PHENETIC ANALYSIS OF THE SUBFAMILY CARDINALINAE USING EXTERNAL AND SKELETAL CHARACTERS

JENNA J. HELLACK AND GARY D. SCHNELL

The subfamily Cardinalinae includes 37 species of cardinals, buntings, and grosbeaks, which have been divided into from 9 (Paynter 1970) to 15 genera (Hellmayr 1938). Previously using skeletal variables, Hellack (1976) investigated phenetic relationships of the subfamily with cluster analysis. In that study 3 species in the genus *Saltator* clustered differently from that suggested in previous classifications (Hellmayr 1938, Paynter 1970). The 3 *Cardinalis* species grouped together only in analyses using 14 skull characters, and all 31 species included in the study were very similar in relative measurements of the pelvic region. In this paper, we examine further the phenetic affinities of the subfamily by analyzing an additional set of external characters.

MATERIALS AND METHODS

We used 75 external morphologic characters in 10 analyses; in 2 of these Hellack's (1976) 49 skeletal characters were included. Table 1 lists the species, the number assigned to each, and common names (nomenclature follows Paynter 1970).

Table 1 of Hellack (1976) indicates the number of skeletons measured. The 49 measurements are from all skeletal regions. Due to lack of skeletal materials, only 31 of the 37 species were compared.

In the analyses of external morphologic characters, similar problems of obtaining material occurred. The Appendix lists the 75 external morphologic characters, which can be separated into 3 categories: (1) 33 study skin measurements of the tail, wing, toes, and bill; (2) color measurements (dominant wave length) from 8 body regions; (3) contrast characters in which 33 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; the means for each species are in Appendix IV of Hellack (1975).

Hellack measured study skin characters on 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 nominate race. Study skins were available for females of all 37 species, but only 36 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* (Munsell 1973) which specifies a given color in terms of 3 characters—hue, value, and chroma. We converted these to dominant wave lengths, excitation purity, and % reflectance using tables supplied by the Munsell company (Anonymous 1970); these conversions are discussed by Newhall et al. (1943). Only the dominant wave length of each region was included in the analysis. Color measurements were obtained for males of 34 species and females of 33. *Caryothraustes humeralis*, *Saltator cinctus*, and *S. albicollis* were not included in color analyses of the males. These species plus *S. maxillosus* were not included in color analyses of females.

Table 1

Species Included in the Study

Species No.	Scientific Name[1]	Common Name[2]	Species No.	Scientific Name[1]	Common Name[2]
1	*Spiza americana*	Dickcissel	22	*S. cinctus*	Masked Saltator
2	*Pheucticus chrysopeplus*	Yellow Grosbeak	23	*S. atricollis*	Black-throated Saltator
3	*P. aureoventris*	Black-backed Grosbeak	24	*S. rufiventris*	Rufous-bellied Saltator[3]
4	*P. ludovicianus*	Rose-breasted Grosbeak	25	*S. albicollis*	Streaked Saltator
5	*P. melanocephalus*	Black-headed Grosbeak	26	*Passerina glaucocaerulea* (*Cyanoloxia glaucocaerulea*)	Indigo Grosbeak
6	*Cardinalis cardinalis*	Cardinal			
7	*C. phoeniceus*	Vermilion Cardinal	27	*P. cyanoides* (*Cyanocompsa cyanea*)	Blue-back Grosbeak
8	*C. sinuatus*	Pyrrhuloxia			
9	*Caryothraustes canadensis*	Yellow-green Grosbeak	28	*P. brissonii* (*Cyanocompsa cyanea*)	Ultramarine Grosbeak
10	*C. humeralis*	Yellow-shouldered Grosbeak			
11	*Rhodothraupis celaeno*	Crimson-collared Grosbeak	29	*P. parellina* (*Cyanocompsa parellina*)	Blue Bunting
12	*Periporphyrus erythromelas*	Red-and-black Grosbeak			
13	*Pitylus grossus*	Slate-colored Grosbeak	30	*P. caerulea* (*Guiraca caerulea*)	Blue Grosbeak
14	*Saltator atriceps*	Black-headed Saltator			
15	*S. maximus*	Buff-throated Saltator	31	*P. cyanea*	Indigo Bunting
16	*S. atripennis*	Black-winged Saltator	32	*P. amoena*	Lazuli Bunting
17	*S. similis*	Green-winged Saltator	33	*P. versicolor*	Varied Bunting
18	*S. coerulescens*	Grayish Saltator	34	*P. ciris*	Painted Bunting
19	*S. orenocensis*	Orinocan Saltator	35	*P. rositae*	Rose-bellied Bunting
20	*S. maxillosus*	Thick-billed Saltator	36	*P. leclancherii*	Orange-breasted Bunting
21	*S. aurantiirostris*	Golden-billed Saltator	37	*P. caerulescens* (*Porphyrospiza caerulescens*)	Blue Finch

[1] Scientific names are those of Paynter (1970). In parentheses 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).

[2] Common names are those used by de Schauensee (1970) or Peterson and Chalif (1973) unless otherwise specified.

[3] Common name from Hellmayr (1938).

When all available characters were used (skeletal, study skin, and color) we had complete data for only 30 of the 37 species. Therefore the analyses of combined data include neither the 4 above mentioned species nor *Periporphyrus erythromelas*, *S. rufiventris*, and *Passerina caerulescens*.

To assess phenetic similarity, we used multivariate statistical programs from the Numerical Taxonomy System (NT-SYS, developed by F. James Rohlf, John Kishpaugh, and David Kirk). Both Q- and R-type studies were conducted.

In the Q-type analysis, characters were standardized so that each had a mean of 0 and a standard deviation of 1. Then a product-moment correlation coefficient or an average distance coefficient was calculated for all pairs of species (Sneath and Sokal 1973). Species were clustered by the unweighted pair-group method using arithmetic averages (UPGMA, Sneath and Sokal 1973) and the results summarized in phenograms.

We extracted 3 principal components from a matrix of character correlations in the R-type analysis (Sneath and Sokal 1973), and phenetic relationships are presented as 3-dimensional models of species projected onto these components (Rohlf 1968). A shortest minimally connected network (Rohlf 1970) computed from the original distance matrix is superimposed on the 3-D models to point out possible distortions.

To eliminate or reduce the size factor, study skin characters were used as ratios (see Appendix), and skeletal measurements were divided by the first principal component extracted from a matrix of unstandardized skeletal characters. Skeletal data were handled this way because the method produced the "best" phenetic classification from the skeletal data (see Hellack 1976).

Ten phenetic classifications were produced using the various combinations of the 4 data sets (study skin, contrast, color, and skeletal characters) and 2 similarity coefficients (correlation and distance). Males and females were analyzed separately to: (1) see if there were major differences among the resulting classifications, and (2) include all species in some analyses without having to compare species with complete data with those for which some information was lacking. Various data combinations were made so as to include all the characters available for any one species in an analysis.

When all available data were used they were handled as follows: study skin characters of both males and females were averaged; for contrast and color characters male and female averages were included separately; and skeletal characters were averaged for a species without regard to sex (as done in Hellack 1976). This resulted in 168 "characters" per species.

Matrices were produced from the classification systems of Paynter (1970) and Hellmayr (1938; see Hellack 1976). These 2 matrices, the 10 from the various combinations mentioned above, and 2 from the analyses of skeletal characters (SKEL/COMP I ALL CORR and SKEL/COMP I ALL DIST, Hellack 1976) were compared by computing the coefficient of correlation between each pair of basic similarity matrices. Similarities were summarized as a dendrogram that indicates which basic similarity matrices are most alike; phenograms were compared in a similar manner.

The following abbreviations are used. CORR or DIST refer to the use of correlation or distance to analyze similarity among species. SKIN denotes the use of study skin measurements and contrast characters. COLOR refers to the use of 8 color characters of dominant wave length. SKEL indicates the use of skeletal characters divided by unstandardized principal component I (SKEL/COMP I ALL of Hellack 1976). BSM is the abbreviation for basic similarity matrix.

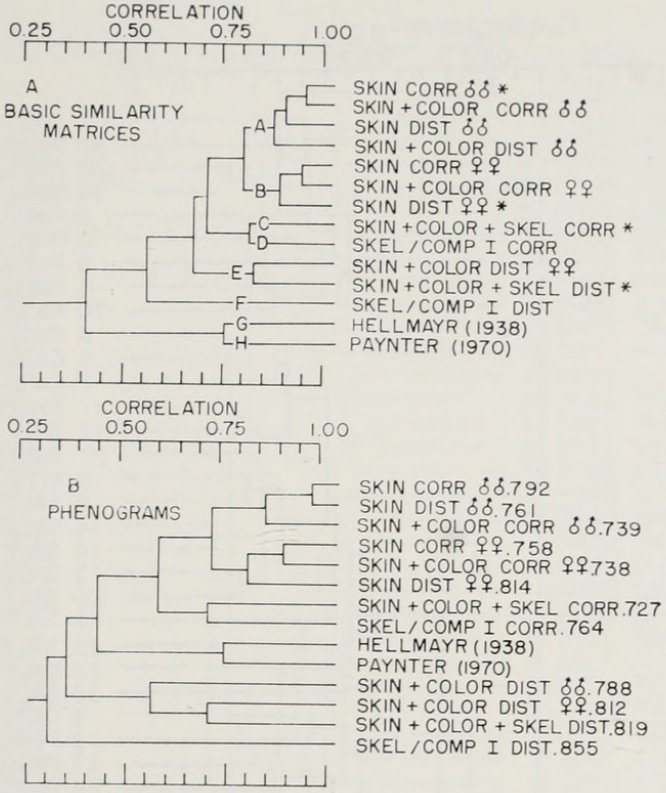

FIG. 1. Dendrograms showing relationships among: (A) basic similarity matrices; (B) phenograms. Letters indicate groups of very similar BSMs. Asterisks indicate the phenogram chosen to represent each of these groups—the one with the highest cophenetic correlation. These representative phenograms are shown in Figs. 2a–b.

RESULTS

Phenograms.—In Fig. 1A, which is a dendrogram of similarities among BSMs, 9 groups are labeled. The 4 BSMs of group A (in which only males are compared) differ in similarity coefficient and/or the number of characters (the BSMs also differ in the number of species included, although the dendrogram, Fig. 1A, is comparing placement of only those species each pair of analyses has in common). Group B has 3 BSMs (where only females were compared) which like those of group A, differ in similarity coefficient and/or the number of characters. The 2 BSMs of group E differ in character set but are alike in the similarity coefficient used. The 5 remaining groups contain 1 BSM each.

The main difference between the dendrogram showing similarities among phenograms (Fig. 1B) and Fig. 1A is that 1 BSM of group A (SKIN + COLOR DIST ♂♂) clusters in group E. Also distance analyses of groups E and F show less similarity to the other clusters than they did in Fig. 1A.

BSMs within groups A, B, and E are very similar (Fig. 1A). We have depicted only 1 from each—the phenogram with the highest cophenetic cor-

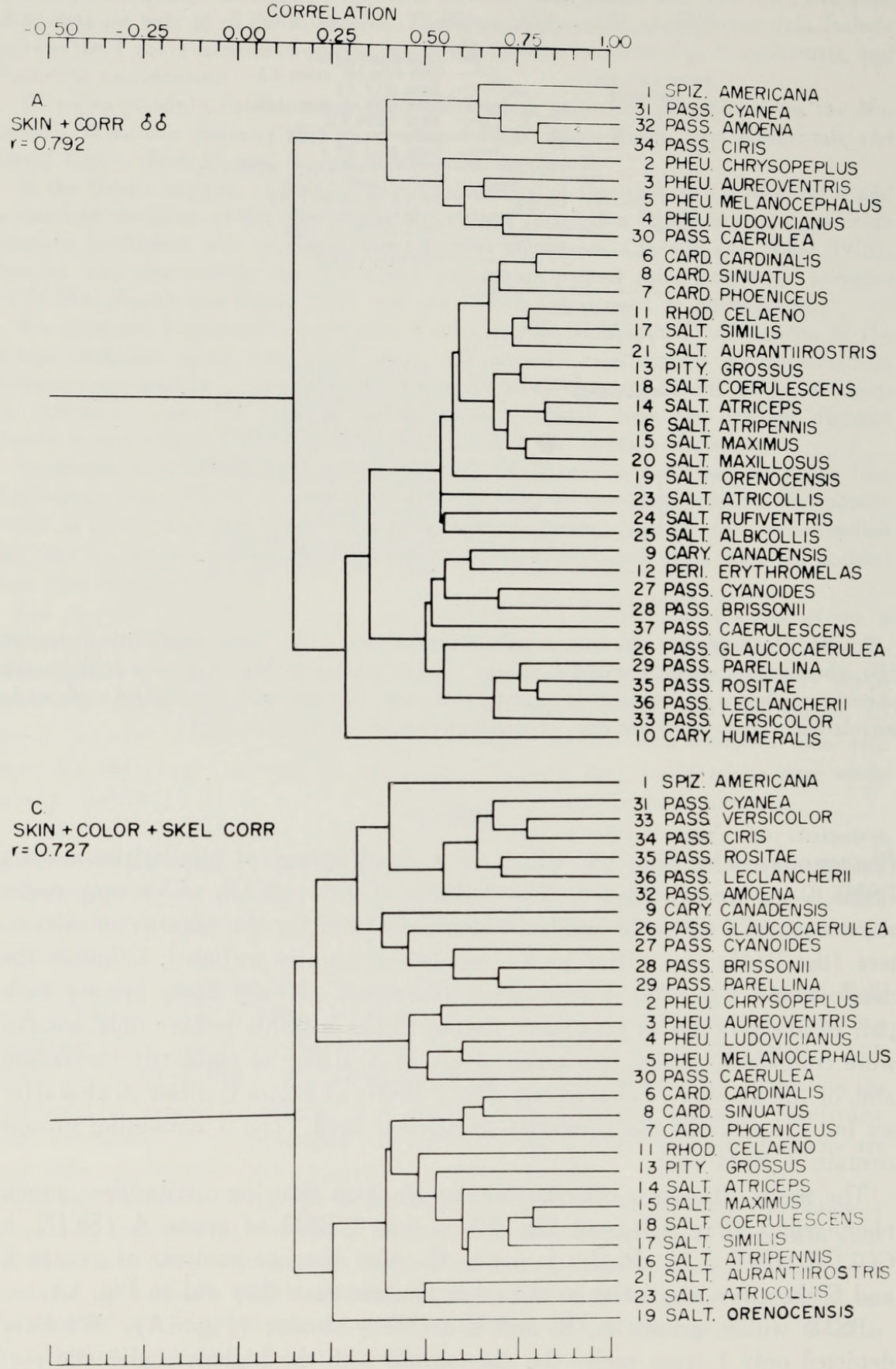

FIG. 2 a. Phenogram representatives of groups A and C of Fig. 1: (A) study skin characters of males with correlations; (C) all characters and correlations.

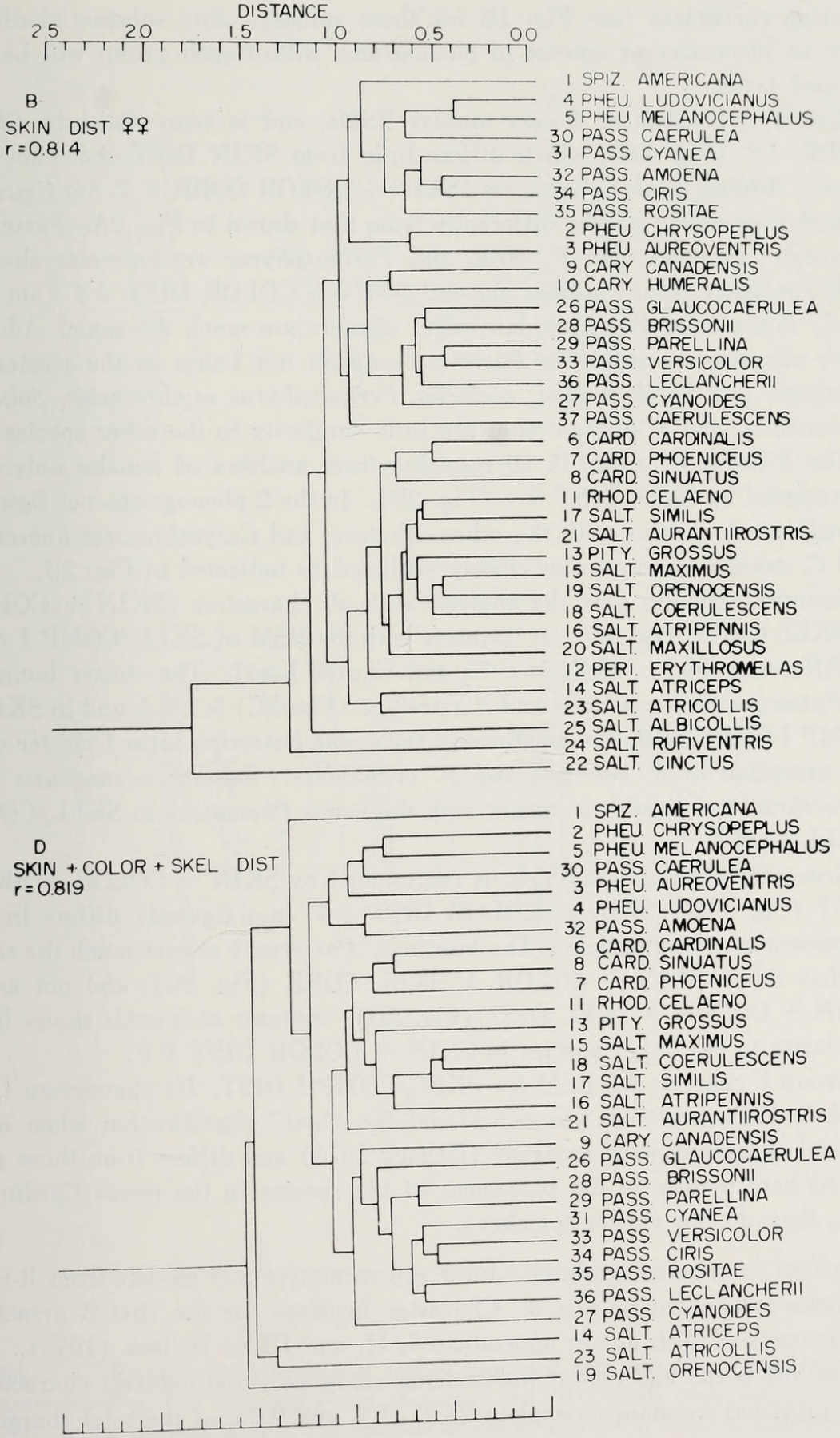

FIG. 2 b. Phenogram representatives of groups B and D of Fig. 1: (B) study skin characters of females with distances; (D) all characters and distances.

relation coefficient (see Fig. 1B for these values). Any substantial difference in placement of species in phenograms within each group will be described below.

Group A consists of 4 very similar BSMs, and is represented by SKIN CORR ♂♂ (Fig. 2A), which differs little from SKIN DIST ♂♂ (not figured). Adding 8 color characters (SKIN + COLOR CORR ♂♂, not figured) caused 2 species to cluster differently from that shown in Fig. 2A. *Passerina versicolor* grouped with *P. ciris*, and *Periporphyrus erythromelas* showed little similarity to any species cluster. SKIN + COLOR DIST ♂♂ (not figured) is the most divergent, but major clusters are much the same. Adding color characters resulted in *Passerina amoena* not being in the cluster of buntings; and *Rhodothraupis caelaeno*, *Periporphyrus erythromelas*, *Saltator orenocensis*, and *S. atriceps* showing little similarity to the other species.

The 3 BSMs of group B, all resulting from analyses of females only, are represented by SKIN DIST ♀♀ (Fig. 2B). In the 2 phenograms not figured, *S. rufiventris* clusters with the other saltators, and *Caryothraustes humeralis* and *C. canadensis* are not as closely affiliated as indicated in Fig. 2B.

Group C includes only the analysis with all characters (SKIN + COLOR + SKEL CORR, Fig. 2C). It connects with the BSM of SKEL/COMP I ALL CORR (described in Hellack 1976, not figured here). 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 1 cluster with the exception of *P. caerulea* and *P. cyanoides*). *Saltator orenocensis* and *Caryothraustes canadensis* cluster with the genus *Pheucticus* in SKEL/COMP I ALL CORR.

Group E, containing 2 BSMs, is represented by SKIN + COLOR + SKEL DIST (Fig. 2D). SKIN + COLOR DIST ♀♀ (not figured) differs in the placement of several species. The buntings (*Passerina*) cluster much the same as they do in SKIN + COLOR + SKEL CORR (Fig. 2C), and not as in SKIN + COLOR + SKEL DIST (Fig. 2D). *Saltator atripennis* shows little similarity to any other species in SKIN + COLOR DIST ♀♀.

Group F contains the BSM for SKEL/COMP I DIST. Its phenogram (figured in Hellack 1976) was considered the "best" classification when only skeletal characters were analyzed (Hellack 1976) and differs from those presented here mainly in the placement of the species in the genus *Cardinalis* (i.e., they do not cluster together).

Principal component analyses.—Four representative 3-D models from R-type analyses are shown in Fig. 3. Character loadings for the first 3 principal components of each are in appendices I, II, and III of Hellack (1975).

Fig. 3A is the analysis of males using study skin and contrast characters. The principal components explain 21.2, 11.7, and 9.0% of the total character

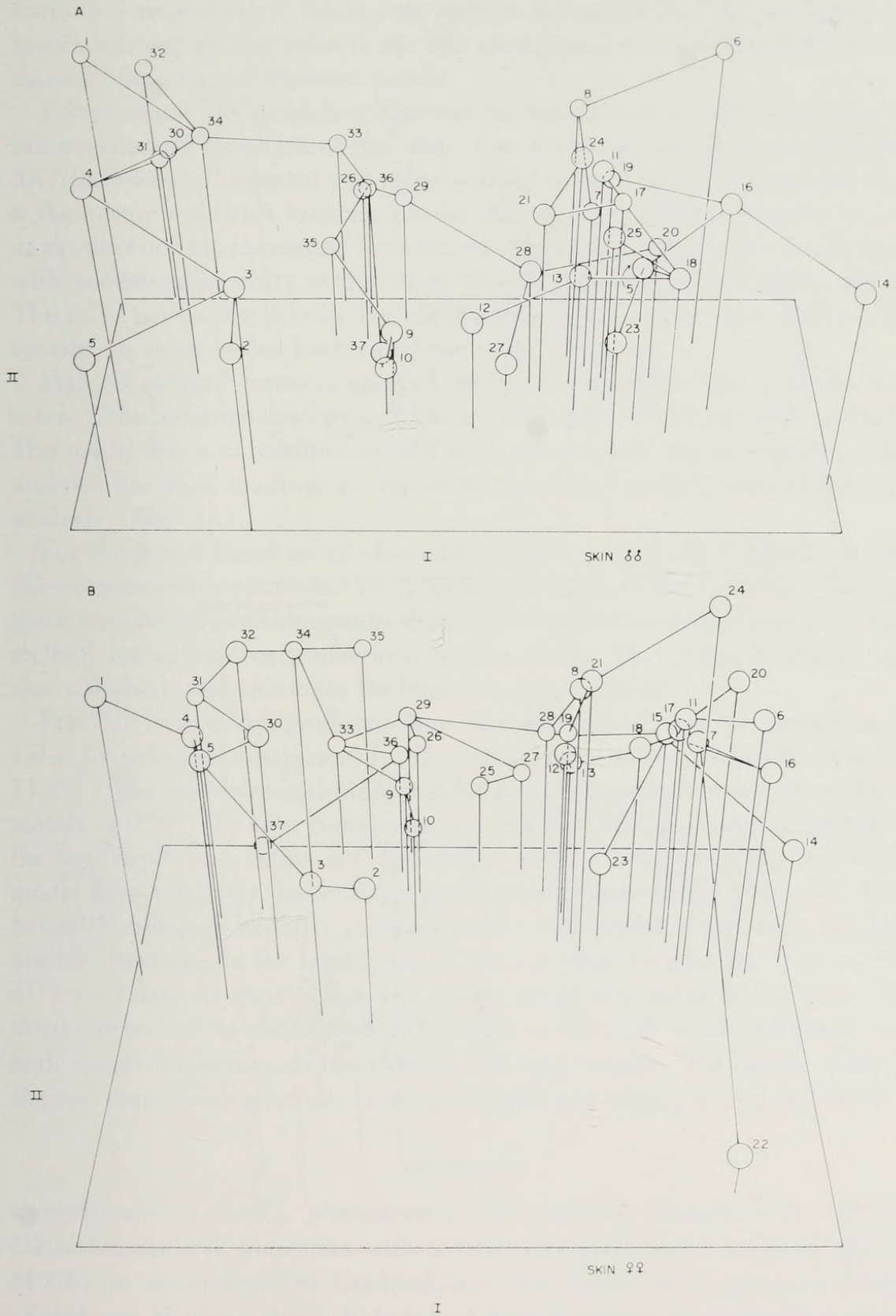

FIG. 3 a. Representative models of species projected onto the first 3 principal components based on (A) male study skin characters and (B) female study skin characters. Species names corresponding to the numbers on the models are in Table 1. Components I and II are labelled, III is the height. The shortest minimally connected network is projected onto each of the models.

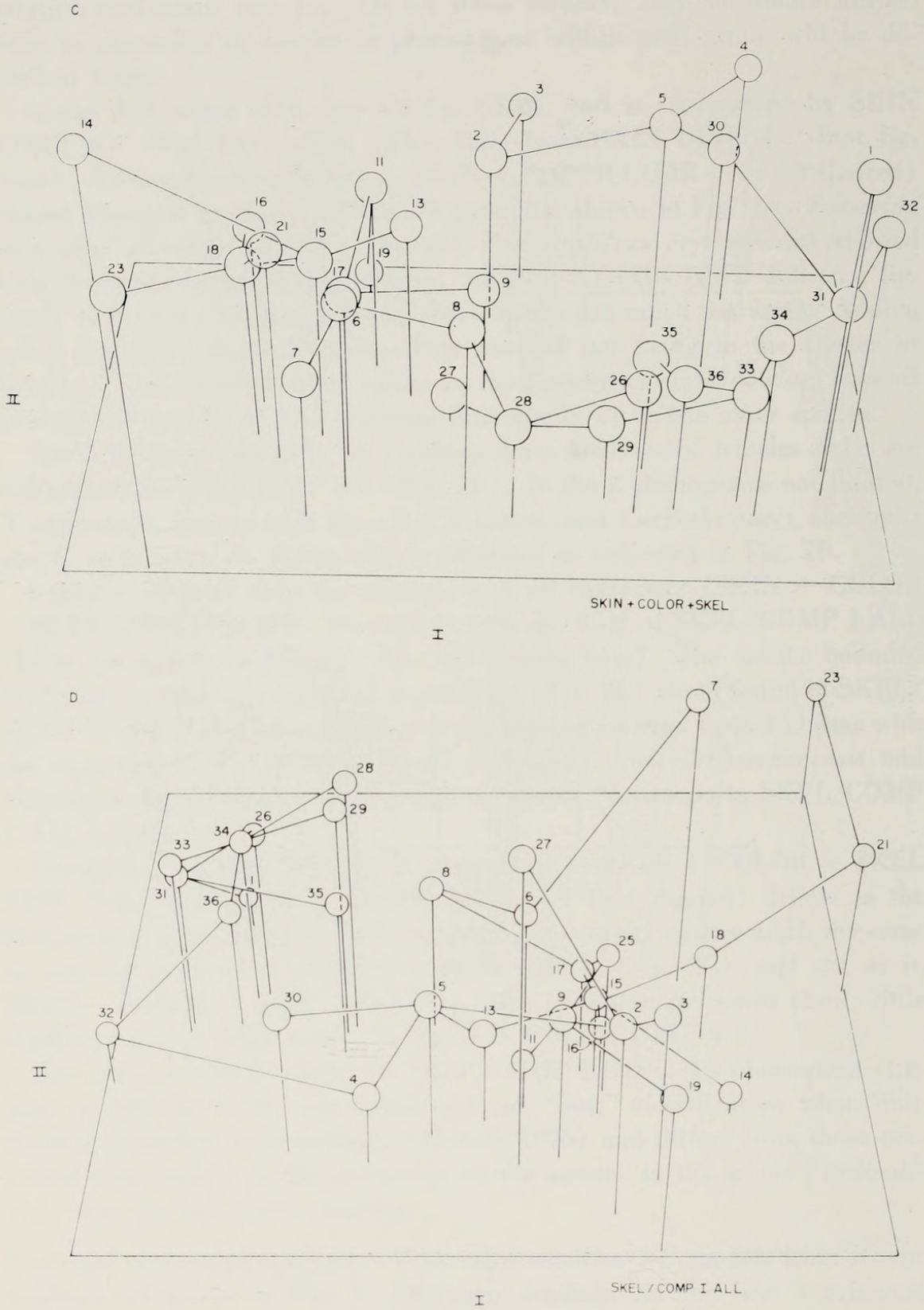

FIG. 3 b. Representative models of species projected onto the first 3 principal components based on (C) all available characters and (D) skeletal characters.

variation, respectively. While only 42% is accounted for, the euclidian distances between species pairs in the 3-D model have a correlation of 0.90 with those in the original distance matrix.

Component I has its highest loadings on the amount of tail covered by the tail coverts and the shape of the wing. Species on the left in the 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, as well as on the contrast characters for white in the wing and tail. The larger birds with considerable white in the wing and tail are in the front of the model. The third component has its highest loadings on the wing vane widths. The species on short stems have relatively wide primaries.

Fig. 3B resulted from an analysis of female study skin and contrast characters. The 3 components explain 20.2, 11.9, and 9.7% of the total variation. The model has a correlation of 0.91 with the original distance matrix. This analysis has high loadings on the same characters as does that of the male analysis (Fig. 3A).

For the model based on all characters (SKIN + COLOR + SKEL) in Fig. 3C, components account for 23.3, 13.0, and 9.2% of the variation. 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 used, and character loadings are not available.

Fig. 3D is a model produced from the analysis of skeletal characters divided by principal component I. The components account for 27.0, 18.2, and 11.2% of the character variation, and the model's correlation with the distance matrix is 0.90. The first component is a contrast with its highest loadings on the keel depth and femur and tibiotarsus widths. Species on the left in the model have relatively deeper keels and narrower femurs and tibiotarsi. Component II has high negative loadings on the long bones of the wing and high positive loadings on the long bones of the leg. Species near the front of Fig. 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 lengths. The species with the shorter stems have relatively narrower skulls and longer sterna and keels.

DISCUSSION

Comparisons of BSMs, phenograms, and previous classifications.—Highly correlated skeletal characters with a large size factor were used by Hellack (1976) in an analysis of Cardinalinae. We 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 use of the distance coefficient. The analyses in this study in which external

characters (SKIN or SKIN + COLOR) were used did not follow this tendency. Except for SKIN + COLOR DIST ♀♀ (not figured), there was considerable correlation among the BSMs of similar character sets irrespective of similarity coefficient (Fig. 1A). That BSMs do not group according to similarity coefficient probably indicates there is no large size factor or other significant trend in the ratios used.

As in analyses of skeletal characters, affinities among phenograms (Fig. 1B) changed some from those expressed for BSMs (Fig. 1A). In the comparison of phenograms (Fig. 1B), SKIN + COLOR DIST ♂♂ (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 ♀♀ (not figured) and SKIN + COLOR + SKEL DIST (Fig. 2D). Switching also occurred in some of the major branches (e.g., 4 distance phenograms show less similarity to other analyses than did their respective BSMs).

In comparing the 12 classifications in this study with those of Hellmayr (1938) and Paynter (1970), 9 BSMs were more similar to previous classifications than were their respective phenograms. All 12 BSMs and 10 phenograms were more similar to Paynter (1970) than to Hellmayr (1938). The 2 phenograms more similar to Hellmayr (1938) are SKIN CORR ♂♂ (Fig. 2A) and SKIN + COLOR CORR ♂♂ (not figured). Correlations between BSMs (as well as phenograms) and previous classifications are very low, indicating that the affinities implied by previous workers are different from those determined in our study.

Comparisons of representative phenograms.—SKIN DIST ♀♀ (Fig. 2B) of group B is the only representative phenogram in which all species included in Cardinalinae by Paynter (1970) were analyzed. The placement of species in the other representative phenograms will be compared below with their placement in SKIN DIST ♀♀ (Fig. 2B).

In the representative phenogram of group A (SKIN CORR ♂♂, Fig. 2A) some changes in close affinities are evident; however, major clusters are composed of many of the same species. *Passerina rositae*, *Saltator albicollis*, *S. rufiventris*, *Periporphyrus erythromelas*, and *Caryothraustes humeralis* in SKIN CORR ♂♂ are not placed in the same groups as they are in SKIN DIST ♀♀.

The phenogram of group C (SKIN + COLOR + SKEL CORR, Fig. 2C) differs primarily in the main stem connections of its smaller clusters. For example, the cluster bounded by *Pheucticus chrysopeplus* and *Passerina caerulea* is found as 2 clusters in SKIN DIST ♀♀ 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 as they are in SKIN DIST ♀♀.

The species showing little affiliation to any of the clusters in SKIN DIST ♀♀ were not included in the phenogram of group C.

SKEL/COMP I CORR (group D, not figured) differs 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. There is one cluster of 9 species with the other 2 species, *P. caerulea* and *P. cyanea*, not clustering with these.

The phenogram representative of group E (SKIN + COLOR + SKEL DIST) is shown in Fig. 2D. The majority of the clusters are much the same as those of SKIN DIST ♀♀ (Fig. 2B). *Saltator orenocensis* differs in its placement and the species in the genus *Passerina* do not form 2 large groups. Only 2 species, *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 Fig. 5B of Hellack (1976). It was the "best" phenetic classification of Cardinalinae when only skeletal measurements were used. Several differences are noticeable in comparing this phenogram with the others. Only 2 of the species in the genus *Cardinalis* cluster together; the other (*C. phoeniceus*) shows little similarity to them. Most species in the genus *Passerina* cluster together (except *P. cyanea* and *P. caerulea*) rather than forming 2 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.—We have presented a number of phenetic classifications of the subfamily Cardinalinae. Each represents a facet of the phenetic relationships of the group. However, it may at times be useful to have one "best" classification of a group.

Schnell (1970) proposed several guides for choosing the "best" phenetic classification, when more than one are available. The phenogram selected should: (1) be based on a large number of characters; (2) have transformations applied to reduce any general size factor and; (3) have a relatively high cophenetic correlation. These guides while useful are not totally sufficient for this study. The phenogram used for general purposes should also have a relatively high correlation with the other phenetic analyses of the study.

For 2 of our analyses, all available characters were used 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 is SKIN + COLOR + SKEL DIST. 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 ♀♀ (not figured) and SKEL/COMP I DIST (figured in Hellack 1976) of the BSMs are more similar to SKIN + COLOR + SKEL

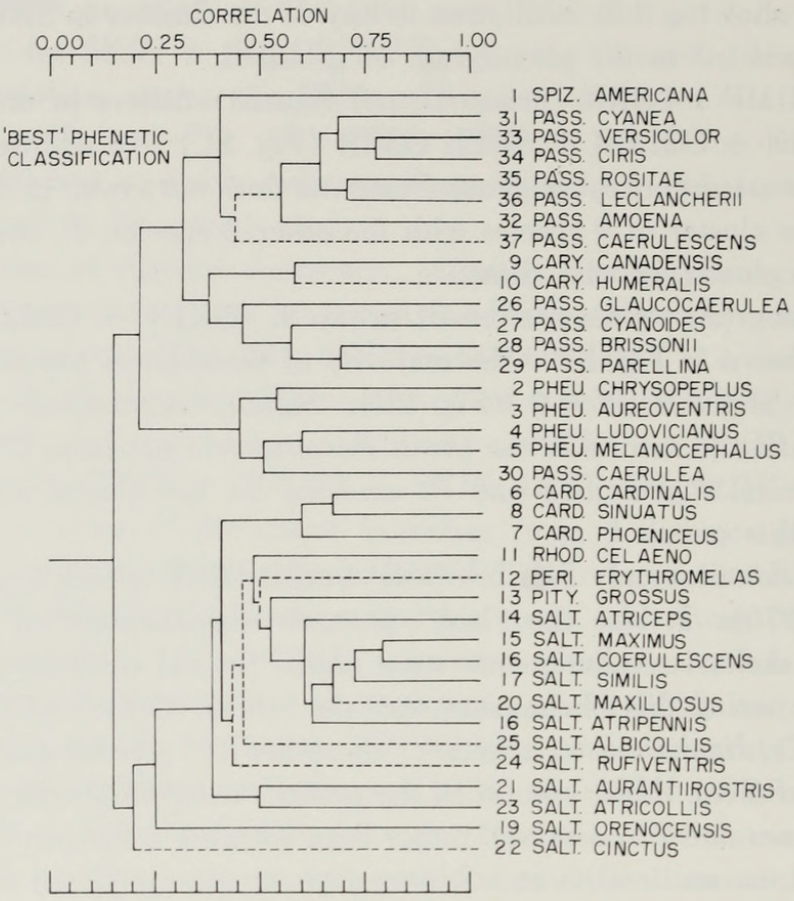

FIG. 4. The "best" phenetic classification of this study. Seven species not included in the SKIN + COLOR + SKEL CORR (Fig. 2A) analysis are represented by dotted lines.

DIST. The 2 phenograms of these analyses plus SKIN + COLOR DIST ♂ ♂ (not figured) are more similar in the comparison of phenograms. SKIN + COLOR + SKEL CORR (Fig. 2C), while not having the highest cophenetic correlation, is probably the best representative phenogram.

Using all available characters resulted in 7 species not being included in the SKIN + COLOR + SKEL CORR analysis. As these species (*Caryothraustes humeralis*, *Periporphyrus erythromelas*, *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, we evaluated their placement in other phenograms and 3-D models. SKIN + COLOR + SKEL CORR (Fig. 2C) was used for the placement of all species which it included and we positioned the 7 species into the clusters they probably would have joined had they been included in the analysis. This "best" phenetic classification is shown in Fig. 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 ♀♀ (Fig. 2B) and in the 3-D models of both SKIN ♀♀ (Fig. 3B) and SKIN ♂♂ (Fig. 3A), *C. humeralis* is most similar to *C. canadensis*. The average similarity of these 2 in the correlation analyses of both SKIN CORR ♀♀ (not figured) and SKIN CORR ♂♂ (Fig. 2A) is 0.58. This average similarity is used for the placement of *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 analyses where *Periporphyrus erythromelas* was included (all of those based on external characters) it was most similar to *P. celaeno* or *Pitylus grossus*. This was true in the phenograms and 3-D models (except for SKIN CORR ♂♂; Fig. 2A).

Saltator maxillosus was included in the analyses of skin and contrast characters (Figs. 2A,B; 3A,B). In the 2 cluster analyses where we evaluated male characters (Fig. 2A), *S. maxillosus* showed close affinity to *S. maximus*, while in the cluster analyses using female characters (Fig. 2B) it was similar to both *S. atripennis* and *S. similis*. In the 3-D models (Fig. 3A,B), *S. maxillosus* separated 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. Thus 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. Considerable feather wear was evident in the only specimen of this species. We placed it in the "best" classification (Fig. 4) as we found it in the analyses of female characters (Figs. 2B, 3B), but because of the lack of specimens we are not certain that this appropriately represents the phenetic affinities of this species.

Saltator rufiventris was included in all the external character analyses. It clustered with the saltators; however, it showed no close affinities to any one saltator. Its closest affinities are perhaps to *S. aurantiirostris*, the species to which it is connected by the minimum connecting network of the 3-D models (Fig. 3A,B). *S. rufiventris* separates from the other saltators in component III of the 3-D models. The primaries are relatively narrower. Its placement in Fig. 4 represents more similarity to the major cluster of saltators than to any other species cluster. *S. rufiventris* is also more similar to the saltator cluster than are *S. aurantiirostris* and *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 1976) and in the analyses of male study skin characters (Figs. 2A, 3A). In the analyses of female study skin characters (Figs. 2B,3B), less simi-

larity to the saltators is shown. 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. leclancherii*, the species to which it appears most similar. Its connection is at some distance from that of the other species to indicate 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*, *Pheucticus*, and *Cardinalis*. Hellmayr (1938) divides the species of Paynter's (1970) genus *Passerina* into 5 genera (*Passerina*, *Cyanocompsa*, *Cyanoloxia*, *Porphyrospiza*, and *Guiraca*) and the 4 species of *Pheucticus* into 2 genera (*Pheucticus* and *Hedymelas*). Hellmayr (1938) placed the Pyrrhuloxia (*Cardinalis sinuatus*) in a genus by itself (*Pyrrhuloxia sinuatus*).

The "best" phenetic classification (Fig. 4) divides the species into 3 large clusters. While these groups were not found in all the analyses, one or more groups occurred in every analysis (Fig. 2). The 3 groups are: (1) most of the species in the genus *Passerina* plus *Spiza* and *Caryothraustes*; (2) the genus *Pheucticus* 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 *Pheucticus* are most similar to Hellmayr's groupings. 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 clusters showed more similarity to the genus *Caryothraustes* or species of the genus *Pheucticus*.

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 *Pheucticus*. The Pyrrhuloxia clusters with the other species in the genus *Cardinalis*, as suggested by Paynter's (1970) classification.

The groupings of Hellmayr (1938) and Paynter (1970) are the same for the remaining species, but our phenetic analyses 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 6 very similar saltators (*S. atriceps*, *S. maximus*, *S. coerulescens*, *S. similis*, *S.*

maxillosus, and *S. atripennis*). The remaining 6 saltator species show little affiliation to any of the species clusters. It is possible that the material available was inadequate to get a reliable estimate of similarities for the species *S. rufiventris*, *S. albicollis*, and *S. cinctus*. This is not true for *S. atricollis*, *S. aurantiirostris*, and *S. orenocensis*. Ridgway (1901) suggested that several of the South American saltators did not belong in the genus, a conclusion which is supported by this study.

Taxonomic conclusions.—In this study the phenetic similarity found among the species in the subfamily Cardinalinae is somewhat different from the affiliations suggested by previous classifications. This is particularly 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 (*P. 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. *P. 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, Mayr and Short 1970). In our study it was not closely associated with any one group although it clustered most often with the genus *Pheucticus*.

Our results indicate that the genus *Saltator*, as classified at present, is a heterogenous group and consideration should be given to dividing it into several genera. We believe that *S. albicollis* and *S. rufiventris* are saltators and if adequate materials 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. We do not feel in a position to comment on *S. cinctus*.

The species in Paynter's (1970) genus *Passerina* could in our opinion be grouped according to either former classification—with the exception of *P. caerulea* which should remain *Guiraca caerulea*. *Pheucticus* appears to be composed of 2 rather different groups as indicated by Hellmayr (1938), and we suggest that his recommendations should be followed. We agree with Paynter on the classification of the genus *Cardinalis* (that it contains *Cardinalis sinuatus*) and the remaining species of this subfamily.

SUMMARY

We analyzed affinities of 37 species in the subfamily Cardinalinae using 75 external morphological characters and 49 skeletal characters. Affinities are presented in phenograms and 3-D models. The phenograms are compared among themselves and with previous classifications. A "best" phenetic classification was constructed using the guide-

lines of Schnell (1970) and taking into account correlation between basic similarity matrices.

The phenogram thus chosen did not include 7 of the species. These 7 species were placed 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 these species had been included.

This phenogram was then used to look at similarities and compare these similarities with the classifications 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 *Pheucticus* 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.

ACKNOWLEDGMENTS

We are grateful to the curators of a number of collections who allowed us to use material in their care (they are listed in Hellack 1976). We thank Harley P. Brown, Charles C. Carpenter, and James R. Estes for critically reviewing the manuscript, and 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.

LITERATURE CITED

Anonymous. 1970. Dominant wavelength and excitation purity for designated Munsell color notations. Munsell Color Company, Inc., Newburgh, N.Y.

Blake, C. H. 1969. Notes on the Indigo Bunting. Bird Banding 40:133–139.

de Schauensee, R. M. 1970. A guide to the birds of South America. Livingston Publ. Co., Narbert, Pa.

Hellack, J. J. 1975. A phenetic analysis of the subfamily Cardinalinae, Aves. Ph.D. thesis. Univ. of Oklahoma, Norman.

———. 1976. Phenetic variation in the avian subfamily Cardinalinae. Occas. Pap. Mus. Nat. Hist., Univ. Kans. 57:1–22.

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

Mayr, E. and L. L. Short. 1970. Species taxa of North American Birds. Publ. of the Nuttall Ornithol. Club No. 9. Cambridge, Mass.

Munsell, A. H. 1973. Munsell book of color. Macbeth Color and Photometry Division, Kollmorgen Corporation, Newburgh, N.Y.

Newhall, S. M., D. Nickerson, and D. B. Judd. 1943. Final report of the O. S. A. subcommittee on the spacing of the Munsell colors. J. Opt. Soc. Am. 33:385–418.

Paynter, R. A. 1970. Subfamily Cardinalinae. Pp. 216–245 *in* Check-list of birds of the World. Vol. 13 (R. A. Paynter and R. W. Storer, eds.), Mus. Comp. Zool., Heffernan Press, Worcester, Mass.

Peterson, R. T. and E. L. Chalif. 1973. A field guide to Mexican birds. Houghton Mifflin Co., Boston.

PHILLIPS, A. R., J. MARSHALL, AND G. MONSON. 1964. The birds of Arizona. Univ. of Arizona Press, Tucson.

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

ROBINS, J. D. AND G. D. SCHNELL. 1971. Skeletal analysis of the *Ammodramus-Ammospiza* grassland sparrow complex: a numerical taxonomic study. Auk 88:567–590.

ROHLF, F. J. 1968. Stereograms in numerical taxonomy. Syst. Zool. 17:246–255.

———. 1970. Adaptive hierarchical clustering schemes. Syst. Zool. 19:58–82.

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

SNEATH, P. H. A. AND R. R. SOKAL. 1973. Numerical taxonomy. W. H. Freeman and Co., San Francisco.

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

DEPT. OF ZOOLOGY AND STOVALL MUSEUM, UNIV. OF OKLAHOMA, NORMAN 73019.
ACCEPTED 15 DEC. 1975.

APPENDIX

DESCRIPTION OF STUDY SKIN, CONTRAST, AND COLOR CHARACTERS

Study skin.—(1) Rectrix length, distance from where skin joins shaft of middle pair of rectrices to tip of longest rectrix. Five characters represent shape of tail and are divided by rectrix length to reduce size factor; measurement is coded as negative until longest feather is measured then positive from longest feather. Characters are as follows: (2) distance from tip of outer rectrix to tip of 2nd, (3) distance from tip of 2nd rectrix to tip of 3rd, (4) distance from tip of the 3rd to tip of 4th rectrix, (5) distance from tip of 4th rectrix to tip of 5th, (6) distance from tip of 5th rectrix to tip of 6th. Two measures of feather widths (from center of feather), each divided by rectrix length to reduce size factor. Characters are: (7) outer rectrix width, and (8) outer vane of outer rectrix. The relative amount of tail covered by coverts was measured by the following 2 characters (divided by rectrix length): (9) distance from tip of under-tail coverts to tip of longest rectrix, (10) distance from tip of the upper-tail coverts to tip of longest rectrix.

Wing length (11), distance from carpal joint (bend of wing to tip of longest primary). Five characters represent shape of wing and are divided by wing length to reduce size factor, coded as negative numbers until longest feather is measured then a positive number. Characters are: (12) distance from tip of 9th primary to tip of 8th, (13) distance from tip of 8th to tip of 7th, (14) distance from tip of 7th primary to tip of 6th, (15) distance from tip of 6th primary to tip of 5th, (16) distance from tip of 5th primary to tip of 4th. Ten characters represent the widths of wing feathers and are divided by wing length in order to reduce size factor (all measurements were taken at the center of the feather). Characters are: (17) width of the 9th primary, (18) width of outer vane of 9th primary, (19) width of 8th primary, (20) width of outer vane of 8th primary, (21) width of 7th primary, (22) width of outer vane of 7th primary, (23) width of 6th primary, (24)

width of outer vane of 6th primary, (25) width of 1st secondary, (26) width of outer vane of 1st secondary, (27) distance from the tip of longest secondary to tip of longest primary; measurement divided by wing length.

(28) Hallux length, measured without claw. Three toe lengths divided by hallux length to reduce size factor are: (29) length of middle toe, (30) length of 2nd toe, (31) length of 4th toe. Two angles were recorded from bill: (32) angle of commissural point relative to tomia, and (33) an angle measurement of arc of mandibular ramus.

Contrast characters.—Thirty-three 2-state characters were used. They were recorded as either present or absent characters, or contrast or no contrast characters. They are: (34) white spots in tail, (35) under-tail coverts contrasting to belly, (36) white present at apex of primaries, (37) white at base of primaries, (38) white on primary coverts, (39) white on secondary coverts, (40) marginal coverts contrasting to other coverts, (41) malar region contrasting to auricular, (42) lore region contrasting to forehead, (43) forehead contrasting to crown, (44) occiput contrasting to nape, (45) occiput contrasting to crown, (46) nape contrasting to back, (47) chin contrasting to gular, (48) gular contrasting to jugulum, (49) eye ring, (50) breast streaking, (51) back streaking, (52) side of body streaked, (53) flanks streaked, (54) abdomen contrasting to breast, (55) rump contrasting to back, (56) presence of a crest, (57) color sexual dimorphism, (58) middle wing coverts contrasting to other coverts, (59) superciliary line contrasting to crown, (60) auricular white, (61) white spot at base of lower mandible, (62) stripes on throat, (63) upper-tail coverts contrasting to rump, (64) streaking on crown, (65) flanks contrasting to abdomen, (66) sides contrasting to breast.

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