BIOCHEMICAL SYSTEMATICS WITHIN PALAEOTROPIC FINCHES (AVES: ESTRILDIDAE)

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ABSTRACT.—Differentiation at 38 presumptive loci was examined among 30 species of palaeotropic finches (Estrildidae) by protein electrophoresis. Three species of Ploceidae, two of Fringillidae, and one of Emberizidae were included for comparison and the establishment of out-groups. Phenetic and cladistic analyses were employed, and both produced concordant patterns of relationships among the species. I conclude that all four families are closely related, with Estrildidae and Ploceidae grouped on one major sublineage and Fringillidae and Emberizidae on the other. Within the Estrildidae, three distinct radiations are identified, corresponding to the waxbill (Estrildae), mannikin (Lonchurae), and grassfinch (Poephilae) groupings in current classifications. Contrary to prevailing views, *Aidemosyne* is shown to be a member of Poephilae, not Lonchurae, and to be allied with *Neochmia* and *Aegintha*. Similarly, the relationships of *Aegintha* as currently presumed with the Estrildae are not consistent with the electrophoretic data. Overall, the data suggest a monophyletic origin for the Australasian Poephilae. Within this assemblage, however, *Emblema* and *Poephila* are clearly polyphyletic by current classifications. A major point of ambiguity in the data centers on the interconnections between the three major estrildid assemblages; at present, this can be treated only as an unresolved trichotomy. *Received 24 October 1985, accepted 15 August 1986.*

BEFORE 1980, most ornithological studies using multilocus protein electrophoresis were confined to intraspecific variation (Baker 1974, Corbin et al. 1974, Manwell and Baker 1975), and they revealed levels of variation comparable to those of other vertebrates (Avise 1977). These studies also indicated a marked lack of differentiation between closely related species (Smith and Zimmerman 1976, Barrowclough and Corbin 1978), a result that has now been found to be a consistent feature in the Aves. In a series of papers on comparative protein electrophoresis within passerine families, Avise et al. (1980a–c, 1982) reported that genetic distances in birds were much lower than those observed in other vertebrates. Similar findings also were reported in nonpasserine families (Barrowclough et al. 1981, Gutiérrez et al. 1983, Adams et al. 1984). Whether the observed low isozymic genetic distances are a consequence of a slow rate of protein evolution (Avise et al. 1980c) or an artifact of overestimating the age of avian taxa (Baker and Hanson 1966) remains unresolved (Avise and Aquadro 1982). Such genetic properties place obvious constraints on the use of protein electrophoresis in evolutionary studies. Thus, the low genetic distances between populations (Barrett and Vyse 1982) and subspecies (Barrowclough 1980) of birds limit its use in determining levels of gene flow through hybrid zones or between populations. This weakness becomes its strength in determining relationships among species at generic and family levels. It is only because of the low isozymic divergence encountered among birds that electrophoresis can be used productively up to interfamilial comparisons (Avise et al. 1980c, Barrowclough et al. 1981). Accordingly, I have applied it here in an attempt to resolve species-group relationships in the estrildine finches, Estrildidae.

Delacour (1943) divided the estrildine finches into three tribes on the basis of courtship, mouth markings of nestlings, and life habits. They are the waxbills (Estrildae), which are restricted largely to Africa; the grassfinches (Poephilae), an Australasian-centered group; and the mannikins (Lonchurae), which are pan-palaeotropic from Africa through southern Asia to Australasia. While this grouping has been accepted generally, the exact composition of each tribe has been in constant dispute. In particular, the relationships of the genera *Aegintha, Erythrura, Chloebia, Amadina,* and *Aidemosyne* have never been resolved satisfactorily. Mayr (1968) could not group the genera into three discrete tribes

TABLE 1. Enzymes examined, buffers used, and tissue distribution of each enzyme.

Enzyme (E.C. no.)	Abbreviation	No. of loci	Tissue	Running buffer[a]	Running time[b] (h)
Isocitrate dehydrogenase (1.1.1.42)	IDH	2	Muscle	E	2
Glutamate-oxaloacetate transaminase (2.6.1.1)	GOT	2	Muscle	E	2.5
Glucose-phosphate isomerase (5.3.1.9)	GPI	1	Muscle	B	3
Mannose-phosphate isomerase (5.3.1.8)	MPI	1	Muscle	C	1.5
Glycerophosphate dehydrogenase (1.1.1.8)	GPDH	1	Muscle	A	3
6 Phosphogluconate dehydrogenase (1.1.1.44)	PGDH	1	Muscle	C	2.5
Malate dehydrogenase (1.1.1.37)	MDH	2	Muscle	A	1.5
Glyceraldehyde-3-phosphate dehydrogenase (1.2.1.12)	GAPDH	1	Muscle	D	3
Malic enzyme (1.1.1.40)	ME	2	Muscle	A	1.5
Peptidase C (3.4.11)	PEP L-A	1	Muscle	A	2
Peptidase B (3.4.11)	PEP L-G-G	1	Muscle	B	1.5
Esterase[c] (3.1.1.1)	EST	2	Muscle	A	1
Aldolase (4.1.2.13)	ALD	1	Muscle	D	3
Triose-phosphate isomerase (5.3.1.1)	TPI	1	Liver	D	3
Guanine deaminase (3.5.4.3)	GDA	1	Liver	C	1
Glutamate dehydrogenase (1.4.1.3)	GDH	1	Muscle	D	3
General protein (—)	GP	5	Muscle	A	3
Fumerase (4.2.1.2)	FUM	1	Liver	E	2
Aconitase (4.2.1.3)	ACON	2	Liver, muscle	F	2
Lactate dehydrogenase (1.1.1.27)	LDH	2	Muscle, heart	D	3
Phosphoglucomutase (2.7.5.1)	PGM	2	Liver	E	3
Hexokinase (2.7.1.1)	HK	2	Muscle	C	2
Superoxide dismutase (1.15.1.1)	SOD	1	Muscle	A	2
NADP specific dehydrogenase[d]	NADP nDH	1	Liver	C	2
NAD specific dehydrogenase[d]	NAD nDH	1	Muscle, liver	D	3

[a] A = 50 mM TEM, B = 15 mM TEB, C = 50 mM TEM + NADP, D = 50 mM TEM + NAD, E = 0.1 M Tris-citrate, F = 0.01 M citrate-phosphate. See Baverstock et al. (1980) for buffer recipes.

[b] At 5 mA per 12 cm gel.

[c] Used method A in Harris and Hopkinson (1976) with 4-methyl-umbelliferyl-acetate.

[d] "Nothing" dehydrogenases, i.e. bands were observed without the addition of any substrate to the staining mixture.

and arbitrarily accepted Delacour's (1943) revision with minor modifications. This reflects the fact that the Estrildidae are unusual among birds in that plumage patterns are a relatively poor clue to relationships owing to extensive convergences and parallelisms (Harrison 1963, Mayr 1968). Moreover, the value given to the various morphological and behavioral characters (Goodwin 1982) used is often subjective, both in interpretation and in application. For example, there is a gradation in the patterns of nestling mouth markings between the grassfinches and mannikins (Delacour 1943) such that the separation between these two tribes is arbitrary. Thus, although Mayr's (1968) arrangement was intended to be temporary, it still remains the only practical classification.

I analyzed protein products of 38 presumptive loci in 30 species of estrildid finches by both phenetic and cladistic methods. Six species of Ploceidae, Fringillidae, and Emberizidae were included for comparison and as out-groups in cladistic analyses. The resulting data are used to reassess relationships within the Estrildidae and the affinities of this family to other seed-eating birds.

MATERIALS AND METHODS

Specimens used were obtained from the wild and from aviaries. Wild-caught specimens of several species came from the Fitzroy River region of northwestern Australia, and, whenever possible, preference was given to material from such sources. For other species only aviary-bred birds were readily available. In such cases, each sample was obtained from diverse sources in Victoria and New South Wales to minimize the chance of obtaining related individuals. A list of the specimens examined and their collection localities is presented in the Appendix.

Liver, muscle, and heart tissue were excised and stored in liquid nitrogen. Tissues were homogenized using the recipe of Baverstock et al. (1980). Individuals were screened for 25 enzyme systems representing 38 presumptive loci (Table 1). Enzymes were

stained according to the method of Harris and Hopkinson (1976) except GOT, where the procedure of Shaw and Prasad (1970) was used. All systems were run in a cellulose acetate matrix on a paper support (Cellogel, Chemetron, Italy).

The measures of Nei (1978) and Rogers (1972) were used to estimate genetic distances between taxa. A phenetic analysis by the UPGMA method (Sneath and Sokal 1973) was performed summarizing the matrix of Nei's (1978) $\bar{D}$, while the matrix of Rogers' (1972) $\bar{D}$ was subjected to a distance-Wagner procedure (Farris 1972). In the latter computation, three species of Ploceidae were used as an out-group. Both these analyses were performed on the BIOSYS package (Swofford and Selander 1981). In addition, a qualitative analysis using the method of Hennig (1966) was performed. The rationale and procedure of this analysis has been outlined in Baverstock et al. (1979) and Patton and Avise (1983). After an initial dichotomy within the Estrildidae was determined through the ploceid out-group, each of the sister estrildine lineages were then treated as out-groups to each other from dichotomy to dichotomy.

RESULTS

ALLELIC FREQUENCIES AND HETEROZYGOSITIES AND GENETIC DISTANCE DATA

Allelic frequencies for the 30 variable loci are presented in an appendix that is available from the author. The following loci were monomorphic in all species: GOT-2, HK-2, ME-1, ME-2, MDH-1, MDH-2, NADnDH, GP-4, GP-5, TPI, and GDH. The range of heterozygosity measures (Appendix) is large (0.00–0.06, mean = 0.03), and the average proportion of polymorphic loci is 12% (see Appendix). These values are comparable to the levels of genetic variation reported for birds in general (Selander 1976, Avise and Aquadro 1982).

Matrices of genetic distance values for the Estrildidae are presented in Table 2. Except for *Poephila bichenovii*, in which two subspecies were examined, all comparisons are between species. The Nei (1978) distance between *P. b. bichenovii* and *P. b. annulosa* of 0.01 (Table 2) is similar to that observed between subspecies of other birds (Corbin 1977). In comparison, genetic distances between congeneric species range from 0.10 to 0.25, while those between genera are higher, ranging from 0.30 to 0.77 (Table 3). These values are generally higher than those reported in several other passerine families where mean intra- and intergeneric values of $\bar{D}$ are 0.10 and 0.26, respectively (summarized in Avise and Aquadro 1982).

Distance values for species representing the three related families Ploceidae, Fringillidae, and Emberizidae are given in Table 4. The interfamilial genetic distances are low, ranging from 0.765 to 0.455, in contrast to the recorded distance across avian families of 1.00 (Avise and Aquadro 1982).

CLUSTER ANALYSIS

Phenetic analysis.—The UPGMA-generated phenogram (Fig. 1) weakly separates the Estrildidae from the Ploceidae and groups the estrildids in three clusters corroborating the tribes of Delacour (1943) and Mayr (1968). They are the Poephilae (cluster 1), Estrildae (cluster 2), and Lonchurae (cluster 3) in the nomenclature of Mayr (1968).

Apart from *Aegintha temporalis* and *Aidemosyne modesta*, the species in cluster 1—all Australasian—always have been considered to be closely related (Morris 1958, Mayr 1968). Both *A. temporalis* and *A. modesta* are included here in the Poephilae, aligned with *Neochmia ruficauda* (Fig. 1). The most decisive split is between *Poephila guttata, P. bichenovii,* and the rest of the tribe. Although the genetic distance between *P. guttata* and *P. bichenovii* is relatively high ($\bar{D}$ = 0.21), they stand together apart from other Poephilae. The remaining species of *Poephila* cluster closely with the *Neochmia-Aegintha-Aidemosyne* assemblage, while *Emblema guttata* is grouped with *Neochmia phaeton* and not its congener, *E. picta.*

The limited number of species and genera examined precludes comprehensive analysis of the relationships within cluster 2, the African Estrildae. Two points, however, merit comment. First, *Pytilia melba* and *P. phoenicoptera* cluster together and are close to the rest of the Estrildae, despite their extensive karyotypic differences (Christidis 1983). If Nei's (1978) $\bar{D}$ is related to time since divergence, then the branching patterns (Fig. 1) suggest that the two species of *Pytilia* have diverged rather recently both from each other and from the rest of the Estrildae. This in turn indicates that the marked chromosomal differences within *Pytilia* (Christidis 1983) also have arisen recently. Secondly, the species of Estrildae are phenetically more distant from one another than are those within

the Poephilae. Such a result is not unexpected because it is generally agreed that the Estrildidae arose in Africa (Goodwin 1982), so African estrildine taxa could be expected to be older and more distantly radiated than their Asian and Australian counterparts.

The third cluster, Lonchurae, is subdivided into five groups (Fig. 1). The first group, which includes the genera *Erythrura* and *Chloebia*, and the second, which is the genus *Amadina*, are distinct from the rest of the Lonchurae. With the exception of *Padda oryzivora*, the remaining species belong to *Lonchura* itself and separate into three groups. The first of these is monotypic with *L. pectoralis*. The second is also monotypic with *L. bicolor*, though it may reflect the fact that neither *L. cucullata* nor *L. fringilloides*—both supposed close allies of *L. bicolor*—was included in the analysis. *Padda oryzivora* and the remaining five species of *Lonchura* comprise the final group. Here, extremely short branch points separate the species even though some of them, particularly *P. oryzivora*, are morphologically distinct.

Wagner analysis.—Unlike phenetic analyses, the Wagner tree does not assume a constant rate of protein evolution (Fig. 2). The dendrogram generated in Fig. 2 uses three species of Ploceidae as an out-group. It is clear from the branch lengths that the rate of protein evolution varied along the different lineages. Despite this, there is considerable concordance between the UPGMA and Wagner networks.

The branching patterns for the Poephilae in both networks (Figs. 1 and 2) are essentially the same, the only difference being a minor switch in position between *Aegintha temporalis* and *Neochmia ruficauda*. Moreover, the five clusters within the Lonchurae are the same. In the branching sequences of the Lonchurae, however, there are differences. These are due to unequal amounts of protein change along a lineage, as shown in the differences in the lengths of branches leading to *Amadina* and *Lonchura pectoralis* in both networks. As a result the UPGMA analysis places *L. pectoralis* closer to the genus *Lonchura* than to the genus *Amadina*, while the Wagner network clusters *Amadina* closer. The arrangement in the Wagner tree reflects the greater number of ancestral character states (symplesiomorphies) and derived character states (synapomorphies) that *L. pectoralis* and *Amadina* share with the rest of *Lonchura*, respectively. This also accounts for the discrepancies in the position of *Lagonosticta senegala* of the Estrildae (Figs. 1 and 2).

An alternative to the distance-Wagner procedure for analyzing electrophoretic data is the use of percent fixed differences (Baverstock et al. 1982, Adams et al. 1984). For most species this method produces a Wagner network similar to that presented in Fig. 2, and so it is not repeated here. Some discrepancies occurred. On percent fixed differences, *N. ruficauda* is 8 units from *N. phaeton*, *Aegintha temporalis*, and *Aidemosyne modesta*, while *A. temporalis* and *A. modesta* are 6 units from one another. The problem lies in the position of *N. phaeton*, which is 19 units from *A. modesta*, 14 units from *A. temporalis*, but only 8 units from *N. ruficauda*, a result that produces negative branch lengths. Such inconsistencies are quite common in electrophoretic (Avise et al. 1980c) and immunological (Farris 1981) data and are probably the result of back-mutations and convergences. Here, fixed allelic differences indicate that it is more appropriate to group *N. phaeton* within the *Neochmia-Aidemosyne-Aegintha* cluster than to align it with *Emblema guttata* (Figs. 1 and 2). This alignment is corroborated by morphological, behavioral (Goodwin 1982), and chromosomal (Christidis 1986) data.

Cladistic analysis.—A Hennigian cladogram drawn from qualitative analysis of electromorphs (Fig. 3) was based on three species of Ploceidae as an out-group. This method of analysis takes account of convergence and back-mutation in the construction of phylogenetic trees (Baverstock et al. 1979, Patton and Avise 1983). The specific characters defining each of the branches in the cladogram, the most robust of which are those defined by three or more character states, are listed in Table 5.

In agreement with UPGMA and distance-Wagner analyses, the cladogram resolves the Estrildidae into the three same base clades. The relationships of the Lonchurae to the two other clades, Estrildae and Poephilae, however, are ambivalent. Three derived character states of the electromorphs defining these clades—LDH-1(c), PGDH(g), and PGM-2(g)—link the Lonchurae with the Estrildae; an alternative group—GPDH(c), SOD(j), and NADP nDH(g)—links the Lonchurae to the Poephilae instead, an arrangement supported by the distance-Wagner dendrogram. The UPGMA phenogram groups the

TABLE 2. Genetic distance measures in the Estrildidae. Above diagonal: Rogers (1972) genetic distance; below diagonal: Nei (1978) unbiased distance. Species abbreviations are defined in the Appendix.

Species	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15
1 PGU	—	0.216	0.325	0.320	0.320	0.324	0.357	0.346	0.378	0.381	0.327	0.499	0.482	0.420	0.454
2 PBI	0.213	—	0.291	0.288	0.277	0.315	0.319	0.354	0.361	0.342	0.324	0.472	0.480	0.394	0.437
3 PAC	0.360	0.321	—	0.054	0.085	0.131	0.140	0.255	0.238	0.197	0.227	0.488	0.492	0.349	0.435
4 PCI	0.343	0.297	0.010	—	0.111	0.157	0.166	0.276	0.243	0.224	0.214	0.480	0.489	0.354	0.445
5 PPE	0.363	0.311	0.059	0.069	—	0.156	0.155	0.275	0.259	0.214	0.248	0.517	0.510	0.357	0.438
6 AMO	0.365	0.354	0.105	0.119	0.145	—	0.118	0.236	0.244	0.120	0.211	0.509	0.483	0.353	0.436
7 ATE	0.416	0.356	0.109	0.122	0.140	0.086	—	0.201	0.206	0.125	0.162	0.498	0.464	0.363	0.411
8 EGU	0.402	0.417	0.264	0.279	0.303	0.240	0.194	—	0.286	0.236	0.207	0.562	0.525	0.406	0.508
9 EPI	0.458	0.428	0.240	0.239	0.279	0.241	0.193	0.308	—	0.260	0.238	0.498	0.465	0.402	0.433
10 NRU	0.460	0.402	0.196	0.214	0.228	0.102	0.107	0.247	0.276	—	0.186	0.520	0.464	0.390	0.471
11 NPH	0.370	0.385	0.231	0.195	0.270	0.208	0.147	0.205	0.244	0.182	—	0.521	0.483	0.383	0.438
12 CGO	0.679	0.623	0.660	0.640	0.724	0.710	0.673	0.817	0.675	0.730	0.727	—	0.215	0.387	0.381
13 ETR	0.641	0.641	0.658	0.639	0.707	0.646	0.602	0.725	0.608	0.612	0.650	0.218	—	0.352	0.329
14 LPE	0.531	0.487	0.406	0.395	0.433	0.417	0.432	0.507	0.490	0.484	0.471	0.464	0.422	—	0.292
15 LFL	0.597	0.570	0.562	0.560	0.572	0.561	0.508	0.699	0.561	0.632	0.571	0.462	0.390	0.336	—
16 LAT	0.595	0.569	0.515	0.512	0.528	0.515	0.470	0.700	0.611	0.582	0.570	0.505	0.429	0.365	0.028
17 LMA	0.602	0.576	0.568	0.565	0.581	0.567	0.522	0.705	0.569	0.638	0.577	0.468	0.396	0.333	0.001
18 LCA	0.588	0.560	0.557	0.554	0.570	0.552	0.515	0.687	0.548	0.622	0.566	0.464	0.400	0.329	0.003
19 LPU	0.524	0.562	0.488	0.491	0.488	0.486	0.487	0.648	0.545	0.600	0.534	0.445	0.391	0.338	0.049
20 POR	0.587	0.561	0.553	0.549	0.517	0.556	0.501	0.699	0.553	0.624	0.554	0.481	0.407	0.339	0.045
21 LBI	0.598	0.480	0.450	0.467	0.483	0.478	0.421	0.601	0.562	0.536	0.570	0.419	0.429	0.308	0.232
22 AFA	0.722	0.770	0.617	0.628	0.611	0.568	0.612	0.739	0.835	0.630	0.729	0.484	0.562	0.527	0.407
23 AER	0.711	0.771	0.616	0.627	0.623	0.569	0.611	0.731	0.834	0.635	0.715	0.488	0.561	0.526	0.406
24 ASU	0.707	0.760	0.460	0.472	0.510	0.474	0.418	0.601	0.599	0.455	0.515	0.729	0.623	0.680	0.636
25 AAM	0.663	0.736	0.488	0.518	0.484	0.429	0.413	0.608	0.634	0.417	0.591	0.786	0.775	0.628	0.624
26 EAS	0.497	0.530	0.364	0.375	0.397	0.342	0.352	0.462	0.484	0.327	0.432	0.658	0.702	0.413	0.583
27 UBE	0.673	0.748	0.589	0.630	0.548	0.583	0.502	0.623	0.599	0.556	0.646	0.620	0.565	0.618	0.496
28 LSE	0.778	0.757	0.553	0.569	0.654	0.617	0.524	0.651	0.588	0.592	0.600	0.629	0.672	0.756	0.694
29 PME	0.618	0.654	0.446	0.490	0.467	0.472	0.402	0.565	0.558	0.504	0.563	0.626	0.678	0.585	0.505
30 PPH	0.586	0.641	0.395	0.419	0.402	0.419	0.377	0.553	0.547	0.409	0.453	0.723	0.769	0.573	0.630

TABLE 2. Continued.

Species	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30
1 PGU	0.455	0.458	0.453	0.421	0.450	0.456	0.514	0.511	0.512	0.488	0.402	0.501	0.545	0.470	0.452
2 PBI	0.437	0.440	0.434	0.440	0.436	0.386	0.539	0.539	0.537	0.525	0.419	0.530	0.535	0.490	0.480
3 PAC	0.409	0.438	0.436	0.399	0.434	0.374	0.464	0.463	0.377	0.393	0.322	0.454	0.433	0.376	0.341
4 PCI	0.418	0.447	0.444	0.402	0.438	0.392	0.475	0.474	0.397	0.421	0.336	0.486	0.448	0.407	0.366
5 PPE	0.413	0.442	0.442	0.402	0.411	0.387	0.462	0.465	0.407	0.390	0.335	0.428	0.485	0.383	0.342
6 AMO	0.410	0.439	0.436	0.398	0.433	0.390	0.438	0.438	0.387	0.357	0.303	0.450	0.466	0.390	0.350
7 ATE	0.388	0.417	0.418	0.405	0.411	0.360	0.467	0.467	0.362	0.353	0.315	0.408	0.423	0.354	0.328
8 EGU	0.508	0.511	0.504	0.489	0.509	0.457	0.529	0.524	0.456	0.460	0.378	0.472	0.482	0.440	0.430
9 EPI	0.461	0.437	0.429	0.429	0.433	0.434	0.566	0.565	0.459	0.479	0.396	0.461	0.451	0.442	0.432
10 NRU	0.444	0.473	0.469	0.460	0.469	0.419	0.469	0.473	0.472	0.435	0.287	0.434	0.453	0.403	0.342
11 NPH	0.439	0.441	0.438	0.428	0.431	0.439	0.524	0.514	0.409	0.452	0.363	0.481	0.455	0.442	0.377
12 CGO	0.407	0.383	0.390	0.370	0.396	0.354	0.391	0.396	0.521	0.544	0.486	0.468	0.472	0.470	0.515
13 ETR	0.355	0.332	0.344	0.341	0.348	0.355	0.434	0.434	0.469	0.542	0.510	0.488	0.496	0.500	0.539
14 LPE	0.314	0.290	0.293	0.305	0.301	0.280	0.413	0.413	0.497	0.468	0.349	0.466	0.537	0.449	0.438
15 LFL	0.039	0.007	0.025	0.071	0.063	0.215	0.337	0.336	0.473	0.467	0.448	0.399	0.504	0.403	0.468
16 LAT	—	0.033	0.056	0.096	0.090	0.205	0.310	0.310	0.447	0.445	0.439	0.390	0.504	0.403	0.441
17 LMA	0.027	—	0.023	0.072	0.067	0.208	0.340	0.339	0.476	0.474	0.441	0.393	0.507	0.405	0.471
18 LCA	0.031	0.003	—	0.086	0.085	0.227	0.353	0.352	0.478	0.470	0.442	0.402	0.507	0.410	0.467
19 LPU	0.072	0.050	0.053	—	0.087	0.212	0.312	0.315	0.463	0.461	0.440	0.386	0.493	0.389	0.454
20 POR	0.072	0.050	0.052	0.052	—	0.248	0.326	0.329	0.486	0.461	0.456	0.401	0.517	0.418	0.475
21 LBI	0.223	0.230	0.235	0.214	0.264	—	0.337	0.337	0.447	0.471	0.360	0.390	0.452	0.403	0.442
22 AFA	0.367	0.413	0.415	0.359	0.381	0.406	—	0.013	0.500	0.445	0.479	0.459	0.531	0.439	0.492
23 AER	0.366	0.412	0.414	0.357	0.390	0.405	0.001	—	0.499	0.444	0.478	0.463	0.530	0.439	0.494
24 ASU	0.586	0.641	0.639	0.604	0.653	0.586	0.687	0.686	—	0.239	0.365	0.384	0.323	0.282	0.243
25 AAM	0.586	0.642	0.624	0.604	0.611	0.635	0.587	0.586	0.267	—	0.271	0.349	0.375	0.268	0.260
26 EAS	0.571	0.577	0.567	0.556	0.600	0.438	0.645	0.644	0.443	0.309	—	0.322	0.395	0.262	0.228
27 UBE	0.484	0.491	0.487	0.454	0.493	0.484	0.605	0.616	0.460	0.413	0.373	—	0.315	0.205	0.294
28 LSE	0.693	0.699	0.696	0.658	0.713	0.591	0.749	0.748	0.387	0.462	0.490	0.356	—	0.313	0.326
29 PME	0.504	0.511	0.503	0.474	0.523	0.504	0.574	0.573	0.314	0.304	0.292	0.205	0.355	—	0.151
30 PPH	0.580	0.635	0.620	0.591	0.630	0.580	0.677	0.680	0.267	0.299	0.250	0.323	0.381	0.148	—

TABLE 3. Mean genetic distances at different taxonomic levels within the Estrildidae.

Comparison[a,b]	$\bar{D}$ (Nei 1978)	SD	SE
Congeneric in Poephilae (10)	0.124	0.073	0.007
Congeneric in Lonchurae (17)	0.048	0.049	0.003
Congeneric in Estrildae (2)	0.208	0.084	0.042
Intergeneric in Poephilae (45)	0.281	0.097	0.002
Intergeneric in Lonchurae (49)	0.395	0.085	0.002
Intergeneric in Estrildae (19)	0.352	0.078	0.004
Interfamilial; Estrildidae vs. Ploceidae (93)	0.630	0.046	0.002

[a] Number of pair-wise comparisons is in parentheses.

[b] Species compositions of the genera are based on the revision by Christidis (1987).

Estrildae with the Poephilae on the GOT-1(c) synapomorphy.

There is no single dominant factor that favors any of these three alternative branching patterns, although a closer connection between Poephilae and Lonchurae is supported by the Wagner dendrogram and one of the alternative Hennigian cladograms. Without other independent evidence corroborating any of the alternative alignments, the relationship among the tribes remains an unresolved trichotomy. Although the degree of resolution of the Hennigian cladogram (Fig. 3) is less than in the UPGMA (Fig. 1) and Wagner (Fig. 2) networks, the composition and relationships of species within each of the estrildid tribes is generally consistent across all three analyses. Thus, in the Hennigian cladogram both *Poephila guttata* and *P. bichenovii* form a distinct clade within the Poephilae; *Emblema picta* is separated from all other grassfinches on one electromorph; and the two *Neochmia* species form a distinct clade, consistent with data from fixed allelic differences. Clades within the Lonchurae are all defined by two or more derived character states (Fig. 3), and the clusters of species are similar to those obtained by the Wagner and UPGMA methods. There is parallel correspondence in the Estrildae.

DISCUSSION

The electrophoretic data were analyzed by three different methods, after the approach of Patton and Avise (1983). I produced a best-fit phylogeny by comparing the results of all three methods for agreement or discrepancy. In most instances there was good agreement among the three analyses, and consequently phylogenetic conclusions can be drawn with some confidence. The comparison also pinpointed areas of conflict, identifying discrepancies such as in the relationships between *Neochmia ruficauda* and *N. phaeton*. I tested the phylogenies obtained in the present study by an analysis of estrildid karyotypes (Christidis 1986) and found broad agreement with the electrophoretic data in the composition of Poephilae, Lonchurae, and Estrildae, and the alignment of species internally.

Although the electrophoretic data subdivide the Estrildidae into three groups corresponding largely to the "tribes" of Delacour (1943) and Mayr (1968), they do not establish definitive relationships among the tribes. Other evidence sheds little light on the question. From appendicular musculature, Bentz (1979) suggested that the Estrildae and Lonchurae form a cluster apart from the Poephilae within the Estrildidae; but this is not supported consistently by the elec-

TABLE 4. Genetic distance measures in the families examined. Above diagonal: Rogers (1972) genetic distance; below diagonal: Nei (1978) unbiased distance.

Species	Family	1	2	3	4	5	6	7
1. *Poephila guttata*	Estrildidae	—	0.433	0.450	0.419	0.533	0.504	0.538
2. *Passer domesticus*	Ploceidae	0.547	—	0.081	0.373	0.406	0.363	0.466
3. *P. montanus*	Ploceidae	0.579	0.050	—	0.403	0.422	0.361	0.473
4. *Foudia madagascariensis*	Ploceidae	0.530	0.456	0.504	—	0.445	0.478	0.502
5. *Carduelis carduelis*	Fringillidae	0.751	0.514	0.530	0.589	—	0.254	0.375
6. *C. chloris*	Fringillidae	0.697	0.442	0.423	0.641	0.282	—	0.375
7. *Tiaris canora*	Emberizidae	0.765	0.621	0.632	0.693	0.460	0.455	—

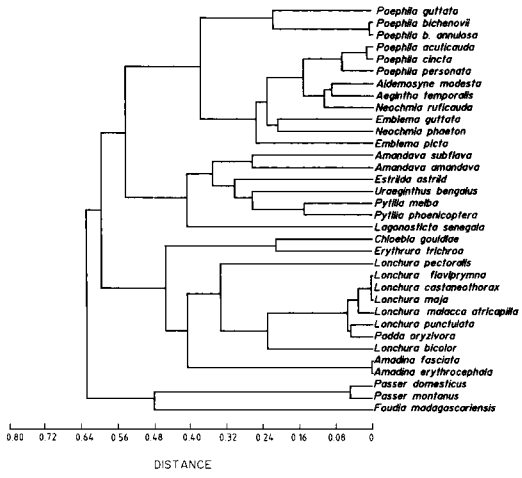

Fig. 1. UPGMA phenogram based on Nei's (1978) $\bar{D}$.

trophoretic evidence (compare Figs. 1–3). Opinion has fluctuated, moreover, as to whether the Australian grassfinch fauna has been derived from one or several successive invasions (Morris 1958; Harrison 1963, 1967). Immelmann (1962) and Harrison (1967) maintained that the Australian genera *Emblema, Neochmia,* and *Aegintha* were all direct descendants of a waxbill (Estrildae) invasion from Africa. This hypothesis was based on the assumption that these genera were more closely related to African *Estrilda* than to other Australian elements. A second invasion by primitive mannikins (Lonchurae) was said to have given rise to *Poephila* and *Aidemosyne.* In contradicting this hypothesis, my results and the myological data of Bentz (1979) suggest instead a single, monophyletic origin for the Australian grassfinches (Poephilae) that includes *Emblema, Neochmia,* and *Aegintha.* The behavioral and morphological similarities between members of these genera and African *Lagonosticta* (Mitchell 1962) and *Estrilda* (Delacour 1943, Mitchell 1962) are evidently the result of convergences and parallelisms, not common ancestry.

Neochmia, Aegintha, and *Aidemosyne* often are placed in three separate tribes (Wolters 1957, 1981; Mitchell 1962). Goodwin (1982) argued for a close relationship among them on the basis of nestling mouth markings and plumage patterns, but the evidence was inconclusive because *Aidemosyne* shared several behavioral characters with the Lonchurae. The electrophoretic data nonetheless support a close relationship among these three genera. The phylogeny of the Poephilae (Figs. 1–3) also highlights the shortcomings in plumage patterns as determi-

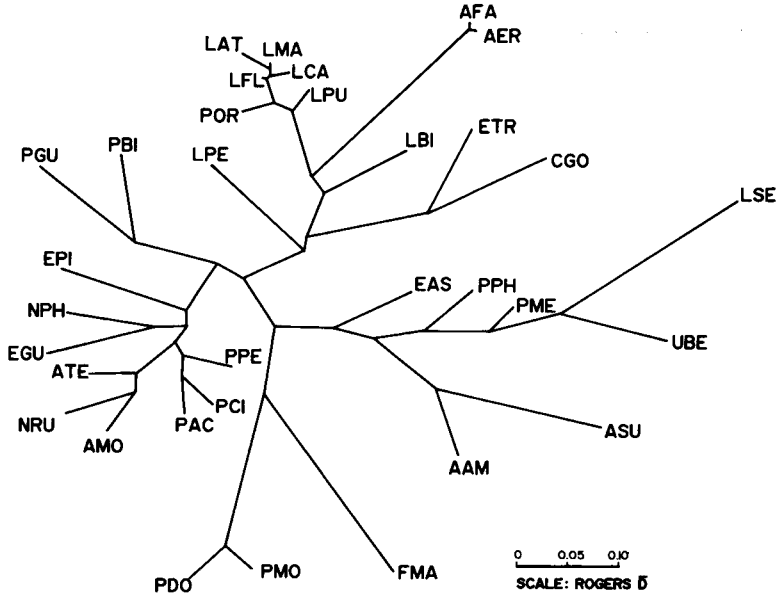

Fig. 2. Distance-Wagner network based on Rogers' (1972) $\bar{D}$. The tree is rooted by the "out-group method" (Farris 1972) using the Ploceidae (PDO, PMO, FMA). Species abbreviations are defined in the Appendix.

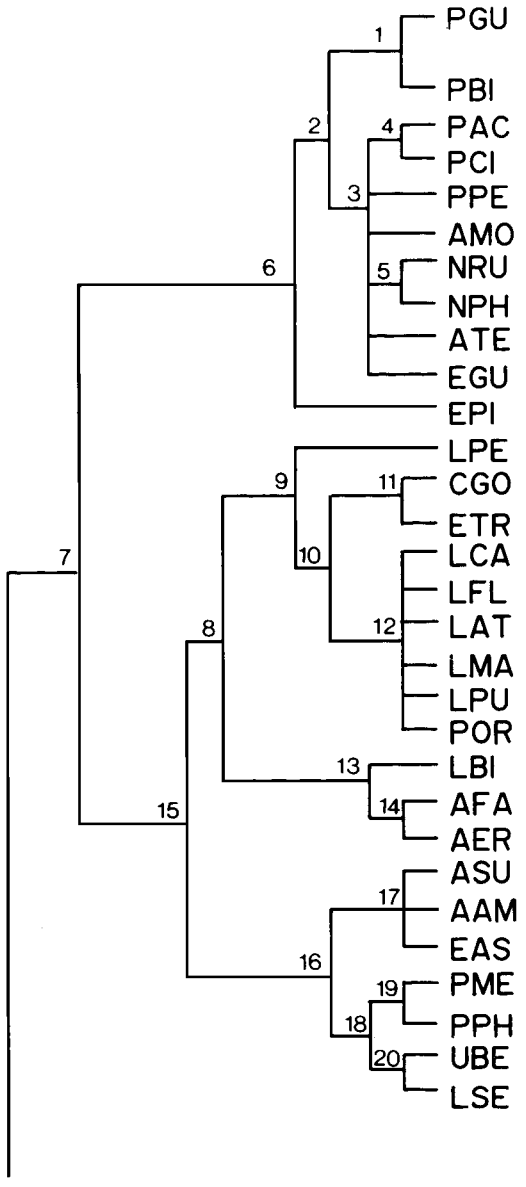

Fig. 3. Cladogram based on electromorphs. Numbers at branch refer to synapomorphies (Table 5).

TABLE 5. Electromorphs that define clades (Fig. 3).

Clade	Apomorphic characters
1	ACON-2(b), PGM-2(d), Ndh(h)[a]
2	PGDH(k)
3	PGDH(h)
4	IDH-2(b), PGM-1(g)
5	GP-2(e)
6	GPDH(a), ACON-1(e),[a] PGM-2(c), LDH-1(f),[a] LDH-2(b)
7	IDH-1(e), GOT-1(e), SOD(j)
8	PGDH(g), MPI(d), HK-1(b), LDH-2(a)
9	GDA(a)
10	PGM-2(g)
11	GOT-1(d), Ald(d), GP-2(c), CP-3(a), LDH-1(e)[a]
12	IDH-1(a), GOT-1(c), ACON-1(a), LA-2(h)
13	GOT-1(i)
14	IDH-1(f), ACON-1(i),[a] PGM-1(c), PGM-2(f), Est-1(d)
15	LDH-1(c), PGDH(g), PGM-2(g)
16	GAPDH(a), ACON-1(h), SOD(c)
17	Ndh(i), Est-1(c)
18	GDA[a](e)
19	LA-2(f)
20	GP-2(a)

[a] Characters in which the plesiomorphic state could not be determined.

nants of relationship. A case in point is the red upper-tail coverts of *Emblema picta*, *E. guttata*, and *Aegintha temporalis*, which have been used to unite these species in a single genus (McKean 1975). This grouping, however, is clearly polyphyletic (Figs. 1–3).

The electrophoretic results also demonstrate that the Lonchurae are a monophyletic assemblage and include *Amadina*. Guttinger (1976) and Goodwin (1982) contended that *Amadina* was a specialized offshoot of the Estrildae because it shared several morphological and behavioral traits (song and nestling mouth markings) with *Pytilia*. Such similarities, however, are evidently convergent or parallelisms. The genera *Chloebia* and *Erythrura*, moreover, are sister members of the Lonchurae and not related to *Poephila* (Delacour 1943). The closeness of *Chloebia* and *Erythrura* (Fig. 1) is consistent with the views of Mitchell (1958) and Schodde and McKean (1976) that the former is an arid-adapted representative of rain forest–inhabiting *Erythrura*. In this assemblage, only *Lonchura* as presently constituted is paraphyletic. In particular, *L. pectoralis* and *L. bicolor* are separate from each other and from the rest of the genus, a distinction consistent with their behavior (Guttinger 1976).

Apart from *Amandava*, the species of Estrildae examined here have always been grouped together. Harrison (1961) believed that *Amandava* was a specialized derivative of the Lonchurae, while Wolters (1957, 1981) saw similarities in behavior and plumage patterns between *Amandava* and poephiline *Aegintha*. Neither view is supported by the protein data, which demonstrate conclusively that *Amandava* is a member of the Estrildae.

The electrophoretic results can also be used to provide relative time scales of divergence. According to the calibration of the avian "molecular clock" by Gutiérrez et al. (1983), most estrildid genera diverged about 8 million years ago and the three underlying tribes about 14 million years ago. Based on an incomplete and depauperate fossil record, however, the average age of most passerine genera is 3.75 million years (Romer 1966, Prager and Wilson 1980). Given the large discrepancy between the protein and fossil time scales—a factor of 2—the accuracy of the latter must be questioned seriously. Here a combination of protein electrophoresis with other corroborative data sets such as DNA-DNA hybridization, microcomplement fixation, and mitochondrial DNA sequence analysis has the potential to provide much more accurate estimates of times of divergence among passerine taxa.

Relationships among the Estrildidae, Ploceidae, Fringillidae, and Emberizidae.—In attempting to determine an outgroup for the Estrildidae, three related families were examined (Fig. 4). The phenogram supports the current view that the Ploceidae and Estrildidae are more closely related to one another than they are to any other group (Bock 1960, Sibley 1970, Bock and Morony 1978). This is substantiated further by the low overall genetic distance of 0.63 (Table 3) between the ploceids and estrildids compared with the average of 1.0 across avian families in general (Avise and Aquadro 1982: fig. 2). However, the placing of *Passer* in the Ploceidae was questioned by Pocock (1966) and Sibley (1970), who argued in favor of fringillid affinities. The electrophoretic data do not support such a conclusion (Fig. 4); instead they show that *Passer* is allied to other ploceids and the Estrildidae, corroborating the results of DNA-DNA hybridization (Sibley and Ahlquist 1985).

The relationships between Old World and New World seed-eating oscines have been controversial, centering on whether similarities in the bony palate are due to monophyly (Tordoff 1954, Mayr 1955) or reflect convergence resulting from similar feeding strategies (Bock 1960, Raikow 1978). Although my electrophoretic data are limited, they are relevant to these questions. First, there is a clear separation between the ploceid-estrildid and the fringillid-emberizid assemblages. The similarity between the Fringillidae and Emberizidae is surprisingly high

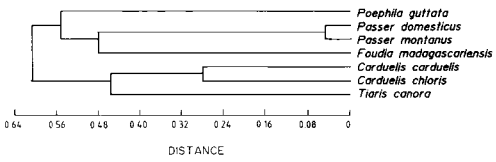

Fig. 4. UPGMA of the relationships between the Estrildidae (*Poephila guttata*), Ploceidae (*Passer domesticus, P. montanus,* and *Foudia madagascariensis*), Fringillidae (*Caraduelis chloris* and *C. carduelis*), and Emberizidae (*Tiaris canora*).

[Nei's (1978) $\bar{D} = 0.46$; see Table 4] and consistent with the classification of Mayr and Amadon (1951), who treated them as subfamilies within the Fringillidae. Second, the separation between Estrildidae-Ploecidae and Fringillidae-Emberizidae (Table 4) is not as great as would be expected if the two groups were unrelated (Bock 1960). On the other hand, affinity between these two assemblages is corroborated by DNA-DNA hybridization data (Sibley and Ahlquist 1985). Thus, the similar palatine processes in these four families may be homologous and evidence for monophyly, and are not convergent as argued by Bock (1960, 1963). The average Nei (1978) distance among the four families is only 0.59, which indicates that they are close phylogenetically. Before their phylogeny can be placed in context among other passerines, however, further work is required on such families as the Nectariinidae, Alaudidae, and Motacillidae. According to evidence from DNA-DNA hybridization (Sibley and Ahlquist 1985), these three families form a natural assemblage with the Ploceidae, Estrildidae, Fringillidae, and Emberizidae. The results of my study clearly indicate that multilocus protein electrophoresis could make a significant contribution in examining the affinities within this assemblage.

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APPENDIX. Species examined, sample sizes, localities, and genetic variability measures.

Species	Abbreviation	Locality[a] (sample size)	Percentage of loci polymorphic[b]	Mean heterozygosity
Estrildidae				
Poephila guttata	PGU	A (15)	21.1	0.053
P. bichenovii bichenovii	PBI	A (4), C (6)	15.8	0.016
P. b. annulosa	PAN	B (3)	5.3	0.026
P. acuticauda	PAC	A (8), B (9)	26.3	0.062
P. cincta	PCI	A (4)	18.4	0.059
P. personata	PPE	A (2), B (2)	7.9	0.026
Aidemosyne modesta	AMO	A (5)	18.4	0.058
Aegintha temporalis	ATE	A (5), C (2)	15.8	0.041
Emblema guttata	EGU	A (4)	13.2	0.046
E. picta	EPI	A (3)	10.5	0.440
Neochmia ruficauda	NRU	A (9), B (16)	26.3	0.011
N. phaeton	NPH	B (5)	10.5	0.037
Chloebia gouldiae	CGO	A (6)	10.5	0.013
Erythrura trichroa	ETR	A (3)	2.6	0.009
Lonchura pectoralis	LPE	A (1), B (11)	13.2	0.015
L. flaviprymna	LFL	A (3), B (1)	2.6	0.013
L. malacca atricapilla	LAT	A (2)	2.6	0.013
L. maja	LMA	A (1)	0.0	0.000
L. castaneothorax	LCA	A (4), B (5)	15.8	0.012
L. bicolor	LBI	A (2)	2.6	0.013
Amadina fasciata	AFA	A (4)	2.6	0.000
A. erythrocephala	AER	A (4)	5.3	0.013
Amandava subflava	ASU	A (3)	5.3	0.018
A. amandava	AAM	A (1)	0.0	0.000
Estrilda astrild	EAS	A (3)	2.6	0.000
Uraeginthus bengalus	UBE	A (3)	7.4	0.044
Lagonosticta senegala	LSE	A (3)	5.3	0.009
Pytilia melba	PME	A (5)	5.3	0.011
P. phoenicoptera	PPH	A (6)	2.6	0.000
Ploceidae				
Passer domesticus	PDO	C (16)	13.2	0.023
P. montanus	PMO	D (3)	7.9	0.018
Foudia madagascariensis	FMA	A (2)	0.0	0.000
Fringillidae				
Carduelis carduelis	CCA	D (2)	2.6	0.009
C. chloris	CCH	D (2)	5.3	0.026
Emberizidae				
Tiaris canora	TCA	A (3)	5.3	0.018

[a] A = aviary stock; B = Fitzroy River region, northwestern Australia; C = Australian Capital Territory region; D = Melbourne, Australia.
[b] A locus was considered polymorphic if the frequency of the most common allele did not exceed 0.99.