PATTERNS OF GENIC AND MORPHOLOGIC VARIATION AMONG SPARROWS IN THE GENERA *ZONOTRICHIA, MELOSPIZA, JUNCO,* AND *PASSERELLA*

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ABSTRACT.—Analyses of genic variation and skeletal morphology were used to examine relationships among 10 species in the genera *Zonotrichia, Junco, Melospiza,* and *Passerella.* Cluster and principal components analyses showed that morphologic differentiation involves size and aspects of the skull, synsacrum, and hind limb. The genera have basically different skeletal morphologies; there is some overlap, however. The phenetic groupings of taxa, based on skeletal morphology, were congruent with neither traditional taxonomic limits nor the genetic analysis. The phenetic groupings seem biased by nondivergence and convergence. I conclude that the analysis of the genic data produces a better estimate of the phylogenetic history of the group than the analysis of morphology.

The genic data show that the genera are distinct lineages, although the affinities of *Z. capensis* need clarification. The branching order of *Zonotrichia, J. hyemalis,* and *Melospiza* is unresolved, while *P. iliaca* is probably a sister taxon to these three genera. *Melospiza melodia* and *P. iliaca* are not closely related, contrary to previous suggestions. The Lincoln's Sparrow and Swamp Sparrow are more similar to each other than either is to the Song Sparrow. Within *Zonotrichia,* the phylogenetic hypothesis suggests that the White-crowned Sparrow and Golden-crowned Sparrow are the most similar species, with the remaining taxa joining them in the following order: Harris' Sparrow, White-throated Sparrow, and Rufous-collared Sparrow. This phylogenetic scheme contradicts previous opinions, which, I suggest, were based on inconclusive evidence. The Harris' Sparrow, which is divergent relative to its congeners in both plumage and skeletal characters, is genically similar to its congeners. The Rufous-collared Sparrow is morphologically and genically differentiated from its north-temperate congeners, and, if it is a valid member of *Zonotrichia,* it must be an early derivative.

Heterozygosity ($\bar{x}$ = 0.039), percentage polymorphic loci ($\bar{x}$ = 20.3), and mean number of alleles per polymorphic locus ($\bar{x}$ = 2.4) were similar to values reported for other birds and support the observation that birds possess levels of within-species genetic variation typical of other vertebrates. However, genetic distances averaged 0.06 between congeneric species and 0.26 for noncongeneric (but confamilial) interspecific comparisons and are lower than those observed at comparable taxonomic levels in other vertebrates. Rates of genic change seem homogeneous. Converting genetic distances into estimates of divergence dates suggests that the genera originated from 1.3 to 6.6 MYBP. Speciation within *Zonotrichia* and *Melospiza* probably occurred in the Pleistocene but before approximately 140,000 yr ago. I suggest that *Passerella, Melospiza, Junco,* and *Zonotrichia* be retained as distinct genera until comparable genetic data from other emberizines are available. *Received 11 November 1981, accepted 26 March 1982.*

THE methods of data gathering and analysis used in systematic biology have greatly expanded in recent years. Biochemical assessments of genetic variation, quantitative analyses of genetic and morphologic data, and progress in the theoretical aspects of systematics have provided powerful means for investigating evolutionary relationships among organisms. The use of electrophoresis to study protein variation has been especially prevalent (see Nevo 1978) and has provided, for example, data on levels of genetic variation in natural populations, on the genetic structure of populations and species, and on phylogenetic relationships among taxa. However, there have been few quantitative multi-locus studies of protein variation at the specific and generic level in birds (e.g. Barrowclough and Corbin 1978; Avise et al. 1980a, b; Yang and Patton 1981) relative to other vertebrate groups (Nevo 1978,

Barrowclough 1980b). Similarly, there have been relatively few phenetic (e.g. Schnell 1970, Robins and Schnell 1971, Hellack and Schnell 1977, Wood 1979) and cladistic (e.g. Payne and Risley 1976, Raikow 1976, Simpson and Cracraft 1981) appraisals of morphologic variation in birds. In few studies (Handford and Nottebohm 1976) were protein and morphologic variation examined in concert. The increasing use of these techniques and analyses, and more than one data set, will be important to (1) evaluate evolutionary and systematic relationships among avian taxa, (2) compare avian evolution at different levels (e.g. morphologic and genic), and (3) generate data that can be compared with results from other vertebrate groups.

The systematic relationships among species in the genera *Zonotrichia, Junco, Melospiza,* and *Passerella* have been addressed by several authors (Linsdale 1928; Dickerman 1961; Paynter 1964, 1970; Short and Simon 1965; Mayr and Short 1970), but there has been little recent systematic work on these taxa. In this paper I analyze patterns of genic (= allozymic) and morphologic (skeletal) variation in order to produce independent, quantitative estimates of the systematic relationships and evolutionary history of these emberizine sparrows. Genic versus morphologic differentiation, rates and levels of genic divergence, and taxonomic relationships are discussed.

Methods and Materials

Morphology.—Taxa examined were: Rufous-collared Sparrow (*Zonotrichia capensis*), White-crowned Sparrow (*Z. leucophrys*), White-throated Sparrow (*Z. albicollis*), Golden-crowned Sparrow (*Z. atricapilla*), Harris' Sparrow (*Z. querula*), Song Sparrow (*Melospiza melodia*), Lincoln's Sparrow (*M. lincolnii*), Swamp Sparrow (*M. georgiana*), Fox Sparrow (*Passerella iliaca stephensi, P. i. canescens, P. i. townsendi*), Dark-eyed Junco (*Junco hyemalis*), and Bachman's Sparrow (*Aimophila aestivalis*); the latter taxon was used as an outgroup. The subspecies of *P. iliaca* were used as separate Operational Taxonomic Units (OTU's) (see below). Specimens used in this study are housed at the Museum of Vertebrate Zoology, University of California, Berkeley; further information concerning these specimens is available from the author. Five skeletons per taxon were measured for 40 characters (described in Robins and Schnell 1971) from most body regions (see Appendix 1). Only adult males were used except for one female each of *Z. leucophrys* and *Z. albicollis* and two of *M. georgiana*. Measurements were recorded to the nearest 0.05 mm with dial calipers. The mean of the five measurements for each character was computed for each taxon. While five individuals cannot encompass within-taxon variation, it has been apparently assumed in other, similar studies (e.g. Schnell 1970, Wood 1979) that such sample sizes are sufficient, because within-taxon variation is much less than among-taxon variation. This assumption, in regard to geographic variation, will be discussed below.

Principal components analysis (PCA) and cluster analyses (UPGMA and WPGMA) were used to study patterns of morphological variation (see Sneath and Sokal 1973). PCA is appropriate for elucidating the major phenetic groupings of taxa. The principal components, orthogonal and unrotated, were extracted from a covariance matrix using the program PNCOMP (Duncan and Phillips 1980). The correlations of characters with the first four components were examined to determine which characters best "summarized" the variation.

Because cluster analysis is most accurate at the level of "branch tips" (i.e. higher levels of similarity), it is not suitable for defining broader groupings, the latter being sensitive to different clustering algorithms and distance coefficients (Presch 1979; see beyond). Therefore, ordination (e.g. PCA) and clustering techniques are complementary and are both employed here to evaluate the morphologic data set.

The raw character means were variance standardized, and the Taxonomic Distance (TD, Sneath and Sokal 1973) measure was used to construct an OTU × OTU distance matrix (available from author). The program CLUST, written by W. W. Moss (Duncan and Phillips 1980), was used to construct phenograms (for morphologic and genetic data) and a PRIM (or minimum spanning) network.

The clustering and ordination analyses were used on the 13-taxon × 40-character matrix. In addition, I constructed phenograms from subsets of the 13 taxa. This procedure involved the removal of one or two subspecies of *P. iliaca* in order to test whether morphologically different subspecies, when used in various combinations, resulted in different among-species patterns.

Electrophoresis.—Sample sizes and general localities for specimens are given in Table 1. Samples of liver, heart, and pectoral muscle were stored at −76°C. For preparation of tissue extracts, samples were thawed, minced with a razor blade, and combined with an equal volume of deionized water. Samples were then centrifuged at 16,000 rpm for 40 min at 4°C. The supernatant was frozen at −76°C for later electrophoretic analysis.

I examined 39 presumptive genetic loci (Appendix 2) using standard starch gel electrophoretic procedures (Selander et al. 1971, Avise et al. 1980a, Barrowclough 1980b, Yang and Patton 1981). Protein assays were prepared following Selander et al. (1971), Harris and Hopkinson (1976), and Yang and Patton

(1981). Further information on electrophoretic conditions is available from the author.

Across all species, the most frequent allele at a locus was designated as 100; higher numbers imply a more anodal migration. Allelic mobilities, relative to 100, were estimated to the nearest 5 units. Isozymes (e.g. GOT-1 and GOT-2) are designated by a 1 for the most anodal and sequentially higher numbers for more cathodal forms. Estimates of within-species variability include average heterozygosity per locus, percentage of loci polymorphic (most frequent allele ≤ 0.99), and mean number of alleles per polymorphic locus (per species). Heterozygosity was determined by direct count for each specimen and then averaged ($\pm$SD) for each species. The methods of Nei (1978) and Rogers (1972) were used to calculate genetic distances between taxa. Phenograms (Sneath and Sokal 1973) and phylogenetic trees, constructed using the methods of Fitch and Margoliash (1967; F-M trees) and Farris (1972; Wagner trees), were used to estimate the branching pattern and amount of divergence among the taxa. Phenograms imply homogeneity of rates of genic change along branches, while the phylogenetic trees do not. The F-M procedure constructs a number of trees by altering the branching pattern and branch lengths. Alternative trees were evaluated by the percentage Standard Deviation (%SD; Fitch and Margoliash 1967) and the magnitude and number of negative branches (the fewer the better). A lower %SD implies a better fit of branching diagram to original distance data. The programs EVOLVE (written by W. M. Fitch) and WAGNER (written by J. S. Farris) were used for the F-M and Wagner trees, respectively (Duncan and Phillips 1980). A cladistic (*sensu* Hennig 1966) analysis, using alleles as character states (see Wake 1981), was partially useful at the generic level; however, few synapomorphic allelic states were discovered (see Appendix 2) that defined clades at lower levels, e.g. groups of species. Alleles in *P. chlorurus* were considered plesiomorphic (ancestral).

RESULTS

SKELETAL MORPHOLOGY

Principal components analysis.—The plot of the taxa on Principal Components (PC) I–III is shown in Fig. 1a and on PC II–IV in Fig. 1b. The first three axes account for 94% of the variation in skeletal characters, and PC IV accounts for an additional 3.1%. Along PC I, the taxa are distributed according to size, from left to right. The correlation of $\sqrt[3]{\text{mass}}$ with scores on PC I, for each species, is 0.847 ($P < 0.01$, df = 11). Most characters load highly and positively on PC I (Appendix 1), further supporting the conclusion that PC I is a "size axis." In Fig. 1a, the genera generally occupy different regions of the 40-character space. The superimposed PRIM network, however, shows that *Z. querula* is the nearest neighbor of *P. i. townsendi* and not of *Z. atricapilla*. Also, *Z. capensis* is nearer to *A. aestivalis* than to other *Zonotrichia*. The PCA reveals that species of *Zonotrichia* differ substantially in size (PC I). The subspecies of *P. iliaca* and the species of *Zonotrichia* are relatively dispersed in the principal component space, whereas species of *Melospiza* are more tightly grouped. The sample of *J. hyemalis* stands apart and is nearest to *Melospiza*.

The separation of taxa on PC II (Fig. 1) is mostly attributable to differences in the sizes and shapes of skulls (Appendix 1). *Passerella i. stephensi*, which has the largest skull of any subspecies of *P. iliaca* (Linsdale 1928, Zink unpubl.), and *Z. querula* represent the extremes of variation on this "skull" axis, with the remaining taxa having intermediate positions.

The taxa are arrayed along PC III from *J. hyemalis* to *A. aestivalis*. Characters contributing to PC III (Appendix 1) include: skull (POW), pectoral region (FPL), leg (FMW, TTW, TMW), and wing (ULL, CML). The highest loadings on PC IV are from the synsacrum (PSL, SMW), leg (FEL, FPE, FDE, TTL, TML, TDE), and wing (ULW, CMD).

The plot of PC II–IV (Fig. 1b), which accounts for 14.5% of the variation, can be interpreted as portraying "shape" rather than size because of the deletion of PC I. Because of the low amount of variation explained, however, and the fact that some nonsize-related variation *is* present on PC I, the results should be interpreted with some caution.

The following groupings appear to occupy different areas of the plot of PC II–IV: species of *Zonotrichia* (excluding *capensis*), *A. aestivalis* and *Z. capensis*, *J. hyemalis*, and two subspecies of *P. iliaca* (*canescens* and *stephensi*). The three subspecies of *P. iliaca* are still dispersed, suggesting considerable shape heterogeneity. In Fig. 1b, the species of *Zonotrichia* (excluding *capensis*) are more tightly grouped than in Fig. 1a, again suggesting that size differences contribute in an important way to their separation in Fig. 1a. The overlap of *Melospiza* and *P. i. townsendi* in Fig. 1b suggests either convergence in "shape" or retention of the ancestral morphology.

Thus, the two plots (Fig. 1) show that there

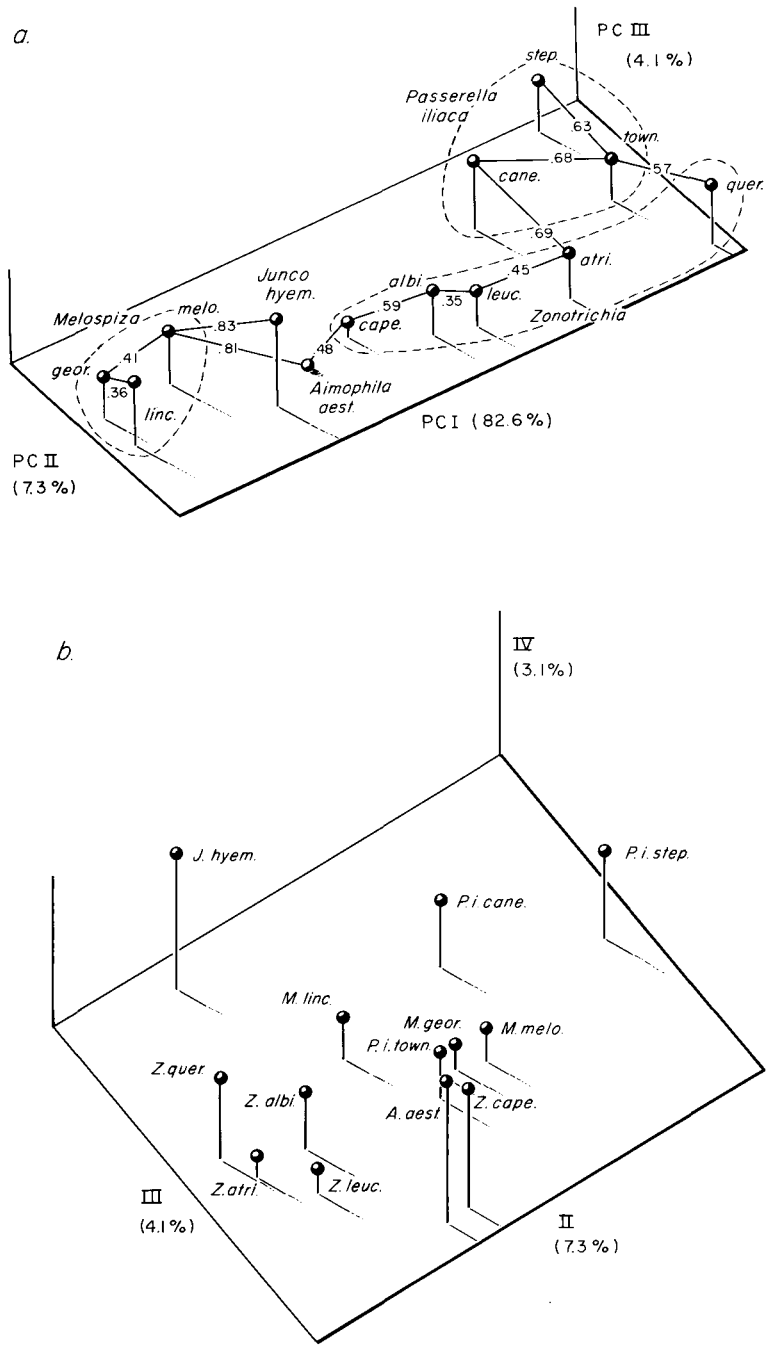

Fig. 1. Three-dimensional representations of principal components analysis of 40 skeletal characters (see Appendix 1). a. Plot of taxa on PC I–III. Because the original 40-dimensional space is reduced here to 3 dimensions by the PCA, a PRIM network is superimposed to indicate a taxon's nearest neighbor in "skeletal morphology space" and to show distortions in this space-reducing procedure. Branch lengths are in units of Taxonomic Distance. The percentage of variance in the data explained by each component is indicated in parentheses. The dashed lines enclose taxa traditionally assigned to *Melospiza*, *Zonotrichia*, and *Passerella iliaca*. b. Plot of taxa on PC II–IV.

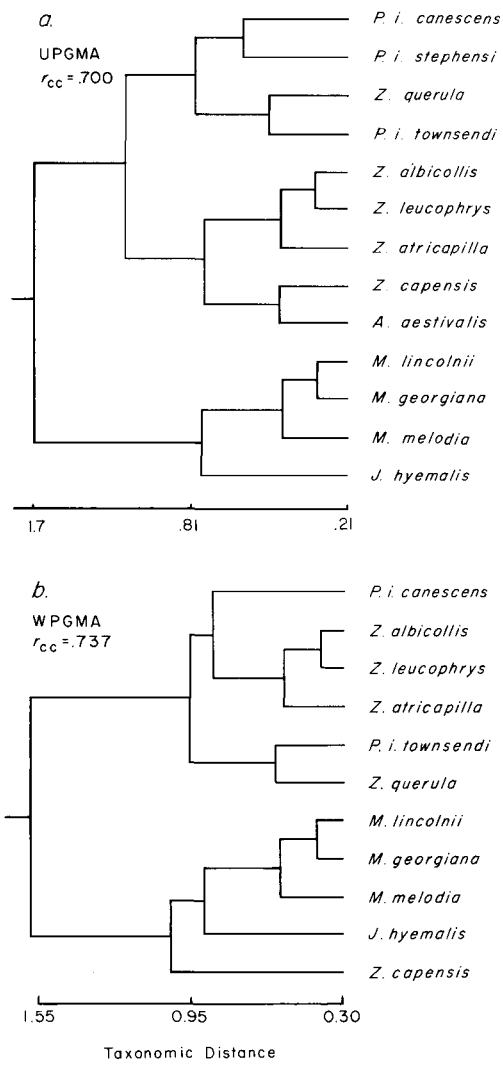

Fig. 2. Phenograms based on the same 40 skeletal characters as in Fig. 1. a. UPGMA analysis of all taxa. b. WPGMA analysis of same taxa excluding *A. aestivalis* and *P. i. stephensi*. The results of analyses of other subsets of taxa are summarized in the text.

are size and shape differences among the genera but that there is also some overlap. Variation in overall skeletal morphology includes most body regions but particularly the skull, pelvic region, and hind limb.

Cluster analysis.—The UPGMA phenogram of the 13 taxa is shown in Fig. 2a. A WPGMA analysis (not shown) of the same 13 taxa differed only in that the *Z. capensis-A. aestivalis* cluster was most similar to *Melospiza-Junco*. There are two basic clusters in Fig. 2a, one consisting of *Zonotrichia* and *Passerella* and one including *Junco* and *Melospiza*. The similarity of *Z. capensis* and *A. aestivalis* (the "outgroup") was unexpected, as was the occurrence of *Z. querula* within the *P. iliaca* cluster. [D. Scott Wood (pers. comm.) also found the latter result in a similar study.] The remaining three species of *Zonotrichia* cluster together fairly tightly, with *Z. leucophrys* and *Z. albicollis* being more similar to each other than either is to *Z. atricapilla*. The subspecies of *P. iliaca* are relatively divergent and more similar to *Zonotrichia* (excluding perhaps *capensis*) than to *Melospiza* or *Junco*. Within *Melospiza, lincolnii* and *georgiana* are more similar to each other than either is to *melodia*. The *J. hyemalis* sample is closer to *Melospiza* than to other taxa. The r_{cc} values for these phenograms, 0.74 for the WPGMA and 0.70 for the UPGMA, suggest that these diagrams are only fair representations of the TD matrix.

Cluster analysis of various subsets consistently placed *Z. querula* with subspecies of *P. iliaca*, although the relationship was ambiguous. For example, in Fig. 2b, *Z. querula* is more similar to *P. i. townsendi* than to other *Zonotrichia*, while *P. i. canescens* is more similar to *Z. atricapilla, leucophrys*, and *albicollis* (TD = 0.80), than to *P. i. townsendi* (TD = 1.0).

By varying either the taxa included and/or the clustering algorithm of the analysis, the phenetic placement of *Z. capensis* oscillated between joining either *Melospiza-Junco* or other *Zonotrichia* (excluding *querula*) as a sister group. Also, in a few instances, the higher-level branching structure was altered. The relationships of *Z. albicollis, Z. leucophrys* and *Z. atricapilla*, the species of *Melospiza*, and *J. hyemalis* were consistent with Fig. 2 in all analyses of subsets; therefore, their phenetic positions seem stable.

GENETIC VARIATION

Levels of intraspecific genetic variation and differentiation.—Allelic frequencies are given in Appendix 2. Heterozygotes were observed at 18 of 39 loci (46.2%), while 6 loci showed only fixed differences across species. The remaining 15 loci were monomorphic and fixed for the same allele for all taxa. Thus, a total of 24 of 39 loci (61.5%) were variable for these 11 species.

A partial correlation analysis (BMDP6R, Frane

TABLE 1. Species examined, sample sizes, localities, and intraspecific genetic variation of species used for electrophoresis.

Species	Number	Locality[a]	$\bar{H}_{obs} \pm$ SD	Percentage polymorphic loci[b]	Mean number alleles[c]
Green-tailed Towhee (*Pipilo chlorurus*)	4	California	0.058 ± 0.038	15.4	2.17
Rufous-collared Sparrow (*Zonotrichia capensis*)	14	Paraguay	0.045 ± 0.031	25.6	2.40
White-crowned Sparrow (*Z. leucophrys*)	19	California (9)**, Oklahoma (10)*	0.036 ± 0.020	23.1	2.44
White-throated Sparrow (*Z. albicollis*)	12	Illinois (5)*, Oklahoma (5)*, Minnesota (2)	0.032 ± 0.016	23.1	2.44
Golden-crowned Sparrow (*Z. atricapilla*)	15	California*	0.039 ± 0.027	15.4	2.67
Harris' Sparrow (*Z. querula*)	18	Nebraska (8)*, Oklahoma (10)*	0.020 ± 0.019	12.8	2.20
Song Sparrow (*Melospiza melodia*)	14	California (5), Illinois (5)*, Minnesota (4)	0.042 ± 0.016	17.9	2.43
Lincoln's Sparrow (*M. lincolnii*)	8	California (2), Nevada (1), Illinois (5)*	0.054 ± 0.046	17.9	2.29
Swamp Sparrow (*M. georgiana*)	16	Minnesota (1), Illinois (15)*	0.042 ± 0.032	23.1	2.33
Fox Sparrow (*Passerella iliaca*)	57	California (51), Oklahoma (1)*, Illinois (5)*	0.036 ± 0.030	30.8	2.42
Dark-eyed Junco (*Junco hyemalis*)	48	South Dakota (25), Montana (23)	0.029 ± 0.022	17.9	2.57
Total	225	Mean[d]	0.039	20.3	2.40

[a] An asterisk denotes specimens taken on migration or during winter. Two asterisks mean sample includes both breeders and nonbreeders. Precise localities are available from author.
[b] Frequency of most common allele ≤ 0.99.
[c] Per polymorphic locus.
[d] Unweighted by sample size.

1977) showed that sample size (i.e. number of animals per species) was not a significant predictor (determined by two-tailed t-tests, $P > 0.05$) of heterozygosity, percentage of loci polymorphic, or number of alleles per polymorphic locus (Table 1). Therefore, the values can be compared directly between species. The Harris' Sparrow has lower levels of genetic variability than the other species, which have similar levels of variation among themselves. The levels of genetic variation shown in Table 1 are similar to those reported for other birds (Barrowclough and Corbin 1978; Barrowclough 1980b; Avise et al. 1980a, b; Yang and Patton 1981).

Even with broad geographic representation for some species (Table 1), within-species genic differentiation was much less than among-species levels. Nei's (1978) D among breeding *M. melodia* from California and Minnesota, and migrants from Illinois, was less than 0.007. The sample of *P. iliaca* is part of a major study (Zink unpubl.) of 619 breeding individuals from a total of 31 localities in California, Oregon, and Nevada; 7 subspecies including *canescens* and *stephensi* have been examined. The largest D-value for any pair of localities is 0.004 ($\bar{x} = 0.001$); the $\bar{D}$ between *canescens* and *stephensi* is 0.0004. Fox Sparrows from Illinois (migrants of the *iliaca* subspecies group) and California (migrants of the *unalaschcensis* subspecies group) are very similar to the breeding birds I examined (discussed above) from the western United States. The sample of *J. hyemalis* is part of a genic analysis by George F. Barrowclough (unpubl.), which includes breeding birds from populations distributed from South Dakota to southern California. The largest D-value between populations is 0.004. These levels of within-species (i.e. population or subspecies) genic divergence are typical for birds (Barrowclough 1980b) and indicate that further sampling of additional individuals and geographic regions would probably not alter the relationships offered below (with the possible exception of *Z. capensis*).

Interspecific genetic distance.—The genetic distances (Nei's and Rogers') between species are given in Table 2. The average genetic distance ($\bar{D} \pm$ SD; Nei 1978) among five species of *Zonotrichia* is 0.118 ± 0.073 (0.063 ± 0.024 excluding *capensis*) and among three species of *Melospiza*, 0.059 ± 0.026. These congeneric, in-

TABLE 2. Matrix of genetic distances between 11 species of emberizine sparrows. Nei's (1978) D-values are above the diagonal, and Rogers' (1972) D-values are below the diagonal.

Species	1	2	3	4	5	6	7	8	9	10	11
1. *Pipilo chlorurus*	—	0.4284	0.3916	0.4454	0.4287	0.3740	0.3654	0.3283	0.4077	0.3769	0.4135
2. *Zonotrichia capensis*	0.3628	—	0.1942	0.1915	0.2134	0.1965	0.2888	0.2519	0.2889	0.3224	0.2269
3. *Z. leucophrys*	0.3327	0.1951	—	0.0677	0.0280	0.0438	0.2726	0.2389	0.2634	0.3434	0.2096
4. *Z. albicollis*	0.3701	0.1932	0.0816	—	0.0938	0.0756	0.1923	0.2200	0.2177	0.3182	0.1709
5. *Z. atricapilla*	0.3566	0.2135	0.0448	0.1125	—	0.0701	0.3062	0.2723	0.2976	0.3796	0.2423
6. *Z. querula*	0.3250	0.2015	0.0596	0.0891	0.0875	—	0.2895	0.2517	0.2741	0.3138	0.1755
7. *Melospiza melodia*	0.3153	0.2674	0.2533	0.1910	0.2796	0.2652	—	0.0464	0.0885	0.2270	0.1763
8. *M. lincolnii*	0.3028	0.2492	0.2359	0.2232	0.2672	0.2473	0.0765	—	0.0415	0.2265	0.1868
9. *M. georgiana*	0.3531	0.2684	0.2495	0.2135	0.2786	0.2567	0.1104	0.0724	—	0.3091	0.1913
10. *Passerella iliaca*	0.3295	0.2917	0.3027	0.2850	0.3305	0.2789	0.2173	0.2265	0.2808	—	0.2519
11. *Junco hyemalis*	0.3524	0.2191	0.2029	0.1725	0.2323	0.1760	0.1781	0.1955	0.1947	0.2363	—

terspecific levels are an order of magnitude greater than the intra-specific levels discussed above. The $\bar{D}$ among species of *Zonotrichia* and *Melospiza* is 0.262 ± 0.033 (15 comparisons); *P. iliaca* and *Zonotrichia*, 0.335 ± 0.027 (n = 5); *P. iliaca* and *Melospiza*, 0.254 ± 0.048 (n = 3); *J. hyemalis* and *Zonotrichia*, 0.205 ± 0.031 (n = 5); *J. hyemalis* and *Melospiza*, 0.185 ± 0.008 (n = 3). The $\bar{D}$ among congeneric species in *Zonotricia* (excluding *capensis*) and *Melospiza*, 0.063 ± 0.024, is clearly less than the $\bar{D}$ for noncongeneric comparisons (0.262 ± 0.033). The implications of the relatively high $\bar{D}$ between *Z. capensis* and its congeners, 0.199 ± 0.010, will be considered below. These levels of genetic differentiation are similar but somewhat larger than those reported by Barrowclough (1980b) for other passerine congeneric ($\bar{x}$ = 0.044) and noncongeneric ($\bar{x}$ = 0.214) interspecific comparisons.

Genic relationships among taxa.—Loci that best discriminate among taxa were analyzed cladistically (see Wake 1981 for discussion); only alleles in high frequency were used. Assuming that the alleles in *P. chlorurus* represent the ancestral condition, the four genera constitute a monophyletic group based on the possession of the same shared-derived alleles (synapomorphies) at GOT-1, GAPDH, and GLUD. *Passerella iliaca* has unique alleles (autapomorphies) at NP, SOD-1, G-6-PDH, and αGPD-1 and shares a synapomorphy with *Melospiza* at LDH-1 (175). The genic monotypy of *J. hyemalis* is supported by autapomorphies at LDH-1 and ACON, but *J. hyemalis* shares a synapomorphy with *Melospiza* at NP (120), with north-temperate *Zonotrichia* at G-6-PDH (100) and an uncommon allele in high frequency with *Z. querula* at αGPD-1 (110). Species of *Zonotrichia* form a monophyletic group based on synapomorphies at LDH-1 (100) and NP (85, 100), and the four north-temperate species share distinctive alleles at ICD-1. Alleles at 6-PGDH and ADA also serve to identify *Zonotrichia* as a genic clade, and alleles at SDH, ACON, GPI, αGPD-1, and LGG contribute to differentiation within the north-temperate species. *Zonotrichia capensis* has unique alleles at PGM-2, G-6-PDH, and αGPD-1 and a unique allele at NP (85) in high frequency. The distribution of synapomorphies at G-6-PDH and NP suggests different cladistic relationships for *J. hyemalis*, *Z. capensis*, and north-temperate *Zonotrichia*. Species of *Melospiza* have shared-derived alleles at GPT (120) and G-6-PDH (110); differentiation within *Melospiza* is due mostly to alleles at ACON, EAP, ACP, and ADA.

Representative branching diagrams summarizing the pairwise matrix of Rogers' D-values (Table 2) are shown in Fig. 3. A total of 17 branching diagrams (14 F-M trees, 2 phenograms, Wagner tree) was examined and the following conclusions were consistently supported: (1) *P. chlorurus* is an appropriate outgroup; (2) *P. iliaca*, *Melospiza*, *J. hyemalis*, north-temperate species of *Zonotrichia*, and possibly *Z. capensis* are distinct lineages, and *P. iliaca* is probably a sister group to these genera; (3) the relationships of species in *Zonotrichia* and *Melospiza* are as shown in Fig. 3; and (4) *Z. capensis* is not closely allied to its north-temperate congeners, and it is of uncertain affinities. Disagreement among branching diagrams of similar efficiency (i.e. similar r_{cc} or %SD) showed that the branching order of *J. hyemalis*, *Melospiza*, and *Zonotrichia* is unresolved. For example, the UPGMA phenogram and the "best" F-M tree had the same branching sequence (Fig. 3a), while the Wagner parsimony tree (Fig. 3b) places *J. hyemalis* closer to *Zonotrichia* than to *Melospiza*. A WPGMA phenogram (r_{cc} = 0.94) and an F-M tree (%SD = 8.45, two negative branches) (neither shown) resembled Fig. 3b; the positions of *J. hyemalis* and *Z. capensis* were exchanged, however, reflecting the conflicting data discussed above for NP, LDH-1, and G-6-PDH. Overall, *Z. capensis* is more similar to its congeners ($\bar{D}$ = 0.199 ± 0.010) and *J. hyemalis* (D = 0.227) than to either *Melospiza* ($\bar{D}$ = 0.277 ± 0.020) or to *P. iliaca* (D = 0.322).

Rates of genic differentiation.—The F-M and Wagner procedures estimate branch lengths, which can be interpreted as rates of genic divergence. There are no confidence limits on these "rates," and they cannot be evaluated statistically. Also, "rates" will be dependent on the loci included in a survey, i.e. the rates are averages across loci.

Within *Zonotrichia* (Fig. 3a), branch lengths in units of Rogers' D (×10) from the "common ancestor" range from 0.85 for *Z. albicollis* to 1.16 for *Z. atricapilla* (mean ± SD = 0.98 ± 0.14). Branch lengths (Fig. 3a) to species of *Melospiza* are 0.39, 0.42, and 0.67 for *M. melodia*, *M. lincolnii*, and *M. georgiana*, respectively ($\bar{x}$ ± SD = 0.49 ± 0.15). If *Z. capensis* is excluded because of its uncertain affinities, the comparable

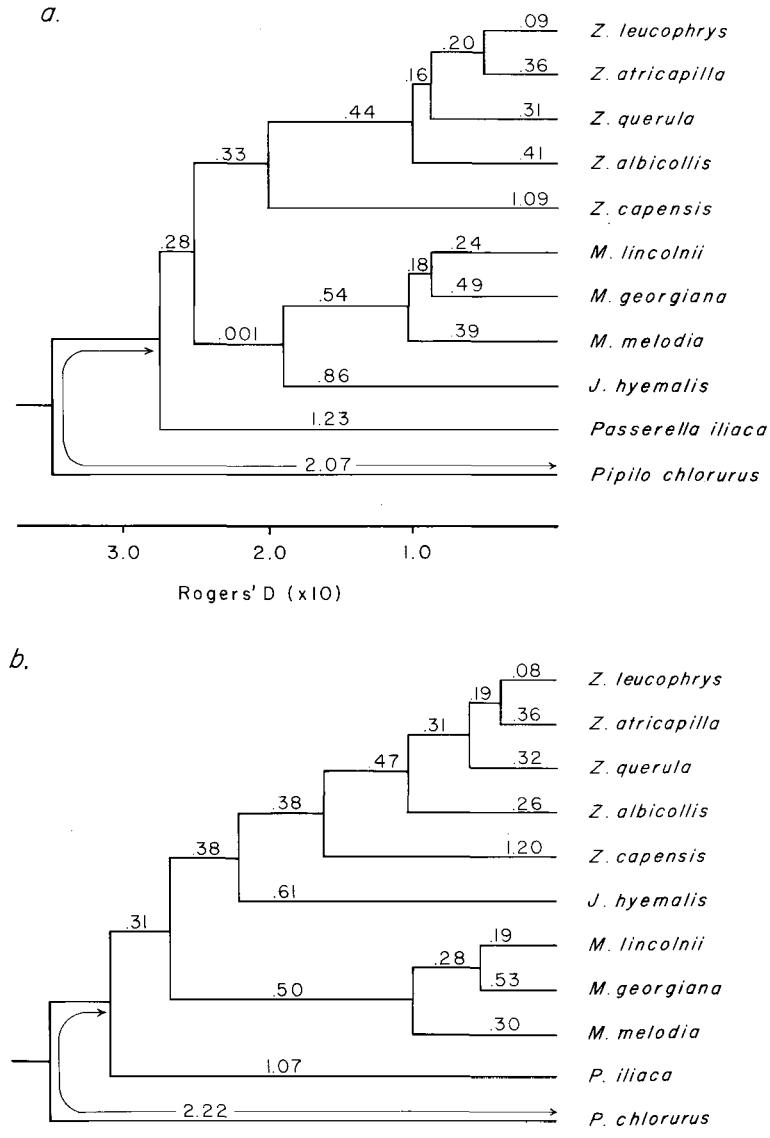

Fig. 3. Branching diagrams summarizing the matrix of Rogers' *D*-values (× 10). a. Branching diagram depicting results of a UPGMA cluster analysis (r_{cc} = 0.95) and an F-M tree. Branch lengths are from the F-M tree, which has a %SD of 7.85. b. Wagner tree, rooted at *P. chlorurus*, with a %SD of 13.8. This branching diagram is an approximation of the most parsimonious, or minimum length, tree (Farris 1972). In both the F-M and Wagner trees, the distance from *P. chlorurus* to the remaining taxa is not partitioned into two branch lengths, because this would require an additional outgroup to *P. chlorurus*.

value for the other species of *Zonotrichia*, 0.51 ± 0.14, is equivalent to that for species of *Melospiza*. I conclude that *within* each genus there is no compelling evidence to reject a hypothesis of homogeneity of rates. The distances from the joining of *P. chlorurus* to *P. iliaca*, *J. hyemalis*, *Melospiza* (distances averaged), and *Zonotrichia* (distances averaged), are 1.23, 1.14, 1.31 ± 0.15, and 1.59 ± 0.14, respectively, for the F-M tree. The same comparisons for the Wagner tree are 1.07, 1.30, 1.34 ± 0.26, and 2.15 ± 0.22, respectively, and suggest a faster relative rate for *Zonotrichia*. Because the Wagner tree has a higher %SD than the F-M tree, however, I note

only that genic change in *Zonotrichia* may be rapid, relative to the other genera, but it is not proven. The suggestion of rate heterogeneity among genera does warrant the use of tree-constructing methods, such as F-M and Wagner, which take into account this possibility.

Discussion

Evaluation of morphologic analyses.—Several aspects of the phenetic analysis deserve attention. The subspecies of *P. iliaca* are as divergent as *Z. atricapilla*, *Z. leucophrys*, and *Z. albicollis*, and species in *Melospiza*, are from each other (Fig. 2a). Although these subspecies consistently cluster with *Z. querula*, the analysis suggests that geographic variation should be evaluated before addressing among-species relationships. While *P. iliaca* and *M. melodia* are both highly polytypic, the remaining species examined here are less variable. Therefore, I assume that the samples (number of characters and individuals and geographic representation) used here are sufficient for documenting patterns of phenetic variation in all forms except *M. melodia* (discussed below).

The stability of phenetic groupings can be examined by altering clustering algorithms (see also Presch 1979, Wood 1979, Duncan et al. 1980). In Fig. 2 for example, a comparison of the UPGMA and WPGMA phenograms (each with similar r_{cc}'s) shows that the phenetic placement of *Z. capensis* is inconsistent. Conclusions drawn from the phenograms should mainly involve the "stable" phenetic groupings. Previous avian phenetic studies (e.g. Schnell 1970, Wood 1979) have examined alternative phenograms, but assessments of geographic variation and independent phylogenetic analyses are rarely included (see Payne and Risley 1976).

The phenetic groupings of *P. iliaca* and *Zonotrichia* (especially *Z. querula*), *Melospiza* and *J. hyemalis*, *Z. capensis* and *A. aestivalis*, and the relationships of *Z. leucophrys*, *Z. albicollis*, and *Z. atricapilla* (Fig. 2) contradict traditional taxonomic arrangements (Mayr and Short 1970, Paynter 1970). The clustering of *P. i. townsendi* with *Z. querula* rather than with its conspecifics does not reflect biological species limits. Only the phenetic relationships of species of *Melospiza* in Fig. 2 resemble previous taxonomic opinions (Mayr and Short 1970). The instances of disagreement cited above could be attributable to incorrect taxonomy, nondivergence (i.e. plesiomorphy) at the level of overall skeletal morphology, homoplastic evolution (e.g. convergence), or methodological factors (e.g. small sample sizes used here; see above). Thus, it is difficult to evaluate the significance of the phenetic groupings proposed by this analysis.

Comparison of morphologic and genic patterns of variation.—Here, I compare the phenetic groupings (Figs. 1, 2) to the independent genic estimates (Fig. 3) of relationships and analyze specific cases of noncongruence. The phenetic analysis of skeletal morphology is designed to identify groups of taxa based on measures of overall similarity. In such analyses, contributions of individual characters are obscured due to their combination into a single measure, such as Taxonomic Distance (e.g. Fig. 2), or into principal components; in PCA, examination of character "loadings" can help recover some information about individual characters. Thus, patterns of change in divergent characters may be swamped out by inclusion of nondivergent characters (i.e. plesiomorphic or ancestral) or characters that exhibit convergence, parallelism, or reversals. In cluster analysis, for example, the degree to which phenetic groupings reflect phylogeny will depend on how well the TD measure tracks divergent evolution, which is a point of contention among systematists (Mickevich 1978, Presch 1979, Rohlf and Sokal 1980). Independent analyses are necessary to establish whether or not phenetic groups of taxa represent phylogenetic groupings.

It is useful to document patterns of phenetic variation, because they may provide general indications of evolutionary trends in morphology or identify instances of ecological convergence between species. The $\bar{D}$ among *Z. albicollis*, *Z. atricapilla*, and *Z. leucophrys*, 0.06 ± 0.03, is two orders of magnitude higher than the $\bar{D}$ between *P. i. canescens* and *P. i. stephensi* (0.0004, Zink unpubl.), yet the subspecies of *P. iliaca* show greater levels of morphologic divergence (Fig. 2). These species of *Zonotrichia* breed in similar habitats (Godfrey 1966), but the subspecies of *P. iliaca* breed in quite different habitats (Linsdale 1928). It seems clear, in this example, that genic divergence in *Zonotrichia* has proceeded without concomitant morphologic change.

It would be tempting to suggest that the similarity of *P. iliaca* and *Z. querula* (Fig. 2) rep-

resents a "hidden" link between the genera. However, Nei's D between these species, 0.314, is greater than most comparisons between noncongeners. *Passerella iliaca* is a separate clade in Fig. 3, and *Z. querula* is clearly similar to its congeners. Therefore, the phenetic resemblance is attributable to convergence, plesiomorphy, or the fact that both are "large." A phylogenetic analysis (Hennig 1966) of morphology is required to prove convergence vs. plesiomorphy. Research on comparative aspects of the ecology of *P. iliaca* and *Z. querula* might show whether or not adaptation to similar environments or niches could explain the apparently similar morphologies.

The branching sequence among the other species of *Zonotrichia* is not congruent between the data sets. *Zonotrichia albicollis* and *Z. leucophrys* are more similar to each other than either is to *Z. atricapilla*, based on skeletal morphology, but the genic estimate substitutes *atricapilla* for *albicollis*. The genic and morphologic data sets agree, however, that *Z. capensis* is divergent relative to its congeners.

Melospiza lincolnii and *M. georgiana* cluster together in analyses of both data sets. Wood (pers. comm.) found that, by accounting for the morphologic variation among subspecies of *M. melodia*, the relationships suggested by Fig. 2 were substantially altered. Hence, concordance between morphologic and genic data sets for species in *Melospiza* may be tenuous. The genic data (Fig. 3) show that the relationship between *J. hyemalis* and *Melospiza* is unresolved. This conflicts with the closer relationship of these taxa shown in Fig. 2.

Thus, the morphologic (Fig. 2) and genic (Fig. 3) estimates of relationships among taxa are not congruent. The correlation between the genetic distance and taxonomic distance matrices is 0.47 (excluding outgroups and *P. i. townsendi*). The genic data are congruent with traditional generic limits, however, (A.O.U. 1957), with the possible exception of these for *Z. capensis*. There is no a priori reason to expect concordance between the genic and morphologic data sets (Schnell et al. 1978, Templeton 1981, Wake 1981). Genic evolution can occur without concomitant morphologic change (Gorman and Kim 1977, Highton and Larson 1979), and organisms with different morphologies may be genically similar (Turner 1974, Avise et al. 1975, King and Wilson 1975, Yang and Patton 1981).

Voous (1980: 1232) proposed that "morphology is a better index to ecology than to phylogeny," and, although I doubt the generality of this claim (see Simpson and Cracraft 1981), Voous' idea may pertain here. Phenetic analysis of species, based on skeletal morphology, probably measures, at least in part, phenotypic responses to ecological conditions. That is, the genetic basis of these groupings is unknown. At the allozymic level, almost certainly genetic, the data, which are bands on gels, have a simple and better understood relationship to the genotype.

In summary, based on 39 presumptive genetic loci, the $\bar{D}$'s between conspecific populations, congeneric species, and noncongeneric species are 0.002 (Zink unpubl.), 0.06, and 0.26, respectively, and show a monotonic increase of $\bar{D}$ as the taxonomic (and probably biological) unit examined becomes more inclusive. Thus, I propose, based on the hierarchical levels of genic variation found here, that the analysis of genic data (Fig. 3) best depicts phylogenetic relationships among these emberizine taxa. The morphologic groupings in this study include instances of nondivergence (some *Zonotrichia*) and probably convergence (*P. iliaca* and *Z. querula*).

Evolutionary history and levels of genic differentiation.—Genetic distances can be used to estimate dates of divergence among taxa (Nei 1975, Sarich 1977, Yang and Patton 1981). There are few independent estimates of divergence times against which to calibrate the avian electrophoretic clock; such calibrations are badly needed. Also, genetic distances are assumed to be linear functions of time since divergence (Wilson et al. 1977, Vawter et al. 1980; but see Lessios 1981), and this assumption needs verification for avian systems, especially at low levels of D.

Estimates presented here are offered as "ballpark" figures. Values were derived using the formula $t = c \times 10^6 D$, where D is Nei's (1978) D-value; the value of c was varied from 5 (Nei 1975) to 26.3. The latter value was estimated by Gutiérrez et al. (in press) based on a calibration of $\bar{D}$ and the fossil record of some New World Quail (Odontophorinae).

The genetic distinctness of the genera (excluding *Pipilo*) examined here, $\bar{D} = 0.25$, converts to ages of from 1.3 to 6.6 million years before present (MYBP)—a wide range, but important in suggesting that late Pleistocene glaciations were probably not responsible for the

origin of these lineages. At the generic level, given the unresolved branching order (Fig. 3) and the wide overlap in breeding ranges (A.O.U. 1957), a biogeographic reconstruction is not possible. That is, the data do not allow prediction of the time and place of the origin of these lineages.

Congeneric species in *Zonotrichia* (excluding *capensis*) and *Melospiza* ($\bar{D}$ = 0.06) are about 300,000–1,600,000 yr old, suggesting that speciation in these genera occurred in the Pleistocene but probably not more recently than 140,000 yr ago (based on the lowest observed D, 0.028, between *Z. leucophrys* and *Z. atricapilla*, and c = 5). Thus, it is unlikely that glaciations of Wisconsinian and possibly Illinoian ages influenced speciation in these genera, in contrast to the suggestion by Hubbard (1973) that speciation in other passerine groups was affected by such glacial events.

Within north-temperate species of *Zonotrichia*, *Z. albicollis* originated the earliest (Fig. 3). The "primitiveness" of *Z. albicollis* is possibly corroborated by the breast streakings in the first winter plumage, reminiscent of the condition in *M. lincolnii* but different from the remaining three species of *Zonotrichia*. *Zonotrichia querula*, which presently breeds in Mackenzie, Keewatin, and northern Manitoba (Godfrey 1966), differentiated next. The divergent plumage and skeletal morphology of *Z. querula* has probably developed in a relatively short span of time. Last, a sister lineage to *Z. querula*, possibly widely distributed across northern North America, fragmented into *Z. atricapilla* in the west and *Z. leucophrys* presumably in the east; subsequent dispersal would explain the occurrence of *Z. leucophrys* across all of North America.

The $\bar{D}$ of *Z. capensis* to its congeners, 0.19, represents from 1.0 (c = 5) to 5.0 (c = 26.3) MYBP. This species is distributed from México to southern South America (Edwards 1974). If *Z. capensis* is indeed a member of a monophyletic *Zonotrichia* clade, it is an early offshoot that has undergone considerable anagenetic evolution, as evidenced by the branch lengths in Fig. 3. *Zonotrichia* (and *Junco*) possibly originated in South America and subsequently dispersed northward. Intraspecific genic differentiation, however, must be evaluated in *Z. capensis* before its systematic position can be resolved. The possibility exists that *Z. capensis* is more closely related to other South American emberizines.

Passerine birds are less differentiated genically, at comparable taxonomic levels, than other vertebrates (Barrowclough 1980b, Avise et al. 1980b, this study). Heterozygosity levels in passerines including those studied here, approximately 4%, are similar to other vertebrates (Nevo 1978); therefore, birds are not lacking the "stuff" of genic divergence.

Large effective population sizes and high rates of gene flow typify many avian populations (Barrowclough 1980a), and these factors may inhibit genic divergence at this level. Avian species limits are often clearly defined, however, because of the numerous "tests of sympatry" among breeding species. Therefore, the low interspecific genic differences ($\bar{D}$ = 0.04; Barrowclough 1980b) among passerines seem to be a real result. Recency of common ancestry (e.g. Baker 1981) or slow rates of protein evolution and rapid rates of morphological change are possible explanations. Tests among such alternatives should be pursued at the species level; comparisons at other levels in vertebrates may be biased, because taxonomists partition variation in different ways in different groups.

Summary and critique of previous taxonomic opinions.—Evidence cited for close relationships among the taxa discussed here has not been critically evaluated; a brief review of previous ideas follows. Mayr and Short (1970) agreed with Linsdale's (1928) merger of *Melospiza* into *Passerella* and suggested that these genera were closely allied to *Junco* and *Zonotrichia*. Mayr and Short considered *Z. albicollis* and *Z. atricapilla* to be components of a superspecies and included these with *Z. leucophrys* as a species group. Paynter (1964, 1970) suggested that *Passerella* and *Melospiza* should be merged with *Zonotrichia*, and Short and Simon (1965) recommended the merger of *Zonotrichia* (*sensu* Paynter) into *Junco*. Morony et al. (1975) use the taxonomic scheme of Paynter (1970), and their treatment is used in some recent literature (e.g. Avise et al. 1980b). Edwards (1974) and the A.O.U. Check-list (1957) maintain separate genera; see also Parkes (1954).

Paynter (1964) stated that *Melospiza* and *Passerella* have similar morphologies, song, nests, eggs, and habits. He stated that ". . . after an elaborate comparison of skull osteology, as well [as] external morphology and habits, Linsdale

(1928) proposed their generic merger" (Paynter 1964: 278). Linsdale's study was not elaborate, however. He (1928) presented three skull measurements for six subspecies each of the Fox and Song sparrows and showed that they were basically similar, by inspection. Although *Passerella* and *Melospiza* overlap in multivariate space (Fig. 1b), largely because of the influence of skull characters (Appendix 1), this does not a priori point to a close relationship (also see Figs. 1a, 2). Similarities in song between *P. iliaca* and *M. melodia* are discussed by Martin (1977), and they are not as clear-cut as Paynter suggested. In any event, the value of song as a "generic character" is uncertain. For example, the song of *Pipilo chlorurus* is more similar to that of *Passerella iliaca* than the latter is to *M. melodia*. I doubt that many systematists would favor the generic merger of *Pipilo* and *Passerella* on the basis of this similarity in song. *Passerella* and *Melospiza* are genically distinct ($\bar{D}$ =. 0.254), and the apparent phenotypic similarities cited above are not indicative of a close phylogenetic relationship.

The result (Fig. 3) that *Z. atricapilla* and *Z. albicollis* are the most divergent members of *Zonotrichia* conflicts with Mayr and Short's (1970) claim that these two species comprise a superspecies. Mayr and Short apparently reasoned that the essentially allopatric breeding distributions of *Z. atricapilla* and *Z. albicollis* meant that they were sister taxa (i.e. superspecies). The genic data, however, show that *Z. leucophrys* is most similar to *Z. atricapilla* (Fig. 3).

Dickerman (1961) and Short and Simon (1965) suggested that the apparent high frequency of hybridization between *Z. albicollis* and *J. hyemalis* indicated a close evolutionary relationship. This implies a direct relationship between frequency of hybridization and genomic similarity (Short 1969) and predicts that hybrids should be more frequent between (sympatric) congeners, a hypothesis not supported here. Hybridization may occur between species pairs of birds that are well separated phylogenetically (Prager and Wilson 1975). Therefore, the phyletic significance of hybrids between *Z. albicollis* and *J. hyemalis* is unknown.

Shields (1973) and Shields and Straus (1975) showed that the karyotypes of *Junco* and *Zonotrichia* were similar, although Shields (1980) noted that avian karyotypic evolution is conservative. Therefore, like hybridization potential, phylogenetically distant birds may have similar karyotypes. Similarity of karyotypes between *Junco* and *Zonotrichia* is not necessarily conclusive of a close phylogenetic relationship. Karyotypic analysis, especially with newer banding techniques (Shields 1980) should be explored in avian phylogenetic studies.

The genic data do not resolve whether or not *J. hyemalis* and *Zonotrichia* are nearest relatives, a hypothesis offered by previous authors (cited above). The $\bar{D}$ from *J. hyemalis* to *Zonotrichia* (0.205) is similar to the $\bar{D}$ between *J. hyemalis* and *Melospiza* (0.185); further work is needed to clarify the cladistic relationships of these and the other genera studied here.

An electrophoretic study by Avise et al. (1980b) of 21–22 loci revealed lower levels of genic divergence among the Song Sparrow, Swamp Sparrow, White-throated Sparrow, and Dark-eyed Junco than those reported here. To compare our studies, I first recalculated *D*-values from the allelic frequencies given by Avise et al. (1980b) using Nei's (1978) correction for sampling error. The major difference between the original and corrected *D*-values of Avise et al. (1980b) was that their *D*-value for *M. georgiana-M. melodia*, 0.028, was reduced to 0.0007. Other corrected values were lower in general. Based on either original or corrected *D*-values of Avise et al. (1980b), the species in *Melospiza* and *Zonotrichia* appear closely related [*D*-values of 0.086 (corrected 0.053) for *M. melodia* and *Z. albicollis* and 0.057 (corrected 0.055) for *M. georgiana* and *Z. albicollis*]. In contrast, the values obtained in the present study for the same comparisons, 0.192 and 0.218, suggest a more distant relationship. The allelic frequencies reported by Avise et al. (1980b) are very similar to mine (Appendix 2) for the 21 loci in common between the two studies. The additional 18 loci examined here, however, account for the differences. The results of Avise et al. (1980b) seem not to portray adequately the level of divergence between *Junco, Zonotrichia,* and *Melospiza*; they did not examine *P. iliaca*.

In conclusion, I suggest that the evidence cited by previous workers in support of various taxonomic rearrangements of *Zonotrichia, Junco, Passerella,* and *Melospiza* is inconclusive and that the proposed generic mergers cited above would obscure significant genetic differentiation. Thus, I propose that the four genera be maintained separately, at least until evidence is advanced that corroborates their monophyly

and degree of differentiation relative to other passerines.

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APPENDIX 1. Correlation of characters with first four principal components (PC).

Character	PC I	PC II	PC III	PC IV
Premaxilla length (PML)	0.8737	0.4598	−0.1193	0.0727
Premaxilla length from narial opening (PNO)	0.7780	0.4669	−0.2078	0.1610
Premaxilla depth (PMD)	0.8549	0.4848	0.0753	0.0243
Nasal bone width (NBW)	0.9708	0.0505	0.0311	0.0181
Postorbital width (POW)	0.5274	−0.7403	−0.3034	−0.1444
Skull width (SKW)	0.9548	0.2064	0.0701	−0.0218
Skull depth (SKD)	0.9559	0.2385	−0.0132	−0.0679
Skull length (SKL)	0.9501	0.2181	−0.1434	−0.1110
Mandible length (MAL)	0.9201	0.3433	−0.1118	0.0389
Minimum mandible length (MML)	0.7269	0.6445	0.0037	0.1339
Mandible depth (MAD)	0.7539	0.6154	0.1252	0.0835
Coracoid length (COL)	0.9670	−0.1926	0.0789	0.0020
Scapula length (SCL)	0.9626	−0.1374	0.2128	−0.0224
Scapula width (SCW)	0.9754	−0.1243	0.1547	0.0291
Furcular process length (FPL)	0.9195	−0.0880	0.3468	0.1263
Sternum length (STL)	0.9650	−0.1700	0.1402	0.0490
Keel length (KEL)	0.9365	−0.1692	0.2150	0.0644
Sternum width (STW)	0.9660	−0.0618	0.1309	−0.1211
Keel depth (KED)	0.9371	−0.2226	0.2040	0.0858
Posterior synsacrum length (PSL)	0.9271	−0.0996	−0.1150	−0.2400
Anterior synsacrum length (ASL)	0.9241	−0.1835	−0.2385	−0.1813
Synsacrum width (SYW)	0.9648	−0.0108	0.0502	−0.2158
Synsacrum minimum width (SMW)	0.9545	−0.1425	−0.0023	0.0240
Femur proximal end width (FPE)	0.9741	−0.0025	−0.0643	−0.2106
Femur minimum width (FMW)	0.9039	−0.1161	−0.3900	0.0954
Femur distal end width (FDE)	0.9577	0.1239	−0.0768	−0.2146
Femur length (FEL)	0.9486	−0.1024	−0.1639	−0.2177
Tibiotarsus width (TTW)	0.8485	−0.2261	−0.4398	0.1509
Tibiotarsus length (TTL)	0.9241	−0.0159	0.0420	−0.3413
Tarsometatarsus length (TML)	0.8998	−0.0343	0.0563	−0.3337
Tarsometatarsus width (TMW)	0.7567	0.1371	−0.5816	0.1838
Tarsometatarsus distal end width (TDE)	0.9262	0.1571	−0.1086	−0.2484
Humerus trochanter length (HTL)	0.9636	−0.0964	0.1290	0.1510
Deltoid crest depth (DCD)	0.9218	−0.2530	−0.0514	0.1973
Humerus distal end width (HDE)	0.9529	−0.0108	0.2546	0.1110
Humerus length (HUL)	0.9806	−0.1524	0.0498	0.0511
Ulna length (ULL)	0.9304	−0.0809	0.2985	0.1678
Ulna width (ULW)	0.8242	−0.2868	−0.1201	0.4536
Carpometacarpus length (CML)	0.9258	−0.1665	0.3208	−0.0091
Carpometacarpus depth (CMD)	0.8847	−0.2190	−0.0913	0.3715
Percentage of variance explained	82.6%	7.3%	4.1%	3.1%

APPENDIX 2. Allelic frequencies for variable loci (localities combined). Numbers in parentheses are frequencies of alleles at a locus. Abbreviations for enzyme names (and E.C. numbers) follow Harris and Hopkinson (1976). All taxa are monomorphic and fixed for the same allele at the following 15 loci: GOT-2, SOD-2, CK-1,2 (2.7.3.2), AK (2.7.4.3), MDH-1,2 (1.1.1.37), ADH (1.1.1.1), LAP (3.4.11), ICD-2, PGM-1, LDH-2, general proteins (Hb, Pt-1,2; stained with Amido Black).

Locus	*Pipilo chlorurus*	*Zonotrichia*					*Melospiza*			*Passerella iliaca*	*Junco hyemalis*
		capensis	*leucophrys*	*albicollis*	*atricapilla*	*querula*	*melodia*	*lincolnii*	*georgiana*		
LDH-1 (1.1.1.27)	200	100	100	100	100	100	175	175	175	175	120
SDH (= SORDH) (1.1.1.14)	−100	−100	−100	−100	−60	−100	−100	−100	−100	−100	−100
GOT-1 (2.6.1.1)	180	170 (0.04) 100 (0.96)	100 (0.97) 20 (0.03)	170 (0.04) 100 (0.92) 20 (0.04)	100	100	100	100	100	100	100
GAPDH (1.2.1.12)	50	−100	−100	−100	−100	−100	−100	−100	−100	−100	−100
6-PGDH (1.1.1.44)	100 (0.63) 85 (0.25) 80 (0.12)	105 (0.21) 85 (0.75) 50 (0.04)	100 (0.74) 90 (0.03) 85 (0.21) 80 (0.02)	100 (0.79) 85 (0.21)	100 (0.53) 90 (0.03) 85 (0.40) 80 (0.04)	120 (0.03) 100 (0.86) 85 (0.11)	120 (0.07) 100 (0.89) 90 (0.04)	100 (0.94) 80 (0.06)	100	125 (0.01) 100 (0.97) 90 (0.02)	125 (0.03) 100 (0.92) 75 (0.05)
NP (2.4.2.1)	75	100 (0.07) 85 (0.93)	100	100	100	100	120	120	120	130	120
PGM-2 (2.7.5.1)	100 (0.88) 90 (0.12)	105 (0.11) 95 (0.89)	100 (0.97) 90 (0.03)	100	100 (0.93) 90 (0.07)	100 (0.94) 90 (0.06)	100	100	110 (0.03) 100 (0.94) 90 (0.03)	110 (0.02) 100 (0.96) 90 (0.02)	100
SOD-1 (1.15.1.1)	100	100	100	100	100	100	100	100	100	200 (0.90) 120 (0.10)	100
GLUD (= GDH) (1.4.1.3)	120	100	100	100	100	100	100	100	100	100	100
Est-D (3.1.1.1)	120 (0.13) 100 (0.87)	100	100 (0.97) 80 (0.03)	100	100	100	120 (0.10) 100 (0.90)	120 (0.13) 100 (0.87)	120 (0.03) 100 (0.97)	120 (0.03) 100 (0.94) 65 (0.01) 60 (0.02)	120 (0.01) 100 (0.98) 60 (0.01)
MPI (5.3.1.8)	100	115 (0.04) 100 (0.96)	100	115 (0.04) 100 (0.96)	115 (0.08) 100 (0.92)	100	100 (0.96) 90 (0.04)	100	100	115 (0.01) 100 (0.99)	100
ACON (4.2.1.3)	100	170 (0.04) 100 (0.96)	100	110	100	100	110	100	115	100	95
EAP (3.1.3.2)	60	100	100	100	100	100	60	100 (0.38) 60 (0.62)	100	105 (0.03) 60 (0.97)	100

APPENDIX 2. Continued.

Locus	*Pipilo chlorurus*	*Zonotrichia*					*Melospiza*			*Passerella iliaca*	*Junco hyemalis*
		capensis	*leucophrys*	*albicollis*	*atricapilla*	*querula*	*melodia*	*lincolnii*	*georgiana*		
ACP (3.1.3.2)	100	100	100	100	100	100	100	120 (0.44) 100 (0.56)	120 (0.78) 100 (0.22)	100	100
ADA (3.5.4.4)	70 (0.13) 50 (0.87)	100 (0.75) 80 (0.25)	135 (0.02) 125 (0.03) 100 (0.95)	130 (0.08) 120 (0.04) 100 (0.88)	100	100	100 (0.07) 60 (0.72) 50 (0.21)	60 (0.13) 50 (0.87)	60 (0.03) 50 (0.97)	70 (0.10) 60 (0.90)	60
GPT (2.6.1.2)	95	100	100	100	100	100	120	120	120	100	100
ICD-1 (1.1.1.42)	140 (0.13) 100 (0.87)	100 (0.89) 70 (0.04) 50 (0.07)	165 (0.05) 150 (0.95)	150	165 (0.03) 150 (0.84) 110 (0.13)	150	140 (0.07) 100 (0.93)	100	100 (0.81) 50 (0.19)	140 (0.03) 100 (0.97)	100
GPI (= PGI) (5.3.1.9)	180	100	180 (0.97) 100 (0.03)	180 (0.04) 100 (0.96)	240 (0.03) 180 (0.94) 100 (0.03)	240 (0.03) 180 (0.97)	170 (0.05) 100 (0.95)	100	180 (0.09) 100 (0.91)	180 (0.01) 100 (0.99)	100
G-6-PDH (= GD) (1.1.1.49)	80	105	100	100	100	100	110	110	110	90	100
αGPD-1 (1.1.1.8)	125	120	100	100 (0.95) 95 (0.05)	100	110 (0.95) 100 (0.05)	100	100	110 (0.03) 100 (0.94) 95 (0.03)	130	115 (0.02) 110 (0.98)
αGPD-2	100	100	100	160 (0.04) 100 (0.96)	100	160 (0.14) 100 (0.86)	100	100	100	150	150 (0.01) 100 (0.99)
Peptidase (3.4.11)											
LGG	110 (0.25) 100 (0.75)	125 (0.07) 110 (0.68) 100 (0.25)	100 (0.16) 85 (0.84)	100 (0.88) 90 (0.08) 75 (0.04)	100 (0.26) 85 (0.74)	100	110 (0.14) 100 (0.79) 85 (0.07)	110 (0.06) 100 (0.88) 75 (0.06)	100 (0.91) 85 (0.09)	110 (0.06) 100 (0.94)	110 (0.11) 100 (0.62) 85 (0.27)
LA-1	100	120 (0.04) 110 (0.07) 100 (0.89)	120 (0.06) 110 (0.02) 100 (0.92)	110 (0.02) 100 (0.96) 90 (0.02)	100	100	100	120 (0.07) 110 (0.12) 100 (0.81)	130 (0.03) 125 (0.09) 100 (0.88)	110 (0.02) 100 (0.98)	110 (0.04) 100 (0.94) 90 (0.02)
LA-2	85	100	100	100	100	100	100	100	100	100 (0.15) 85 (0.80) 75 (0.05)	100 (0.87) 85 (0.13)