SKELETAL ANALYSIS OF THE *AMMODRAMUS-AMMOSPIZA* GRASSLAND SPARROW COMPLEX: A NUMERICAL TAXONOMIC STUDY

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THE sparrows considered include species generally placed in the genera *Myospiza, Passerculus, Ammodramus, Passerherbulus, Xenospiza,* and *Ammospiza.* Murray (1968) reviews the numerous taxonomic revisions attempted for this group of sparrows. Although use of 6 genera for 13 species suggests considerable diversity, the grassland sparrows have usually been considered to be closely related cladistically (i.e. relationship through recency of common ancestry; Cain and Harrison, 1960). Even a casual look at representative specimens indicates close phenetic (i.e. phenotypic) affinities. The first edition of the A.O.U. Check-list (1886), Ridgway (1887), and Chapman (1895) included all of the known North American species in the genus *Ammodramus.* In 1901 Ridgway (see Figure 1) allocated the North American species to four genera (*Passerculus, Centronyx, Coturniculus,* and *Ammodramus*), still assuming close cladistic affinities within the group. He considered two South American species referable to a fifth genus, *Myospiza,* which was most similar to *Coturniculus.* After Bangs (1931) named a new genus and species, *Xenospiza baileyi,* the grassland sparrow group included 13 species, which Hellmayr (1938) placed in six genera (see Figure 1). The most recent A.O.U. Check-list (1957) retains the generic nomenclature of Hellmayr, and like Hellmayr, implies close cladistic relationships among North American members of the complex.

Tordoff and Mengel (1951), Graber (1955), Dickerman et al. (1967), Dickerman (1968), and Murray (1968) made detailed studies of several of the species, focusing attention mainly on molt, plumage, and song in attempts to elaborate a phyletic taxonomy. As no studies to date, other than the taxonomic treatment of Hellmayr (1938), have covered all species in this group of sparrows, we undertook detailed phenetic analyses of skeletons using multivariate statistical techniques. We thought that a comparative analysis of all species in the group, in addition to clarifying phenetic affinities, would be most helpful in assigning logical generic limits. Pitelka (1947) and Dickerman et al. (1967) have pointed out the difficulty involved in discussing "generic relationships" among the grassland sparrows solely in terms of external morphology. Hopefully, this work will shed some light on the problem.
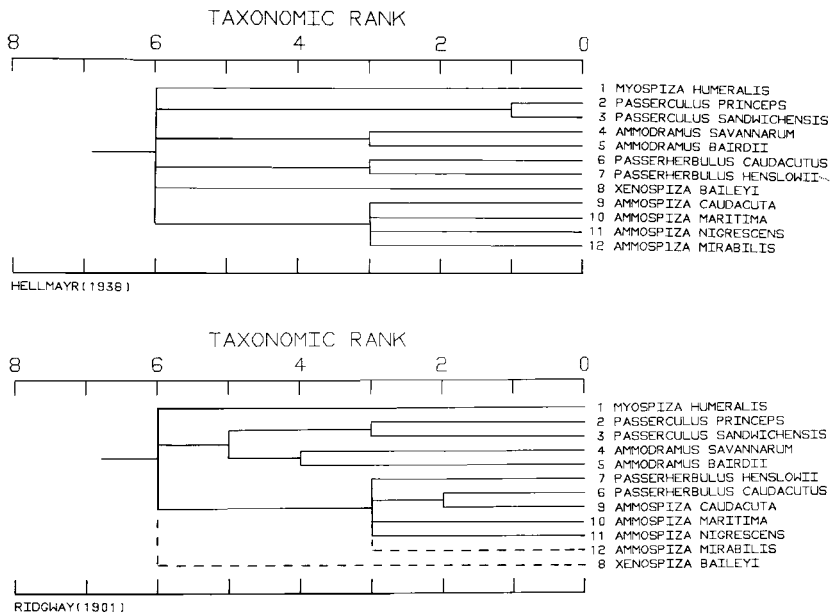
FIGURE 1. Dendrograms depicting classifications proposed by Hellmayr (1938) and Ridgway (1901). Junctions between stems indicate taxonomic levels. The following arbitrary similarity coefficients were assigned to formal taxonomic levels: (1) sub-species, (3) genus, and (6) family. Other levels were used to quantify more detailed statements about similarity by Ridgway. The generic names used by Ridgway were: *Myospiza* (OTU 1), *Passerculus* (OTUs 2 and 3), *Coturniculus* (OTU 4), *Centronyx* (OTU 5), and *Ammodramus* (OTUs 6, 7, 9, 10, and 11). The dotted lines represent our estimate of where Ridgway (1901) would have placed *Ammospiza mirabilis* and *Xenospiza baileyi* described in 1919 and 1931, respectively. *Myospiza aurifrons* has not been included (see Materials section).

MATERIALS

Table 1 lists the 12 OTUs (Operational Taxonomic Units; Sokal and Sneath, 1963) studied. The generic and specific designations are those of Hellmayr (1938), except for *Passerculus princeps* which he considered a subspecies of *P. sandwichensis*. The A.O.U. Check-list (1957) recognizes *P. princeps* as a full species, and we have treated it in this manner. The choice of which OTUs to include in the study was based on these works and does not necessarily imply support of the species limits indicated in them; decisions about species limits are beyond the scope of this paper. Table 1 includes a brief description of the geographic distribution of each species, the OTU numbers used throughout this work, and the number of specimens measured. Lack of material prevented study of *Myospiza aurifrons*, which Hellmayr (1938) and Meyer de Schauensee (1966) recognize as a full species with reservations; *M. humeralis* and *M. aurifrons* are very similar, and may or may not be best considered conspecific.

We measured the 48 skeletal characters to the nearest 0.1 mm with dial calipers (Figure 2; Table 2). All measurements, from adult specimens, are the same as those

TABLE 1

OTU Numbers, Number of Skeletons Measured, and Geographic Distribution of Species Studied[1]

OTU No.	Species	No. skeletons	Breeding season distribution[2]
1	*Myospiza humeralis*	6	South America, east of Andes (6 Argentina)
2	*Passerculus princeps*	5	Sable Island, Nova Scotia (1 New Jersey, 2 New York, 2 Massachusetts)
3	*Passerculus sandwichensis*	10	Widespread in North America (10 Kansas)
4	*Ammodramus savannarum*	10	Southern Canada, U. S., local in Middle America to northern South America (9 Kansas, 1 Texas)
5	*Ammodramus bairdii*	6	Restricted, northern Great Plains, North America (1 Arizona, 3 North Dakota, 1 Saskatchewan, 1 unknown)
6	*Passerherbulus caudacutus*	10	North central U. S. and prairie provinces of Canada (10 Kansas)
7	*Passerherbulus henslowii*	10	Northeastern quarter of U. S. and adjacent Canada (1 Florida, 4 Kansas, 5 Michigan)
8	*Xenospiza baileyi*	5[3]	Southwestern Mexico (5 Mexico)
9	*Ammospiza caudacuta*	10	Disjunct in prairie provinces, James Bay of Canada, and northern Atlantic coast, North America (1 Florida, 6 New Jersey, 3 North Dakota)
10	*Ammospiza maritima*	10	Atlantic and Gulf coasts, North America (1 Florida, 1 Georgia, 3 New Jersey, 4 North Carolina, 1 unknown)
11	*Ammospiza nigrescens*	9[4]	Very restricted in eastern Florida, U. S. (9 Florida)
12	*Ammospiza mirabilis*	7[5]	Very restricted in southwestern Florida, U. S. (7 Florida)

[1] *Myospiza aurifrons*, that occurs in the northern half of South America, is not included (see Materials section). Data on distributions is summarized from Hellmayr (1938), the A.O.U. Check-list (1957), and Dickerman et al. (1967).

[2] The number of specimens used in this study from various states, provinces, or countries are given in parentheses. More detailed data can be obtained from the authors.

[3] Including two partial skeletons.

[4] Including three partial skeletons.

[5] Including five partial skeletons.

taken by Schnell (1970a) and described in his Appendix 1, with the following exceptions. Measurements SK 20, 25, and 51 were omitted. The postorbital width (SK 7) was taken transversely just posterior to the postorbital processes of the frontals. SK 8 (skull width) was the maximum transverse dimension of the posterior portion of the skull. Mandible depth (SK 14) was the maximum dimension from the surangular to, and perpendicular with, the ventral edge of the mandible. We took tibiotarsus width (SK 35) as the dorsoventral dimension of the tibiotarsus near the distal end of the fibula. These changes were necessary because the sparrows are
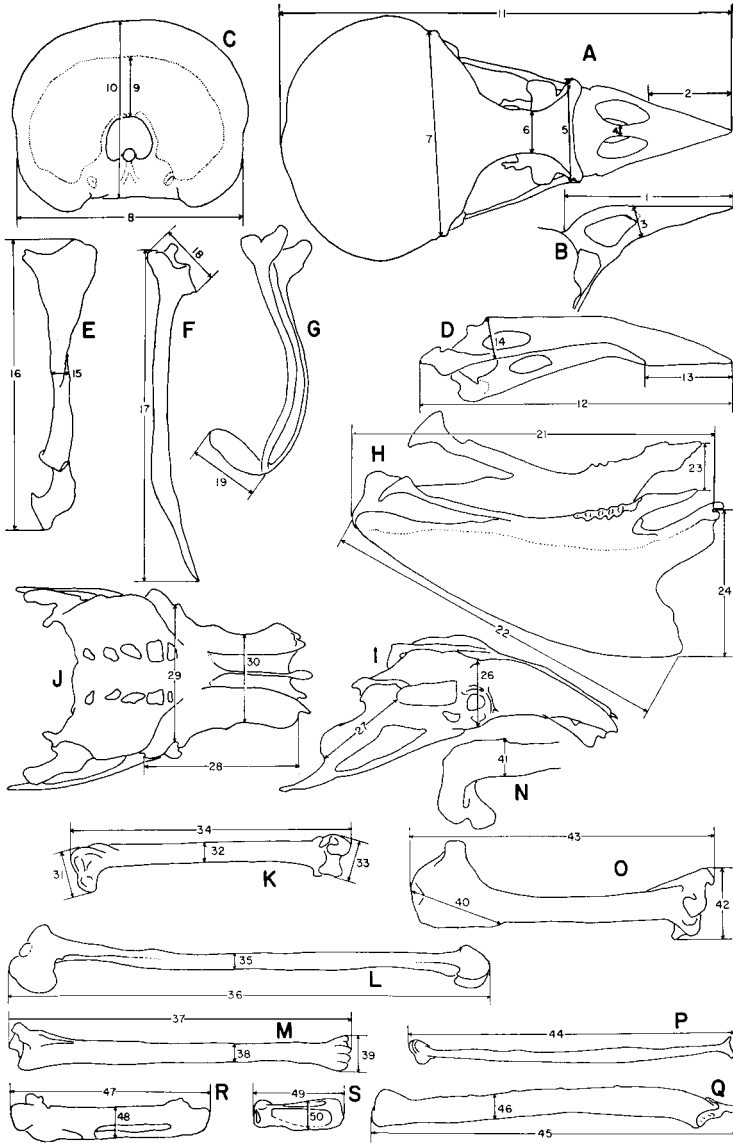
FIGURE 2. Skeletal elements of *Passerculus sandwichensis* illustrating the measurements taken. A, skull, dorsal view; B, premaxilla, lateral view; C, skull, posterior view; D, mandible, lateral view; E, coracoid, ventral view; F, scapula, ventral view; G, furcula, dorsal view; H, sternum, lateral view; I, synsacrum, lateral view; J, synsacrum, dorsal view; K, femur, posterior view; L, tibiotarsus, lateral view; M, tarsometatarsus, anterior view; N, proximal end of humerus, internal view; O, humerus, palmar view; P, radius, palmar view; Q, ulna, anconal view; R, carpometacarpus, internal view; S, phalanx, internal view.

TABLE 2

LIST OF 48 SKELETAL MEASUREMENTS[1]

SK No.	Characters	SK No.	Characters
1	Premaxilla length	27	Posterior synsacrum length
2	Premaxilla length from narial opening	28	Anterior synsacrum length
		29	Synsacrum width
3	Premaxilla depth	30	Synsacrum minimum width
4	Internarial width	31	Femur proximal end width
5	Nasal bone width	32	Femur minimum width
6	Interorbital width	33	Femur distal end width
7	Postorbital width	34	Femur length
8	Skull width	35	Tibiotarsus width
9	Occipital depth	36	Tibiotarsus length
10	Skull depth	37	Tarsometatarsus length
11	Skull length	38	Tarsometatarsus width
12	Mandible length	39	Tarsometatarsus distal end width
13	Minimum mandible length		
14	Mandible depth	40	Humerus trochanter length
15	Coracoid width	41	Deltoid crest depth
16	Coracoid length	42	Humerus distal end width
17	Scapula length	43	Humerus length
18	Scapula width	44	Radius length
19	Furcular process length	45	Ulna length
21	Sternum length	46	Ulna width
22	Keel length	47	Carpometacarpus length
23	Sternum width	48	Carpometacarpus depth
24	Keel depth	49	Phalanx length[2]
26	Synsacrum depth	50	Phalanx depth[2]

[1] Numbers assigned to characters follow those of Schnell (1970a, 1970b). Refer to text for notes concerning measurements omitted or modified.
[2] Digit 2, phalanx 1 of Howard (1929).

notably smaller than the Lari that Schnell (1970a) measured, and a number of the bones are shaped differently.

Measurements represent mean values for up to 10 specimens (see Table 1). We attempted to obtain one-half males and one-half females, but this was not possible for five of the species. We did not try to obtain specimens from throughout the range of each species, or all from one locality, but measured the first five males and five females encountered. We recognize that this is not an optimum sampling procedure and that as a result the reliability of our estimates of phenetic similarity between different pairs of OTUs may vary considerably. However, the general lack of adequate skeletal material in collections essentially precluded sampling by a less arbitrary procedure. A list of specific specimens used, together with appropriate locality and other data, is available from the authors.

METHODS

The terminology and definitions of numerical taxonomy are used throughout this study, and the reader is referred to Sokal and Sneath

(1963) if clarification is needed. Also, Sokal (1966), Sneath (1969), and Michener (1970) give more recent reviews of the theory, rationale, and procedures of numerical taxonomy. Most computations were carried out using NT-SYS (Numerical Taxonomy System), a system of multivariate computer programs developed by F. James Rohlf, John Kishpaugh, and Ron Bartcher.

Multivariate techniques to measure phenetic resemblance may be grouped conveniently into two types: an R-type study involves the analysis of correlations among characters; an analysis of correlations or distances between pairs of OTUs is a Q-type analysis (Cattell, 1952). Both types were used and are described below.

R-TYPE ANALYSIS

Phenetic relationships can be graphically presented as scatter diagrams or three-dimensional models of OTUs plotted with respect to the first few principal components extracted from a matrix of correlations among characters (Rohlf, 1968). These components can be thought of as a set of new orthogonal axes in the 48-dimensional character space (or 47 where characters are divided by one of the measurements). As our characters are correlated and there are many fewer OTUs than characters, it is possible to describe most of the phenetic variation in terms of only a few "new" coordinate axes. (Distances between OTUs can be represented exactly in a dimensional space equal to the number of characters or the number of OTUs minus one, whichever is smaller.) All axes in a principal components analysis are rotated so that the first component "explains" the maximum character variance, the second axis is orthogonal to the first and placed so that it explains a maximum of the total remaining character variance, the third is placed orthogonal to the first and second in a similar way, etc. Orthogonal axes are by definition uncorrelated.

The resulting 3-D models (plots of projections of OTUs onto the first three components) usually represent overall structure well, although there may be distortion in phenetic affinities implied among very similar OTUs. In this way these diagrams are complementary to phenograms, because terminal branches of phenograms usually represent affinities satisfactorily, but one can have less confidence in the main branches (Moss, 1967; Rohlf, 1967, 1968; Hendrickson and Sokal, 1968; Crovello, 1969; Schnell, 1970a, 1970b). To point out where possible distortions in the 3-D models occur, we have superimposed a shortest minimally connected network (Rohlf, 1970) computed from the original matrix of distances between OTUs.

As Rohlf (1968) points out, one advantage of this method of summarizing the results of a phenetic analysis is that no assumptions are made that OTUs must fall into a nested series of clusters or that clusters even

exist. Rohlf (1965, 1967, 1968) describes the computational procedures for obtaining principal components, discusses their theoretical aspects, and shows how to compute projections. We used logarithms of the original measurements and standardized characters.

Q-TYPE ANALYSIS

As above, all characters were transformed to logarithms and standardized, so that each would have a mean of zero and a standard deviation of one. Thus character state codes are independent of original measurement units and are expressed in standard deviation units. The rationale for using logs is given by Schnell (1970a). Missing measurements were recorded as no comparison (NC; Sokal and Sneath, 1963) and were ignored during computation.

Product moment correlation coefficients (r) and average distance coefficients (d) were calculated for all pairs of OTUs by the standard formulae given below (Sokal and Sneath, 1963):

$$r_{jk} = \frac{\sum\limits_{i=1}^{n} (X_{ij} - \overline{X}_j)(X_{ik} - \overline{X}_k)}{\sqrt{\sum\limits_{i=1}^{n} (X_{ij} - \overline{X}_j)^2 \sum\limits_{i=1}^{n} (X_{ik} - \overline{X}_k)^2}},$$

$$d_{jk} = \sqrt{\frac{\sum\limits_{i=1}^{n} (X_{ij} - X_{ik})^2}{n}},$$

where X_{ij} stands for the character state value of character i in OTU j; X_{ik} for the character state value of character i for OTU k; $\overline{X}_j$ and $\overline{X}_k$ for the mean of all state values for OTU j and OTU k, respectively; and n for the total number of characters. Correlations can range from $+1$ to -1 and high positive values indicate similarity. Distances are always non-negative values, with low values indicating similarity.

Cluster analyses (unweighted pair-group method using arithmetic averages, UPGMA; Sokal and Sneath, 1963) were performed on correlation and distance matrices, and the results are summarized in phenograms (diagrams of phenetic relationships; Camin and Sokal, 1965). The UPGMA procedure was selected because, when compared with other clustering procedures, it has yielded the highest cophenetic correlation (i.e. correlation between a phenogram and its similarity matrix) in numerical taxonomic studies to date (see Sokal and Rohlf, 1962; Farris, 1969; Rohlf, 1970).

For some analyses we divided all other measurements (before standardization) by sternum length (SK 21) or humerus length (SK 43) to reduce the overall effect of size. In principal components analyses of data similar

to these, the first component is often a general size factor; hence, we tried to eliminate the size effect by removing the influence of the first principal component mathematically from a matrix of distances between OTUs. The formula used is:

$$DP_{jk} = \sqrt{\frac{n(d_{jk})^2 - (p_j - p_k)^2}{n - 1}},$$

where DP_{jk} is the reduced average distance between OTUs j and k; d_{jk} is the distance between OTUs j and k; p_j and p_k are the projections of OTUs j and k on the first principal component; and n is the total number of characters.

Cophenetic correlation coefficients (Sokal and Rohlf, 1962) were computed between coefficients in the original similarity matrix and those implied by the phenogram; this gives an indication of how well a phenogram summarizes its similarity matrix. We compared different phenograms with the coefficient of correlation of cophenetic values (Crovello, 1969). This is the correlation between sets of coefficients implied by the diagrams. We also calculated coefficients of correlation of similarity matrices (a correlation between the half matrices of two basic similarity matrices, excluding the principal diagonal). Phenograms were compared with the classifications of Ridgway and Hellmayr (Figure 1) in a similar way by assigning arbitrary numerical values to different taxonomic ranks (see Basford et al., 1968; Schnell, 1970b).

RESULTS

Principal components analyses are given first (to indicate the positioning of OTUs in the character spaces) and then the phenograms. Within each of these sections results are presented in the following order: skeletal characters; characters divided by sternum length; characters divided by humerus length; characters minus the effect of principal component I (for phenograms only).

We used shorthand notation similar to that of Schnell (1970a, 1970b) to refer to specific phenograms. Prefixes CORR or DIST refer to the clustering of correlations or distances between OTUs. Hyphenated to one of the above will be SKEL, SKEL/STERNUM, SKEL/HUMERUS, or SKEL(-PC I).

When a particular branching in a phenogram occurs, the placement of one or the other of the resulting branches nearer the top of the page is arbitrary. Therefore, one can rotate branches on their "trunks" without distorting in any way the relationships the phenogram implies.
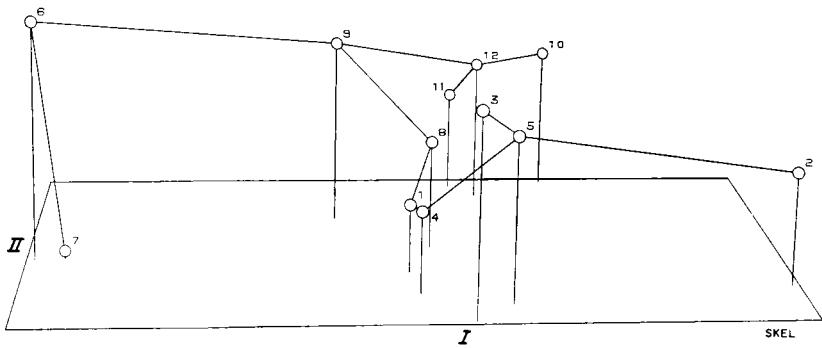
FIGURE 3. Projection of the 12 OTUs onto the first three principal components based on a matrix of correlations among *characters*. I and II are indicated in the figure and III is the height. The shortest minimally connected network is projected onto the principal component space to indicate where possible distortions may be present. Species names corresponding to the OTU numbers can be found in Table 1 and Figure 1.

PRINCIPAL COMPONENTS

Figure 3 shows species projected onto the first three principal components from the analysis of skeletal measurements. The components explain 57.02, 26.58, and 5.81 per cent of the total character variation, respectively. Thus, with about 90 per cent of the total variance explained, reducing the character space to three dimensions distorts the distances between OTUs very little.

Principal component I is essentially a general size factor with high loadings (over 0.75; see Table 3) on many characters, except for most skull measurements; it separates the relatively small *Passerherbulus caudacutus* (6) and *P. henslowii* (7) and the large *Passerculus princeps* (2) from the other OTUs. Component II is a contrast, mainly of SK 1, 2, 11, 12, and 13 (all skull length measurements) against furcular process length (SK 19) and tends to divide off the *Ammospiza* species (9–12), which are relatively larger for the former and smaller for the latter, from the other species. The third factor has its highest correlations with SK 3–6 and 14 (skull widths and bill depths). *Passerherbulus henslowii* (7), which tends to be relatively large for these measurements, is set off from the other OTUs by this factor, while other species fall along a continuum.

Figure 4 is a 3-D model of OTUs projected onto principal components from an analysis of characters divided by sternum length. Two distinct clusters emerge, one containing OTUs 1–5 and the other with OTUs 6–12. The first three components explain 61.47, 12.97, and 7.99 per cent of the variance (total of 82.43). Component I separates the two groups and has

ROBINS AND SCHNELL [Auk, Vol. 88

TABLE 3

THE FIRST THREE PRINCIPAL COMPONENTS BASED ON MATRICES OF CORRELATIONS
AMONG CHARACTERS TREATED IN THREE DIFFERENT WAYS

| SK No.	Skeletal characters			Characters/sternum length			Characters/humerus length		
	I	II	III	I	II	III	I	II	III
1	.398	−.845	−.123	−.952	.084	.062	−.884	−.235	.097
2	.473	−.804	−.001	−.892	.059	.288	−.861	.048	.227
3	.340	−.496	−.514	−.697	.086	−.091	−.503	−.278	−.246
4	.376	.262	−.781	−.319	.224	−.819	.166	−.816	−.243
5	.682	.148	−.517	−.738	.358	−.419	−.097	−.779	−.447
6	.313	−.404	−.578	−.791	.093	−.493	−.477	−.663	−.337
7	.871	−.248	.241	−.920	.048	.096	−.617	−.351	.177
8	.800	−.205	−.173	−.892	.171	−.229	−.459	−.708	−.222
9	.669	−.104	−.174	−.850	.013	−.286	−.300	−.715	−.059
10	.712	−.540	−.279	−.928	.137	−.246	−.586	−.723	−.208
11	.604	−.787	.063	−.992	.003	.013	−.917	−.335	.081
12	.517	−.823	.014	−.987	−.016	.020	−.905	−.308	.150
13	.459	−.781	−.117	−.888	.033	.158	−.820	−.068	.198
14	.227	−.237	−.807	−.603	.134	−.519	−.266	−.663	−.326
15	.760	.586	−.138	.235	−.306	−.634	.767	−.489	.181
16	.953	.279	.055	−.871	−.472	−.017	.762	−.450	.414
17	.896	.435	.035	−.776	−.446	−.239	.834	−.478	.162
18	.795	.567	−.013	.677	−.235	.012	.934	−.029	−.085
19	.595	.777	−.072	.940	−.156	−.096	.947	−.046	.161
21	.868	.472	−.044	—	—	—	.871	−.273	.126
22	.788	.606	−.052	.923	−.248	−.083	.946	−.116	.146
23	.891	−.067	−.056	−.906	−.081	−.174	−.321	−.724	.203
24	.755	.611	.040	.744	−.412	.096	.922	−.050	.242
26	.733	−.616	.006	−.963	−.090	.044	−.903	−.142	.114
27	.697	−.635	.213	−.964	−.092	.164	−.880	−.135	.370
28	.960	−.207	.018	−.977	−.030	.029	−.605	−.581	.458
29	.777	.130	.111	−.753	−.321	−.355	−.040	−.677	.400
30	.793	.465	−.112	−.635	−.200	−.640	.370	−.820	.062
31	.832	−.506	.133	−.934	−.012	.260	−.916	.125	.230
32	.860	−.457	−.004	−.931	.096	.213	−.848	−.066	.149
33	.807	−.512	.065	−.928	.087	.253	−.894	.076	.037
34	.788	−.578	.131	−.984	−.036	.115	−.953	−.173	.126
35	.864	−.431	.202	−.894	−.130	.357	−.835	.291	.344
36	.809	−.529	.207	−.933	−.068	.298	−.883	.110	.375
37	.850	−.416	.288	−.910	−.153	.365	−.846	.308	.356
38	.716	−.675	.029	−.967	.022	.184	−.971	−.063	.047
39	.755	−.614	.178	−.964	−.051	.207	−.951	−.013	.236
40	.879	.422	.058	−.293	−.793	−.076	.919	−.038	.056
41	.829	.549	−.019	.736	−.411	−.062	.906	−.165	.251
42	.893	.405	−.005	−.072	−.788	.081	.867	−.063	.291
43	.977	.042	.086	−.922	−.257	.178	—	—	—
44	.801	.551	.068	.291	−.801	−.003	.970	.043	−.031
45	.810	.553	.060	.187	−.880	−.128	.974	−.054	.021
46	.793	.532	−.021	.123	−.647	−.123	.863	−.250	.232
47	.872	.428	.095	−.251	−.853	.208	.943	.028	.125
48	.826	.426	−.053	−.676	−.182	−.300	.524	−.642	.044
49	.843	.475	.126	−.288	−.824	−.009	.864	−.190	.321
50	.725	.551	.195	.424	.003	.404	.754	−.138	.422
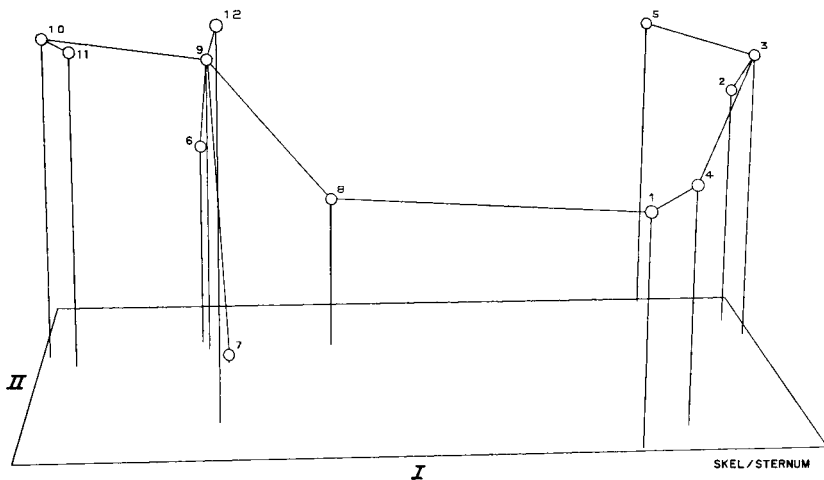
FIGURE 4. Three-dimensional projection of 12 OTUs onto the first three principal components based on a matrix of correlations among *characters divided by sternum length*. I and II are indicated and III is the height. The shortest minimally connected network is projected onto the component space. Species names referring to OTU numbers are listed in Table 1 or Figure 1.

high loadings (over 0.90; see Table 3) on all leg measurements (SK 31–39), synsacrum lengths and depth (SK 26–28), and various other characters (SK 1, 7, 10–12, 19, 22, 23, 43). Relative to sternum length, OTUs 1–5 are smaller than OTUs 6–12 for all of these measurements except furcular process length (SK 19), for which they are larger. The second component has high loadings (over 0.75) on wing elements, particularly bone lengths (SK 40, 42, 44, 45, 47, 49). In the OTU 1–5 group it separates *Myospiza humeralis* (1) and *Ammodramus savannarum* (4) from *Passerculus princeps* (2), *P. sandwichensis* (3), and *A. bairdii* (5). In the other cluster, component II separates *Ammospiza mirabilis* (12) from other OTUs. Birds short-winged relative to sternum length are in the foreground of the diagram. Component III has high loadings on internarial, coracoid, and synsacrum minimum widths (SK 4, 15, 30). *Passerherbulus henslowii* (7) is relatively larger in these measurements and is separated from the other sparrows.

The model in Figure 5 depicts species projections onto principal components from an analysis of characters divided by humerus length. Not unexpectedly, it shows marked similarities with Figure 4, although the two main groups in the latter are not so distinct in Figure 5. Components I, II, and III explain 60.93, 16.53, and 5.88 per cent of the character variance (total 83.34). Factor I is a contrast (positive versus negative load-
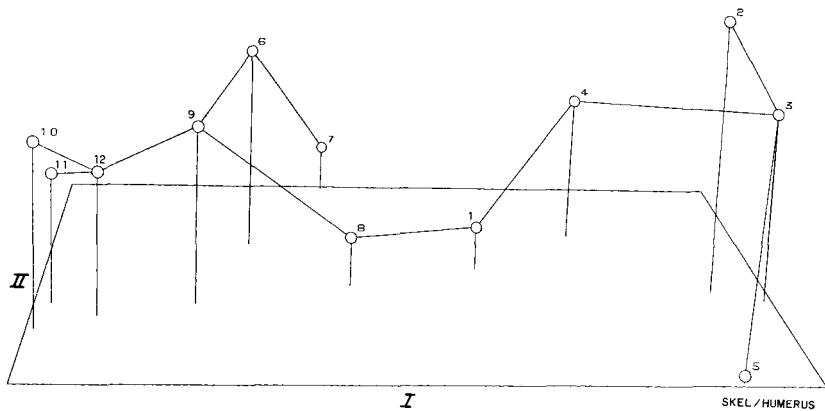
FIGURE 5. A model of 12 OTUs projected onto the first three principal components of a matrix of correlations among *characters divided by humerus length.* I and II are shown and III is the height. The shortest minimally connected network is projected onto the component space. Table 1 or Figure 1 list species names corresponding to the OTU numbers.

ings over 0.90; see Table 3) of pectoral girdle measurements (SK 18, 19, 22, 24, 40, 41, 44, 45, 47) against some pelvic girdle measurements and skull lengths (SK 11, 12, 26, 31, 34, 38, 39). OTUs with longer skulls, a less prominent keel, wider leg bones, and smaller wings (relative to humerus length) are on the right side of the figure. The second component has high correlations (over 0.70) with skull widths and depths (SK 5, 6, 8–10), sternum width (SK 23), and synsacrum minimum width (SK 30). OTUs with relatively small values for these characters are in the foreground of the model. The highest correlations with III (over 0.35) form a contrast of nasal bone width (SK 5) with synsacrum measurements (SK 27–29), tibiotarsus and tarsometatarus lengths (SK 36, 37), and phalanx depth (SK 50).

PHENOGRAMS

The CORR-SKEL analysis (Figure 6) divides OTUs into two main groups: OTUs 1–5 and 8; and OTUs 6, 7, and 9–12. The two groups correspond to the OTUs located in the front right and back left, respectively, of the model in Figure 3. While *Ammospiza* (9–12) remains intact, other traditionally recognized groups do not. For example, *Passerherbulus caudacutus* (6) lies closer to *Ammospiza* than to *P. henslowii* (7). The cophenetic correlation of 0.880 indicates a relatively good fit of the phenogram to the similarity matrix.
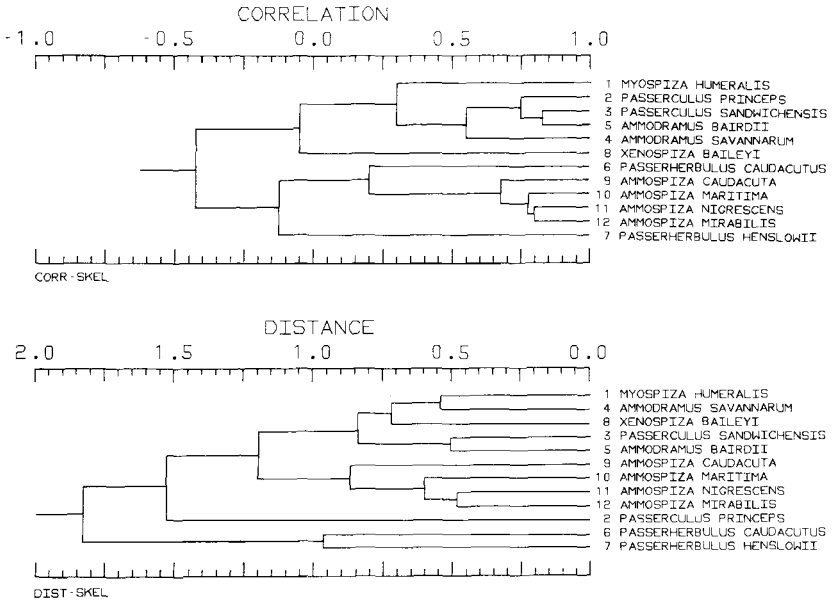
FIGURE 6. Correlation (CORR-SKEL) and distance (DIST-SKEL) phenograms of 12 OTUs based on an unweighted pair group of cluster analyses using arithmetic averages (UPGMA) for the 48 skeletal measurements. The cophenetic correlations are 0.880 and 0.848, respectively.

The clusters formed in DIST-SKEL (Figure 6) differ considerably from those in CORR-SKEL and reflect a decided effect of size. Clustering occurs much as one would group OTUs visually in the 3-D model (Figure 3). The intermediate-sized species were joined before the larger *Passerculus princeps* (2) was included; then the small *Passerherbulus caudacutus* (6) and *P. henslowii* (7) were connected. The cophenetic correlation (0.848) indicates a reasonable fit of DIST-SKEL to its similarity matrix.

CORR-SKEL/STERNUM (Figure 7) is very similar to CORR-SKEL, the fundamental change being the placement of *Xenospiza baileyi* (8) with the *Passerherbulus* (6–7) and *Ammospiza* (9–12) species. A few other minor changes appear in the figures. The phenogram fits its similarity matrix well.

DIST-SKEL/STERNUM (Figure 7) includes the same two major groups as CORR-SKEL/STERNUM; these are also obvious in the 3-D model (Figure 4). Clustering is carried out as one would do by eye from Figure 4, and the distances between OTUs implied by the phenogram are close to those in the original similarity matrix.
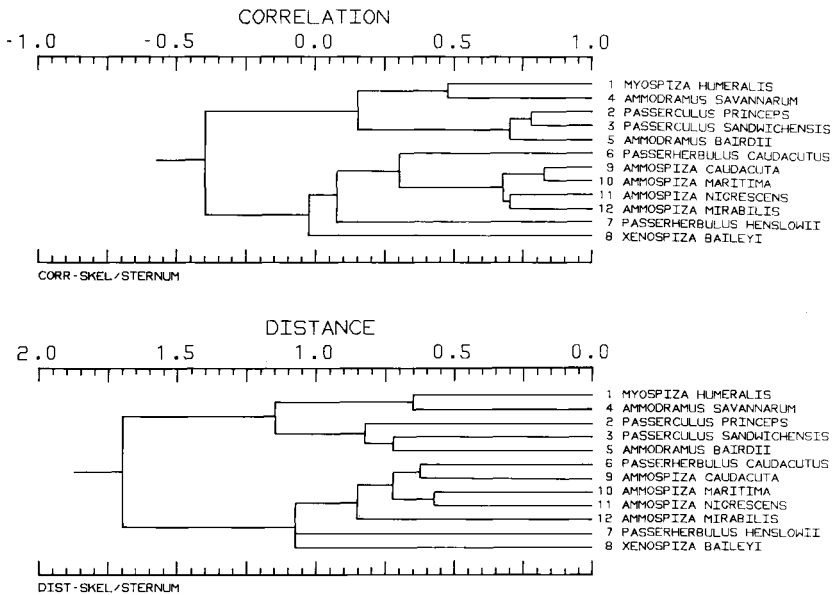
CORRELATION

-1.0   -0.5   0.0   0.5   1.0

1 MYOSPIZA HUMERALIS
4 AMMODRAMUS SAVANNARUM
2 PASSERCULUS PRINCEPS
3 PASSERCULUS SANDWICHENSIS
5 AMMODRAMUS BAIRDII
6 PASSERHERBULUS CAUDACUTUS
9 AMMOSPIZA CAUDACUTA
10 AMMOSPIZA MARITIMA
11 AMMOSPIZA NIGRESCENS
12 AMMOSPIZA MIRABILIS
7 PASSERHERBULUS HENSLOWII
8 XENOSPIZA BAILEYI

CORR-SKEL/STERNUM

DISTANCE

2.0   1.5   1.0   0.5   0.0

1 MYOSPIZA HUMERALIS
4 AMMODRAMUS SAVANNARUM
2 PASSERCULUS PRINCEPS
3 PASSERCULUS SANDWICHENSIS
5 AMMODRAMUS BAIRDII
6 PASSERHERBULUS CAUDACUTUS
9 AMMOSPIZA CAUDACUTA
10 AMMOSPIZA MARITIMA
11 AMMOSPIZA NIGRESCENS
12 AMMOSPIZA MIRABILIS
7 PASSERHERBULUS HENSLOWII
8 XENOSPIZA BAILEYI

DIST-SKEL/STERNUM

FIGURE 7. Correlation (CORR-SKEL/STERNUM) and distance (DIST-SKEL/ STERNUM) phenograms based on characters divided by sternum length. The cophenetic correlations are 0.905 and 0.908, respectively.

The groups resulting from the CORR-SKEL/HUMERUS analysis (Figure 8) are very similar to CORR-SKEL/STERNUM, although slight shifting occurs within the main clusters. The cophenetic correlation of 0.925 was the highest recorded in this study.

DIST-SKEL/HUMERUS (Figure 8) also produced similar clusters, but the cophenetic correlation of 0.795 indicates considerable distortion in the original distances. The reader is referred to Figure 5 to see how clustering took place.

The phenogram in Figure 9, DIST-SKEL(-PC I), results from removing the effect of principal component I (presumably a gross size factor) from the distance matrix based on skeletal characters. The two main groups formed, one containing *Ammospiza* (9–12) and the other the rest of the OTUs, differ from those produced in any other analysis. The cophenetic correlation of 0.789 shows considerable distortion in the phenogram representation of the similarity matrix.

DISCUSSION

The three parts of this section discuss (1) general relationships between classifications, (2) selecting the "best" phenetic classification, and (3) nomenclatural recommendations.
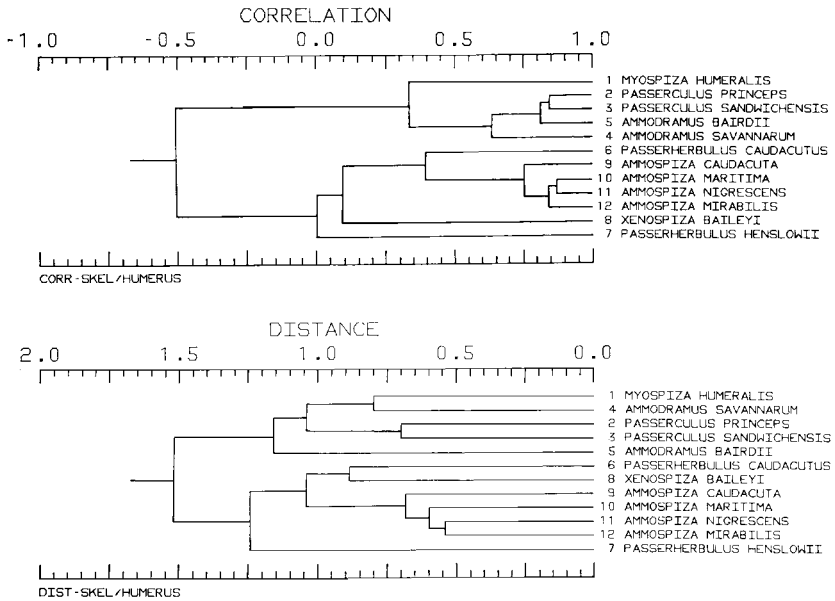
FIGURE 8. Correlation (CORR-SKEL/HUMERUS) and distance (DIST-SKEL/HUMERUS) phenograms based on characters divided by humerus length. Cophenetic correlations are 0.925 and 0.795, respectively.

CLASSIFICATION OF CLASSIFICATIONS

The previous section mentions some similarities between phenograms; this part includes a more precise summary of relationships between these classifications. We analyzed the coefficients of correlation of basic similarity matrices (referred to hereafter as BSMs) and coefficients of correlation of cophenetic values. The relationships between numerical classifications are of particular interest in a general way, as it is important to know something about what techniques will provide similar results, irrespective of the taxonomic group being studied. Such a knowledge should also help clarify our understanding of grassland sparrow affinities.

Table 4 presents the coefficients of correlations of BSMs (lower left) and coefficients of correlation of cophenetic values (upper right) for all possible comparisons. Also, the classifications of Hellmayr (1938) and Ridgway (1901) have been compared with both BSMs and cophenetic values. The negative signs encountered when comparing distance and correlation analyses (because similarities are represented by low values in one and high in the other) are ignored. Figure 10 summarizes in dendrograms the relationships implied by coefficients of BSMs and of cophenetic
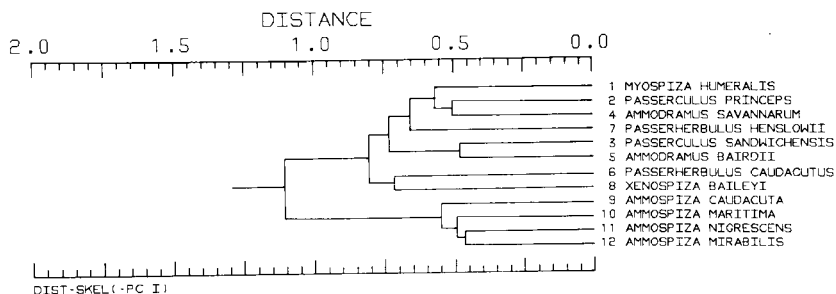
FIGURE 9. DIST-SKEL(-PC I), a phenogram derived from a distance matrix between OTUs (based on skeletal characters) with the effect of principal component I removed. The cophenetic correlation is 0.789.

values in Table 4. The cophenetic correlations of these diagrams indicate that they give good summaries of their respective matrices.

In Figure 10, the BSMs for CORR- and DIST-SKEL/STERNUM and CORR- and DIST-SKEL/HUMERUS are all very similar. The BSM of CORR-SKEL also shows a marked likeness to these four. Ridgway's classification is on the average more similar to these five BSMs than is Hellmayr's. The most divergent BSMs are DIST-SKEL(-PC I), where size was presumably eliminated completely, and DIST-SKEL, where the effect of size went unchecked.

The affinities between phenograms (Figure 10) were changed slightly from those expressed in BSMs, the main modification being in DIST-SKEL(-PC I). Clustering resulted in DIST-SKEL(-PC I) being much more similar to the main group of similar classifications (3-7). DIST-SKEL is the most divergent classification. While Hellmayr's and Ridgway's classifications are on the average more similar to each other than they are to the main group of phenograms, they are more dissimilar than are the phenograms among themselves (in the main phenogram group). Actually, Ridgway's classification has higher (although relatively low) correlations with three of our phenograms than it does with Hellmayr's classification (see Table 4).

As previously found by Sokal and Michener (1967) and Schnell (1970b), correlations tend to give more uniform results than distances when differently treated sets of data are analyzed for the same OTUs (see Figure 10). The similarity we found between distance and correlation phenograms when analyzing characters divided by sternum or humerus lengths is greater than that found for comparisons of appropriate classifications of the Lari (Schnell, 1970b).
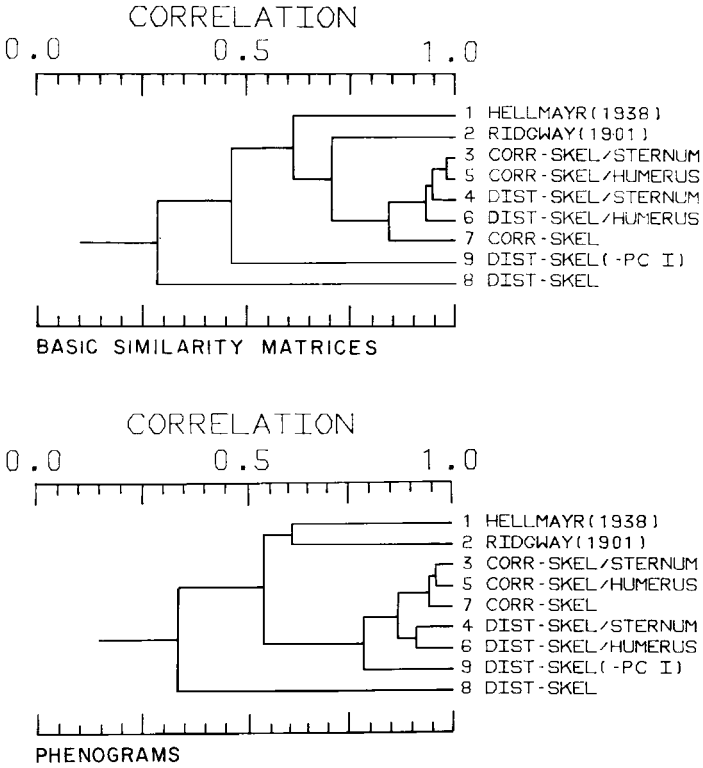
FIGURE 10. Dendrograms showing relationships among basic similarity matrices (BSMs) and among phenograms. Both were constructed using the UPGMA. Cophenetic correlations are 0.925 and 0.927, respectively. The numbers associated with the labels indicate their sequence in Table 4.

TABLE 4

CORRELATIONS BETWEEN ALL PAIRS OF THE NINE BASIC SIMILARITY MATRICES (LOWER LEFT) AND CORRELATIONS BETWEEN ALL PAIRS OF NINE PHENOGRAMS (UPPER RIGHT)

		1	2	3	4	5	6	7	8	9
1	Hellmayr (1938)		.613	.584	.498	.570	.510	.548	.372	.405
2	Ridgway (1901)	.613		.692	.690	.645	.542	.586	.071	.353
3	CORR-SKEL/STERNUM	.648	.752		.919	.957	.882	.928	.387	.761
4	DIST-SKEL/STERNUM	.485	.754	.944		.889	.889	.826	.430	.700
5	CORR-SKEL/HUMERUS	.607	.702	.971	.933		.879	.957	.404	.791
6	DIST-SKEL/HUMERUS	.657	.675	.930	.914	.930		.827	.489	.799
7	CORR-SKEL	.638	.657	.896	.767	.905	.791		.354	.853
8	DIST-SKEL	.394	.012	.314	.193	.320	.334	.459		.250
9	DIST-SKEL (-PC I)	.479	.169	.515	.363	.527	.497	.654	.304	

Schnell (1970b) 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 investigators. He concluded for his data that "The placing (or forcing) of OTUs into a hierarchical system of clusters resulted in an indication of relationships between OTUs more in accord with the opinions of previous workers, who also represented relationships in a hierarchy." Our data do not yield this result, for in 9 of 12 comparisons the BSMs are more similar than are their phenograms to previous classifications (Table 4).

With the exception of the two most divergent phenograms—DIST-SKEL and DIST-SKEL(-PC I)—BSMs and phenograms were more similar to Ridgway's than Hellmayr's classification. The reason is not evident, in good part because the basis of the classification of Hellmayr for this group is not clear.

THE "BEST" PHENETIC CLASSIFICATION

Multiple phenetic classifications of a group are of particular interest, since phenetic relationships often are complicated and each grouping of OTUs expresses a slightly different facet of these relationships. The principal component models, which are classifications at least in the sense of DuPraw (1964, 1965), are particularly useful in elucidating affinities, because we need not assume in such a classification that OTUs fall into a nested series of clusters (Rohlf, 1968).

At times it may be useful to have a single phenogram that in some way best estimates overall phenetic affinities. We have followed the guides outlined by Schnell (1970b) for choosing such a classification. Briefly summarized, these guides suggest: (1) that when correlated characters are used, one should pick a classification that in some way takes these correlations into account; (2) that a classification based on a large number of characters should give a better overall representation than one based on fewer characters; (3) that from classifications meeting the criteria above, the one that best represents its BSM with a minimum distortion should be chosen; and (4) that if other classifications or BSMs indicate particular OTUs are poorly placed, this should be taken into account in the final overall phenetic representation (see the original paper for more detailed discussion of these guides).

On the basis of (1) the only phenogram eliminated from consideration is DIST-SKEL, although it is questionable whether in an overall classification one would want to remove the effects of size completely as we did mathematically in DIST-SKEL(-PC I). As all of our classifications are based on essentially the same number of characters, (2) need not be considered. From (3) we conclude that CORR-SKEL/HUMERUS (Figure

8) is probably the best overall representation of phenetic affinities. We see no evidence of "poorly placed" OTUs from other representations.

NOMENCLATURAL RECOMMENDATIONS

We believe that the classifications presented here are the best currently available estimates of phenetic relationships for this sparrow complex. The question of whether a formal classification should be based strictly on phenetics has been debated vigorously (see summaries of differing viewpoints in Sokal and Sneath, 1963; Hennig, 1966; Mayr, 1969). Our own opinion is that, in extant bird classifications at least, we are dealing for the most part with a type of phenetic classification, although some may not wish to recognize it as such. For example, Schnell (1970a, 1970b) has analyzed classifications of the Lari proposed by earlier workers and concluded that they are mainly phenetic. In the case of the Lari, Schnell (1970b) suggested no nomenclatural changes because he felt that a "good" general (i.e. formal) classification was currently available. For the grassland sparrows considered here, we feel that this is not the case. This group has been fragmented into numerous genera (at least 6 for 13 species) on the basis of single or few characters, and these genera are poorly characterized in the literature. Also, we are unaware of the documentation by any author of even a single character for all of the species; no "comparative" study of this group to date has included all the species involved.

As we have dealt only with these 12 species, we can say little about their relation to other members of the Fringillidae. This study was begun assuming that we were dealing with, if not a monophyletic group, at least a phenetically distinct cluster within the fringillids. Future investigators may show this assumption to be invalid, in which case our conclusons will have to be modified. Within the group our analyses indicate two main phenetic clusters—one containing OTUs 1–5 and the other OTUs 6–12. Within these clusters, species are remarkably similar in skeletal morphology; therefore, we propose these similarities be emphasized and two genera be recognized including the following:

Ammodramus Swainson
  humeralis (Bosc), OTU 1
  princeps (Maynard), OTU 2
  sandwichensis (Gmelin), OTU 3
  bairdii (Audubon), OTU 5
  savannarum (Gmelin), OTU 4

Ammospiza Oberholser
  leconteii [*caudacutus*] (Audubon), OTU 6
  caudacuta (Gmelin), OTU 9
  maritima (Wilson), OTU 10
  nigrescens (Ridgway), OTU 11
  mirabilis (Howell), OTU 12
  baileyi (Bangs), OTU 8
  henslowii (Audubon), OTU 7

We arbitrarily ordered the species according to CORR-SKEL/HUMERUS (Figure 8). The treatment above follows Murray (1968) in

using the specific name *leconteii* in place of *caudacutus* (6); see his paper for the nomenclatural rationale. OTUs 1, 2, 3, 6, 7, and 8 are placed in genera different from treatments in the fifth A.O.U. Check-list (1957) or Hellmayr (1938) or both. If *Myospiza aurifrons* is recognized as a full species, it should probably be called *Ammodramus aurifrons* (Spix).

We think it undesirable to recognize subgenera, as phenetic affinities below the designated generic level are rather variable depending on the particular technique or transformation used. The only cluster that might deserve such recognition is the *Ammospiza caudacuta*(9)-*maritima*(10)-*nigrescens*(11)-*mirabilis*(12) group, which remained quite stable throughout our analyses. To be consistent, every other species that we now place in this genus should be given its own subgenus to reflect phenetic affinities. Certainly (except for the one mentioned above), if subgenera are recognized, they should not follow previous generic splits.

According to Ridgway (1898, 1901), Bangs (1931), and Pitelka (1947), *Myospiza* (1) and *Xenospiza* (8) are the most divergent genera included in this group of sparrows. Only in CORR-SKEL/HUMERUS (Figure 8) is there any suggestion that *Ammodramus humeralis* (1) is the most divergent of the *Ammodramus* (1–5) sparrows. On the basis of four external characters, Ridgway (1898) removed the South American species (*humeralis* [1] and *aurifrons*) from *Coturniculus* and placed them in a new genus, *Myospiza*. Previously, *Coturniculus* also included *savannarum* (4). Thus, our action with regard to *Ammodramus humeralis* (1) is not unprecedented.

Presumably as a result of Pitelka's (1947) study, Miller et al. (1957) listed *Xenospiza baileyi* (1) between *Passerella iliaca* and *Melospiza lincolnii*. In the most extensive study to date on *Xenospiza baileyi* (1), Dickerman et al. (1967) suggested that it should remain as a monotypic genus closely related to the grassland sparrows. For Bangs (1931), Pitelka (1947), and Dickerman et al. (1967), the choice of naming or retaining *Xenospiza* as a monotypic genus was admittedly dictated in part by the lack of information suitable for comparison with supposed relatives. In Figures 3, 4, 5, 7, and 8, *Xenospiza baileyi* (8) has the greatest affinity with OTUs 6, 7, and 9–12. Bangs (1931) considered *Xenospiza* to be closest to *Passerherbulus caudacutus* (6), and Dickerman et al. (1967) noted that Mayr considered it closest to *Passerherbulus henslowii* (7).

Murray (1968) recommended dropping *Passerherbulus*, suggesting that *P. caudacutus* (6) be placed in *Ammospiza* (taking the specific name *leconteii*)—a suggestion with which we concur—but he then placed *P. henslowii* (7) in the genus *Ammodramus*. Worthington and Todd (1926) and Hellmayr (1938: 502) anticipated us in thinking that generic separa-

tion of *Ammospiza leconteii* (6) and *A. henslowii* (7) would serve to obscure their similarity to each other and to the other *Ammospiza* (8–12).

Dickerman et al. (1967) suggested that the genus *Ammodramus* might be enlarged to include *Passerculus, Passerherbulus,* and *Ammospiza,* with *Xenospiza* remaining as a monotypic genus. This opinion is not unlike that of the first A.O.U. Check-list (1886), Ridgway (1887), and Chapman (1895). Later, Dickerman (1968 and pers. comm.) suggested that the genera *Myospiza* and *Xenospiza* might also be included in the enlarged genus *Ammodramus.* As mentioned above, we favor placing the OTUs into two genera.

The question now arises as to why our analyses tended to split the sparrows into two groups. This may reflect the presence of two cladistic groups, but the proof of such a statement seems elusive (as is apparent from *all* work done previously on this group). The most obvious possibility —and probably the most important—is the presence in all species within a given group of a set of adaptations to a similar array of environmental pressures. In the proposed genus *Ammospiza* (6–12), OTUs 6 and 9–12 breed in or near fresh or salt water marshes; *A. henslowii* (7) breeds in marshes, meadows, and neglected fields (Robins, 1967); and *A. baileyi* (8) breeds in marshes (Bangs, 1931), medium and tall bunch grasses (Dickerman et al., 1967), and grassy montane habitats (Miller et al., 1957). Thus all species in *Ammospiza* (6–12) breed in or near marshes, and those that are the least restricted in their choice of breeding habitat (*A. henslowii* [7] and *A. baileyi* [8]) are often on the periphery of the *Ammospiza* cluster in our skeletal analyses (see Figures 4, 5, 7, and 8). The five species included in the proposed genus *Ammodramus* (1–5) do not normally breed in areas as wet as do the *Ammospiza* (6–12). Indeed, the proposed *Ammodramus* sparrows are more aptly named "grassland sparrows," as opposed to the seven "marshland sparrows" of the genus *Ammospiza.*

Brodkorb); University of Kansas (R. F. Johnston, R. M. Mengel); University of Miami (O. T. Owre); University of Michigan (R. W. Storer); University of Minnesota (D. W. Warner); University of South Florida (G. E. Woolfenden); Yale University (N. P. Ashmole).

SUMMARY

Multivariate statistical techniques were used to evaluate 48 skeletal characters and determine phenetic affinities among 12 sparrow species in the genera *Myospiza, Passerculus, Ammodramus, Passerherbulus, Xenospiza,* and *Ammospiza.* Phenetic relationships are presented in phenograms and three-dimensional models of OTUs projected onto principal components based on a matrix of correlations among characters. For the phenograms, average distances and product moment correlations are used as similarity coefficients and the UPGMA for clustering. In some analyses, all measurements are divided by sternum or humerus length to reduce the overall effect of size. In another, the influence of size is eliminated by removing the effect of the first principal component from distances between OTUs.

Seven resulting phenograms are compared among themselves and with the classifications of Ridgway and Hellmayr. Using distances without any attempt to reduce the effect of size resulted in the most divergent classification. Regardless of whether size was taken into account, correlations produced very similar results when the data were treated in different ways. Hellmayr's and Ridgway's classifications were on the average more similar to each other than to the main group of phenograms, but were more dissimilar than were the phenograms among themselves.

The guides of Schnell (1970b) were used to determine which was the "best" phenetic classification, although the usefulness of multiple classifications is stressed. Based on the phenetic groupings obtained, we recommend that two genera be recognized. The first, *Ammodramus,* can be referred to as the grassland sparrows, and includes *humeralis, princeps, sandwichensis, bairdii,* and *savannarum.* The second, *Ammospiza,* can be called the marshland sparrows and contains *leconteii, caudacuta, maritima, nigrescens, mirabilis, baileyi,* and *henslowii.*

LITERATURE CITED

AMERICAN ORNITHOLOGISTS' UNION. 1886. The code of nomenclature and check-list of North American birds. New York, Amer. Ornithol. Union.

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

BANGS, O. 1931. A new genus and species of American buntings. Proc. New England Zool. Club, 12: 85–88.

BASFORD, N. L., J. E. BUTLER, C. A. LEONE, AND F. J. ROHLF. 1968. Immunologic

comparisons of selected Coleoptera with analyses of relationships using numerical taxonomic methods. Syst. Zool., 17: 388–406.

CAIN, A. J., AND G. A. HARRISON. 1960. Phyletic weighting. Proc. Zool. Soc. London, 135: 1–31.

CAMIN, J. H., AND R. R. SOKAL. 1965. A method for deducing branching sequences in phylogeny. Evolution, 19: 311–326.

CATTELL, R. B. 1952. Factor analysis. New York, Harper and Bros.

CHAPMAN, F. M. 1895. Handbook of birds of eastern North America. New York, D. Appleton and Co.

CROVELLO, T. J. 1969. Effects of change of characters and of number of characters in numerical taxonomy. Amer. Midl. Naturalist, 81: 68–86.

DICKERMAN, R. W. 1968. A hybrid Grasshopper Sparrow × Savannah Sparrow. Auk, 85: 312–315.

DICKERMAN, R. W., A. R. PHILLIPS, AND D. W. WARNER. 1967. On the Sierra Madre Sparrow, *Xenospiza baileyi*, of Mexico. Auk, 84: 49–60.

DuPRAW, E. J. 1964. Non-Linnean taxonomy. Nature, 202: 849–852.

DuPRAW, E. J. 1965. Non-Linnean taxonomy and the systematics of honeybees. Syst. Zool., 14: 1–24.

FARRIS, J. S. 1969. On the cophenetic correlation coefficient. Syst. Zool., 18: 279–285.

GRABER, R. R. 1955. Taxonomic and adaptive features of the juvenal plumage in North American sparrows. Unpublished Ph.D. dissertation, Norman, Univ. Oklahoma.

HELLMAYR, C. E. 1938. Catalogue of birds of the Americas. Field Mus. Nat. Hist., Zool. Ser., vol. 13, part 11.

HENDRICKSON, J. A., JR., AND R. R. SOKAL. 1968. A numerical taxonomic study of the genus *Psorophora* (Diptera: Culicidae). Ann. Entomol. Soc. Amer., 61: 385–392.

HENNIG, W. 1966. Phylogenetic systematics. Urbana, Univ. Illinois Press.

HOWARD, H. 1929. The avifauna of Emeryville Shellmound. Univ. California Publ. Zool., 32: 301–394 .

MAYR, E. 1969. Principles of systematic zoology. New York, McGraw-Hill Book Co.

MEYER DE SCHAUENSEE, R. 1966. The species of birds of South America and their distribution. Narberth, Pennsylvania, Livingston Publ. Co.

MICHENER, C. D. 1970. Diverse approaches to systematics. Pp. 1–38 *in* Evolutionary biology, vol. 4 (T. Dobzhansky et al., Eds.). New York, Appleton-Century-Crofts.

MILLER, A. H., H. FRIEDMANN, L. GRISCOM, AND R. T. MOORE. 1957. Distributional check-list of the birds of Mexico, part 2. Pacific Coast Avifauna, No. 33.

MOSS, W. W. 1967. Some new analytic and graphic approaches to numerical taxonomy, with an example from the Dermanyssidae (Acari). Syst. Zool., 16: 177–207.

MURRAY, B. G., JR. 1968. The relationships of sparrows in the genera *Ammodramus*, *Passerherbulus*, and *Ammospiza* with a description of a hybrid LeConte's × Sharp-tailed Sparrow. Auk, 85: 586–593.

PITELKA, F. A. 1947. Taxonomy and distribution of the Mexican sparrow *Xenospiza baileyi*. Condor, 49: 199–203.

RIDGWAY, R. 1887. A manual of North American birds. Philadelphia, J. B. Lippincott Co.

RIDGWAY, R.   1898.   Descriptions of supposed new genera, species and subspecies of
    American birds. I. Fringillidae. Auk, 15: 223–230.
RIDGWAY, R.   1901.   The birds of North and Middle America. Part I. Family Fringil-
    lidae—the finches. U. S. Natl. Mus. Bull. 50: 1–715.
ROBINS, J. D.   1967.   Ecology of Henslow's Sparrow. Unpublished M.A. thesis,
    Kalamazoo, Western Michigan Univ.
ROHLF, F. J.   1965.   Character correlations in numerical taxonomy. Proc. 12th In-
    tern. Congr. Entomol. (London, 1964), pp. 109–110.
ROHLF, F. J.   1967.   Correlated characters in numerical taxonomy. Syst. Zool., 16:
    109–126.
ROHLF, F. J.   1968.   Stereograms in numerical taxonomy. Syst. Zool., 17: 246–255.
ROHLF, F. J.   1970.   Adaptive hierarchical clustering schemes. Syst. Zool., 19: 58–82.
SCHNELL, G. D.   1970a.   A phenetic study of the suborder Lari (Aves)/I. Methods
    and results of principal components analyses. Syst. Zool., 19: 35–57.
SCHNELL, G. D.   1970b.   A phenetic study of the suborder Lari (Aves)/II. Pheno-
    grams, discussion, and conclusions. Syst. Zool., 19: 264–302.
SNEATH, P. H. A.   1969.   Recent trends in numerical taxonomy. Taxon, 18: 14–20.
SOKAL, R. R.   1966.   Numerical taxonomy. Sci. Amer., 215(6): 106–116.
SOKAL, R. R., AND C. D. MICHENER.   1967.   The effects of different numerical tech-
    niques on the phenetic classification of bees in the *Hoplitis* complex (Megachilidae).
    Proc. Linnean Soc. London, 178: 59–74.
SOKAL, R. R., AND F. J. ROHLF.   1962.   The comparison of dendrograms by objective
    methods. Taxon, 11: 33–40.
SOKAL, R. R., AND P. H. A. SNEATH.   1963.   Principles of numerical taxonomy. San
    Francisco, W. H. Freeman and Co.
TORDOFF, H. B., AND R. M. MENGEL.   1951.   The occurrence and possible significance
    of a spring molt in Leconte's Sparrow. Auk, 68: 519–522.
WORTHINGTON, W. W., AND W. E. C. TODD.   1926.   The birds of the Choctawhatchee
    Bay region of Florida. Wilson Bull., 38: 204–229.

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