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GENETIC RELATIONSHIPS OF NORTH AMERICAN CARDUELINE FINCHES[1]

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Abstract. Starch gel electrophoresis was used to examine variation at 33 genetic loci in 19 taxa (15 species in 6 genera) of cardueline finches (family Fringillidae). Levels of heterozygosity and genetic distances were comparable to those reported from surveys of other avian taxa. Twenty-three loci (70%) were polymorphic within taxa and/or were fixed at alternative alleles among taxa. Rogers' genetic distances were used to construct phenograms, distance Wagner trees, and F–M trees; these provided hypotheses for the evolutionary relationships of taxa. The genetic data indicate that: (1) *Coccothraustes, Pinicola, Leucosticte, Carpodacus, Carduelis,* and *Loxia* are distinctive genera that vary in estimated age (as measured from nearest branch point) from approximately 14 MY (*Coccothraustes*) to 5 MY (*Loxia*); (2) species treated by the AOU (1983) as congeners within *Carpodacus, Carduelis,* and *Loxia* are correctly classified to genus; (3) the subgenera *Acanthis, Astragalinus, Spinus,* and *Carduelis,* within the genus *Carduelis,* are recognizable; (4) the crossbills (*Loxia*) are most closely allied to *Carduelis* among the genera examined; (5) *Carpodacus purpureus* and *C. cassinii* are closely related sister species whereas *C. mexicanus* is very distinct; (6) *Loxia curvirostra* and *L. leucoptera* are moderately different electrophoretically; (7) in contrast, the redpolls, *Carduelis flammea* and *C. hornemanni exilipes,* are similar genetically; (8) most speciation events in North American carduelines range from mid-late Pliocene (4 MY) to mid-Pleistocene (500,000 years) in age; but (9) subspecies diverged in the late Pleistocene. A phylogeny of cardueline genera derived from these electrophoretic data agrees in major respects with one proposed by Raikow on the basis of hindlimb myology. The sequence of appearance of older taxa is still not resolved with certainty, however, because of partially conflicting molecular and morphologic results.

Key words: Cardueline finches; Coccothraustes; Pinicola; Leucosticte; Carpodacus; Carduelis; Loxia; *allozymes; phylogenetic inference; genetic distance.*

INTRODUCTION

Modern studies of the relationships of nine-primaried oscines agree that the cardueline finches (subfamily Carduelinae, family Fringillidae) are closely related; they share a reasonably consistent combination of similar morphologic and behavioral traits (Tordoff 1954a, 1954b; Bock 1960, Raikow 1978). This consensus is reflected in the classifications of Howell et al. (1968), Mayr and Short (1970), and the AOU (1983). Within the cardueline finches, however, relationships are still poorly understood. Limits of genera are controversial, particularly among Old World forms. The proper sequence of taxa in systematic lists is another continuing problem. The position of the genus *Leucosticte,* for example, illustrates the disagreement often encountered when sequences are compared. Although Mayr and Short (1970) began their sequence of North American genera with *Carpodacus,* and placed *Leucosticte* next to last, Raikow (1978), in an analysis of limb myology, deemed *Leucosticte* to be the most primitive cardueline of the genera he examined. The AOU (1983) agreed with Raikow and began their sequence with *Leucosticte.* The treatment of Howell et al. (1968) contrasts with all three of the aforementioned sequences. Considering only the North American genera in their world list, they placed *Leucosticte* between *Acanthis* and *Carpodacus,* approximately one-third of the way from the beginning.

Because previous systematic approaches have failed to reconcile the differing views on the internal classification of carduelines, the group seemed eminently suitable for the fresh perspective offered by biochemical methods. Accordingly, we electrophoretically compared 19 taxa, representing 15 species in 6 genera, most of which are native to North America. The analysis includes all species in the AOU (1983), except vagrants and introduced forms.

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Because the greatest diversity within the subfamily occurs in the Old World (where all of the 18 genera listed by Howell et al. [1968] occur and where 11 [61%] of the total genera are endemic), we do not attempt to interpret relationships beyond the North American taxa.

Avian electrophoretic research is still in an expanding phase (see reviews of existing studies and citations in Barrowclough 1983, Corbin 1983, Matson 1984, Zink and Johnson 1984, and Barrowclough et al. 1985). Therefore, the new information on carduelines adds to the gradually growing base of avian genetic data. Finally, because we make genetic comparisons at the familial level, the cardueline data are also of "macrotaxonomic" interest. As Barrowclough has noted (1983:228), renewed investigation of the utility of electrophoresis in the systematics of higher categories of birds is just beginning. Only a few recent examples exist of studies in which genetic comparisons have been made above the generic level; these include Barrowclough et al. (1981) on the Procellariiformes, Gutiérrez et al. (1983) on Galliformes, and Johnson and Zink (1985) on the Vireonidae.

MATERIALS AND METHODS

Using starch gel electrophoresis, we analyzed tissue from 96 specimens representing 19 taxa (15 species of 6 genera) of cardueline finches. All but one of these forms, the European Goldfinch (*Carduelis carduelis*), are native to North America. A single specimen of the Sage Sparrow (*Amphispiza belli*; subfamily Emberizinae, family Emberizidae) was used as an outgroup. Taxa studied, sample sizes and geographic sources of specimens are listed in Table 1. Nomenclature follows the most recent Check-list of North American birds (AOU 1983).

Procedures for the collection and storage of tissue samples have been described elsewhere (Johnson et al. 1984). Electrophoretic methods essentially followed Selander et al. (1971) and Yang and Patton (1981), with the slight modifications outlined by Johnson et al. (1984). Thirty-three presumptive genetic loci were scored. Alleles at a locus were coded by their mobility from the origin. The most anodal locus was designated as "a," with successively slower alleles denoted as "b," "c," etc. Isozyme nomenclature follows Yang and Patton (1981). From banding patterns on gels (presumptive individual genotypes), we derived a table of allelic frequencies (Table 2). Observed heterozygosity ($H_{obs.}$) was determined by direct count for each specimen and then averaged (±SE) for each sample. The computer program BIOSYS-1 (Swofford and Selander 1981) was used to compute expected heterozygosity ($H_{exp.}$) per sample, percentage polymorphic loci, average number of alleles per polymorphic locus, Nei's (1978) and Rogers' (1972) genetic distances (Table 3), UPGMA and WPGMA phenograms (Sneath and Sokal 1973), and distance Wagner trees (Farris 1972, 1981; Swofford 1981). The distribution of observed and expected number of heterozygotes (Table 1), over all loci in a sample was examined for departure from Hardy-Weinberg expectation (Hartl 1981) with a χ^2 test (Barrowclough 1980). Fitch-Margoliash (F–M) trees (Fitch and Margoliash 1967) were generated with the computer program EVOLVE. The various branching diagrams portray patterns of genetic similarity and provide estimates, under differing assumptions, of the evolutionary relationships among taxa (Felsenstein 1983, 1985).

RESULTS

VARIATION AT LOCI AND HETEROZYGOSITY

Of the 33 loci scored, 14 (42.4%) showed at least a single heterozygote. At nine other loci (Glud, Eap, Got-1, Ald, Acon, Ck-1, Gda, Ck-2 and Ldh-1) the species (including the outgroup taxon) were fixed at alternative alleles. Thus, we regard 23 (70%) of the total loci as being variable within the taxa surveyed. Allelic frequencies at the polymorphic loci are listed by taxon in Table 2. The 10 monomorphic loci were: Icd-2, Sod-2, Got-2, Mdh-1, Mdh-2, Ldh-2, Ab-hemoglobin, Pgm-2, Ab-1 and Ab-2. We also attempted to analyze five additional loci, Gpt, La-2, Est-D, Gsr and Acp, but these proved to be unscorable.

Levels of genetic variation within taxa are shown in Table 1. $H_{obs.}$ ranged from 0.0 (in *Carpodacus p. purpureus, Loxia c. grinnelli* and *Carduelis lawrencei*) to 0.103 (in *Loxia l. leucoptera*). Average $H_{obs.}$ over all taxa was 0.034, a value 21% lower than the average of 0.043 reported for birds in general (Barrowclough 1980) and a value 36% lower than the average of 0.053 reported for large single breeding populations of 30 species (summarized in Barrowclough 1983:228–229). Few patterns were observed; however, we note that the three species of North American goldfinches (subgenus *Astragalinus*) all have low observed heterozygosities (X = 0.012). Percentage of polymorphic loci ranged from 0.0 (again involving *C. p. purpureus, L. c. grinnelli* and *C. lawrencei*) to 20.7 (in *Loxia l. leucoptera*), with a mean of 8.97. The average number of alleles per polymorphic locus ranged from 1.00 in the three monomorphic forms already cited to 1.45 (in *Carpodacus m. frontalis*), with a mean of

TABLE 1. Taxa studied, sample sizes, sources of specimens, and intraspecific genetic variation.

Taxon	n	Sample region[a]	No. alleles at polymorphic loci	$H_{obs} \pm SE$	$H_{exp} \pm SE$	Percentage polymorphic loci[b]	Average number of alleles[c]
Rosy Finch							
(*Leucosticte arctoa littoralis*)	3	Idaho	26	0.034 ± 0.019	0.034 ± 0.019	10.34	1.10
Pine Grosbeak							
(*Pinicola enucleator alascensis*)	4	Alaska	27	0.034 ± 0.014	0.047 ± 0.023	13.79	1.14
(*P. e. leucura*)	3	Minnesota	28	0.069 ± 0.034	0.064 ± 0.027	17.24	1.17
Purple Finch							
(*Carpodacus purpureus purpureus*)	4	Michigan	23	0.0	0.0	0.0	1.00
(*C. p. californicus*)	15	California[d]	29	0.034 ± 0.009	0.041 ± 0.021	13.79	1.21
Cassin's Finch							
(*Carpodacus cassinii*)	12	California[d] (11), Montana[d] (1)	31	0.026 ± 0.007	0.038 ± 0.014	13.79	1.28
House Finch							
(*Carpodacus mexicanus frontalis*)	19	California[d]	36	0.040 ± 0.009	0.056 ± 0.022	20.69	1.45
Red Crossbill							
(*Loxia curvirostra grinnelli*)	1	California[d]	23	0.0	0.0	0.0	1.00
White-winged Crossbill							
(*Loxia leucoptera leucoptera*)	3	Alaska	31	0.103 ± 0.034	0.094 ± 0.038	20.69	1.28
Common Redpoll							
(*Carduelis flammea flammea*)	5	Alaska	24	0.021 ± 0.008	0.016 ± 0.016	3.45	1.03
Hoary Redpoll							
(*Carduelis hornemanni exilipes*)	2	Alaska	26	0.052 ± 0.018	0.052 ± 0.029	10.34	1.10
Pine Siskin							
(*Carduelis pinus pinus*)	6	California[d] (3), Minnesota (3)	28	0.035 ± 0.015	0.033 ± 0.016	13.79	1.17
Lesser Goldfinch							
(*Carduelis psaltria hesperophilus*)	4	California[d]	25	0.017 ± 0.010	0.016 ± 0.016	3.45	1.07
Lawrence's Goldfinch							
(*Carduelis lawrencei*)	3	California[d]	23	0.0	0.0	0.0	1.00
American Goldfinch							
(*Carduelis tristis tristis*)	5	Michigan	24	0.014 ± 0.008	0.012 ± 0.012	3.45	1.03
(*C. t. salicamans*)	2	California[d]	24	0.017 ± 0.017	0.017 ± 0.017	3.45	1.03
European Goldfinch							
(*Carduelis carduelis*)	1	Australia (cagebird)	25	0.069	0.069 ± 0.048	6.90	1.07
Evening Grosbeak							
(*Coccothraustes vespertinus vespertinus*)	2	Minnesota	25	0.052 ± 0.018	0.040 ± 0.028	6.90	1.07
(*C. v. brooksi*)	2	Oregon[d]	25	0.036 ± 0.034	0.034 ± 0.024	6.90	1.07
Sage Sparrow							
(*Amphispiza belli nevadensis*)	1	Nevada[d]	24	0.034	0.034 ± 0.034	3.45	1.03
Total and means[e]	97			0.034	0.035	8.97	1.12

[a] Exact localities available from authors.
[b] Frequency of most common allele ≤ 0.95.
[c] Per locus.
[d] From breeding grounds.
[e] Unweighted by sample size.

1.12. These values are all very dependent on sample size.

For all comparisons (Table 1), $H_{obs.}$ and $H_{exp.}$ are similar. The greatest difference occurs in *Carpodacus cassinii,* in which $H_{obs.}$ is approximately 32% less than $H_{exp.}$. However, chi-square tests reveal that genetic variation in none of the 20 population samples departs significantly ($P > 0.05$) from Hardy-Weinberg expectations.

GENETIC DISTANCES

Genetic distances (Nei's D 1978) between samples differentiated at several taxonomic levels

TABLE 2. Allelic frequencies for polymorphic loci. Numbers in parentheses are frequencies for alleles (coded as letters), when a particular allele was not fixed. Abbreviations for proteins follow Harris and Hopkinson (1976).

Locus	*L. a. littoralis*	*P. e. alascensis*	*P. e. leucura*	*C. p. pur-pureus*	*C. p. californicus*	*C. cassinii*	*C. m. frontalis*	*L. c. grinnelli*	*L. l. leucoptera*	*C. f. flammea*
Mpi	e	c	c	b	b	b	d (0.97) e (0.03)	b	b	b
Gpd	b (0.17) c (0.83)	c	c	c	c	a (0.04) c (0.88) d (0.08)	b (0.03) c (0.97)	b	b	c
Icd-1	e	b (0.25) e (0.75)	b (0.17) e (0.83)	b	b	c (0.08) e (0.92)	c (0.05) e (0.95)	b	a (0.17) c (0.17) e (0.66)	a (0.30) c (0.70)
Adh	e	a	a	f	f	f (0.83) g (0.17)	c (0.18) f (0.82)	b	b	f
Glud	c	c	c	b	b	c	c	c	c	c
Pgm-1	d	d	d	d	d	d (0.96) e (0.04)	d (0.97) e (0.03)	b	a (0.17) b (0.83)	b
Eap	b	d	d	b	b	b	e	a	a	e
Sdh	c	d	d	e	e	c	a (0.03) c (0.97)	c	c	c
Got-1	a	b	b	d	d	d	e	c	c	b
Np	b	c	c	d	d	d	d	b	b	e
Gpi	b	e	d (0.17) e (0.83)	e	c (0.10) e (0.90)	e (0.96) f (0.04)	e (0.03) f (0.97)	c	c	c
Lgg	e	c (0.25) d (0.75)	d (0.83) f (0.17)	c	b (0.10) c (0.67) d (0.23)	c (0.96) d (0.04)	a (0.05) c (0.95)	c	a (0.33) c (0.33) d (0.34)	c
Est	a (0.17) c (0.83)	c	c	c	c	c	a	c	a (0.17) c (0.83)	c
Ada	g (0.83) l (0.17)	h	h	c	a (0.07) b (0.07) c (0.86)	f	i (0.94) k (0.03) l (0.03)	e	c	c
La-1	e	b (0.13) f (0.87)	b (0.17) f (0.83)	f	c (0.13) f (0.87)	d (0.08) f (0.92)	a (0.05) b (0.40) c (0.55)	f	c (0.17) f (0.83)	f
Ald	a	a	a	a	a	a	a	a	a	a
Acon	c	a	a	c	c	c	c	c	c	c
6-Pgd	c	c (0.87) d (0.13)	c (0.33) d (0.67)	b	b	b	a (0.11) b (0.89)	b	a (0.17) b (0.83)	b
Ck-1	c	c	c	b	b	b	c	c	c	c
Sod-1	e	b	b	c	c	c	c	b	b	b
Gda	b	b	b	a	a	a	b	b	b	b
Ck-2	b	b	b	b	b	b	b	b	b	b
Ldh-1	a	a	a	a	a	a	a	a	a	a

Locus	*C. h. exilipes*	*C. p. pinus*	*C. p. hesperophilus*	*C. lawrencei*	*C. t. tristis*	*C. t. salicamans*	*C. carduelis*	*C. v. vespertinus*	*C. v. brooksi*	*A. b. nevadensis*
Mpi	b	b	b	c	b	b	a	b (0.50) e (0.50)	d (0.75) e (0.25)	f
Gpd	c	c	c	c	c	c	c	b	b	c (0.50) e (0.50)
Icd-1	e	c (0.08) e (0.92)	b	b	a (0.20) c (0.80)	c (0.75) e (0.25)	f	d	d	e
Adh	f	f	f	f	f	f	f	f	f	d
Glud	c	c	c	c	c	c	c	c	c	a
Pgm-1	b	b (0.17) d (0.83)	d	d	d	d	c (0.50) d (0.50)	d	d	d
Eap	e	e	e	e	e	e	e	e	e	c
Sdh	c	c	c	c	c	c	c	b	b	c
Got-1	b	d	d	d	d	d	e	b	b	d
Np	d (0.25) e (0.75)	b	b	b	b	b	b	f	f	a
Gpi	c	a (0.08) c (0.92)	c	c	c	c	e	e	e	e

TABLE 2. Continued.

Locus	*C. h. exilipes*	*C. p. pinus*	*C. p. hesperophilus*	*C. lawrencei*	*C. t. tristis*	*C. t. salicamans*	*C. carduelis*	*C. v. vespertinus*	*C. v. brooksi*	*A. b. nevadensis*
Lgg	a (0.25) c (0.75)	c	a (0.13) c (0.74) d (0.13)	c	c	c	c (0.50) g (0.50)	c	c	c
Est	c	c	c	c	c	c	c	a	a	b
Ada	c	c	d	d	d	d	c	j	j	f
La-1	f	f	f	f	f	f	f	c	c	f
Ald	a	a	a	a	a	a	a	b	b	c
Acon	c	c	b	c	c	c	c	d	d	c
6-Pgd	b (0.75) c (0.25)	b (0.84) c (0.08) f (0.08)	b	b	b	b	b	e	d (0.25) e (0.75)	g
Ck-1	c	c	c	c	c	c	c	b	b	a
Sod-1	b	b	b	b	b	b	b	a (0.75) e (0.25)	a	d
Gda	b	b	b	b	b	b	b	b	b	c
Ck-2	b	b	b	b	b	b	b	b	b	a
Ldh-1	a	a	a	a	a	a	a	a	a	b

are summarized in Table 4. In general, average *D* increases with increasing taxonomic level. Thus, subspecies are differentiated at *D* of 0.0048, species of the same genus differ at 0.1739, species from different genera are differentiated at 0.5209, and species from different families have average Nei's *D* of 0.9239.

CLADISTIC ANALYSIS

In addition to comparisons of genetic distances between taxa, distances computed from allelic frequencies, it is of interest to examine the occurrence of alleles from a cladistic viewpoint (Hennig 1966, Avise et al. 1980a, Nelson and Platnick 1981, Matson 1984). Of special concern are unique alleles (autapomorphies), those confined to particular taxa, and shared-derived alleles (synapomorphies), those alleles that by their pattern of occurrence define clusters of species.

We observed unique alleles in 10 of the 15 species of carduelines: *L. a. littoralis* (6 autapomorphies, of which 5 [Adh, allele e; Got-1, a; Gpi, b; Lgg, e; La-1, e] are fixed), *P. enucleator* (8, of which 6 [Adh, a; Eap, d; Sdh, d; Np, c; Ada, h; Acon, a] are fixed), *C. purpureus* (5), *C. cassinii* (5), *C. mexicanus* (5), *L. curvirostra* (1), *L. leucoptera* (1), *C. pinus* (2), *C. carduelis* (4), and *C. vespertinus* (8, of which 6 [Icd-1, d; Sdh, b; Np, f; Ada, j; Ald, b; Acon, d] are fixed). The scarcity or absence of unique alleles in the seven species of *Carduelis* is notable. Only *C. pinus* and *C. carduelis* possessed autapomorphies; *C. flammea, C. hornemanni, C. psaltria, C. lawrencei,* and *C. tristis* lacked unique alleles. The degree to which the occurrence of autapomorphies is sample-size dependent deserves further study in these taxa.

A few examples of shared alleles that were possibly derived (synapomorphies) were uncovered; *L. curvirostra* and *L. leucoptera* shared Adh, b; Eap, a; and Got-1, c. Pgm-1, b, united *L. curvirostra, L. leucoptera, C. flammea, C. hornemanni,* and *C. pinus.* Sod-1, c, occurred only in the three species of *Carpodacus. C. purpureus* and *C. cassinii* were synapomorphic at Gda, a. All species of *Carpodacus, Loxia,* and *Carduelis* shared 6-Pgd, b. Otherwise, patterns of allelic occurrence among taxa did not clearly agree with clusters defined by genetic distances. The latter are of course influenced both by frequencies and occurrence of alleles. Avise et al. (1980a, b), Patton and Avise (1983), and Zink and Johnson (1984) have reported similar results for other avian taxa.

Finally, the outgroup, *Amphispiza belli nevadensis,* was fixed at the following 13 alleles that were not represented in any of the carduline finches: Mpi, f; Adh, d; Glud, a; Eap, c; Np, a; Est, b; Ald, c; 6-Pgd, g; Ck-1, a; Sod-1, d; Gda, c; Ck-2, a; and Ldh-1, b. From a cladistic viewpoint, such alleles in the outgroup taxon could represent the primitive or pleisiomorphic character state for each of the loci. One way to examine this possibility would be to survey additional outgroups.

BRANCHING DIAGRAMS

Relationships among taxa, based on genetic distance values, were analyzed with four branching methods: distance Wagner (Fig. 1), F–M tree (Fig. 2), WPGMA (Fig. 3), and UPGMA. We consider the four branching protocols to represent different hypotheses on the phylogenetic relationships of the taxa and

TABLE 3. Matrix of Nei's (1978; above diagonal) and Rogers' (1972; below diagonal) genetic distances between forms of *Leucosticte, Pinicola, Carpodacus, Loxia, Carduelis, Coccothraustes* and *Amphispiza* (Outgroup).

	1.	2.	3.	4.	5.	6.	7.	8.	9.	10.	11.	12.	13.	14.	15.	16.	17.	18.	19.	20.
1. *L. a. littoralis*	—	.535	.554	.735	.714	.531	.493	.577	.494	.590	.495	.415	.528	.478	.472	.455	.489	.837	.883	.998
2. *P. e. alascensis*	.430	—	.005	.678	.666	.580	.608	.611	.560	.495	.425	.452	.478	.432	.497	.483	.464	.739	.739	.995
3. *P. e. leucura*	.444	.036	—	.707	.686	.594	.609	.626	.553	.503	.431	.457	.487	.444	.505	.490	.474	.761	.752	1.023
4. *C. p. purpureus*	.526	.502	.516	—	.004	.149	.527	.595	.621	.469	.464	.372	.428	.423	.417	.414	.459	.774	.785	.833
5. *C. p. californicus*	.516	.494	.503	.022	—	.150	.521	.597	.611	.476	.467	.377	.421	.422	.415	.413	.469	.746	.787	.858
6. *C. cassinii*	.421	.452	.458	.153	.161	—	.365	.522	.502	.415	.363	.284	.380	.376	.316	.303	.410	.674	.713	.622
7. *C. m. frontalis*	.401	.466	.463	.419	.418	.317	—	.576	.517	.405	.349	.319	.421	.364	.356	.341	.343	.586	.543	.900
8. *L. c. grinnelli*	.446	.468	.474	.448	.458	.411	.443	—	.073	.268	.273	.263	.280	.276	.270	.268	.379	.821	.865	1.056
9. *L. l. leucoptera*	.402	.439	.439	.478	.466	.414	.419	.107	—	.226	.195	.193	.322	.330	.267	.259	.321	.799	.844	1.023
10. *C. f. flammea*	.453	.400	.404	.375	.391	.351	.346	.238	.236	—	.028	.125	.227	.224	.149	.151	.228	.665	.703	.999
11. *C. h. exilipes*	.407	.367	.369	.388	.393	.332	.319	.255	.217	.057	—	.089	.226	.227	.178	.164	.226	.663	.702	.912
12. *C. p. pinus*	.357	.381	.382	.318	.334	.263	.288	.242	.211	.133	.114	—	.110	.109	.062	.051	.165	.667	.706	.758
13. *C. p. hesperophilus*	.419	.393	.398	.352	.349	.328	.356	.249	.298	.211	.216	.123	—	.073	.067	.064	.256	.682	.721	.930
14. *C. lawrencei*	.388	.364	.370	.345	.354	.324	.317	.241	.306	.203	.221	.116	.076	—	.065	.063	.214	.708	.711	.833
15. *C. t. tristis*	.385	.401	.405	.342	.351	.285	.313	.239	.264	.141	.183	.077	.074	.066	—	.002	.208	.666	.705	.827
16. *C. t. salicamans*	.308	.396	.400	.341	.351	.279	.308	.238	.260	.148	.178	.071	.073	.066	.008	—	.206	.664	.702	.804
17. *C. carduelis*	.401	.384	.394	.379	.388	.356	.313	.323	.298	.216	.222	.173	.238	.207	.204	.203	—	.690	.693	.899
18. *C. v. vespertinus*	.581	.528	.538	.531	.538	.502	.457	.566	.564	.493	.498	.497	.504	.509	.494	.493	.509	—	.010	1.141
19. *C. v. brooksi*	.595	.528	.535	.545	.552	.516	.436	.579	.578	.507	.512	.511	.518	.510	.508	.507	.510	.040	—	1.144
20. *A. b. nevadensis*	.631	.640	.649	.569	.585	.471	.597	.641	.644	.634	.605	.539	.611	.569	.566	.560	.603	.677	.678	—

equate congruence among them with relative robustness of results. Thus, we interpret any difference in topology among the trees to imply ambiguity in the resolution of relationships and order of evolutionary descent of taxa, ambiguity resulting from the nature of evolution of alleles at allozyme loci and/or different assumptions of the tree-constructing algorithms. For discussion of the likelihood that these various branching methodologies reveal real phylogenetic relationships, see the differing views of Felsenstein (1984) and Farris (1981).

The structure of the UPGMA dendrogram (not shown) was similar to that of the WPGMA tree, with two important differences. First, *C. mexicanus* did not link with its congeners. Instead, it formed a sister group with a cluster that included both forms of *Loxia* and all species of *Carduelis*. Second, *Pinicola, Leucosticte,* and the stem of a large cluster comprised of all species of *Carpodacus, Loxia,* and *Carduelis* formed an unresolved trichotomy. Other differences between the UPGMA and WPGMA dendrograms were trivial.

Based on the foregoing premises, the branching diagrams consistently support the following results: (1) the named subspecies of *P. enucleator, C. purpureus, C. tristis,* and *C. vespertinus* cluster together within their respective species and therefore are very closely related; (2) in the genus *Carduelis,* species within the subgenera *Acanthis* and *Astragalinus* group "properly" according to subgenus and the monotypic subgenera *Spinus* (*C. pinus*) and *Carduelis* (*C. carduelis*) stand somewhat apart; therefore all the subgenera maintain their integrity; (3) traditional generic limits are supported within *Carpodacus, Loxia,* and *Carduelis* with two exceptions, both involving the House Finch (in the distance Wagner tree, *C. mexicanus* clusters with *C. vespertinus* and in the UPGMA dendrogram, *C. mexicanus* clusters with *Loxia-Carduelis*); (4) within *Carpodacus, C. purpureus* and *C. cassinii* are closely-related sister species, distinct from *C. mexicanus*; (5) within *Loxia, L. curvirostra* and *L. leucoptera* are moderately different genetically; (6) in contrast, the two forms of redpolls, *C. flammea* and *C. hornemanni* are similar genetically; (7) the closest ally of the crossbills (*Loxia*) in all four analyses is the cluster of species that comprises *Carduelis*; (8) radiations of species in *Loxia* and *Carduelis* occurred over several million years, starting 5 MYBP (million years before present; see beyond); (9) in contrast, genesis of species in *Carpodacus* was prolonged, with *C. mexicanus* splitting from the lineage leading to its congeners, *C. purpureus* and *C. cassinii,* at least several million years prior to the split of the

TABLE 4. Mean genetic distances (Nei 1978) among samples from populations differentiated at several taxonomic levels.

Taxonomic level	Number of comparisons	D ± SE	Range	*D* ± SE for other birds[a]
Intraspecific (subspecies)	4	0.0048 ± 0.0021	0.000–0.010	0.0048 ± 0.0005
Interspecific congeners	33	0.1739 ± 0.0206	0.028–0.527	0.0440 ± 0.0026
Within *Carpodacus*	5	0.3424 ± 0.0839	0.149–0.527	
Within *Loxia*	1	0.047	—	
Within *Carduelis*	27	0.1465 ± 0.0138	0.028–0.256	
Same subgenus of *Carduelis*	6	0.0600 ± 0.0066	0.028–0.073	
Different subgenera of *Carduelis*	21	0.1712 ± 0.0132	0.051–0.256	
Intergeneric confamilial	134	0.5209 ± 0.0143	0.193–0.883	0.2136 ± 0.0141
Interfamilial: *Amphispiza belli* (Emberizidae) vs. all 19 taxa of Carduelines (Fringillidae)	19	0.9239 ± 0.0303	0.622–1.144	0.6829 ± 0.0304

[a] Data from Barrowclough (1980:661), who summarized values for Nei's *D* from a variety of passerine birds (mostly emberizids and sturnids).

latter taxa at approximately 3 MYBP; (10) *Coccothraustes, Pinicola, Leucosticte,* and *Carpodacus* are older than either *Loxia* or *Carduelis*; and (11) all six genera considered in this study are clearly defined by the new genetic data.

The following results are less certain. (1) Although the F–M tree and WPGMA analyses suggest that the three oldest genera appeared in the order *Coccothraustes, Pinicola,* and *Leucosticte,* the rather deviant pattern shown by the Wagner tree, the close placement of branching nodes in the WPGMA analysis, and the miniscule branch lengths separating these taxa on the F–M tree indicate that this sequence of their cladogenesis is tentative; (2) the phylogenetic relationships and age of *Carpodacus* are unclear, although the sum of the results suggests an intermediate position for this genus, between *Leucosticte* and *Carduelis*; (3) despite the alliance of the crossbills (*Loxia*) to the redpolls in the distance Wagner analysis, according to the structure of both the F–M tree and the WPGMA dendrogram the relationship of crossbills to particular species or subgenera of *Carduelis* is unresolved; and (4) none of the trees suggest a monophyletic relationship between any two of the three species of goldfinches (*C. psaltria, C. lawrencei,* and *C. tristis*) in the subgenus *Astragalinus.*

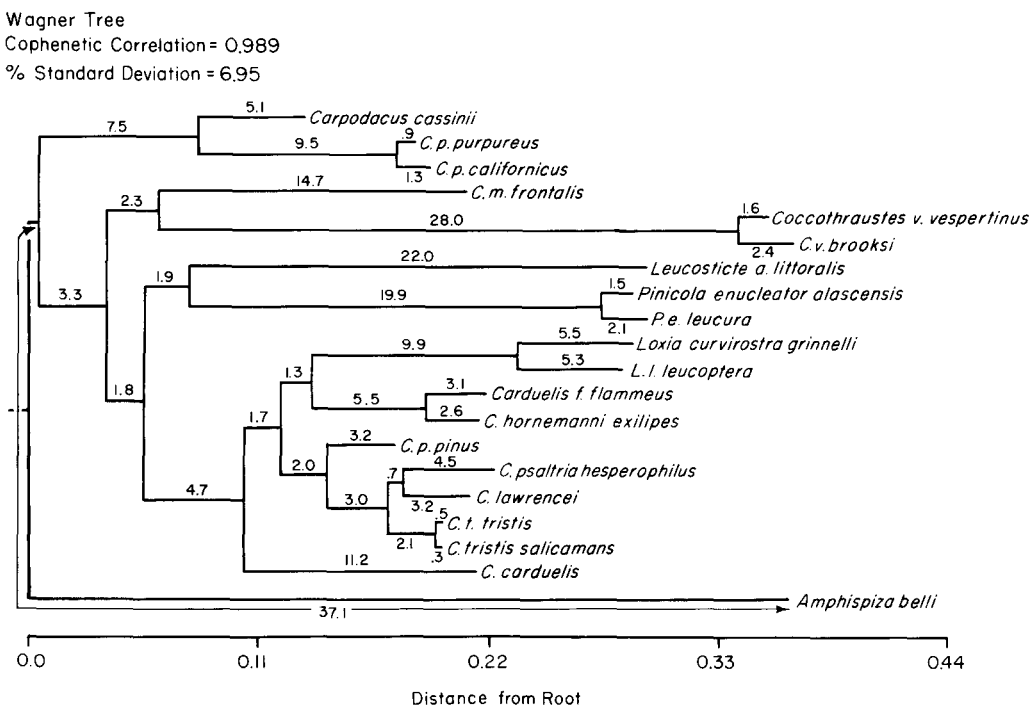

FIGURE 1. Distance Wagner tree rooted at the outgroup, *Amphispiza belli.* This analysis produced no negative branches.

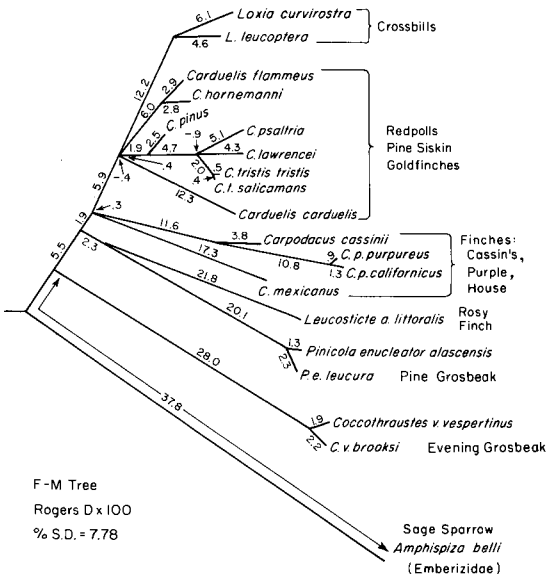

FIGURE 2. Branching diagram derived by the procedure of Fitch and Margoliash (1967). Branch lengths are in units of Rogers' D ($\times 100$). The tree is rooted (see Farris 1972) at *Amphispiza belli*. Of 5 F–M trees examined, the one illustrated best summarized the original matrix based on the fewest (2) negative branches and lowest percentage standard deviation.

DISCUSSION

TIMING OF CLADOGENETIC EVENTS

Nei (1975), Sarich (1977), Yang and Patton (1981) and Gutiérrez et al. (1983), among others, proposed calibrations applied to Nei's D values among existing species in attempting to date phyletic divergence. The calibration of Gutiérrez et al. (1983), based on galliform taxa, is the only such estimate available so far specifically for birds. They calculated that one unit of Nei's (1978) D accumulated over approximately 26.3 MY, a figure arrived at by dividing the age of a fossil quail, *C. cooki* (Wetmore 1934), which is presumed to be mid-Miocene (16 million years before the present [MYBP]) by the average Nei's D (= 0.609) between *C. montezumae* and its Odontophorine sister taxa. Thus, $t = 26.3 \times 10^6 D$, where t is the time since divergence and D is Nei's (1978) genetic distance. Such calibrations assume the operation of a molecular clock (Wilson et al. 1977, Thorpe 1982) whereby allelic differences among populations accrue randomly in a more or less steady, time-dependent manner. The report of Barrowclough et al. (1985), that patterns of genetic divergence in a variety of birds agree with the predictions of Kimura's (1979, 1982) neutral, mutation-drift model, supports both the notion of a clock and the attempts to derive calibrations based on the magnitude of Nei's D.

However, recent evaluation of the circumstances surrounding the dating of *C. cooki* has revealed an ambiguity that suggests that the conversion figure of 26.3 offered by Gutiérrez et al. (1983) could be too large by a factor of two. For this clarification we are indebted to Carl Swisher, Department of Paleontology, University of California, Berkeley. Regarding the type specimen of *C. cooki* (Amer. Mus. Nat. Hist. No. 8301; coll. by Harold Cook [HC No. 647] in 1933 at Aphelops Draw, Sioux Co., Nebraska), Swisher wrote (undated letter received by NKJ on April 15, 1985): "According to Morris Skinner [et al.] (1977) and Cook's notes, the 'specimen came from the upper Sheep Creek beds, above the heavy ash layer, western exposures.' Skinner states that *C. cooki* came from Aphelops Draw. The geologic section provided by Skinner includes only one prominent ash bed, the Sheep Creek Ash (#3). This is the most prominent ash in the Sheep Creek and is with little doubt the ash Cook referred to. Unfortunately, Skinner points out that all Sheep Creek localities are below this ash bed. Fossil localities above this ash are present in Aphelops Draw and very fossiliferous, but are much younger. Skinner says the fossil is from the Sheep Creek Fm which would be below the ash. This gets more complicated . . . the ash has been dated by K-Ar methods at 15.1 MY. If type came from below the ash, I feel it is fair to say it is 15 to 16 MY, but could be as old as 17 MY (L. Early Miocene to Early-Middle Miocene). If Cook was right and it came from above the ash bed, then it would be as young as 9 to 7 MY (or Late Miocene)."

Because the collector of the fossil stated clearly that it was found "above the heavy ash layer," we believe that there is sufficient probability that it came from the younger upper stratum, approximately 8 MY in age. But because of the uncertainties alluded to above, and in view of the stratigraphic data of Skinner et al. (1977), we propose that a compromise figure of 12 MYBP would be the most appropriate estimated age of *C. cooki*. The formula for the calibration would then read: $t = 19.7 \times 10^6 D$. (If an age of 8 MYBP is applied to *C. cooki*, then the formula would read: $t = 13.1 \times 10^6 D$.

The scale of Figure 1 is based upon the conversion factor of 19.7. In interpreting this figure it should be kept in mind that because large standard errors accompany genetic distance values and because of uncertainty regarding the calibration, the following *dates* proposed for the splitting of lineages can be only very gross approximations. We feel that the *se-*

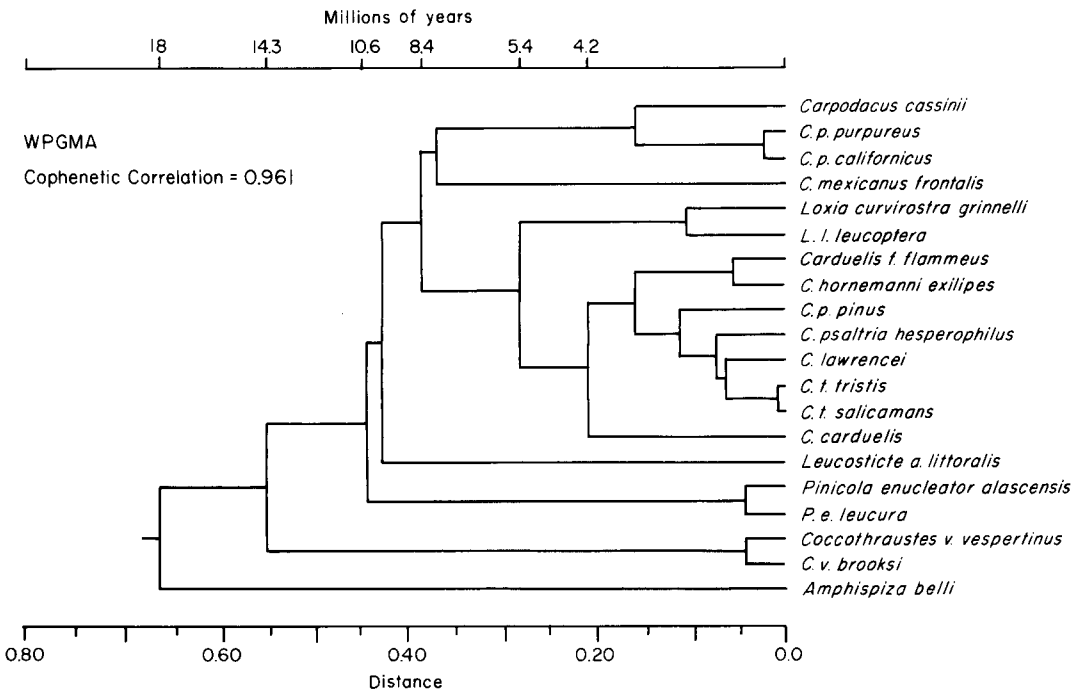

FIGURE 3. Phenogram based on Rogers' D-values and derived by the WPGMA method. The high cophenetic correlation coefficient (r_{cc} = 0.961) indicates excellent agreement between the distances shown in the phenogram and the original data matrix. The dating scale is based on a modification of the calibration offered by Gutiérrez et al. (1983); see text.

quence of appearance of the various taxa, however, is more trustworthy.

Using the compromise conversion factor of 19.7, the split between the emberizids and the lineage leading to the modern carduelines considered here occurred at 18 MYBP, the divergence of *C. vespertinus* took place at 14.3 MYBP, the separation of the ancestors of *Pinicola* from the rest of its sister taxa happened at 10.6 MYBP, the predecessors of *Leucosticte* split at 10.5 MYBP, the lineage leading to *Carpodacus* divided from that leading to *Loxia-Carduelis* at 8.4 MYBP, and the ancestors of *Loxia* diverged from those of *Carduelis* at 5.4 MYBP. Except for the separation of the lineage leading to *C. mexicanus,* which split from the clade leading to *C. cassinii* and *C. purpureus* at 9.3 MYBP, speciation events within genera occurred generally over the period of time from the late Pliocene to mid-Pleistocene. For example, the ancestors of *C. carduelis* divided from those leading to its congeners at 4.2 MYBP. The two forms of redpolls, in contrast, seem to have split 550,000 years ago. The approximate time of divergence of subspecies is illustrated by three comparisons: within *C. purpureus,* 78,000 years; *Pinicola enucleator,* 98,500 years; and *C. vespertinus,* 197,000 years, all of which would represent late Pleistocene events.

LEVELS OF GENETIC VARIATION

A major surprise of the study was the comparatively great genetic divergence of *C. mexicanus* from its phenetically very similar congeners, *C. purpureus* and *C. cassinii.* Wide genetic separation of species within one genus is not without precedent, however. In the woodpecker genus *Sphyrapicus,* for example, the phenetically similar *S. nuchalis* and *S. varius* are separated by a substantial genetic distance (Johnson and Zink 1983). Another example occurs in *Vireo,* in which *V. flavoviridis* is apparently fixed at alleles that differ from the predominant allele found in its extremely similar allopatric relative, *V. olivaceus* at 6 loci (Johnson and Zink 1983). The opposite situation occurs in the goldfinches of the subgenus *Astragalinus,* in which the three species examined, although phenetically distinctive, are genetically very similar. Furthermore, both in certain sapsuckers (*S. nuchalis* and *S. ruber,* Johnson and Zink 1985) and in warblers (*Dendroica coronata* complex, Barrowclough 1980), forms with obviously different plumages also show miniscule genetic differentiation. Clearly, the relationship between phenotypic divergence and protein divergence at the near-species level deserves much further study in birds. At present, too few studies have been conducted to support generalization. Our finding of low

levels of heterozygosity and scarcity or lack of unique alleles in certain subgenera of *Carduelis* and in *Loxia* is also noteworthy. Although low values of *H* in *L. curvirostra* are almost certainly related to sample size, such is probably not the complete explanation for the reduced genetic variability found in *C. flammea, C. psaltria, C. lawrencei,* or *C. tristis.* Perhaps historical patterns of gene flow, drift, and/or fluctuations in effective population size have been important in the maintenance of low levels of genetic variation in these species. Such stochastic phenomena have been invoked in explanations of relative genetic variability in other avian examples (Barrowclough et al. 1985).

EVOLUTIONARY RELATIONSHIPS OF CONGENERIC SPECIES

In most instances the electrophoretic data agree with relationships of congeners proposed on the basis of conventional taxonomic practice. For example, the protein evidence clearly supports Mayr and Short's (1970:79) view that the "Cassin's Finch is closely related to *C. purpureus* and can be considered a sibling species with it . . . ." However, under the account of the House Finch they comment, in apparent conflict with the aforementioned statement, that "Conceivably *mexicanus* and *cassinii* represent an older invasion of *Carpodacus* from Eurasia, and *purpureus* a more recent entrant into North America." Perhaps the possible close relationship of *mexicanus* and *cassinii,* implied by their proposed association in the same early invasion, was unintentional. In any event, the genic information does support both the notion of an older entry from the Old World of the lineage leading to *mexicanus* but not including *cassinii,* and the close relationship of *C. purpureus* and *C. cassinii.* Presumably, the lineage leading to the latter two species either arrived in the New World from Eurasia comparatively recently, as suggested by Mayr and Short (1970), or was derived in the New World from the older *mexicanus* lineage after its arrival and subsequent establishment.

Several species of *Carduelis* have been identified as probable close relatives. For example, the frequent hybridization and similar morphologic features of *C. flammea* and *C. hornemanni exilipes* point to their possible conspecificity (Mayr and Short 1970, Troy and Brush 1983, Troy 1985), a status with which the protein evidence would not conflict. However, low genetic distances alone are unrelated to species status; perfectly good biologic species can have genetic distances approaching zero (Yang and Patton 1981, Johnson and Zink 1983). Even if *C. flammea* and *C. hornemanni exilipes* prove to be conspecific, it will still be desirable to compare the enzyme genes of these forms with those of the morphologically different Hornemann's Redpoll (*C. hornemanni*), which may be specifically distinct from the *flammea-exilipes* complex (Todd 1963, AOU 1983).

Although we assume that the New World goldfinches, *C. tristis, C. psaltria,* and *C. lawrencei* are all near relatives, as is evident from their placement in the subgenus *Astragalinus* (AOU 1983), the molecular data do not identify any pair of the three species as closest relatives. Indeed, conclusions on this point are unwarranted because several Central and South American species of *Carduelis,* one or more of which could be the nearest relatives of these species (Mayr and Short 1970), were unrepresented in our comparison group.

EVOLUTIONARY RELATIONSHIPS OF GENERA

The most explicit phylogeny of genera of North American carduelines was offered by Raikow (1978, 1985). Other taxonomic works in recent years (Howell et al. 1968, Mayr and Short 1970, AOU 1983) have simply listed species, leaving the reader to interpret evolutionary affinities from the sequence in which taxa were treated. Raikow's phylogeny was based on the precepts of cladistics (Hennig 1966) applied to an analysis of morphologic characters, mostly those of appendicular myology. He recognized two major clusters of cardueline finches. The first cluster included *Leucosticte* as the oldest genus and as a sister taxon to a clade formed of *Fringilla, Pinicola, Carpodacus,* and *Hesperiphona* (=*Coccothraustes* of the present study). The latter two genera were aligned as sister taxa; they lack M. plantaris of the hindlimb, the loss of which is considered to be a derived character state. Raikow's second major cluster included four genera, *Pyrrhula, Chloris, Loxia,* and *Carduelis.* These genera share the presumably derived features of the presence of a tibial head on M. peroneus brevis (a trait also shared with the Hawaiian honeycreepers) and loss of a patellar band. *Pyrrhula* and *Chloris* have also lost M. obturatorius dorsalis; *Loxia* and *Carduelis* both have lost M. plantaris. Loss of either muscle is presumably a derived character state. The latter two pairs of genera are thus sister groups.

In major features the phylogeny derived from the protein data agrees with that based on the morphologic information. Both phylogenies divide cardueline genera into an older group comprised of *Coccothraustes, Pinicola, Leucosticte,* and *Carpodacus,* and a more recent clade consisting of *Carduelis* and *Loxia.* The latter relationship is also supported by the discovery of a hybrid between the Red Crossbill

and the Pine Siskin (Tallman and Zusi 1984). The ability to hybridize provides strong evidence for considerable genetic compatability between the taxa involved.

Within the older cluster of genera, however, the two proposed phylogenies are discordant with regard to the sequence of genera. Although all are apparently old, distinctive lineages, there is no evidence from the electrophoretic results that *Leucosticte* is *the* oldest genus. Instead, based on its greater accumulation of genic differences compared with the other taxa, *Coccothraustes* is probably the oldest genus, followed by *Pinicola, Leucosticte,* and *Carpodacus.* Another disagreement of the protein and morphologic results involves the linkage of *Coccothraustes* with *Carpodacus* as sister taxa (Raikow 1978). The genetic data maintain *Coccothraustes* as a well-separated lineage in all but one analysis, the distance Wagner tree. There, a single species of *Carpodacus,* the House Finch, joins with the Evening Grosbeak. However, because the other two species of *Carpodacus* were excluded from this clade, and in view of the very short branch lengths separating all of the older genera, we consider relationships at that level to be essentially unresolved by the Wagner procedure.

Despite these differences, which we judge to be minor, the phylogenies developed independently from electrophoretic and morphologic information are in basic agreement. The lack of identity in sequence of older genera is not surprising and should not detract from the fundamental compatibility of our genetic findings with the earlier myologic results on the carduelines. The occurrence of incomplete congruence of molecular and morphologic data sets is becoming increasingly recognized as a commonplace and thus far rather unyielding problem in comparative phylogenetics (Lewin 1985).

Because this study was restricted to North American taxa (plus *C. carduelis*), our ability to interpret phylogenetic relationships has been somewhat compromised in view of the possibility that some of the taxa are closely related to forms occurring in other geographic regions. Therefore, the larger question of genetic relationships of cardueline taxa worldwide awaits the assembly of tissue of the remaining taxa for biochemical study. Many of these forms can be obtained only with great difficulty, if at all. Hopefully, someone with access to specimens in the Old World will accept this challenge.

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LITERATURE CITED

AMERICAN ORNITHOLOGISTS' UNION. 1983. Check-list of North American birds, 6th ed. American Ornithologists' Union, Washington, DC.

AVISE, J. C., J. C. PATTON, AND C. F. AQUADRO. 1980a. Evolutionary genetics of birds. I. Relationships among North American thrushes and allies. Auk 97:135–147.

AVISE, J. C., J. C. PATTON, AND C. F. AQUADRO. 1980b. Evolutionary genetics of birds. II. Conservative protein evolution in North American sparrows and relatives. Syst. Zool. 29:323–334.

BARROWCLOUGH, G. F. 1980. Genetic and phenotypic differentiation in a wood warbler (Genus *Dendroica*) hybrid zone. Auk 97:655–668.

BARROWCLOUGH, G. F. 1983. Biochemical studies of microevolutionary processes, p. 223–261. *In* A. H. Brush and G. A. Clark, Jr. [eds.], Perspectives in ornithology. Cambridge Univ. Press, England.

BARROWCLOUGH, G. F., K. W. CORBIN, AND R. M. ZINK. 1981. Genetic differentiation in the procellariiformes. Comp. Biochem. Physiol. 69:629–632.

BARROWCLOUGH, G. F., N. K. JOHNSON, AND R. M. ZINK. 1985. On the nature of genic variation in birds, p. 135–154. *In* R. F. Johnston [ed.], Current ornithology. Vol. 2. Plenum Press, New York.

BOCK, W. J. 1960. The palatine process of the premaxilla in the Passeres. Bull. Mus. Comp. Zool. 122:361–488.

CORBIN, K. W. 1983. Genetic structure and avian systematics, p. 211–244. *In* R. F. Johnston [ed.], Current ornithology. Vol. 1. Plenum Press, New York.

FARRIS, J. S. 1972. Estimating phylogenetic trees from distance matrices. Am. Nat. 106:645–668.

FARRIS, J. S. 1981. Distance data in phylogenetic analysis, p. 1–23. *In* V. A. Funk and D. R. Brooks [eds.], Advances in cladistics. Vol. 1. Proceedings Willi Hennig Society. New York Botanical Garden, New York.

FELSENSTEIN, J. 1983. Numerical methods for inferring evolutionary trees. Q. Rev. Biol. 57:379–404.

FELSENSTEIN, J. 1984. Distance methods for inferring phylogenies: a justification. Evolution 38:16–24.

FELSENSTEIN, J. 1985. Confidence limits on phylogenies: an approach using the bootstrap. Evolution 39:783–791.

FITCH, W. M., AND E. MARGOLIASH. 1967. Construction of phylogenetic trees. Science 155:279–284.

GUTIÉRREZ, R. J., R. M. ZINK, AND S. Y. YANG. 1983. Genic variation, systematic, and biogeographic relationships of some galliform birds. Auk 100:33–47.

HENNIG, W. 1966. Phylogenetic systematics. Univ. Illinois Press, Chicago, IL.

HOWELL, T. R., R. A. PAYNTER, JR., AND A. L. RAND. 1968. Subfamily Carduelinae, Serins, Goldfinches, Linnets, Rose Finches, Grosbeaks, and Allies, p. 207–306. *In* R. A. Paynter, Jr. [ed.], Check-list of birds of the world; Vol. XIV. Museum of Comparative Zoology, Cambridge, MA.

JOHNSON, N. K., AND R. M. ZINK. 1983. Speciation in sapsuckers (*Sphyrapicus*): I. Genetic differentiation. Auk 100:871–884.

JOHNSON, N. K., AND R. M. ZINK. 1985. Genetic evidence for relationships among the red-eyed, yellow-green, and Chivi vireos. Wilson Bull. 97:421–435.

JOHNSON, N. K., R. M. ZINK, G. F. BARROWCLOUGH, AND J. A. MARTEN. 1984. Suggested techniques for modern avian systematics. Wilson Bull. 96:543–560.

KIMURA, M. 1979. The neutral theory of molecular evolution. Sci. Am. 241:98–126.

KIMURA, M. 1982. The neutral theory as a basis for understanding the mechanism of evolution and variation at the molecular level, p. 3–56. *In* M. Kimura [ed.], Molecular evolution, protein polymorphism and the neutral theory. Japan Scientific Societies Press, Tokyo, Japan.

LEWIN, R. 1985. Molecules vs. morphology: of mice and men. Science 229:743–745.

MATSON, R. H. 1984. Applications of electrophoretic data in avian systematics. Auk 101:717–729.

MAYR, E., AND L. L. SHORT. 1970. Species taxa of North American birds. A contribution to comparative systematics. Publ. Nuttall Ornithol. Club 9:1–127.

NEI, M. 1975. Molecular population genetics and evolution. North Holland Publ. Co., Amsterdam, Netherlands.

NEI, M. 1978. Estimation of average heterozygosity and genetic distance from a small number of individuals. Genetics 89:583–590.

NELSON, G., AND N. PLATNICK. 1981. Systematics and biogeography: cladistics and vicariance. Columbia Univ. Press, New York.

PATTON, J. C., AND J. C. AVISE. 1983. An empirical evaluation of qualitative Hennigian analyses of protein electrophoretic data. J. Mol. Evol. 19:244–254.

RAIKOW, R. J. 1978. Appendicular myology and relationships of the New World nine-primaried oscines (Aves: Passeriformes). Bull. Carnegie Mus. Nat. Hist. 7:1–43.

RAIKOW, R. J. 1985. Problems in avian classification, p. 187–212. *In* R. F. Johnston [ed.], Current ornithology. Vol. 2. Plenum Press, New York.

ROGERS, J. S. 1972. Measures of genetic similarity and genetic distance. Univ. Texas Stud. Genet. 7:145–153.

SARICH, V. M. 1977. Rates, sample sizes, and the neutrality hypothesis for electrophoresis in evolutionary studies. Nature 265:24–28.

SELANDER, R. K., M. H. SMITH, S. Y. YANG, W. E. JOHNSON, AND J. B. GENTRY. 1971. Biochemical polymorphism and systematics in the genus *Peromyscus*. I. Variation in the old-field mouse (*Peromyscus polionotus*). Univ. Texas Publ. 7103:49–90.

SKINNER, M. F., S. M. SKINNER, AND R. J. GOORIS. 1977. Stratigraphy and biostratigraphy of L. Cenozoic deposits in C. Sioux Co., Western Nebraska. Bull. Amer. Mus. Nat. Hist. 158:265–371.

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

SWOFFORD, D. L. 1981. On the utility of the distance Wagner procedure, p. 25–43. *In* V. A. Funk and D. R. Brooks [eds.], Advances in cladistics. Vol. 1. Proc. Willi Hennig Society, New York Botanical Garden, New York.

SWOFFORD, D. L., AND R. B. SELANDER. 1981. A computer program for the analysis of allelic variation in genetics. J. Hered. 72:281–283.

TALLMAN, D. A., AND R. L. ZUSI. 1984. A hybrid Red Crossbill-Pine Siskin (*Loxia curvirostra* × *Carduelis pinus*) and speculations on the evolution of *Loxia*. Auk 101:155–158.

THORPE, J. P. 1982. The molecular clock hypothesis: biochemical evolution, genetic differentiation and systematics. Annu. Rev. Ecol. Syst. 13:139–168.

TODD, W.E.C. 1963. Birds of the Labrador Peninsula. Univ. Toronto Press, Canada.

TORDOFF, H. B. 1954a. A systematic study of the avian family Fringillidae based on the structure of the skull. Misc. Publ. Mus. Zool. Univ. Mich. 81:1–42.

TORDOFF, H. B. 1954b. Relationships in the New World nine-primaried oscines. Auk 71:273–284.

TROY, D. M. 1985. A phenetic analysis of the redpolls *Carduelis flammea flammea* and *C. hornemanni exilipes*. Auk 102:82–96.

TROY, D. M., AND A. H. BRUSH. 1983. Pigments and feather structure of the redpolls, *Carduelis flammea* and *C. hornemanni*. Condor 85:443–446.

WETMORE, A. 1934. A fossil quail from Nebraska. Condor 36:30.

WILSON, A. C., S. S. CARLSON, AND T. J. WHITE. 1977. Biochemical evolution. Annu. Rev. Biochem. 46:573–639.

YANG, S. Y., AND J. L. PATTON. 1981. Genic variability and differentiation in the Galapagos finches. Auk 98: 230–242.

ZINK, R. M., AND N. K. JOHNSON. 1984. Evolutionary genetics of flycatchers. I. Sibling species in the genera *Empidonax* and *Contopus*. Syst. Zool. 33:205–216.