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GENETIC EVIDENCE FOR THE ORIGIN AND RELATIONSHIPS OF HAWAIIAN HONEYCREEPERS (AVES: FRINGILLIDAE)[1]

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Dedication. It is a pleasure to dedicate this paper to Dr. Dean Amadon, pioneering investigator of Hawaiian honeycreepers, on the occasion of his 76th birthday.

Abstract. Using starch gel electrophoresis of proteins, we examined variation at 36 genetic loci in nine species (eight genera) of Hawaiian honeycreepers (Class Aves; Family Fringillidae; Subfamily Drepanidinae). Two species of cardueline finches and two emberizids served as outgroup taxa. Twenty-three loci (64%) were either polymorphic within taxa and/or were fixed at alternative alleles among taxa. In seven of nine species, low levels of mean H_{obs} (0.015), percentage of polymorphic loci (4.16), and average number of alleles per polymorphic locus (2.03) may reflect population bottlenecks that occurred either during or after initial colonization. Phenograms, distance Wagner trees, F-M trees, and a cladistic analysis provided hypotheses for the evolutionary relationships of taxa and suggest that: (1) The drepanidines are monophyletic. (2) The Hawaiian honeycreepers are more similar genetically to the two species of emberizids than to the two species of carduelines, a result that conflicts with a recent consensus of opinion based on morphologic and other biochemical data. (3) The species ancestral to modern drepanidines colonized the Hawaiian Archipelago at an estimated 7–8 million years before present (MYBP). This date agrees generally with the timing of emergence of Nihoa, now largely submerged, but antedates the appearance of Kauai (5 MYBP), the oldest of the present "high" Hawaiian Islands. (4) The creepers *Oreomystis* and *Paroreomyza* represent the oldest and most divergent lineage of living drepanidines. (5) The youngest lineages are represented by the nectar feeders (*Himatione* and *Vestiaria*), the thick-billed "finch types" (*Loxioides* and *Telespiza*), and a diverse array of other forms (*Loxops* and *Hemignathus*). (6) *Hemignathus "virens" stejnegeri* is a full species, possibly allied to *Loxops coccineus*. Our genetic data conflict with the two major phylogenetic hypotheses that have been proposed for the radiation of the drepanidines: (1) origin from tubular-tongued, nectar-feeding ancestors; and (2) origin from thick-billed and thick-tongued, seed- and fruit-eating ancestors. Instead, the evidence suggests that the earliest Hawaiian honeycreepers had generalized bills, tongues, and diets. This ancestral group gave rise to the lineages that eventually led to both (1) modern *Paroreomyza* and *Oreomystis* and (2) a complex group of (a) nectar feeders (*Himatione, Vestiaria,* and relatives); (b) seed and fruit eaters (*Loxioides, Telespiza,* and relatives); and (c) a diverse group of species that feed on both arthropods and nectar (*Loxops, Hemignathus,* and relatives). We speculate that the most immediate ancestor of all of the heavy-billed species was a thin-billed, tubular-tongued, nectarivorous form and that this major morphologic shift was expedited by the alteration of developmental patterns and rates.

Key words: Hawaiian honeycreepers; Drepanidinae; allozymes; insular colonization; phylogenetic inference.

INTRODUCTION

As a showcase for the products of evolutionary diversification following colonization, the Hawaiian Archipelago is unsurpassed. Among the endemic birds, the honeycreepers are especially renowned. The profound divergence in bill shape and ecology shown by the 28 living or very recently extinct species has long served as a textbook example of adaptive radiation. In recent

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decades a stream of publications has dealt with the distribution, morphology, ecology, systematics, and evolution of these unique birds (Amadon 1947, 1950, 1986; Baldwin 1953; Bock 1970; Sibley 1970; Richards and Bock 1973; Raikow 1974, 1976, 1977a, 1977b, 1978; Zusi 1978; Berger 1981; Olson and James 1982a, 1982b, 1988; Sibley and Ahlquist 1982; James et al. 1987; Pratt et al. 1987; Bledsoe 1988a). Most of the foregoing authors agree that the drepanidines are monophyletic, having evolved from a single ancestral species that colonized the Hawaiian Islands from either Asia or the Americas. However, current literature reveals little agreement on relationships of species or on generic limits within the group.

Using starch gel electrophoresis of proteins, we compared 15 populations of nine species of drepanidines. Although 18 living species are known, six of the nine forms omitted are rare and endangered and, hence, difficult to obtain. Sequence and nomenclature of taxa follow the AOU (1983). Our use of this standard reference does not imply agreement with either the classification or nomenclature therein because as Olson and James (1988) have argued recently the AOU nomenclature for both the Kauai population of the Common Amakihi (*Hemignathus "virens" stejnegeri*) and the Kauai Akialoa (*Hemignathus procerus*) is incorrect. Olson and James' proposals are currently under study by the Committee on Classification and Nomenclature of the AOU.

From the perspective offered by the genetic data set, we address the following issues: (1) the origin of the Drepanidinae; (2) the timing of colonization of the Hawaiian Archipelago; (3) the evidence for population bottlenecks and founder effects; (4) the phylogenetic relationships of modern species; and (5) the taxonomic implications of the genetic results.

MATERIALS AND METHODS

Sixty-two specimens of honeycreepers representing eight genera, nine species, and 15 populations were collected in the spring of 1977 and 1978 in the Hawaiian Islands. Two species of Emberizidae, the Western Tanager (*Piranga ludoviciana*) and Saffron Finch (*Sicalis flaveola*) and two species of carduelines, the Purple Finch (*Carpodacus purpureus*) and Red Crossbill (*Loxia curvirostra*), were selected as outgroup taxa. Taxa studied, sample sizes, and geographic sources of specimens are listed in Table 1. Procedures for the collection and storage of liver and heart tissue followed Johnson et al. (1984). Tissue homogenates (a combination of liver, heart, and an equal volume of de-ionized water) were centrifuged at 4°C and 15,000 rpm for 40 min. The aqueous protein extracts were then stored at −76°C for later electrophoretic analysis. Thirty-six presumptive genetic loci were examined by horizontal starch gel electrophoresis using standard procedures (Selander et al. 1971, Yang and Patton 1981). Protein assays were prepared according to Harris and Hopkinson (1976) and Selander et al. (1971). Our specific buffer system-assay combinations are available upon request. Alleles (=electromorphs) at each locus were designated alphabetically in decreasing order of mobility. For multiple isozymes of proteins the most anodal locus was identified as 1; more cathodal loci were indicated by progressively higher numbers. Hemoglobin was the only cathodal protein detected on LiOH gels. From banding patterns on gels (presumptive individual genotypes), we derived a table of allelic frequencies (Table 2).

Heterozygosity levels were determined by direct count. Allelic frequencies were converted to genetic distances (Table 3) using the methods of Rogers (1972) and Nei (1978). To compare patterns of population and/or species similarity or relatedness, phenograms (UPGMA and WPGMA, Sneath and Sokal 1973), and phylogenetic trees (F-M trees, Fitch and Margoliash 1967; distance Wagner trees, Farris 1972) were constructed from Rogers' genetic distance values.

Using the program PAUP (Swofford 1985), we also conducted a cladistic analysis in which loci were characters and alleles at a given locus were character states. Because a cladistic analysis using *alleles* as characters may yield intermediate taxa with no alleles (Buth 1984) and because data reduction by "presence/absence" coding is undesirable for other reasons (Swofford and Berlocher 1987) we did not attempt this method. For the cladistic analysis by locus, alleles were lettered consecutively among taxa. When polymorphic at a locus, a taxon was assigned the state for its commonest allele. If two alleles were equally common (e.g., ICD-2, *H. s. sanguinea* [Maui]), the first allele was chosen. Because the direction of character state transformation was unknown, character states (alleles at each locus) were not ordered on input. The addition sequence, CLOSEST, the branch swapping option, ALT, the rooting procedure, OUTGROUP, and the method of detecting all equally parsimonious

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

Taxon	n	Source of specimens	$H_{obs} \pm SE$	Percent polymorphic loci	Average no. alleles per polymorphic locus
Family Emberizidae					
Subfamily Thraupinae					
Western Tanager					
(*Piranga ludoviciana*)	1	California	0.083	8.3	2.00
Subfamily Emberizinae					
Saffron Finch					
(*Sicalis flaveola pelzelni*)	1	Paraguay	0.028	2.8	2.00
Family Fringillidae					
Subfamily Carduelinae					
Purple Finch					
(*Carpodacus purpureus californicus*)	1	California	0.083	8.3	2.00
Red Crossbill					
(*Loxia curvirostra grinnelli*)	1	California	0.0	0.0	1.00
Subfamily Drepanidinae—Tribe Psittirostrini					
Laysan Finch					
(*Telespiza cantans cantans*)	4	Laysan Island	0.007 ± 0.008	2.8	2.00
Palila					
(*Loxioides bailleui*)	1	Hawaii	0.0	0.0	—
Tribe Hemignathini					
Common Amakihi					
(*Hemignathus virens virens*)	12	Hawaii	0.039 ± 0.009	22.0	2.25
(*H. v. wilsoni*)	4	Maui	0.048 ± 0.020	11.1	2.25
(*H. v. chloris*)	3	Oahu	0.046 ± 0.030	8.3	2.30
(*H. v. stejnegeri*)	8	Kauai	0.059 ± 0.013	16.7	2.17
Anianiau					
(*Hemignathus parvus*)	6	Kauai	0.014 ± 0.010	8.3	2.00
Kauai Creeper					
(*Oreomystis bairdi*)	1	Kauai	0.028	2.8	2.00
Maui Creeper					
(*Paroreomyza montana*)	4	Maui	0.049 ± 0.015	11.1	2.25
Akepa					
(*Loxops coccineus caeruleirostris*)	1	Kauai	0.0	0.0	—
Tribe Drepanidini					
Iiwi					
(*Vestiaria coccinea*)	3	Hawaii	0.019 ± 0.011	2.8	2.00
	5	Kauai	0.22 ± 0.012	5.5	2.00
Apapane					
(*Himatione sanguinea sanguinea*)	6	Hawaii	0.005 ± 0.005	5.5	2.00
	1	Maui	0.028	2.8	2.00
	3	Kauai	0.028 ± 0.019	11.1	2.25
Total and means[b]	62		0.026	7.4	2.11

[a] Nomenclature and sequence of species follow AOU (1983).
[b] Drepanidines only; four outgroup species excluded. These values were unweighted by sample size.

trees, MULPARS, were specified. Equally parsimonious trees were input into CONTREE to produce a strict consensus tree.

The FITCH option of the computer program PHYLIP (version 2.8, by J. Felsenstein) was used to determine the lowest least-squares network for several proposed phylogenies. For species represented by two or more sampled populations, Wright's (1965) F_{st}, a measure of gene pool fragmentation, was computed with the modifications of Wright (1978) for small sample size and of Nei (1975) for multiple alleles.

RESULTS

VARIATION AT LOCI AND HETEROZYGOSITY

Of the 36 loci scored, 23 (64%) were variable in that they showed either one or more heterozy-

TABLE 2. Allelic frequencies for polymorphic loci. Alleles are coded as letters, with the most anodal one designated as "a" and successively slower alleles as "b," "c," etc. Numbers in parentheses are frequencies for alleles when a single allele was not fixed. Abbreviations for proteins follow Harris and Hopkinson (1976).

Locus (EC number)	*P. ludoviciana*	*S. f. pelzelni*	*C. p. californicus*	*L. c. grinnelli*	*T. c. cantans*	*L. bailleui*	*H. v. virens*	*H. v. wilsoni*	*H. v. chloris*
EST-2 (3.1.1.1)	b	b	c	c	c	c	b (0.71) c (0.29)	b (0.37) c (0.63)	b (0.33) c (0.67)
MPI (5.3.1.8)	c	c	b	b	c	c	c	c	c
LA-1 (3.4.11)	c	b	c	c	b	b	b (0.04) c (0.96)	c	c
LA-2 (3.4.11)	c	c	c	a	c	c	c	b (0.125) c (0.75) d (0.125)	c
LA-3 (3.4.11)	NP	NP	NP	NP	a	a	NP	NP	NP
LGG (3.4.11)	d (0.50) e (0.50)	e	a (0.50) c (0.50)	c	d	e	d (0.04) e (0.92) f (0.04)	c (0.125) e (0.875)	b (0.17) c (0.17) e (0.66)
CK (2.7.3.2)	b	b	b	c	c	c	c	c	c
PGI (5.3.1.9)	b	a (0.50) b (0.50)	a (0.50) b (0.50)	a	b	b	b	b	a (0.17) b (0.83)
NP (2.4.2.1)	c	a	c	c	e (0.88) g (0.12)	f	c (0.08) e (0.88) g (0.04)	e	e
GOT-1 (2.6.1.1)	c	c	d	d	d	d	d	d	d
GPT (2.6.1.2)	b	b	b	b	b	b	b	b	b
GR (1.6.4.2)	b	a	a	b	a	a	a	a	a
SDH (1.1.1.14)	a	b	d	b	b	b	b	b	b
GPD (1.1.1.8)	b	b	b	a	c	c	c	c	c
EAP (3.1.3.2)	c	c	b	a	c	c	c	c	c

TABLE 2. Continued.

Locus (EC number)	*P. ludoviciana*	*S. f. pelzelni*	*C. p. californicus*	*L. c. grinnelli*	*T. c. cantans*	*L. bailleui*	*H. v. virens*	*H. v. wilsoni*	*H. v. chloris*
ADA (3.5.4.4)	b (0.50) e (0.50)	f	c (0.50) d (0.50)	a	g	g	g	g	g
PGM (2.7.5.1)	b	b	b	a	b	b	a (0.04) b (0.96)	b	b
6-PGD (1.1.1.44)	e (0.50) f (0.50)	e	a	c	c	c	c (0.96) d (0.04)	b (0.125) c (0.875)	c
ICD-1 (1.1.1.42)	a	c	a	a	b	b	a (0.04) b (0.96)	b	b
ICD-2 (1.1.1.42)	b	c	b	b	b	b	b	b	b
SOD-1 (1.15.1.1)	d	d	c	a	d	d	b (0.04) d (0.96)	d	d
ADH-1 (1.1.1.1)	b	b	b	b	b	b	b	b	c
ADH-2 (1.1.1.1)	d	d	d	d	b	c	b	b	b

Locus (EC number)	*H. v. stejnegeri*	*H. parvus*	*O. bairdi*	*P. montana*	*L. c. caeruleirostris*	*V. coccinea* (Hawaii)	*V. coccinea* (Kauai)	*H. s. sanguinea* (Hawaii)	*H. s. sanguinea* (Maui)	*H. s. sanguinea* (Kauai)
EST-2 (3.1.1.1)	c	c	c	a (0.125) b (0.125) c (0.75)	c	c	c	c	c	c
MPI (5.3.1.8)	a (0.19) c (0.81)	c	c	c	c	c	c	c	c	c
LA-1 (3.4.11)	b (0.19) c (0.81)	a (0.08) c (0.92)	b	b	c	b	b (0.80) c (0.20)	c	c	c
LA-2 (3.4.11)	c	c	a	c	c	c	c	c	c	c
LA-3 (3.4.11)	NP	a	NP	NP	NP	a	a	a	a	a
LGG (3.4.11)	e	e (0.92) f (0.08)	d (0.50) e (0.50)	e	d	d (0.67) e (0.33)	d (0.80) e (0.20)	d (0.08) e (0.92)	e	d (0.17) e (0.83)
CK (2.7.3.2)	c	c	c	c	c	c	c	c	c	a (0.17) c (0.83)

TABLE 2. Continued.

Locus (EC number)	*H. v. stejnegeri*	*H. parvus*	*O. bairdi*	*P. montana*	*L. c. caeruleirostris*	*V. coccinea* (Hawaii)	*V. coccinea* (Kauai)	*H. s. sanguinea* (Hawaii)	*H. s. sanguinea* (Maui)	*H. s. sanguinea* (Kauai)
PGI	b (0.94) d (0.06)	b	b	b (0.50) d (0.50)	b	b	b	e	e	c (0.17) d (0.17) e (0.66)
NP (2.4.2.1)	d (0.69) e (0.31)	e	g	g	b	e	e	c (0.17) e (0.83)	e	e
GOT-1 (2.6.1.1)	d	d	e	b (0.25) e (0.75)	d	d	d	d	d	a (0.33) d (0.67)
GPT (2.6.1.2)	b	b	a	a	b	b	b	b	b	b
GR (1.6.4.2)	a	a	a	a	a	a	a	a	a	a
SDH (1.1.1.14)	b	b	c	c	c	b	b	b	b	b
GPD (1.1.1.8)	c	c	b	b	c	c	c	c	c	c
EAP (3.1.3.2)	c	c	c	c	c	c	c	c	c	c
ADA (3.5.4.4)	g	g	g	g	g	g	g	g	g	g
PGM (2.7.5.1)	b	b	b	b	b	b	b	b	b	b
6-PGD (1.1.1.44)	c (0.63) d (0.37)	c (0.92) d (0.08)	c	c	c	c	c	c	c	c
ICD-1 (1.1.1.42)	a (0.19) b (0.56) c (0.25)	b	b	b (0.875) c (0.125)	b	b	b	b	b	b
ICD-2 (1.1.1.42)	b	b	b	b	b	b	b	b	a (0.50) b (0.50)	b
SOD-1 (1.15.1.1)	d	d	d	d	d	d	d	d	d	d
ADH-1	b	b	b	b	b	a	a	a	a	a
ADH-2 (1.1.1.1)	a	b	c	b	a	d	d	d	d	d

TABLE 3. Matrix of Nei's (1978; below diagonal) and Roger's (1972; above diagonal) genetic distances between forms of *Piranga, Sicalis, Carpodacus, Loxia, Telespiza, Loxioides, Hemignathus, Oreomystis, Paroreomyza, Loxops, Vestiaria,* and *Himatione.*

	1.	2.	3.	4.	5.	6.	7.	8.	9.	10.	11.	12.	13.	14.	15.	16.	17.	18.	19.
1. *P. ludoviciana*	—	.232	.272	.378	.366	.368	.289	.304	.333	.309	.340	.354	.317	.312	.358	.356	.361	.381	.354
2. *S. f. pelzelni*	.212	—	.354	.486	.346	.319	.300	.317	.341	.303	.347	.361	.336	.375	.338	.347	.358	.354	.352
3. *C. p. californicus*	.258	.412	—	.302	.394	.395	.355	.352	.366	.328	.368	.419	.425	.340	.391	.387	.372	.392	.378
4. *L. c. grinnelli*	.449	.652	.321	—	.415	.417	.376	.369	.387	.363	.392	.441	.442	.389	.413	.409	.383	.403	.397
5. *T. c. cantans*	.423	.409	.468	.536	—	.082	.107	.105	.125	.151	.059	.233	.239	.137	.068	.070	.141	.156	.148
6. *L. bailleui*	.427	.371	.472	.539	.083	—	.135	.134	.161	.131	.087	.208	.243	.167	.102	.111	.139	.153	.154
7. *H. v. virens*	.296	.330	.394	.458	.097	.129	—	.029	.059	.099	.058	.255	.226	.133	.154	.152	.140	.156	.153
8. *H. v. wilsoni*	.318	.349	.386	.443	.089	.124	.002	—	.049	.099	.053	.246	.228	.129	.148	.146	.139	.148	.145
9. *H. v. chloris*	.362	.392	.417	.472	.113	.156	.032	.027	—	.127	.081	.275	.248	.149	.140	.138	.130	.140	.135
10. *H. v. stejnegeri*	.318	.328	.350	.431	.132	.111	.063	.055	.087	—	.107	.256	.252	.113	.171	.170	.161	.175	.175
11. *H. parvus*	.381	.409	.423	.493	.053	.085	.043	.032	.061	.080	—	.264	.246	.142	.102	.100	.095	.104	.102
12. *O. bairdi*	.412	.420	.506	.574	.247	.220	.268	.255	.297	.254	.290	—	.128	.208	.255	.264	.315	.333	.312
13. *P. montana*	.332	.388	.520	.576	.251	.259	.227	.228	.261	.252	.258	.100	—	.243	.289	.298	.309	.322	.308
14. *L. c. caeruleirostris*	.341	.456	.383	.492	.146	.182	.128	.120	.145	.092	.148	.220	.259	—	.175	.167	.190	.208	.200
15. *V. coccinea* (Hawaii)	.419	.391	.465	.532	.060	.100	.145	.136	.130	.149	.096	.285	.315	.186	—	.009	.076	.088	.080
16. *V. coccinea* (Kauai)	.341	.456	.383	.492	.059	.108	.140	.130	.124	.146	.092	.290	.325	.172	.001	—	.075	.086	.078
17. *H. s. sanguinea* (Hawaii)	.413	.431	.435	.478	.146	.146	.136	.125	.119	.142	.089	.364	.352	.207	.067	.062	—	.021	.029
18. *H. s. sanguinea* (Maui)	.435	.420	.458	.501	.152	.152	.138	.126	.120	.147	.089	.377	.362	.220	.071	.066	.000	—	.040
19. *H. s. sanguinea* (Kauai)	.401	.416	.439	.490	.135	.146	.131	.120	.112	.141	.082	.352	.340	.202	.057	.051	.002	.003	—

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

Level of comparison	Number of comparisons	$\bar{D} \pm$ SE	Range
Local populations[a]	4	0.0015 ± 0.0006	0.0–0.003
Intraspecific (subspecies)[b]	6	0.0443 ± 0.0123	0.002–0.087
(excluding *H. v. stejnegeri*)[c]	3	0.0203 ± 0.0093	0.002–0.032
Interspecific congeners[d]	4	0.0540 ± 0.0106	0.032–0.080
Intergeneric confamilial	91	0.1683 ± 0.0089	0.051–0.377
Intratribal	29	0.1543 ± 0.0173	0.032–0.297
Intertribal	66	0.1675 ± 0.0104	0.053–0.377
Intersubfamilial[e]	30	0.4669 ± 0.0105	0.350–0.576
Interfamilial[f]	30	0.3862 ± 0.0083	0.296–0.456

[a] *Vestiaria coccinea* and *Himatione sanguinea* only.
[b] *Hemignathus virens* only.
[c] *H. "v." stejnegeri* is a probable species.
[d] *Hemignathus virens* vs. *H. parvus* only.
[e] Drepanidines vs. carduelines.
[f] Drepanidines vs. emberizids (*Piranga ludoviciana* and *Sicalis flaveola*).

gotes (15 loci) or were fixed at alternative alleles among species, including outgroup taxa (8). The 13 monomorphic loci were: EST-1, GDA, LAP, LDH-1, PT-1, AB-2 (hemoglobin), ACON, GOT-2, ALD, GLUD, MDH-1, MDH-2, and G-6-PDH. Six additional loci could not be scored: ACP, SOD-2 (absent), PK, LDH-2, CK-3, and ME.

Levels of genetic variation within taxa are provided in Table 1. For the honeycreepers, observed heterozygosities are not correlated with sample size ($r = 0.3671$; $P > 0.05$). H_{obs} ranged from 0.0 (in *Loxioides bailleui* and *Loxops coccineus*) to 0.059 (in *Hemignathus "virens" stejnegeri*). Average H_{obs} over all drepanidines was 0.026, a value 39.5% lower than the average of 0.043 reported for birds in general (Barrowclough 1980) and a value 51% lower than the average of 0.053 reported for large single breeding populations of 30 species (summarized by Barrowclough 1983:228–229). A reduction in observed heterozygosity below typical levels is apparent in all drepanidines except the four populations of *Hemignathus virens* and *Paroreomyza montana*. Mean H_{obs} for the 10 populations of the remaining seven species was 0.015. None of the 15 population samples departed significantly ($P < 0.05$; χ^2 test) from Hardy-Weinberg expectations.

GENETIC DISTANCES

In Table 4 we summarize average Nei's D among sample sets differentiated at increasingly inclusive levels, from local populational to interfamilial. In general, Nei's $\bar{D}$ increases at successively higher taxonomic levels of the AOU (1983) classification: local populations are differentiated at $\bar{D}$ of 0.002, subspecies at 0.044, species of the same genus at 0.054, species of different confamilial genera at 0.168, species of different tribes at 0.168, and species of different families at 0.386. The value for subspecies can be refined. Because *Hemignathus "v." stejnegeri* is genetically well-differentiated, we regard it as a species (see beyond). Removal of *stejnegeri* from the calculation of $\bar{D}$ for subspecies results in a figure of 0.020 (Table 4). Both the intertribal and interfamilial level values also require comment. Because the intergeneric confamilial and intertribal values are virtually identical (0.1683 vs. 0.1675), we calculated the value for *intra*tribal comparisons. This value, $\bar{D} = 0.154$, is again very similar to the previous two, a result which indicates that the electrophoretic data for the species assayed do not support the classification of Hawaiian honeycreepers into formal tribes. Unexpectedly, the value obtained when species of different subfamilies of the same family were compared ($\bar{D} = 0.4669$) was *larger* than that found when the honeycreepers were compared with the two species of Emberizidae (0.3862).

It is apparent that the genetic distances do not always change from one taxonomic level to the next according to expectation. This may result from the fact that the AOU classification of honeycreepers is "evolutionary" or eclectic and not cladistic. Thus, we cannot necessarily assume that the levels therein represent hierarchical phylogenetic levels and, therefore, paraphyly cannot

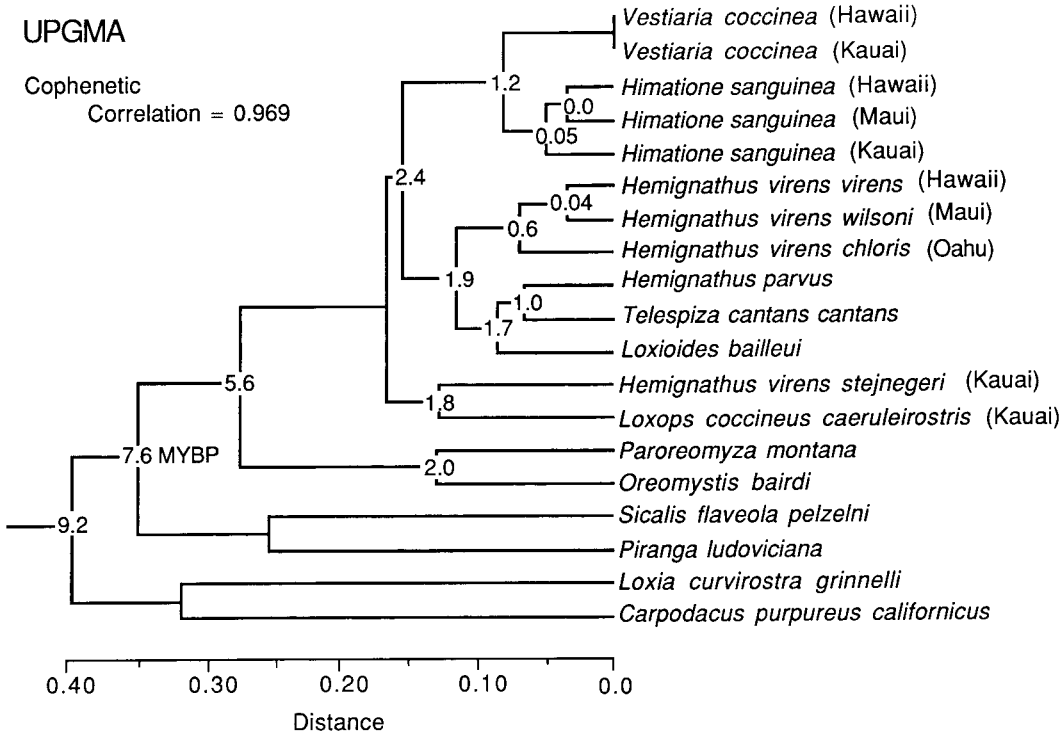

FIGURE 1. Phenogram based on Rogers' *D* values and derived by the UPGMA method. The high cophenetic correlation coefficient (r_{cc}) indicates excellent agreement between the distances shown in the phenogram and the original data matrix. Numbers at branching points provide crude estimates, in millions of years, for the timing of cladogenesis of taxa (see text).

be ruled out (Bledsoe 1988b, p. 6–7; R. J. Raikow, pers. comm.).

GENETIC POPULATION STRUCTURE

Three of the species considered here are represented by two or more samples, permitting the assessment of genetic population structure through the calculation of Wright's (1951) F_{st}. At any locus, an F_{st} value of 1 indicates fixation of alternative alleles between populations and a value of 0 indicates panmixis. In *Hemignathus virens,* F_{st} averaged across subspecies equals 0.3107; in *Himatione sanguinea,* 0.0525; and in *Vestiaria coccinea,* 0.0111. The value for *H. virens* points to clear population subdivision. This is largely a result of the inclusion of the genetically divergent taxon, *H. "v." stejnegeri,* which we regard as a species-level differentiate. The value for *H. sanguinea* indicates modest genetic structuring in that species. The low F_{st} for *Vestiaria coccinea* suggests slight subdivision, in keeping with the very low Nei's *D* (0.001) recorded for the two populations compared (Hawaii and Kauai).

BRANCHING DIAGRAMS

The results of the four analyses, UPGMA, WPGMA, F-M Tree, and Distance Wagner Tree, were broadly similar. The arrangement of branch tips was especially concordant. In the UPGMA (Fig. 1), seven major clusters are evident: (1) the two populations of *Vestiaria coccinea* and the three populations of *Himatione sanguinea*; (2) *Hemignathus virens virens, H. v. wilsoni,* and *H. v. chloris*; (3) *Hemignathus parvus, Telespiza cantans,* and *Loxioides bailleui*; (4) *Hemignathus "virens" stejnegeri* and *Loxops coccineus caeruleirostris*; (5) *Paroreomyza montana* and *Oreomystis bairdi*; (6) the two emberizids, *Sicalis flaveola* and *Piranga ludoviciana* and (7) the two carduelines, *Loxia curvirostra* and *Carpodacus purpureus.* Clusters 2 and 3 are sister groups and these two clusters form a sister group with cluster 1. In turn, the first three clusters form a sister

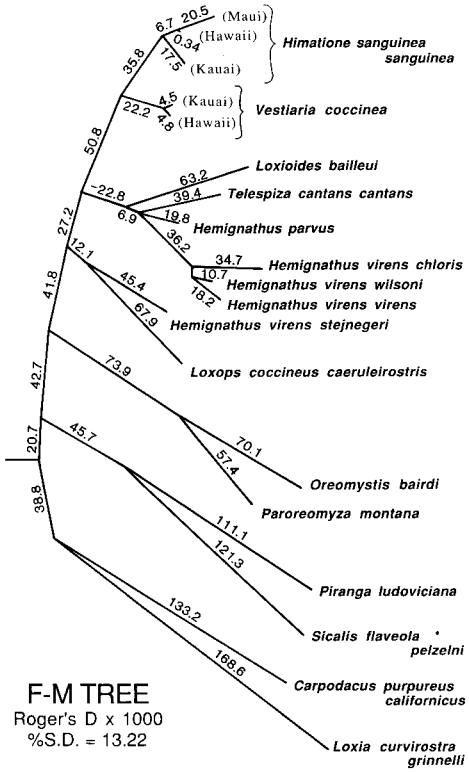

FIGURE 2. Branching diagram derived by the procedure of Fitch and Margoliash (1967). Branch lengths, in units of Rogers' D ($\times 1{,}000$) are drawn proportionately. The tree is rooted at the composite outgroup. A negative branch of miniscule length (-0.7) between the branch of length 6.9 and the bifurcation leading to *Telespiza cantans cantans* and *Hemignathus parvus* is not plotted. Of 21 F-M trees examined, the one illustrated best summarized the original genetic distance matrix based on the fewest (two) negative branches and the lowest percentage standard deviation.

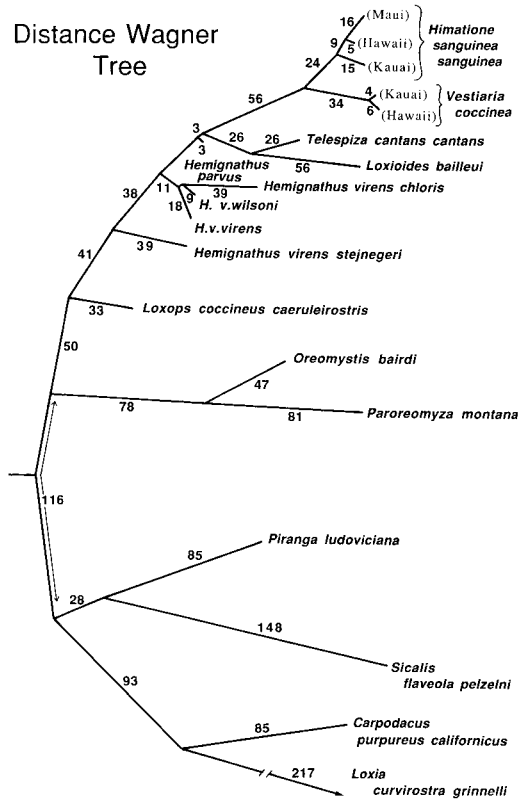

FIGURE 3. Optimized distance Wagner tree rooted at the composite outgroup. This analysis produced no negative branches.

group with cluster 4, the first four clusters form a sister group with cluster 5, and so on.

The WPGMA (not shown) differed from the UPGMA in only two respects: cluster 4 (see above) is combined with cluster 2 in an unresolved trichotomy and this enlarged cluster forms a sister group with clusters 1 and 3 which are in turn sister groups. Thus, the main ambiguity concerns the placement of the species couplet, *H. "v." stejnegeri* and *Loxops coccineus*; otherwise both analyses lead to extremely similar branching schemes. Finally, both UPGMA and WPGMA show the drepanidines closer to the emberizids than to the carduelines, a result that is contrary to expectation.

The F-M tree (Fig. 2) identified the same major groupings of species as revealed by the previous two analyses. Indeed, the F-M tree is essentially identical to the UPGMA phenogram: *Himatione* and *Vestiaria* are sister groups joined to a large cluster comprised of *Hemignathus virens virens, H. v. wilsoni, H. v. chloris, Hemignathus parvus, Telespiza,* and *Loxioides*; *Hemignathus "virens" stejnegeri* and *Loxops coccineus* are sister species linked to all the previously mentioned forms; *Paroreomyza montana* and *Oreomystis bairdi* form a clade tied to all of the previous species; and the closest species to the drepanidines are the two emberizids rather than the two carduelines.

Finally, the distance Wagner tree (Fig. 3) expresses a structure which is again very similar to that of the F-M tree. In the Wagner tree, however, *Loxops coccineus* and *H. "v." stejnegeri* branch off independently rather than being sister taxa. Moreover, the three remaining subspecies of *Hemignathus virens* form a cluster that also

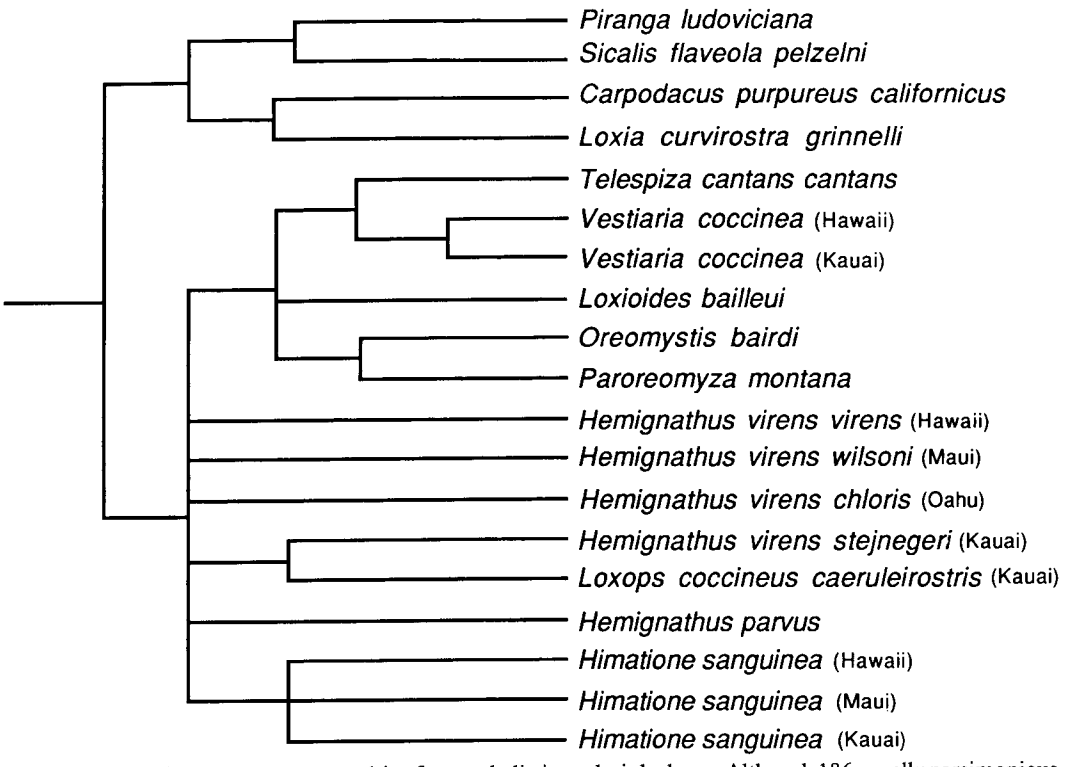

FIGURE 4. Strict consensus tree resulting from a cladistic analysis by locus. Although 186 equally parsimonious trees with 55 construction steps were produced, we stopped the output at 83 trees for production of the consensus tree shown. Statistics derived from this tree are as follows: Consensus fork index (component count) = 10, CF (normalized) = 0.588, Term information = 31, and Total information = 41.

branches off the main stem independently, although still in close proximity to the cluster formed by *H. parvus, Telespiza,* and *Loxioides.*

We interpret the overall congruence and the few discrepancies of the four branching diagrams to indicate substantial robustness in their portrayal of the relationships of taxa as expressed by Rogers' *D.* The minor differences among the four topologies could potentially be resolved through the construction of a "consensus tree." However, for reasons presented elsewhere (Johnson and Marten 1988:185), we do not advocate the use of such trees for determination of congruence among branching patterns derived by different methodologies.

CLADISTIC ANALYSIS

Because cladistic approaches have often provided ambiguous results in other avian studies (Avise et al. 1980, Zink and Johnson 1984, Johnson et al. 1988), we did not anticipate congruence with the various distance techniques. Nonetheless, in most essential features the cladistic analysis by locus (Fig. 4) suggests relationships that support those indicated by the UPGMA, the F-M tree, and the distance Wagner network: (a) the composite outgroup of four species forms a major cluster distinct from that containing all of the drepanidines (only in distance Wagner and cladistic analyses); (b) *Oreomystis bairdi* clusters with *Paroreomyza montana*; (c) *H. "v." stejnegeri* allies with *L. c. caeruleirostris* rather than with the three other forms of *H. virens*; (d) the two populations of *V. coccinea* form a cluster as do the three populations of *H. sanguinea.* In two important respects, however, the topology of Figure 4 differs from any distance analysis, namely, in that *Vestiaria* does not group near *Himatione* and in that the two thick-billed drepanidine taxa, *Telespiza* and *Loxioides,* although part of the same major cluster are not portrayed as sister groups. Furthermore, the basal relationships of many of the species are unresolved in the consensus tree.

DATING OF MAJOR CLADOGENETIC EVENTS

By applying Marten and Johnson's (1986) modification of the calibration of Gutiérrez et al. (1983) to Nei's *D*, we can obtain estimates of the timing of past cladogenetic events. Thus, $t = 19.7 \times 10^6 D$, where t is the time since divergence and D is Nei's (1978) genetic distance. This exercise assumes the operation of a molecular clock (Wilson et al. 1977, Thorpe 1982) in which allelic differences accumulate uniformly over time. The report of Barrowclough et al. (1985), that genic variation in birds generally agrees with the predictions of Kimura's (1979, 1982) neutral, mutation-drift model, supports the hypothesis of a clock and encourages the use of Nei's *D* for the estimation of divergence times. However, because significant problems attend the determination of any calibration value, including ours (Marten and Johnson 1986:416–417), and because genetic distances are accompanied by substantial standard errors, we caution that the figures for the timing of cladogenetic events are best regarded as exploratory, blunt estimates. These figures have been added at the appropriate nodes in Figure 1.

Average Nei's *D*s separating the drepanidines from the carduelines and emberizids are 0.4669 and 0.3862, respectively. These distances translate into divergence times of 9.2 and 7.6 million years before present (MYBP). The next major split, that of the remainder of the drepanidines from the creepers in the genera *Paroreomyza* and *Oreomystis,* occurred at approximately 5.6 MYBP. Generic and specific divergence times ranged from approximately 2.4–1.0 MYBP, that is, from the late Pliocene to the mid-Pleistocene. Subspecific divergences, as calculated from *Hemignathus virens* exclusive of *H.* "*v.*" *stejnegeri* (a probable species), occurred from approximately 580,000 to 39,400 YBP (0.6–0.04 MYBP), into the late Pleistocene.

DISCUSSION

ORIGIN OF THE HAWAIIAN HONEYCREEPERS

Most earlier workers (Gadow 1891, 1899; Amadon 1950; Baldwin 1953; Beecher 1953) believed that the honeycreepers came from New World nine-primaried oscine stock, specifically either the thraupines or coerebines, groups currently placed in the Family Emberizidae. In contrast, Sushkin (1929) proposed that the drepanidines evolved from the cardueline finches of the Family Fringillidae. Recent findings from morphology (Bock 1970; Richards and Bock 1973; Raikow 1976, 1977a, 1977b, 1978; Zusi 1978) and biochemistry (Sibley 1970, Sibley and Ahlquist 1982, Bledsoe 1988a) have strongly supported Sushkin's view.

Our results clearly suggest that the drepanidines are genetically closer to the two species of emberizids than to the two species of carduelines examined. As shown in Table 3, this generalization is violated for only two of 60 Nei's *D* values (in both *Loxops coccineus* and in the Kauai population of *Vestiaria coccinea,* Nei's *D* was larger in the comparison with *Sicalis flaveola* [0.456] than in that with *Carpodacus purpureus* [0.383]) and for only one of 60 Roger's *D* values (*L. coccineus* vs. *S. flaveola* is larger than in the comparison of the same species with *C. purpureus*).

Although this conflict is not easily resolved, four possible explanations come to mind. (1) Our study examined insufficient loci to reveal true relationships. This possibility seems unlikely in view of the fact that the number of loci analyzed here (36) is at the high end of the range typically assayed in avian studies. (2) Because both the emberizids and carduelines are comprised of large clusters of species of widely varying age (note the substantial Nei's genetic distances [Table 3] between the two emberizids [0.212] and between the two carduelines [0.321]), comparison of the drepanidines with species of those groups other than the four chosen here might provide a picture of relationships more in agreement with the current consensus of opinion. Genetic comparison of drepanidines with Asiatic species of carduelines and emberizids would be especially pertinent in view of the possibility that the original colonist arrived from that region rather than from North America, as suggested by Berger (1981). (3) High levels of homoplasy (parallelism and/or convergence) in allozyme expression patterns have obscured true patterns of relationship. (The report of Mindell and Sites [1987] of frequent homoplasy and consequent slight phylogenetic information in *isozyme* patterns, when higher categories of birds were compared, would not be pertinent here.) Homoplasy in allozyme expression has been suspected in other avian studies (Zink and Johnson 1984). Although this possibility is difficult to exclude completely, we note that the drepanidines unambiguously allied more closely with the emberizids than with the car-

duelines. No vagueness was shown in this alliance as might be expected if either parallelism or convergence played a role. (4) The Hawaiian honeycreepers shared a more recent common ancestor with the emberizids than with the carduelines. A. H. Bledsoe (in litt. 21 November 1987) has suggested two additional possibilities: (5) "An increase in the rate of amino acid substitution in the carduelines over the rate typical of the other taxa could yield the pattern observed in Table 3" (for additional comments on the possibility of variable rates see Bledsoe 1987a, 1987b), and (6) "that the drepanidines and carduelines are sister groups but that the effect of a colonization bottleneck was to remove from the drepanidines rare alleles evolved in the stem lineage leading to the cardueline-drepanidine clade. Such alleles would remain among the carduelines but be lacking in both the emberizids and the drepanidines. The effect, like an increase in rate in carduelines, would be to make the drepanidines and emberizines more similar to one another than the drepanidines are to the carduelines."

All but the first of these possibilities seem reasonable. Nonetheless, we see no easy way at present to judge their relative merits. This dilemma notwithstanding, the allozyme data should at least re-open the apparently long-settled question of drepanidine relationships and expose the need for extensive comparisons, molecular and otherwise, among a wide array of potentially related drepanidine, cardueline, and emberizid taxa.

TIMING OF COLONIZATION

Sibley and Ahlquist (1982) proposed that the ancestor of the drepanidines colonized a now-submerged island of the Hawaiian chain at 20–15 MYBP and that "it was the colonization event that caused the dichotomy between the cardueline and drepaninine lineages." Our data indicate a much more recent arrival, at approximately 7.6 MYBP. This younger date agrees generally with that published for the emergence of Nihoa (7 MYBP; Dalrymple et al. 1974), which is now nearly submerged to the northwest of the main Hawaiian Islands. Furthermore, because of the imprecision of the 7.6 MYBP estimate, we cannot rule out colonization of the ancestral species at Kauai, the oldest of the present main islands, when it formed over the hot spot in the ocean floor at an estimated 5 MYBP (McDougall 1979).

Despite our conflicting dates, we agree with Sibley and Ahlquist that the split of the drepanidines from its ancestral species probably occurred at the time of colonization. Furthermore, as foreshadowed by Amadon (1947) and stated explicitly by Sibley and Ahlquist (1982), the fact that the honeycreepers captured so many ecological niches provides excellent evidence that their ancestor was the first passerine species to become established in the islands. Finally, the genetic evidence supports Sibley and Ahlquist's view (1982:138) that "most of the adaptive radiation that produced the 22 known species of Hawaiian honeycreepers probably occurred within the past 5 million yr on the 'high' islands from Kauai to Hawaii."

EVIDENCE FOR POPULATION BOTTLENECKS AND FOUNDER EFFECTS

Insular colonization models typically assume that the initial pioneers were few in number and, therefore, simply by chance introduced an unrepresentative sample of the parental gene pool to the island ("founder effect," Mayr 1942:237). In theory, passage through such a population bottleneck, both during and for a significant period after colonization, should be reflected in diminished levels of genetic variation as demonstrated by low values of observed heterozygosity, percentage of polymorphic loci, and average number of alleles per polymorphic locus (Table 1). Low heterozygosities are also expected if the total population of a species exists currently at low densities (Nei et al. 1975).

The reduced genetic variability recorded in several taxa can be explained by either or both of the above phenomena. For one species, the Laysan Finch, clear evidence for a past bottleneck is available. Although encountered commonly all over Laysan Island in 1912–1913, habitat destruction by rabbits reduced the population to an estimated few dozen individuals in 1923. By 1938 the population had recovered to at least 1,000. Present numbers of the species fluctuate between 7,500 and 14,800 (Berger 1981). Other forms which are presently common, but which have low heterozygosities (e.g., *Vestiaria coccinea* and *Himatione sanguinea*) perhaps reflect past bottleneck events. Three currently scarce species, *Loxioides bailleui* (total population estimated at 1,600 individuals in 1975 [van Riper et al. 1978]), *Oreomystis bairdi* (total population estimated at 6,800 ± 1,900 individuals in 1968–1973, but declining [Scott et al. 1986]) and

Loxops coccineus caeruleirostris (total population estimated at 5,100 ± 1,700 for Kauai in 1968–1973 [Scott et al. 1986]) may illustrate both past bottlenecks and the loss of genetic variability which is expected to accompany small population size. Reduced levels of observed heterozygosity have been reported for other insular taxa of birds (Zink et al. 1987, Johnson and Marten 1988).

PHYLOGENY OF THE DREPANIDINAE

In recent decades, three explicit phylogenies for the Hawaiian honeycreepers have been offered. Amadon (1950:231–233), following Gadow (1891, 1899), envisioned a nectar-feeding, coerebid-like (=thin-billed thraupine) ancestor. Rather early it split into two principal stocks. The first lineage (the "Psittirostrinae") led through intermediate forms, such as *Loxops* (which under Amadon's classification included *H. virens, H. parvus, P. montana,* and *O. bairdi*) and *Hemignathus,* to culminate in thick-billed species, like *Pseudonester* and *Psittirostra* (which then included *T. cantans* and *L. bailleui*). The second lineage (the "Drepaniinae") included specialized nectar feeders and led through *Himatione* and *Vestiaria* to *Drepanis* and *Ciridops.* Thus, Amadon viewed *Loxops* (sensu latu) and *Himatione* to be the least specialized as well as earliest evolved members of each major lineage. Baldwin (1953:386–388) agreed with the essence of Amadon's proposed phylogeny.

Richards and Bock (1973:122–128) also hypothesized an ancestor with a tubular tongue but chose a *Ciridops*-like species for this role. They, too, proposed a rather rapid cladogenetic event soon after colonization in which two major lineages arose from the *Ciridops*-like ancestor. The first lineage (the "Drepanidinae") evolved into the stock that produced definitive *Ciridops,* then *Himatione* and the other advanced nectarivorous species. The other stock (the "Psittirostrinae") passed through an ancestral "*Loxops virens*-like" stage, then bifurcated into a branch leading to *Hemignathus* and the thick-billed forms and a branch leading to modern *Loxops coccineus* and "*L.*" *maculata* (=*Paroreomyza* and *Oreomystis*), "*L.*" *parva,* and "*L.*" *virens.*

The third recently-published phylogeny is that of Raikow (1977a:113–115). Like Sushkin (1929), he believed that a primitive cardueline finch colonized the Hawaiian Islands and evolved into the drepanidines. He envisioned an initial split with one branch producing the lineage of thick-billed forms and the other giving rise in succession to *Paroreomyza, Hemignathus, Loxops, Palmeria, Himatione, Vestiaria,* and *Drepanis.* In the absence of material for detailed dissection, he excluded *Ciridops* from the phylogeny.

The aforementioned three phylogenies were derived from morphologic and ecologic data. Our phylogeny based on allozymes differs fundamentally. First, neither the specialized nectarivorous forms nor the thick-billed species are segregated into distinctive lineages. Thus, no genic evidence supports the views that either *Himatione* or the finch-like forms are primitive. Instead, the creepers (*Paroreomyza* and *Oreomystis*) divide basally from the remaining species. The fact that the flat-tongued, insectivorous creepers represent the modern descendants of the earliest major branch of drepanidines encourages speculation that the common ancestor of both the creepers and the remaining modern drepanidines could have possessed a somewhat similar, generalized bill form, tongue morphology, and diet. Furthermore, it is plausible to envision subsequent radiation from such an ancestor of separate lineages that culminated in modern species representing (a) both generalized (e.g., *H. virens*) and specialized (*L. coccineus*) omnivores, (b) specialized thick-billed and thick-tongued finch taxa (e.g., *Loxioides* and *Telespiza*), and (c) specialized decurved-billed and tubular-tongued nectarivorous taxa (e.g., *Himatione* and *Vestiaria*). Although we do not propose that any modern species evolved from another, that possibility cannot be excluded.

The aforementioned scenario requires the derivation of finch-billed forms with thick, flat tongues from tubular-tongued ancestors, a possibility first proposed by Amadon (1947). Such a route presents no serious difficulty. (Note the close relationship of thick-billed *Telespiza* and *Loxioides* with thin-billed *Hemignathus* suggested by Fig. 1–3.) Even an advanced tubular tongue possesses a moderately thick base. Phylogenetic loss through truncation of the rolled distal portion and subsequent thickening of the basal portion of the tongue could be accomplished through the alteration of developmental patterns and rates. Concomitant change in bill shape also seems reasonable. As Alberch et al. (1979:315) wrote, "We know that slight perturbation in the ontogenetic trajectory of an organ can be amplified through time, by the dynamics of growth and tissue interactions, to produce an

adult phenotype drastically different from that of the ancestor. Clearly, major morphological changes can be the product of minor genetic mutations." Gould (1977) provides elaborate discussion of the crucially important relationship of ontogeny to phylogeny and Olson (1973:31–36) describes an example in rails.

The presence or absence of *M. plantaris,* a small muscle of the shank, has figured prominently in recent discussions of the phylogeny and relationships of the drepanidines (Raikow 1977a). Many forms (e.g., "*Loxops*" *virens, Himatione, Vestiaria,* and *Palmeria*) have lost this muscle, a condition considered to be derived because the muscle is present in many passerine and nonpasserine families (Raikow 1978:22–23). Because each of three thick-billed taxa (including *Telespiza*) examined by Raikow (1978) possess *M. plantaris,* he cites this as evidence for the relative primitiveness of these taxa within the drepanidines. However, several lines of evidence suggest that the presence of this muscle does not argue persuasively for a basal position for the thick-billed forms. First, as Raikow's (1978:21) dissections show, this muscle is not uniformly present in either the emberizids or the cardueliines, groups that have been considered as ancestral to the drepanidines. For example, *M. plantaris* is absent in *Diglossa, Cyanerpes, Carpodacus, Serinus* (present in *S. mozambicus* but absent in *S. serinus*), *Carduelis,* and *Loxia.* Therefore, it is by no means certain that the ancestral drepanidine, whether of emberizid or cardueline origin, possessed *M. plantaris.* But if it were present in the ancestor (and its presence in the creeper *Paroreomyza* argues for this), Raikow (1975) and Raikow et al. (1979) have described a means through which the *M. plantaris* could have reappeared in the thick-billed forms even though absent from their most immediate ancestors. In brief, they review evidence suggesting that the phenotypic expression of particular genetic information can be interrupted for significant periods of time. Later, reactivation of relevant regulatory genes allows the "lost" feature to reappear (Raikow et al. 1979:206). Recently, Raikow (in litt., 27 January 1988) has kindly commented on this hypothesis with respect to the drepanidines: "With regard to the possibility that M. plantaris could be lost and subsequently regained, I see no theoretical impediment. It is a small muscle of dubious functional significance, and seems to be easily dispensed with at no disadvantage to the birds . . . . That your hypothesis would require the reappearance of the muscle would not, I think, be a strong argument against your view. Of course, it offers no support either." We conclude therefore that the presence of *M. plantaris* in the thick-billed species does not preclude the possibility that they were immediately derived from an ancestor that lacked this muscle.

The FITCH option of the program PHYLIP allows an objective, quantitative comparison of phylogenies. Although the phylogenies proposed by Amadon (1950) and by Richards and Bock (1973) are too generalized to permit analysis by this method, that of Raikow is explicit enough to allow comparison with our distance Wagner results. Because our distance Wagner phylogeny (Sum of squares = 3.278, SD = 9.819) has a lower least squares network and lower standard deviation than Raikow's phylogeny (SS = 5.454, SD = 12.666), we conclude that it more accurately portrays the relationships inherent in the original genetic distance matrix. Bledsoe (1987a) discusses the use of the Fitch option to evaluate phylogenetic estimates of distance data.

Hopefully, the continuing research program on fossil depranidines (Olson and James 1982a, 1982b) will eventually shed more direct light on the ancestors of the thick-billed taxa. Unfortunately, fossils presently available are modern in appearance (S. L. Olson, pers. comm.) and much too young (James et al. 1987) to assist in phylogenetic reconstruction.

Our genetic data offer the most convincing evidence yet for monophyly of the drepanidines. Doubts regarding monophyly have persisted in the literature up to the present decade (Bock 1970, Berger 1981). In particular, Pratt (in Berger 1981: 149) felt that members of *Paroreomyza* were dubiously drepanidines based on a combination of behavioral, morphologic, and other evidence. Although the creepers are clearly the phylogenetically most distant taxa of drepanidines considered here, they obviously ally with the other drepanidines, rather than with either the emberizid or cardueline outgroup species. The refined morphologic comparisons of Richards and Bock (1973) and of Raikow (1976, 1977a, 1977b) also indicate that the creepers are drepanidine. However, demonstration of monophyly in the nine species we studied by no means rules out the possibility that unstudied taxa could point to polyphyly. Specifically, the rare and little-known

Melamprosops phaeosoma is suspected of being nondrepanidine (Pratt, in Berger 1981:170).

TAXONOMIC IMPLICATIONS OF THE GENETIC RESULTS

In several instances the electrophoretic data pointed to relationships at variance with those of the most widely used current classifications (e.g., Bock 1970, Berger 1981, AOU 1983). Differences are evident from the subspecific to tribal levels. The genic information suggests that: (1) *Hemignathus "virens" stejnegeri* is a full species possibly allied to *Loxops coccineus caeruleirostris*; (2) *Telespiza cantans* and *Loxioides bailleui* are sister taxa in the distance Wagner treatment and are perhaps congeneric; (3) the relationships of *H. parvus* are unresolved; (4) *Vestiaria coccinea* and *Himatione sanguinea* are sister taxa in several analyses and are possibly congeneric; (5) *Paroreomyza* and *Oreomystis* are valid genera and, although distantly related, are each other's closest relatives among the drepanidines we studied; and (6) among the species of Drepanidinae examined, only two tribes are justified, one for *Paroreomyza* plus *Oreomystis* and another for the remaining species. We recommend that these suggested taxonomic changes be formally considered by the Committee on Classification and Nomenclature of the AOU.

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