; *Eu* = Euclidean distance; *U* = untransformed data; *Ratio* = ratio transformed data; *Log* = log transformed data; *Bat* = measurements selected to encompass bat variation; *Frog* = measurements selected by Cherry et al. (1978) for general changes in body shape.

Distance, transformation, kind of measurement	Clustering method								
	Maximum test			Average test			Minimum test		
	1	2	3	1	2	3	1	2	3
M—U—Bat	F	OK	F	F	OK	F	OK	OK	F
M—U—Frog	F	F	F	F	OK	F	OK	OK	F
M—Ratio—Bat	OK	F	OK	F	F	F	OK	F	OK
M—Ratio—Frog	F	F	F	F	F	F	OK	OK	F
M—Log—Bat	F	F	OK	F	F	F	OK	OK	OK
M—Log—Frog	F	F	F	F	F	F	OK	OK	F
D ² —U—Bat	F	F	F	F	F	F	OK	OK	F
D ² —U—Frog	F	OK	F	OK	OK	F	OK	OK	F
D ² —Ratio—Bat	F	F	OK	OK	OK	OK	OK	OK	OK
D ² —Ratio—Frog	F	F	F	OK	OK	F	OK	OK	F
D ² —Log—Bat	F	F	F	OK	OK	F	OK	OK	F
D ² —Log—Frog	F	F	F	OK	OK	F	OK	OK	F
Eu—U—Bat	OK	OK	F	OK	OK	F	OK	OK	F
Eu—U—Frog	F	OK	F	OK	OK	F	F	OK	F
Eu—Ratio—Bat	OK	OK	F	OK	OK	F	OK	OK	F
Eu—Ratio—Frog	F	F	F	F	F	F	OK	OK	F
Eu—Log—Bat	OK	OK	F	OK	OK	F	OK	OK	F
Eu—Log—Frog	F	OK	F	F	F	F	OK	OK	F

points, whereas UPGMA forms clusters on the basis of an average value. In data such as those displayed in Fig. 1, the different methods would return the same result. However, in some circumstances the results can be very different. If the five species were arranged in a line, it is possible that species 3 might be nearest to species 4, and species 4 be nearest species 5. Yet the distance between species 2 and 3 might be smaller than that between species 3 and 5. Here minimum and maximum distance methods would give different results.

RESULTS

Results of the different combinations of methods are shown in Table 1. Only thrice were all three test criteria met (Mahalanobis' *D*² ratio transformed bat measurements with average distance clustering and minimum distance clustering, and *M*-statistic log transformed bat measurements). Maximum distance clustering showed a low level of success in meeting the three test criteria with minimum distance clustering (14 successes out of 54 tries); average distance clustering was somewhat

more successful, especially with Mahalanobis' D^2 distances (21 out of 54), and minimum distance clustering consistently succeeded in meeting the first two test criteria for all combinations of measurements, data transformations, and distance statistics (failing only twice), but was ineffective (three successes out of 18 tries) on the third criterion.

Chi-square tests of the data show minimum distance clustering (17 successes) to be significantly more successful in meeting the first test criterion than the maximum distance (4 successes) or UPGMA clustering (nine successes) ($\chi^2_1 = 9.45$, $P < 0.01$). The minimum distance clustering was also marginally better than the other clustering methods on the second test criterion ($\chi^2_1 = 3.66$, $P < 0.06$) with 17 successes versus seven successes for maximum and 11 successes for UPGMA clustering. However, none of the three clustering algorithms was consistently more successful in properly grouping the two *Monophyllus* species, three versus one versus three successes for maximum, average and minimum clustering, respectively.

Findley's (1979) point regarding choice of characters to be measured is well taken. But for these data at least, the measurements chosen specifically to emphasize variation within bats were not significantly more effective in differentiating between the nine species than were the measurements used originally for frogs! (43 successes for "bats" versus 29 for "frogs" ($\chi^2_1 = 1.66$, $P > 0.05$). Atchley's (1980) criticism of the use of a ratio transformation by Cherry et al. (1978) is not applicable to our data because ratio transformed, log transformed, and untransformed data were almost equally successful in meeting the three test criteria (25, 23, and 24 successes, respectively). The three distance statistics also showed no consistent differences in meeting the three test criteria ($\chi^2_1 = 2.1$, $P > 0.05$). This suggests that Atchley's (1980) criticism of the M-statistic for its disregard of correlation between characters is, similarly, not applicable to these data. Kunkel et al. (1980) defended the use of the M-statistic stating that its weakness concerning correlation between characters is compensated for by its superiority with small sample sizes, although Cherry et al. (1982) found small sample sizes used with both the M-statistic and Mahalanobis' D^2 led to overestimates of D values. We used a small sample size ($n = 10$) yet the M-statistic was no more successful at meeting the three criteria than were Mahalanobis' D^2 and Euclidean distances.

Distance values, the input for the clustering algorithms, between each possible pair of the nine species were arranged so that the nearest distance (smallest value) and farthest distance (largest value) from any one species to the other eight could be examined for each of the combinations of methods. All the permutations consistently placed the same groups of species in nearest or farthest proximity to one another. Examination of these actual distances between taxa pairs demonstrates

their relative insensitivity to the kinds of measurements, transformations, or distance algorithms used. This suggests that the most critical step, by far, in producing a successful clustering involves the final step—the choice of the clustering algorithms itself.

DISCUSSION

Distance Statistics

Following Findley's (1979) observation that by the particular selection of appropriate anatomical features one could show great similarity or dissimilarity on the basis of distance values, the nine bat measurements in this study included morphological traits that emphasized variation in the bat taxa examined. The nine measurements of Cherry et al. (1978) were said to be chosen objectively to show evolutionary change in all major parts of the body of vertebrate animals. Comparison of results based on the two sets of measurements showed neither set to be superior in successfully meeting our three criteria for differentiating between the nine taxa.

The merits of ratio transformation of data have been hotly debated (Atchley et al., 1976; Atchley, 1978; Hill, 1978). Whereas ratio transformed data resulted in some of the more aberrant placements of taxa, only two of the three sets of measurements, transformations, distance statistics, and clustering algorithms that met all three test criteria involved ratio transformations. Atchley's (1980) criticism of the use of a ratio transformation by Cherry et al. (1978) is not supported by this study because neither ratio transformed, log transformed nor untransformed data were consistently successful in meeting the three test criteria. The three distance statistics showed no consistent differences in meeting the three test criteria suggesting that both Atchley's (1980) criticism of the M-statistic for disregard of correlation between characters and that of Kunkel et al. (1980) concerning Mahalanobis' D^2 over-compensation for correlation between characters are not totally warranted.

Clustering Algorithms

Rohlf (1962) and Sokal and Rohlf (1962) found average distance clustering with UPGMA to be superior to other clustering algorithms and Sneath and Sokal (1973) cite UPGMA as the most frequently used algorithm. Minimum distance clustering, however, has been viewed as defective because of a tendency to cluster together taxa linked by chains of intermediates (Everitt, 1974), and maximum distance clustering has been accused of "space dialating" extremes (Sneath and Sokal, 1973). Yet, none of the three clustering algorithms was consistently able to meet all three test criteria. Whereas the distance statistics yielded the

same results, the clustering algorithms showed different levels of success in accurately portraying these matrices.

Minimum distance clustering, even with its alleged defect of "chaining," was the only clustering algorithm consistently successful in meeting the test criteria. One difficulty encountered in cluster analysis is that each algorithm carries with it assumptions about the type of structures present in the data; for example, the average distance method assumes that taxa will be arrayed spherically in hyperspace (Sokal and Michener, 1967; Everitt, 1974). This study suggests that such spherical clusters may not be the case with these animals and that by allowing for chains of taxa rather than discrete spheres of taxa, minimum distance clustering gives a more accurate representation of phenetic relationships within this group than does average distance or maximum distance clustering.

CONCLUSIONS

Results of this study suggest that the three principal criticisms directed against the *M*-statistic are only of minor importance. Regardless of choice of measurements and allowance for correlation between characters or type of data transformation, the *M*-statistic, Mahalanobis' D^2 , and Euclidean distance statistics yield the same results. The *M*-statistic is shown to be no worse, but certainly no better at accurately measuring morphological distance than either of the other two distance algorithms.

It is of major importance, however, that none of the clustering algorithms could accurately portray the phenetic relationships of the nine taxa on the basis of all three test criteria. This study describes inconsistencies in how the three clustering algorithms interpret the distance matrices. Choice of the best clustering algorithm for a group of taxa hinges on preconception of how those taxa are arrayed in hyperspace. Perhaps, as taxa follow different evolutionary tracks resulting in different patterns in hyperspace, one type of clustering algorithm will most accurately mirror phenetic relationships of one group, whereas a different clustering algorithm will be required to accurately portray phenetic relationships of another group.

Reasons underlying different results from the three clustering algorithms are not evident here. The basis for discordant results may be some facet of the clustering algorithms or it may be traced to some earlier step in the process of measurement, transformation, and distance metric calculation. For example, in our data set, the absence of a tail measurement in desmodontines may confound clustering of the other six taxa which have short and relatively longer tails. Taxa with short tails may actually cluster closer to taxa with no tails than with

those having long tails. Additionally, the consistent failure of test 3, grouping the sibling species of *Monophyllus* is striking. Perhaps the distance statistics used do not accurately portray the extreme morphological similarity of these bats. In such a case, no combination of transformation and clustering could be expected to give predictable results. Alternatively, both the "frog" and "bat" measurements may have been too generalized to be sensitive to variation at this level, or none of the techniques adequately dealt with size bias. Inherent weaknesses of the often indiscriminantly used tool of cluster analysis are made apparent, however. There is now a call for more rigorous tests using other well-characterized taxa to enhance understanding of the circumstances of applicability of distance metrics and clustering algorithms to evolutionary studies.

ACKNOWLEDGMENTS

This study was done in partial fulfillment of requirements for the M.S. degree by McBee while at Texas Tech University. We especially thank Craig S. Hood for a thorough review of the manuscript and thoughtful discussions resulting in improvement of the work. We thank John W. Bickham, Lorraine M. Cherry, Ronald K. Chesser, Robert D. Owen, and A. C. Wilson who read earlier drafts of this manuscript and provided helpful criticism. David J. Schmidly allowed access to specimens housed in the Texas Cooperative Wildlife Collection.

LITERATURE CITED

- ATCHLEY, W. R. 1978. Ratios, regression intercepts, and the scaling of data. *Syst. Zool.*, 27:78-83.
- . 1980. M-statistics and morphological divergence. *Science*, 208:1059.
- ATCHLEY, W. R., C. T. GASKINS, AND D. ANDERSON. 1976. Statistical properties of ratios. I. Empirical results. *Syst. Zool.*, 25:137-148.
- BAKER, R. J. 1979. Karyology. Pp. 107-156, in *Biology of bats of the New World family Phyllostomatidae. Part III* (R. J. Baker, J. K. Jones, Jr., and D. C. Carter, eds.), *Spec. Publ. Mus.*, Texas Tech Univ., 16:1-441.
- BAKER, R. J., AND R. A. BASS. 1979. Evolutionary relationship of the Brachyphyllinae to glossophagine genera *Glossophaga* and *Monophyllus*. *J. Mamm.*, 60:364-372.
- BAKER, R. J., R. L. HONEYCUTT, M. L. ARNOLD, V. M. SARICH, AND H. H. GENOWAYS. 1981. Electrophoretic and immunological studies on the relationship of the Brachyphyllinae and Glossophaginae. *J. Mamm.*, 60:665-672.
- BARR, A. J., J. H. GOODNIGHT, J. P. SALL, W. H. BLAIR, AND D. M. CHILKO. 1979. *SAS User's Guide*, 1979 edition. SAS Institute Inc., Raleigh, North Carolina, 494 pp.
- CHERRY, L. M., S. M. CASE, AND A. C. WILSON. 1978. Frog perspective on the morphological difference between humans and chimpanzees. *Science*, 200:209-211.
- CHERRY, L. M., S. M. CASE, J. D. KUNKEL, J. S. WYLES, AND A. C. WILSON. 1982. Body shape metrics and organismal evolution. *Evolution*, 36:914-933.
- EVERITT, B. S. 1974. *Cluster analysis*. Heinemann Press, London, pp. 1-122 + vi.
- FINDLEY, J. S. 1979. Comparisons of frogs, humans, and chimpanzees. *Science*, 204:434-435.
- GRIFFITHS, T. A. 1982. Systematics of the New World nectar-feeding bats (Mammalia, Phyllostomidae) based on the morphology of the hyoid and lingual regions. *Amer. Mus. Novitates*, 2742:1-45.

- . 1985. Molar cusp patterns in the bat genus *Brachyphylla*: some functional and systematic observations. *J. Mamm.*, 66:544–549.
- HAIIDUK, M. W., AND R. J. BAKER. 1982. Cladistical analysis of G-banded chromosomes of nectar-feeding bats (Glossophaginae: Phyllostomidae). *Syst. Zool.*, 31:252–265.
- HILL, M. 1978. On ratios—a response to Atchley, Gaskins, and Anderson. *Syst. Zool.*, 27:61–62.
- HONEYCUTT, R. L., I. F. GREENBAUM, R. J. BAKER, AND V. M. SARICH. 1981. Molecular evolution of vampire bats. *J. Mamm.*, 62:805–811.
- HOOD, C. S., AND J. D. SMITH. 1982. Cladistical analysis of female reproductive histomorphology in phyllostomatoid bats. *Syst. Zool.*, 31:241–251.
- . 1983. Histomorphology of the female reproductive tract in phyllostomatoid bats. *Occas. Papers Mus., Texas Tech Univ.*, 86:1–38.
- JAMESON, D. L., J. R. MACKEY, AND R. C. RICHMOND. 1966. The systematics of the Pacific tree frogs, *Hyla regilla*. *Proc. California Acad. Sci.*, 33:551–620.
- JAMESON, D. L., AND R. C. RICHMOND. 1971. Parallelism and convergence in the evolution of size and shape in Holarctic *Hyla*. *Evolution*, 25:497–508.
- JOHNSON, S. C. 1967. Hierarchical clustering schemes. *Psychometrika*, 32:241–254.
- KUNKEL, J. G., L. M. CHERRY, S. M. CASE, AND A. C. WILSON. 1980. M-statistics and morphological divergence. *Science*, 108:1060–1061.
- MAHALANOBIS, P. C. 1936. On the generalized distance in statistics. *Proc. Nat. Inst. Sci. (India)*, 2:49–55.
- ROHLF, F. J. 1962. A numerical taxonomic study of the genus *Aedes* (Diptera: Culicidae) with emphasis on the congruence of larval and adult classifications. Unpublished Ph.D. dissertation, Univ. Kansas, 98 pp.
- ROHLF, F. J., J. KISHPAUGH, AND D. KIRK. 1974. Nz-SYS numerical taxonomy system of multivariate statistical programs.
- SCHWARTZ, A., AND J. K. JONES, JR. 1967. Bredin-Archibold-Smithsonian Biological Survey of Dominica. 7. Review of bats of the endemic Antillean genus *Monophyllus*. *Proc. U.S. Nat. Mus.*, 124:1–20.
- SMITH, J. D., AND A. STARRETT. 1979. Morphometric analysis of chiropteran wings. Pp. 229–316, in *Biology of bats of the New World, family Phyllostomatidae, Part III* (R. J. Baker, J. K. Jones, Jr., and D. C. Carter, eds.), *Spec. Publ. Mus., Texas Tech Univ.*, 16:1–441.
- SNEATH, P. H. A., AND R. R. SOKAL. 1973. *Numerical taxonomy*. W. H. Freeman and Co., San Francisco, pp. 1–573 + xv.
- SOKAL, R. R., AND P. H. A. SNEATH. 1963. *Principles of numerical taxonomy*. W. H. Freeman and Co.
- SOKAL, R. R., AND C. D. MICHENER. 1967. The effects of different numerical techniques on the phenetic classification of bees of the *Hoplitis* complex (Megachilidae). *Proc. Linn. Soc. London*, 178:59–74.
- SOKAL, R. R., AND F. J. ROHLF. 1962. The comparison of dendrograms by objective methods. *Taxon*, 11:33–40.

APPENDIX I

Specimens Examined

Brachyphylla cavernarum.—GUADELOUPE; Basse-Terre, 1 km S, 4 km W Vernou, TTU 20968, 1 km W Vernou, TTU 20967, 2 km N Baillif, TTU 20965, Grand-Terre, 1 km N, 1 km W St. Francois, TTU 20974.

Diphylla ecaudata.—HONDURAS; Morazan, 0.3 mi SE Sabana Grande, TTU 30669, Olancho, 40 km NE Catacamas, TCWC 19685, TCWC 19686. MEXICO; Tamaulipas, 67 km S Cd. Victoria on Mex. 85, TTU 10171, Vera Cruz, Ojo de Agua del Rio Atoyac, TTU 10000–10001, 10157, Yucatan, Cueva de Spuril, 3 km NW Komchen, TTU 25899,

3 km S, 1 km W Calcehtoc, TTU 25900. UNITED STATES; Texas, Val Verde Co., Comstock R. R. Tunnel, TTU 5658.

Desmodus rotundus.—MEXICO; Tamaulipas, 68 km S Cd. Victoria, Mex. 85, TTU 8228, Rio Corona, Mex. 101, N Cd. Victoria, TTU 8578, Rancho del Cielo, TTU 7356–7357, TTU 7359–7360, Veracruz, 76 km NW Taxpan, TTU 8193–8195, TTU 8190.

Diaemus youngi.—COSTA RICA; Guanacaste, Finca la Pacifica, 4 km NW Canas, TCWC 22533. EL SALVADOR; La Paz, 3 mi NW La Herradura, TTU 27591. NICARAGUA; Managua, 3 km N Masachapa, TTU 30667, Zelaya, 3 km NW Rama, TTU 30668. TRINIDAD; Maracas Valley, TTU 5428, TTU 5232–5233, Los Cueveus, TTU 5411, St. Patrick, La Brea, TTU 26888.

Erophylla sezekorni.—PUERTO RICO; El Verde Research Station, El Yunque Natl. Forest, TTU 8922, TTU 8923, TTU 8919, El Toro, El Yunque Natl. Forest, TTU 8906–8907, 1 mi W Corozal, TTU 8937–8941.

Glossophaga soricina.—MEXICO; Hidalgo, El Suspiro, 1 km N, 4 km W Tahuetlan, TTU 24192, 4 mi S San Felipe Orizatlan, TTU 15458, TTU 15464, 8 mi S Tlanchinol, TTU 24194, San Luis Potosi, Cueva de Los Savinos, 8 mi NE Cd. Valles, TTU 8341–8342, Yucatan, Colegio Peninsular Colonia Bueno Vista, Merida, TTU 25892–25893, Cueva de Spuril, 3 km S, 1 km W Calchetoc, TTU 25890–25891.

Monophyllus plethodon.—DOMINICA; St. Joseph Parish, Clark Hall, TTU 9337, TTU 31330–31331, St. Paul Parish, Springfield, TTU 31329, 1 mi from mouth of Layou River, TTU 31332. GUADELOUPE; Basse-Terre, Bains Jaunes, 2.5 km E Saint Claude, TTU 20795–20796, 1 km W Vernou, TTU 20798–20800.

Monophyllus redmani.—PUERTO RICO; El Toro, El Yunque Natl. Forest, TTU 9791, El Verde Research Station, El Yunque Natl. Forest, TTU 8927–8928, 1 mi W Corozal, TTU 8934–8936, TTU 9815–9817.

Phyllonycteris aphylla.—JAMAICA; St. Ann Parish, Orange Valley, TTU 21901–21908, TTU 21923–21925.

APPENDIX II

Measurements (mm) from Specimens Examined

Number	TTL TB	TL GLS	EL NL	HF FA	FA VL	GLS MB	CL ET	MD5 HF	MB EN
<i>Brachyphylla cavernarum</i>									
TTU 8896	86.0	0.0	20.0	19.0	66.5	31.6	6.3	58.0	14.8
	26.6	31.6	0.9	66.5	54.4	14.8	12.6	19.0	7.5
TTU 9819	99.0	6.0	22.0	17.0	65.6	31.5	4.7	57.6	14.8
	26.1	31.5	0.8	65.3	67.5	14.8	11.8	17.0	8.1
TTU 9820	98.0	7.0	21.0	15.0	66.6	31.5	4.5	57.3	14.9
	25.6	31.5	1.0	66.6	66.5	14.9	12.5	15.0	8.1
TTU 8892	83.0	6.0	22.0	20.0	62.5	32.3	4.8	51.9	15.2
	21.2	32.3	0.8	62.5	50.7	15.2	12.6	20.0	8.0
TTU 20968	97.0	5.0	22.0	21.0	65.6	31.8	6.8	55.9	15.0
	25.6	31.8	0.7	65.6	65.2	15.0	12.3	21.0	8.2
TTU 20967	102.0	9.0	23.0	20.0	62.3	30.7	5.8	56.3	14.9
	25.0	30.7	0.7	62.3	71.3	14.9	12.5	20.0	7.8
TTU 20965	101.0	6.0	22.0	20.0	64.7	31.5	7.8	55.2	14.6
	24.5	31.5	0.7	64.7	69.5	14.6	13.0	20.0	8.0
TTU 20974	98.0	8.0	24.0	22.0	64.0	30.3	4.1	54.9	14.3
	24.5	30.3	0.6	64.0	67.7	14.3	12.3	22.0	7.6
TTU 8893	86.0	0.0	18.0	16.0	64.5	30.1	4.1	54.5	14.5
	23.3	30.1	0.7	64.5	55.9	14.5	11.9	16.0	7.9
TTU 8894	91.0	0.0	18.0	17.0	61.3	30.7	5.9	54.8	14.7
	22.5	30.7	0.7	61.3	60.3	14.7	12.0	17.0	7.4
<i>Diphylla ecaudata</i>									
TTU 10171	75.0	0.0	7.0	18.0	54.2	22.9	5.0	52.2	11.5
	22.3	22.9	1.2	54.2	52.1	11.5	6.7	18.0	6.5
TTU 10000	88.0	0.0	13.0	14.0	53.6	22.5	8.0	50.8	11.8
	21.2	22.5	1.2	53.6	65.5	11.8	7.0	14.0	6.1
TTU 10001	70.0	0.0	13.0	15.0	54.5	22.6	7.7	50.6	11.8
	21.0	22.6	1.0	54.5	47.4	11.8	6.8	15.0	5.6
TTU 10157	76.0	0.0	12.0	18.0	55.1	23.2	7.5	53.7	11.9
	22.1	23.2	1.2	55.1	52.8	11.9	7.0	18.0	5.9
TTU 25899	78.0	0.0	14.0	18.0	48.9	21.8	6.5	49.2	11.2
	19.9	21.8	1.0	48.9	56.2	11.2	6.5	18.0	5.8
TTU 25900	80.0	0.0	15.0	17.0	50.6	22.0	6.0	50.8	11.4
	20.5	22.0	1.1	50.6	58.0	11.4	7.1	17.0	5.8
TTU 5658	83.0	0.0	16.0	18.0	51.8	23.0	6.2	51.8	12.2
	19.6	23.0	1.2	51.8	60.0	12.2	7.1	18.0	5.6
TTU 30669	84.0	0.0	9.0	17.0	53.8	23.0	7.6	52.8	12.6
	20.6	23.0	1.2	53.8	61.0	12.6	9.5	17.0	5.7
TCWC 19685	83.0	0.0	16.0	14.0	51.5	22.7	6.3	50.5	11.8
	18.7	22.7	1.3	51.5	60.3	11.8	9.2	14.0	5.2
TCWC 19686	87.0	0.0	16.0	16.0	55.3	23.5	5.5	55.0	12.2
	19.5	23.5	1.4	55.3	63.5	12.2	9.0	16.0	6.0

APPENDIX II—Continued.

Number	TTL TB	TL GLS	EL NL	HF FA	FA VL	GLS MB	CL ET	MD5 HF	MB EN
<i>Desmodus rotundus</i>									
TTU 8228	84.0	0.0	17.0	19.0	60.3	24.1	3.9	50.3	12.3
	24.0	24.1	0.6	60.3	59.9	12.3	8.1	19.0	5.8
TTU 8578	84.0	0.0	18.5	17.0	62.9	24.4	3.0	55.8	12.6
	25.9	24.4	1.1	62.9	59.6	12.6	7.8	17.0	6.0
TTU 7356	78.0	0.0	16.0	19.0	56.9	23.5	3.2	48.9	12.0
	23.8	23.5	0.8	56.9	54.5	12.0	7.0	19.0	5.9
TTU 7357	73.0	0.0	15.0	19.0	55.0	23.6	3.0	48.7	12.0
	22.7	23.6	0.7	55.0	49.4	12.0	7.2	19.0	5.9
TTU 7359	70.0	0.0	16.0	19.0	55.8	22.5	2.7	48.6	12.1
	22.4	22.5	0.4	55.8	47.5	12.1	7.0	19.0	5.9
TTU 7360	83.0	0.0	17.0	21.0	62.3	24.5	3.1	52.3	13.0
	25.2	24.5	0.7	62.3	58.5	13.0	7.9	21.0	5.8
TTU 8193	91.0	0.0	18.0	19.0	61.1	24.4	2.9	53.6	12.7
	24.6	24.4	0.8	61.1	66.6	12.7	7.8	19.0	6.0
TTU 8194	84.0	0.0	18.0	16.0	53.8	23.5	2.8	47.5	12.6
	22.8	23.5	1.0	53.8	60.5	12.6	7.7	16.0	5.9
TTU 8195	84.0	0.0	15.0	19.0	54.5	23.0	2.8	40.0	12.2
	24.2	23.0	1.0	54.5	61.0	12.2	7.3	19.0	5.9
TTU 8190	79.0	0.0	15.0	19.0	57.5	23.8	3.5	49.0	12.4
	24.2	23.8	0.7	57.5	55.2	12.4	7.3	19.0	6.2
<i>Diaemus youngi</i>									
TTU 27591	95.0	0.0	14.0	21.0	53.7	25.0	5.8	49.0	13.4
	10.5	25.0	0.9	53.7	70.0	13.4	8.1	21.0	6.1
TTU 5411	79.0	0.0	16.0	14.0	47.3	23.6	3.2	43.6	12.2
	21.4	23.6	0.7	47.3	55.4	12.2	7.3	14.0	5.3
TTU 5428	77.0	0.0	17.0	17.0	48.6	23.7	4.0	45.8	12.4
	21.9	23.7	0.9	48.6	53.3	12.4	7.3	17.0	5.9
TTU 5233	54.0	0.0	14.0	17.0	48.1	23.9	3.8	43.8	11.6
	20.4	23.9	1.0	48.1	30.1	11.6	7.6	17.0	5.9
TTU 5232	53.0	0.0	15.0	17.0	48.4	23.1	3.7	46.0	12.4
	20.7	23.1	1.0	48.4	29.9	12.4	7.0	17.0	5.5
TTU 26888	87.0	0.0	11.0	18.0	50.3	23.7	5.2	46.9	12.4
	19.7	23.7	1.2	50.3	63.3	12.4	9.6	18.0	5.5
TTU 30667	87.0	0.0	15.0	20.0	55.3	25.4	6.1	49.6	13.6
	22.2	25.4	1.2	55.3	61.6	13.6	10.7	20.0	6.1
TTU 30668	90.0	0.0	12.0	19.0	56.9	26.0	5.3	53.0	13.3
	23.8	26.0	1.3	56.9	64.0	13.3	11.0	19.0	6.3
TCWC 22533	92.0	0.0	19.0	20.0	55.2	25.6	4.7	49.8	13.0
	23.6	25.6	1.2	55.2	66.4	13.0	10.2	20.0	6.4
<i>Erophylla sezekorni</i>									
TTU 8922	80.0	14.0	18.0	14.0	47.1	24.0	3.2	38.4	10.5
	19.5	24.0	0.4	47.1	56.0	10.5	8.9	14.0	6.8

APPENDIX II—*Continued.*

Number	TTL TB	TL GLS	EL NL	HF FA	FA VL	GLS MB	CL ET	MD5 HF	MB EN
TTU 8923	74.0 20.7	15.0 23.6	17.0 0.4	14.0 44.0	44.0 50.4	23.6 10.5	3.1 8.5	39.3 14.0	10.5 6.6
TTU 8919	79.0 19.2	13.0 24.2	19.0 0.4	13.0 45.9	45.9 54.8	24.2 10.7	2.8 8.7	37.1 13.0	10.7 6.3
TTU 8937	79.0 19.5	11.0 24.2	15.0 0.5	14.0 47.9	47.9 54.8	24.2 11.0	2.8 8.9	38.8 14.0	11.0 6.3
TTU 8906	82.0 19.8	13.0 24.8	15.0 0.5	14.0 47.1	47.1 57.2	24.8 10.6	3.2 9.0	39.4 14.0	10.6 6.9
TTU 8941	74.0 19.5	12.0 24.3	17.0 0.4	14.0 46.6	46.6 49.7	24.3 10.6	2.9 8.7	38.3 14.0	10.6 6.6
TTU 8940	73.0 20.2	12.0 23.8	19.0 0.4	14.0 47.0	47.0 49.2	23.8 10.6	3.3 8.5	38.6 14.0	10.6 6.7
TTU 8939	79.0 20.6	14.0 23.9	19.0 0.5	14.0 49.1	49.1 55.1	23.9 10.8	3.0 8.8	40.0 14.0	10.8 6.5
TTU 8938	75.0 19.9	13.0 24.8	15.0 0.5	14.0 47.2	47.2 50.2	24.8 11.0	2.9 8.9	38.4 14.0	11.0 6.4
TTU 8907	75.0 19.4	15.0 24.4	15.0 0.5	15.0 47.2	47.2 50.6	24.4 10.7	3.4 8.9	39.0 15.0	10.7 6.8
<i>Glossophaga soricina</i>									
TTU 25893	63.0 12.8	8.0 20.8	14.0 0.3	11.0 34.2	34.2 42.2	20.8 9.0	5.8 7.2	29.1 11.0	9.0 5.4
TTU 25892	63.0 —	6.0 20.9	15.0 0.4	10.0 34.0	34.0 42.1	20.9 8.9	5.5 7.5	31.3 10.0	8.9 5.5
TTU 25891	69.0 14.2	9.0 21.4	15.0 0.4	11.0 36.1	36.1 47.6	21.4 8.9	5.1 7.5	31.7 11.0	8.9 5.7
TTU 25890	59.0 12.5	7.0 20.7	15.0 0.4	10.0 32.9	32.9 38.3	20.7 8.7	6.2 7.0	28.7 10.0	8.7 5.4
TTU 8342	68.0 13.8	6.0 21.6	14.0 0.4	10.0 35.0	35.0 46.4	21.6 8.9	6.8 7.7	30.6 10.0	8.9 5.5
TTU 8341	65.0 13.0	7.0 21.7	13.0 0.4	10.0 35.8	35.8 43.3	21.7 9.2	6.5 7.5	32.0 10.0	9.2 5.9
TTU 24194	58.5 12.5	9.0 20.8	14.5 0.2	11.0 34.8	34.8 37.7	20.8 8.8	5.1 7.6	30.8 11.0	8.8 5.2
TTU 15458	55.0 12.8	— 20.8	13.0 0.3	11.0 35.4	35.4 34.2	20.8 8.9	6.9 7.0	31.6 11.0	8.9 5.3
TTU 15464	61.0 12.7	4.0 20.9	15.0 0.3	9.0 36.5	36.5 40.1	20.9 8.6	6.8 7.3	31.4 9.0	8.6 5.6
TTU 24192	56.0 12.0	6.0 20.5	14.0 0.2	12.0 33.9	33.9 35.5	20.5 8.8	6.5 7.1	30.3 12.0	8.8 5.4
<i>Monophyllus plethodon</i>									
TTU 9337	78.0 17.0	13.0 22.9	15.5 0.5	15.0 40.3	40.3 55.1	22.9 10.0	4.6 8.2	32.7 15.0	10.0 6.1

APPENDIX II—*Continued.*

Number	TTL TB	TL GLS	EL NL	HF FA	FA VL	GLS MB	CL ET	MD5 HF	MB EN
TTU 20795	79.0	13.0	15.0	17.0	39.1	23.3	4.1	29.6	10.0
	16.1	23.3	0.5	39.1	55.7	10.0	9.0	17.0	5.5
TTU 20796	81.0	13.0	16.0	13.0	42.0	23.6	3.6	32.8	10.1
	16.4	23.6	0.5	42.0	57.4	10.1	8.5	13.0	6.1
TTU 20798	79.0	12.0	15.0	9.0	40.8	23.3	3.7	32.3	9.5
	16.8	23.3	0.3	40.8	55.7	9.5	8.5	9.0	6.2
TTU 20799	80.0	13.0	13.0	13.0	41.0	23.4	4.0	31.9	9.6
	16.5	23.4	0.4	41.0	56.6	9.6	8.2	13.0	6.5
TTU 20800	74.0	11.0	16.0	13.0	40.9	23.2	3.7	31.3	10.1
	16.8	23.2	0.3	40.9	50.8	10.1	8.3	13.0	6.1
TTU 31329	78.0	14.0	16.0	12.0	41.1	23.0	3.1	33.1	9.6
	17.7	23.0	0.3	41.1	55.0	9.6	8.1	12.0	6.2
TTU 31330	78.0	12.0	15.0	14.0	40.9	23.6	3.5	30.4	9.5
	17.3	23.6	0.5	40.9	54.4	9.5	8.5	14.0	6.4
TTU 31331	78.0	12.0	14.0	14.0	40.0	23.6	2.8	30.5	9.6
	16.2	23.6	0.3	40.0	54.4	9.6	8.3	14.0	6.4
TTU 31332	72.0	12.0	15.0	13.0	40.1	22.9	3.5	31.6	9.6
	16.1	22.9	0.4	40.1	49.1	9.6	8.6	13.0	5.7
<i>Monophyllus redmani</i>									
TTU 8933	61.0	7.0	9.0	14.0	36.8	20.0	4.2	28.5	8.5
	15.1	20.0	0.3	36.8	41.0	8.5	6.7	14.0	5.3
TTU 8927	48.0	6.0	10.0	11.0	35.7	19.8	4.0	28.5	8.2
	14.7	19.8	0.2	35.7	28.2	8.2	6.8	11.0	5.0
TTU 8928	52.0	6.0	8.0	11.0	35.6	19.9	3.4	28.1	8.1
	15.1	19.9	0.3	35.6	32.1	8.1	6.6	11.0	5.2
TTU 8935	61.0	10.0	11.0	12.0	36.0	19.8	3.6	28.5	8.2
	14.3	19.8	0.4	36.0	41.2	8.2	6.5	12.0	5.7
TTU 8936	51.0	—	10.0	10.0	35.3	19.3	4.1	26.6	8.1
	13.1	19.3	0.2	35.3	31.7	8.1	6.3	10.0	5.1
TTU 9791	65.0	10.0	9.5	11.0	36.1	19.7	4.3	28.5	8.2
	14.5	19.7	0.2	36.1	45.3	8.2	6.6	11.0	4.8
TTU 8934	53.0	6.0	13.0	11.0	36.4	19.8	3.8	27.8	8.2
	15.0	19.8	0.3	36.4	33.2	8.2	6.4	11.0	5.1
TTU 9816	62.0	8.5	9.5	12.5	36.3	20.1	4.0	28.6	8.5
	14.8	20.1	0.2	36.3	41.9	8.5	6.6	12.5	5.1
TTU 9815	60.0	10.0	10.0	12.0	35.7	19.5	4.7	28.6	8.2
	15.0	19.5	0.2	35.7	40.5	8.2	6.1	12.0	5.1
TTU 9817	63.0	10.0	9.0	12.0	36.3	19.3	4.0	28.6	8.3
	15.4	19.3	0.2	36.3	43.7	8.3	6.6	12.0	5.0
<i>Phyllonycteris aphylla</i>									
TTU 21923	75.0	7.0	17.0	15.0	45.5	25.2	2.2	38.2	11.1
	22.9	25.2	0.9	45.5	49.8	11.1	8.6	15.0	7.9
TTU 21908	85.0	8.0	18.0	16.0	44.8	24.9	1.5	38.0	11.1

APPENDIX II—*Continued.*

Number	TTL TB	TL GLS	EL NL	HF FA	FA VL	GLS MB	CL ET	MD5 HF	MB EN
	22.2	24.9	0.8	44.8	60.1	11.1	9.3	16.0	7.0
TTU 21907	85.0	8.0	19.0	15.0	46.1	24.6	2.0	38.9	11.2
	22.9	24.6	1.2	46.1	60.4	11.2	9.4	15.0	6.8
TTU 21906	85.0	10.0	17.0	15.0	43.7	25.2	1.9	37.3	11.3
	22.2	25.2	1.1	43.7	59.8	11.3	9.4	15.0	7.3
TTU 21905	82.0	10.0	19.0	16.0	47.2	25.9	2.2	40.5	11.2
	23.6	25.9	1.1	47.2	56.1	11.2	9.9	16.0	7.3
TTU 21904	83.0	9.0	18.0	15.0	46.0	26.2	2.2	38.1	11.6
	22.3	26.2	1.1	46.0	56.8	11.6	10.1	15.0	7.5
TTU 21903	84.0	11.0	19.0	15.0	46.6	25.6	1.6	39.9	11.7
	23.5	25.6	1.1	46.6	58.4	11.7	9.8	15.0	7.3
TTU 21902	82.0	10.0	19.0	14.0	45.9	25.5	1.4	37.7	11.4
	21.5	25.5	0.9	45.9	56.5	11.4	9.8	14.0	7.3
TTU 21901	82.0	10.0	19.0	15.0	46.7	25.8	1.8	39.9	11.4
	23.6	25.8	0.8	46.7	56.2	11.4	9.5	15.0	7.7
TTU 21925	72.0	9.0	17.0	14.0	45.6	25.0	2.2	39.0	11.1
	21.8	25.0	1.2	45.6	47.0	11.1	9.8	14.0	7.4

TTU—The Museum, Texas Tech University; TCWC—Texas Cooperative Wildlife Collection, Texas A&M University; TTL—total length; TL—tail length; EL—ear length; HF—hind foot length; FA—forearm length; GLS—greatest length of skull; CL—calcar-leg width; EN—distance from lacrimal canal to anterior margin of nasals; ND5—length of metacarpal of digit five; MB—mastoidal breadth; TB—tibia length; ML—width of maxilla at first incisors; VL—vertebral length; ET—distance from anterior margin of auditory meatus to lacrimal canal.

APPENDIX III

Matrices of Distance Values

<i>Brachyphylla</i> —1					<i>Glossophaga</i> —6				
<i>Diphylla</i> —2					<i>Monophyllus plethodon</i> —7				
<i>Desmodus</i> —3					<i>Monophyllus redmani</i> —8				
<i>Diaemus</i> —4					<i>Phyllonycteris</i> —9				
<i>Erophylla</i> —5									
M-statistic untransformed frog measurements									
1	2	3	4	5	6	7	8	9	
1	—	4.066	2.844	3.332	4.707	7.509	5.757	7.905	3.895
2	4.795	—	1.262	0.989	2.052	4.153	2.777	4.548	1.566
3	4.028	1.686	—	1.245	2.437	4.699	3.244	5.095	2.057
4	4.250	1.514	1.190	—	1.930	4.657	2.913	5.053	1.435
5	6.187	3.382	2.971	2.789	—	2.966	1.251	3.362	1.410
6	8.418	4.509	5.710	5.010	3.760	—	1.752	0.935	4.053
7	7.343	3.948	4.075	3.712	1.450	2.333	—	2.148	2.301
8	9.332	5.475	6.172	5.667	4.165	1.405	2.738	—	4.448
9	5.512	3.367	2.937	2.713	1.158	4.299	2.377	4.704	—
M-statistic untransformed bat measurements									
M-statistic ratio transformed frog measurements									
1	2	3	4	5	6	7	8	9	
1	—	1.476	1.351	1.147	1.099	0.926	1.199	0.805	1.273
2	1.674	—	0.867	0.847	1.691	2.152	1.997	1.501	1.352
3	1.405	1.394	—	1.248	1.602	2.149	2.020	1.343	1.622
4	1.017	1.384	1.126	—	1.450	1.776	1.856	1.193	1.173
5	1.717	2.939	2.461	2.438	—	0.987	0.701	0.679	1.152
6	2.206	2.847	3.487	2.972	1.802	—	0.822	1.004	1.435
7	2.188	3.456	3.278	2.955	0.953	1.768	—	0.867	1.049
8	1.689	2.088	2.671	2.050	1.466	1.302	1.705	—	1.273
9	1.761	3.079	2.542	2.577	1.042	1.486	1.340	1.482	—
M-statistic ratio transformed bat measurements									
M-statistic log transformed frog measurements									
1	2	3	4	5	6	7	8	9	
1	—	3.460	2.368	2.867	4.053	7.373	5.335	7.817	3.356
2	4.399	—	1.113	0.950	2.065	4.553	2.928	4.998	1.526
3	3.715	1.671	—	1.180	2.406	5.025	3.323	5.470	2.013
4	3.878	1.489	1.214	—	1.924	4.947	2.991	5.392	1.486
5	5.535	3.272	2.797	2.644	—	3.380	1.376	3.825	1.322
6	8.435	5.088	6.291	5.551	4.042	—	2.038	1.158	4.426
7	6.864	4.037	4.138	3.779	1.619	2.444	—	2.482	2.388
8	9.459	6.119	6.871	6.327	4.659	1.665	3.061	—	4.871
9	5.170	3.533	3.042	2.887	1.134	4.865	2.571	5.482	—
M-statistic log transformed bat measurements									

APPENDIX III.—*Continued.*D² untransformed frog measurements

	1	2	3	4	5	6	7	8	9
1	—	2.293	1.286	1.288	2.298	5.000	3.604	5.678	2.095
2	3.251	—	0.369	0.271	1.279	2.314	1.684	2.611	6.994
3	2.859	0.572	—	0.379	1.242	3.088	2.118	3.266	1.064
4	1.865	0.466	0.507	—	1.179	2.516	1.740	3.062	0.510
5	2.709	1.644	1.995	1.398	—	0.737	0.273	0.856	0.513
6	5.433	2.288	3.941	2.660	1.127	—	0.186	0.185	1.223
7	3.976	2.334	3.225	2.160	0.326	0.463	—	0.399	0.649
8	6.532	2.191	3.364	2.788	1.139	0.460	0.675	—	1.696
9	1.857	1.986	2.100	1.125	0.393	1.629	0.632	2.041	—

D² untransformed bat measurementsD² ratio transformed frog measurements

	1	2	3	4	5	6	7	8	9
1	—	1.840	0.951	0.989	2.106	4.823	3.516	5.467	1.862
2	2.710	—	0.349	0.263	1.293	2.645	1.819	2.934	0.687
3	2.284	0.565	—	0.357	1.198	3.285	2.170	3.399	1.000
4	1.490	0.455	0.492	—	1.246	2.774	1.909	3.370	0.534
5	2.360	1.762	2.073	1.481	—	0.786	0.289	0.841	0.512
6	5.628	3.246	5.144	3.564	1.490	—	0.201	0.266	1.340
7	3.849	2.736	3.639	2.514	0.392	0.601	—	0.372	0.707
8	6.005	2.874	4.149	3.316	1.128	0.559	0.530	—	1.901
9	1.716	1.961	2.053	1.146	0.341	1.964	0.678	1.910	—

D² ratio transformed bat measurementsD² log transformed frog measurements

	1	2	3	4	5	6	7	8	9
1	—	1.693	0.949	0.910	2.083	5.553	3.632	6.429	1.819
2	2.888	—	0.315	0.239	1.367	3.132	1.977	3.639	1.673
3	2.482	0.583	—	0.365	1.353	4.002	2.444	4.360	1.077
4	1.505	0.473	0.556	—	1.299	3.274	2.034	4.091	0.527
5	2.223	1.496	1.765	1.168	—	1.083	0.333	1.265	0.527
6	5.790	3.171	5.068	3.399	1.527	—	2.941	0.282	1.590
7	3.696	2.489	3.406	2.184	0.437	0.537	—	0.562	0.739
8	7.091	2.986	4.452	3.669	1.620	0.615	0.898	—	2.246
9	1.694	2.273	2.123	1.220	0.412	2.415	0.836	2.940	—

D² log transformed bat measurements

APPENDIX III. — *Continued.*

Euclidean untransformed frog measurements

	1	2	3	4	5	6	7	8	9
1	—	8.021	6.696	6.825	10.567	17.861	13.057	18.669	7.639
2	8.654	—	1.325	1.200	3.518	10.137	5.398	10.883	1.057
3	6.230	2.867	—	0.163	4.469	11.387	6.592	12.155	1.087
4	7.545	1.566	1.382	—	4.307	11.234	6.435	11.999	1.152
5	11.608	5.980	6.045	5.433	—	7.342	2.865	8.181	3.182
6	17.022	9.233	10.867	9.707	6.110	—	4.845	0.883	10.262
7	13.971	7.390	8.144	7.283	2.459	3.811	—	5.659	5.426
8	18.892	11.064	12.741	11.577	7.836	1.874	5.433	—	11.052
9	10.073	2.078	4.844	4.542	2.634	7.680	4.082	9.437	—

Euclidean untransformed bat measurements

Euclidean ratio transformed frog measurements

	1	2	3	4	5	6	7	8	9
1	—	3.368	3.710	2.043	3.440	4.763	4.729	3.298	2.174
2	2.014	—	1.038	2.324	4.791	7.840	6.586	5.314	3.390
3	2.690	1.121	—	2.097	5.689	8.398	7.453	5.794	4.224
4	2.180	0.909	1.989	—	5.044	6.777	6.582	4.146	3.547
5	5.800	7.183	8.406	7.782	—	4.220	1.815	3.017	1.520
6	7.895	9.696	10.568	9.337	3.621	—	3.332	2.637	4.770
7	8.645	10.649	11.258	10.574	2.852	3.416	—	3.457	3.229
8	2.927	7.403	8.314	6.993	3.270	2.375	4.774	—	2.705
9	5.628	7.640	8.210	7.635	0.271	3.877	3.056	3.415	—

Euclidean ratio transformed bat measurements

Euclidean log transformed frog measurements

	1	2	3	4	5	6	7	8	9
1	—	7.262	6.172	6.285	9.096	17.601	12.008	18.678	6.371
2	7.519	—	1.097	0.989	3.357	10.889	5.505	11.820	1.745
3	4.962	2.812	—	0.290	4.005	7.026	6.225	12.869	1.539
4	6.352	1.458	1.438	—	3.725	11.691	6.202	12.663	1.254
5	9.882	5.426	5.596	4.985	—	8.523	2.956	9.643	2.890
6	16.482	10.028	11.683	10.526	6.775	—	5.593	1.293	11.263
7	12.547	7.109	8.020	7.125	2.724	4.278	—	6.690	5.678
8	18.510	11.886	13.675	12.477	8.996	2.061	6.321	—	12.315
9	8.684	5.630	4.957	4.778	1.641	8.525	4.259	10.576	—

Euclidean log transformed bat measurements