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A PHENETIC ASSESSMENT OF THE CICONIIDAE (AVES) USING
SKELETAL MORPHOLOGY

The University of Oklahoma

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(AVES) USING SKELETAL MORPHOLOGY

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D. SCOTT WOOD

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A PHENETIC ASSESSMENT OF THE CICONIIDAE
(AVES) USING SKELETAL MORPHOLOGY

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PREFACE

The following dissertation is divided into three distinct parts each of which is designed as a manuscript to be submitted for publication. The first paper is a summary of the phenetic affinities expressed by those skeletal elements of the storks that were analyzed; it is basically descriptive in nature. The second paper presents a new mathematical transformation for continuous mensural data to be used in phenetic studies; this transformation was used in the other parts of the study. The third paper contains comparisons between the phenetic morphologic results and the similarities based on ritualized courtship behavior; nomenclatural recommendations are discussed. Papers I and III are to be submitted to the Annals of Carnegie Museum; paper II is to be submitted to Systematic Zoology.

PHENETIC RELATIONSHIPS WITHIN THE CICONIIDAE (AVES)

D. Scott Wood

Abstract

The major skeletal elements of all 17 species of storks were analyzed using techniques from multivariate statistics to assess the phenetic affinities within the family Ciconiidae. The common-part transformation and the use of taxonomic distances clustered by the unweighted pair-group method with arithmetic averages gave significantly more stable phenetic arrangements than the other methods used. My results are very similar to the classification of Kahl (1979b) at the generic level with the exception that Jabiru is more similar to Ephippiorhynchus than would be indicated from Kahl's classification. Also, Kahl's placement of these two genera in the tribe Leptoptilini is not supported by results based on skeletal data; these genera are phenetically similar to the Ciconia species.

Introduction

The cosmopolitan avian family Ciconiidae is composed of the 17 species of storks (Table 1, nomenclature from Kahl 1971a, 1972a). By 1901 there was agreement as to the membership of the family except for the Shoebill (*Balaeniceps*), which most authors considered to be in a separate family (e.g., Beddard 1886, 1896, 1901, Garrod 1875, 1877, 1878, Parker 1860, Weldon 1883) and is currently recognized as such (Kahl 1979a). The classification of Peters

(1931, Fig. 1A) summarized the systematic findings with the 17 species allocated to 11 genera in two tribes. Prior to Peters' classification, virtually all studies involving storks either focused on the relationships of the Ciconiidae as a whole to other birds (or vice versa) rather than on relationships within the family or were concerned with describing a new feature of some particular species. More recent morphological studies also have focused on the relationships of the family to other birds (e.g., Cottam 1955, Ligon 1967). With the exception of Verheyen (1959), there has been no comprehensive investigation of the comparative morphology of members of the Ciconiidae although Furbringer (1888), Garrod (1873), and Vanden Berge (1970) included representatives of the family in their comparative studies of muscles.

Verheyen (1959) examined a wide range of characters in an attempt to clarify the relationships within the order Ciconiiformes (sensu Wetmore 1960) and included all but one species of stork (Anastomus oscitans) in his analysis. He proposed a classification for this family (Fig. 1B) that differed in several important respects from that of Peters (1931). In the process, he only reduced the number of genera to nine, referring the genera Jabiru and Xenorhynchus of Peters to Ephippiorhynchus and placing the genus Dissoura in the Leptoptilini, one of the four tribes he recognized.

Kahl (1966, 1971a, 1972a-e, 1973) compared the ritualized courtship behavior of all 17 storks and considerably improved our knowledge of the intrafamilial relationships. His classification

(Kahl 1979b) is shown in Fig. 2. Kahl also made important departures from both Peters' (1931) and Verheyen's (1959) classifications, reducing the number of genera to six and allocating these genera to three tribes. Significantly, he combined several genera into Ciconia and placed Anastomus and Mycteria in a separate tribe. He also associated Jabiru and Ephippiorhynchus with Leptoptilos, although not on behavioral grounds (Kahl 1973).

As part of a larger study involving the relationships of the Ciconiidae, I investigated the phenetic associations within the family as implied by the structure of a number of different skeletal elements. I also use my empirical results to evaluate the efficacy of the phenetic methods chosen, some of which have received little critical attention.

Materials and Methods

Skeletons of the 17 species were obtained (Table 1). Because of the paucity of material, I measured the first five or six specimens encountered, as listed in Appendix I, regardless of origin (unless a specimen was damaged); for some species fewer than five specimens were available. I chose characters by: (1) comparing among a reference series of ciconiiforms in the University of Oklahoma collections; (2) rejecting skeletal elements for which I could discern only small variation over the series; (3) identifying points on each of the remaining bones in such a way that for any individual I could identify the point homologous to that of the reference series; (4) choosing interpoint distances that would,

when measured, describe variation visible to my eye. The interpoint distances were also chosen so that they formed the sides of triangles; in this way I could calculate the angles subtended by the sides of the triangles and thus have a relatively size-independent measure of the shape of the bone. Using this procedure I chose 107 points spread over nine bones or bone complexes. Fig. 3 shows the points chosen for each of the bones. From this network I selected 215 measurements; these delimited 99 triangles giving 297 angular characters (Table 2). Descriptions of the points, characters and angles are listed in Appendix II; nomenclature is taken from Baumel et al. (1979) and Bock and McEvey (1969). The data for each bone were analyzed separately; in addition, I analyzed the total data set (as defined below).

Computations were performed on the IBM 370-158 at the University of Oklahoma. Some analysis was done using FORTRAN routines but most employed the packages NT-SYS (Rohlf, Kishpaugh and Kirk 1979) and SAS (Barr et al. 1979). The three-dimensional models were plotted using the program GRAFPAC developed by F.J. Rohlf.

Each species was represented by the means of each character over all individuals. Missing values were estimated; of the approximately 12,000 measurements used in this study, only 9 were coded as missing.

Angles were calculated in radians in the following way: Let A, B, and C be the sides of the triangle (the measured characters) and X be the angle opposite A. Then $\underline{X} = 2 * \arctan (\underline{R} / (\underline{S} - \underline{A}))$

where $\underline{S} = (\underline{A} + \underline{B} + \underline{C}) / 2$ and $\underline{R} = ((\underline{S} - \underline{A}) * (\underline{S} - \underline{B}) * (\underline{S} - \underline{C})) / \sqrt{\underline{S}}$.

The angles were calculated for all individuals and means were computed to represent each species. Where, due to measurement error, angles could not be calculated (the sum of the lengths of two sides of a triangle was less than the third), the angles were estimated by comparing the relative lengths of the sides and then assigning values representing angles of a very obtuse triangle of similar proportions.

Size (at least its linear effects) is considered by many workers to be a poor indicator of taxonomic relationships (Sneath and Sokal 1973). For many taxonomic studies using continuous characters, size has thus been considered a problem; using untransformed data, large (or small) species cluster together regardless of shape (see discussion in Sneath and Sokal 1973:169-174). The problem of size has two facets: (1) the definition of size; and (2) how to remove or reduce its effects. Sneath and Sokal (1973) suggested that if in an ordination the first axis has mostly positive loadings then this axis represents a size axis. They proposed removing the effect by collapsing the ordination by that dimension and using the remaining axes. Alternatively, they suggested removing a measure of size through the use of ratios, a common and widespread practice.

More recently Atchley, Gaskins and Anderson (1976), Atchley and Anderson (1978) and Atchley (1978) have demonstrated potential dangers of using ratios. They suggested using regression analysis to remove the effects of size (or some other variable). I expected

size to have a considerable influence on the magnitude of the raw measurements since the family includes some of the largest of flying birds as well as a few of only moderate size (range in height 76cm - 152cm; Harrison 1978). Principal component I (based on a matrix of correlations among the characters from the total data set as defined below) did not represent size since the high loadings were restricted to a specific set of characters and were not all positive. However, clusters of species derived from the raw data (using the unweighted pair-group method with arithmetic averages; UPGMA) appeared to reflect a large size influence.

I operationally defined size as the mean of three length characters corresponding to the lengths of the tarsometatarsus, tibiotarsus and ischium (TA-DN, TI-EL, SY-CJ; see Appendix II). To check that this variable reflected size, I clustered the species according to size by eye and compared these groups to the UPGMA clusters formed using the size variable only. The results were concordant and were also very similar to clusters derived from the raw data. I then regressed each variable against the size variable to obtain the regression estimate, subtracted the estimate from the original value and used the residual as the character state.

Explicitly, this procedure is as follows: Let $\underline{Y}$ be a vector of measurements for a given character over all species. Let $\underline{X}$ be the size vector over all species. The estimate of $\underline{Y}_1$ ($= \hat{\underline{Y}}_1$) can be found from the equation $\hat{\underline{Y}} = \alpha + \beta \underline{X}$, where $\alpha = \bar{\underline{Y}} - \beta \bar{\underline{X}}$ and $\beta = r_{(\underline{Y}, \underline{X})} * (\underline{s}_Y / \underline{s}_X)$. The quantity $r_{(\underline{Y}, \underline{X})}$ is the correlation

between the variables $\underline{Y}$ and $\underline{S}$; $\underline{s}_Y$ and $\underline{s}_X$ are the standard deviations of these variables. The residual, $\underline{R}$, is found from $\underline{R}_i = \underline{Y}_i - \hat{\underline{Y}}_i$. These residuals are uncorrelated with $\underline{X}$ (size). Size accounted for between 60% and 90% of the variance of the data for the various bones. The angular data provided a second transformation to reduce the effects of size; tests indicate the correlation with the size variable to be much reduced.

For another transformation I removed the "common part" from each of the data sets. This idea is described and developed more fully in Wood (1982b). Briefly, the variable representing a particular stork (the vector of measurements on that stork) can be thought of as having two parts: (1) a part predictable by regression from some reference variable (some bird other than a stork) and (2) a part not predictable from the reference variable. If the reference variable is chosen to estimate the essence of the stork family as closely as possible, then I will refer to the first component as the common part. The second part I will call the clustering part; the variance accounted for by the latter concerns differences between the various storks as well as variation due to measurement error.

The clustering part is of most use when evaluating relationships within a group. The common part can be removed in a manner analagous to the procedure outlined above for removing size if an estimate of the common part can be found. In phenetic studies, a species (or several species that is very similar to the members of the group under study can be used to estimate the common part; the more similar

the outside species is, the better will be the estimate. For this study I used two species to estimate the common part: Balaeniceps rex and Scopus umbretta. They are osteologically very similar to the storks and several authors have suggested they are related to the storks (e.g., Mitchell 1913, Parker 1860, Peters 1931, Wetmore 1960). The regression equation used in this case is: $\hat{\underline{Y}}_i = \alpha + \beta_1 \underline{X}_1 + \beta_2 \underline{X}_2$, where $\hat{\underline{Y}}_i$ is the estimate of all variables for species i , $\underline{X}_1$ and $\underline{X}_2$ are the vectors of character measurements for Scopus and Balaeniceps, and α and β are as above (β_1 and β_2 correspond to Scopus and Balaeniceps, respectively). Between 80% and 90% of the variance was removed from the various data sets by this procedure. A separate estimate of the common part was also calculated from four other species (one pelican, one cormorant, and two New World vultures). Average taxonomic distances (Sneath and Sokal 1973) were calculated between all storks for each set of estimates for each bone. The average matrix correlation between estimates (over all bones) was 0.91 indicating that the transformation (removal of the common part) is robust to the choice of estimator for the common part.

The use of means obscures variability within each species and, consequently, the overlap in phenetic space. If substantial overlap exists, there may be insufficient information present to discern the relationships among the elements (taxa). Partitions from such a data set should give less consistent taxonomic results than partitions taken from a case showing much less overlap because in the first case the variation is more nearly random with

respect to the taxa. For all of the transformations (size removed, angles, common part), I subjected each of the data sets to a multiple discriminant function analysis (using PROC DISCRIM of SAS). My interest was in the resolution afforded by the data: how many individuals were misclassified? If the resolution was poor (i.e., poor discrimination among species resulting in many misclassifications, particularly if they were misclassified to species thought on other grounds to be relatively dissimilar or unrelated) then I judged that using means would be likely to compound errors and give discordant results. Of the nine bones originally used (Table 2), five showed sufficient resolution to be useful in subsequent analyses (the remaining four produce far less consistent results). Thus, the remainder of the analyses were restricted to the following: skull, humerus, sternum, synsacrum and tarsometatarsus. One reason for the poor resolution resulting from use of the other bones is that the original measurements were devised to describe variation over all ciconiiforms (sensu Wetmore 1960); the elements not used further (axis, clavicle, coracoid and tibiotarsus) are very uniform within the Ciconiidae but show considerable variation over the several families of the Ciconiiformes.

All subsequent analyses (except as noted) were performed on each of the 18 data sets: six partitions (skull = SK, humerus = HU, sternum = ST, synsacrum = SY, tarsometatarsus = TA, all characters from these five bones = ALL) with three transformations for each (size removed by regression = SIZE, size effect reduced by using

angles = ANGLES, common part removed = COMMON). A given data matrix is named by concatenating the transformation code with the partition code (e.g., SIZE-SK, ANGLES-SY). The following analyses were performed after standardization of the data: (1) A phenogram summarized the results of a UPGMA cluster analysis on a matrix of average taxonomic distances. (2) Factor analysis using a matrix of correlations among taxa (Q-type) was performed with a secondary factor structure matrix obtained by oblique rotation using the functionplane technique of Katz and Rohlf (1974). Communalities were estimated using the maximum of the absolute values of the elements for each variable in the correlation matrix and all factors with eigenvalues greater than 1.0 were retained. The secondary structure matrix was interpreted as a taxon by character matrix and used to produce inter-taxon correlations as the similarity measure. These were subjected to a UPGMA cluster analysis and the results summarized in a phenogram. This procedure seeks to identify patterns of common variation (clusters of taxa) and emphasize these by rotating the axes to be coincident with the clusters. An oblique rotation was used because there is no a priori reason to expect clusters of biological organisms to be orthogonal. The analysis reconstitutes the among-taxa correlation matrix but emphasizes the similarities between members of a cluster because the components of variance unique to a given taxon are discarded. Thus, the phenograms closely resemble phenograms produced by UPGMA clustering of the original inter-taxon correlation matrix except that the

clusters are better defined and phenograms based on different partitions of the data are slightly more consistent (i.e., have a higher average matrix correlation among results).

(3) Projections of the taxa on axes from a principal components analysis (the number of components was determined by the number of eigenvalues greater than 1.0) were subjected to a cluster analysis using the adaptive hierarchical clustering scheme (AHCS) of Rohlf (1970); these results were summarized in a phenogram. AHCS can find elongated clusters in multidimensional space rather than only the hyperspheroidal clusters searched for by most clustering algorithms (including UPGMA). The degree of elongation sought is controlled by a parameter of the program (set to 1.0 for this study). The technique uses inter-taxon distances for the similarity measure and so may give results similar to UPGMA clustering of these distances, particularly if elongated clusters do not exist. Because of computer limitation, AHCS was not run on the combined (ALL) data sets. (4) Non-metric multidimensional scaling (MDS) was used to reduce the dimensionality of the data to three. The species were plotted on these axes using GRAFPAC to produce three-dimensional (3-D) models; these give better visual representation of the distances among taxa than is usually possible using phenograms. (5) Minimum-spanning trees (for taxa) were derived from average distance matrices and superimposed on the 3-D models. (6) Matrix correlations were calculated between all pairs of phenograms and between a phenogram and its basic similarity matrix (cophenetic

correlations).

Codes for the three phenogram-producing analyses are: DIST (UPGMA clustering of distances), AHCS (AHCS clustering of distances) and CORR (Q-type factor analysis). Phenograms, basic similarity matrices and other results were named by concatenating these codes with the codes for transformation and partition (e.g., COMMON-SK-DIST, SIZE-ALL-CORR). A dendrogram of phenograms was created by applying UPGMA to the matrix of correlations among phenograms (after changing the sign on the matrix correlations between distance analyses and correlation analyses). Further discussion of these techniques may be found in Sneath and Sokal (1973) or in the documentation to NT-SYS (Rohlf, Kishpaugh and Kirk 1979).

Results and Discussion

Fifty-one phenograms were constructed to represent the similarities among the storks. Fig. 4 is a dendrogram of these phenograms based on correlations between all pairs of cophenetic matrices. The cophenetic correlation of this dendrogram is 0.693, an indication of some distortion in the original associations. Figs. 5-7 show phenograms representative of the major clusters present in the dendrogram (using an arbitrary level of 0.4); additional phenograms are shown in Figs. 8-10 and in Wood (1982a, c).

Fig. 5A depicts the phenogram for ANGLES-HU-DIST, a representative of one of the two largest clusters in Fig. 4. Except for Anastomus oscitans, which is well separated from the other species, the clusters correspond closely to the genera of Kahl (1979b, Fig. 2). In addition

to A. lamelligerus being associated with Ciconia, Jabiru clusters with the Ciconia species. This is one of only four phenograms to support Kahl's placement of Ephippiorhynchus with Leptoptilos (the others are ANGLES-HU-AHCS, COMMON-HU-CORR and COMMON-SK-CORR). The cophenetic correlation is 0.737 due to distortion among the major branches of the phenogram.

The phenogram of COMMON-SK-AHCS (Fig. 5B) is a representative of the other large cluster in Fig. 4. The structure of this phenogram matches the structure of Kahl's (1979b) classification (Fig. 2) closely with the exceptions that Anastomus and Ephippiorhynchus are associated with Ciconia, and Jabiru clusters with Mycteria.

In the phenogram for COMMON-ALL-CORR (Fig. 6A), the species cluster very tightly, a phenomenon generally true of the CORR analyses because of the emphasis placed on close similarities by the factor analytic procedure used. The composition of the clusters is similar to that found in the previous examples with the exception of Ciconia which is split among two groups. Jabiru is most similar to Ephippiorhynchus and Ciconia whereas Leptoptilos is closer to Mycteria. The cophenetic correlation of 0.893 indicates relatively little distortion in the phenogram.

The phenograms in Figs. 6B, 7A and 7B are representatives of relatively small clusters of the dendrogram of phenograms (Fig. 4). The phenogram for COMMON-SY-CORR (Fig. 6B) shows several clusters that are similar to Kahl's genera but both Mycteria and Ciconia are split. Mycteria leucocephala clusters with Ephippiorhynchus and C. abdimii

is associated with Anastomus. The cophenetic correlation (0.715) is relatively low; the relationships of the storks implied by the phenogram are somewhat distorted from the basic similarities. Mycteria and Anastomus cluster together in the phenogram SIZE-ALL-DIST (Fig. 7A). Four of the five species of Ciconia also cluster together but Leptoptilos javanicus is separated from its congeners. Some distortion is present (cophenetic correlation of 0.818). The phenogram ANGLES-TA-DIST (Fig. 7B) represents a cluster in Fig. 4 composed of the three analyses using the data set ANGLES-TA. These three phenograms are the only results concordant with Verheyen's (1959) suggestion that Ciconia episcopus is closely related to Leptoptilos. Only the Mycteria cluster resembles the groups proposed by Kahl (1979b, Fig. 2). The cophenetic correlation of 0.730 is relatively low for this study.

Clearly, there are considerable differences between some phenograms (the range of matrix correlations is -0.10 to 0.95). These differences are not only between transformations and analyses but also between data sets for a given transformation and analysis.

Rohlf and Sokal (1981) pointed out that methods that produce more stable classifications (other factors being equal) would be preferred over those that produce less stable classifications. They also noted that stability, by itself, is not a good criterion since perfect stability can be achieved by making the results independent of the data. However, this criterion can be useful when comparing methods chosen for reasons other than stability (e.g., to emphasize

a particular aspect of the data).

Rohlf and Sokal (1980,1981) have discussed several definitions of stability, of which robustness of a classificatory procedure to changes in character sets (congruence of resultant classifications) is applicable here. They defined congruence as "agreement of separate classifications arrived at by the same algorithms and based on the same set of operational taxonomic units but on different sets of characters" (Rohlf and Sokal 1981). The sets of characters should not represent different classes of characters since such an evaluation of stability would be confounded with an evaluation of the non-specificity hypothesis (Rohlf and Sokal 1980). Matrix correlations are a useful measure of the relative congruence of classifications although this measure may not be optimal for evaluating absolute levels of concordance (Rohlf 1982).

The partitions of the characters used in this study provide an opportunity to evaluate the stability of the methods employed. Both the transformations of the data as well as the analyses applied to these data are evaluated with respect to the stability of the resulting classifications. Table 3 lists the average matrix correlations among phenograms over all partitions (five bones) for all transformations and analyses considered. Ranges and standard deviations are included. Within each transformation and analysis (e.g., ANGLES-DIST) the 10 correlations used to calculate the mean are not independent since they represent all possible comparisons among the five partitions. However, at least four comparisons are

independent and the degrees of freedom in all significance tests are adjusted accordingly. Significant heterogeneity exists among the means listed in Table 3 (analysis of variance, $F = 3.35$, $F_{0.5 [4,36]} < 2.69$). If the means are ranked, no significant differences exist between adjacent means. However, the analysis COMMON-DIST has a significantly higher mean than any analysis except COMMON-AHCS ($t = 2.71$, $t_{0.5 [8]} = 1.86$ [one tailed] between COMMON-DIST and COMMON-CORR). If the analyses are pooled so that the differences between transformations can be evaluated, then the COMMON transformation gives significantly more congruent results (i.e., a higher mean) than does SIZE ($t = 2.274$, $t_{0.5 [16]} = 1.746$ [one tailed]). The ANGLE transformation gives results with lower average congruence than SIZE. These findings are supported by a more detailed analysis of a subset of the data which is presented elsewhere (Wood 1982b).

The mean matrix correlation among partitions is very low for both the SIZE and ANGLE transformations (Table 3). These transformations were chosen to emphasize the shape of the skeletal elements used as the source of information about relationships among the storks. Shape was defined in two different ways: in the SIZE transformation shape was the residual variance remaining from a statistical removal of a size estimate; in the ANGLE transformation shape was defined as the angles subtended by pairs of measurements on the bones. The emphasis on shape (or the de-emphasis of size) has been commonly used in phenetic studies because the single

characteristic "size" often has such a pervasive influence as to mask the information about relationships present in the other characters used in the study. However, the classifications I have derived from the size transformations show rather low stability (as measured by matrix correlations) regardless of the analysis employed.

In contrast to findings of some other investigators (e.g., Schnell 1969, Robins and Schnell 1971, Hellack 1976) but similar to my earlier results on cranes (Wood 1979), distances gave the most stable (consistent) results. However, this may be more an effect of the transformation than of other considerations since the transformations used by the investigators cited above were quite different from those used here.

Both analyses (UPGMA and AHCS) of distances among the taxa using the COMMON transformation produced results that were more stable than the CORR analysis but only the UPGMA (DIST) was significantly higher. The DIST (UPGMA) and AHCS analyses are very similar except that AHCS can also find clusters that are not hyperspheroidal. If the clusters are elongated then AHCS should better detect them and, hence, give more stable results. This is not the case here although the difference in stability (measured by matrix correlation) is not significant. Inspection of the 3-D models (Figs. 11-16; these represent the interspecific distances very closely) reveals little elongation of clusters.

Thus, for the purpose of revealing phenetic structure consistent

over different sets of characters, the transformation and analysis COMMON-DIST is most effective. Figs. 8-10 show the phenograms from the six partitions (five bones plus the combined data) for this transformation and analysis. All except COMMON-SY-DIST are relatively good representations of the basic similarity matrices (cophenetic correlations greater than 0.830). The cophenetic correlation for COMMON-SY-DIST is 0.737, indicating distortion in the phenogram. Figs. 11-16 show the 3-D models derived from MDS analyses of the COMMON transformed data sets. These give more accurate representations of the dissimilarities (distances) among the storks than the phenograms but are much more difficult to interpret as hierarchically nested sets of clusters (classifications in the usual sense). The minimum spanning networks superimposed on the models give further information on the close affinities of the storks.

The six phenograms of Figs. 8-10 have many clusters in common (the average matrix correlation between them is 0.531). In particular, some of the genera proposed by Kahl (1972a, 1979b) appear consistently as clusters. The four species placed by Kahl in the genus Mycteria cluster together in all analyses, as do the two species of Anastomus and the three of Leptoptilos. Within the Mycteria association, M. ibis and M. leucocephala are a mutually close pair in all analyses except COMMON-SY-DIST (Fig. 10A). In the latter, M. ibis is the species most similar to M. leucocephala but not vice versa (see Fig. 15). Mycteria

americana and M. cinerea form a mutually close pair in three of the analyses (COMMON-ALL-DIST, Fig. 8A; COMMON-HU-DIST, Fig. 9A; and COMMON-TA-DIST, Fig. 10B) but in the remaining three, M. americana is represented as the most divergent of the group. This latter arrangement is not new; M. americana has traditionally been separated generically from the other wood storks (Fig. 1A).

The two species of Ephippiorhynchus cluster less consistently, being a mutually close pair in only three of the phenograms (Figs. 8A, B and 10A). However, E. senegalensis is more similar to E. asiaticus than to any other species in analyses of both the humerus and sternum (Figs. 13-14). For the tarsometatarsus data, E. senegalensis is nearly as similar to E. asiaticus as is Jabiru (Fig. 16).

The relationships of the species placed by Kahl into the genus Ciconia are less consistently portrayed. In only two phenograms (Fig. 8A and 8B) are all five species clustered together to the exclusion of the other storks. However, some close similarities are more consistently found: C. abdimii and C. episcopus group together in all analyses and in four cases are mutually close pairs; C. nigra, C. maguari and C. ciconia are present in the same cluster in four analyses. Table 4 summarizes the nearest neighbors (along the minimum spanning network in the multidimensional character space) of each of the Ciconia species for each data set. For two species, the results are the same regardless of data set: the most similar species to C. abdimii is always C. episcopus and the most

similar to C. maguari is in every case C. ciconia. The converse is not true; that is, C. maguari is not always the most similar species to C. ciconia. In fact, in only one of the six analyses (symsacrum) is this true. However, in all but 2 of 30 cases the nearest (most similar) species to a member of the genus Ciconia is a congener (C. episcopus is most similar to Anastomus oscitans in the sternal analysis and C. ciconia is most similar to Ephippiorhynchus asiaticus in the analysis of tarsometatarsal data; see Figs. 14 and 16). C. nigra is intermediate between the two pairs of species discussed above; C. ciconia is most similar to it in four analyses (and vice versa in three of those) and C. episcopus is most similar to it in the remaining two (sternal and symsacral data). These results suggest that for summarizing the phenetic relationships among the Ciconia species using a phenogram, COMMON-ALL-DIST (Fig. 8A) is the best consensus. C. maguari should be shown more similar to C. ciconia and C. nigra than is depicted. The 3-D model for this analysis (Fig. 11) gives a good graphic summary of the phenetic relationships of the Ciconia species.

The relationships of Jabiru are less consistent than for other storks. In the phenograms it is associated with Ephippiorhynchus in COMMON-ALL-DIST (Fig. 8A) and COMMON-TA-DIST (Fig. 10B), and with Ciconia ciconia and/or C. maguari in COMMON-HU-DIST (Fig. 9A), COMMON-ST-DIST (Fig. 9B) and COMMON-SY-DIST (Fig. 10A); it is very different from other storks when only the skull is considered (see Figs. 8B, 12). However, in the analyses using data from

either the humerus of sternum, the species most similar to Jabiru is Ephippiorhynchus asiaticus (Figs. 13,14). Jabiru thus shows closest similarities to Ephippiorhynchus but is also clearly to some members of the Ciconia group.

The relationships among the groups discussed above (corresponding to the genera of Kahl) also show some consistent features. Leptoptilos is divergent from other groups in five of the six analyses, COMMON-TA-DIST (Fig. 10B) being the exception, and in all but COMMON-SK-DIST (Fig. 8B) is the most divergent group. In this latter exception (Fig. 8B), Anastomus is the most divergent but since the two storks of this genus have such highly modified bills and associated skull structures adapted to a particular feeding method (Kahl 1971b), it is not surprising that an analysis of skull characters shows them to be quite divergent. In four of the other five analyses, Anastomus is closely linked with Mycteria; in the fifth (COMMON-ST-DIST, Fig. 9B), the association is much less close but, as can be seen from the corresponding 3-D model (Fig. 14), Mycteria is more similar to Anastomus than to any other genus or group. Members of the Ephippiorhynchus-Jabiru group are associated with the Ciconia species in three of the phenograms (Figs. 8A, 9) but in every 3-D model this group (or a majority of the group) is linked in the minimum spanning network to Ciconia species

Summary of Phenetic Results

My purpose in constructing phenograms and 3-D models was to summarize the overall similarity of the organisms under study in

a concise form. Many phenograms (and models) were produced during this study, each emphasizing a different aspect of the phenetic relationships among the storks. Both the technique employed to examine the relationships and the character set used affect the results produced. For the data analyzed in this paper, the COMMON transformation is clearly preferred as is the use of average distance as a similarity measure. UPGMA is appropriate because there is little evidence for elongated clusters among the storks. Thus, the COMMON-DIST analysis is the most suitable to summarize the phenetic similarities.

The classifications derived from analyses of each bone are most appropriate where further study concerns the particular aspect emphasized by the classification. For example, predictions of the similarities in feeding habits and apparatus of the storks would likely be most accurately obtained from a classification emphasizing characteristics of the head region of the skeleton. However, for a general summary statement, a classification representing the similarity over all characters is most appropriate provided it shows little distortion of the consensus of relationships implied by the different partitions of the data. The phenogram COMMON-ALL-DIST (Fig. 8A) satisfies these criteria except that Ciconia maguari should be shown more similar to C. ciconia and C. nigra. A better summary but one that is not composed of hierarchic non-overlapping groups, is given by the 3-D model for this analysis (Fig. 11).

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Table 1.--Taxa and number of specimens used in this study (nomenclature from Kahl 1972a)

Name	No. specimens	Geographic range (Kahl 1979b)
<i>Mycteria americana</i>		
American Wood Stork	5	Southern United States to Paraguay
<i>Mycteria cinerea</i>		
Milky Stork	2	Cambodia to Java
<i>Mycteria ibis</i>		
Yellowbilled Stork	6	Africa, from Senegal to Sudan; south to Natal
<i>Mycteria leucocephala</i>		
Painted Stork	5	India and Sri Lanka to Vietnam
<i>Anastomus oscitans</i>		
Asian Openbill Stork	5	India and Sri Lanka to Vietnam
<i>Anastomus lamelligerus</i>		
African Openbill Stork	4	Africa, from Senegal to Sudan; south to Transvaal
<i>Ciconia nigra</i>		
Black Stork	4	Much of Palearctic; South Africa

Table 1 continued

Ciconia abdimii

Abdim's Stork	5	Africa, from Senegal to Uganda and Yemen
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Ciconia episcopus

Woolynecked Stork	5	India and Sri Lanka to Borneo and the Philippines
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Ciconia maguari

Maguari Stork	5	Colombia to Argentina
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Ciconia ciconia

White Stork	6	Europe to Turkistan; Cape Province; Eastern Siberia
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Ephippiorhynchus asiaticus

Blacknecked Stork	5	India and Sri Lanka to Northeastern Australia
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Ephippiorhynchus senegalensis

Saddlebill Stork	5	Africa, from Senegal to Sudan; south to Transvaal
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Jabiru mycteria

Jabiru Stork	5	Mexico to Argentina
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Leptoptilos javanicus

Lesser Adjutant Stork	5	Eastern India to Borneo
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Table 1 continued

Leptoptilos dubius

Greater Adjutant Stork	5	Northeastern India to Vietnam
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Leptoptilos crumeniferus

Marabou Stork	6	Africa, from Senegal to Sudan; south to Natal
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Table 2.--*Bones used to infer phenetic relationships among the Storks; numbers of points and characters defined on each bone.*

Bone	Number of		
	points	linear	angles
Ossa cranii, ossa faciei	16	39	51
Axis ¹	8	18	24
Humerus	17	36	57
Clavicula ¹	10	15	18
Coracoideum ¹	10	16	21
Sternum	9	21	33
Synsacrum, os coxae	11	21	30
Tibiotarsus ¹	12	20	24
Tarsometatarsus	15	29	39

¹Used only in preliminary analyses.

Table 3.--*Statistics on matrix correlations between all pairs of cophenetic matrices derived from each of the five data partitions. Each treatment of the data is analyzed separately; for each analysis the number of possible intercorrelations is 10.*

Analysis	Mean	Standard deviation	Range
COMMON-DIST	.352	.182	.805 - .291
COMMON-AHCS	.407	.193	.833 - .177
COMMON-CORR	.353	.100	.471 - .190
SIZE-DIST	.312	.145	.520 - .051
SIZE-AHCS	.275	.151	.568 - .107
SIZE-CORR	.339	.171	.679 - .102
ANGLES-DIST	.303	.192	.597 - .102
ANGLES-AHCS	.187	.209	.667 - -.007
ANGLES-CORR	.291	.108	.475 - .151

Table 4.--Nearest neighbor in phenetic space (average taxonomic distances for members of the genus *Ciconia* for each data partition; SK = skull, HU = humerus, ST = sternum, SY = synsacrum, TA = tarsometatarsus, ALL = all characters.

Reference species	<i>Ciconia</i>					Other (see text)
	<i>nigra</i>	<i>abdimii</i>	<i>episcopus</i>	<i>maguari</i>	<i>ciconia</i>	
<i>Ciconia</i>						
<i>nigra</i>			ST, SY		SK, HU, TA, ALL	
<i>abdimii</i>			SK, HU, ST, SY, TA, ALL			
<i>episcopus</i>	SY	SK, HU, ST ALL				TA
<i>maguari</i>					SK, HU, ST, SY, TA, ALL	
<i>ciconia</i>	HU, TA, ALL	SK		SY		ST

Figure Legends

Fig. 1. Dendrograms representing (A) the classification of Peters (1931) and (B) the relationships postulated by Verheyen (1959).

Fig. 2. Dendrogram representing the classification of Kahl (1979b).

Fig. 3. Representative skeletal elements of the storks showing the points defined in this study. The characters defined from these points are listed in Appendix II. The specimens illustrated are Leptoptilos sp. (UOMZ 7722, views 1-4), Ciconia ciconia (CM S-1813, views 5-8, 10-15), Jabiru mycteria (UOMZ 6794, view 9), and Mycteria americana (UOMZ 7720, views 16-23). The following bones and views are illustrated: (1) skull and palate, ventral view; (2) skull and palate, left lateral view; (3) axis, right lateral view; (4) axis, caudal view; (5) left humerus, proximal portion, cranial view; (6) left humerus, proximal portion, caudal view; (7) left humerus, distal portion, cranial view; (8) left humerus, distal portion, dorsal view; (9) clavicle, right dorsolateral view; (10) left coracoideum, dorsal view; (11) left coracoideum, ventral view; (12) sternum, left lateral view; (13) sternum, cranial view; (14) synsacrum, dorsal view; (15) synsacrum, left lateral view; (16) left tibiotarsus, proximal portion, dorsal view; (17) left tibiotarsus, distal portion, dorsal view; (18) left tibiotarsus, proximal end; (19) left tibiotarsus, distal portion, medial view; (20) left tarsometatarsus, proximal portion, dorsal view; (21) left tarsometatarsus, proximal end;

(22) left tarsometatarsus, distal portion, dorsal view; (23) left tarsometatarsus, distal portion, plantar view.

Fig. 4. Dendrogram of phenograms derived from a UPGMA analysis of all possible matrix comparisons between the cophenetic matrices for the 51 phenograms of this study (scale is in correlation units).

Fig. 5. Phenograms representative of the major clusters of the dendrogram of phenograms: (a) derived from UPGMA clustering of taxonomic distances based on angular characters of the humerus; (B) derived from an AHCS analysis of taxonomic distances based on the COMMON transformation of skull characters. Scales of both phenograms are in units of average taxonomic distance.

Fig. 6. Phenograms representative of the major clusters of the dendrogram of phenograms. Both are derived from UPGMA clustering of correlations taken from a Q-type factor analysis of characters transformed using the COMMON transformation: (A) based on all characters; (b) based on synsacral characters. Scales of both are in correlation units.

Fig. 7. Phenograms representative of the major clusters of the dendrogram of phenograms: (A) derived from UPGMA clustering of taxonomic distances based on the SIZE transformation of all characters; (B) derived from UPGMA clustering of taxonomic

distances based on angular characters of the tarsometatarsus.

Scales of both are in average taxonomic distance units.

Fig. 8. Phenograms derived from UPGMA clustering of average taxonomic distances based on the COMMON transformation of the data: (A) all characters; (B) skull characters. Scales of both are in units of average taxonomic distance.

Fig. 9. Phenograms derived from UPGMA clustering of average taxonomic distances based on the COMMON transformation of the data: (A) characters of the humerus; (b) characters of the sternum. Scales of both are in units of average taxonomic distance.

Fig. 10. Phenograms derived from UPGMA clustering of average taxonomic distances based on the COMMON transformation of the data: (A) synsacrum characters; (B) tarsometatarsus characters. Scales of both are in units of average taxonomic distance.

Fig. 11. Three-dimensional model showing arrangement of storks in phenetic space based on a multidimensional scaling analysis of all characters transformed using the COMMON procedure. A minimum spanning network derived from taxonomic distances calculated from the transformed data is superimposed on the model.

Fig. 12. Three-dimensional model depicting an arrangement of storks

in phenetic space based on a multidimensional scaling analysis of skull characters transformed using the COMMON procedure. A minimum spanning network derived from taxonomic distances calculated from the transformed data is superimposed on the model.

Fig. 13. Three-dimensional model showing arrangement of storks in phenetic space based on a multidimensional scaling analysis of humerus characters transformed using the COMMON procedure. A minimum spanning network derived from taxonomic distances calculated from the transformed data is superimposed on the model.

Fig. 14. Three-dimensional model showing arrangement of storks in phenetic space based on a multidimensional scaling analysis of sternum characters transformed using the COMMON procedure. A minimum spanning network derived from taxonomic distances calculated from the transformed data is superimposed on the model.

Fig. 15. Three-dimensional model showing arrangement of storks in phenetic space based on a multidimensional scaling analysis of synsacrum characters transformed using the COMMON procedure. A minimum spanning network derived from taxonomic distances calculated from the transformed data is superimposed on the model.

Fig. 16. Three-dimensional model showing arrangement of storks in phenetic space based on a multidimensional scaling analysis of

tarsometatarsus characters transformed using the COMMON procedure.

A minimum spanning network derived from taxonomic distances
calculated from the transformed data is superimposed on the model.

Fig. 1.

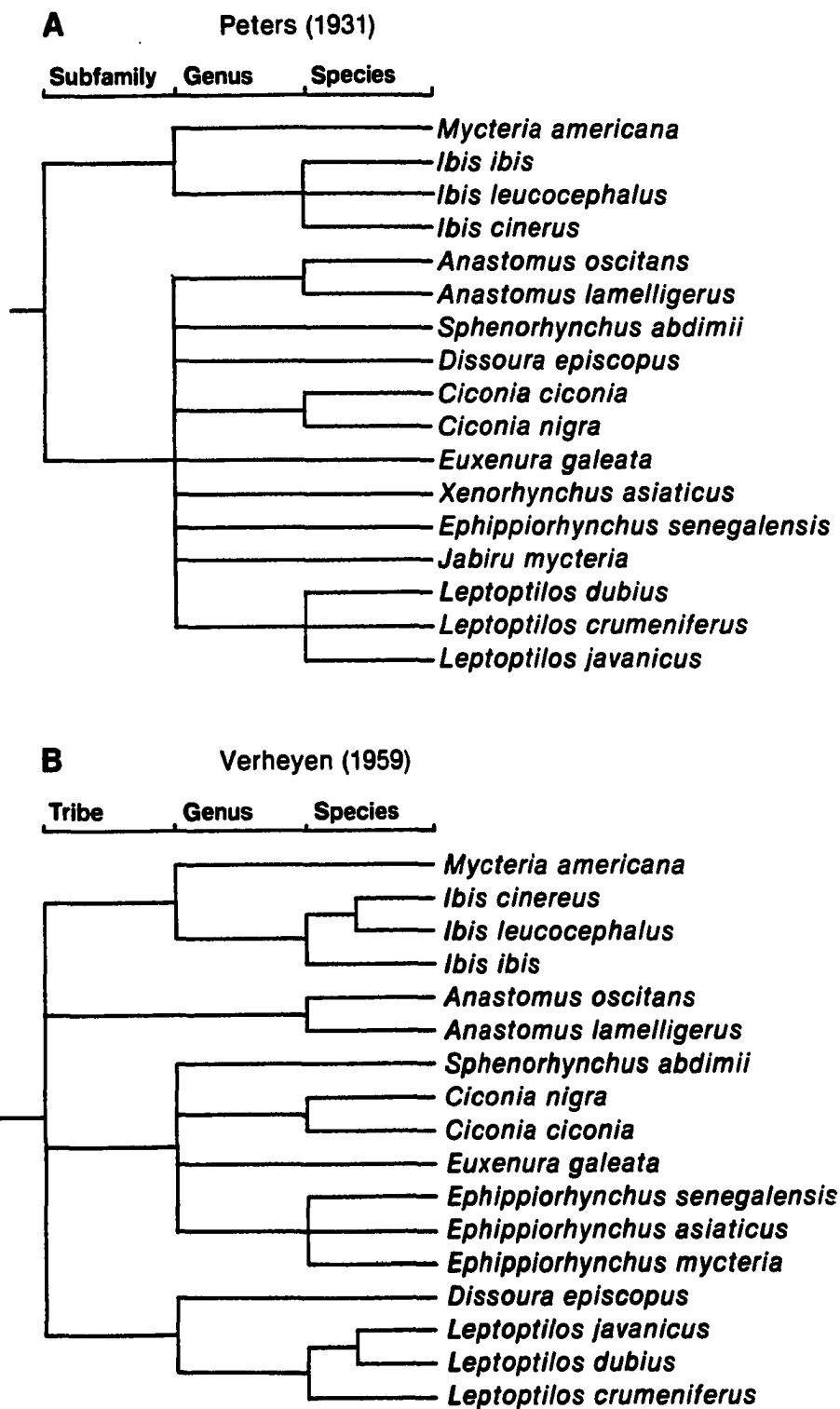


Fig. 2.

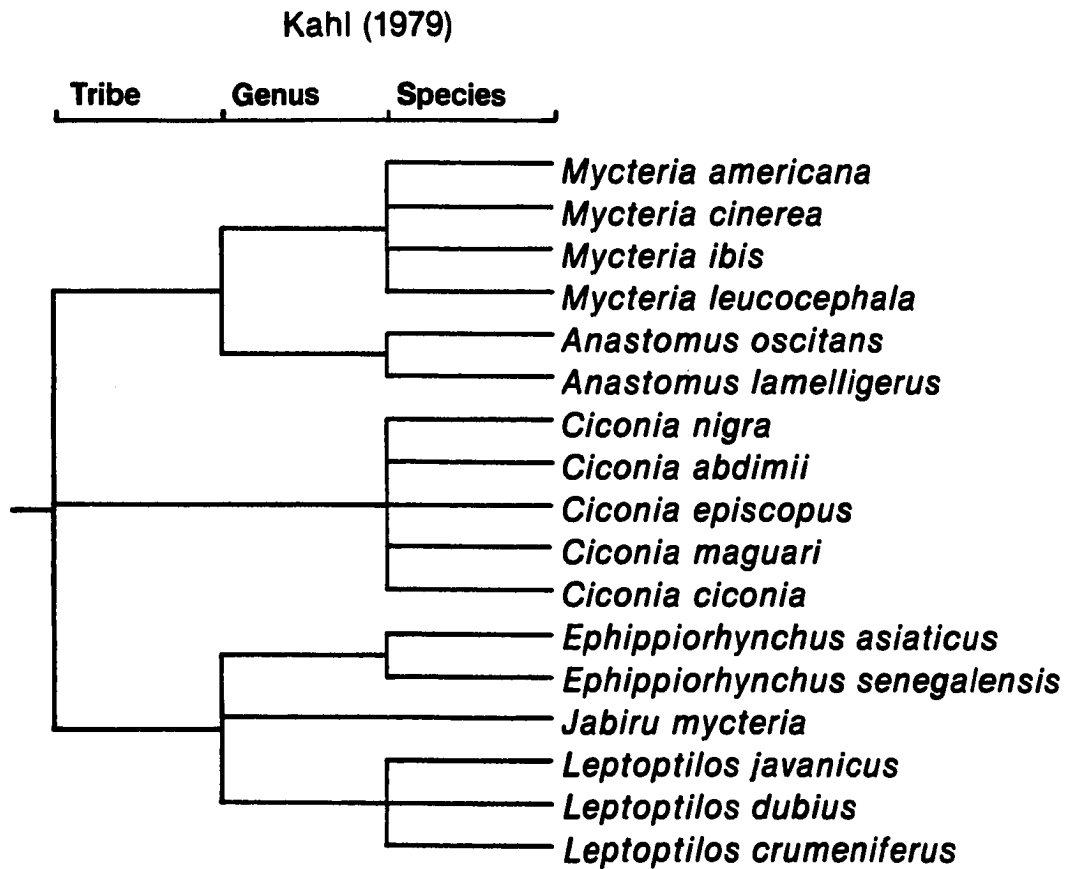


Fig. 3. (part)

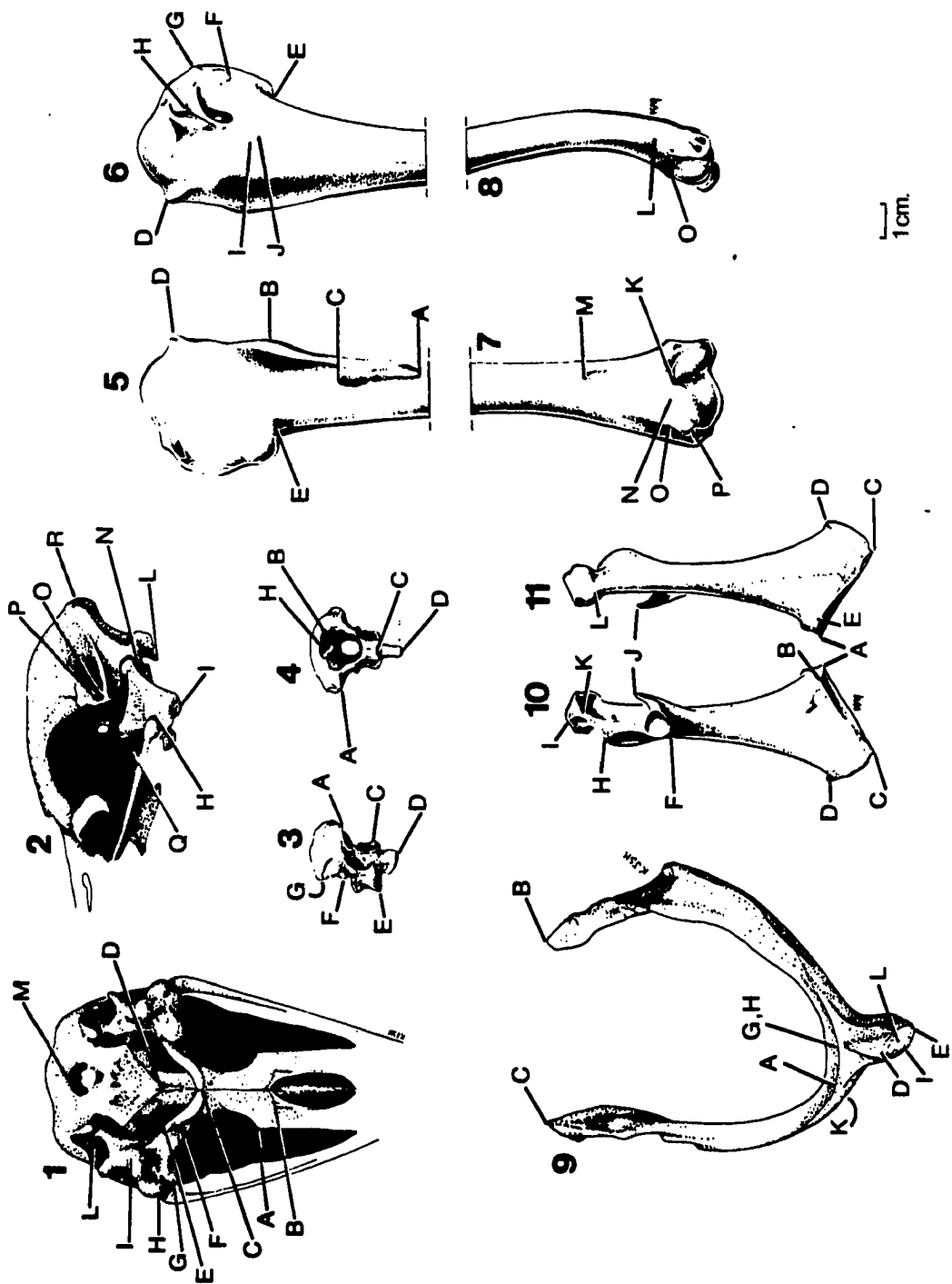
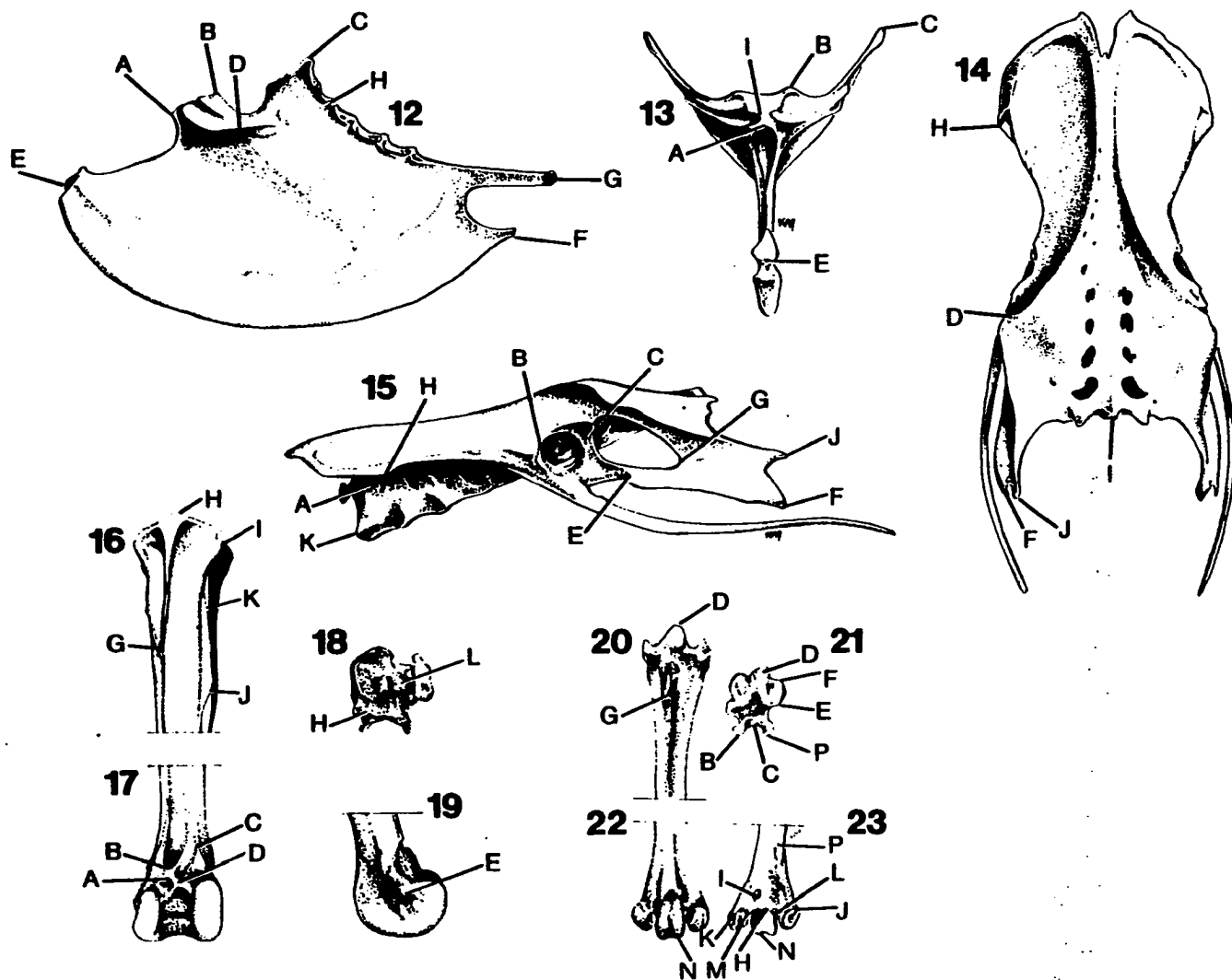


Fig. 3. (concl.)



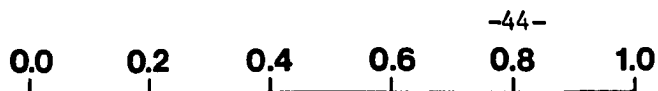


Fig. 4.

$r_{cc} = 0.693$

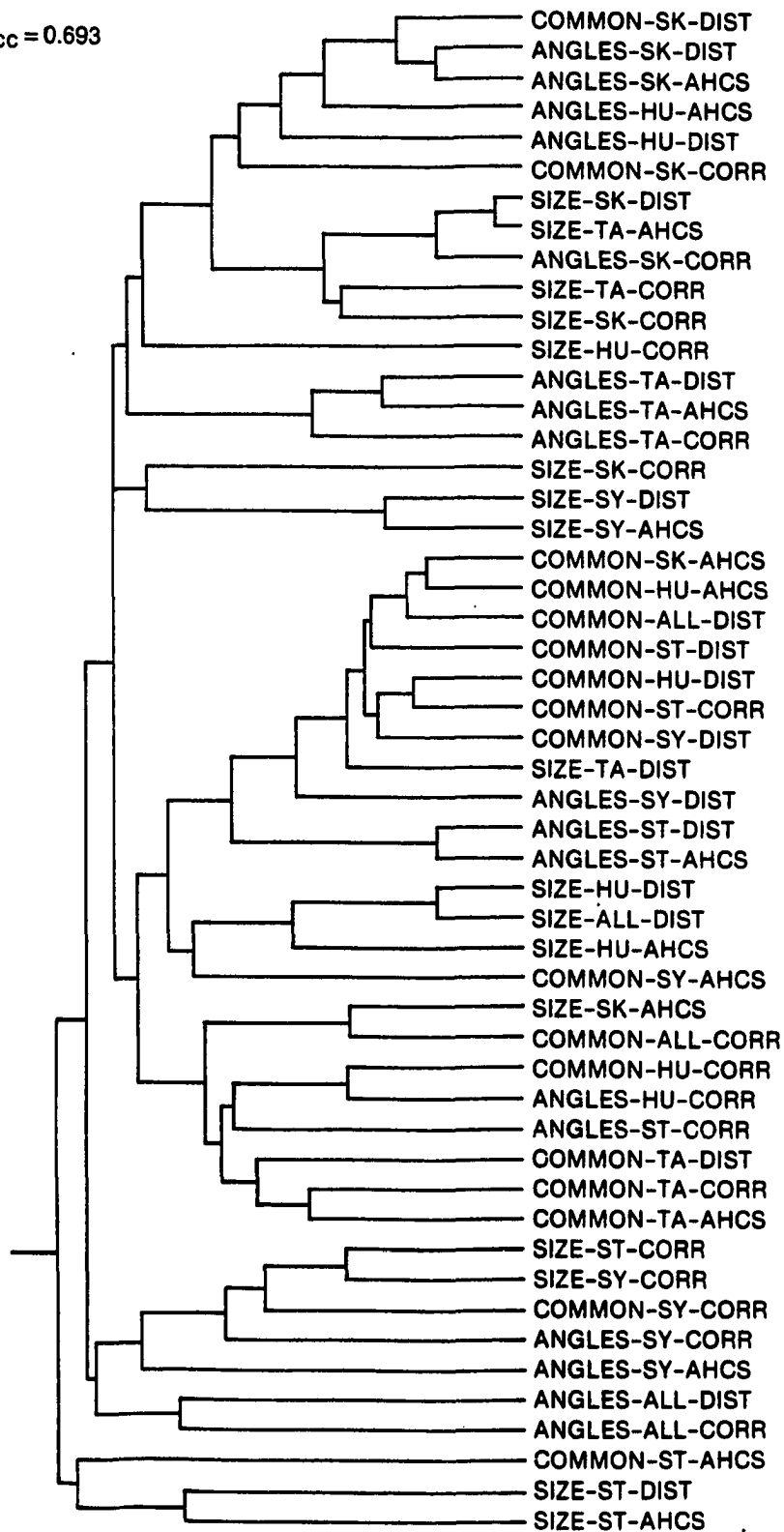


Fig. 5.

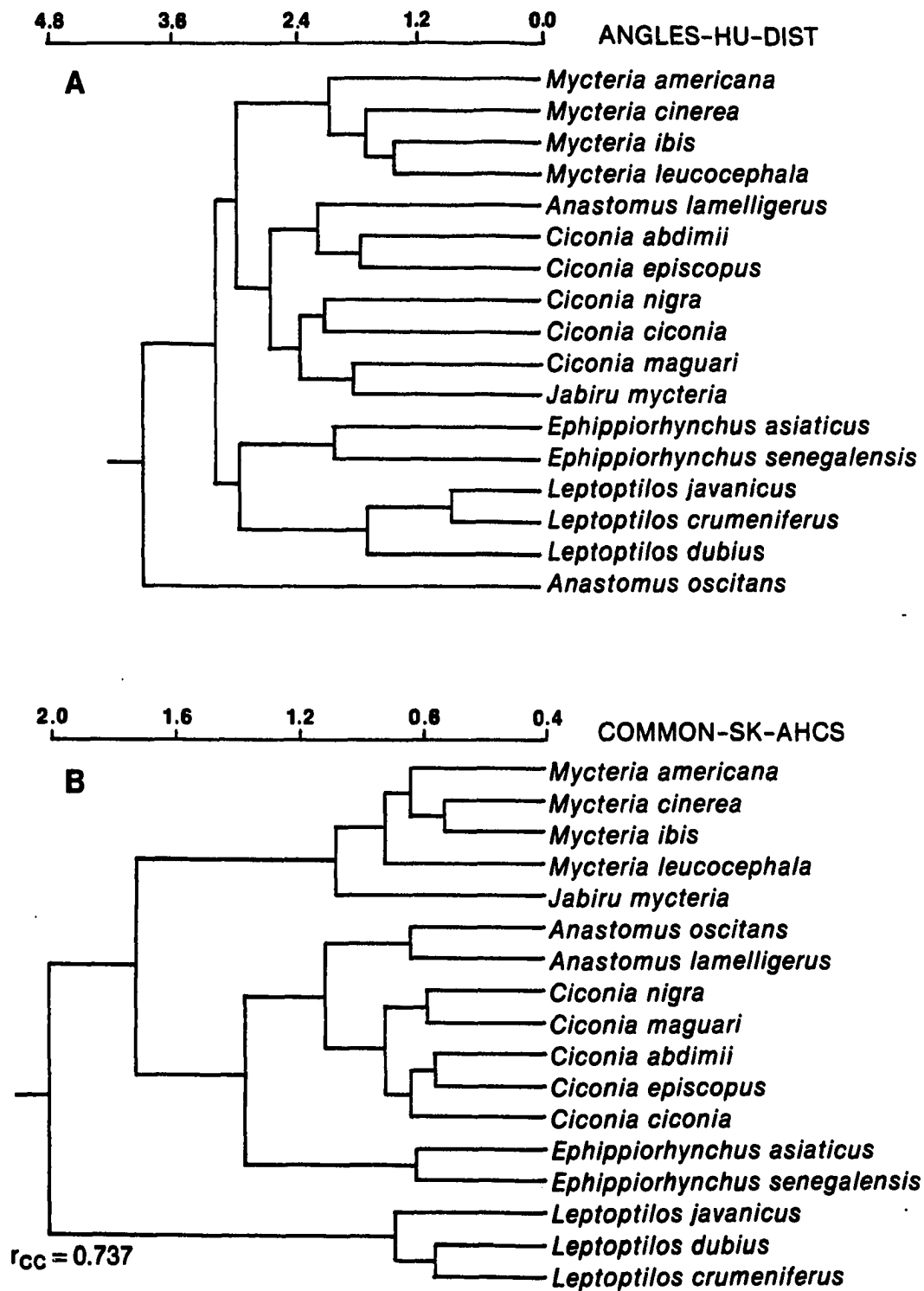


Fig. 6.

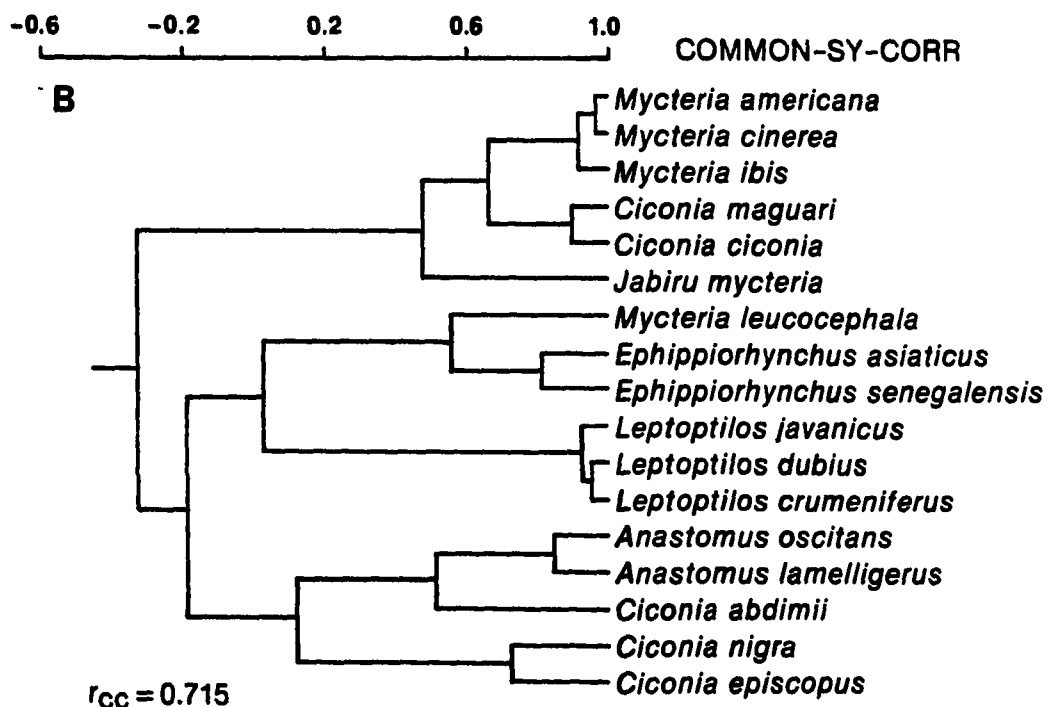
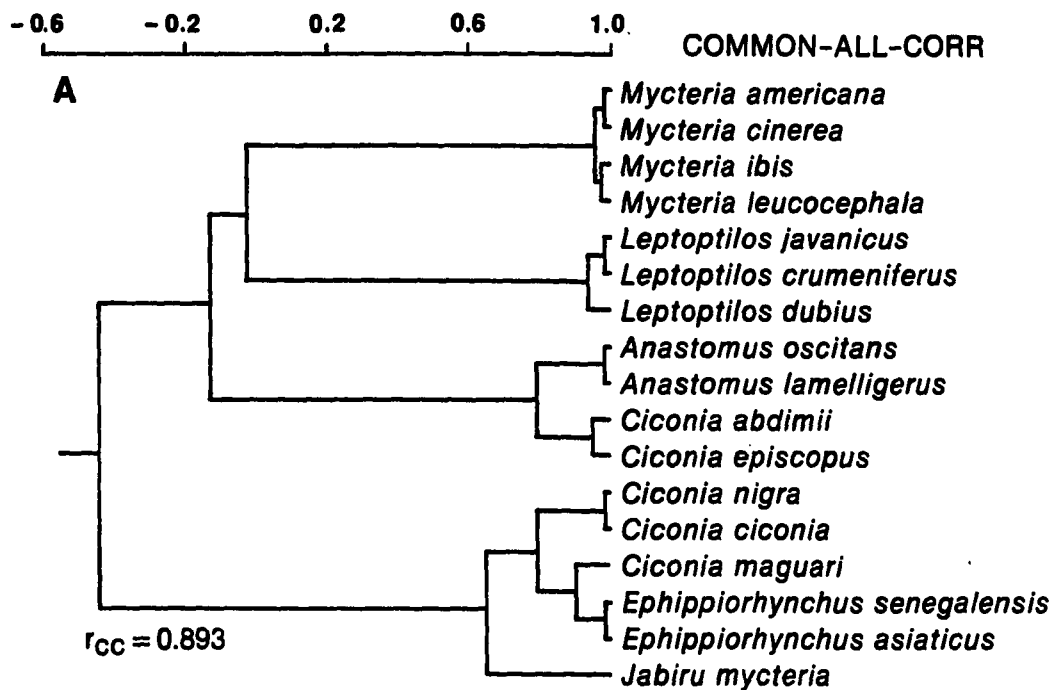


Fig. 7.

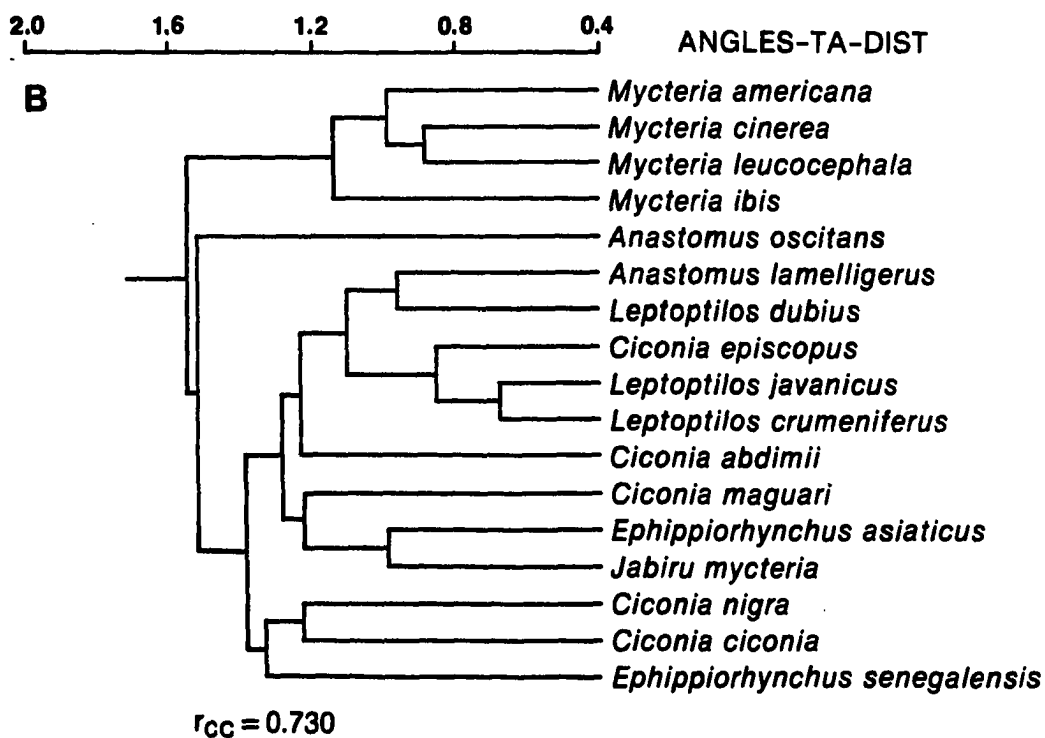
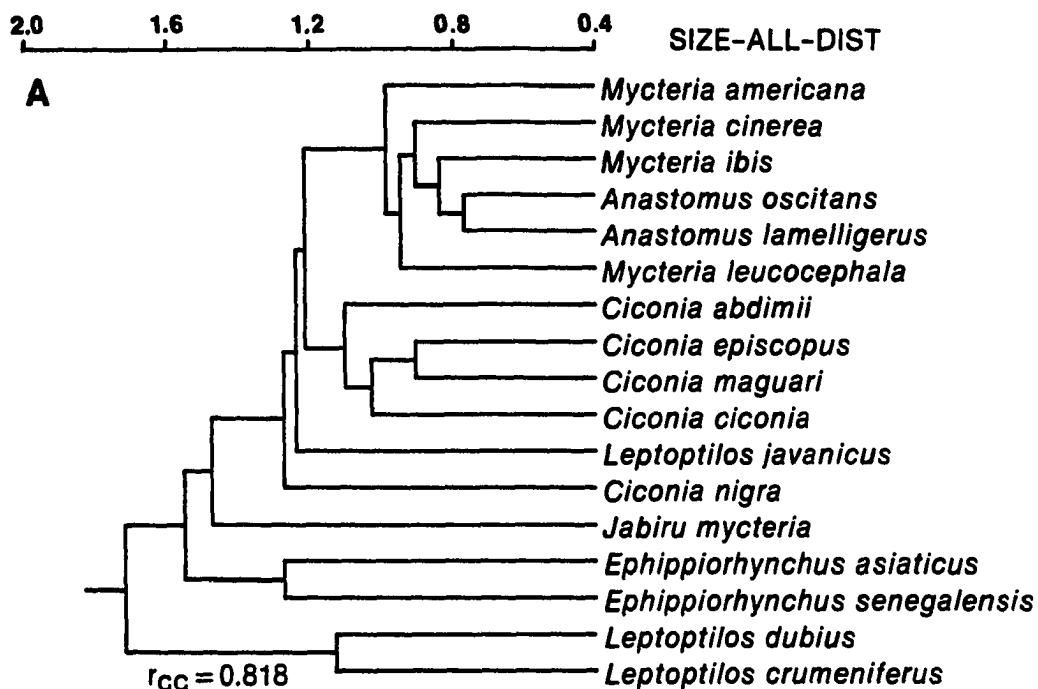


Fig. 8.

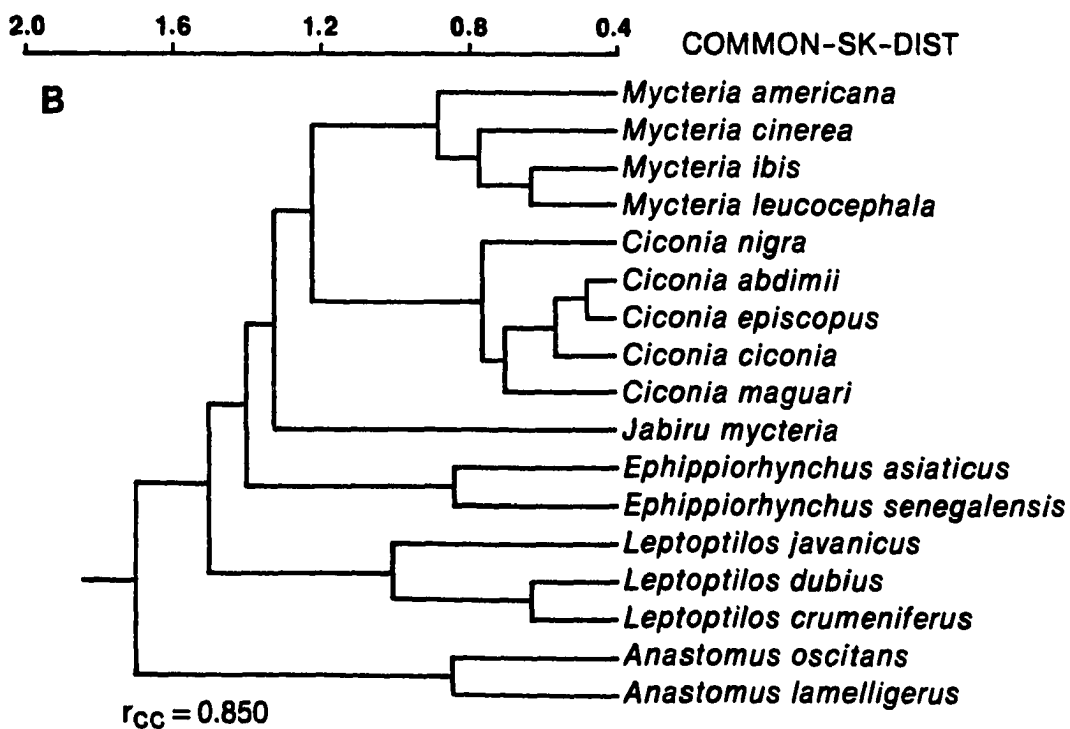
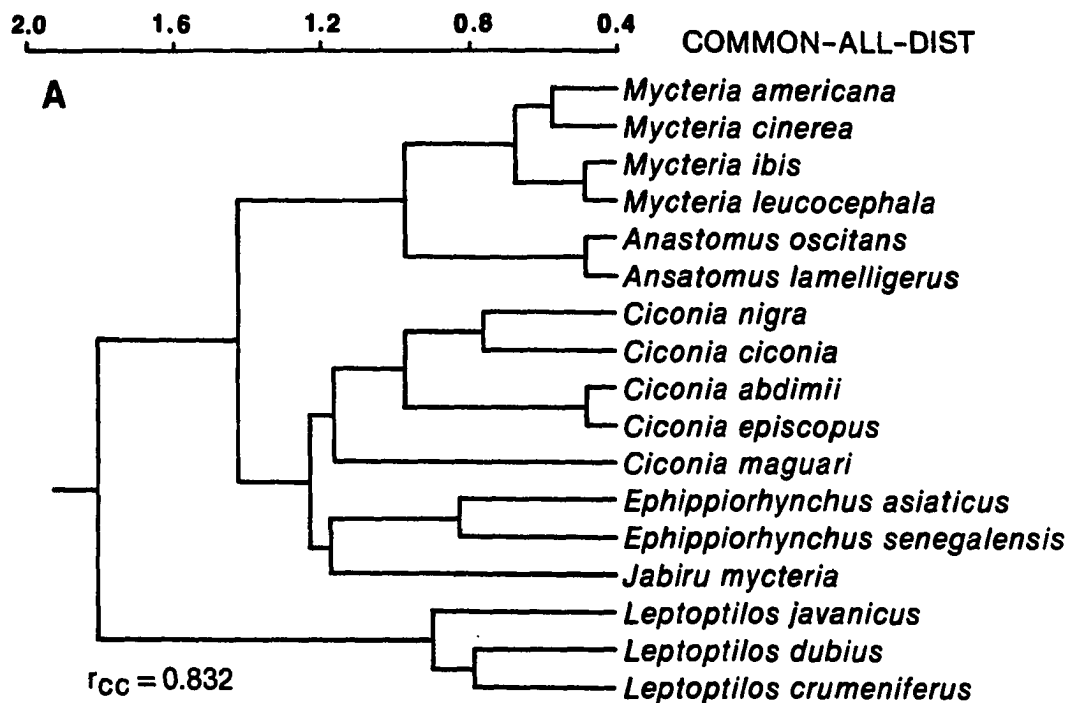


Fig. 9.

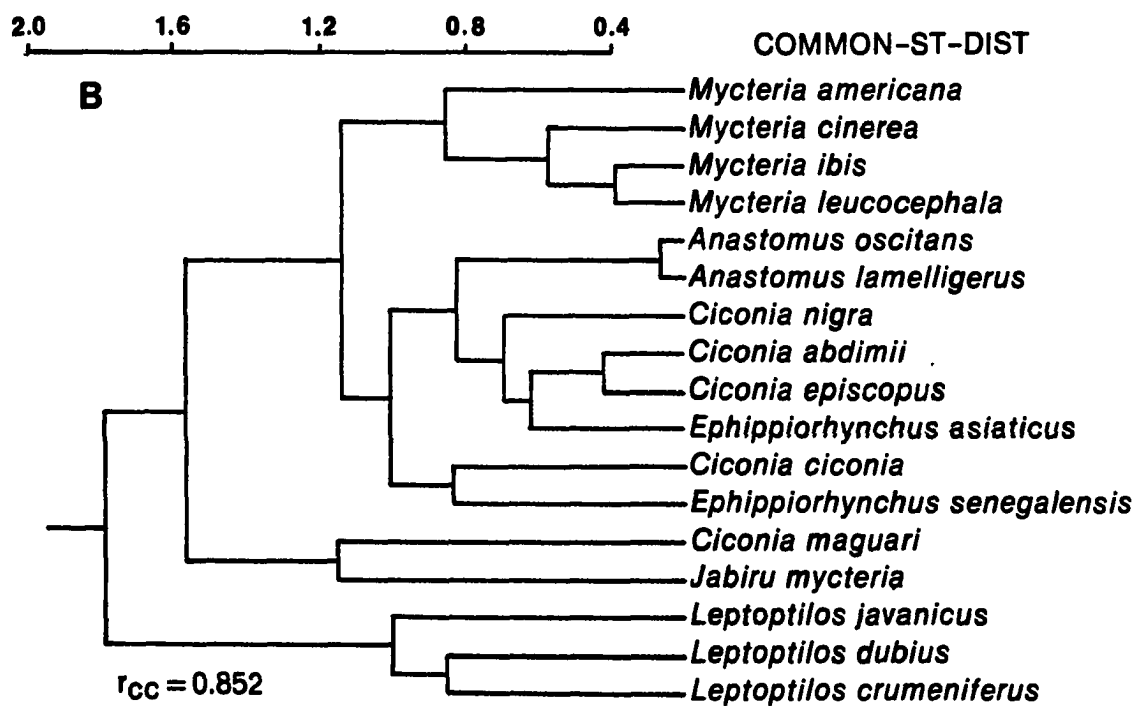
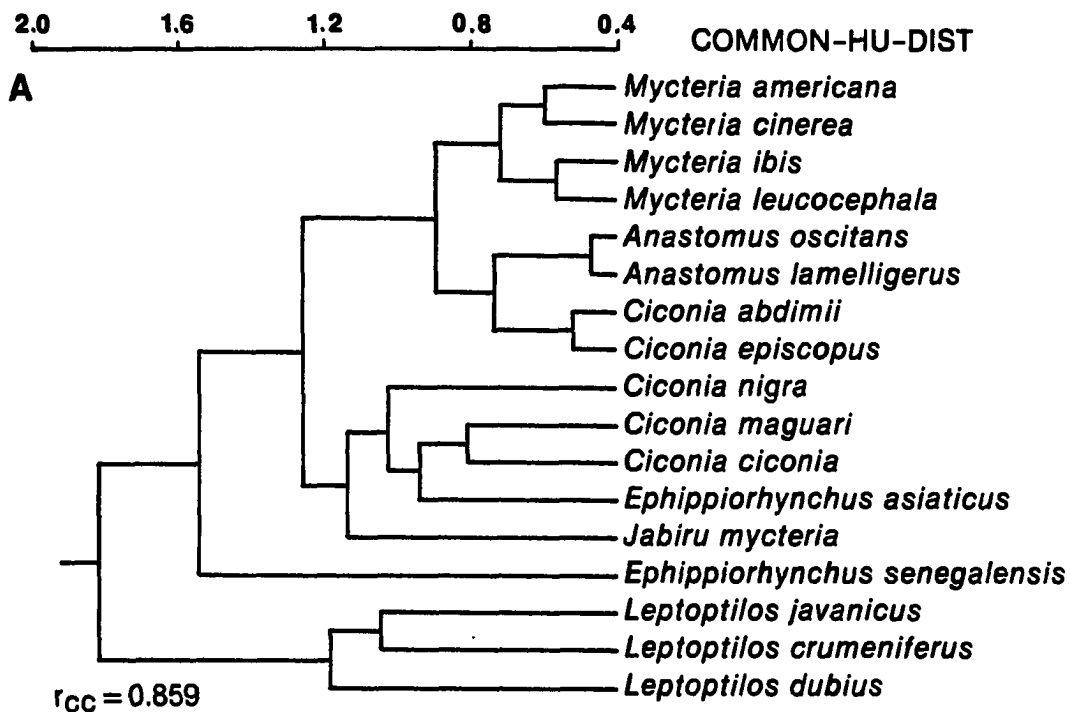


Fig. 10.

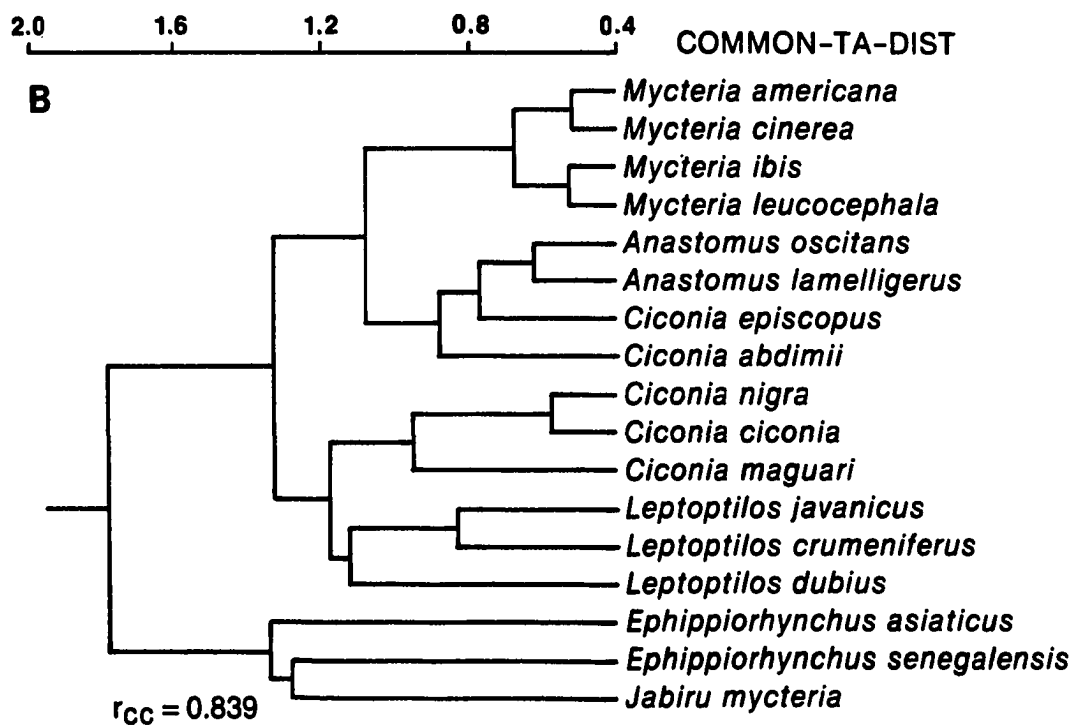
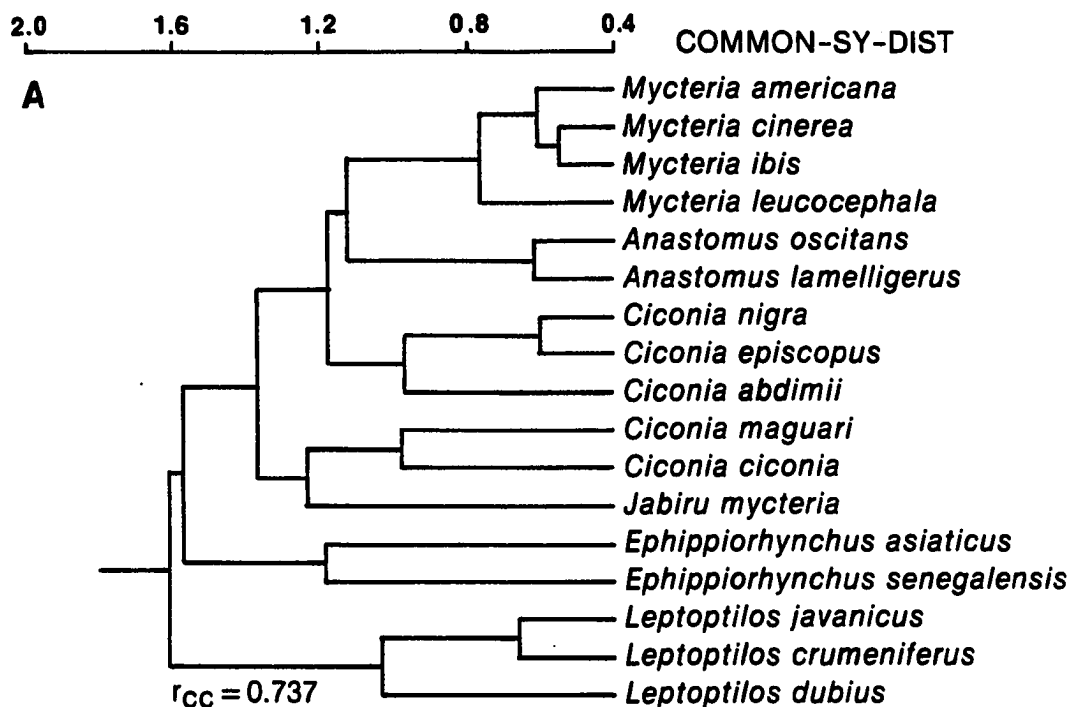
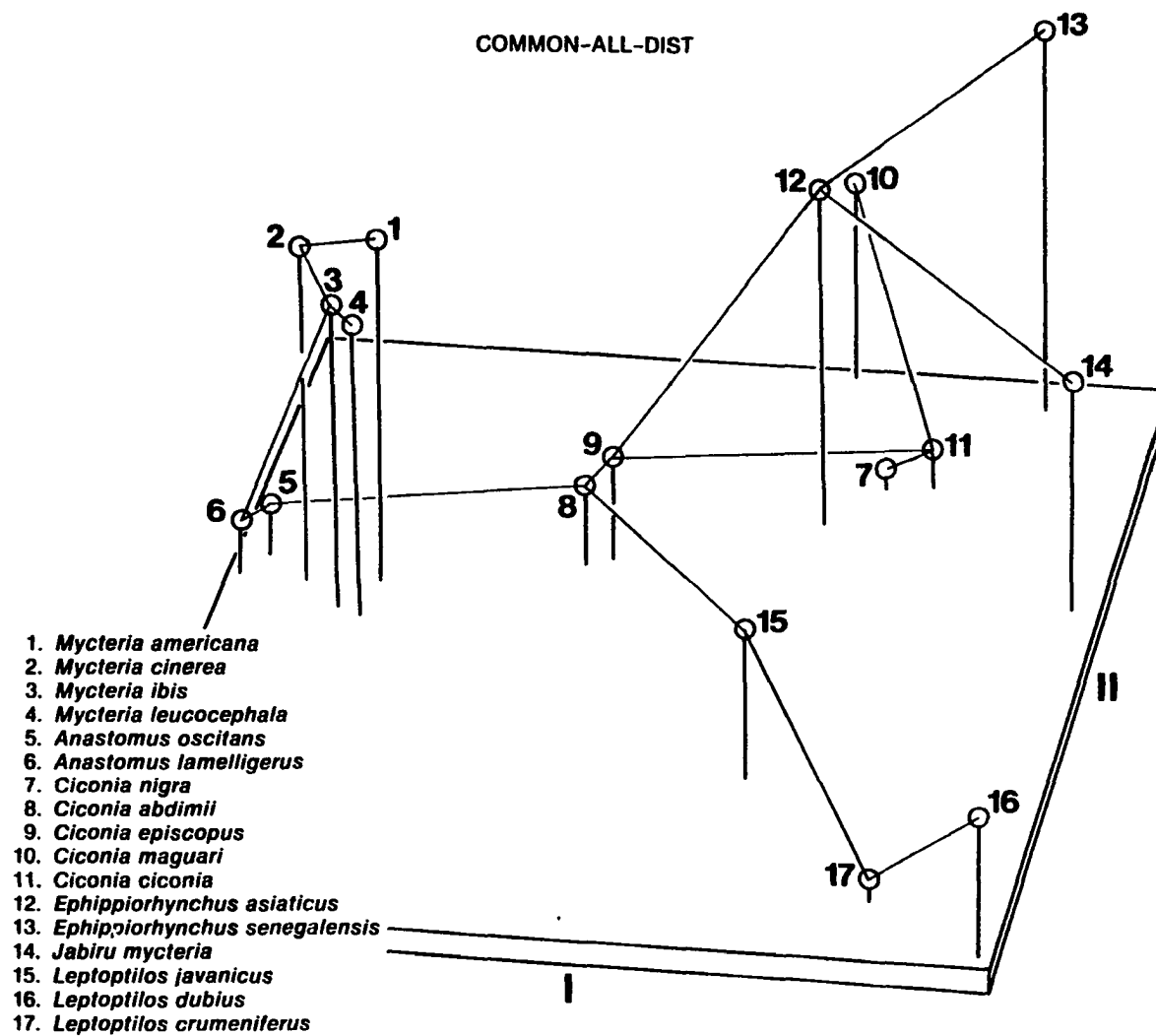


Fig. 11.



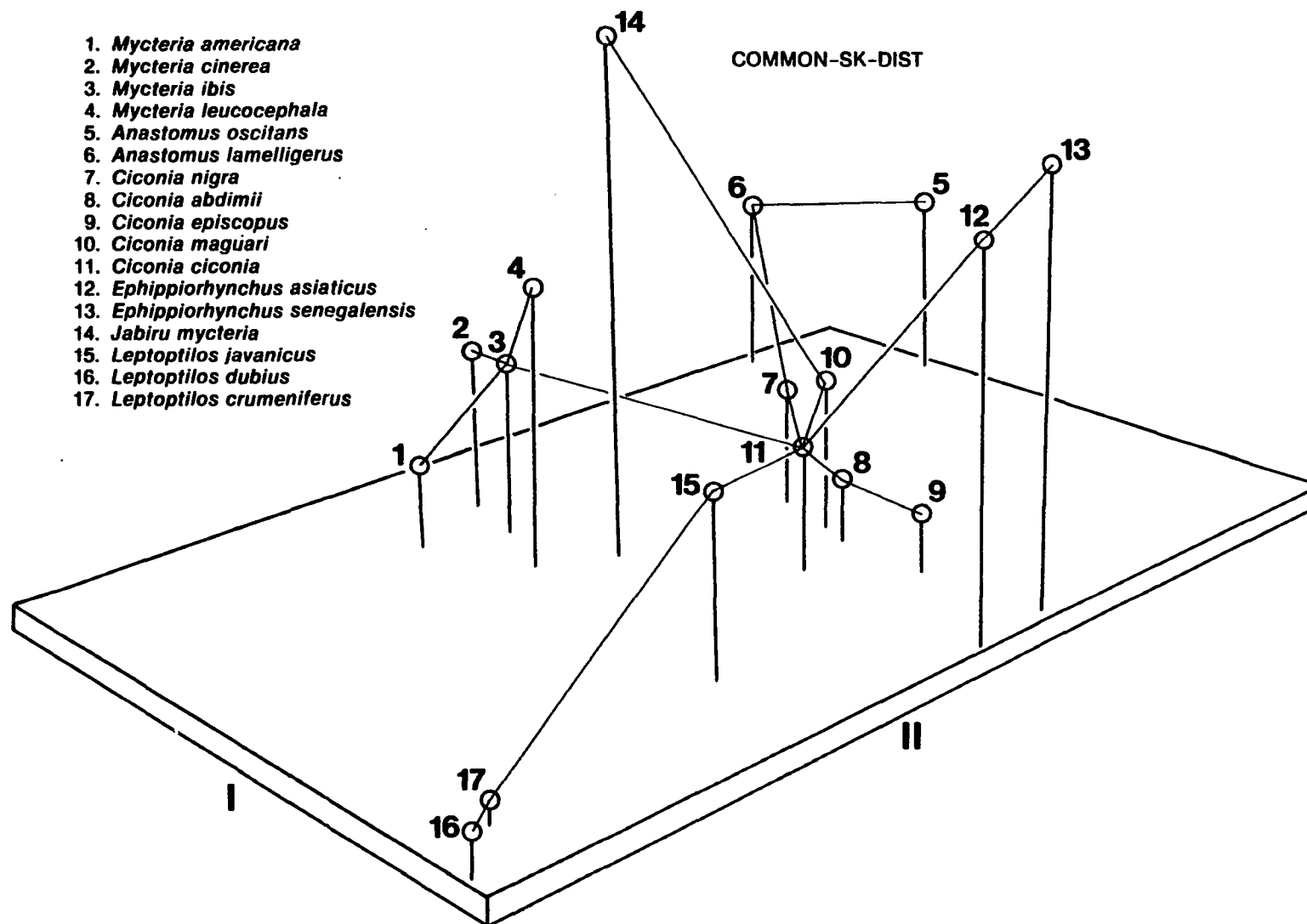


Fig. 12.

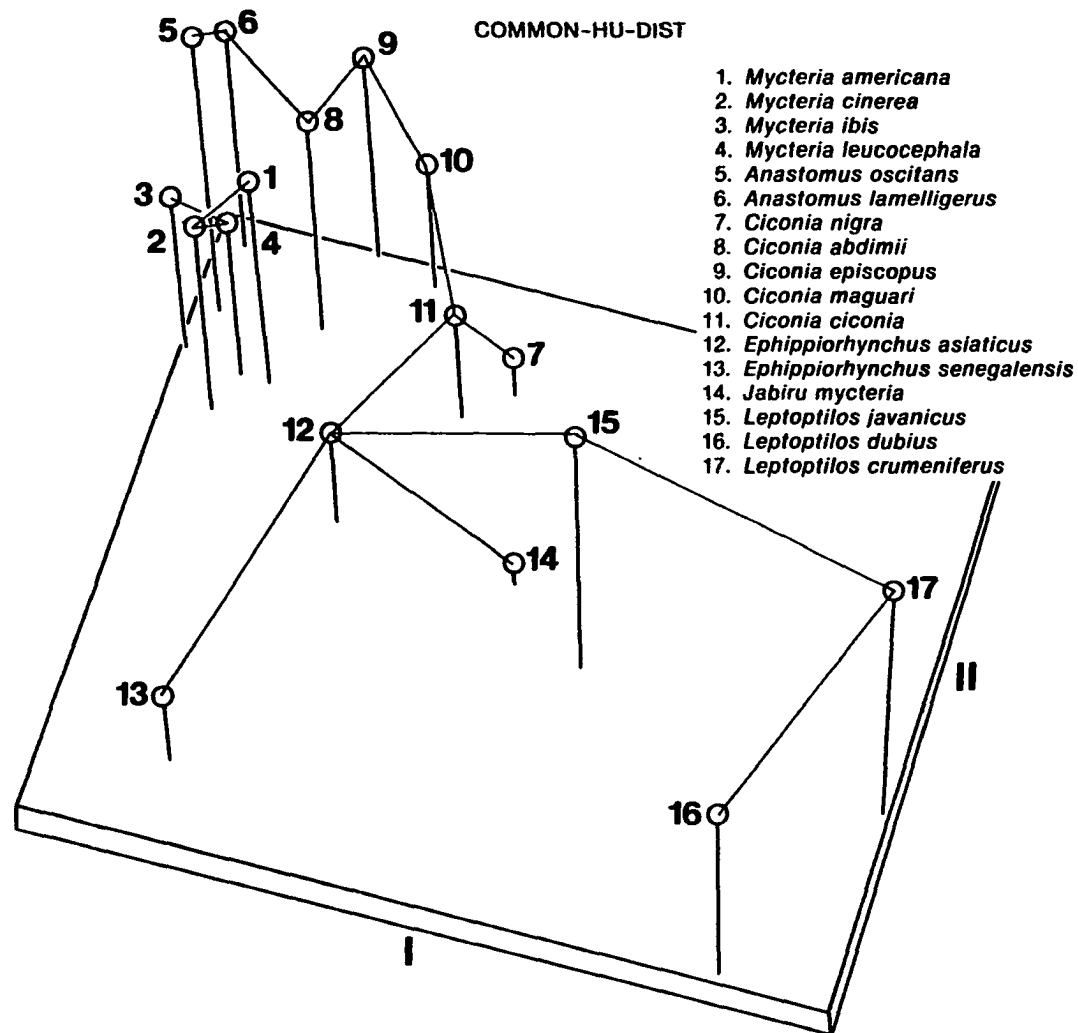


Fig. 13.

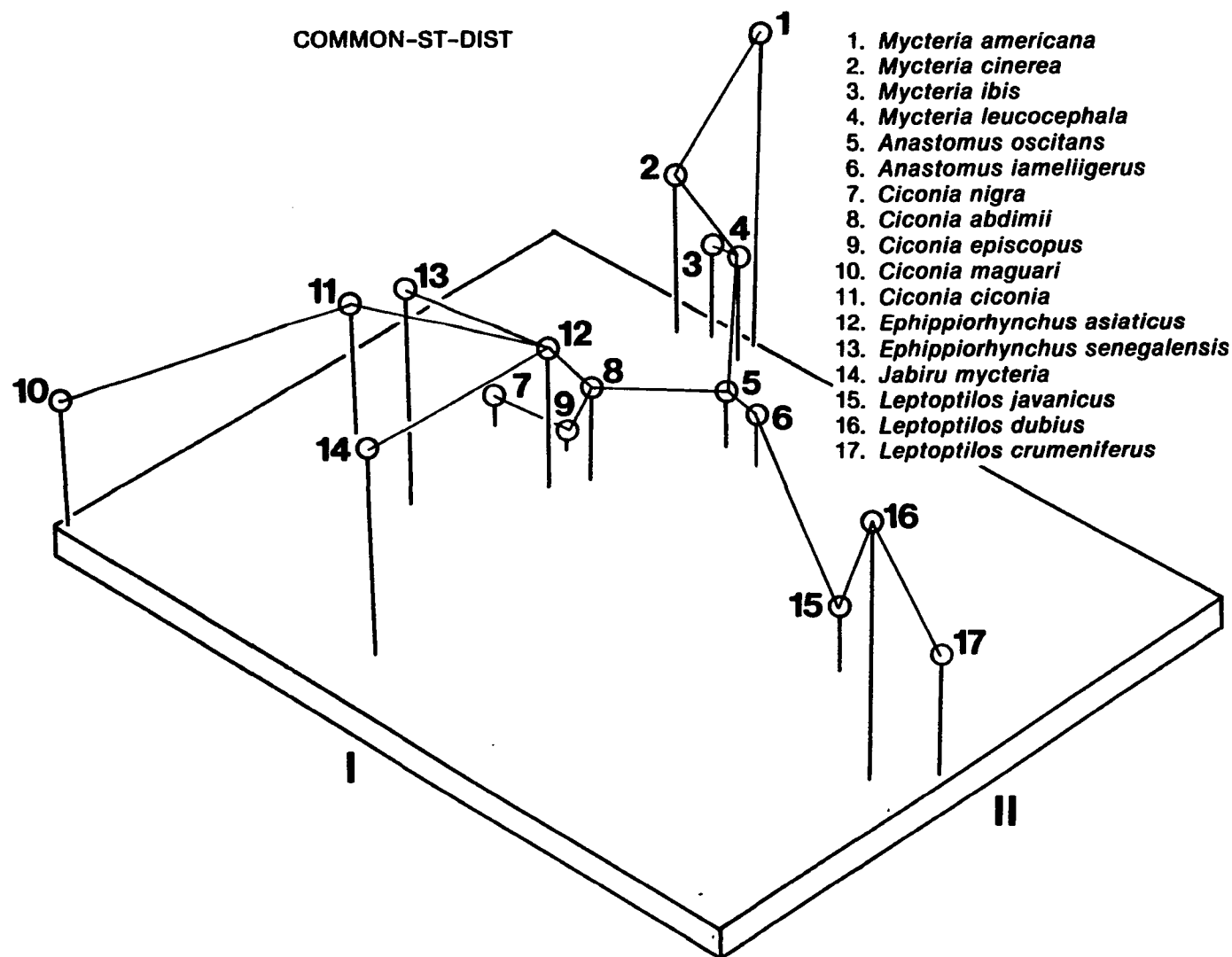


Fig. 14.

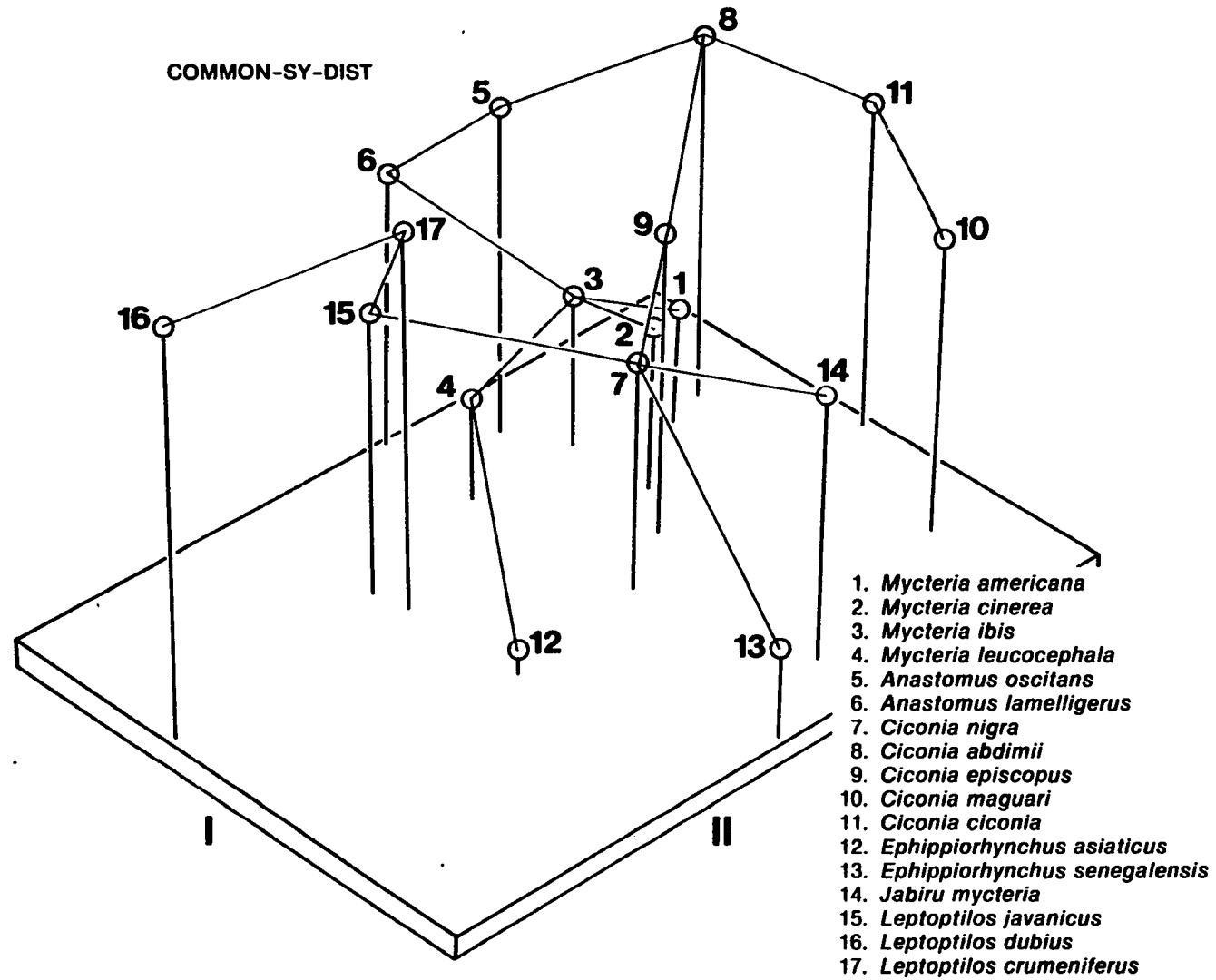


Fig. 15.

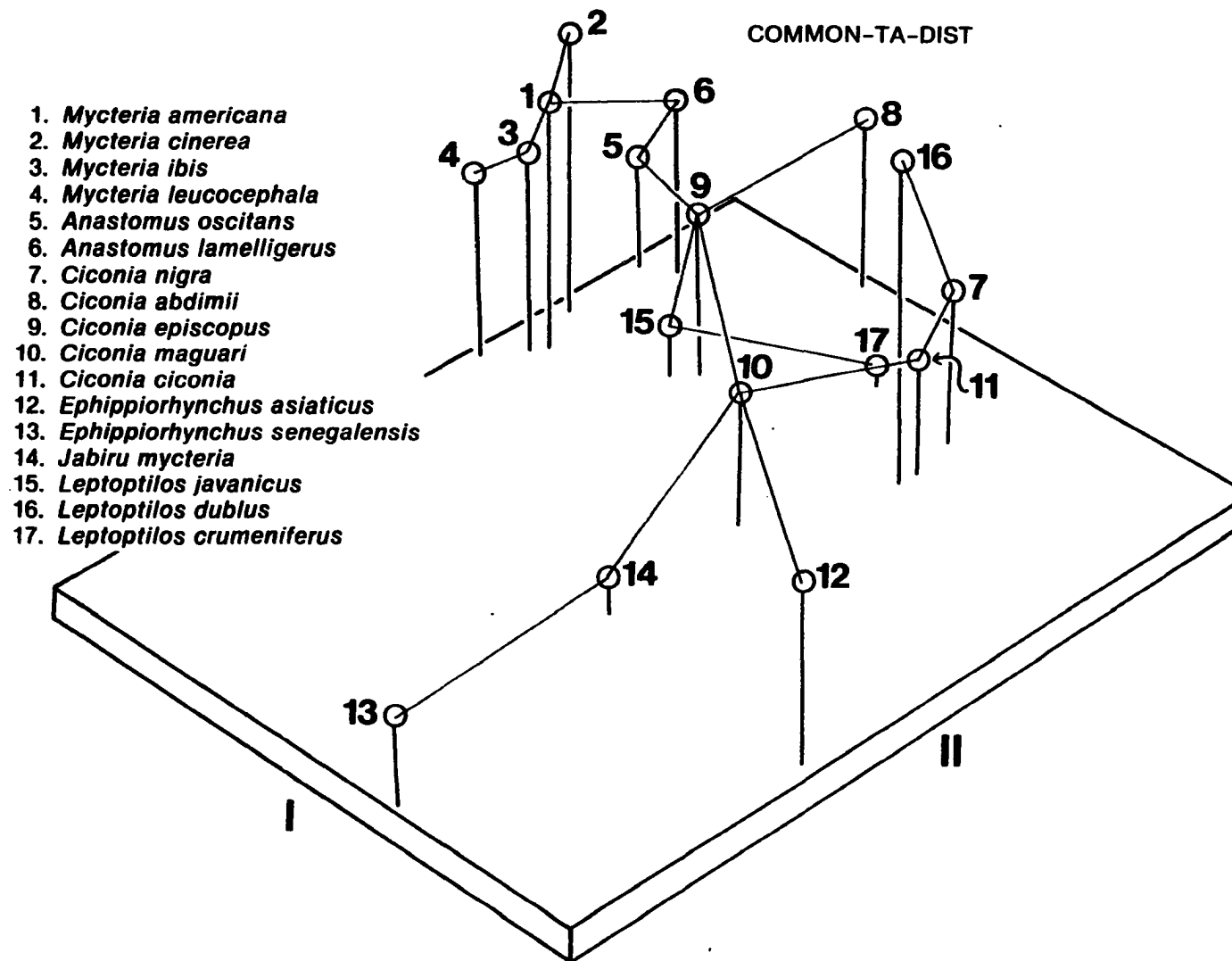


Fig. 16.

Appendix I. Specimens used in this study. The following abbreviations for museums are used: AMNH, American Museum of Natural History, New York, New York; FM, Field Museum of Natural History, Chicago, Illinois; KU, Museum of Natural History, University of Kansas, Lawrence, Kansas; MCZ, Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts; MVZ, Museum of Vertebrate Zoology, University of California, Berkeley, California; NMNH, National Museum of Natural History, Smithsonian Institution, Washington, D.C.; OU, Stovall Museum of Science and History, University of Oklahoma, Norman, Oklahoma; UMMZ, Museum of Zoology, University of Michigan, Ann Arbor, Michigan; YPM, Peabody Museum, Yale University, New Haven, Connecticut

Mycteria americana -- AMNH 605, 9856; KU 30867; NMNH 19532; OU 7720.

Mycteria cinerea -- NMNH 345229, 430169.

Mycteria ibis -- AMNH 2626; FM 104694; KU 70791; NMNH 431651;

UMMZ 215038; YPM 7526.

Mycteria leucocephala -- NMNH 432506, 432507; UMMZ 153055, 154507;

YPM 406.

Anastomus oscitans -- NMNH 488759, 489353, 553234; UMMZ 216572,

216573.

Anastomus lamelligerus -- MVZ 133407; NMNH 291418, 291419, 291420.

Ciconia nigra -- MCZ 6997; NMNH 19784, 291560; YPM 4350.

Ciconia abdimii -- AMNH 4860; NMNH 430455, 430456, 430528; YPM 7588.

Ciconia episcopus -- AMNH 3553, 1370, 4952; NMNH 225807, 226001.

Ciconia maguari -- NMNH 19940; OU 10611; UMMZ 156986, 156987,
158608.

Ciconia ciconia -- AMNH 1723, 1724, 2286; NMNH 343156, 430168;
UMMZ 151110.

Ephippiorhynchus asiaticus -- AMNH 1729, 2083, 3891; NMNH 19694,
346193.

Ephippiorhynchus senegalensis -- AMNH 2433, 2903; FM 104380;
UMMZ 211561, 211562.

Jabiru mycteria -- NMNH 343465; OU 6794, 10612, 14386; UMMZ 154788.

Leptoptilos javanicus -- AMNH 2721, 4392, 5059; NMNH 223897;
UMMZ 218204.

Leptoptilos dubius -- AMNH 4023; FM 104387; NMNH 225988, 429220;
YPM 409.

Leptoptilos crumeniferus -- AMNH 1731, 5862; NMNH 488129; OU 14385;
UMMZ 210451, 218203.

Balaeniceps rex -- AMNH 5935, 8817; NMNH 344963, 345070;
UMMZ 215884.

Scopus umbretta -- NMNH 18898; UMMZ 154762, 158164, 158419, 158435.

Appendix II.--Descriptions of the points, linear measurements and angular characters used in this study. The letters identifying the points correspond to those labeled on Fig. 3. Nomenclature follows Baumel, et al. (1979) and Bock and Mc Evey (1969). The linear measurements are inter-point distances; they are listed as pairs of letters corresponding to the described points. References to these measurements use a combination of the two letter code for the bone and the two letters for the points (e.g., SK-CR, TA-JP). The interconnections between any three points form a triangle; angles subtended by the sides of these triangles are used as angular characters. Specific angles are named using the letters of the three points forming the triangle with the point at the vertex of the angle listed second (i.e., character AEB is the angle subtended by lines connecting point A with point E and point B with point E). As with the linear measurements, references to the characters include the code for the bone (e.g., AX-BCH, HU-KMN). Since all angles for each triangle are used as angular characters, only the triangles are listed.

Ossa cranii, ossa faciei -- SK

Points

- A. Os palatinum; lamella caudolateralis; caudolateralmost point
- B. Os palatinum; crista ventralis; caudoventralmost point
- C. Os palatinum; margo ventralis articularis pterygoideum;
medialmost point

- D. Lamina basisphenoidalis; processus medialis; rostralmost point
- E. Os pterygoideum; facies articularis quadratum; medialmost point
- F. Os quadratum; condylus medius; rostralmost point
- G. Os quadratum; condylus medius; lateralmost point
- H. Os quadratum; cotyla quadratojugalis; caudoventralmost point
- I. Os quadratum; condylus caudalis; ventralmost point
- L. Ala occipitalis; processus exoccipitalis; medioventralmost point
- M. Foramen magnum; margo dorsalis; medial point
- N. Processus suprameaticus; ventralmost point
- O. Processus zygomaticus; rostralmost point
- P. Processus postorbitalis; ventralmost point
- Q. Processus orbitalis quadrati; medialmost point
- R. Os parietalis; margo caudalis articularis supraoccipitalis;
medialmost point

Linear measurements

AB AC BC CD CE CH CM CN AR DE DH DI DL DM DN EF
EF EH EN FG FH FI FM GH HI HL HN HO HQ IL IN LM
MR NP NR OP OQ OR PR

Triangles

ABC CDE CDH CDN CMR DLH DLI DLM EFG EGH ENH FHN FHI
HIN HOQ NPR OPR

Axis -- AX

Points

- A. Processus articularis caudalis; facies articularis;

caudolateralmost point

- B. Arcus axis; caudomedialmost point
- C. Corpus axis; facies articularis caudalis; ventromedialmost point
- D. Corpus axis; processus ventralis; ventralmost point
- E. Corpus axis; facies articularis atlantica; ventralmost point
- F. Processus articularis cranialis; facies articularis; cranialmost point
- G. Arcus axis; craniomedialmost point
- H. Area ligamentum elastici caudalis; dorsalmost point

Linear measurements

AB AC AD AE AF BC BD BE BG BH CD CE CG CH DE EF
EG FG

Triangles

ABC ABD AEF BCE BCG BCH CDE EFG

Humerus -- HU

Points

- A. Impressio m. pectoralis pars profundus; distalmost point
- B. Crista pectoralis; cranialmost point
- C. Impressio m. pectoralis pars profundus; proximalmost point
- D. Tuberculum dorsale; dorsalmost point
- E. Junctura intumescencia, margo ventralis
- F. Impressio m. scapulohumeralis caudalis; distalmost point
- G. Impressio m. biceps brachii; proximalmost point
- H. Tuberculum ventrale; dorsolateralmost point

- I. Impressio m. latissimus dorsi caudalis; proximalmost point
- J. Impressio m. latissimus dorsi caudalis; distalmost point
- K. Condylus dorsalis; cranioventralmost point
- L. Impressio m. supinator; proximalmost point
- M. Fossa m. brachialis; proximalmost point
- N. Fossa m. brachialis; distalmost point
- O. Tuberculum supracondylare ventrale
- P. Epicondylus ventralis; ventralmost point
- Q. Epicondylus dorsalis; caudodistalmost point

Linear measurements

AB AC AD AE BC BD BE BI CE DE DF DH DI DJ EF EH
FG FH FI GH IJ KL KM KN KO KP KQ LM LN LQ MN MO
NO NP OP OQ

Triangles

ABC ABE ACE ADE BDI BED DEF DEH DIF DIJ FGH KLM KLQ
KMN KMO KOP KOQ LMN NOP

Clavicula -- FU
~~~~~

Points

- A. Synostosis interclaviculare; point sinister to craniodorsalmost point; points A and I are on same plana paramediana
- B. Processus acromialis; caudodorsalmost point; sinister
- C. Processus acromialis; caudodorsalmost point; dexter
- D. Apophysis furculae; facies articularis apex carinae sterna; dorsalmost point

E. Apophysis furculae; facies articularis apex carinae sterna;  
ventralmost point

G. Synostosis interclaviculare; craniodorsalmost point

H. Same as point G (in the Ciconiidae)

I. Apophysis furculae; facies articularis apex carinae sterna;  
Lateralmost point

K. Point to give maximum thickness of extremitas sternalis  
claviculae at point A

L. Apophysis furculae; facies articularis apex carinae sterna;  
midpoint

Linear measurements

AB AC AD AE AG AH AI AK AL BC DE GH GL IK IL

Triangles

ABC ADE AGH AGL AIK AIL

Coracoideum -- CO

Points

A. Angulus medialis; medialmost point

B. Facies articularis sternalis; lateralmost point

C. Processus lateralis; dorsolateralmost point

D. Facies articularis sternalis; crista ventralis;  
craniolateralmost point

E. Facies articularis sternalis; crista dorsalis; caudalmost point

F. Junctura facies articularis humeralis, cotyla scapularis;  
ventralmost point



- H. Facies articularis humeralis; dorsalmost point
- I. Impressio ligamentum acrocoracohumeralis; dorsolateralmost point
- J. Processus procoracoideus; dorsalmost point
- K. Facies articularis clavicularis; caudalmost point
- L. Processus acrocoracoideus; tuberculum brachialis

Linear measurements

AB AC AD AJ BC BD BJ FH FI FJ HI HJ HL JK JL KL

Triangles

ABC ABD ABJ FHI FHJ JHL JLK

Sternum -- ST

Points

- A. Spina externa; cranialmost point
- B. Spina interna sinister; dorsalmost point
- C. Processus craniolateralis; craniolateralmost point
- D. Tuberculum labri ventralis (junctura labrum ventralis, lineae intermusculare); sinister
- E. Apex carinae; facies articularis; ventralmost point
- F. Margo caudalis; median point
- G. Trabecula lateralis sinister; caudolateralmost point
- H. Process costalis 2 sinister; facies articularis; midpoint
- I. Facies articularis coracoideus dexter; medialmost point

Linear measurements

AB AC AD AE BC BD BE BH BI CD CE CF CH DE DF DG  
DH DI EF EH FG

Triangles

ABD ABE ACD BCD BDE BDI BEH CDH DCF DFG ECF

Synsacrum, os coxae -- SY

Points (all sinister or median)

- A. Fovea costalis for caudalmost costa vertebralis
- B. Fossa acetabuli; margo cranialis; cranialmost point
- C. Antitrochanter; caudalmost point
- D. Processus lateralis crista iliaca; lateralmost point
- E. Foramen obturatum; margo caudalis; caudodorsalmost point
- F. Processus terminalis ischii; caudalmost point
- G. Foramen ilioischadicum; caudalmost point
- H. Ala preacetabularis ilii; lateralmost point
- I. Extremitas caudalis synsacri; middorsal point
- J. Processus dorsolateralis ilii; caudalmost point
- K. Extremitas cranialis synsacri; ventromedialmost point

Linear measurements

AC AF AH AK BC BD BE CD CE CF CG CI CJ CK DE EF  
EG EJ FI HK IK

Triangles

ACF AHK BCE BDE CDE CEF CEG CEJ CFI CIK

Tibiotarsus -- TI

Points

- A. Pons supratendineus; margo proximalis

- B. Pons supratendineus; margo distalis
- C. Impressio lateralis ligamentum transversum; distalmost point
- D. Tuberculum intercondylare; cranialmost point
- E. Epicondylus medialis; medialmost point
- F. Sulcus cartilaginis tibialis; proximomedialmost point
- G. Impressio m. gastrocnemius medialis; distalmost point
- H. Crista cnemialis cranialis; proximalmost point
- I. Crista cnemialis lateralis; lateralmost point
- J. Foramen interosseum distale; proximalmost point
- K. Foramen interosseum proximale; distalmost point
- L. Area interarticularis; proximalmost point

Linear measurements

AB AD BC BD BE BF CD EF EL GH GI GJ GK HI HJ HL  
IK IL JK JL

Triangles

ABD BCD BEF GHI GIK GJK HLI HLJ

Tarsometatarsus -- TA

Points

- A. Crista medialis hypotarsi; margo plantaris; proximalmost point
- B. Crista lateralis hypotarsi; margo plantaris; proximalmost point
- C. Sulcus hypotarsi; facies plantaris; proximomedialmost point
- D. Eminentia intercondylaris; proximalmost point
- E. Cotyla medialis; margo lateralis; plantolateralmost point
- F. Cotyla medialis; margo dorsalis; dorsalmost point

G. Sulcus extensorius; midpoint between margo distalis

impressiones retinaculi extensorii

H. Trochlea metatarsi III; facies plantaris; proximalmost point

I. Foramen vasculare distale; facies plantaris; margo distale

J. Trochlea metatarsi IV; margo lateralis; proximalmost point

K. Trochlea metatarsi II; margo medialis; proximalmost point

L. Trochlea metatarsi IV; margo medialis; proximalmost point

M. Trochlea metatarsi II; margo lateralis; proximalmost point

N. Trochlea metatarsi III; condylus lateralis; distalmost point

P. Fossa metatarsi I; margo proximalis; proximalmost point

Linear measurements

AB AC AE BC BE CD CE CF DF DG DN FG HI HJ HK HP

IK IM IP JK JL JN JP KM KN LM LN LP MN

Triangles

ABC ABE ACE CDF DFH HIK HIP HJK HJP IMK JKN JLP LMN

## PAPER II

CHARACTER TRANSFORMATIONS IN PHENETIC  
STUDIES USING CONTINUOUS MORPHOMETRIC VARIABLES

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*Character transformations in phenetic studies using continuous morphometric variables. Syst. Zool. -- The stability (measured using matrix correlations) of phenetic classifications based on partitions of continuous morphometric data (skeletal measurements from three groups of birds) was compared for analyses involving two transformations: removal of size and removal of the common part (an estimate of the taxon of the study group). Linear regression was used in both transformations to remove that portion of the variance accounted for by the estimate of either size or the common part. The size estimate was a composite variable computed as the mean of three measurements. The estimate of the common part was the set of measurements used to form the data set to be analyzed but taken on a similar species outside the study group. Results derived from three similarity measures (product-moment correlations, average taxonomic distances and Manhattan distances) were also compared. In all cases distance measures produced significantly higher average congruence between classifications than did correlations. For two data sets the transformation to remove the common part resulted in*

significantly higher mean congruence (for distances) than did the transformation to remove size; for the third data set there was no significant difference. The common-part transformation is suggested for use in phenetic studies of continuous morphometric data. [Phenetics, continuous characters, regression, congruence].

An analysis of continuous morphometric measurements in phenetic studies typically includes one or more transformations of the initial data (Sneath and Sokal, 1973). Standardization of each character over all taxa, for example, is routinely conducted to reduce the heterogeneity of vectors representing taxa. Transformations to reduce or eliminate size are also commonly employed (see Sneath and Sokal, 1973:168). The purpose of such transformations is to change the emphasis on a particular feature of the data (e.g., give each character equal weight, remove a size influence). Clearly, some of these, such as size removal, represent attempts to reduce the variance present in the data; some portion of the variance (e.g., that of size) is thought to be unimportant or even misleading. My purpose is to suggest a transformation that emphasizes a component of the variance that could be considered as most useful in phenetic studies. I compare classifications derived from data transformed in this way with classifications derived from data transformed to remove size.

#### COMMON PART TRANSFORMATION

Given a set of criterion variables and a second set of one or more reference variables, each of the criterion variables can be thought of as having two parts: (1) a part predictable by regression from the reference variables, and (2) a part not predictable from the reference variables. For example, if the set of reference variables represents size and the criterion variables are morphometric skeletal measurements of birds, then the two parts of each criterion variable would be (1) a size part and (2) a non-size part. Alternately, if the reference variables represent the concept of "bird" then the parts of the criterion variables (which, in this case, are vectors of measurements for each of the members of the group of birds under study) are (1) a bird part and (2) a part not correlated with the general notion of "bird". This latter component includes the variance concerning the differences among the birds under study as well as variance attributable to measurement error. If the criterion variables are the members of a particular bird taxon, the reference variables can be chosen to represent an estimate of the essence of that taxon. In this case I will refer to the first part of the criterion variables as the common part. For example, if the criterion variables are each of the species of storks (Aves: Ciconiidae), then the common part of each of the variables is the "stork" part. I will refer to the second part as the clustering part. This concerns, in this example, the differences among the storks not correlated with the common part.



Taxonomically, for analyses within a group of organisms, the first part is not useful because it is common to all members of the group under study (hence the common part) and the analyses deal with the similarities and differences between clusters within the group. If the common part accounts for a large portion of the variance of each of the variables (the usual case due to relatively high overall similarity among the members of the group), it can have an over-riding influence (in a manner analagous to size) when cluster analyses are performed. To eliminate this influence and emphasize the clustering part a transformation to remove the common part is needed.

If an estimate of the common part can be found, regression analysis could be used to remove it from the data (Atchley, 1978, has suggested such a technique for the removal of size). Any taxon (of comparable rank to those in the study) from outside the limits of the group under investigation can be used as an estimate of the common part. From a phenetic viewpoint, the more similar the outside taxon, the better will be the estimate. If more than one estimate is available (or desired), multiple regression can be used. The procedure is to calculate the estimate of each character state for each taxon from regression on the outside taxon, subtract these estimates from the original values and retain the residuals. The residuals are uncorrelated with the variable representing the outside taxon.

Let  $\underline{Y}$  be a vector of measurements for a given taxon of the

group under study over all characters and  $\underline{X}$  be the vector of measurements for the outside taxon. The estimate of the common part (the vector  $\hat{\underline{Y}}$ ) is found from  $\hat{\underline{Y}} = \hat{\alpha} + \hat{\beta}\underline{X}$  where  $\hat{\alpha} = \bar{\underline{Y}} - \bar{\underline{X}}$  and  $\hat{\beta} = \underline{r}_{\underline{Y},\underline{X}} * (\underline{s}_{\underline{Y}} / \underline{s}_{\underline{X}})$ . The quantities  $\underline{s}_{\underline{X}}$  and  $\underline{s}_{\underline{Y}}$  are the standard deviation of  $\underline{X}$  and  $\underline{Y}$ , respectively, and  $\underline{r}_{\underline{Y},\underline{X}}$  is the product-moment correlation between  $\underline{Y}$  and  $\underline{X}$ . The vector of residuals ( $\underline{R}$ ) is found from  $\underline{R} = \underline{Y} - \hat{\underline{Y}}$ . These residuals are uncorrelated with  $\underline{X}$ , the estimate of the common part, and make up the transformed data. The procedure is depicted graphically in Fig. 1.

#### MATERIALS AND METHODS

Three data sets, all of continuous measurements taken on the skeletons of birds, were used in this analysis. The measurements of the CICON data set were taken from the synsacrum and tarsometatarsus of the 17 species of storks (Ciconiidae). After defining 9 points on the surface of the synsacrum and 15 on the tarsometatarsus, I took 50 measurements between various pairs of the points. These measurements were chosen to reflect skeletal variation present among the stork species. Each species was represented by the means of up to six individuals. These data are part of a larger set (of nine bones) analyzed in Wood (1982a,b).

The GRUINAE data are mostly lengths and widths involving all major skeletal elements from the 13 species of typical cranes (Gruidae: Gruinae). A similar set of measurements was used to form the SPARROW data set based on the nine species of the genera Zonotrichia, Passerella and Melospiza (Emberizidae: Emberizinae).

I measured 55 characters for the GRUINAE data set and 48 for the SPARROW data. These were taken on each skeleton and each species was represented by the means of up to 10 individuals. A very similar measurement set was first devised by Schnell (1970) for use with gulls and related birds, and then modified for use with a group of grassland sparrows (Robins and Schnell, 1971). The average similarity among the storks was higher than among the cranes but considerably lower than among the sparrows.

All data were transformed to remove the common part as described above. The estimate of the common part for the SPARROW data was derived from Junco vulcani, a member of a group of birds thought to be closely related to the sparrows analyzed here, and very similar phenetically to the Zonotrichia and Melospiza species (Paynter, 1966, pers. obs.). The estimates used for the CICON and GRUINAE common parts each involved two species: for the CICON data I employed Balaeniceps rex and Scopus umbretta; for the GRUINAE data I used the two species of Balearica that comprise the second subfamily of the Gruidae. In both cases, the species selected to estimate the common part are thought to be related to the group being analyzed (Olson, 1978, Walkinshaw, 1973), and are phenetically similar to members of the group.

Each data set was subjected to a transformation to remove size. As suggested by Atchley (1978), regression analysis was used. The procedure is identical to that described above for the removal of the common part except that to remove size the variable X is a

vector of measurements for a given character over all species, and the variable Y is an estimate of size for each species. The estimate of size used for the CICON data was a composite variable computed as the average of tarsometatarsus length, tibiotarsus length and synsacrum length (characters TA-SN, TI-EL and SY-CJ of Wood, 1982a, b). The size estimate for the GRUINAE and SPARROW data was a similar composite variable computed as the average of tarsometatarsus length, tibiotarsus length and sternum length (characters 37, 35 and 21 of Schnell, 1970, Robins and Schnell, 1971, and Wood, 1979).

Comparisons of the resulting classifications were done using the idea of congruence, defined by Rohlf and Sokal (1981) as "agreement of separate classifications arrived at by the same algorithms and based on the same set of taxa but on different sets of characters." It is generally agreed that a procedure producing higher congruence would be preferred when creating classifications (Rohlf and Sokal, 1981). As pointed out by these authors, congruence by it self is a poor criterion since perfect congruence can be achieved by making the results independent of the data. However, when the procedures are chosen using criteria other than congruence (as they are here), it is a useful measure of performance. Congruence was assessed using the matrix correlation (Sneath and Sokal, 1973). This is a good measure of the relative congruence of phenetic classifications although it may not be optimal for evaluating absolute levels of concordance (Rohlf 1982).

The following procedure was carried out on each of the three

data sets: (1) The raw data were transformed by (a) removing size and (b) removing the common part as described above. (2) Twenty-five characters were chosen at random using a standard random number generator (GGUBS subroutine of the IMSL FORTRAN library; IMSL, 1980) from each of the transformed matrices. (3) Each of the random character sets was standardized by characters and then similarity matrices were computed of (a) product-moment correlations, (b) average taxonomic distances and (c) Manhattan distances. Phenograms were constructed using the unweighted pair-group method with arithmetic averages (UPGMA) on the similarity matrices. Discussions of these standard phenetic techniques are in Sneath and Sokal (1973). (4) Steps 2 and 3 were run 10 times, each starting with a different random seed. (5) Matrix correlations were calculated between all matrices of a given type (e.g., within size-removed correlations, within common-part Manhattan distances). (6) Steps 4 and 5 were performed 10 times. The resulting samples ( $n = 450$ ) of correlations from each similarity measure from each transformation were tested for differences in means. The null hypothesis in these cases was: the mean congruence using the  $i^{\text{th}}$  analysis on data transformed by the removal of size is equal to the mean for the same analysis on data transformed by the removal of the common part. There are nine analyses corresponding to all combinations of three data sets and three similarity measures. The observations within each sample are not independent; thus the degrees of freedom in the  $t$ -test must be adjusted. At least nine

comparisons within each of the runs (steps 2 and 3) are independent and the replicates (step 5) are independent. Thus, the degrees of freedom were adjusted from 898 ( $2 \times \text{sample size} - 2$ ) to 162 ( $9 \text{ comparisons} \times 9 \text{ replicates} \times 2$ ). A similar adjustment was used by Birch et al. (1963). For the common-part transformation, differences in means were tested for between pairs of values within each data set. Degrees of freedom were adjusted as above. All computations were done on the IBM 370-158 at the University of Oklahoma using SAS (Barr et al., 1979), NT-SYS (Rohlf, Kishpaugh and Kirk, 1979) and FORTRAN routines.

#### RESULTS AND DISCUSSION

Ratios of the total variance in the transformed data to the total variance in the original data are listed for both transformations in Table 1. The common part accounts for a large portion of the variance in all three data sets (87-98%). Size also accounts for a considerable portion (76-89%). Clearly, either the common part of size could mask other relationships implied by these data.

The differences in the amount of variance explained by the common part for the three data sets are due both to the average similarity among the taxa and to the similarity of the estimator to the taxa in the group. For the SPARROW data the average similarity is very high and the outside taxon is also very similar whereas the levels of similarity for the CICON data are considerably less. This is predictable from the relationships expressed by the

current classification of birds; the estimator for the SPARROW common part (Junco vulcani) is a member of the same subfamily as the SPARROW species; the estimators for the GRUINAE are in a different subfamily of the family containing the GRUINAE species, while the estimators of the common part of the CICON data are in separate families in the Ciconiiformes.

Three similarity measures were used as the basis for producing classifications from data transformed by the removal of the common part. The mean congruence values for each transformation using each of these three similarity measures are given in Table 2 (along with other pertinent statistics). A considerable range of average congruence values (0.165 to 0.942 from a possible range of -1.0 to 1.0) are present when all similarity measures and data sets are considered. However, the use of correlations as a similarity gives significantly lower average congruence values than do the distance measures (comparisons between correlation and average distance values:  $t_{.001[\infty]} = 3.29$ ,  $t_{[CICON]} = 35.21$ ,  $t_{[GRUINAE]} = 18.67$ ,  $t_{[SPARROW]} = 12.52$ ). The values are exceptionally low for the CICON and GRUINAE data sets (0.175 and 0.165, respectively). There is relatively little difference between the values for the distance similarity measures although for two of the data sets (CICON and SPARROW) the Manhattan distances give significantly higher average congruence ( $t_{[CICON]} = 3.73$ ,  $t_{[SPARROW]} = 6.48$ ).

The use of correlations as similarity measures on these

data sets produces results that are highly dependent on the character set chosen for analyses. Distance measures provide much greater stability and should be preferred in taxonomic analyses using data similar to those treated here. The level of stability (measured by average congruence) is dependent on the particular data analyzed; it is very high for the SPARROW data. The lower values for the distance measures for the CICON and GRUINAE data still reflect considerable similarity among the phenograms. An example is the comparison between the two phenograms in Fig. 2 (taken from Wood 1982b). The matrix correlation is 0.489 but most of the major groups are the same in both and many of the details of the relationships among the species correspond.

Comparisons between the common-part transformation and the size-removed transformation for values of average congruence of classifications are also given in Table 2. I will not consider further the use of correlations because this similarity measure results in classifications of very low average congruence. For two of the data sets (CICON and SPARROW), a statistically significant increase in average congruence resulted from the removal of the common part compared to removal of size (see Table 2 for test values). For the SPARROW data the increase is especially notable since the average congruence is very high for the size-removed transformation. For the GRUINAE data the congruence means for average taxonomic distances are not statistically different; for the Manhattan distances the mean for the common-part



transformation is significantly lower than for the size-removed transformation.

Thus, for two of the three data sets analyzed the removal of the common part of the variables resulted in an increase in congruence between classifications based on random partitions of the data over the congruence obtained from the transformation removing size. This increase resulted when distances (either average taxonomic or Manhattan) were used as a similarity measure; when correlations were used, the average congruence was significantly lower regardless of the transformation. Removal of the common part emphasizes the variance relevant to the formation of classifications and may produce more stable results than the removal of size. I suggest that this transformation (removal of the common part) may be useful in phenetic studies using continuous morphometric data.

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TABLE 1. RATIO OF THE TOTAL VARIANCE IN TRANSFORMED DATA TO TOTAL VARIANCE IN ORIGINAL DATA FOR THREE DATA SETS (SEE TEXT FOR DESCRIPTION).

| Data set | Transformation |                     |
|----------|----------------|---------------------|
|          | Size removed   | Common part removed |
| CICON    | 0.136          | 0.092               |
| GRUINAE  | 0.238          | 0.083               |
| SPARROW  | 0.111          | 0.018               |

TABLE 2. MATRIX CORRELATIONS WITHIN ANALYSES FOR THREE SIMILARITY MEASURES IN TWO DIFFERENT TRANSFORMATIONS FOR THE THREE DATA SETS (SEE TEXT FOR DESCRIPTION). MEANS ( $\bar{X}$ ), STANDARD DEVIATIONS (SD) AND RANGES (Min., Max.) GIVEN. SAMPLE SIZE IS 450 IN EACH CASE. THE  $t$ -VALUE REFERS TO HYPOTHESIS OF EQUALITY OF MEANS BETWEEN TRANSFORMATIONS. SIGNIFICANCE LEVELS ARE: \*,  $P < .01$ ; \*\*\*,  $P < .001$ ; ns, NOT SIGNIFICANT. CRITICAL  $t$ -VALUE USED IN ALL CASES IS  $t_{.001[\infty]} = 3.29$ .

| Data set and<br>similarity measure | Size removed |      |       |      | Common part removed |      |       |      | <i>t</i> |
|------------------------------------|--------------|------|-------|------|---------------------|------|-------|------|----------|
|                                    | $\bar{X}$    | SD   | Min.  | Max. | $\bar{X}$           | SD   | Min.  | Max. |          |
| CICON                              |              |      |       |      |                     |      |       |      |          |
| Correlation                        | .265         | .153 | -.066 | .876 | .174                | .155 | -.133 | .730 | 8.83***  |
| Average distance                   | .516         | .165 | .032  | .891 | .557                | .171 | -.053 | .928 | 3.63***  |
| Manhattan distance                 | .472         | .195 | -.190 | .952 | .559                | .167 | .018  | .921 | 10.45*** |
| GRUINAE                            |              |      |       |      |                     |      |       |      |          |
| Correlation                        | .198         | .200 | -.220 | .827 | .165                | .196 | -.178 | .685 | 2.52*    |
| Average distance                   | .438         | .242 | -.301 | .882 | .427                | .224 | -.249 | .878 | 0.73ns   |
| Manhattan distance                 | .510         | .243 | -.183 | .907 | .425                | .245 | -.286 | .947 | 5.24***  |

Table 2 continued

| SPARROW            |      |      |      |      |      |      |      |      |          |
|--------------------|------|------|------|------|------|------|------|------|----------|
| Correlation        | .703 | .140 | .237 | .975 | .818 | .125 | .470 | .996 | 13.09*** |
| Average distance   | .713 | .181 | .176 | .997 | .911 | .096 | .406 | .997 | 20.47*** |
| Manhattan distance | .771 | .178 | .194 | .995 | .942 | .033 | .794 | .998 | 19.96*** |

# Figure Legends

Fig. 1. Schematic plot illustrating removal of the common part. Coordinates of dots are the corresponding values for characters from the  $i^{th}$  taxon in group under study (ordinate) and the outside taxon (estimate of the common part; abscissa). Line represents estimate (using linear regression) of  $i^{th}$  taxon of study group based on outside taxon. Residual (marked  $R_k$ ) is the vertical distance (distance along the ordinate) between a given point and the line; this is the transformed value for the  $k^{th}$  character of the  $i^{th}$  taxon in the data matrix.

Fig. 2. Two phenograms chosen to illustrate similarities between phenograms for which the matrix correlation between their respective cophenetic matrices is less than 0.6 (actual correlation is 0.535). Taxa are members of the avian family Ciconiidae (storks) and characters were taken from the skull (SK) and synsacrum (SY), and transformed by removal of the common part. The scales are in units of average taxonomic distance.

Fig. 1.

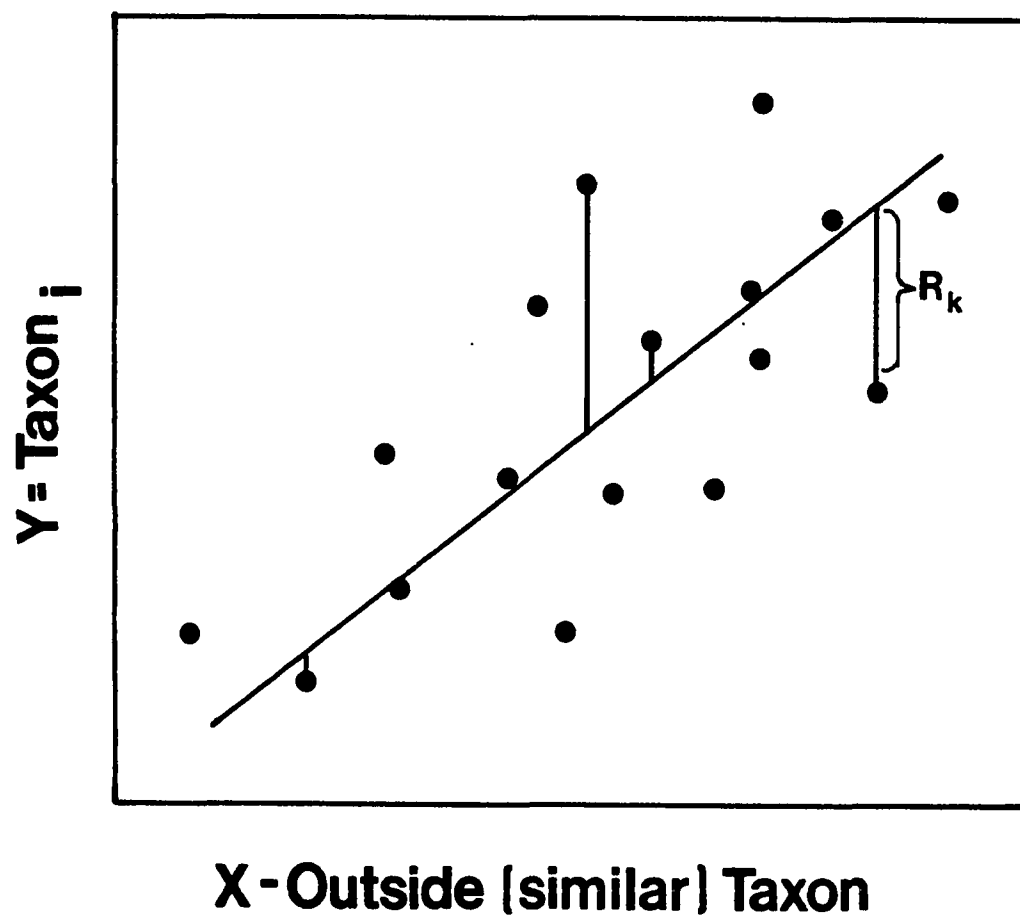
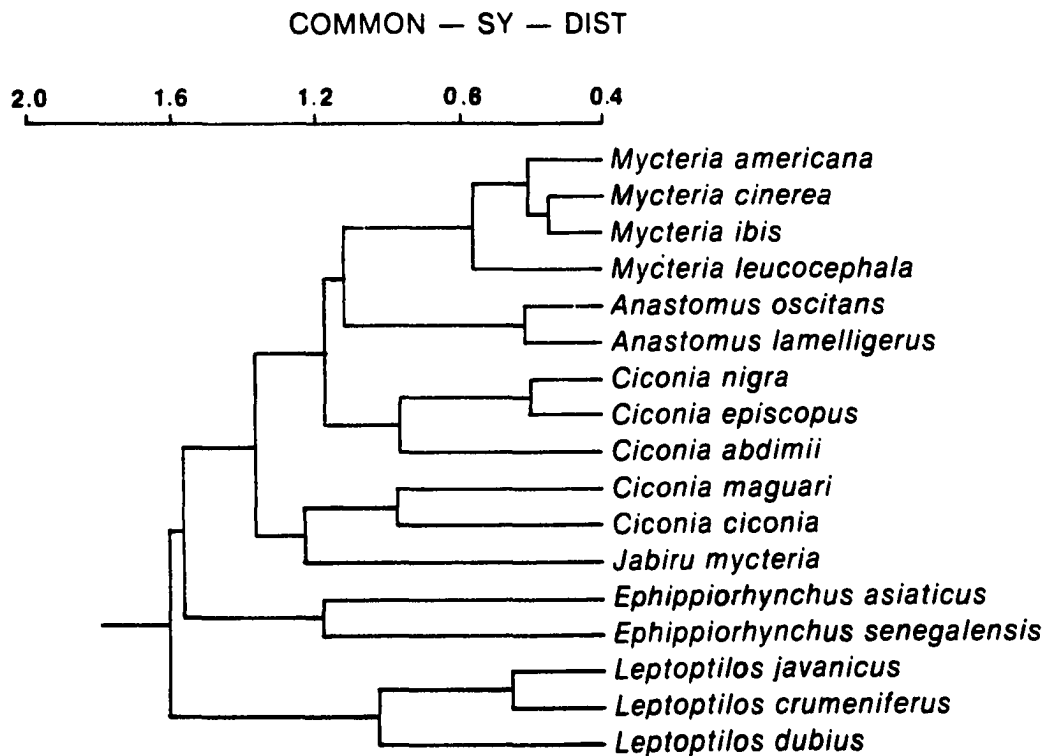
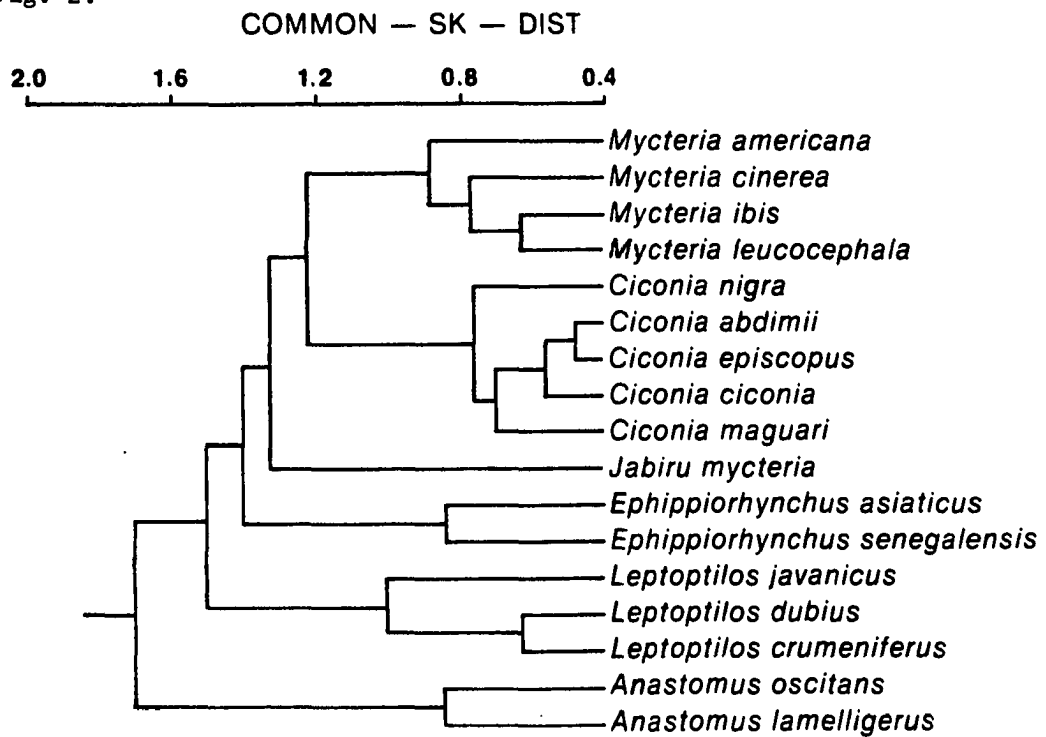




Fig. 2.



### PAPER III

CONCORDANCE BETWEEN CLASSIFICATIONS OF THE CICONIIDAE  
(AVES) BASED ON BEHAVIORAL AND MORPHOLOGICAL DATA

D. Scott Wood

ABSTRACT

Kahl's data on courtship behavior in the Ciconiidae were recoded and analyzed from a phenetic viewpoint. The resultant classification reflects his published results except for the placement of Ciconia nigra and the genera Jabiru and Ephippiorhynchus. Classifications based on skeletal morphology are highly congruent with those recalculated from the behavioral data. The classification suggested by both sets of data is similar to that proposed by Kahl with the following changes: (1) Jabiru is included with Ephippiorhynchus; (2) Ephippiorhynchus is transferred into the Ciconiini.

INTRODUCTION

Kahl's (1966, 1971, 1972a-e, 1973) studies of the ritualized courtship behavior of the 17 species of storks (Ciconiidae) are among the most complete comparative descriptions of behavior for any family of birds. He considered the taxonomic implications of the behavioral traits and recommended significant changes in the classification of this group (Kahl 1972a, 1979). Previous to Kahl's work, the classification most often used was that of Peters

(1931; Fig. 1), who split the family into 11 genera and two subfamilies. Verheyen (1959) included all but one of the storks (Anastomus oscitans) in his analysis of the Ciconiiformes (sensu Wetmore 1960). He used a large suite of characters taken from many aspects of the morphology and behavior of the birds to construct a classification (Fig. 2A). His significant deviations from Peters' classification were: (1) the merger of Xenorhynchus and Jabiru into Ephippiorhynchus and (2) the association of Dissoura with Leptoptilos. Verheyen's classification recognized nine genera grouped into four tribes but has not been widely accepted. Kahl (1972a, 1979: Fig. 2B) further reduced the number of genera (to six) and split the family into three tribes. His significant modifications were: (1) the merger of the five typical storks into Ciconia; (2) the association of Anastomus with Mycteria; and (3) the association (on other than behavioral grounds) of Ephippiorhynchus (including Xenorhynchus) and Jabiru with Leptoptilos. These three groupings form the tribes Ciconiini, Mycteriini and Leptoptilini, respectively.

For Kahl's summary to be useful as a general classification for this family, it should be predictive of character state distributions from suites of characters not used to form the classification (Sneath and Sokal 1973). Thus, it is of interest to compare Kahl's classification with those obtained using different sets of characters. I have presented elsewhere (Wood 1982a, b) a detailed phenetic study of the 17 species of storks

based on continuous osteological characters. In this paper I compare classifications of the storks based on behavioral characters with those based on skeletal morphology.

#### MATERIALS AND METHODS

Because Kahl's treatment of behavioral characteristics was primarily qualitative, I recoded his descriptions of behaviors in numerical (multi-state) form. Descriptions were taken from Kahl (1966, 1972b-e, 1973), and the characters and character states used are listed in Appendix I; the data matrix is included as Appendix II. In the three instances where Kahl did not actually record a particular behavior but was confident of its presence (Head Shaking Crouch in C. maguari, Forward Threat in M. cinerea, Up-Down in E. senegalensis), I included the predicted character states. Average taxonomic distances (Sneath and Sokal 1973) were computed among all species; these were subjected to clustering using the unweighted pair-group with arithmetic averages (UPGMA) method, and the results summarized in a phenogram.

The phenetic morphological results used in comparisons are taken from Wood (1982a, b). The basic data are the 156 measurements (means of up to six individuals) from five skeletal elements of each of the 17 stork species. Fig. 3 shows a representative bone (proximal end of a humerus) with the points and measurements that were taken (those that are visible in this view). The other bones (skull, sternum, synsacrum and tarsometatarsus, as well as the distal end of the humerus) were similarly described. These data

were split into five partitions corresponding to the five bones measured; a combined set of all measurements was also analyzed. Data in each of the six sets were transformed in three ways: (1) the effect of size was reduced by calculating the angles subtended by pairs of measurements sharing a vertex (the characters were originally chosen so as to make these calculations possible). (2) Size was removed from the data using regression as suggested by Atchley (1978). (3) The common part of the variance was removed using regression. Complete descriptions of these transformations are in Wood (1982, a, b, c). This last transformation treats each species of stork as a variable and then removes the variance accounted for by an estimate of a generalized stork. Multiple regression is used if the estimate of the common part involves more than one non-stork species.

The choice of an estimator organism (which needs to be outside the group under consideration) for the common part of the storks is not immediately clear. The relationship of the Ciconiidae to other birds has received considerable scrutiny but little consensus (Parkes 1978, Olson 1978). The two peculiar monotypic African forms Balaeniceps rex and Scopus umbretta are considered by many to be more closely related to the storks than are other birds; they are more similar skeletally to the storks than are other groups although in different ways (pers. obs.). Thus, I used these two species together to estimate the common part.

The following analyses were performed: (1) A phenogram

summarized the results of a UPGMA cluster analysis on a matrix of average taxonomic distances. (2) Factor analysis using a matrix of correlations among taxa (Q-type factor analysis) was performed with a secondary factor structure matrix obtained by oblique rotation using the functionplane technique (Katz and Rohlf 1974). Communalities were estimated using the maximum of the absolute values of the elements for each variable of the correlation matrix, and all factors with eigenvalues greater than 1.0 were retained. The secondary structure matrix was interpreted as a taxon by character matrix and used to produce inter-taxon correlations that were clustered using UPGMA and summarized in a phenogram. (3) Projections of the taxa onto axes from a principal components analysis (the number of components retained was determined by the number of eigenvalues greater than 1.0) were subjected to cluster analysis using the adaptive hierarchical clustering scheme (AHCS) of Rohlf (1970); these results were summarized in a phenogram. (4) Multidimensional scaling (MDS) was used to reduce the dimensionality of the data to three. The species were plotted on the three MDS axes using the computer package GRAFPAC (developed by F.J. Rohlf).

Phenograms were named by concatenating codes representing transformations, data partitions and analyses. Codes for the transformations are (in order of their description above): (1) ANGLES, (2) SIZE and (3) COMMON. Codes for the data partitions are the first two letters of the bone name: SK (skull), HU (humerus),

ST (sternum, SY (synsacrum), TA (tarsometatarsus) and ALL (all characters. Codes for the analyses are (in order of their description above): (1) DIST, (2) CORR and (3) AHCS. Combining transformations, data partitions and analyses in all possible ways gives a total of 54 phenograms. However, only 51 were produced because AHCS was not run on the ALL partition due to computer limitations.

Concordance between the behavioral and morphological data was measured with the matrix correlation (Sneath and Sokal 1973), a widely used coefficient for comparisons in phenetic studies (Rohlf 1982). The phenogram representing the behavioral data was compared with each of the 51 morphological phenograms using this measure.

#### RESULTS AND DISCUSSION

Although Kahl's classification (Fig. 2B) gives no detail to the relationships of the storks within each genus, he provided such information in the text of one of his reports (Kahl 1972d). Fig. 4A shows this more detailed classification in the form of a dendrogram. The differences in Fig. 4A compared to Fig. 2B are the placement of Jabiru closer to Ephippiorhynchus and the arrangement of the species within Ciconia; Kahl considered C. nigra and C. ciconia to be the least closely related of all the Ciconiini. He also judged Leptoptilos crumeniferus to be very closely related to L. dubius.

The phenogram representing the behavioral data is shown in



Fig. 4B. The cophenetic correlation of 0.97 indicates an extremely good fit to the basic similarity matrix. It is very similar to Kahl's classification. My recoding of the behavioral data suggests that Leptiptilos is not similar to the Jabiru-Ephippiorhynchus group. Furthermore, Leptoptilos is nearly as similar to Mycteria as is Anastomus and the phenetic affinities between the Jabiru-Ephippiorhynchus cluster and the Ciconiini are greater than between Mycteria and Anastomus. It appears from Kahl's (1972a, b) discussions that he considered the similarities between Mycteria and Leptoptilos to be primitive (i.e., symplesiomorphis) and, thus, irrelevant to inferring phylogenetic relationships among the groups. He also considered Jabiru to be closely related (in a cladistic sense) to the Leptoptilos species, a conclusion based primarily on external morphology--that is, "massive bill, inflatable throat sac, unfeathered head and neck, iris color" (Kahl 1973). His conclusion that this species is a link between Ephippiorhynchus and Leptoptilos is not well supported by behavioral information. Small differences in the arrangement of species in the Ciconia and Leptoptilos clusters are apparent when comparing the behavior phenogram (Fig. 4B) with Kahl's detailed classification (Fig. 4A); these appear to also be the result of the inclusion of cladistic considerations in Kahl's detailed classification.

The 51 phenograms resulting from the phenetic skeletal analyses are discussed in Wood (1982a, b). The matrix correlations between the behavioral phenogram (Fig. 4B) and each of these phenograms are

listed in Table 1. Obviously, the behavioral classification does not predict some of these morphological results particularly well, which is not surprising since some of the morphological phenograms are uncorrelated with each other. Figs. 5 and 6 depict a representative set of phenograms to show the variation in the phenetic results. Clearly, some of these are quite dissimilar to the behavior phenogram. A number of morphological phenograms, however, are very similar (correlation greater than 0.7) to the behavior results. Included in these morphological results is the phenogram that I indicated best represented the morphological findings (Wood 1982a, b); this latter phenogram (COMMON-ALL-DIST) is depicted in Fig. 7A. The choice of the best phenogram was based primarily on stability defined in terms of congruence of classifications using partitions of the data (Rohlf and Sokal 1981). The transformation to remove the common part provided a significant increase in stability compared with the other transformations employed and the use of average taxonomic distances as a similarity measure produced more stable results for this transformation than did correlations. The COMMON-ALL-DIST phenogram summarized the variation over all characters rather than for only a portion of the data thus providing a better overall summary of the phenetic affinities than the phenograms of other less inclusive partitions.

Figs. 7 and 8 show the four phenograms with the highest correlation with the behavioral classification. In addition to COMMON-ALL-DIST these are: SIZE-TA-CORR (Fig. 7B); ANGLES-SK-CORR

(Fig. 8A); and SIZE-SK-DIST (Fig. 8B). The cophenetic correlation for each is shown on the figures; all are higher than 0.8 except that for SIZE-SK-DIST which is only 0.71. Based on matrix correlations, the behavioral phenogram predicts each of these approximately equally well.

Based on the analysis of the recoded behavior data (Fig. 4B), the storks are split into five distance clusters corresponding to the genera proposed by Kahl (1979), with the exception that Jabiru and Ephippiorhynchus are in the same cluster. There are few instances in the phenograms of Figs. 7 and 8 where the major clusters defined by behavior are not expressed. The two Anastomus species are placed in the same cluster in SIZE-TA-CORR (Fig. 7B) only by the inclusion of Leptoptilos, and in SIZE-SK-DIST (Fig. 8B) the Ciconia cluster also includes Ephippiorhynchus. Jabiru is associated with a number of different clusters: Ciconia in SIZE-TA-CORR (Fig. 7B), Mycteria in ANGLES-SK-CORR (Fig. 8A) and Anastomus in SIZE-SK-DIST (Fig. 8B). Of these four phenograms only in COMMON-ALL-DIST (Fig. 7A) is Jabiru associated with Ephippiorhynchus. The major difference between this phenogram (Fig. 7A) and the behavioral phenogram (Fig 4B) is the placement of Leptoptilos; it is clustered with Mycteria and Anastomus in the phenogram based on behavior whereas the morphological data indicate that it is distinct from all other storks.

The behavior phenogram is a very good representation of the behavioral similarities. However, some distortion of relationships

has occurred in the COMMON-ALL-DIST phenogram (cophenetic correlation of 0.83). Fig. 9 shows the three-dimensional model derived from the same basic similarity matrix; this model represents the basic similarity matrix very well (correlation of 0.99). A comparison of the phenogram with the three-dimensional model indicates that most of the distances represented in the phenogram are similar to those in the model except for those of the Leptoptilos species to the remainder of the storks--these are greater in the phenogram. The distance between the Ciconiini and the Mycteriini clusters appears from the model to be much more similar to the distance between the Ciconiini and the Leptoptilini clusters than would be inferred from the phenogram.

#### TAXONOMIC RECOMMENDATIONS

As noted above, a general classification should be predictive of character states from as wide a range of characters as possible. The genera proposed by Kahl are good representations of the close affinities of the storks as implied by either behavior or skeletal morphology, except that the association of Jabiru mycteria with Ephippiorhynchus asiaticus and E. senegalensis is not recognized. The tribes proposed by Kahl also summarize the phenetic relationships of the storks well except for the association of Leptoptilos with Jabiru and Ephippiorhynchus. These latter two genera are similar to the Ciconia species both behaviorally and on the basis of skeletal morphology. For these reasons I propose the following modifications to the classification of Kahl (1979) which allow

greater accuracy in predicting character state distributions not only for skeletal morphology but also for ritualized courtship behavior: (1) Include Jabiru mycteria in the genus Ephippiorhynchus which has priority; this genus now contains three members, asiaticus, senegalensis and mycteria. (2) Transfer the expanded genus Ephippiorhynchus from the tribe Leptoptilini to the tribe Ciconiini. The family Ciconiidae would consist of five genera assigned to three tribes: Mycteriini, Mycteria and Anastomus; Ciconiini, Ciconia and Ephippiorhynchus; and Leptoptilini, Leptoptilos.

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(submitted for publ.).



Table 1.--Matrix correlations between phenogram based on behavior and phenograms for morphologic data sets (based on cophenetic matrices).

|                 | Common parts |      |      | Size removed |      |      | Angles |      |      |
|-----------------|--------------|------|------|--------------|------|------|--------|------|------|
|                 | removed      |      |      |              |      |      |        |      |      |
|                 | DIST         | CORR | AHCS | DIST         | CORR | AHCS | DIST   | CORR | AHCS |
| Skull           | .738         | .710 | .676 | .760         | .427 | .550 | .662   | .788 | .755 |
| Humerus         | .426         | .446 | .682 | .291         | .467 | .408 | .595   | .338 | .458 |
| Sternum         | .438         | .481 | .282 | .314         | .451 | .301 | .335   | .488 | .282 |
| Synsacrum       | .561         | .337 | .570 | .458         | .446 | .470 | .439   | .357 | .216 |
| Tarsometatarsus | .400         | .456 | .558 | .451         | .834 | .729 | .450   | .516 | .395 |
| All characters  | .784         | .698 |      | .336         | .626 |      | .244   | .266 |      |

FIGURE LEGENDS

Fig. 1. Dendrogram representing the classification of Peters (1931).

Fig. 2. Dendrograms representing classifications presented by (A) Verheyen (1959) and (B) Kahl (1979)

Fig. 3. Cranial view of the proximal end of the left humerus of Ciconia ciconia (CM S-1813). Characters (measurements) visible from this view that were used in this study are (using the points marked): A-B, A-C, A-D, B-C, B-D, B-E, C-E, and D-E.

Fig. 4. (A) Dendrogram representing the classification of Kahl (1979) but including further details (taken from Kahl 1972a) on subtribal and subgeneric relationships. (B) Phenogram derived from UPGMA clustering of taxonomic distances based on the recoded behavioral data of Kahl (1966, 1972a-e, 1973).

Fig. 5. Phenograms showing variation in the morphological results (A) Phenogram derived from UPGMA clustering of correlations taken from a Q-type factor analysis of sternal characters. The data were transformed by the removal of the common part. (B) Phenogram derived from UPGMA clustering of taxonomic distances calculated from sternal characters transformed by removing size.

Fig. 6. Phenograms showing the variation in morphological results.

- (A) Phenogram derived from UPGMA clustering of correlations taken from a Q-type factor analysis of angular characters on the humerus.
- (B) Phenogram derived from UPGMA clustering of correlations taken from a Q-type factor analysis of all angular characters used in the study.

Fig. 7. Phenograms highly correlated with the behavior phenogram.

- (A) Phenogram derived from UPGMA clustering of taxonomic distances using all characters of the study. The data were transformed by removing the common part. This phenogram was considered the best representation of the morphological results (Wood 1982a, b).
- (B) Phenogram derived from UPGMA clustering of correlations taken from a Q-type factor analysis of tarsometatarsus characters. The data were transformed by removing size.

Fig. 8. Phenograms highly correlated with the behavior phenogram.

- (A) Phenogram derived from UPGMA clustering of taxonomic distances based on angular skull characters.
- (B) Phenogram derived from UPGMA clustering of taxonomic distances based on skull characters transformed by the removal of size.

Fig. 9. Three-dimensional model based on a multi-dimensional scaling analysis of all morphological characters used in this study. The shortest minimally connecting network is superimposed on the character space.

Fig. 1.

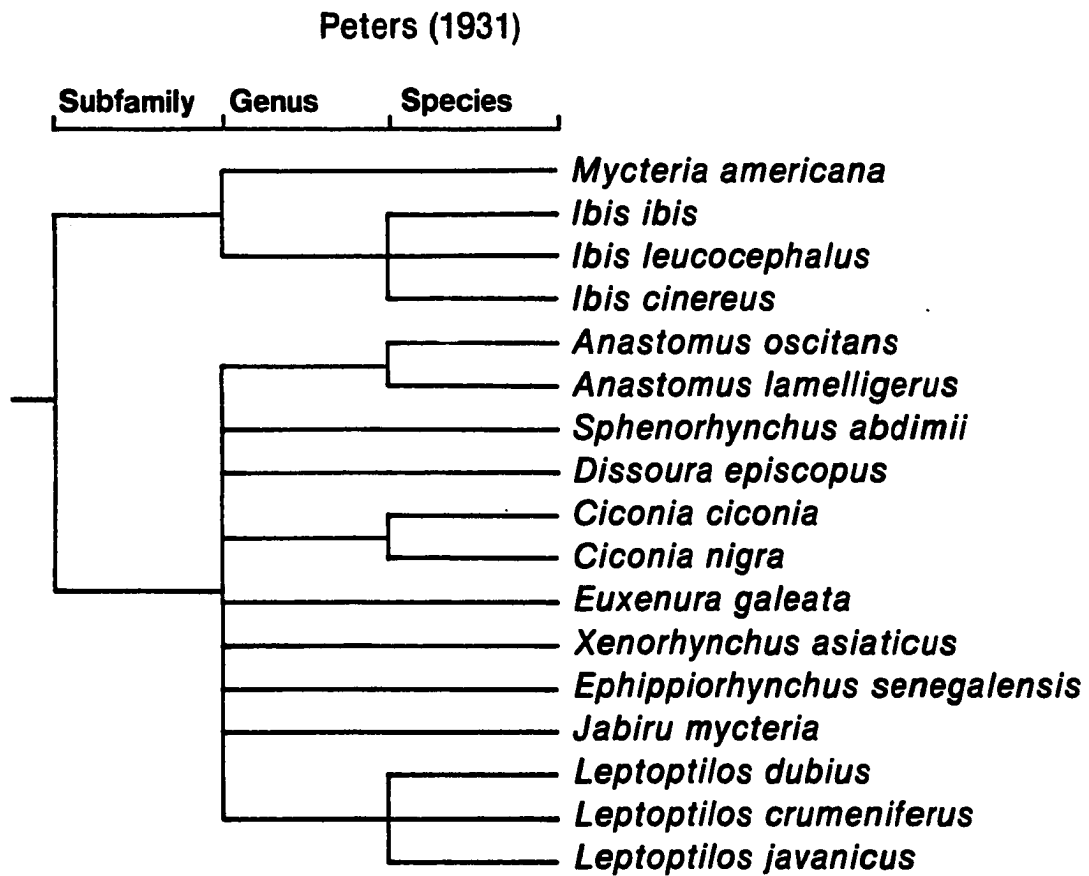


Fig. 2.

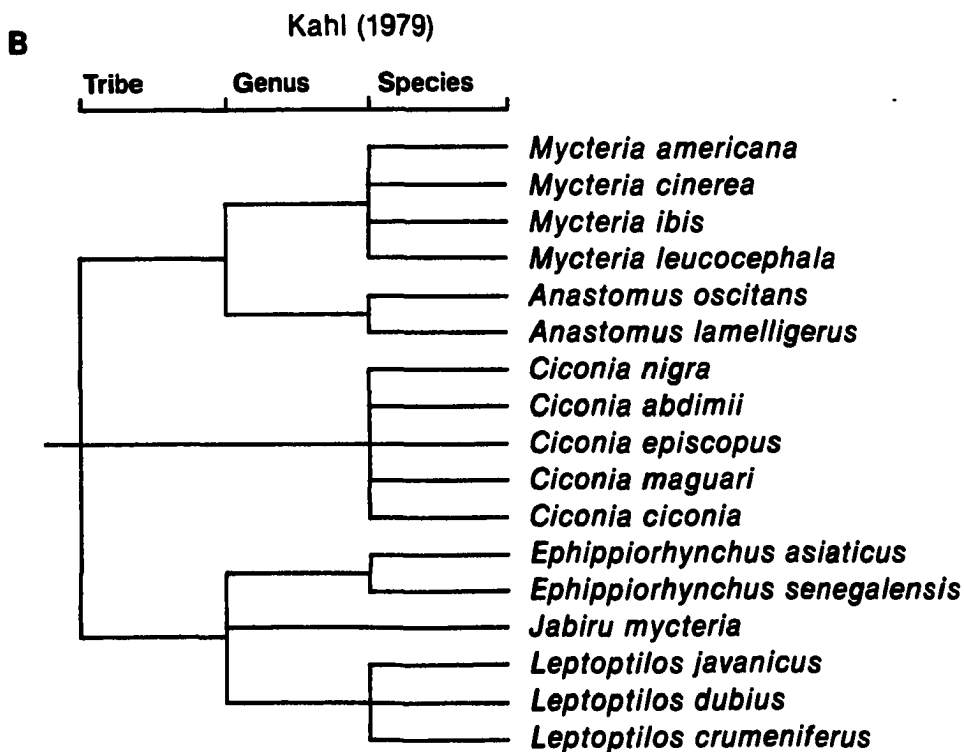
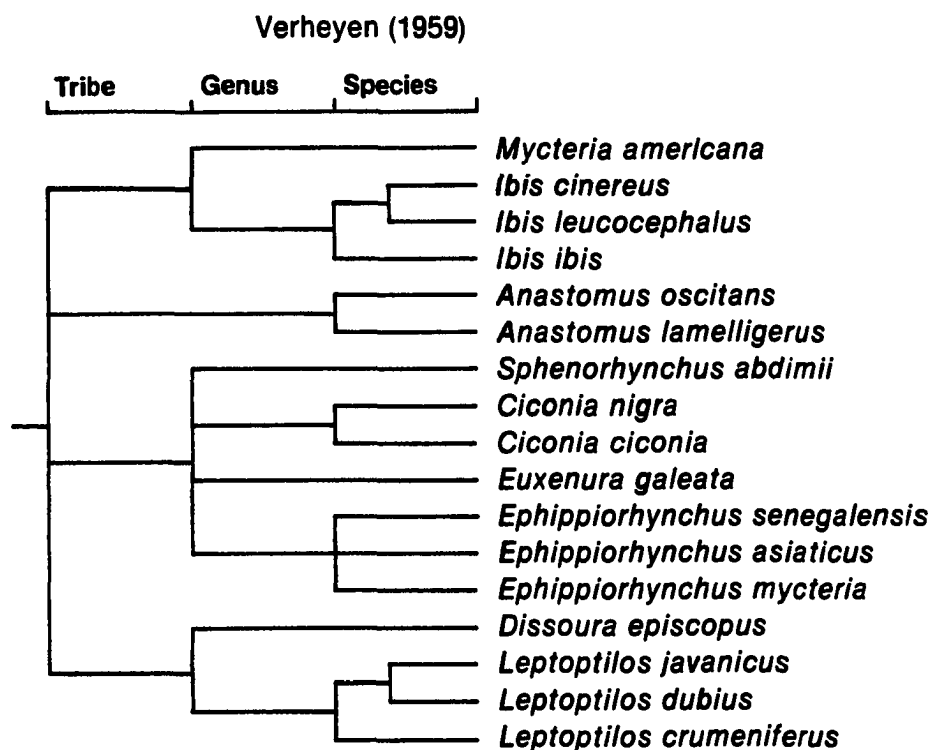


Fig. 3.

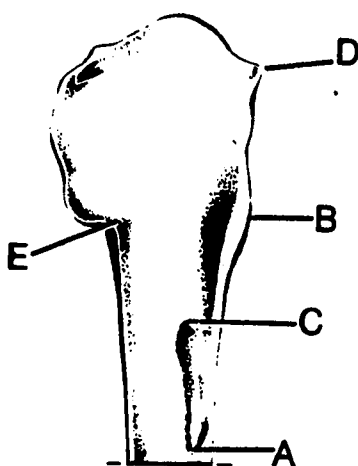
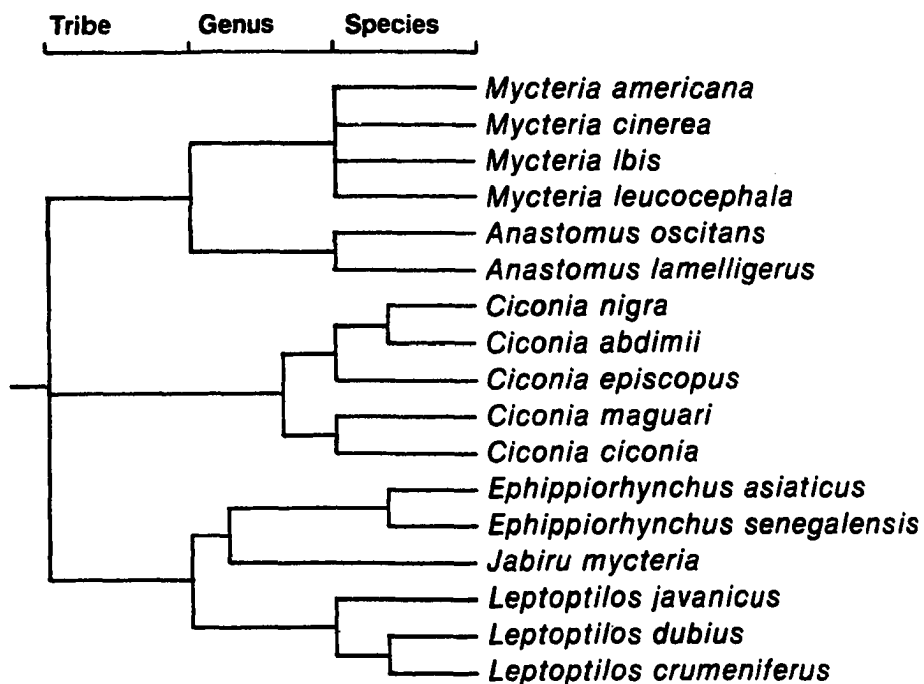


Fig. 4.

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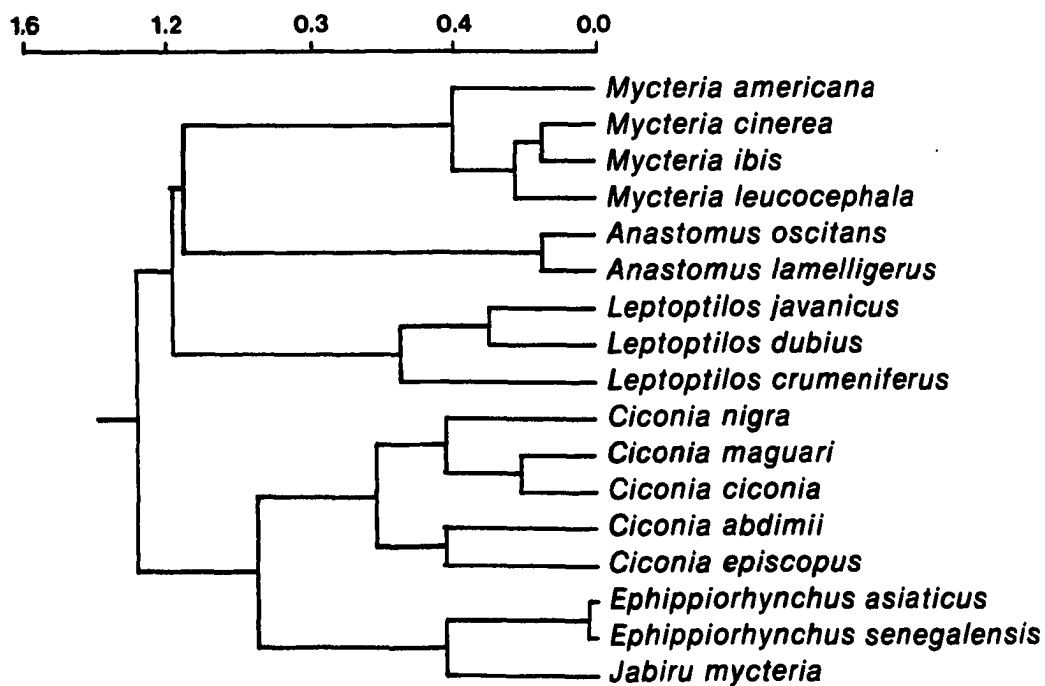
**A**

**Kahl Descriptions**



**B**

**Behavior**



$r_{cc} = 0.970$

Fig. 5.

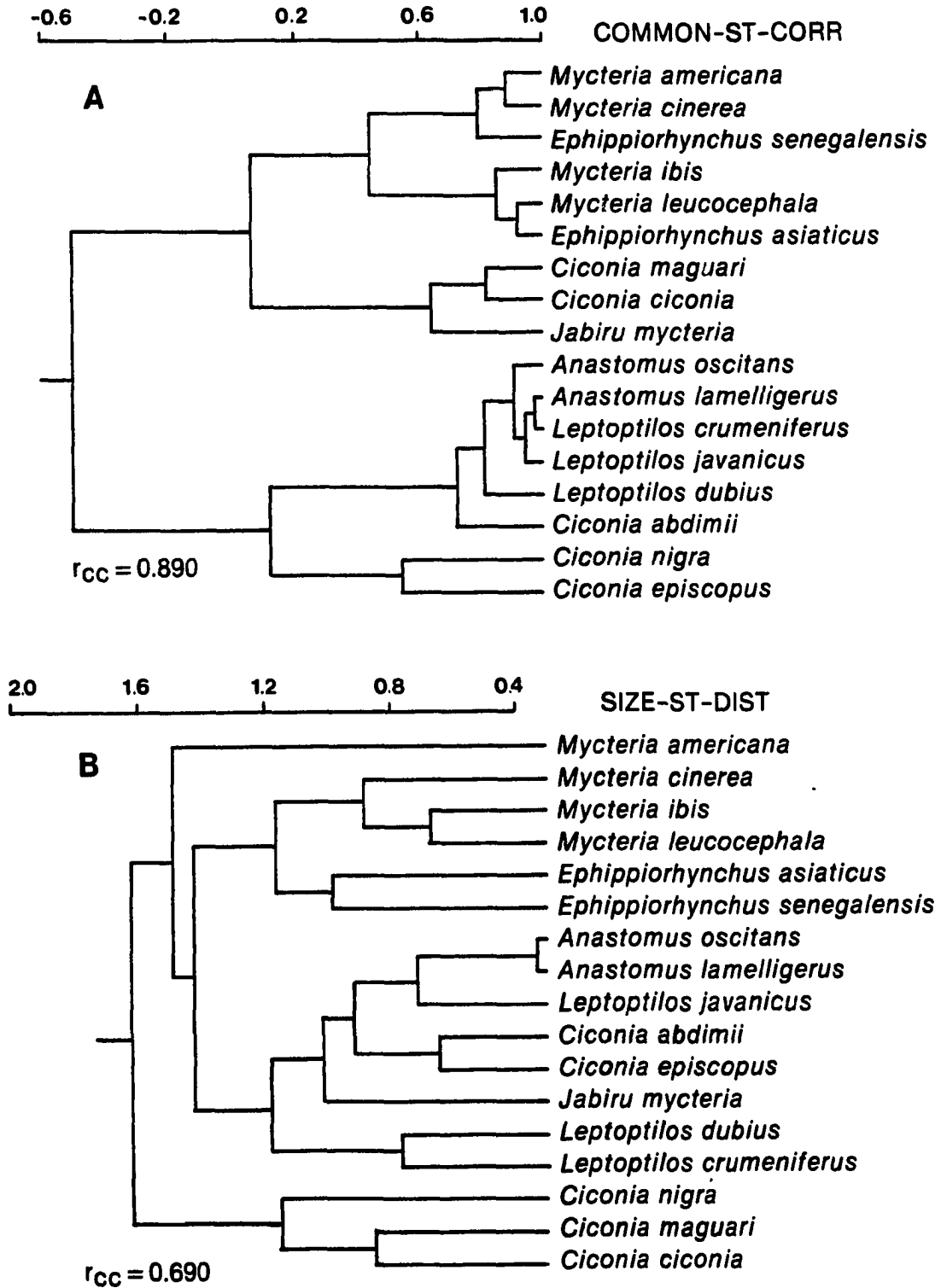




Fig. 6.

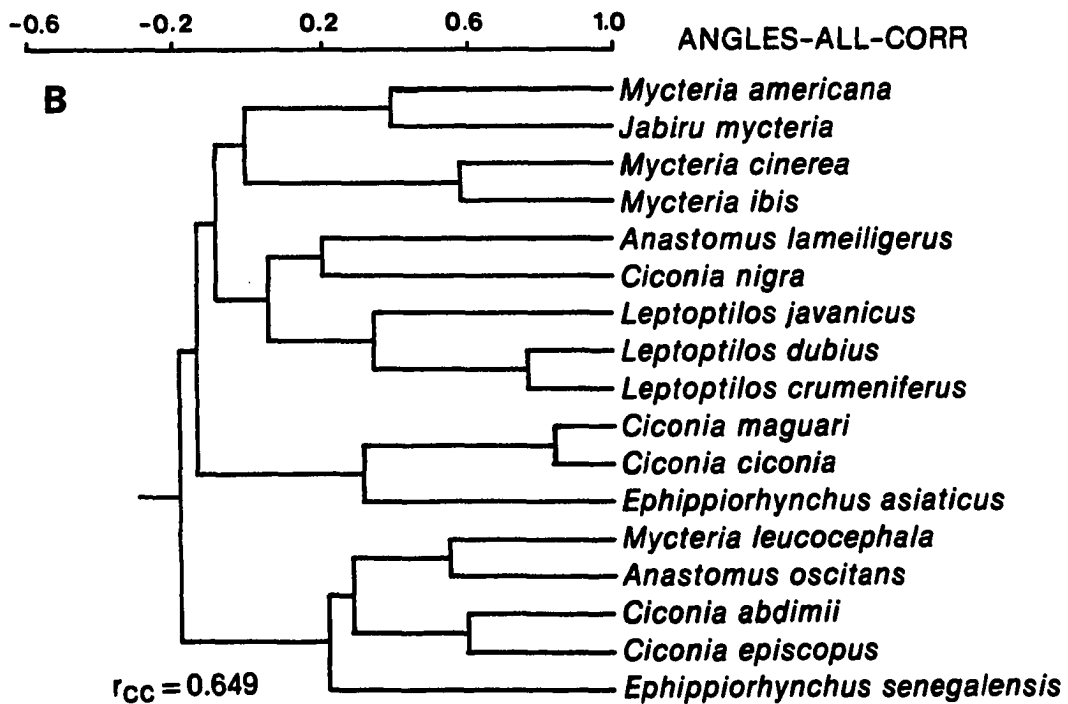
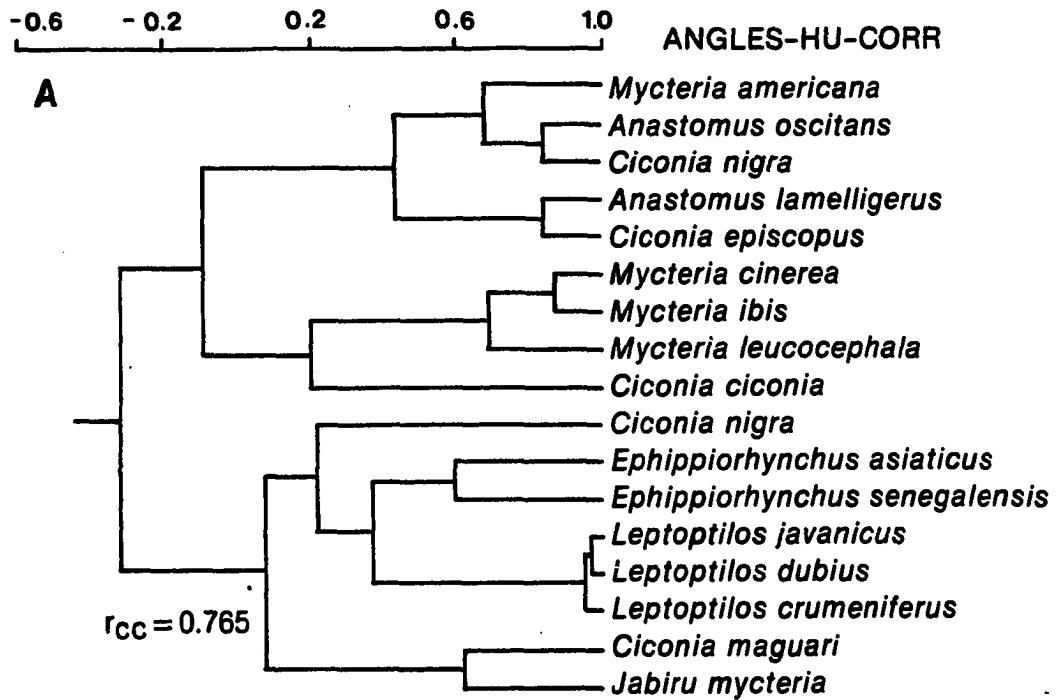


Fig. 7.

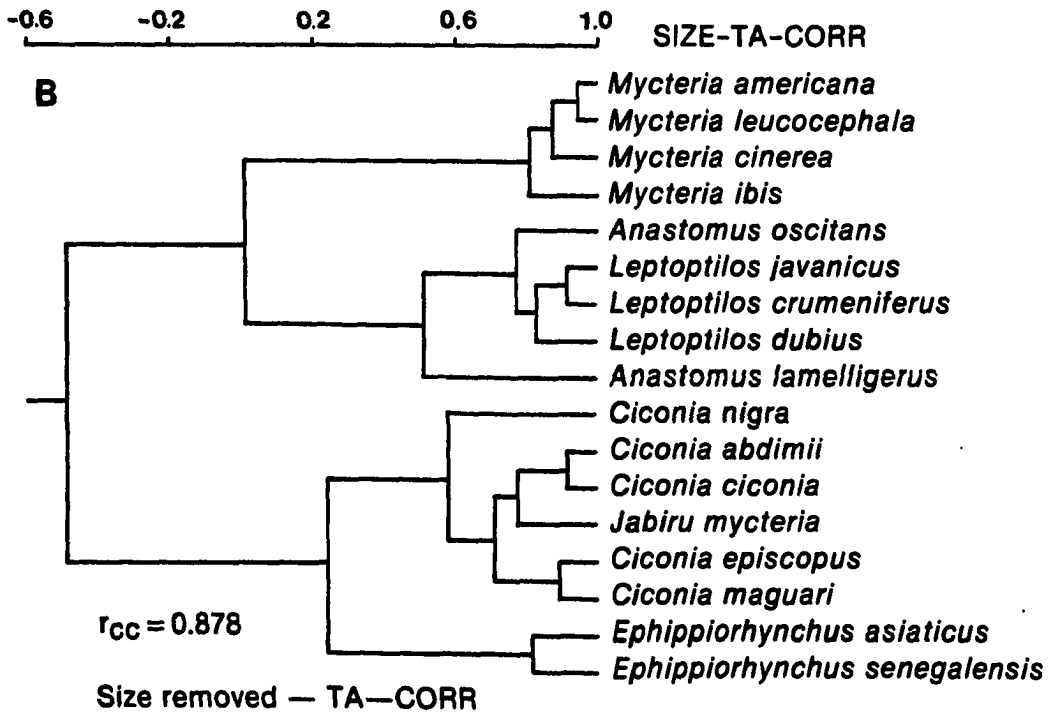
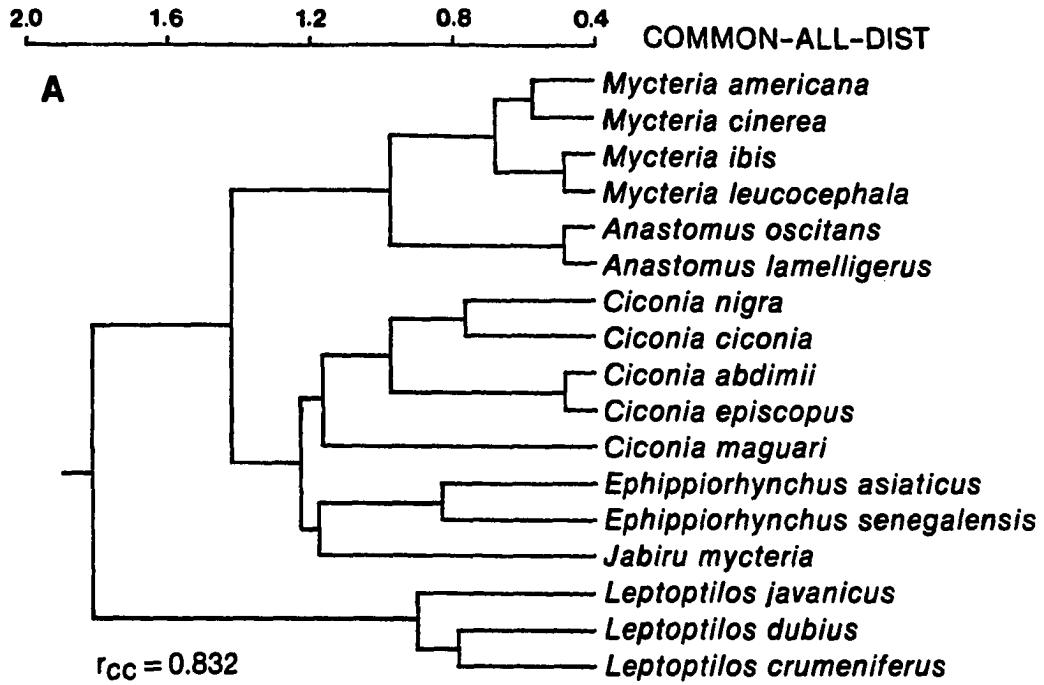


Fig. 8.

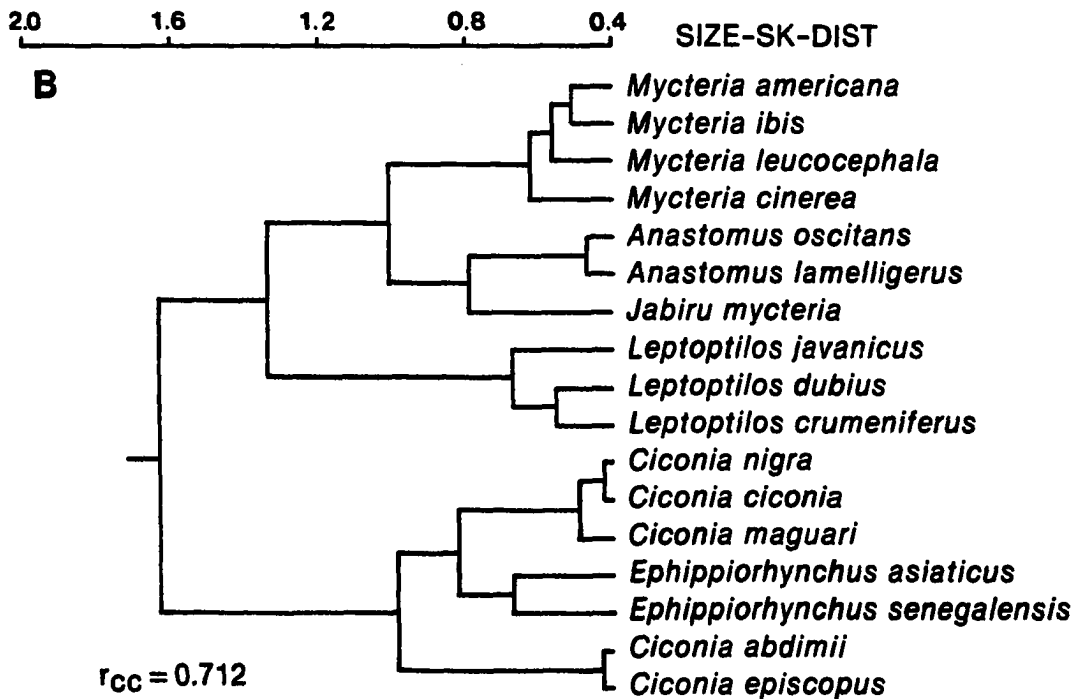
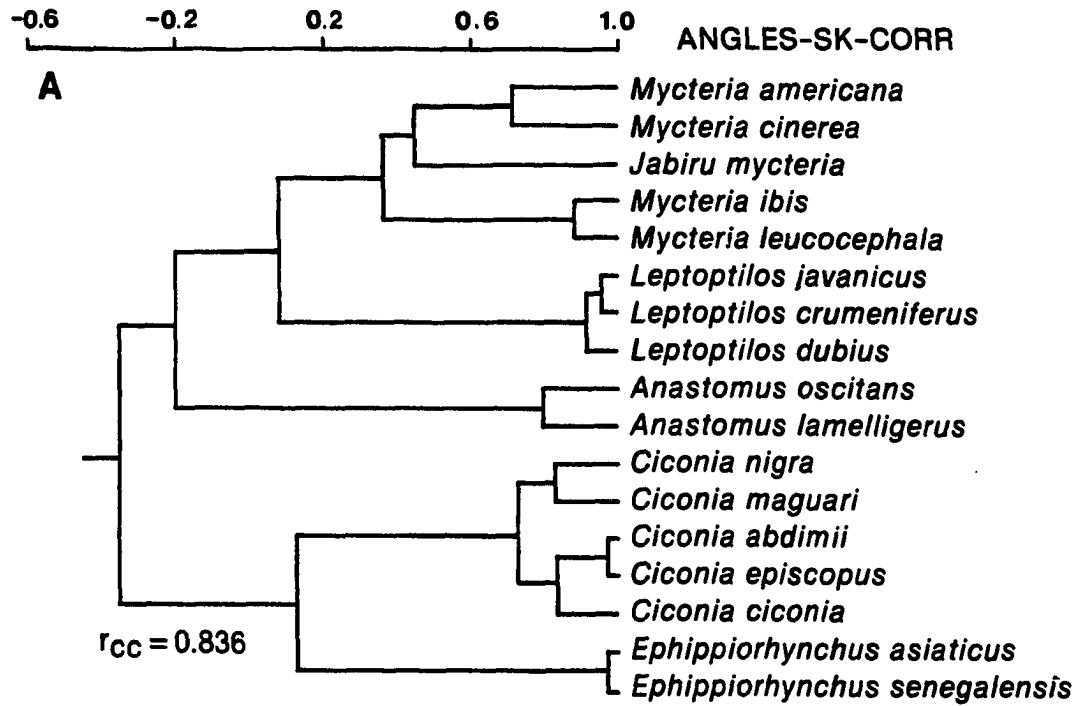
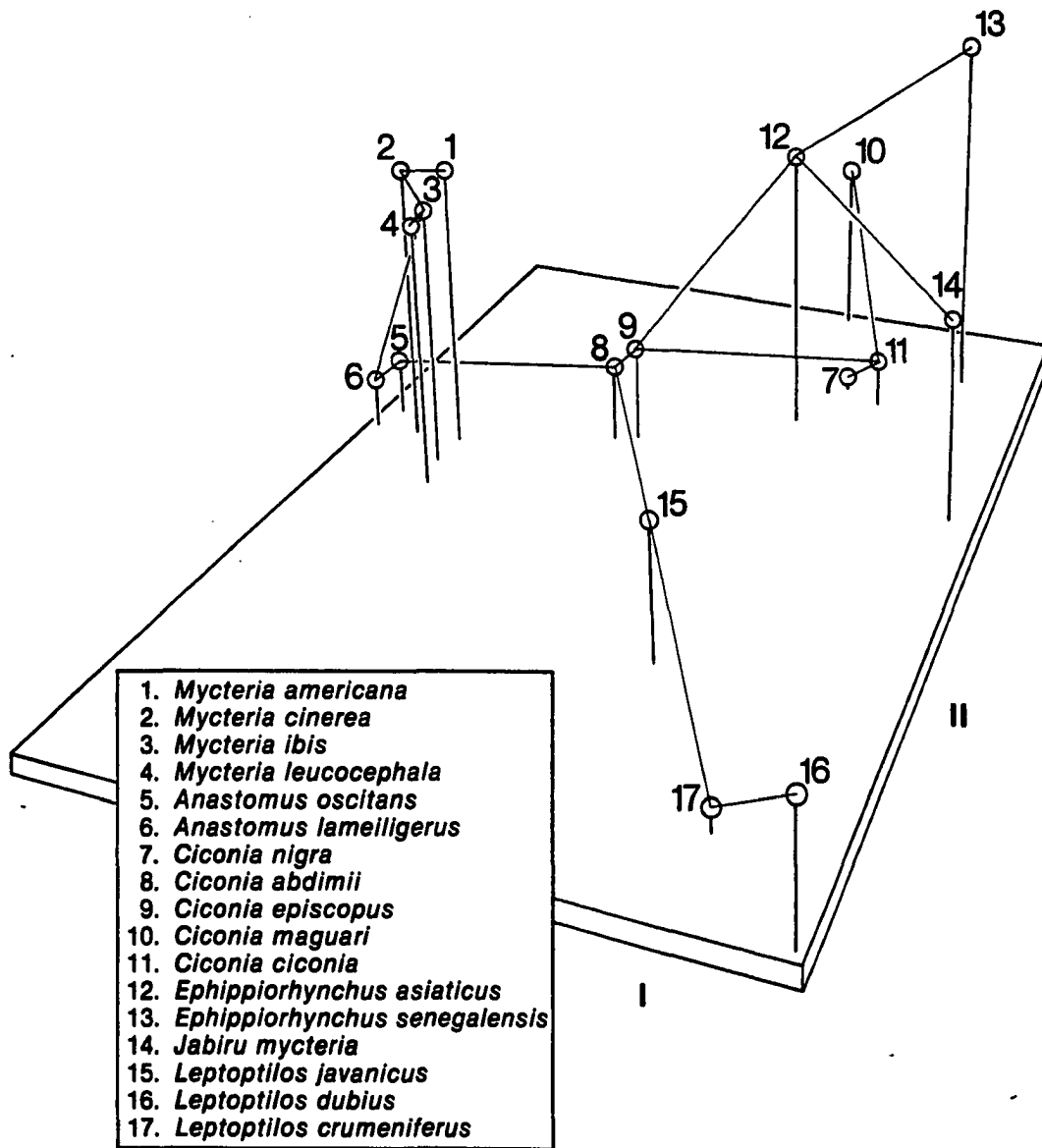


Fig. 9.



APPENDIX I

The following ritualized courtship displays were recoded from qualitative descriptions into quantitative multi-state form. Since many displays are complex, the component parts were coded as separate characters. The states 0, 1 and 2 were used in the following way: for characters coded only as present or absent 1 corresponds to present and 0 to absent; for characters with variable intensity of expression or of variable occurrence, state 2 corresponds to full intensity or regular occurrence, state 1 to reduced intensity or occasional occurrence, and state 0 to absence. The qualitative descriptions are taken from Kahl (1966, 1972a-e, 1973) and the recoded data are presented in Appendix II. In the following list the name of the display is given first followed by the list of specific components or aspects; these latter are the numbered characters.

Copulation Clattering: 1. bill clattered; 2. neck retracted; 3. under-tail coverts displayed. Up-Down: 4. bill clattered on down motion; 5. bill clattered on up motion; 6. bill snapped; 7. head shaking; 8. neck extended; 9. wings partly spread; 10. wings fully spread; 11. tail cocked. Swaying Twig Grasping: 12. bill snapped; 13. bill gaped; 14. wings partly spread; 15. under-tail coverts displayed; 16. tail cocked. Anxiety Stretch: 17. bill snapped; 18. wings partly spread; 19. wings fully spread; 20. under-tail coverts displayed. Snap Display: 21. occurrence of display; 22. head shaking; 23. neck extended. Forward Clattering

Threat: 24. bill clattered; 25. bill snapped; 26. head shaking;  
27. neck retracted; 28. under-tail coverts displays. Upright  
Display: 29. occurrence of display. Forward Threat: 30. occurrence  
of display; 31. head shaking; 32. wings partly spread; 33. Under-tail  
coverts displayed; 34. tail cocked. Head Shaking Crouch: 35.  
occurrence of display. Aerial Clattering Threat: 36. occurrence of  
display. Flying Around: 37. occurrence of display. Display  
Preening: 38. occurrence of display. Flap Dash: 39. occurrence of  
display. Balancing: 40. occurrence of display; 41. bill snapped.  
Gaping: 42. occurrence of display. Erect Gape: 43. occurrence of  
display.

# Appendix II

Recoded behavior data. See Appendix I for character descriptions.

|                        | Characters |   |   |   |   |   |   |   |   |   |   |   |   |   |   |   |   |   |   |   |   |   |   |   |   |   |   |   |   |   |   |   |   |   |   |   |   |   |   |   |   |   |   |   |   |
|------------------------|------------|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Species                | 1          | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 0 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 2 | 2 | 2 | 2 | 2 | 2 | 2 | 2 | 2 | 2 | 3 | 3 | 3 | 3 | 3 | 3 | 3 | 3 | 3 | 4 | 4 | 4 | 4 |   |   |
| <i>M. americana</i>    | 2          | 2 | 2 | 0 | 0 | 0 | 0 | 2 | 0 | 0 | 0 | 0 | 0 | 0 | 2 | 0 | 0 | 1 | 0 | 0 | 2 | 0 | 2 | 2 | 0 | 0 | 2 | 1 | 1 | 2 | 1 | 0 | 2 | 2 | 0 | 2 | 1 | 2 | 0 | 2 | 1 | 1 | 0 |   |   |
| <i>M. cinerea</i>      | 2          | 2 | 2 | 0 | 0 | 2 | 0 | 2 | 0 | 0 | 0 | 0 | 0 | 0 | 2 | 0 | 0 | 1 | 0 | 0 | 2 | 0 | 2 | 2 | 0 | 0 | 2 | 1 | 1 | 2 | 0 | 0 | 2 | 2 | 0 | 2 | 2 | 2 | 0 | 2 | 2 | 2 | 0 |   |   |
| <i>M. ibis</i>         | 2          | 2 | 2 | 0 | 0 | 1 | 0 | 2 | 0 | 0 | 0 | 0 | 0 | 0 | 2 | 0 | 0 | 1 | 0 | 0 | 2 | 0 | 2 | 2 | 0 | 0 | 2 | 1 | 1 | 2 | 0 | 0 | 2 | 2 | 0 | 2 | 2 | 2 | 0 | 2 | 2 | 2 | 0 |   |   |
| <i>M. leucocephala</i> | 2          | 2 | 2 | 0 | 0 | 2 | 0 | 2 | 0 | 0 | 0 | 1 | 0 | 0 | 2 | 0 | 0 | 1 | 1 | 0 | 2 | 0 | 2 | 2 | 0 | 0 | 2 | 1 | 1 | 2 | 0 | 0 | 2 | 2 | 0 | 2 | 2 | 2 | 0 | 2 | 2 | 2 | 0 |   |   |
| <i>A. oscitans</i>     | 0          | 2 | 1 | 0 | 0 | 0 | 1 | 2 | 1 | 0 | 1 | 0 | 1 | 1 | 2 | 1 | 0 | 0 | 0 | 0 | 2 | 1 | 0 | 0 | 2 | 1 | 2 | 2 | 2 | 2 | 1 | 2 | 2 | 2 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |   |   |
| <i>A. lamelligerus</i> | 0          | 2 | 1 | 0 | 0 | 0 | 2 | 2 | 1 | 0 | 1 | 0 | 1 | 1 | 2 | 1 | 0 | 0 | 0 | 0 | 2 | 1 | 0 | 0 | 2 | 1 | 2 | 2 | 2 | 2 | 1 | 2 | 2 | 2 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |   |   |
| <i>C. nigra</i>        | 2          | 0 | 0 | 1 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 2 | 2 | 0 | 0 | 0 | 1 | 2 | 0 | 0 | 0 | 0 | 0 | 0 |   |   |
| <i>C. abdimii</i>      | 2          | 0 | 0 | 2 | 2 | 0 | 0 | 0 | 2 | 2 | 2 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 2 | 2 | 0 | 0 | 0 | 1 | 2 | 2 | 0 | 0 | 0 | 0 | 0 |   |   |
| <i>C. episcopus</i>    | 2          | 0 | 0 | 2 | 0 | 0 | 0 | 0 | 2 | 2 | 2 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 2 | 2 | 0 | 0 | 0 | 1 | 2 | 0 | 0 | 0 | 0 | 0 | 0 |   |   |
| <i>C. maguari</i>      | 2          | 0 | 0 | 2 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 2 | 2 | 0 | 0 | 0 | 1 | 2 | 1 | 0 | 0 | 0 | 0 | 0 |   |   |
| <i>C. ciconia</i>      | 2          | 0 | 0 | 0 | 2 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 2 | 2 | 0 | 0 | 0 | 1 | 2 | 1 | 0 | 0 | 0 | 0 | 0 |   |   |
| <i>E. asiaticus</i>    | 2          | 0 | 0 | 2 | 0 | 0 | 0 | 2 | 2 | 2 | 0 | 0 | 0 | 0 | 0 | 0 | 2 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 2 | 0 | 0 | 0 |
| <i>E. senegalensis</i> | 2          | 0 | 0 | 2 | 0 | 0 | 0 | 2 | 2 | 2 | 0 | 0 | 0 | 0 | 0 | 0 | 2 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 2 | 0 | 0 | 0 |
| <i>J. mycteria</i>     | 2          | 0 | 0 | 2 | 0 | 0 | 0 | 2 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 2 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 2 | 0 | 0 | 0 |
| <i>L. javanicus</i>    | 2          | 0 | 0 | 2 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 2 | 2 | 0 | 0 | 2 | 2 | 2 | 2 | 0 | 0 | 2 | 0 | 0 | 2 | 2 | 2 | 2 | 0 | 0 | 2 | 0 | 0 | 2 | 0 | 0 | 0 | 2 | 2 | 0 | 2 |   |
| <i>L. dubius</i>       | 2          | 0 | 0 | 0 | 2 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 2 | 2 | 0 | 0 | 2 | 2 | 2 | 2 | 0 | 0 | 2 | 0 | 0 | 2 | 2 | 2 | 2 | 0 | 0 | 2 | 0 | 0 | 2 | 0 | 0 | 0 | 2 | 0 | 0 | 2 |   |
| <i>L. crumeniferus</i> | 2          | 0 | 0 | 2 | 0 | 0 | 0 | 0 | 2 | 0 | 0 | 0 | 0 | 0 | 2 | 2 | 0 | 0 | 2 | 2 | 2 | 2 | 0 | 0 | 2 | 0 | 0 | 2 | 2 | 2 | 2 | 0 | 0 | 2 | 0 | 0 | 2 | 0 | 0 | 0 | 2 | 0 | 0 | 2 |   |