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PHENETIC RELATIONSHIPS WITHIN THE FAMILY GRUIDAE

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The monographs on the Gruidae by Blythe and Tegetmeier (1881) and Blaauw (1897) indicate that the cranes were studied extensively in the 19th century. However, opinions of taxonomists of that time differed widely as to the generic and specific limits within the family. Sharpe (1899) listed 19 species and 9 genera while Blythe and Tegetmeier (1881) and Blaauw (1897) recognized 16 species in 2 and 3 genera, respectively. Little systematic work has been conducted on cranes in the 20th century except to address questions of nomenclature and to describe subspecies (e.g., Peters 1925, Grant 1948, Walkinshaw 1965). Peters (1934) proposed the classification in general use today (4 genera, 14 species) and the only changes in generic or specific limits have concerned *Balearica* (Walkinshaw 1964). Archibald (1975) reevaluated phylogenetic relationships within the Gruidae by examining the structure of the unison calls. He studied 13 of the 15 species (recognizing 2 species of *Balearica*) and recently obtained data on *Grus leucogeranus* (pers. comm.). The classifications of Peters and Archibald are represented in Fig. 1.

Taxonomic investigations and studies dealing with evolutionary patterns or adaptations are particularly reliant on morphologic information. Detailed comparative morphological studies (particularly skeletal) do not exist for the Gruidae and it is my purpose to evaluate the phenetic similarities among the cranes (both external and skeletal) and compare the results with current classifications.

MATERIALS AND METHODS

Up to 10 skins for each of the 15 crane species were measured. Usually the first 10 specimens encountered were measured, but in the few cases where larger series existed (e.g. *Grus canadensis*) I measured equal numbers of males and females. Skeletons of 14 of the 15 species were located. Table 1 details the material used along with the current ranges of the species. The nomenclature is that of Peters (1934) except that 2 species of *Balearica* are recognized in light of Walkinshaw's (1964) work. The original data are contained in appendices to Wood (1976).

I coded 95 external characters (EXT) from each skin including characters from all parts of the body. For coding color characters I used the Munsell system (1973), a numerical scheme which specifies colors using 3 components. Only the component representing the lightness or darkness (gray scale) of the color was used because the remaining components (representing hue and intensity) showed little variation. Measurements of plumage such as lengths of primaries and vane widths of rectrices were made with a rule to the nearest 1.0 mm, and those of other parts with dial calipers to 0.1 mm.

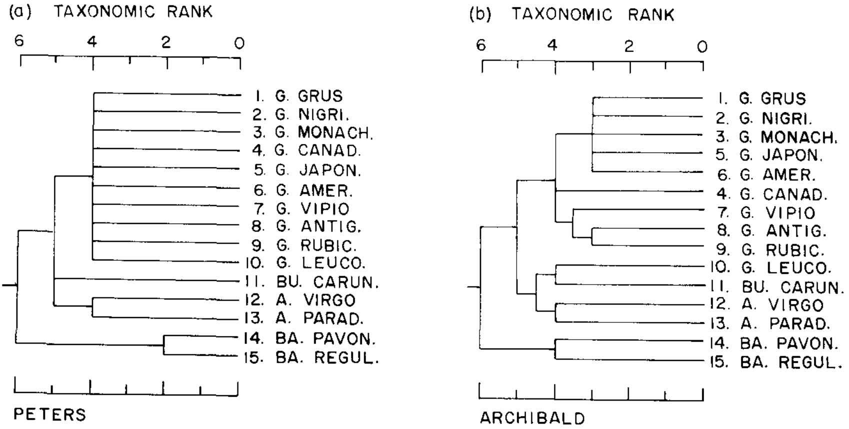

FIG. 1. Dendrograms representing the classifications of cranes proposed by Peters (1934) and Archibald (1975, pers. comm.). Taxonomic levels have been arbitrarily assigned the following values: (2) species, (3) subgenus, (4) genus, (5) subfamily, (6) family.

The head and neck region was divided into 19 areas and each coded for the amount of feathering using a scale of 0 (no feathers) to 5 (fully feathered). I coded 21 two-state (presence or absence) characters to take into account the special features of the various species.

A total of 55 skeletal measurements (SKEL) was taken with either dial or vernier calipers to the nearest 0.1 mm. Characters 1–50 are those of Schnell (1970a) with appropriate modifications due to differently shaped bones in the cranes. Characters 51–55 are designed to measure the tracheal invagination into the sternum. Both external and skeletal characters are described in the appendix of Wood (1976).

Models (based on principal component analyses) and phenograms were constructed using techniques such as those employed by Schnell (1970a,b), Robins and Schnell (1971) and Hellack (1976). Computations were performed on the IBM 370 computer using the computer program package NT-SYS developed by F. J. Rohlf, J. Kishpaugh and D. Kirk. The reader is referred to Schnell (1970a) and Sneath and Sokal (1973) for full details on these methods.

A preliminary principal component analysis was conducted on the data after logarithmic transformation and standardization to evaluate the effect of size. Size has been shown to be a major component of the variation in other phenetic studies on birds (Schnell 1970a, Robins and Schnell 1971, Hellack 1976, Hellack and Schnell 1977). Thus, I followed their suggestions and transformed my data to reduce this effect. Sternum length and humerus length were used as divisors of all skeletal measurements to form 2 transformed data matrices composed of ratios (SKEL/STERNUM, SKEL/HUMERUS). External dimensional measurements were divided by a size factor (sum of wing length, length of bare tibia and tarsus length) and combined with the 2-state characters to form a data set (EXT-WO/COLOR). The color characters were added to these data to form a second data set of external characters (EXT/LENGTHS). SKEL/STERNUM and EXT/LENGTHS were combined to form a data set over all characters (COMBINED).

TABLE 1

NUMBER ASSIGNED TO EACH SPECIES OF CRANE. NUMBER OF SKINS AND SKELETONS MEASURED AND GEOGRAPHIC DISTRIBUTION OF SPECIES[a]

Name[b]	No. skins	No. skeletons	Current distribution (B) Breeding; (W) Wintering; (R) Resident
1. *Grus grus* Common Crane	10	10	(B) Northern Eurasia, India; (W) Mediterranean, India, China
2. *Grus nigricollis* Black-necked Crane	10	0	(R) Tibet, Kashmir, to Viet Nam
3. *Grus monacha* Hooded Crane	9	1	(B) Central Siberia; (W) Japan, S. Korea, S. China
4. *Grus canadensis* Sandhill Crane	10	10	(B) Northern N. Am., southeast U.S.A., Cuba; (W) southern U.S.A., Mexico, Cuba
5. *Grus japonensis* Manchurian Crane	10	8	(B) Eastern Siberia, Manchuria, Japan; (W) Japan, Korea
6. *Grus americana* Whooping Crane	10	10[c]	(B) Wood Buffalo Park, Canada; (W) Aransas Natl. Wildl. Ref., Texas, U.S.A.
7. *Grus vipio* White-naped Crane	9	8[c]	(B) Southeast Siberia, northwest Mongolia; (W) Central China, South Korea
8. *Grus antigone* Sarus Crane	10	10	(R) India, Burma, Malaya, northeast Australia
9. *Grus rubicunda* Brolga	10	7	(R) Western and northern Australia
10. *Grus leucogeranus* Siberian Crane	9	6	(B) Northern Siberia; (W) Asia Minor (?), India, China
11. *Bugeranus carunculatus* Wattled Crane	9	7	(R) East and south Africa
12. *Anthropoides virgo* Demoiselle Crane	10	10	(B) North Africa, southern U.S.S.R. to Mongolia; (W) North Africa to Burma
13. *Anthropoides paradisea* Stanley Crane	8	10	(R) Africa south of the Zambesi River
14. *Balearica pavonina* West African Crowned Crane	10	10	(R) Africa between 0° and 15° N latitude
15. *Balearica regulorum* Gray Crowned Crane	10	10	(R) Africa south of the equator

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[a] Distributions taken from Walkinshaw (1973).

[b] Species names from Peters (1934) and Walkinshaw (1964); common names from Walkinshaw (1973).

[c] Includes 2 partial skeletons.

For all data matrices, characters were standardized to a mean of 0 and standard deviation of 1. A matrix of correlations among characters was computed and from it principal components were extracted. The crane species were projected onto the first 3 components and plotted using the computer package GRAFPAC developed by F. J. Rohlf. The shortest minimally connecting network was superimposed on each of the 3-dimensional models to indicate distortion. Character loadings were computed for each of the components to identify the sources of variation; loadings of the first 3 principal components for each analysis are contained in appendices to Wood (1976). The correlation between (1) a matrix of euclidean distances between species in the 3-d model and (2) the corresponding distance matrix (described below) was calculated to give a matrix correlation coefficient. This coefficient gives an indication of how well the 3-d model represents the distance matrix.

Product-moment correlation and average distance coefficients were computed for all pairs of species. Cluster analyses using the unweighted pair-group method with arithmetic averages (UPGMA) were performed on all correlation and distance matrices (basic similarity matrices, abbreviated BSMs) and the results summarized in phenograms. Matrix correlation coefficients were calculated to indicate the degree of concordance between similarity values in a phenogram and its BSM.

To compare the results of this study with the work of other authors, similarity matrices were constructed from the classifications of Peters (1934) and Archibald (1975, pers. comm.). For details of this procedure see Schnell (1970a). These were combined with the BSMs and correlations between all pairs of matrices were computed. The similarity matrix produced was subjected to clustering using UPGMA and the results summarized in a phenogram. The classifications of Peters and Archibald were compared to my phenograms in a similar manner.

The following abbreviations are used. Specific BSMs are named by hyphenating CORR or DIST (depending on the type of similarity coefficient used) to the appropriate data matrix (e.g. CORR-EXT/LENGTHS). Phenograms derived from specific BSMs bear the name of the BSM. The classifications of Peters (1934) and Archibald (1975, pers. comm.) are denoted by PETERS and ARCHIBALD, respectively.

RESULTS

Three-dimensional models.—The ordination of the crane species with respect to the first 3 principal components derived from EXT/LENGTHS is shown in Fig. 2. Components I, II and III explain 28.6, 17.2 and 11.2% of the character variance for a total of 56.9. In spite of the low percentage, the model is an excellent representation of the BSM DIST-EXT/LENGTHS; the matrix correlation being 0.97. Other 3-d models also show a high matrix correlation regardless of how much character variance is explained by the principal components. The *Balearica* species (14, 15) are separated by principal component I (PC-I) which has high (absolute value >0.8) negative loadings on a complex of wing (EXT 32, 36, 38, 40, 42), tarsus (EXT 53) and feathering (EXT 66, 70) characters and high positive loadings on 2 tail (EXT 48, 49) and 4 two-state (EXT 81, 85, 89, 93) characters. Crowned cranes have narrower outer vanes on the primaries, shorter tarsi, longer tails

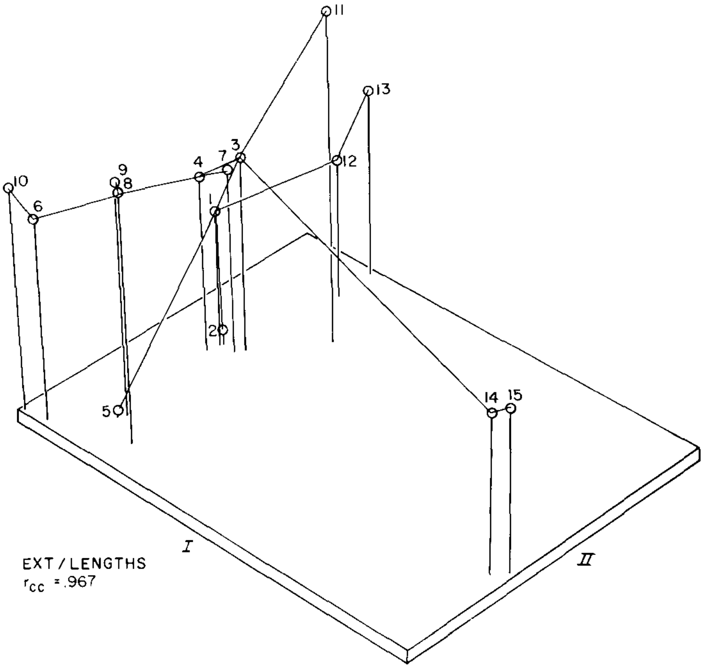

FIG. 2. Projection of the crane species onto the first 3 principal components based on a matrix of correlations among external characters divided by the sum of wing and leg lengths (see text). I and II are indicated and the height represents component III. The shortest minimally connecting network is superimposed on the character space. Species names corresponding to the numbers can be found in Table 1.

and less feathering on the gular and auricular areas than other cranes (all measurements except feathering are relative to the size factor and are ratios). The 2-state characters indicate the presence of special features such as the crest and the oval nostrils.

The remaining cranes are spread along a continuum by PC-II which has high positive loadings (0.7) on characters dealing with lengths of secondaries (EXT 43, 45, 47), color of the outer secondaries (EXT 19) and the width of the mandibular ridge (EXT 29). *Grus americana* (6) and *G. leucogeranus* (10) are whiter than other cranes and larger (relative to the size factor) for the dimensional measurements listed. *Anthropoides* spp. (12, 13) are smaller relative to the size factor and darker than other cranes. PC-III has high positive loadings on the colors of 3 neck regions (EXT 7, 13, 17) and a high negative loading on EXT 80 (a feather contrast). *Bugeranus* (11), *G. japonensis* (5) and *G. nigricollis* (2) are separated from all other cranes

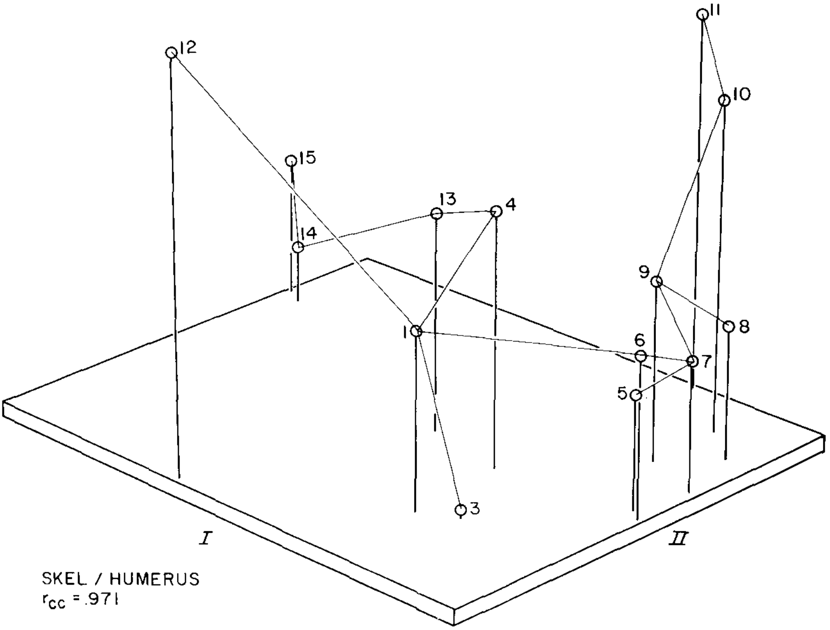

FIG. 3. Projection of the crane species onto the first 3 principal components based on a matrix of correlations among skeletal characters divided by humerus length. Principal components I and II are indicated and the height represents III. The shortest minimally connecting network is superimposed on the character space. Species names corresponding to the numbers can be found in Table 1.

by this component. *Bugeranus* (11) has very light colors for these neck regions and no contrast in the secondary coverts whereas the 2 *Grus* (2, 5) have the opposite condition. The other species are intermediate or exhibit a mixture of these characteristics.

Fig. 3 depicts the 3-d model of SKEL/HUMERUS. *Anthropoides virgo* (12) is separated from the others and among the other species 3 relatively tight groups are present: (A) *G. japonensis*, *G. americana*, *G. vipio*, *G. antigone* and *G. rubicunda* (5–9); (B) *G. leucogeranus* and *Bugeranus* (10, 11); and (C) *Balearica* (14, 15). In the center is a loose aggregation of the remaining *Grus* (*G. grus*, *G. monacha*, *G. canadensis* [1, 3, 4]) and *Anthropoides paradisea* (13). The matrix correlation coefficient is 0.97 and the components explain 37.8, 17.8, and 13.6% of the variance, respectively (total 69.2). PC-I has high positive loadings on several bill and furcular characters (SKEL 1, 2, 11, 12, 13, 19, 20), posterior synsacrum length (SKEL 27) and sternal head width (SKEL 51) and high negative loadings on skull width

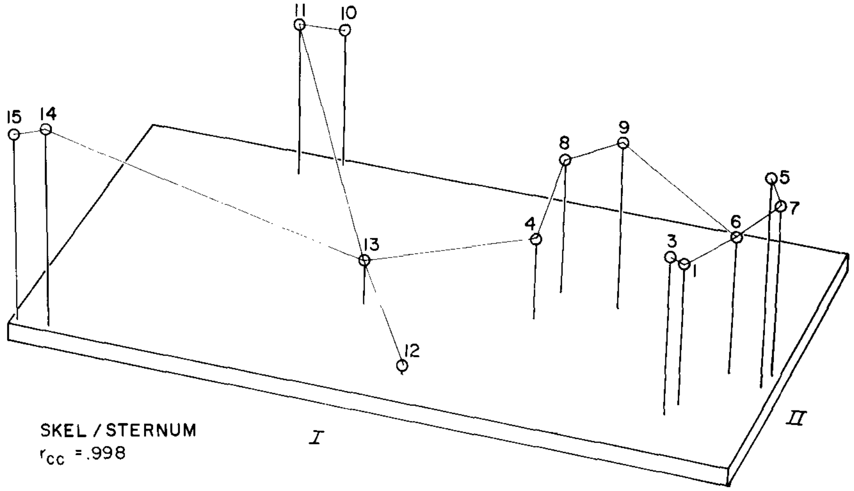

FIG. 4. Projection of the crane species onto the first 3 principal components based on a matrix of correlations among skeletal characters divided by sternum length. Principal components I and II are indicated and the height represents III. The shortest minimally connecting network is superimposed on the character space. Species names corresponding to the numbers can be found in Table 1.

(SKEL 8) and carpometacarpus depth (SKEL 45). The *Balearica* (14, 15) have, relative to humerus length, shorter bills, furculae and synsacra and narrower sternal heads but wider skulls and carpometacarpi than other cranes. PC-II is a contrast of carpometacarpus and phalanx lengths (SKEL 47, 49) and tibiotarsus length (SKEL 36). Relative to humerus length, *A. virgo* (12) has longer hand bones, a shorter tibiotarsus and deeper mandibles than other cranes. Species at the back of the diagram (e.g. *G. leucogeranus* [10] and *Bugeranus* [11]) have the opposite condition. PC-III separated *G. leucogeranus* (10) and *Bugeranus* (11) from the other species as well as further isolating *A. virgo* (12). These species have (relative to humerus length) narrower leg bones than other cranes. This is shown by high negative loadings on characters SKEL 32, 35, and 39.

As in SKEL/HUMERUS, *Balearica* (14, 15) and *G. leucogeranus* and *Bugeranus* (10, 11) form distinct clusters in the 3-d model of SKEL/STERNUM (Fig. 4). *Anthropoides* spp. (12, 13) are found in the center of the model and remaining *Grus* spp. (1–9) are in a loose group (with 2 parts) on the right. The first 3 components explain more than 90% of the variation (71.6, 16.2, 4.7%) and the matrix correlation is 0.998. PC-I has high negative loadings on all but 14 characters and PC-II has high negative loadings on 7 of these 14 (SKEL 1, 2, 4, 11, 12, 13, 20: all from the bill and furcula).

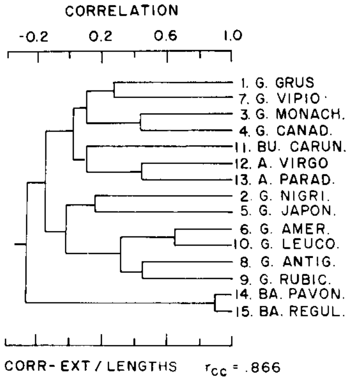

FIG. 5. Correlation phenogram of cranes based on external characters divided by the sum of wing and leg lengths (see text).

Thus, relative to sternum length, the *Balearica* species (14, 15) as well as *Bugeranus* (11) and *G. leucogeranus* (10) are larger than other cranes in all dimensions except bill length, furcula length and keel depth (PC-I). *Bugeranus* (11) and *G. leucogeranus* (10) also have (relative to sternum length) the longest bills and furculae of the cranes whereas *Balearica* (14, 15) have the shortest (PC-II). PC-III has a high negative loading on keel depth (SKEL 23). This means that *Anthropoides* (12, 13) have shallow keels relative to sternum length. PC-I also has high loadings (positive) on SKEL 51–55 (tracheo-sternal characters). Thus, PC-I is a contrast between the sternal invagination by the trachea and most of the rest of the skeleton; the *Balearica* (14, 15) and *Bugeranus* (10, 11) groups show little or no tracheal invagination.

Phenograms.—In the CORR-EXT/LENGTHS phenogram (Fig. 5) there are 3 major clusters: (A) *Balearica*; (B) *Bugeranus*, *Anthropoides*, and 4 *Grus* species (*G. grus*, *G. monacha*, *G. vipio* and *G. canadensis*); and (C) the remaining species of *Grus*. The *Grus* species form species pairs and are separate from *Bugeranus* and *Anthropoides* in group B. The matrix correlation of 0.87 indicates a relatively good fit of the phenogram to its BSM.

Except for 3 species, the clusters using distances (DIST-EXT/LENGTHS; see Fig. 6b in Wood [1976]) are the same as in CORR-EXT/LENGTHS. *G. japonensis* and *Bugeranus* are each quite distant from all other species (shown by component III of Fig. 2) and *G. nigricollis* clusters with *G. grus*, *G. vipio*, *G. monacha* and *G. canadensis*. The matrix correlation of 0.92 indicates a good fit of the BSM.

The 2 phenograms derived from EXT-WO/COLOR (only the distance phenogram is shown; Fig. 6; see Fig. 7a in Wood [1976] for the correlation

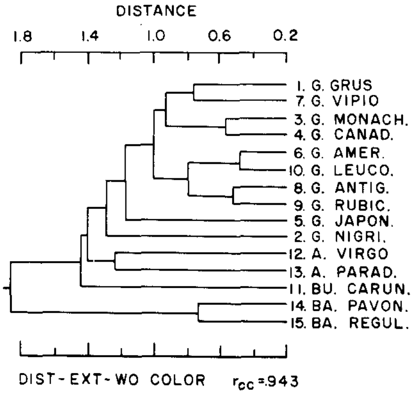

FIG. 6. Distance phenogram of cranes based on external dimensional characters (EXT 28–58) and 2-state characters (EXT 75–95) (dimensional characters divided by the sum of wing and leg lengths).

phenogram) differ from those of EXT/LENGTHS mainly in the placement of the *Anthropoides* species and *Bugeranus*: these species are not associated with any *Grus* species in both CORR- and DIST-EXT-WO/COLOR. As in EXT/LENGTHS, *G. nigricollis* and *G. japonensis* do not cluster consistently with other species: otherwise the *Grus* species show the same split in both analyses. The matrix correlation of 0.94 for DIST-EXT-WO/COLOR is the highest recorded in this study. CORR-EXT-WO/COLOR has a matrix correlation of 0.84 indicating a moderately good fit of the BSM.

CORR-SKEL/HUMERUS (Fig. 7a) is quite different from the external analyses. Two major groups are apparent: (A) *Balearica*, *Anthropoides*, *G. grus*, *G. monacha* and *G. canadensis*; and (B) *Bugeranus* plus the remaining *Grus*. Group A is split into 2 subgroups with *Anthropoides paradisea* and *Balearica* being separated from *Grus* and *A. virgo*. Group B shows a less distinct split and most species are arranged in pairs. Certain species associations are similar to ones found in the external analyses: (1) *G. grus*, *G. monacha*, *G. canadensis*; (2) *Balearica;* and (3) *G. antigone*, *G. rubicunda.* The matrix correlation of 0.77 indicates that the phenogram represents its BSM less well than do others in this study.

DIST-SKEL/HUMERUS (Fig. 7b) is different from both CORR-SKEL/HUMERUS and from the external analyses. *Anthropoides* is split, as in CORR-SKEL/HUMERUS, but *A. paradisea* clusters with *G. grus* and *G. canadensis* while *A. virgo* is relatively distant from all other species. *G. leucogeranus* and *Bugeranus* cluster as in CORR-SKEL/HUMERUS but the arrangement of the other *Grus* species is different from that analysis. The

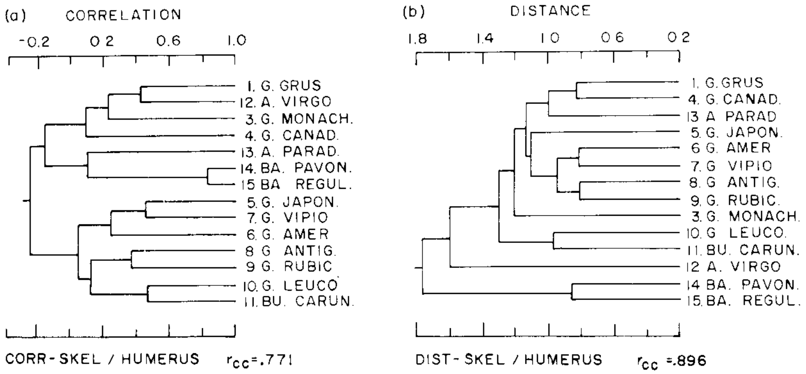

FIG. 7. Correlation (a) and distance (b) phenograms of cranes based on skeletal characters divided by humerus length.

only similarities to the external analyses are the association of *G. americana*, *G. antigone* and *G. rubicunda* and the separation of *Balearica* from other species. The matrix correlation of 0.90 indicates a good fit to the BSM.

With the exception of *G. leucogeranus*, the major groups of CORR-SKEL/STERNUM (Fig. 8) correspond to the genera recognized by Peters (1934, Fig. 1a). *G. leucogeranus* is very close to *Bugeranus* as in SKEL/HUMERUS. The high matrix correlation of 0.92 indicates a good fit of the BSM.

Like CORR-SKEL/STERNUM, the major clusters of DIST-SKEL/STERNUM (see Fig. 9b of Wood [1976]) correspond closely to the groupings of Peters (1934). *G. leucogeranus* is the only exception, clustering (as in all

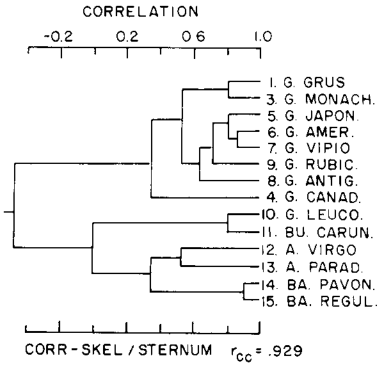

FIG. 8. Correlation phenogram of cranes based on skeletal characters divided by sternum length.

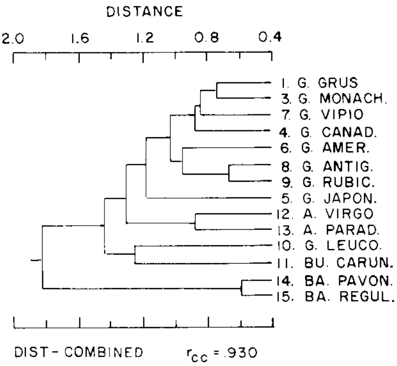

FIG. 9. Distance phenogram of cranes based on external characters divided by the sum of wing and leg lengths and skeletal characters divided by sternum length.

skeletal analyses) with *Bugeranus*. Within *Grus* the species associations are the same as CORR-SKEL/STERNUM except that *G. antigone* and *G. rubicunda* cluster with *G. canadensis*. *Anthropoides* is on the average closer to the *Grus* cluster than to the other species. The matrix correlation of 0.87 indicates a good fit of the BSM.

Two major groups are present in CORR-COMBINED (see Fig. 10a of Wood [1976]): (A) *Anthropoides*, *Balearica* and *Bugeranus*; and (B) *Grus*. Within the first group, *Anthropoides* is separated from *Bugeranus* and *Balearica* and within the second, *G. antigone*, *G. rubicunda* and *G. leucogeranus* are separated from the remaining *Grus*. The arrangement of the *Grus* species is most similar to the external analyses except that *G. americana* clusters with *G. grus* and *G. monacha* in CORR-COMBINED rather than with *G. antigone* and *G. rubicunda*. The matrix correlation of 0.83 is low for this study but still indicates a good fit.

With the exception of *G. leucogeranus*, the clusters in DIST-COMBINED (Fig. 9) correspond to Peters' (1934) genera. This species is most similar to *Bugeranus* (as in the skeletal analyses). *Anthropoides* is closer to *Grus* than to *Bugeranus* and *Balearica* is distant from all other species. The matrix correlation is 0.93.

DISCUSSION

Stability of clusters.—The most stable cluster throughout the analyses is that of the *Balearica* species. In every analysis these 2 species are more similar to each other than either is to another species. *Balearica* is divergent from all other species in 6 of 10 analyses. In the 4 remaining analyses it is always more similar to *Anthropoides* or *Bugeranus* than to *Grus.*

The *Anthropoides* species cluster together in all but SKEL/HUMERUS. This appears to be due to the choice of humerus length as a divisor. Apparently the humerus of *A. virgo* (relative to other bones) has evolved in a manner slightly different from the humeri of other cranes. *Anthropoides* is more often closer to *Grus* species (5 of 8 analyses) than to either *Bugeranus* or *Balearica.*

Grus (excluding *G. leucogeranus*) exists as a major group in all of the analyses except CORR-EXT/LENGTHS, DIST-EXT/LENGTHS and CORR-SKEL/HUMERUS. Within the *Grus* group(s), species are often loosely connected with several species demonstrating no consistent associations. However, several clusters appear relatively constant. *G. antigone* and *G. rubicunda* represent the most stable *Grus* pair appearing in the same cluster in all analyses and as a species pair in all but one (CORR-SKEL/STERNUM). That these 2 species are very similar is further evidenced by their successful hybridization in a recently developed area of sympatry in Australia (J. G. Blackman: quoted by G. W. Archibald, pers. comm.).

Except for SKEL/HUMERUS, *G. grus*, *G. monacha,* and *G. vipio* cluster in the same major group and are often closely associated. Like the *G. antigone-G. rubicunda* pair, these 3 species are sympatric over parts of their ranges and at least 2 (*G. grus* and *G. monacha*) are known to hybridize in the wild (Walkinshaw 1973).

The remaining *Grus* species cluster much less consistently with other species of the genus: *G. nigricollis* is represented only in the external analyses but does not cluster consistently; *G. canadensis* clusters with *G. monacha* in the external analyses but is not consistent elsewhere; *G. americana* clusters with *G. leucogeranus* in the external analyses but is more similar to *G. vipio* in the others; finally, *G. japonensis* forms its own group in more than half of the analyses.

Grus leucogeranus is very similar to *G. americana* in the external analyses but clusters with *Bugeranus* in the skeletal analyses and in DIST-COMBINED. This is a contrast to the phenetic relationships among the other gruid species, for which the external and skeletal analyses produce similar results.

Relationships among classifications.—To give a more detailed analysis of the relationships among similarity matrices and among phenograms, comparisons were made among all pairs of BSMs as well as all pairs of phenograms. Table 2 gives coefficients of correlation for all pairs of BSMs (lower left) and coefficients of cophenetic values for pairs of phenograms (upper right). Fig. 10 summarizes these relationships in the form of dendrograms.

The matrix correlation coefficient of the dendrogram of BSMs is only 0.68,

TABLE 2

COEFFICIENTS OF CORRELATION FOR PAIRS OF BSMs (LOWER LEFT) AND COEFFICIENTS OF COPHENETIC VALUES FOR PAIRS OF PHENOGRAMS (UPPER RIGHT)[a]

	1	2	3	4	5	6	7	8	9	10	11	12
1. ARCHIBALD		.852	.614	.818	.446	.705	.623	.899	.723	.828	.293	.812
2. PETERS	.852		.788	.943	.640	.820	.666	.883	.570	.671	.387	.831
3. CORR-EXT-WO/COLOR	.509	.691		.833	.922	.830	.685	.710	.446	.468	.473	.603
4. DIST-EXT-WO/COLOR	.783	.894	.787		.688	.878	.605	.870	.500	.618	.348	.816
5. CORR-EXT/LENGTHS	.440	.629	.885	.670		.823	.569	.614	.276	.336	.482	.486
6. DIST-EXT/LENGTHS	.744	.844	.760	.903	.722		.521	.877	.338	.575	.382	.730
7. CORR-COMBINED	.655	.658	.766	.632	.776	.683		.606	.712	.615	.392	.448
8. DIST-COMBINED	.850	.832	.659	.821	.640	.891	.815		.626	.847	.332	.836
9. CORR-SKEL/STERNUM	.748	.634	.462	.516	.442	.505	.817	.756		.766	.354	.542
10. DIST-SKEL/STERNUM	.817	.686	.443	.609	.398	.630	.787	.910	.858		.282	.673
11. CORR-SKEL/HUMERUS	.559	.575	.527	.491	.520	.501	.749	.635	.732	.653		.366
12. DIST-SKEL/HUMERUS	.769	.794	.557	.709	.506	.700	.665	.798	.696	.750	.746	

[a] The absolute value of the coefficients are used since similarity for a distance BSM or phenogram is opposite that for a correlation type.

an indication that considerable distortion exists among the main branches of the dendrogram. All distance BSMs cluster together with PETERS and ARCHIBALD but the correlation BSMs are contained in 3 distinct clusters. In contrast to what has generally been found by other workers (e.g., Schnell 1970b, Robins and Schnell 1971, Hellack 1976, Hellack and Schnell 1977)

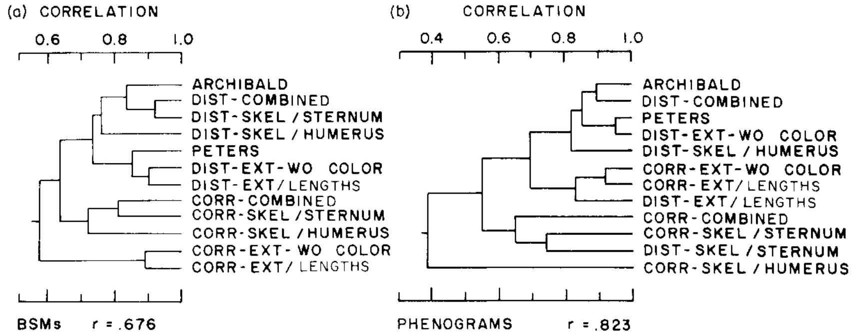

FIG. 10. Dendrograms of cranes showing relationships among basic similarity matrices (BSMs) (a) and phenograms (b). The classifications of Peters (1934) and Archibald (1975, pers. comm.) are included in both dendrograms.

distances give the most uniform results. The average correlation between distance matrices is 0.77 whereas the average between correlation matrices is only 0.67 (see Table 2). Within both the correlation and distance clusters external analyses are grouped together. Skeletal and combined analyses are likewise grouped. There is greater similarity within either the external analyses (mean correlation 0.79) or the group of skeletal and combined analyses (mean correlation 0.76) than between these groups (mean correlation 0.60).

The previous classifications used in this study (PETERS, ARCHIBALD) are each more similar to 1 or more of the BSMs than to each other. This does not reflect a lack of similarity between PETERS and ARCHIBALD but rather demonstrates the close similarities between previous classifications and results of this study. ARCHIBALD is more similar to the skeletal analyses whereas PETERS is more similar to the external analyses. Archibald (1975) based his classification on the unison calls of cranes which directly reflect a portion of the skeletal features (tracheo-sternal), but not the external characters. Peters (1934) apparently relied more heavily on external morphology in constructing his classification.

The relationships among phenograms appear somewhat changed from those among BSMs. The general dichotomy between distance and correlation analyses is apparent but CORR-EXT/LENGTHS, CORR-EXT-WO/COLOR and DIST-SKEL/STERNUM have switched clusters. However, DIST-SKEL/STERNUM and DIST-EXT/LENGTHS are most similar to other distance phenograms (see Table 2). The phenogram of CORR-SKEL/HUMERUS is very divergent from all others and also is a relatively poor representation of its BSM (matrix correlation of 0.77, the lowest of any phenogram).

The relationships discussed for BSMs exist also for the phenograms, although less well defined (i.e. greater similarity exists within either the external group or skeletal plus combined group of phenograms than between these groups; correlations average higher within the skeletal plus combined group than within the correlation group). As found for the BSMs, PETERS and ARCHIBALD are most similar to the distance analyses. PETERS is highly correlated (0.94) to DIST-EXT/LENGTHS and ARCHIBALD is correlated to DIST-COMBINED.

Schnell (1970b) found that phenograms were more similar to previous classifications than were the BSMs. He concluded that species were placed (forced) into hierarchical clusters both in previous classifications as well as phenograms. Robins and Schnell (1971), Hellack (1976) and Hellack and Schnell (1977), however, obtained results at variance with these findings. In the present study, 6 of 10 phenograms are more similar to the previous classifications than are their BSMs (not the same 6 for each classification).

However, in only 4 of the 20 comparisons (20%) are the differences in correlation (correlation of phenogram to classification vs. BSM to classification) greater than 0.051. Data from both Schnell (1970b) and Robins and Schnell (1971) show a much higher percentage of differences greater than 0.055 (54% and 71%, respectively) even though the matrix correlation coefficients of the phenograms to their BSMs are similar to those in the present study. This is further evidence that cranes do fall into relatively well defined clusters and are not "forced" into them by the clustering procedure.

Final considerations.—Close similarity exists between PETERS (the classification of the Gruidae currently accepted by most researchers) and DIST-COMBINED (a good representative phenogram of this study). *Grus leucogeranus* is the only species placed in different major clusters in the 2 classifications. As discussed previously, this species shows phenetic affinities to both *G. americana* (external) and *Bugeranus* (skeletal). Clearly 1 set of similarities is convergent since no evidence exists to link *Bugeranus* with *G. americana* (either phenetically or from other taxonomic studies). Further investigation is needed to evaluate the cladistic relationships of these 3 species.

SUMMARY

Techniques from multivariate statistics were employed to evaluate the phenetic (morphologic) similarities among the cranes (Gruidae). Both external and skeletal characters were analyzed using different data sets constructed by transforming and partitioning the data. The analyses included both principal component analysis and cluster analyses using distance or correlation coefficients. The results were summarized in 3-dimensional diagrams and phenograms. Phenograms as well as similarity matrices were compared and contrasted among themselves and with classifications of other authors. Phenetically the cranes form quite distinct groups; these are similar to the groups found in the classification currently in general use (Peters 1934) with the exception of *Grus leucogeranus.* This species is very similar to *Bugeranus carunculatus,* particularly with regard to skeletal characteristics and the two may in the future be considered congeneric.

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