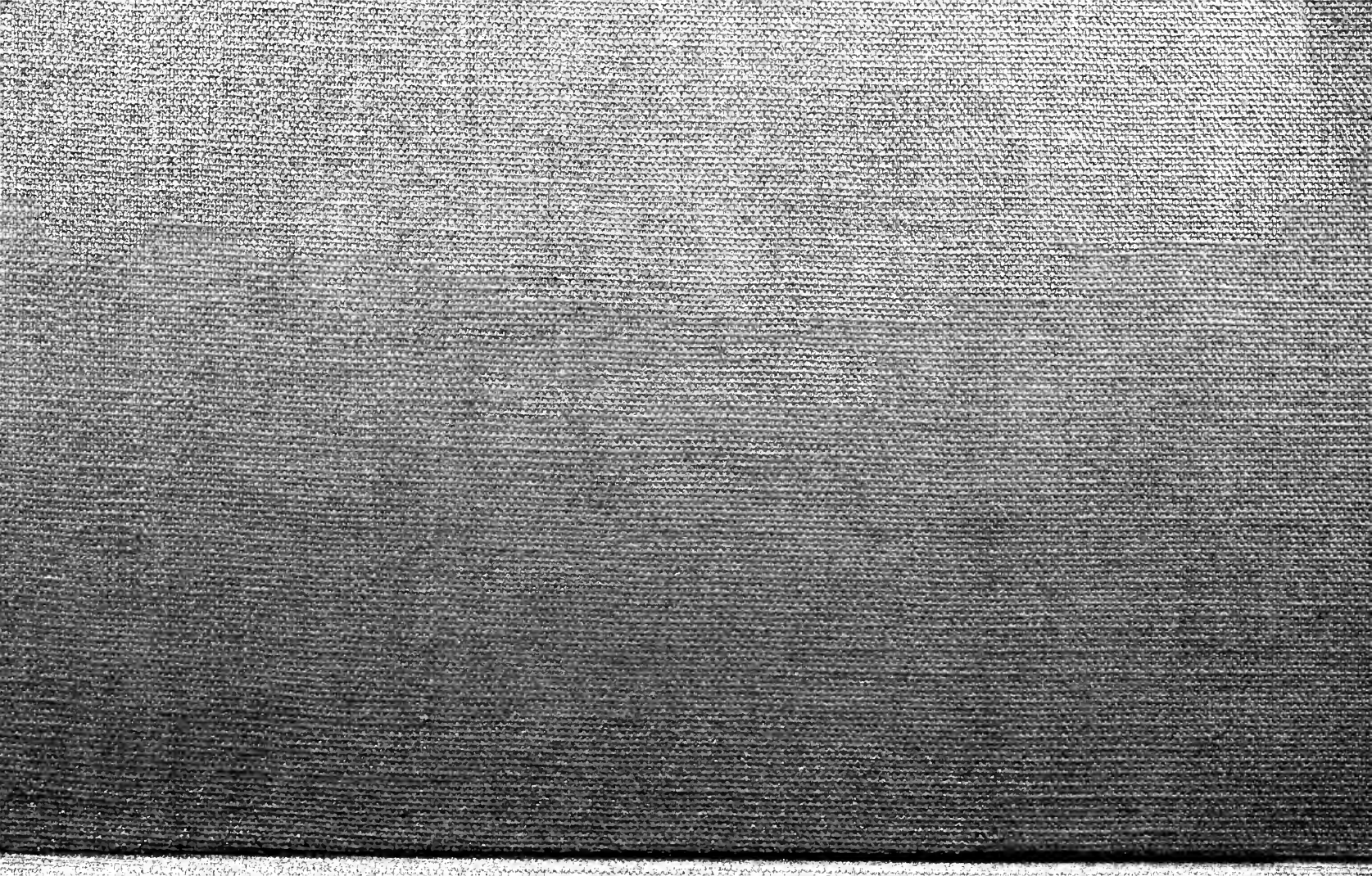

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PHENETIC VARIATION IN THE AVIAN SUBFAMILY CARDINALINAE

By

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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 *(C. sinuatus)* (Bock, 1964), and hybridization in grosbeaks, *Pheucticus melanocephalus* and *P. ludovicianus* (West, 1962) and buntings, *Passerina cyanea* and *P. amoena* (Sibley and Short, 1959).

This study employs numerical analysis of skeletal measurements to assess phenetic affinities of the species in the subfamily Cardi-

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nalinae. 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.

Materials and Methods

The generic and specific designations used in this study are those of Paynter (1970). Table 1 lists these 37 species, a brief description

Table 1.—Number Assigned to Each Species, Number of Skeletons Measured, and Geographic Distribution of Species.[1]

Species Number	Species[2]	Number of Skeletons	Breeding Season Distribution
1	*Spiza americana*	10	E North America
2	*Pheucticus chrysopeplus*	8	Northern South America and W Mexico
3	*Pheucticus aureoventris*	2	Subtropical to temperate zone, South America
4	*Pheucticus ludovicianus*	10	S Canada, E U.S.
5	*Pheucticus melanocephalus*	10	SW Canada, W U.S. to S Mexico
6	*Cardinalis cardinalis*	10	S Ontario to gulf states; SW U.S. to Guatemala
7	*Cardinalis phoeniceus*	3	Coastal N South America
8	*Cardinalis sinuatus*	10	SW U.S. to C Mexico
9	*Caryothraustes canadensis*	9	Tropical zone of South America
10	*Caryothraustes humeralis*	—	Tropical zone of South America
11	*Rhodothraupis celaeno*	7	E Mexico
12	*Periporphyrus erythromelas*	—	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	S 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, E Ecuador
23	*Saltator atricollis*	3	S Brazil, Paraguay 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* (*Cyanoloxia glaucocaerulea*)	2	S Brazil, Uruguay and E Argentina
27	*Passerina cyanoides* (*Cyanocompsa cyanoides*)	11	SE Mexico to Amazonia

TABLE 1.—Continued

Species Number	Species[2]	Number of Skeletons	Breeding Season Distribution
28	*Passerina brissonii* (*Cyanocompsa cyanea*)	3	Tropical and lower subtropical zones of South America
29	*Passerina parellina* (*Cyanocompsa parellina*)	6	Mexico to Nicaragua
30	*Passerina caerulea* (*Guiraca caerulea*)	10	Central and S U.S. S to NW Costa Rica
31	*Passerina cyanea*	10	SE Canada to gulf States
32	*Passerina amoena*	9	SW Canada, W U.S., NW Mexico
33	*Passerina versicolor*	7	SW border of U.S. to Guatemala
34	*Passerina ciris*	10	S U.S., N Mexico
35	*Passerina rositae*	7	S Mexico
36	*Passerina leclancherii*	10	SW Mexico
37	*Passerina caerulescens* (*Porphyrospiza caerulescens*)	—	Compos of Brazil and E Bolivia

[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.O.U. Check-list, 1957) when at variance with those used by Paynter (1970).

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 exclude *Caryothraustes humeralis*, *Periporphyrus erythromelas*, *Saltator maxillosus*, *S. cinctus*, *S. rufiventris*, and *Passerina caerulescens*. The skeletal characters were those examined by Robins and Schnell (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 characters permitted all regions of the bird to be represented in the analyses. 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 mutivariate statistical techniques from the Numerical Taxonomy system of computer programs (NT-SYS) developed by F. J. Rohlf, J. Kishpauph, and D. Kirk. Two techniques were used: R-type, involving the analysis of correlations among characters, and Q-type, an anlysis 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. Character state codes are thus independent of original units of

measurement 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 tree diagrams (phenograms). The R-type analysis extracts principal components from a matrix of correlations 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) were 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 distances 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 skull 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, tree-diagram representations of which have been generated (Fig. 1), plus the 27 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 tree diagram indicating 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. SKEL-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. SKEL/COMP-I indicates characters divided by unstandardized principal component I; SKEL/HUMER characters divided by the humerus length; SKEL/STERN characters divided by the sternum length; and SKEL/TIBIO characters divided by the tibiotarsus length.

FIGURE 1

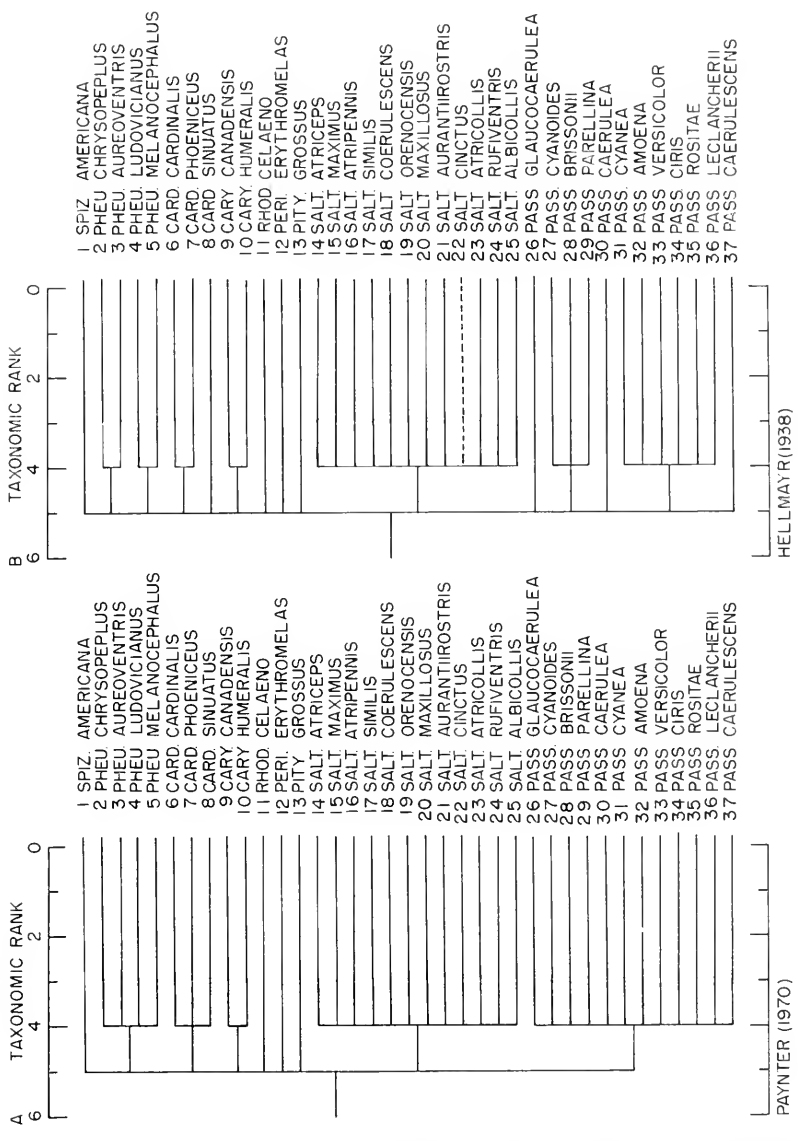


FIG. 1.—Dendrograms depicting two former classifications of the subfamily Cardinalinae: (A) that proposed by Paynter (1970); (B) that proposed by Hellmayr (1938). The following arbitrary similarity values were assigned to each taxonomic level: 1, subspecies; 2, species; 3, subgenus; 4, genus; 5, subfamily.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

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. Thus, the vertical sequence in a phenogram does not imply relationships among the species.

Results

The dendrogram summary of the similarities between the 27 Basic Similarity Matrices (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 2B. Several differences in groupings can be seen in comparing the dendrogram of similarities between BSMs with that of the phenograms. Clustering enhanced differences between many of the BSMs. Phenograms with low 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. 2B), 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

FIGURE 2

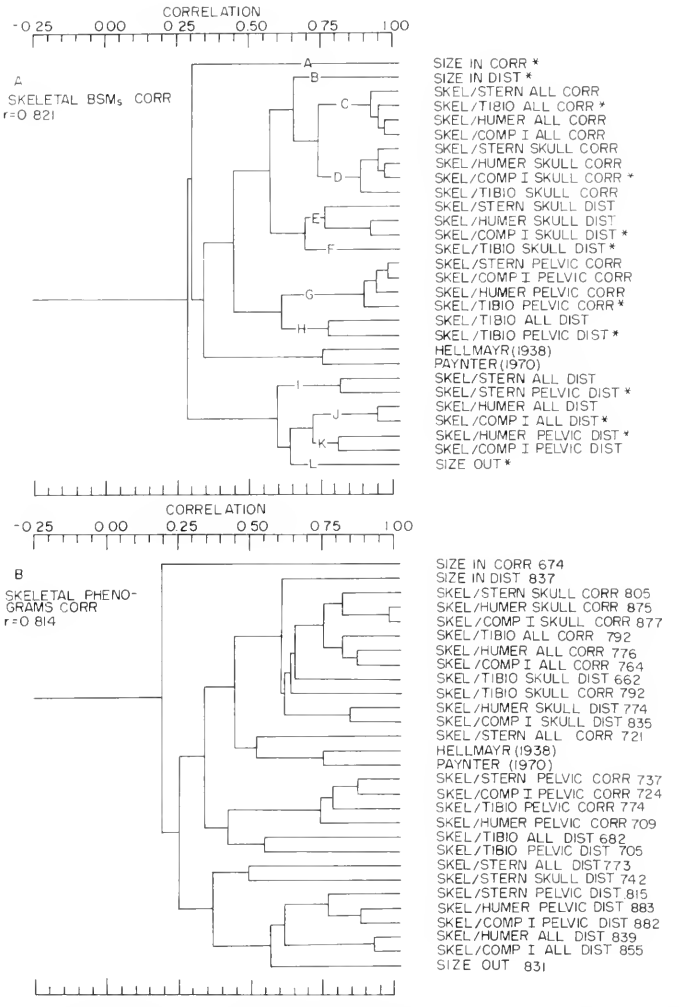


FIG. 2.—Dendrograms showing relationships among: (A) basic similarity matrices; (B) phenograms. Letters indicate groups of similar basic similarity matrices. Asterisks indicate the phenogram chosen to represent each of these groups—the phenogram with the highest cophenetic correlation coefficient. Cophenetic correlation coefficients are shown in the dendrogram of phenograms. Representative phenograms are shown in Figs. 3, 4, and 5.

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

FIGURE 3

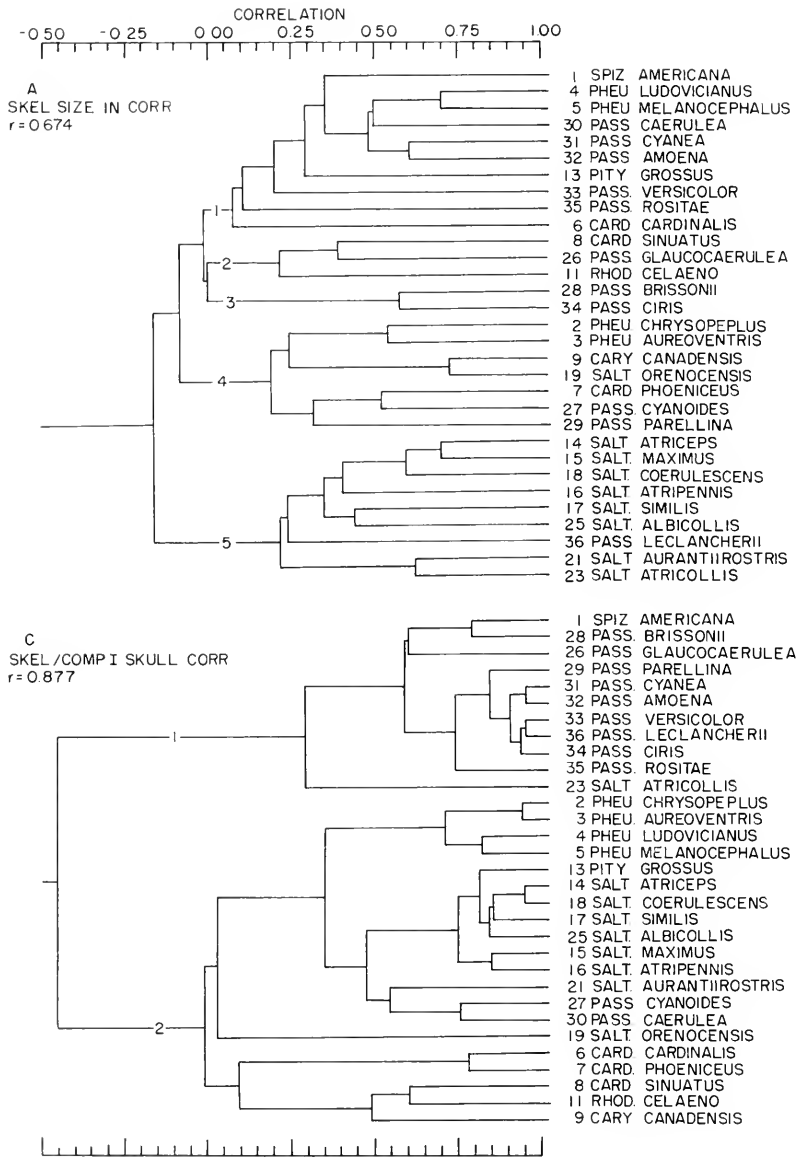
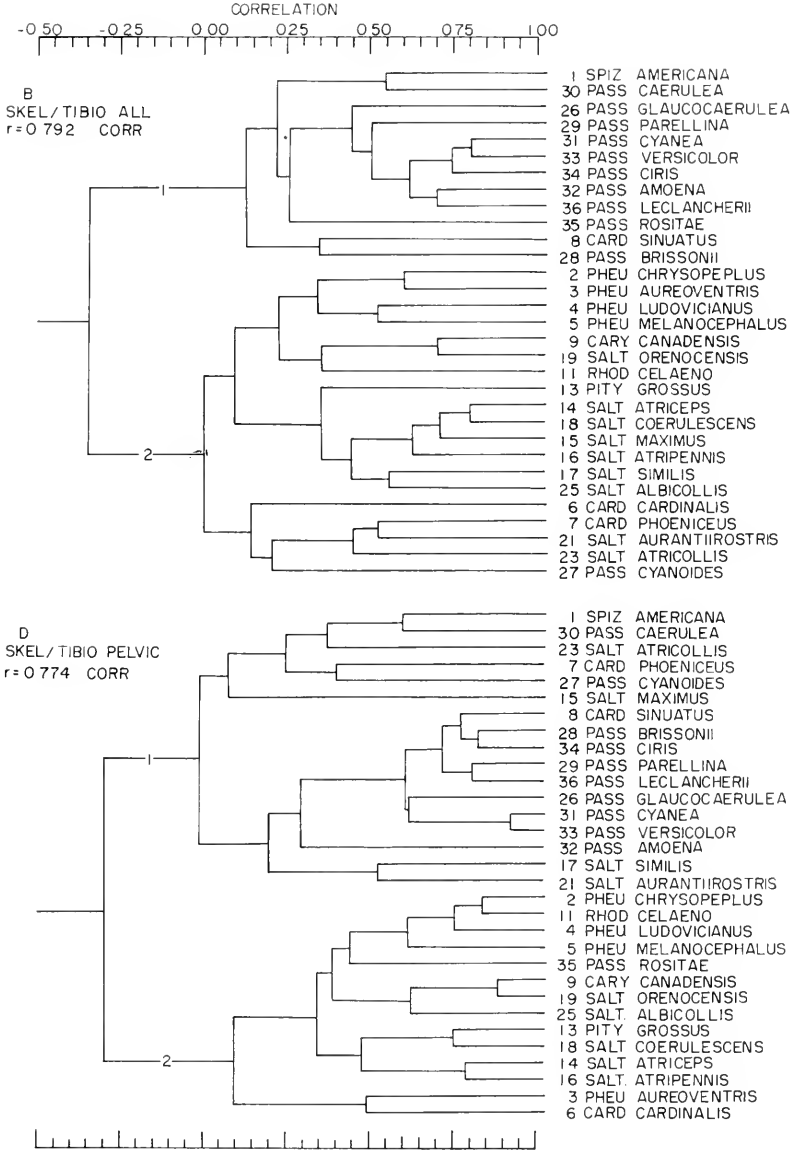


FIG. 3.—Phenogram representatives of groups A, C, D, and G (Fig. 2A). Numbers on the branches of the phenograms indicate clusters discussed in the results. These are four correlation analyses in which: (A) no attempt was made to reduce size; (B) all characters were divided by tibiotarsus length; (C)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



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 *(Pheucticus)* 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 sinatus*, *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 *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 tend 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. 4C) 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 tibiotarsus length) were used; however, the character sets were different (all characters, 14 pelvic characters). Both phenograms of this group (Fig. 2B) have relatively low cophenetic correlation coefficients. The representative phenogram is SKEL/TIBIO PELVIC DIST (Fig. 4D). The two major branches seen in Figure 4D 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 *P. brissonii* and *P. leclancerii* are added to the cluster in the phenogram not figured. The cluster bounded by *Pheucticus 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

FIGURE 4

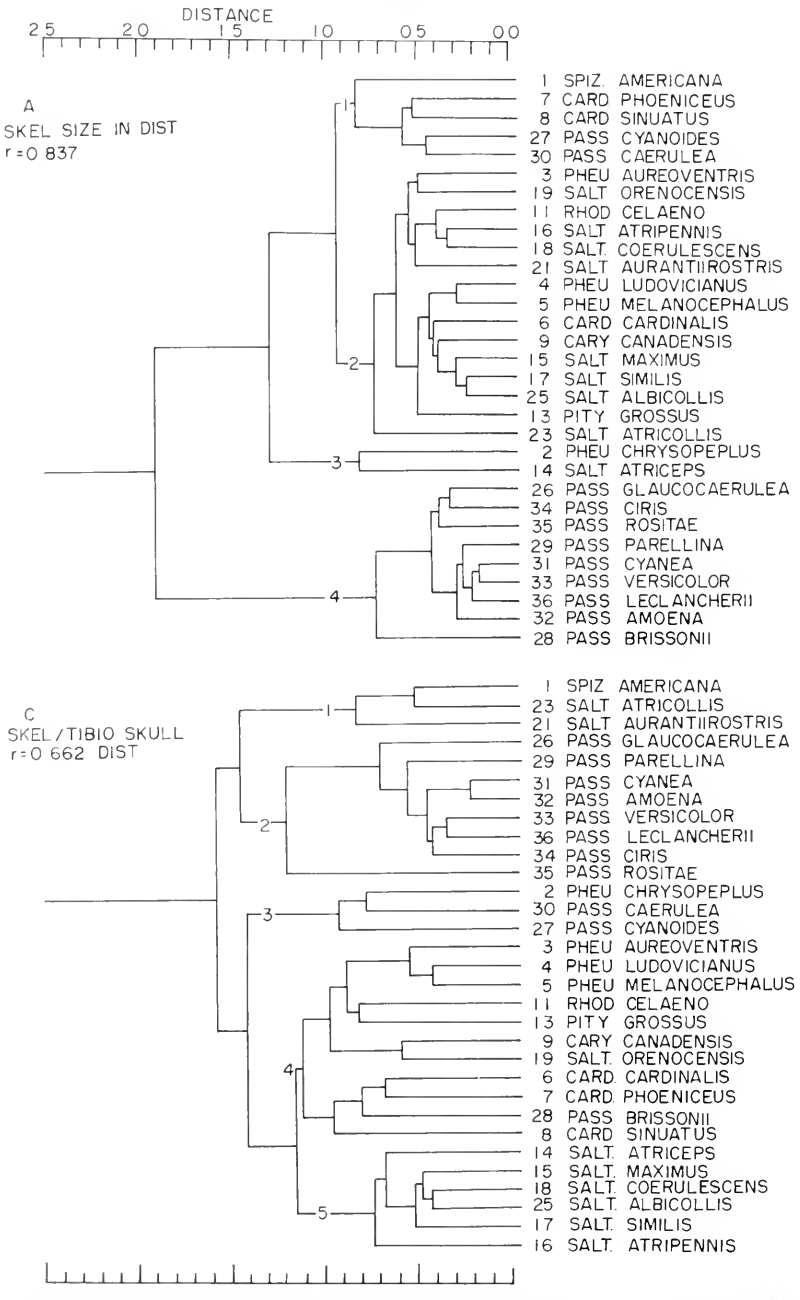
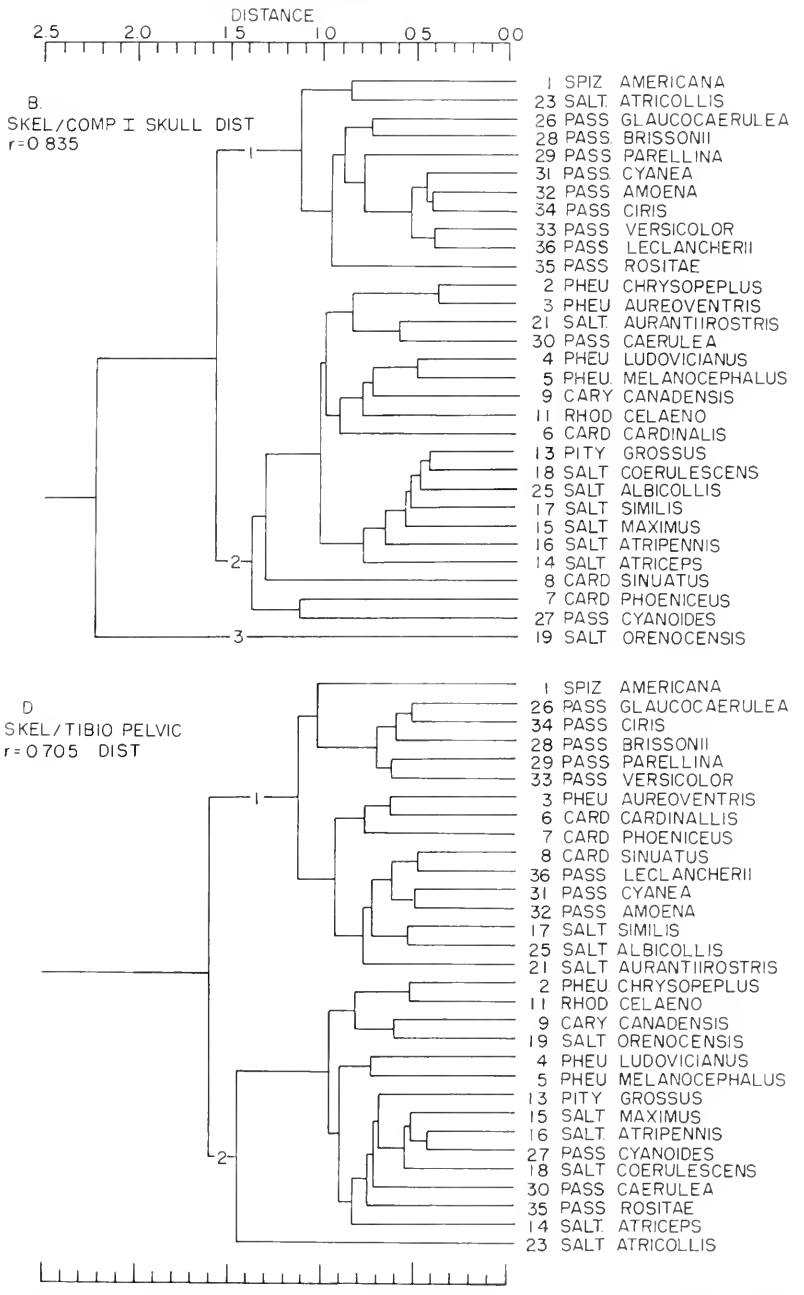


FIG. 4.—Phenogram representatives of groups B, E, F, and H (Fig. 2A). Numbers on the branches of the phenograms indicate clusters discussed in



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; (C) 14 skull characters were divided by tibiotarsus length; (D) 14 pelvic characters were divided by tibiotarsus length.

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 *Pheucticus ludovicianus* and *Passerina rositae* is found in both phenograms with three species (*Cardinalis 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 *Pheucticus chrysopeplus* and *Passerina parellina* in Figure 5A lost *Pheucticus chrysopeplus*, *P. aureoventris*, *Passerina brissonii*, and *P. parellina* while it gained *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). SKEL/COMP 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 *Pheucticus ludovicianus*) do not cluster the same in SKEL/HUMER ALL DIST as they do in Figure 5B. In SKEL/HUMER ALL 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/HUMER PELVIC DIST, 0.883; SKEL/COMP I PELVIC DIST, 0.882). SKEL/HUMER 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 *Pheucticus chrysopeplus* and *Rhodothraupis celaeno* contains *Pheucticus ludovicianus* and the cluster bounded by *Cardinalis sinuatus* and *Passerina versicolor* contains *P. glaucocaerulea*.

Group L contains one BSM (SIZE 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 gradual 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 anlyses of the 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 C, Fig. 2A, 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 that 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 for grassland sparrows. 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/HUMER 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 the 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 having the highest cophenetic correlation 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 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. maximus*, *S. similis* (in SKEL/TIBIO PELVIC 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. 3C) 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/TIBIO PELVIC CORR (Figs. 3B 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 representing each of these groups are more heterogeneous than the phenograms representing the groups of correlation BSMs.

The species of *Passerina*, as found in the cluster bounded by *P. glaucocaerulea* and *P. leclancherii* (SKEL/COMP I ALL DIST, Fig. 5B), 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 often join the group. For example, in SKEL/HUMER PELVIC DIST (Fig. 5C) the cluster in which most of these species are found does not contain *Passerina rositae* and *P. glaucocaerulea*.

Pheucticus 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 are found in most of the phenograms; one is composed of several species in the genus *Saltator*, the other of species of *Passerina*. The remaining species differ in their affinities in each of the phenograms. This possibly indicates that a gradual interspecific variation exists rather than discontinuous variation that would give 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. How-

ever, 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 correlation 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 that 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 ALL 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. *Pheucticus 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 *Pheucticus* 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 consistencies between SKEL/COMP I ALL DIST (Fig. 5B) and the other phenograms which should be emphasized. Three saltators (*S. 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, 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 (*S. aurantiirostris* and *S. atricollis*) probably represented distinct genera. The cluster of the remaining saltators is found in almost every phenogram much the same as in SKEL/COMP I ALL DIST.

The three species of *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 *P. caerulea* also seem to be different from the other species in this study. They tend to change their affinities in each of the

FIGURE 5

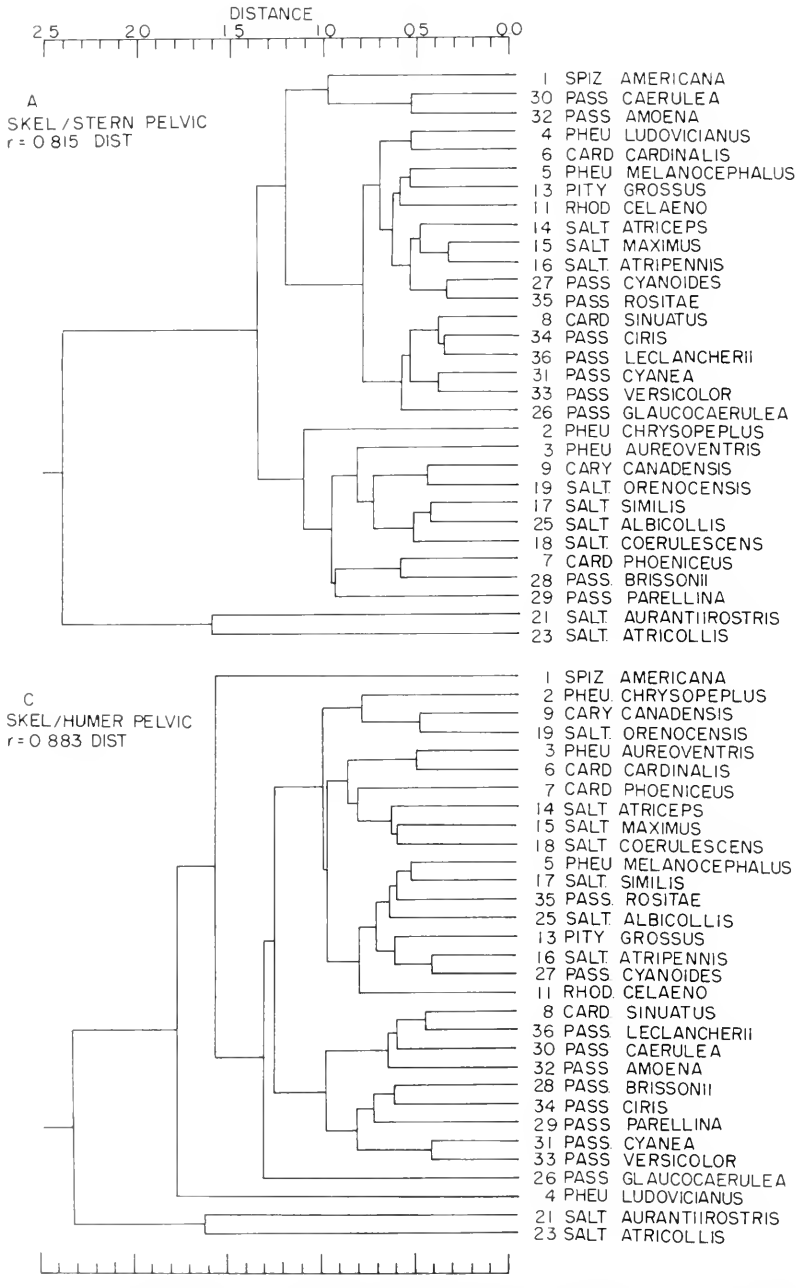
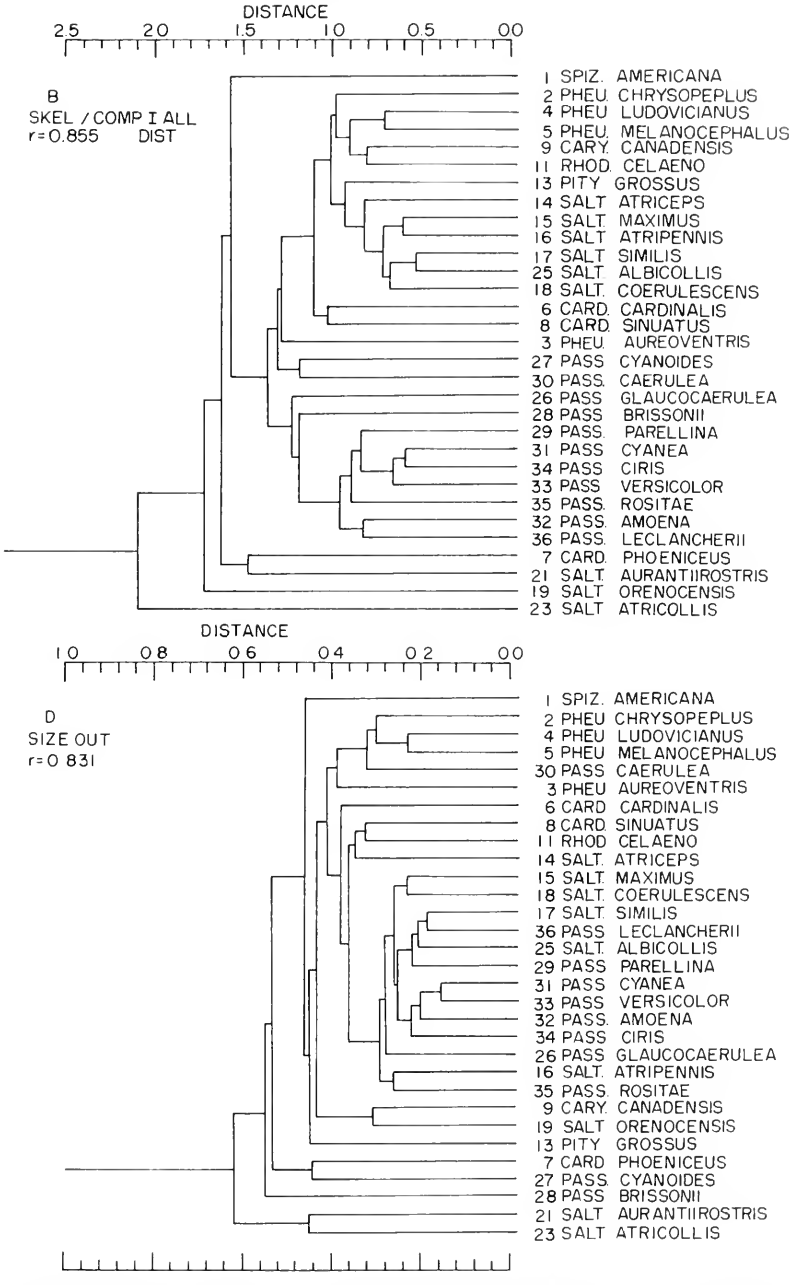


FIG. 5.—Phenogram representatives of groups I, J, K, and L (Fig. 2A). These are four distance analyses in which: (A) 14 pelvic characters were



divided by sternum length; (B) all characters were divided by unstandardized principal component I; (C) 14 pelvic characters were divided by humerus length; (D) the influence of the first principal component was removed mathematically from the distance matrix.

phenograms. The cluster of the remaining species in *Passerina* is found in almost every phenogram much the same as in SKEL/COMPT 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 (*S. orenocensis*, *S. aurantiirostris*, 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 often 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 restricted to the 14 pelvic characters; all of the species were 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 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. That distinct clusters are 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 influences 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) reflected kind of character sets employed. 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.

Based on phenetic groups, three saltators (*S. orenocensis*, *S. aurantiirostris* and *S. atricollis*) show little similarity to the other

species in the genus *Saltator*. This indicates that the saltators, as presently classified, are perhaps a heterogenous group. The three species in the genus *Cardinalis* showed little phenetic affinity to one another in the analysis 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. The remaining species of the subfamily cluster into groups of phenetically similar species which could be interpreted according to either former classification. Because of the above discrepancies, behavioral and ecological, as well as other morphological characters, should be examined.

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Literature Cited

American Ornithologists' Union. 1957. Check-list of North American birds, fifth ed. Baltimore, Amer. Ornithol. Union.

Beecher, W. J. 1953. A phylogeny of the Oscines. Auk, 70:270-333.

Bock, W. J. 1964. Bill shape as a generic character in the cardinals. Wilson Bull., 76:50-61.

de Schauensee, R. M. 1966. *Species Birds of South America*. Livingston Publ. Co., Narberth, Pa.

de Schauensee, R. M. 1970. *A Guide to the Birds of South America*. Livingston Publ. Co., Narberth, Pa.

Hellack, J. J. 1975. *A Phenetic Analysis of the Subfamily Cardinalinae*, Aves. unpubl. Ph.D. Dissertation. Univ. of Oklahoma.

Hellmayr, C. E. 1938. Catalogue of birds of the Americas. Field Mus. Nat. Hist. Publ. Zool. Ser. 13, pt. 11.

Johnson, W. W., Selander, R. K. 1971. Protein variation and systematics in Kangaroo rats (genus *Dipodomys*). Syst. Zool., 20:377-405.

Paynter, R. A. 1970. Subfamily Cardinalinae. Pages 216-245, *in* R. A. Paynter and R. W. Storer, eds. *Check-list of Birds of the World*, Vol. 13. Heffernan Press, Worcester, Mass.

Peterson, R. T., Chalif, E. L. 1973. *A Field Guide to Mexican Birds*. Houghton Mifflin Co., Boston.

Ridgway, R. 1901. The birds of North and Middle America. Bull. U.S. Natl. Mus., 50, pt. 1.

Robins, J. D., Schnell, G. D. 1971. Skeletal analysis of the *Ammodramus-Ammospiza* grassland sparrow complex; a numerical taxonomic study. Auk, 88:567-590.

Schnell, G. D. 1970. A phenetic study of the suborder Lari (Aves) II. Phenograms, discussion, and conclusions. Syst. Zool., 19:264-302.

Sibley, C. G., Short, L. L., Jr. 1959. Hybridization in the buntings (*Passerina*) of the Great Plains. Auk, 76:443-463.

Sneath, P. H. A., Sokal, R. R. 1973. Numerical taxonomy. W. H. Freeman and Co., San Francisco.

Sokal, R. R., Michener, C. D. 1967. The effects of different numerical techniques on the phenetic classification of bees of the *Hoplitis* complex (Megachilidae). Proc. Linn. Soc. London, 178:59-74.

Stallcup, W. B. 1954. Myology and serology of the avian family Fringillidae. Univ. Kansas Publ. Mus. Nat. Hist., 8:157-211.

Tordoff, H. B. 1954. A systematic study of the avian family Fringillidae based on the studies of the skull. Univ. Michigan Mus. Zool. Misc. Publ., 81:1-42.

West, D. A. 1962. Hybridization in grosbeaks (*Pheucticus*) of the Great Plains. Auk, 79:399-421.