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HELLACK, Jenna Jo, 1945-
    A PHENETIC ANALYSIS OF THE SUBFAMILY
    CARDINALINAE (AVES).
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    Zoology
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## THE UNIVERSITY OF OKLAHOMA GRADUATE COLLEGE

## A PHENETIC ANALYSIS OF THE SUBFAMILY CARDINALINAE (AVES)

A DISSERTATION

SUBMITTED TO THE GRADUATE FACUITY
in partial fulfillment of the requirements for the degree of DOCTOR OF PHILOSOPHY

BY

JENNA J. HELLACK

Norman, Oklahoma
1975

# A PHENETIC ANALYSIS OF THE SUBFAMILY CARDINALINAE (AVES) 



# A PHENETIC ANALYSIS OF THE SUBFAMILY <br> CARDINALINAE (AVES) 

by: Jenna Jo Hellack
Major professor: Gary D. Schnell
?ultivariate statistical techniques were used to evaluate 169 steletal, external slan and color characters, and determine phenetic affirities among 37 species in the subfamily Cardinalinae. Phenctic similarity was assessed usins distances and product moment correlations as similarity coefficients ard URGin (unweirhted pair-group method using arithmetic averaces) for clustering. Finenetic relationships are presented in Ehenorrans ani 3-D models of species projected onto principal components baseci on a matrix of correlations amons characters.

The 37 resulting thenosrams are conpared among themselves and with tio formar classifications, Basic similarity matrices were grouped and within each group, the whenoran wich best represented its basic similarity natrix has ciosen to represent the group. A "best" phenetic classification was chosen using previously determined guides.

The chenoran chosen in this manner used all characters available. This resulted in seven species not being included in the analysis. As these species should be included in a "best" phenetic classjfication, a Ehenogran was constructed using the phenogram chosen as the best representetive of this study for the placement of all species it analyzed, and Elacirg the seven remainine species into the clusters they would probabl; ioin if the $\quad$ had been included in the analysis. This was accomplished by studuing the phenograms and 3-D models in which the seven species had been incluried.

This Genogram was then used to look at similarities and compare these similarities :ith two former classifications. Based on phenetic crounines, several saltators ( $\mathcal{S}$. rufivertris, S. albicollis, S. cinctus, S. atoicollis, S. 2wantirostris, and 2 . orenocensis wore found to have İtile similarity to the remaining saltators. In the case of $\underline{S}$. Mrivertris, $\underline{\underline{3}}$. 1 Dicollis and $\underline{E}$. cinctus, insufficient data may be the reason $=0$ their lacis of similerity to the saltator cluster. However, 3. Etricoliis, S. onenocensis and S. aurantiirostris are clearly distinct.

The genus Fhevticis clusters much as one would expect from one former classification. The species placed in the genus Passerina could be grouped accordircs to either former classification. The results of this study are presented in tro papers prepared in the style of the wilson Bulltin

## ACKNOWLHEDGNENTS

I am greatly indebted to the members of my committee: Drs. Harley P. Brown, Charles C. Carpenter, James R. Estes, and Gary D. Schnell. Dr. Hubert H. Frings, an original committee member, also aided in planning my work. I am very grateful to Robert G. Richardson who spent valuable time reviewing my manuscript. I also wish to thank curators of a number of collections who allowed me to use material in their care (they are listed in the acknowledgments of the first paper).

Several other people gave valuable assistance to me in preparation and completion of this study. Elizabeth A. Bergey assisted with the measurement of specimens. Troy L. Best and Dick T. Stalling were a great help with the original planning of the study. Ginna Davidson and Sharon Swift aided in the preparation of figures. I also wish to thank my parents Mr. and Mrs. Joe Hellack and my grandmother Mrs. R. E. Rirtherford, without whose encouragement and assistance this study would not have been possible. This study was supported in part by a travel grant from the Smithsonian Institution and a Sigma Xi Grant-in Aid.

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APPENDICES

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A PHENETIC ANALYSIS OF THE SUBFAMILY CARDINALINAE (AVES)

## INTRODUCTION

The subfamily Cardinalinae is a group of finches including cardinals, saltators and certain grosbeaks. The subfamily at present is placed in the family Fringillidae. However, a number of authors have proposed sharply differing arrangements for the genera traditionally included in the family Fringillidae (Beecher, 1953; Tordoff, 1954; Stallcup, 1954). The Cardinalinae are closely allied to Thraupidae as well as the fringillid subfamily Emberizinae (de Schauensee, 1966).

There is disagreement on the generic grouping of the species traditionally included in the subfamily Cardinalinae as well as family allocations. The 37 species placed in this subfamily by Paynter (1970) are divided into nine genera. Hellmayr (1938) divides these 37 species into 15 genera. My objectives are to look at interspecific relationships of 37 species in the subfamily Cardinalinae utilizing numerical taxonomic techniques to determine phenetic affinities.

The resuits and conclusions of this study are presented in two papers prepared in the style of the Wilson Bulletin. The first is a study
of phenetic affinities of the subfamily Cardinalinae using skeletal characters; external morphological characters are analyzed in the second paper.

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## PAPER I

A PHENETIC ANALYSIS OF THE AVIAN SUBFAMILY CARDINALINAE, BASED UPON SKELETAL CHARACTERS

# A PHENETIC ANALYSIS OF THE AVIAN SUBFAMILY 

CARDINALINAE, BASED UPON SKELETAL GHARACTERS

Jenna J. Hellack

The subfamily Cardinalinae (Fringillidae) is closely allied to Thraupidae (Beecher, 1953; Tordoff, 1954; de Schauensee, 1966). Considerable disagreement exists on which species should be included in the subfamily. In the most recent revision Paynter (1970) included 9 genera and 37 species. Hellmayr's (1938) subfamily included these species (divided into 15 genera) plus 9 others in Gubernatrix, Paroaria, and Tiaris. Tordoff (1954) on the basis of the structure of the palatomaxillaries placed the latter three genera plus Porphyrospiza (Passerina caerulescens of Paynter, 1970) in the subfamily Emberizinae (Fringillidae). Spiza americana, although included in Cardinalinae by both Hellmayr (1938) and Paynter (1970), is of uncertain affinity. Tordoff (1954) and Stallcup (1954) consider it an aberrant cardinal-grosbeak, but Beecher (1953) believed it was an icterid.

While the relationships of the aberrant species have been the subject of considerable debate, few taxonomic studies have been conducted on the affinities of species traditionally included in the subfamily (Ridgway,

1901; Hellmayr, 1938; and Paynter, 1970), these studies include congeneric considerations of such species as the Cardinal (Cardinalis cardinalis) and the Pyrrhuloxia (́. sinuatus) (Bock, 1964), and hybridization in grosbeaks, Pheuticus melanocephalus and $\underline{P}$. Iudovicianus (West, 1962) and buntings, Passerina cyanea and P. amoena (Sibley and Short, 1959).

This study is a numerical analysis utilizing skeletal measurements to assess phenetic affinities of the species in the subfamily Cardinalinae. Results obtained using restricted character sets will be compared. Several methods to reduce the effect of size in this study were tried and these will also be compared.

## MATERTALS AND METHODS

The generic and specific designations used in this study are the same as those used by Paynter (1970). Table 1 lists these 37 species, a brief description of their geographic distribution, the species number assigned to each, and the number of skeletons measured of each. Skeletal measurements were obtained for 31 of the 37 species; thus my analyses excludes Caryothraustes humeralis, Periporphyrus erythromelas, Saltator maxillosus, S. cinctus, S. rufiventris, and Passerina caerulescens. The skeletal characters were the same as those examined by Robins and Schneil (1971), in their analysis of the Ammodramus-Ammospiza grassland sparrow complex, with the addition of the length of the caudal vertebrae (taken from synsacrum to back of pygostyle). These 49 characters were measured on adult specimens to the nearest 0.1 mm with dial calipers. A mean for each species was obtained from the skeletal material available without regard to sex. Original mean character measurements for each species may be found in Appendix IV of Hellack (1975).

Phenetic similarity was assessed using multivariate statistical techniques from the Numerical Taxomony system of computer prograns (NT-SYS) developed by F. J. Rohlf, J. Kishpauph, and D. Kirk. Two types of techniques were used: R-type involving the analysis of correlations among characters; and Q-type an analysis of correlations or distances between pairs of species.

Characters were standardized in the Q-type of analysis so that each would have a mean of zero and a standard deviation of one. Thus character state codes are independent of orginal measurement units and are expressed in standard deviation units. Product moment correlation coefficients and average distance coefficients were calculated for all pairs of species. Cluster analyses, utilizing the unweighted pair-group method using arithmetic averages (UPGMA), were performed on both correlation and distance matrices, and the results summarized in phenograms. The R-type analysis extracts principal components from a matrix of correlation among characters (Sneath and Sokal, 1973).

To eliminate or reduce the size factor, several analyses were undertaken. All measurements (before standardization) were divided by either sternum length, humerus length, or tibiotarsus length. In addition an R-type analysis was performed on unstandardized characters and then the projections on the first principal component (which was considered to be a general size factor) used as the divisors of their respective species characters. Still another method was tried. This involved the removal of the influence of the first component mathematically from a matrix of distance between species (Sneath and Sokal, 1973).

I produced 27 phenetic classifications using various combinations of the two similarity coefficients (correlation and distance) and the six
transformations (humerus, sternum, tibiotarsus, principal component I, first component removed mathematically, and untransformed). In 11 of these, 49 characters were used; 8 classifications were produced using 14 skuli characters; and 8 produced using 14 pelvic characters.

Matrices were produced from the classifications of Paynter (1970) and Hellmayr (1938) by assigning arbitrary numerical values to different taxonomic ranks (see Schnell, 1970; Robins and Schnell, 1971, and Johnson and Selander, 1971). These two matrices plus 27 matrices (produced from the various combinations mentioned above) were compared by computing the coefficient of correlation between the basic similarity matrices. The correlations were then used to produce a matrix showing the similarities between these matrices. Similarities were summarized in a dendrogram. This sumnary indicates which matrices are most alike. The 27 phenograms were compared in a similar manner.

The following abbreviations will be used throughout the paper. CORR or DIST refer to the use of correlation or distance to analyze similarity between species. SKFL-SIZE-IN denotes the use of skeletal characters in which no adjustment for size was made. SIZE-OUT refers to the mathematical elimination of size. SKBL/COMP-I indicates characters divided by unstandardized principal component I; SKEL/HUNER characters divided by the humerus length; SKEL/STERN characters divided by the sternum length; and SKEL/TIBIO characters divided by the tibiotarsus length. ALL denotes inclusion of all characters in the analysis, PELVIC the use of only the 14 characters of the pelvic girdle and lower limbs, and SKULL the use of 14 characters of the skull. BSM is used as the abbreviation for basic similarity matrix.

When branches occur in phenograms, the placement of the two branches is arbitrary. Branches may be rotated about their axis without changing relationships implied by the phenograms.

RESULTS
The dendrogram summary of the similarities between the 27 BSMs is shown in Figure 2A. Ten groups of BSMs are labeled. Within each of six groups ( $C, D, E, G, J$, and $K$ ) the BSMs are based on the same character groups and similarity coefficients. For example, group C encompasses four BSMs where correlation coefficients were computed and all characters used. However, a different transformation was used for each of the four BSMs (i.e., one where the characters were divided by sternum length, the second where they were divided by the tibiotarsus length, etc.). Groups $H$ and $I$, in contrast, include BSMs based on the same transformations and similarity coefficients, but differ in character groups. The BSMs in which no transformations were used are found in groups A and B. SIZE OUT (group L) is the BSM in which size was eliminated mathematically from a distance matrix. SKEL/TIBIO SKULL DIST (group F) connects to group E which is composed of BSMs having the same character groups and similarity coefficients as itself.

The dendrogram of similarity between phenograms is shown in Figure 2 b . In comparing the dendrogram of similarities between BSMs with that of the phenograms, several changes in groupings can be seen. Clustering enhanced differences between many of the BSMs. Phenograms with lower cophenetic correlation coefficients were more likely to group differently from their BSMs. When both the similarity of BSM to other members of its group and the cophenetic correlation coefficients were low, major group changes are
seen. For example, in group $C$ of the BSMs, SKEL/STERN ALL CORR has a cophenetic correlation coefficient of 0.721 and is the most divergent of the four BSMs in this group. In the dendrogram of the phenograms (Fig. $2 B$ ), it shows little similarity to the other phenograms.

There is considerable correlation within each group of BSMs (Fig. 2A). As an alternative to presenting each phenogram, I have depicted only one phenogram from each highly correlated group of BSMs--the phenogram with the highest cophenetic correlation coefficient. Any substantial difference in placement of species in phenograms within a particular group of BSMs will be described below.

The single BSM in group A (SIZE IN CORR) has little similarity to the remaining groups (Fig. 2A). The resulting phenogram (Fig. 3A) has five major clusters; the majority of species within these clusters have little similarity to each other. The low cophenetic correlation coefficient ( 0.674 ) shows that considerable distortion of the BSM occurred as a result of clustering.

The phenogram representing the one BSM in group B (SKEL SIZE IN DIST) is depicted in Figure 4A. There is little similarity between the four major clusters seen in this phenogram and those found in group A. Size appears to have had considerable effect on the formation of clusters in SKEL SIZE IN DIST. Cluster 3 (Fig. 4A) is composed of the two largest species; Cluster 4 contains the smallest forms.

Group C consists of four very similar BSMs based upon correlation analyses using all characters. All phenograms constructed from these BSMs have relatively low cophenetic correlation coefficients. The phenogram which was chosen to represent the group (SKEL/TIBIO ALL CORR, Fig. 3B) has
a cophenetic correlation coefficient of 0.792 . The two major clusters found in this phenogram are also found in the other phenograms of the group, but two of the species "switch" major clusters (cluster with a different group of species in different phenograms). Passerina caerulea is found with the grosbeaks (Pheuticus) in the other three phenograms. Cardinalis sinuatus switches clusters in one instance. Other than these two major cluster switches, considerable consistency is found between three of the four phenograms of the group (SKEL/STERN ALL CORR being the exception). The differences among the three similar phenograms are the switching of affinities by species which in Figure 3B show little similarity to the cluster their stem joins. Pitylus grossus is most similar to Rhodothraupis celaeno in the other phenograms.

The four BSMs in group D have the same character group (14 skull characters) and the same similarity coefficient (correlation). The phenogram which represents the group is SKEL/COMP I SKULL CORR (Fig. 3C; cophenetic correlation coefficient $=0.877$ ). As in the phenogram representative of group C (Fig. 3B), this phenogram has two major clusters. The species composition of these three clusters are also much the same. Three of the four phenograms representing the BSMs of group D are very similar. The fourth SKEL/TIBIO SKULL CORR, while having two major clusters, has several switches between these clusters. The branching within smaller clusters, however, is much the same. Five of the species represented in these four phenograms (Cardinalis sinuatus, Caryothraustes canadensis, Rhodothraupis celaeno, Saltator aurantiirostris, and S. atricollis) show different affinities in each phenogram. These five show little similarity to the clusters they join in any of the four phenograms. Spiza americana,
which clusters rather closely with the buntings (Passerina), in two of the phenograms (SKEL/COMP I CORR and SKEL/HUMER SKULL CORR), groups with the saltators in the other two.

The three BSMs in group E were produced by using 14 skull characters and distance as a measure of similarity. They differ in the type of transformation used. The correlation between these BSMs is not as high as that found in other groups of BSMs. The phenogram which represents this group (SKEL/COMP I SKULL DIST) is shown in Figure 4B. Its cophenetic correlation coefficient ( 0.835 ) is considerably higher than that of the other two phenograms of the group ( $0.774,0.742$ ). SKEL/COMP I SKULL DIST can be divided into two large branches, with a third branch composed of the single species Saltator orenocensis. Cluster 1 (Fig. 4B) is much the same in all three phenograms of this group, but Passerina brissonii clusters differently in the two phenograms not figured (SKEL/STERN SKULL DIST and SKEL/HUMER SKULL DIST). The second major branch in Figure 4B is not as easily seen in the other two phenograms. The small cluster bounded by Pitylus grossus and $\underline{S}$. atriceps is present in all three phenograms, but the species in the other small clusters of Cluster 2 are not the same in the phenograms not shown. Again, outlying species tena to show different affinities when clustering was undertaken on different BSMs. Cardinalis cardinalis, C. phoeniceus, C. sinuatus, Saltator orenocensis, Passerina cyanoides and as mentioned above $P$. brissonii, differ in their placement in all three phenograms.

The phenogram constructed from the one BSM in group $F$ is SKEL/TIBIO SKULL DIST (Fig. 4C). The character set ( 14 skull characters) and the similarity coefficient (distance) are the same as in group $D$, to which
the stem of the BSMs fuses. Comparing SKEL/TIBIO SKULL DIST (Fig. 4 C ) with SKEL/COMP I SKULL DIST (Fig. 4B), Clusters 1 plus 2 of SKEL/TIBIO SKULL DIST have the same species composition as Cluster 1 of SKEL/COMP I SKULL DIST with the addition of Saltator aurantiirostris and the loss of Passerina brissonii. Cluster 5 of SKEL/TIBIO SKULL DIST is also present in SKEL/COMP I SKULL DIST with Pitylus grossus being the only species missing.

Group $H$ is composed of two BSMs in which the same measure of similarity (distance) and the same transformation (dividing by tiblotarsus length) were used; however, the character sets were different (all characters, 14 pelvic characters). Both phenograms of this group (Fig. zB) have relatively low cophenetic correlation coefficients. The representative phenogram is SKEL/TIBIO PELVIC DIST (Fig. 4D.). The two major branches seen in Figure $4 D$ are also found in the other phenogram. The placement of four species in Figure 4D changes in the phenogram not figured: Saltator atricollis, S. coerulescens, and S. maximus are found in Cluster 1; Passerina amoena in contrast switches to Cluster 2. The small cluster bounded by Spiza americana and Passerina versicolor (Cluster 1, Fig. 4D) is present in both phenograms, but $\underline{P}$. brissonii and $P$. leclancerii are added to the cluster in the phenogram not figured. The cluster bounded by Fheuticus aureoventris and S. aurantiirostris has most of the same species in both phenograms.

Group I is composed of two BSMs with the same character set and similarity coefficient as in group $H$; the transformation (sternum length) is different. The phenogram with the highest cophenetic correlation coefficient is SKEL/STERN PELVIC DIST ( 0.815 , Fig. 5A). The major branches of this phenogram are not present in the other phenograms of the group; however, smaller clusters are comparable. The cluster (Fig. 5A) bounded
by Spiza americana and Passerina amoena is present in both phenograms. The cluster bounded by Pheuticus ludovicianus and Passerina rositae is found in both phenograms with three species (Caxdinalis cardinalis, Passerina cyanoides, and Passerina rositae) not being in the cluster in the phenogram not figured. The Cluster bounded by Cardinalis sinuatus and Passerina glaucocaerulea lost Cardinalis sinuatus and gained P. parellina and $P$. rositae. The cluster bounded by Pheuticus chrysopeplus and Passerina parellina in Figure 5A lost Pheuticus chrysopeplus, P. aureoventris, Passerina $^{\text {brissonii }} L_{2}$ and $\underline{P}$. parellina while it gained $\underline{P}$. cyanoides in the phenogram not figured.

The two BSMs of group J have the same character set (ALL) and the same similarity coefficient (distance), but differ in the transformation used (humerus length, component I), SKE: /rom I ALL DIST is the phenogram representing the group (Fig. 5B). It is highly correlated with SKEL/HUMER ALL DIST (Fig. 2A). Only three species (Cardinalis cardinalis, C. sinuatus, and Pheuticus ludovicianus) do not cluster the same in SKEL/HUNER ALL DIST as they do in Figure 5B. In SKEL/HUMER ALI DIST these three species show little similarity to the clusters they join.

Group K contains two BSMs with the same character set (14 pelvic characters) and the same similarity coefficient (distance). They differ in the transformation used (component I, humerus). The cophenetic correlation coefficients of both phenograms are about the same (SKEL/HUNER PELVIC DIST, 0.883; SKEL/COMP I PELVIC DIST, 0.882). SKEL/HOMER PELVIC DIST is shown in Figure 5C. While the two phenograms of this group are very similar, several species affinities change. In SKEL/COMP I PELVIC DIST, the cluster bounded by Pheuticus chrysopeplus and Rhodothraupis celaeno
contains Pheuticus ludovicianus and the cluster bounded by Cardinalis sinuatus and Passerina versicolor contains P. glaucocaerulea.

Group L contains one BSM (SIRE OUT) which shows similarities to the distance BSMs of group $J$ and $K$ (Fig. 2A). The phenogram has a cophenetic correlation coefficient of 0.831 (Fig. 5D). While clusters are present in the phenogram there are no major branches. More of a gxadual change in phenetic differences appears to occur.

## DISCUSSION

Relationships between BSMs, phenograms, and previous classifications
Several authors (Sokal and Michener, 1967; Schnell, 1970; Robins and Schnell, 1971) have found that correlations tend to give more uniform results than do distances when differently treated data sets are analyzed for the same species. In general, I found that correlation analyses of the same character set but using different transformations gave more uniform results than distance analyses of these same data. However, SIZE IN CORR (the correlation analysis in which no transformation was used) differed considerably from the BSMs of the remaining analyses (Fig. 2A.).

The correlation analyses, where transformations were used, grouped according to character sets (e.g. group G, Fig. 2i, in which all characters were used). The distance analyses, in which transformations were used, grouped together either by character set or in two instances by the type of transformation. In the BSMs, the similarity within groups of distance was not as great as the within group similarity of the correlation analyses.

The affinities between phenograms (Fig. 2B) were slightly changed from those expressed by the BSMs. The phenograms were less similar to each other than were their BSMs. This reduction in similarities was
particularly noticeable in phenograms which had low cophenetic correlation coefficients (e.g. SKEL/TIBIO SKULL DIST, $r=0.662$; Fig. 2B).

Schnell (1970) found, when comparing phenograms and BSMs with previous classifications of the Lari, that phenograms were more similar than their BSMs to the results of previous investigations. Robins and Schnell (1971) noted the opposite of this in 9 of 12 comparisons. In comparing the 27 classifications of this study, 14 of the BSMs were more similar to the previous classifications than were their phenograms. For the 27 analyses, 23 BSMs and 22 of the phenograms were more similar to Paynter's classification (1970) than to Hellmayr's (1938). The four BSMs more similar to Hellmayr's classification (1938) are SIZE IN CORR (Fig. 3A), SKEL/STERN ALL DIST (not figured); SKEL/HUNER SKULL DIST (not figured); and SKEL/STERN SKULL DIST (not figured). Correlations between BSMs and previous classifications, or phenograms and previous classifications are very low. In some instances a BSM or a phenogram is more similar to Paynter (1970) than to Hellmayr (1938) by a correlation of less than 0.002. Comparisons of the representative phenograms

The BSMs produced using correlation as a measure of similarity clustered into four groups (Fig. 2A, groups A, C, D, G). The phenogram which had the highest cophenetic comrelation coefficient within each group of BSMs was selected as a representative of the group. When the representative phenograms of these groups (Fig. 3) are compared there are two clusters which are generally found in all four phenograms. These clusters can be seen in SKEL/COMP I SKULL CORR (Fig. 3C). One is composed of seven species and is bounded by Pitylus grossus and Saltator atripennis. Three of these species--S. manimus, S. Similis (in SKEL/TIBIO FELVIC CORR)
and Pitylus grossus (in SIZE IN CORR)-- are not found in the same cluster in all four correlation phenograms. The second cluster as seen in SKEL/COMP I SKULL CORR (Fig. 30) is composed of seven species which are bordered by Passerina parellina and P. rositae. Several species join this group in the other phenograms. Passerina glaucocaerulea in both SKEL/TIBIO ALL CORR and SKEL/TTBIO PELVIC CORR (Figs. 3 B and 3D, respectively). Passerina brissonii and Cardinalis sinuatus are included in the cluster in SKEL/TIBIO PELVIC CORR, while P. rositae is not. This cluster is not found in SIZE IN CORR.

The BSMs constructed using average distances as a measure of similarity formed seven rather distinct groups (Fig. 2A, groups E, F, H, I, J, K, L). The phenograms which represent each of these groups are more heterogeneous than the phenograms representing the groups of correlation BSMs.

The species in the genus Passerina, as found in the cluster bounded by P. glaucocaerulea and P. leclancherii (SKEL/COMP I ALL DIST, Fig. 58), are present in most of these phenograms. However, the cluster is not always totally intact. Sometimes species are placed in other clusters, while additional species of ten join the group. For example, in SKEL/HUMER PELVIC DIST (Fig. 5G) the cluster in which most of these species are found does not contain Passerina rositae and P. glaucocaerulea.

Pheuticus ludovicianus and P. melanocephalus cluster together in six of the phenograms (Figs. 4 and 5), but they, as a cluster, differ in affinities to other species or clusters. In five of the phenograms Caryothraustes canadensis and Saltator orenocensis show more similarity to each other than to other species. There is also a tendency for several of the species of the genus Saltator to group together in the different
phenograms.
Comparison of these representative phenograms (both distance and correlation analyses) indicates two rather distinct clusters of species which are found in most of the phenograms; one composed of several species in the genus Saltator and the other of species in the genus Passerina. The remaining species differ in their affinities in each of the phenograms. This possibly indicates that a gradual cline of variation exists rather than distinct clusters of species.

## The "best" single phenetic classification

As should now be evident, many different phenetic classifications of the subfamily Cardinalinae are possible. Each of these classifications expresses a facet of the phenetic relationships present in the group. However, it is often useful to have a single general purpose classification.

Schnell (1970) proposed several guidelines by which he chose the "best" phenetic classification of the Lari, and these seem appropriate for this study. The "best" single phenetic classification of the Cardinalinae (i.e., the phenogram in which a large number of characters was used, a transformation was utilized to reduce the general size factor and there was a relatively high cophenetic correiation coefficient) is SKEL/COMP I ALL DIST (Fig. 5B).

SKEL/COMP I ALL DIST (Fig. 5B) has a cophenetic correlation coefficient of 0.855 . While this is the highest of any phenogram which fulfills the other criteria of a "best" phenetic classification, some distortion has occurred as a result of clustering. Comparison of SKEL/COMP I ALL DIST with the other phenograms may indicate where some of this distortion lies. SKEL/COMP I ALJ DIST differs considerably from any one of the other
phenograms; however, each cluster in SKEL/COMP I ALL DIST is found in at least one of the other phenograms. Pheuticus aureoventris is one species perhaps placed "poorly" in the phenogram. In all of the phenograms representing correlation analyses it shows considerably more similarity to the other species included in the genus Pheuticus by Paynter (1970). Caryothraustes canadensis and Saltator orenocensis are also species for which distortion may have caused poor placement in the phenogram. In most of the other phenograms, these two species are similar.

There are several consistancies between SKEL/COMP I ALL DIST (Fig. 5B) and the other phenograms which should be emphasized. Three saltators (́ㅡ. aurantiirostris, s. orenocensis and S. atricollis) rarely if ever are found to cluster with the other species placed in the genus Saltator. Two possible explanations for this are: 1) the skeletal material available on these species was limited; 2) they have been misplaced in the past. The second possibility seems more likely. In my study, very little intraspecific variation was found in the skeletal measurements of species in which a large series of skeletons were available. This would probably be true for these species as well. Ridgway (1901) suggested that two of these species (ㅇ. aurantiirostris and S. atricollis) were probably distinct genera. The cluster of the remaining saltators are found in almost every phenogram much the same as in SKEL/COMP I ALL DIST.

The three species in the genus Cardinalis cluster together only in the analyses in which the characters were restricted to 14 skull measurements. In the remaining analyses they varied in their placement showing little similarity to any group of species. Passerina cyanoides and $\underline{P}$. caerulea also seem to be different from the other species in this study. They
tend to change their affinities in each of the phenograms. The cluster of the remaining species in Passerina are found in almost every phenogram much the same as in SKEL/COMP I ALL DIST (Fig. 5B).

## Conclusions

Similarities expressed by previous classifications and the phenetic similarities found in this study show somewhat different affiliations among the species in this subfamily. This is particularly noticeable for three saltator species (ㄴ. orenocensis, s. aurantilirostris, and s. atricollis) and the genus Cardinalis.

With the exception of a cluster of nine buntings (Passerina) and another of six saltators, species in this subfamily of ten show different affinities from phenogram to phenogram. This fact--plus the somewhat low cophenetic correlation coefficient of many of the phenograms--may indicate that clustering is forcing species into groups, when in reality distinct clusters do not exist. There are some parts of the phenetic space that have a relatively high correlation of species, but these areas are not distinct from one another. There are species placed between these correlated areas. This is particularly evident in the analyses which were restricted to the 14 pelvic characters; all of the species were very similar in these characters. Stallcup (1954) observed that muscular patterns of the legs exhibit little variation even at the ordinal level in Passeriformes. Therefore it is not surprising to find the attachment site for these muscles showing little variation in the subfamily Cardinalinae. When only the 14 characters of the skull were used, the phenograms had much higher cophenetic correlation coefficients and more distinct clusters were formed. Tordoff (1954) and Bock (1964) have noted the adaptability
of the bill in the family Fringillidae and have suggested that most present classifications of the group are based on characters of the bill. The distinct clusters formed in the analyses of skull characters supports this; more specialization has occurred in the skull region in this group of birds.

The use of different similarity coefficients, character sets, and transformations influence the apparent species affinities. There is a tendency for the BSMs and phenograms to form two groups depending on similarity coefficient, but several of the analyses did not follow this trend (e.g. the analysis in which skull characters and distance were used, and the distance analysis in which all characters and no transformations were used). Using a restricted character set had considerable affect on the resulting phenograms. Most of the clusters formed in the phenogram of correlation among BSMs (Fig. 2A) did so on the basis of character sets. The use of transformations to reduce the size factor resulted in some differences, particularly in distance analyses, but caused fewer changes than did the use of restricted character sets or similarity coefficients.

My results indicate that several species (e.g. S. aurantiirostris, S. atricollis, S. orenocensis) are not as similar to each other or to a particular group of species as the classifications proposed by Hellmayr (1938) or Paynter (1970) would suggest. Because of this discrepancy, behavioral and ecological, as well as other morphological characters, should be examined.

SUMMARY
Multivariate statistical techniques were used to evaluate 49 skeletal characters and determine phenetic affinities among 31 species in the subfamily Cardinalinae. Analyses were also made using restricted numbers
of characters; 14 characters of the skull or pelvic region. Phenetic similarity was assessed using distances and product moment correlations as similarity coefficients and UPGMA (unweighted pair-group method using arithmetic averages) for clustering. To reduce or eliminate the effect of size, all measurements were either divided by sternum length, humerus length, or tibiotarsus length, or by the first component in an unstandardized principal component analysis. Another method for reducing the size factor involved the removal of the first principal component from a distance matrix.

The resulting 27 phenograms are compared among themselves and with classifications of Hellmayr (1938) and Paynter (1970). In analyses in which correlation was used as the coefficient of similarity, basic similarity natrices clustered according to character set (e.g. 14 pelvic characters or all characters) and transformations of the data to reduce the size factor had little effect. Distance analyses of the same data resulted in more similarity between analyses which involved character sets of the pelvic and of all characters, but enhanced differences of differently treated data.

Basic similarity matrices were grouped, and within each group the phenogram which best represented its basic similarity matrix was chosen to represent the group. These representative phenograms were compared to one another for differences in placement of species. The guides of Schnell (1970) were used to determine which phenogram was the "best" phenetic classification and this phenogram was used to look at similarity among species. Based on phenetic groupings, three saltators (́․ orenocensis, S. aurantilrostris and S. atricollis) show little similarity to the other
species in the genus Saltator. The three species in the genus Cardinalis showed little similarity to one another in analyses in which all characters were utilized, but the three show considerable similarity in 14 skull characters, Passerina cyanoides and P. caerulea are considerably different from the other species placed in the genus by Paynter (1970). The remaining species of the subfamily cluster into groups of phenetically similar species much as one would expect from either Paynter's (1970) or Hellmayr's (1938) classifications.

## ACKNOWIEDGMENTS

I am grateful to the following persons who allowed me to use material in their care: W. E. Lanyon, Amer. Mus. Nat. Hist; E. R. Blake, Field Mus. Nat. Hist.; J. R. Northern, Los Angeles Co. Mus. Nat. Hist.; L. F. Bejiista, Moore Lab. Zool. Occidental College; P. Slud and J. S. Weske, Nat. Mus. Nat. Hist.; A. M. Rea, private collection; N. K. Johnson, Univ. California, Berkeley; P. Brodkorb, Univ. Florida; R. M. Mengel, Univ. Kansas; R. B. Payne, Unîv. Michigan; J. C. Barlow, Royal Ontario Museum; G. M. Sutton and G. D. Schnell, Univ. Oklahoma. I wish to thank Gary D. Schnell, my major professor and Harley P. Brown, Charles C. Carpenter, and James R. Estes for critically reviewing the manuscript. I also wish to thank Elizabeth A. Bergey who assisted with the measurement of specimens. Ginna Davidson and Sharon Swift aided in the preparation of figures. This study was supported in part by a travel grant from the Smithsonian Institution and a Sigma Xi Grant-in Aid.

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TABLE 1
Number assigned to each species, Number of skeletons measured, and geographic distribution of species ${ }^{1}$

|  |  |  |  |
| :---: | :---: | :---: | :---: |
| Species |  | No. |  |
| No. | Species ${ }^{2}$ | Skel. | Breeding season distribution |
| 1 | Spiza americana | 10 | Eastern North America |
| 2 | Pheucticus chrysopeplus | 8 | Northern South America and w. |
|  |  |  | Mexico |
| 3 | Pheucticus aureoventris | 2 | Subtropical to temperate zone, |
|  |  |  | South America |
| 4 | Pheucticus Iudovicianus | 10 | South Canada, eastern U. S. |
| 5 | Pheucticus melanocephalus | 10 | Sw. Canada, w. U. S. to south- |
|  |  |  | ern Mexico. |
| 6 | Cardinalis cardinalis | 10 | S. Ontario to gulf states; Sw. |
|  |  |  | U. S. to Guatemala South |
|  |  |  | America |
| 7 | Cardinalis phoeniceus | 3 | Costal northern South America |
| 8 | Cardinalis sinuatus | 10 | Sw. U. S. to central Mexico |
| 9 | Caryothraustes canadensis | 9 | Tropical zone of South America |
| 10 | Caryothraustes humeralis | - | Tropical zone of South America |
| 11 | Rhodothraupis celaeno | 7 | Eastern Mexico |
| 12 | Periporphyrus exythromelas | - | Tropical zone of South America |
| 13 | Pitylus grossus | 5 | Tropical zone of South America |
| 14 | Saltator atriceps | 11 | Mexico to Panama |


| 15 | Saltator maximus | 10 | Southern Mexico to Brazil |
| :---: | :---: | :---: | :---: |
| 16 | Saltator atripennis | 4 | Upper tropical and subtropical |
|  |  |  | zones of South America |
| 17 | Saltator similis | 9 | South America (se. Brazil, ne. |
|  |  |  | Bolivia, Paraguay and ne. |
|  |  |  | Argentina) |
| 18 | Saltator coerulescens | 10 | Mexico to Costa Rica; Colombia |
|  |  |  | to n. Argentina |
| 19 | Saltator orenocensis | 1 | Tropical zone Venezuela and |
|  |  |  | ne. Colombia |
| 20 | Saltator maxillosus |  | E. Brazil, ne. Colombia |
| 21 | Saltator aurantiirostris | 3 | Subtropical to temperate zone |
|  |  |  | South America |
| 22 | Saltator cinctus |  | Tropical zone, east Ecuador |
| 23 | Saltator atricollis | 3 | East and south Brazil, Para- |
|  |  |  | guay and ne. Bolivia |
| 24 | Saltator rufiventris | - | Tropical zones of $n$. and e. |
|  |  |  | Bolivia |
| 25 | Saltator albicollis | 11 | Tropical, subtropical zones |
|  |  |  | of South America |
| 26 | Passerina glaucocaerulea | 2 | South Brazil, Uruguay and east |
|  | (Cyanoloxia glaucocaerulea) |  | Argentina |
| 27 | Passerina cyanoides | 11 | Southeastern Mexico to Amazonia |
|  | (Gyanocompsa cyanoides) |  |  |
| 28 | Passerina brissonii | 3 | Tropical and lower subtropical |
|  | (Gyanocompsa cyanea) |  | zones of South America |

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1 Distributions are summaries from Paynter (1970), de Schauensee (1970) and Peterson and Chalif (1973).
2 Scientific names are those of Paynter (1970). In parenthesis are names used by other authors (Hellmayr, 1938; Peterson and Chalif, 1973; A.0.U. Check-list, 1957) when at variance with those used by Paynter (1970).

FIGURE 1. Dendrograms depicting two former classifications of the subfamily Cardinalinae: A) classification proposed by Paynter (1970); B) classification proposed by Hellmayr (1938). The following arbitary similarity values were assigned to each taxonomic level: (1) subspecies; (2) species; (3) subgenus; (4) genus; (5) subfamily. Saltator cinctus which was not included in Hellmayr's (1938) classification is represented by a dotted line indicating where it probably would have been placed.

FIGURE 2. Dendrograms showing relationships among: A) basic similarity matrices; B) phenograms. Letters indicate groups of very similar basic similarity matrices. Asterisks indicate the phenogram chosen to represent each of these groups--the phenogram with the highest cophenetic correlation coefficient. The cophenetic correlation coefficients are shown in the dendrogram of phenograms. The representive phenograms are shown in Figures 3, 4, and 5.

FIGURE 3. Phenogram representatives of groups $A, C, D$, and $G$ ( $F i g .2 A$ ). Numbers on the branches of the phenograms indicate clusters discussed in the results. These are four correlation analyses in which: A) no attempt was made to reduce size; B) all characters were divided by the tibiotarsus length; C) 14 skull characters were divided by unstandardized principal component I; D) 14 pelvic characters were divided by the tibiotarsus length.

FIGURE 4. Phenogram representatives of groups B, E, F, and H (Fig. 2A). Numbers on the branches of the phenograms indicate clusters discussed in the results. These are four distance analyses in which: A) no attempt was made to reduce size; B) 14 skull characters were divided by unstandardized principal component $I$; 6) 14 skull characters were divided by the tibiotarsus length; D) 14 pelvic characters were divided by the tibiotarsus length.

FIGURE 5. Phenogram representatives of groups $I, J, K$, and $L$ (Fig. 2A). These are four distance analyses in which: A) 14 pelvic characters were divided by the sternum length; B.) all characters were divided by unstandardized principal component I; c) 14 pelvic characters were divided by the hunerus length; D) the influence of the first principal component was removed mathematically from the distance matrix.


Figure 1
(


Figure 3


Figure 4


Figure 5

PAPER II

A PHENETIC ANALYSIS OF THE SUBFAMILY CARDINALINAE:
USING EXTERNAL MORPHOLOGICAL CHARACTTERS AND SKELKITAL CHARACTERS

## A PHENETIC ANALYSIS OF THE SUBFAMILY CARDINALINAE:

 USING EXTERNAL MORPHOLOGICAL CHARACTERS AND SKELETAL CHARACTERSJenna J. Hellack

The subfamily Cardinalinae includes 37 species of cardinals, buntings, and grosbeaks. The group has been divided into from nine (Paynter, 1970) to 15 genera (Hellmayr, 1938). Previously using skeletal variables, I (Hellack, 1975b) investigated the phenetic relationships of the subfamily using cluster analyses. In that study three species in the genus Saltator clustered differently from that suggested in previous classifications (Hellmayr, 1938; Paynter, 1970). The three species in the genus Cardinalis were found to cluster together only in analyses utilizing 14 skull characters and all 31 species included in the study were found to be very similar in relative measurements of the pelvic region. In this paper, I wish to examine further the phenetic affinities between species of the subfamily by analyzing an additional set of external characteristics.

MATERTALS AND METHODS

This study involved the utilization of 75 external morphological characters in 10 phenetic analyses and the inclusion in two of these analyses, the 49 skeletal characters used by Hellack (1975b). The generic
and specific designations used are those of Paynter (1970). Table 1 of Hellack (1975b) lists the species, a brief description of their geographic distribution, the species number assigned to each, and the number of skeletons measured of each. The 49 measurements are from all regions of the skeleton. Due to the lack of skeletal materials, only 31 of the 37 species (included in the subfamily by Paynter; 1970) were compared.

In the analyses of external morphological characters, similar problems of obtaining materials occurred. The Appendix indicates the 75 external morphological characters selected for this study, which can be separated into three categories: (1) 33 external skin measurements of the tail, wing, phalanges, and bill; (2) color measurements (dominant wave length) from 8 regions of the body; (3) contrast characters in which 34 comparisons were made between various regions of the bird (e.g. contrast between the nape and the crown; $0-$ no contrast, 1 - contrast). All measurements were taken from adult specimens. Original mean character measurements for each species may be found in Appendix IV of Hellack (1975a).

For the external skin characters, I measured 10 males and 10 females of each species, if specimens were available. When more than one race was involved, measurements were taken from specimens of the nominant race. External skin measurements were available for feinales of all 37 species, but only 36 species are included in the analysis of males (the only known specimen of Saltator cinctus is a female).

Color was measured using the Munsell Book of Color (1973) which specifies a given color in terms of three characters--hue, value, and chroma. These values were then converted to dominant wave lengths, excitation purity, and percent reflectance by using the tables supplied by
the Munsell company (anonymous, 1970). For discussions of these conversions the reader is referred to Newhall, Nickerson, and Judd (1943). Only one value, the dominant wave length of each region was included in the analysis. Color measurements were obtained for males of 34 species and for females of 33 species. Caryothraustes humeralis, Saltator cinctus, and S. albicollis were not included in color analyses of the male species. These species plus $\underline{S}$. maxillosus were not included in color analyses of females. When the 49 skeletal characters were combined with the external morphological characters, only 30 of the 37 species had complete data. These analyses therefore do not include the four above mentioned species plus Periporphyrus exythromelas, Saltator rufiventris, and Passerina caerulescens.

For the purpose of assessing phenetic similarity, multivariate statistical programs were employed from the Numerical Taxonomy System (NT-SYS, developed by F. James Rohlf, John Kishpauph, and David Kirk). Both Q- and R-type studies were conducted.

In the Q-type analysis, characters were standardized and either a product moment correlation coefficient or an average distance coefficient was calculated for all pairs of species (Sneath and Sokal, 1973). Species were then clustered by the unweighted pair-group using arithmetic averages (UPGMA), and the results were summarized in phenograms.

Principal components were extracted from a matrix of correlations among characters in the R-type analysis (Sneath and Sokal, 1973). Phenetic relationships were graphically presented as 3-D models of species plotted with respect to the first few principal components extracted from the matrix of correlation among characters (Rohlf, 1968). A shortest
minimally connected network (Rohlf, 1970) computed from the original matrix of distances is superimposed on the 3-D models to point out possible distortions.

To eliminate or reduce the size factor, the external morphological characters were used as ratios (see Appendix), and the skeletal measurements were divided by the first principal component extracted from a matrix of unstandardized skeletal characters (Hellack, 1975b). The skeletal data were handled this way because in Hellack (1975b) it was the method which produced what was considered the "best" phenetic classification from the skeletal data.

Ten phenetic classifications were produced using the various combinations of available data sets (external skin characters, contrast characters, color characters, and skeletal characters) and two similarity coefficients (correlation and distance). Males and females were analyzed separately for two reasons: (1) to see if there were major differences between the resulting classifications: (2) to include all species in some analyses without the use of a large number of NGs (no comparison, i.e. no data to compare). Various data combinations were made so as to include all the characters available for any one species in an analysis. Characters from the skeletal data were averaged for the species without regard to sex; therefore when all available data were utilized, the data were handled in the following manner: external skin characters of both males and females were averaged to produce mean external skin measurements; the contrast characters and the color characters were doubled (male and female averages included separately); and the skeletal characters of the previous study (Hellack, 1975b) were included. This produced

168 "characters" per species.
Matrices were produced from the classification systems of Paynter (1970) and Hellmayr (1938) (see Hellack, 19756). These two matrices, the 10 matrices produced from the various combinations mentioned above, and two matrices produced from the analyses of skeletal characters (SKEL/COMP I ALL CORR and SKEL/COMP I ALL DIST; Hellack, 1975b) were compared by computing the coefficient of correlation between the basic similarity matrices. These correlations were then used to produce a matrix showing the similarities between these matrices. Similarities were then summarized into a dendrogram that indicates which basic similarity matrices are most alike. The phenograms were compared in a similar manner.

The following abbreviations will be used. CORR or DIST refer to the use of correlation or distance to analyze similarity between species. SKIN will denote the use of external skin measurements and contrast characters, COLOR refers to the use of eight color characters of dominant wave length. SKEH indicates the use of skeletal characters divided by unstandardized principal component I (SKBL/COMP I ALL of Hellack, 1975b). BSM is used as the abbreviation for basic similarity matrix.

RESUITS

## Phenograms

The dendrogram which sumarizes the similarity between 10 BSMs of this study, two BSMs from the analyses of skeletal characters (Hellack, 1975b), and the classifications of Hellmayr (1938) and Paynter (1970) is shown in Figure 1A, Nine groups of BSMs are labeled. The four BSNs of group A are analyses in which only the males of each species are compared. The BSMs differ in similarity coefficient and/or the number of characters
(the BSMs also differ in the number of species compared, although the phenogram, Figure 1A, is comparing placement of only those species each analysis has in common). Group B has three BSMs where only the females for each species were compared. These BSMs like those of group A differ in similarity coefficient and/or the number of characters. Group E is composed of two BSMs. They differ in character set but are alike in the similarity coefficient used. The remaining five groups contain one BSM each.

The dendrogram of similarity between phenograms is shown in Figure 1B. In comparing the dendrogram of similarity between BSMs (Fig, 1A) with that of the phenograms (Fig. 1B), one BSM of group A (SKIN + COLOR DIST $\delta \mathbf{\delta}$ ) is in a different cluster; it shows more similarity to group E. This was the least similar of the four BSMs in group A. The remaining phenograms cluster much as their BSMs do in Figure 1A, although the distance analyses of groups E and F show considerably less similarity to the other clusters of phenograms than they did in Figure 1A. The similarities found in the comparison of BSMs (Fig. 1A) appear to be reduced in the phenogram comparisons (Fig. 1B).

There is considerable correlation of BSMs within groups A, B, and E (Fig. 1A). Instead of presenting all phenograms of these groups, I have depicted only one from each--the phenogram with the highest cophenetic correlation coefficient. Any substantial difference in placement of species in phenograms within each group will be described below.

Group A consists of four very similar BSMs. The phenogram chosen to represent the group (SKIN CORR ס $\delta$, Fig. 2A) has a cophenetic correlatic. 1 coefficient of 0.792 . There is essentially no difference between this
phenogram and that of SKIN DIST $\delta \delta$ (not figured). The addition of eight color characters (SKIN + COLOR CORR $\delta \delta$, not figured) caused two species to cluster differently from that shown in Figure 2A. Passerina versicolor groups with $\underset{P}{ }$. ciris and Periporphyrus erythromelas shows little similarity to any cluster of species. SKIN + COLOR DIST $\delta \delta$ (not figured) is the most divergent of the four phenograms. However, major clusters are much the same. The addition of color characters in this case resulted in Passerina amoena not being found in the cluster of buntings and Rhodothraupis caelaeno, Periporphyrus erythromelas, Saltator orenocensis, and S. atriceps to show little similarity to the other species of the analysis.

The three BSMs of group B are all the result of analyses in which only females of each species were compared. The phenogram which represents this group (SKIN DIST 와, Fig. 2B) has a cophenetic correlation of 0.814 . The major clusters found in Figure $2 B$ are much the same in all phenograms of group B. However, in the two phenograms not figured, Saltator rufiventris clusters with the other saltators. Another difference is the similarity between Caryothraustes humeralis and C. canadensis. They are in the same large cluster, but are not as closely affiliated with each other as is seen in Figure 2 B .

Group C (Fig. 2C) with its one BSM is an analysis with all characters (SKIN + COLOR + SKEL CORR). The phenogram has a cophenetic correlation of 0.727. Its stem connects with the BSM of SKEL/COMP I ALL CORR which was described in Hellack (1975b) and not figured here. Several major cluster changes occur if the two phenograms are compared. The cluster bounded by Passerina glaucocaerulea and P. parellina (Fig. 2C) is not found in SKEL/COMP I ALL CORR (the members of the genus Passerina form one cluster with the
exception of P. caerulea and P. cyanoides). Saltator orenocensis and Caryothraustes canadensis cluster with the genus Pheuticus in SKEL/COMP I ALL CORR (not figured).

Group E contains two BSMs. The phenogram representative of this group (SKIN + COLOR + SKEL DIST, FIG. 2D) has a cophenetic correlation of 0.819 . SKIN + COLOR $+9 \$$ DIST (not figured) differs in the placement of several species. The buntings (Passerina) cluster much the same in SKIN + COLOR $9 \%$ DIST as they do in SKIN + COLOR + SKEL CORR (Fig. 2C), whereas only two of the species in the genus ( P . amoena and P. caerulescens) are not found in the same cluster in SKIN + COLOR + SKEL DIST (Fig. 2D). Saltator atripennis shows little similarity to any other species in SKIN + COLOR 99 DIST.

Group F contains the BSM for SKEL/COMP I DIST. The phenogram resulting from this BSM was considered the "best" classification for the Cardinalinae when only skeletal characters were included in the analyses (Hellack, 1975b). Its phenogram (figured in Hellack, 1975b) had a cophenetic correlation of 0.855 and differs from those presented here mainly in the placement of the species in the genus Cardinalis. In SKEL/COMP I ALL DIST, the cardinals did not cluster together.

Principal component analyses
The different character sets of this study were also subjected to an R-type analysis. Four representative three-dimensional models of these analyses are shown in Figure 3. Character loadings for the first three principal components of each of the 3-D models are in Appendix I, II, and III of Hellack (1975a).

Figure 3A shows species projected onto the first three principal components from the analysis of males using external skin measurements and
contrast characters. The components explain 21.16, 11.73, and 9.01\% of the total character variation, respectively. While only $42 \%$ of the total variation is accounted for, the euclidian distances between species in the 3-D model have a correlation of 0.900 with those in the original distance matrix.

Principal component I has its highest loadings on the amount of tail covered by the tail coverts (Ex9, Ex10) and the shape of the wing (Ex12-16). Species on the left in the 3-D model (Fig. 3A) have less tail exposed and more sharply pointed wings. Component II is a size factor with high loadings on the tail, wing and hallux lengths (Ex1, Ex11, Ex28). This component also has relatively high loadings on the contrast characters for white in the wing and tail (Ex34, Ex36-39). The larger birds with large amounts of white in the wing and tail are in the front of the $3-D$ model. The third component has its highest loadings on the wing vane widths (Ex17-24). The short sticks represent species with relatively wider primaries.

Figure 3B represents the analysis of females utilizing external skin measurements and contrast characters. The first three components explain $20.24,11.85$, and 9.67 \% of the total character variation, respectively. Less than $42 \%$ of the total variation is accounted for in the first three components, however; the 3-D model has a correlation of 0.913 with the original distance matrix. This analysis has high loadings on the same characters as does that of the male analysis (Fig. 3A).

The 3-D model of the analysis utilizing all characters (SKIN + COLOR + SKEL) is shown in Figure 3C. The first three components account for 23.33, 12.96, and $9.22 \%$ of the character variation, respectively (total, 45.51). Because there were many more characters than species in this analysis,

Gower's (1966) method for computing projections from a matrix of correlation among species was utilized. As the 3-D model produced is from a matrix of correlation among species, character loadings are not available.

Figure 3D is the 3-D model produced from the analysis of skeletal characters divided by principal component I. The first three components account for $26.97,18.24$, and $11.18 \%$ of the character variation, respectively (total, 56.39). The 3-D model has a correlation of 0.903 with the distance matrix. The first principal component is a contrast with its highest loadings on the keel depth and femur and tibiotarsus widths. Species on the left in the 3-D model (Fig. 3d) have relatively deeper keels and narrower femurs and tibiotarsi. Component II has its highest loadings on the long bones of the wing and leg. It also is a contrast with negative loadings on the long bones of the wing and positive loadings on the long bones of the leg. Species near the front of Figure 3D have relatively shorter legs and longer wings than those at the back. The third component has high positive loadings on the skull width and depth, and high negative loadings on the sternum and keel length. The species with the shorter sticks have relatively narrower skulls and longer sterna and keels.

Comparisons of BSMs, phenograms, and previous classifications
Highly correlated skeletal characters with a large sige factor were used by Hellack (1975b) in an analysis of Cardinalinae. I found, as in previous studies (Sokal and Michener, 1967; Robins and Schnell, 1971), that using correlation as a measure of similarity tends to give more uniform results than did the uso of the distance coefficient. The analyses in this study in which external character sets (SKIN or SKIN + COLOR) were used did not show this tendency. There was considerable correlation between the BSMs of similar character sets irrespective of similarity coefficient (Fig. 1A). The only exception was SKIN + COLOR DIST 9 ( $n$ ( figured). The lack of a tendency for the BSMs to group according to similarity coefficient perhaps indicates there is not a large size factor or other significant trend in the ratios used as external characters.

As found in the analyses of skeletal characters, the affinities between phenograms (Fig, 1B) changed some from those expressed for the BSMS (Fig. 1A). In the comparison of phenograms (Fig. 1B), SKIN + COLOR DIST $\delta \delta$ (not figured) switched (i.e., clustered with a different group of species or in this case phenograms) affinities, and showed more similarity to SKIN + COLOR DIST 앙( $n o t$ figured) and SKIN + COLOR + SKEL DIST (Fig. 2D). Switching also cecurred in some of the major branches (e.g., four distance phenograms show less similarity to the other analyses than did their respective BSMs).

In comparing the 12 classifications in this study with the classifications of Hellmayr (1938) and Paynter (1970), nine of the BSMs were more
similar to previous classifications than were their respective phenograms. All 12 BSMs and 10 of the phenograms were more similar to Paynter (1970) than to Hellmayr (1938). The two phenograms more similar to Hellmayr (1938) are SKIN CORR $\delta \delta($ Fig. 2A) and SKIN + COLOR CORR $\delta \delta$ (not figured). Correlations between the BSMs and previous classifications are very low, indicating that the affinities implied by previous workers are different from those determined in my study.

Comparisons of representative phenograms
Six phenograms were chosen to represent the groups of BSMs shown in Figure 1A. These had relatively high cophenetic correlation coefficients. The phenogram representative of group B (SKIN DIST \$f, Fig. $2 B$ ) is the only representative phenogram in which all the species included in the subfamily Cardinalinae by Paynter (1970) were analyzed. Below the placement of the species in the other representative phenograms will be compared with their placement in SKIN DIST 9 ㅇ (Fig. 2B).

The representative phenogram of group A (SKIN CORR $\delta \delta$, Fig. 2A) is very similar to SKIN DIST $9 \%$ (Fig. 2b). While some changes in close affinities are evident, the major clusters are composed of many of the same species. Passerina rositae, Saltator albicollis, S. rufiventris, Periporphyrus exythromelas and Caryothraustes humeralis in SKIN CORR 88 are not placed in the same major groups that they are found in SKIN DIST $\$$ 우.

The phenogram of group C (SKIN + COLOR + SKEL CORR, Fig. 2C) differs from SKIN DIST 오 (Fig. 2B) primarily in the main stem connections of its smaller clusters. For example, the cluster bounded by Pheuticus chrysopeplus and Passerina caerulea in SKIN + COLOR + SKEL CORR is found
as two clusters in SKIN DIST 00 with Spiza americana and a few species in the genus Passerina added. Passerina leclancherii and P. versicolor are not included in the same major groups in SKIN + COLOR + SKEL CORR as they are in SKIN DIST 아. The species showing little affiliation to any of the clusters in SKIN DIST $\%$ 아 were not included in the phenogram of group C. SKEL/COMP I CORR (group D, not figured) differs from SKIN DIST 우 (Fig. 2B) in much the same way as SKIN + COLOR + SKEL CORR (Fig. 2C). In addition to the differences discussed above, the genus Passerina does not group in the same way as in SKEL/COMP I CORR. There is one cluster of nine species with the other two species $\underline{P}$. caerulea and $\underset{P}{P}$. cyanea not clustering with these species.

The phenogram representative of group E (SKIN + COLOR + SKEL DIST) is shown in Figure 2D. Again the majority of the clusters are much the same as those of SKIN DIST 9 (Fig. 2B). Saltator orenocensis differs in its placement and the species in the genus Passerina do not form two large groups in SKIN + COLOR + SKEL DIST. Only the two species $\underline{P}$. caerulea and P. amoena do not cluster with the other species of this genus.

Group F contains only SKEL/COMP I ALL DIST, which is in Figure 5B of Hellack (1975b). It was the "best" phenetic classification of the Cardinalinae when only skeletal measurements were used (Hellack, 1975b). Several differences are noticeable in comparing this phenogram to SKIN DIST $9 \%$ (Fig. 2B). Only two of the species in the genus Cardinalis cluster together; the other (ㄷ. phoeniceus) shows little similarity to them. Most species in the gemus Passerina cluster together (exceptions being P. cyanea and $P$. caerulea) rather than forming two distinct clusters. Two saltators (S. aurantiirostris and S. orenocensis) are not found
with the other saltators in SKEL/COMP I DIST.
The "best" phenetic classification
I have presented a number of phenetic classifications of the subfamily Cardinalinae. Each represents a facet of the phenetic relationships present in the group. However, as mentioned in the study of the skeletal characters (Hellack, 1975b), it may at times be useful to have ore "best" classification of a group.

Schnell (1970) proposed several guides for choosing the "best" phenetic classification, when more than one was available. These guides are selection of a phenogram in which: 1) a large number of characters are used; 2) transformations to reduce the general size factor are utilized, and 3) there is a relatively high cophenetic correlation coefficient. These guides while useful are not totally sufficient for this study. In my opinion, the phenogram used for general purposes should have a relatively high correlation with the other phenetic analyses of this study.

There are two analyses (in this study) in which all available characters were utilized and transformations reduced the size factor--SKIN + COLOR + SKEL CORR (FIg. 2C) and SKIN + COLOR + SKEL DIST (Fig. 2D). The phenogram with the highest cophenetic correlation coefficient is SKIN + COLOR + SKEL DIST (Fig. 2D). However, this phenogram is not as highly correlated to the BSMs and phenograms of the other analyses as is SKIN + COLOR + SKEL CORR. Only SKIN + COLOR DIST 9 ㅇ (not figured) and SKEL/COMP I DIST (figured in Hellack, 1975b) of the BSMs are more similar to the distance analysis. The two phenograms of these analyses plus SKIN + COLOR DIST $\delta \dot{\prime} \delta($ not figured) are more similar to SKIN + COLOR + SKEL DIST in the comparison of phenograms. SKIN + COLOR + SKEL CORR (FIg. 2C),
while not having the highest cophenetic correlation coefficient, is probably the best representative phenogram of this.study for the above reason and will be used as such here.

Using all available characters resulted in seven species not being included in the analysis SKIN + COLOR + SKEL CORR (Fig. 2C). As these species (Caryothraustes humeralis, Periporphyrus exythromelas, Saltator maxillosus, S. cinctus, S. rufiventris, S. albicollis, and Passerina caerulescens) are included in the subfamily by various authors (Hellmayr, 1938; Paynter, 1970), they should be represented in a "best" phenetic classification of the group. To accomplish this, I evaluated their placement in other phenograms and 3-D models of analyses. A phenogram was then constructed utilizing SKIN + COLOR + SKEL CORR (Fig. 2C) for the placement of all species which it included and I placed the seven species into the clusters they probably would have joined had they been included in the analysis. This "best" phenetic classification is shown in Figure 4. The reason or reasons for the placement of each of these species are discussed below.

Caryothraustes humeralis was included only in the analyses of skin and contrast characters. In SKIN DIST 9 (Fig. 2B) and in the 3-D models of both SKIN $9 \$$ (Fig. 3B) and SKIN 88 (Fig. 3A), C. humeralis is most similar to C. canadensis. The average similarity of these two in the correlation analyses of both SKIN CORR 99 (not figured) and SKIN CORR dó (Fig. 2A) is 0.577 . This average similarity is used for the placement of $\underline{C}$. humeralis in the "best" classification (Fig. 4).

Periporphyrus erythromelas was placed between Rhodothraustes celaeno and Pitylus grossus and near the saltators in the "best" classification.

In the analyses in which Periporphyrus exythromelas was included (all of uhose based on external characters) it was found to be most similar with R. celaeno or with Pitylus grossus. This was true in both the phenograms and the 3-D models with the only exception being SKIN CORR $\delta \delta$ (Fig. 2A).

Saltator maxillosus was included in the analyses of skin and contrast characters (Figs. 2A, B; 3A,B). It varied in affinities in these analyses. In the two cluster analyses where I evaluated male characters (Fig. 2A), S. maxillosus showed close affinity to $\underline{\text { S }}$. maximus, while in the cluster analyses utilizing female characters (Fig. 2B) it was similar to both S. atripennis and S. similis. In the 3-D models (Fig. 3A,B), S. maxillosus separates from the other saltators primarily in component III--the vanes of its primaries are somewhat wider than found in those species of the major saltator cluster. Based on these analyses, in the "best" classification (Fig. 4) it is placed in the saltator cluster and is depicted as more similar to the central group of species than either S. atripennis or S . atriceps.

Saltator cinctus was included only in the analyses of female skin and contrast characters. Only one specimen is available for this species and considerable feather wear was evident. It is placed in the "best" classification (Fig. 4) as it is found in the analyses of female characters (Figs. 2B,3B), but because of the lack of specimens I am not certain that this represents the true phenetic affinities of this species.

Saltator rufiventris was a part of all the external character analyses. It clustered with the saltators in all analyses; however, it showed no close affinities to any one saltator. Its closest affinities are perhaps to $\underline{\text { S }}$ aurantiirostris, the species to which it is connected by the mininum
connecting network of the 3-D models (Fig. 3A,B). S. mufiventris tends to separate from the other saltators in component III of the $3-\mathrm{D}$ models. The primaries are relatively narrower in S. rufiventris than in the other species in the genus Saltator. Its placement in Figure 4 represents the appearance of more similarity to the major cluster of saltators than to any other species cluster. S. mufiventris is more similar to the saltator cluster than are $\underline{S}$. aurantiirostris or S. atricollis.

Saltator albicollis was represented in all analyses except those in which color was included. It clustered with the saltators in the skeletal analyses (Hellack, 1975b) and in the analyses of external male characters (Figs. 2A, 3A). In the analyses of female external characters (Figs. 2B,3B), it shows much less similarity to the saltators. Its placement as that of S. rufiventris is rather arbitrary, but it is apparently most similar to the saltators.

Passerina caerulescens was included in all the external character analyses. It always clustered with species in the genus Passerina (Figs. 2A,B; 3A,B), but was relatively less similar to them. In the "best" classification (Fig. 4) it is placed in the cluster which includes P. Ieclancherii, the species to which it appears most similar. At the same time, its connection is at some distance from that of the other species indicating its relatively low affiliation with the group. Comparison of former classifications with the "best": phenetic classification

Hellmayr's (1938) and Paynter's (1970) proposed classifications of the 37 species (included in this study) differ in the placement of species that Paynter (1970) assigned to the genera Passerina, Pheuticus and Cardinalis. Hellmayr (1938) divides the eleven species of Paynter's
(1970) genus Passerina into five genera (Passerina, Cyanocompsa, Cyanoloxia, Porphyrospiza, and Guiraca) and the four species of Pheuticus into two genera (Pheuticus and Hedymelas). Hellmayr (1938) places the Pyrrhuloxia (Cardinalis sinuatus) in a genus by itself (Pyrrhuloxia sinuatus).

The "best" phenetic classification of this study (Fig. 4) divides the species in this study into three large clusters. These groups were not found in all the analyses of this study. However, one or more of these three groups occurred in every analysis (Fig. 2). The three groups are: 1) most of the species in the genus Passerina plus Spiza and Caryothraustes; 2) the genus Pheuticus plus Passerina caerulea; 3) the remaining genera in the subfamily (Saltator, Rhodothraustis, Periporphyrus, Pitylus and Cardinalis).

In comparing the "best" phenetic classification to the classifications of Hellmayr (1938) and Paynter (1970), the clusters of the species in the genera Passerina and Pheuticus are most similar to Hellmayr's groupings. It should be pointed out however that, while there is a tendency for Passerina to form more than one cluster in all analyses, these groups were often more similar to each other than to any other species cluster. When this was not true, one of the ciusters of Passerina showed more similarity to the genus Caryothraustes or species of the genus Pheuticus.

Passerina caerulea has been considered very similar to the Indigo Bunting (Phillips et al., 1964; Blake, 1969). In this study P. caerulea never grouped with the other species included in the genus Passerina and in most analyses it clustered with the genus Pheuticus. The Pyrrhuloxia (Cardinalis sinuatus) clusters with the other species in the genus Cardinalis, the same as suggested by Paynter's (1970) classification.

The groupings of Hellmayr (1938) and Paynter (1970) are the same for the remaining species in the subfamily, but the phenetic analyses of my study differ from the previous classifications in the similarities of the species they both place in the genus Saltator. The "best" phenetic classification (Fig. 4) shows one cluster of six very similar saltators (S. atriceps, $\underline{\text { S. maximus, }}$ S. coerulescens, $\underline{\text { S. similis, }}$. maxillosus, and S. atripennis). The remaining six species included in this genus in previous classifications show little affiliation to any of the species clusters. It is possible that the limited material available was inadequate to get a rellable estimate of similarities for the species S. rufiventris, S. albicollis and S. cinctus. This is not true for S. atricollis, $\underline{\text { S }}$. aurantiirostris and S. orenocensis. They differ from this cluster in every analysis. Ridgeway (1901) suggested that several of the South American saltators did not belong in the genus, a conclusion which is supporied by this study.

## Taxonomic Conclusions

In this study the phenetic similarity found between the species in the subfamily Cardinalinae is somewhat different from the affiliations suggested by previous ciassirications. This is pariicularly evident in the genus Saltator. Six species of this genus do not show close affinities to any of the other saltators.

The species in the genus Passerina show considerable similarity to each other in their skeletal characters (ㄹ. caerulea being the exception), but separate into groups much like those suggested by Hellmayr (1938) when external measures were considered along with these skeletal measurements. Passerina caerulea, which was never found clustering with the other species

Paynter (1970) places in the genus, is particularly noticeable. It has been suggested that this species is closely allied to the Indigo Bunting (Phillips et al., 1964; Blake, 1969; and Mayr and Short, 1970). In this study it was not closely assocjated with any one group although it clustered most often with the genus Pheuticus.

My results indicate that the genus Saltator as classified at present is a heterogenous group and consideration should be given to dividing it
 are saltators and if adequate material were available they would cluster with the major group of saltators. S. aurantiirostris, S. atricollis and S. orenocensis are different and should be removed from the genus Saltator. I do not feel in a position to comment on S. cinctus.

The species in Paynter's (1970) genus Passerina could in my opinion be grouped according to either former classification--with the exception of $\underline{P}$. caerulea which should remain Guiraca caerulea. Pheuticus appears to be composed of two rather different groups as indicated by Hellmayr (1938), and I suggest that his recommendations should be followed. I agree with Paynter on the classification of the genus Cardinalis (that it contains Cardinalis sinuatus) and the remaining species of this subfamily.

SUMMARY
Multivariate statistical techniques were used to determine phenetic affinities of 37 species in the subfamily Cardinalinae. Various analyses were made using 75 external morphological characters and 49 skeletal characters. Phenetic similarity was assessed using distances and product moment correlations as similarity coefficients; UPGMA (unweighted
pair-group method using arithmetic averages) was used for clustering. Phenetic relationships are presented in phenograms and 3-D models of species projected onto principal components based on a matrix of correlation among characters.

The resulting 10 phenograms are compared among themselves, with two classifications of skeletal characters (Hellack, 1975b), and with classifications of Hellmayr (1938) and Paynter (1970). Basic similarity matrices grouped together according to the character set utilized or similarity coefficient. The use of different similarity coefficients had little effect on the external character sets.

BSMs were grouped, and within each group the phenogram which best represented its BSM was chosen to represent the group. These representative phenograms were compared to each other for differences in placement of species. The phenogram which best represented the phenetic affinities of the species was determined by utilizing the guidelines of Schnell (1970) and the coefficient of correlation between each of the basic similarity matrices.

The phenogram chosen in this manner used all characters available, but did not include seven of the species. As these species should be represented in a "best" phenetic classification, a phenogram was constructed using the phenogram chosen as the best representative of this study for the placement of all species it analyzed, and placing the seven remaining species into the clusters they would probably join if they had been included in the analysis. This was accomplished by studying the phenograms and 3-D models in which the seven species had been included.

This phenogram was then used to look at similarities and compare
these similarities with the classification of Hellmayr (1938) and Paynter (1970). Based on phenetic groupings several saltators (S. rufiventris, S. albicollis, S. cinctus, S. atricollis, S. aurantiirostris, and S. orenocensis) were found to have little similarity to the remaining saltators. In the case of S. rufiventris, S, albicollis and S. cinctus, insufficient data may be the reason for their lack of similarity to the saltator cluster. However, S. atricollis, S. orenocensis and S. aurantiirostris are clearly distinct.

The genus Pheuticus clusters much as one would expect from Hellmayr's (1938) classification. The species placed in the genus Passerina by Paynter (1970) could be grouped according to either former classification.

## AGKNOWLEDGMENTS

I am grateful to the curators of a number of collections who allowed me to use material in their care (they are listed in Hellack, 1975b). I wish to thank Gary D. Schnell, Harley P. Brown, Charles C. Carpenter, and James R. Estes for critically reviewing the manuscript. I also wish to thank Elizabeth A. Bergey who assisted with the measurement of specimens. Ginna Davidson and Sharon Swift aided in the preparation of figures. This study was supported in part by a travel grant from the Smithsonian Institution and a Sigma Xi Grant-in Aid.

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## FIGURE LEGENDS

FIGURE 1. Dendrograms showing relationships among: A) basic similarity matrices; B) phenograms. Letters indicate groups of very similar basic similarity matrices. Asterisks indicate the phenogram chosen to represent each of these groups--the phenogram which has the highest cophenetic correlation coefficient. These representative phenograms axe shown in Figure 2.

FIGURE 2. Phenogram representatives of groups A, B, C, and E. These are four analyses in which: A) skin cizaracters of males were utilized using correlation as a measure of similarity; B) skin characters of females were used with distance as the similarity coefficient; C) all available characters were used and correlation was the measure of similarity; D) all characters were used and distance was the similarity coefficient.

FIGURE 3. Four representative models of species projected onto the first three principal components of a matrix of correlations among characters. A) the 3-D model in which male skin characters were used, B) the 3-D model in which female skin characters were used, C) the 3-D model in which all available characters were used, D) the 3-D model in which skeletal characters were used. Species names corresponding to the numbers on the models are: 1. Spiza americana; 2. Pheuticus chrysopeplus; 3. P. aureoventris; 4. P. Iudovicianus; 5. P. melanocephalus; 6. Cardinalis cardinalis; 7. G. phoeniceus; 8. C. sinuatus; 9. Caryothraustes canadensis; 10. C. humeralis; 11. Rhodothraupis celaeno; 12. Periporphyrus erythromelas; 13. Pitylus grossus; 14. Saltator atriceps; 15. S. maximus; 16. S.
atripennis; 17. S. similis; 18. S. coerulescens; 19. S. orenocensis; 20. S. maxillosus; 21. S. aurantiirostris; 22. S. cinctus; 23. S. atricollis; 24. S. rufiventris; 25. S. albicollis; 26. Passerina glaucocaerulea; 27. P. cyanoides; 28. P. brissonii; 29. P. parellina; 30. P. caerulea; 31. P. cyanea; 32. P. amoena; 33. P. versicolor; 34. P. ciris; 35. P. rositae; 36. P. leclancherii; 37. P. caerulescens. Principal components I and II are shown and III.is the height. The shortest minimally connected network is projected onto the component space in each of the models.

FIGURE 4. The "best" phenetic classification of this study. Seven species not included in the analysis SKIN + COLOR + SKEL CORR (Fig. 2C) are represented by dotted lines.


Figure 1


Figure 2


Figure 3


Figure 4

APPENDIX
DESCRIPIION OF EXTERNAL SKIN, CONTRAST, AND COLOR CHARACTERS

The abbreviation "Ex" is used for skin measurements and contrast characters. "Col" indicates the color measurements.

Ex1- Rectrix length, distance from where skin joins shaft of middle pair of rectrices to tip of longest rectrix.
(Ex2-Ex6 represent the shape of the tail and are divided by Exi in order to reduce the size factor; measurement is coded as negative until longest feather is measured then positive from longest feather).

Ex2- Distance from the tip of the outer rectrix to the tip of the second rectrix.

Ex3- Distance from the tip of the second rectrix to the tip of the third rectrix.

Ex4- Distance from the tip of the third rectrix to the tip of the fourth rectrix.

Ex5- Distance from tip of the fourth rectrix to the tip of the fifth rectrix.

Ex6- Distance from the tip of the fifth rectrix to the tip of the sixth rectrix.

Ex7- The width of the outer rectrix measured at the center of the feather and divided by Ex1.

Ex8- The width of the outer vane of the outer rectrix measured at the center of the feather and divided by Ex1.

Ex9- Distance from the tip of the undertail coverts to the tip of the longest rectrix divided by Exi.

Exi0- Distance from the tip of the uppertail coverts to the tip of the longest rectrix divided by Ex1.

Ex11- Wing length, distance from carpal joint (bend of wing) to tip of longest primary.
(Ex12-Ex16 represent the shape of the tail and are divided by Exil in order to reduce the size factor, coded as negaiive numbers until the longest feather is measured then a positive number.

Ex12- Distance from the tip of the ninth primary to the tip of the eighth primary.

Ex13- Distance from the tip of the eighth primary to the tip of the seventh primary.

Ex14- Distance from the tip of the seventh primary to the tip of the sixth primary

Ex15- Distance from the tip of the sixth primary to the tip of the fifth primary

Ex16- Distance from the tip of the fifth primary to the tip of the fourth primary

Exi7- Width of the ninth primary measured at the center of the feather and divided by Ex11.

Ex18- Width of the outer vane of the ninth primary measured at the center of the feather and divided by Exil.

Ex19- Width of the eight primary measured at the center of the feather and divided by Ex11.

Ex20- Width of the outer vane of the eight primary measured at the center of the feather and divided by Ex11.

Ex21- Width of the seventh primary measured at the center of the
feather and divided by Ex11.
Ex22- Width of the outer vane of the seventh primary measured at the center of the feather and divided by Exil.

Ex23- Width of the sixth primary measured at the center of the feather and divided by Ex11.

Ex24- Width of the outer vane of the sixth primary measured at the center of the feather and divided by Exil.

Ex25- Width of the first secondary measured at the center of the feather and divided by Ex11.

Ex26- Width of the outer vane of the first secondary measured at the center of the feather and divided by Exil.

Ex27- Distance from the tip of the longest secondary to the tip of the longest primary; measurement divided by Exil.

Ex28- Hallux length.
Ex29- Length of the middle toe divided by Ex28.
Ex30- Length of the second toe divided by Ex28.
Ex31- Length of the fourth toe divided by Ex28.
Ex32- Angle of the commissural point relative to the tomia.
Ex33- An angle measurement of the arc of the mandibular ramus.
Ex34- White spots in the tail. Coded: 0) absent; 1) present.
Ex35- Under-tail coverts contrasting to belly. Coded: 0) no contrast;

1) contrast.

Ex36- White present at apex of primaries. Coded: 0) absent; 1) present.
Ex37-White at base of primaries. Coded: o) absent; 1) present.
Ex38- White on primary coverts. Coded: 0) absent; 1) present.
Ex39- White on secondary coverts. Coded: 0) absent; 1) present.

Ex40-Marginal coverts contrasting to other coverts. Coded: 0) no contrast; 1) contrast.

Ex41-Malar region contrasting to auricular. Coded: 0) no contrast; 1) contrast.

Ex42- Lore region contrasting to forehead. Coded: 0) no contrast; 1) contrast.

Ex43- Forehead contrasting to crown. Coded: 0) no contrast; 1) contrast.

Ex44- Occiput contrasting to nape. Coded: 0) no contrast; 1) contrast.
Ex45- Occiput contrasting to crown. Coded: 0) no contrast; 1) contrast.

Ex46- Nape contrasting to back (base color). Coded: 0) no contrast; 1) contrast.

Ex47-Chin contrasting to gular. Coded: 0) no contrast; 1) contrast.
Ex48-Gular contrasting to jugulum. Coded: 0) no contrast; 1) contrast.

Ex49-Eye ring. Coded: 0) absent; 1) present.
Ex50- Breast streaking. Coded: 0) absent; 1) present.
Ex51- Back streaking. Coded: 0) absent; 1) present.
Ex52- Side of body streaked. Coded: 0) absent; 1) present.
Ex53-Flanks streaked. Coded: 0) absent; 1) present.
Ex54- Abdomen contrasting to breast. Coded: 0) no contrast;

1) contrast.

Ex55- Rump contrasting to back. Coded: 0) no contrast; 1) contrast.
Ex56- Presence of a crest. Coded: 0) absent; 1) present.
Ex57- Color sexual dimorphism. Coded; 0) absent; 1) present.

Ex58-Middle wing coverts contrasting to other coverts. Coded:
0 ) no contrast; 1) contrast.
Ex59- Superciliary line contrasting to crown. Coded: 0) no contrast; 1) contrast.

Ex60-Auricular white. Coded: 0) no; 1) yes.
Ex61- White spot at base of lower manaible. Coded: 0) absent;

1) present.

Ex62- Stripes on throat. Coded: 0) absent; 1) present.
Ex63- Upper-tail coverts contrasting to rump. Coded: 0) no contrast; 1) contrast.

Ex64- Streaking on the crown. Coded: 0) absent; 1) present.
Ex65-Flanks contrasting to abdomen. Coded: 0) no contrast;

1) contrast.

Ex66-Sides contrasting to breast. Coded: 0) no contrast; 1) contrast.

Color characters ( COl ) of the bird were recorded using the dominant wave length as the measurement of color. Color measurements were taken from eight regions of the bird: 1) crown; 2) back; 3) rupp ; 4) upper-tail coverts; 5) gular, jugulum region; 6) breast; 7) abdomen; 8) crissum.

APPENDIX I
The First Three Principal Components Based on Matrices of Correlations Among Characters treated in Two Different Ways

| Ex | Mal | Skin Char | ters | Fema | Skin Cha | cters |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: |
| No. | I | II | III | I | II | III |
| 1 | 0.674 | $-0.576$ | 0.382 | 0.726 | -0.567 | 0.036 |
| 2 | -0.706 | -0.084 | -0.021 | -0.631 | 0.431 | 0.355 |
| 3 | -0.746 | 0.235 | -0.028 | -0.573 | 0.428 | 0.419 |
| 4 | -0.638 | 0.339 | -0.023 | -0.663 | 0.159 | 0.245 |
| 5 | -0.620 | 0.238 | -0.021 | -0.529 | 0.459 | 0.443 |
| 6 | -0.295 | 0.089 | -0.061 | -0.353 | -0.272 | -0.155 |
| $?$ | -0.289 | 0.077 | -0.455 | -0.320 | 0.639 | 0.005 |
| 8 | 0.353 | -0.036 | -0.443 | 0.233 | 0.343 | -0.494 |
| 9 | 0.821 | -0.219 | -0.189 | 0.763 | -0.166 | -0.303 |
| 10 | 0.834 | -0.187 | -0.124 | 0.794 | -0.193 | -0.132 |
| 11 | 0.409 | -0.712 | 0.384 | 0.483 | -0.606 | 0.093 |
| 12 | -0.849 | -0.103 | -0.003 | -0.847 | -0.299 | -0.025 |
| 13 | -0.886 | 0.021 | 0.007 | -0.909 | -0.082 | -0.069 |
| 14 | -0.628 | 0.058 | 0.244 | -0.670 | -0.179 | 0.167 |
| 15 | -0.872 | -0.099 | 0.209 | -0.838 | -0.340 | 0.067 |
| 16 | -0.798 | -0.101 | 0.181 | -0.704 | -0.270 | 0.169 |
| 17 | -0.178 | 0.009 | -0.609 | -0.270 | 0.381 | -0.731 |
| 18 | -0.076 | -0.209 | -0.505 | -0.222 | 0.454 | -0.541 |
| 19 | -0.439 | -0.188 | -0.611 | -0.313 | 0.173 | -0.729 |
| 20 | -0.602 | -0.205 | -0.510 | -0.621 | 0.031 | -0.494 |
| 21 | -0.191 | -0.317 | -0.688 | -0.135 | 0.124 | -0.798 |


| 22 | -0.358 | -0.485 | -0.559 | -0.432 | 0.098 | -0.634 |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: |
| 23 | -0.017 | -0.261 | -0.694 | -0.069 | 0.182 | -0.720 |
| 214 | -0.189 | -0.480 | -0.574 | -0.340 | 0.031 | -0.746 |
| 25 | 0.607 | -0.246 | -0.437 | 0.275 | 0.524 | 0.028 |
| 26 | 0.010 | -0.475 | -0.548 | -0.010 | 0.026 | -0.224 |
| 27 | -0.788 | -0.215 | 0.269 | -0.488 | -0.372 | $-0.117$ |
| 28 | 0.474 | -0.68i | 0.328 | 0.456 | -0.617 | 0.084 |
| 29 | -0.192 | 0.289 | 0.499 | 0.221 | -0.494 | 0.271 |
| 30 | 0.195 | -0.309 | 0.140 | 0.291 | -0.470 | 0.011 |
| 31 | 0.250 | -0.256 | 0.187 | 0.340 | -0.664 | 0.128 |
| 32 | 0.449 | -0.183 | -0.185 | 0.437 | -0.029 | -0.253 |
| 33 | -0.480 | 0.378 | 0.055 | -0.426 | 0.200 | 0.262 |
| 34 | -0.491 | -0.651 | 0.176 | -0.318 | -0.723 | -0.188 |
| 35 | 0.078 | -0.684 | -0.007 | 0.183 | -0.304 | -0.287 |
| 36 | -0.384 | -0.662 | 0.047 | -0.336 | -0.458 | 0.008 |
| 37 | -0.544 | -0.694 | 0.174 | -0.482 | -0.547 | 0.018 |
| 38 | -0.511 | -0.532 | 0.186 | -0.259 | -0.451 | -0.148 |
| 39 | -0.612 | -0.546 | 0.255 | -0.525 | -0.481 | 0.109 |
| 40 | 0.092 | -0.475 | 0.149 | 0.055 | -0.528 | -0.029 |
| 41 | 0.217 | -0.043 | 0.001 | -0.037 | -0.158 | 0.252 |
| 42 | -0.211 | 0.431 | -0.376 | -0.111 | -0.258 | -0.328 |
| 43 | 0.299 | 0.115 | 0.324 | 0.324 | -0.094 | -0.055 |
| 44 | 0.025 | 0.006 | 0.247 | 0.305 | -0.022 | -0.040 |
| 45 | 0.133 | 0.241 | 0.043 | 0.468 | -0.099 | 0.236 |
| 46 | -0.241 | 0.407 | 0.032 | -0.122 | -0.102 | 0.049 |
| 47 | -0.113 | 0.075 | 0.124 | 0.139 | 0.087 | 0.062 |


| 48 | -0.243 | 0.081 | -0.048 | 0.021 | -0.216 | -0.089 |
| :--- | :---: | :---: | :---: | :---: | :---: | :---: |
| 49 | -0.237 | 0.469 | -0.135 | -0.109 | 0.319 | 0.124 |
| 50 | -0.032 | -0.080 | 0.074 | -0.387 | 0.071 | -0.018 |
| 51 | -0.364 | -0.512 | 0.122 | -0.642 | -0.327 | -0.023 |
| 52 | -0.176 | -0.136 | 0.153 | -0.717 | -0.265 | -0.049 |
| 53 | -0.255 | -0.047 | 0.133 | -0.731 | -0.347 | -0.077 |
| 54 | -0.440 | -0.039 | 0.319 | -0.387 | -0.262 | 0.344 |
| 55 | -0.312 | 0.279 | 0.128 | -0.079 | 0.319 | -0.165 |
| 56 | 0.282 | 0.168 | 0.383 | 0.288 | -0.057 | 0.257 |
| 57 | -0.505 | 0.362 | 0.043 | -0.467 | 0.133 | 0.220 |
| 58 | -0.386 | 0.273 | -0.031 | -0.332 | -0.273 | -0.051 |
| 59 | 0.376 | -0.245 | 0.333 | 0.184 | -0.201 | 0.317 |
| $* 1$ | -0.538 | -0.556 | 0.219 | 0.016 | -0.711 | -0.412 |
| 60 | 0.247 | -0.038 | 0.103 | 0.256 | -0.106 | 0.037 |
| 61 | 0.146 | 0.003 | 0.101 | 0.098 | 0.041 | -0.022 |
| 62 | -0.038 | -0.072 | -0.317 | -0.049 | -0.026 | -0.191 |
| $* 2$ | 0.876 | -0.191 | -0.065 | 0.824 | 0.191 | -0.195 |
| 63 | -0.502 | -0.627 | 0.147 | -0.322 | -0.278 | -0.056 |
| 64 | -0.290 | -0.299 | 0.106 | -0.594 | -0.311 | -0.057 |
| 65 | 0.081 | 0.138 | 0.349 | 0.185 | -0.218 | -0.449 |
| 66 | 0.183 | 0.058 | 0.260 | 0.172 | -0.323 | -0.547 |
| 6 |  |  | -0.37 |  |  |  |

*1- Number of rectrices with large white spots. Coded: 0) none;

1) one; 2) two; 3) three; 4) four; 5) five; 6) six.
*2- Number of primaries which are slotted. Coded; 0) none; 1) one; 2) two; 3) three; 4) four; 5) five; 6) six.

## APPENDIX II

The First Three Principal Components Based on Matrices of Correlations among Skeletal Characters/ Comp I

| Sk |  |  |  | Sk |  |  |  |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
| No. | I | II | III | No. | I | II | III |
| 1 | 0.659 | $-0.474$ | 0.247 | 28 | 0.587 | 0.245 | -0.401 |
| 2 | 0.514 | -0.526 | 0.262 | 29 | 0.614 | -0.064 | -0.241 |
| 3 | 0.033 | 0.195 | 0.012 | 30 | 0.119 | -0.465 | 0.037 |
| 4 | 0.780 | -0.272 | -0.022 | 31 | 0.849 | 0.311 | $-0.276$ |
| 5 | 0.385 | -0.642 | 0.379 | 32 | 0.727 | 0.509 | -0.192 |
| 6 | 0.225 | -0.658 | 0.339 | 33 | 0.824 | 0.501 | -0.090 |
| 7 | -0.630 | 0.262 | 0.262 | 34 | 0.479 | 0.698 | -0.176 |
| 8 | -0.519 | 0.324 | 0.644 | 35 | 0.841 | 0.025 | -0.190 |
| 9 | -0.185 | 0.121 | 0.499 | 36 | 0.075 | 0.824 | 0.050 |
| 10 | -0.592 | 0.236 | 0.606 | 37 | -0.108 | 0.829 | 0.164 |
| 11 | -0.256 | 0.011 | 0.372 | 38 | 0.506 | 0.687 | -0.133 |
| 12 | 0.734 | -0.419 | 0.067 | 39 | 0.649 | 0.488 | -0.110 |
| 13 | 0.487 | -0.722 | 0.167 | 40 | 0.626 | .. 0.416 | -0.191 |
| 14 | 0.580 | -0.308 | 0.444 | 41 | -0.302 | 0.037 | -0.496 |
| 15 | 0.331 | -0.389 | -0.664 | 42 | 0.431 | $-0.317$ | -0.279 |
| 16 | -0.768 | 0.114 | -0.364 | 43 | $0.19 ?$ | 0.440 | -0.446 |
| 17 | -0.560 | 0.130 | -0.544 | 44 | $-0.267$ | -0.637 | -0.381 |
| 18 | -0.233 | -0.062 | -0.141 | 45 | $-0.278$ | -0.653 | -0.396 |
| 19 | -0.655 | -0.194 | -0.356 | 46 | 0.085 | -0.524 | -0.269 |
| 21 | -0.440 | 0.233 | -0.618 | 47 | $-0.243$ | -0.586 | -0.506 |

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| 22 | -0.299 | -0.029 | -0.639 | 48 | -0.032 | -0.144 | -0.039 |
| :--- | ---: | ---: | ---: | ---: | ---: | ---: | ---: |
| 23 | 0.351 | -0.329 | 0.019 | 49 | -0.699 | -0.275 | -0.260 |
| 24 | -0.867 | 0.044 | -0.028 | 50 | -0.678 | -0.192 | -0.117 |
| 26 | 0.515 | 0.520 | -0.116 | 51 | -0.426 | 0.259 | -0.034 |
| 27 | 0.465 | 0.461 | -0.181 |  |  |  |  |

















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| 1 | SKEL | 11．Clio |
| 2 | SKEL | 5.750 |
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| 4 | Skri | C．580 |
| 5 | SKEL | 7.410 |
| 5 | SkEL | 3.830 |
| 7 | SkEL | 12.1 cs |
| 5 | SkEL | 13.510 |
| 9 | SkEL | 3.150 |
| 10 | SKEL | 11.630 |
| 11 | jkEL | 2t．390 |
| 12 | SKLL | 17.340 |
| 1.3 | SKEL | 4.600 |
| 14 | SHEL | 2．69J |
| 15 | StEL | C．E50 |
| 16 | SKFL | 15．350 |
| 17 | SKFL | 17.360 |
| 19 | 5k：L | 3.270 |
| 19 | SKFL | 3.640 |
| 21 | SKEL | 17.480 |
| 22 | SkEL | －16．4．70 |
| 23 | SK「L | 7.9 \％ |
| 24 | ckel | 8.250 |
| 2 n | SKFL | 3.050 |
| 27 | SKEL | 4.52 C |
| く8 | SKFL | 7.990 |
| 29 | SKEL | 8.450 |
| 36 | SKEL | 5.36 C |
| 11 | SKFL | 2.640 |
| 3. | SKEL | 1.190 |
| 35 | Skr | 2.630 |
| 34 | SKEL | 14.820 |
| 35 | SAFL | C． 970 |
| 36 | SKEL | 24.900 |
| 37 | Skrel | 17.400 |
| 32 | SKEL | C． 920 |
| 39 | SKEL | 1.720 |
| 40 | SKFL | 5.520 |
| 41 | SKEL | 2．640 |
| $4{ }^{4}$ | SKEL | 4.220 |
| 43 | SKこL | 16.530 |
| 44 | SAEL | 17.750 |
| 45 | SKEL | 19.040 |
| 4 t | SKEL | 1.330 |
| 47 | Skel | 16．16is |
| 48 | SKEL | 2.160 |
| 49 | SkEt | 4.650 |
| 50 | SKFL | 1.720 |
| 51 | SMEL | 8.740 |




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|  | 1-spl2 A | 2-PrFU C | 3-PHFU A | 4-PHEU L | 5-PrELI H |  | 7-CARO ${ }^{\circ}$ | 8-CARES | 9-CADY C | 11FHCD C |
| Col 1 | 579.300 | 576.700 | 581.100 | 579.000 | 582.200 | 579.000 | 577.700 | 575.500 | $574 . \cos$ | 0.0 |
| Col 2 | 582.000 | 576.000 | 581.100 | 579.000 | 150.500 | 575.000 | 579.000 | 575.500 | 574.c00 | 574.000 |
| Col 3 | 578.600 | 574.000 | 579.9C0 | 579.000 | 578.000 | 579.000 | 579.000 | 575.500 | $574 . \mathrm{COJ}$ | 574.600 |
| Col 4 | 518.200 | 576.000 | 576.500 | 579.00 C | 579.030 | 579.00 C | 579.000 | 575.500 | $574 . \mathrm{COJ}$ | 574.600 |
| Col 5 | 514.700 | 576.000 | 581.000 | $\leq 76 . t 00$ | 579.100 | 578.50 C | 577.300 | 578.000 | 574.c39 | C.0 |
| $\operatorname{col} 6$ | 57\%.Uく0 | 575.000 | 574.CCO | 575.00 C | 578.000 | 576.400 | 577.300 | 577.000 | 574.c00 | 574.500 |
| Col 7 | 575.000 | ¢75.030 | 574.000 | 575.00 C | 575.000 | 576.400 | 577.000 | 577.000 | 574.603 | 574.000 |
| col 8 | 515.000 | 575.000 | 573.500 | 577.00C | 575.030 | 577.10C | 577.000 | 577.000 | 574.000 | 574.000 |
|  | 12F1ct | 1301 TY G | 145 ATR 1 | 155 maxI | 1654101 | 1753141 | 195 COEK | 1 CS OFFN | 215 AUEA | 2354121 |
| Col 1 | 0.3 | 481.200 | 577.060 | 574.000 | 0.0 | 572.000 | 572.000 | 0.0 | 576.800 | 5E2.590 |
| Col 2 | 573.030 | 523.600 | 574.500 | 574.000 | 57..CCO | 572.000 | 572.000 | 0.0 | 575.700 | 563.030 |
| Col 3 | 57E.cco | 544.900 | 574.500 | 574.000 | 574.060 | 577.000 | 572.000 | 0.0 | 575.703 | 578.500 |
| Col 4 | 518.203 | 523.800 | 574.500 | 574.000 | 574.000 | 572.00 C | 572.000 | 0.0 | 575.703 | 563.000 |
| Col 5 | 573.CCO | 0.0 | 0.0 | 581.000 | 575.000 | 575.00 C | $5 \mathrm{BC}$. | 575.600 | $578 . \mathrm{coj}$ | C.1] |
| Col 6 | 577.500 | 576.000 | 0.0 | 577.50 C | 575.3 CO | 577.000 | 575.700 | 574.000 | 578.600 | 577.500 |
| Col 7 | 577.500 | 516.000 | 0.0 | 577.000 | 0.0 | 571.000 | 58.6 .700 | 575.600 | 590.003 | 579.000 |
| Col 8 | 571.500 | 576.830 | 582.000 | 581.000 | 578.500 | 577.00 C | 581.300 | 581.300 | 59C. 503 | 58:.500 |
|  | 245 RUFI | 255 ALBI | 26P GLAU | 27 PCVAN | 28 P GRIS | TQP PADE | 30 Cl CYFP | 2ir cyan | 32 D ANO | 33 P VER1 |
| Col 1 | 485.500 | 450.830 | 582.0c0 | 581.500 | 582.000 | 561.500 | 579.600 | 579.000 | 579.800 | 566.230 |
| Col 2 | 4 E5.500 | 531.400 | 582.000 | 581.50 C |  | 581.50 C | 579.600 | 579.000 | 575,900 | $5 t 6.300$ |
| Col 3 | 455.500 | 581.000 | 582.C00 | 582.000 | 5 AZ .200 | 578.000 | 579.600 | 4P1. 500 | 585.300 | 500.300 |
| Col 4 | 495.500 | 531.300 | 582.060 | 582.600 | $5 \mathrm{H2.000}$ | 575.000 | 579.600 | 576.000 | 579.c03 | 506.330 |
| Ccl 5 | 51c.cco | 581.300 | 581. CCO | 581.000 | $5 \mathrm{B2.0c0}$ | 578.000 | 577.500 | 560.000 | 579.coo | 571.200 |
| Col 6 | 574.550 | 511.5J0 | 282.060 | 582.000 | 5H2.000 | 577.100 | 575.500 | ¢ ¢0.000 | 579.500 | 575.30 C |
| Col 7 | 514.500 | 581.000 | 581.500 | 581.000 | 5月1.000 | $577.00 C$ | 575.000 | 579.000 | 578. 500 | 575.300 |
| Col 8 | 574.500 | 531.000 | 582.CCO | 581.000 | 582.0C0 | 577.000 | 575.000 | 579.000 | 575.cos | 575.300 |
|  | 340 CIPE | 35 P ROS 1 | 309 LECL |  |  |  |  |  |  |  |
| Col 1 | 574.060 | 509.500 | 591.560 |  |  |  |  |  |  |  |
| Col 2 | 575.030 | 509.500 | 531.000 |  |  |  |  |  |  |  |
| Col 3 | 4 E1. ${ }^{\text {cieu }}$ | 535.530 | 581. 000 |  |  |  |  |  |  |  |
| COI 4 | $4 E 1.500$ | 491.500 | 581.050 |  |  |  |  |  |  |  |
| col 5 | 5ec.bcu | 576.000 | 577.000 |  |  |  |  |  |  |  |
| Col 6 | 575.500 | 575.00 C | $577 . \mathrm{CCC}$ |  |  |  |  |  |  |  |
| COI 7 | 583.000 | 575.03 C | 577.000 |  |  |  |  |  |  |  |
| Col 8 | 575.5c0 | 574.000 | 572.600 |  |  |  |  |  |  |  |

Appendix III E,1/1

