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SKELETAL CHARACTERS AND THE SYSTEMATICS OF ESTRILDID FINCHES (AVES: ESTRILDIDAE)

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ABSTRACT. The family Estrildidae contains 108 to 140 species arranged in 15 to 40 genera and two to nine tribes or subfamilies. In this study 401 skeletons belonging to 103 species and 27 genera were compared, as well as 75 skeletons of 15 genera of possibly related forms; skeletal characters add to the existing characters of behavioral, external anatomical, and molecular features. Best skeletal characters for generic separation were shape of the caudal basibranchial and a combination (PCA) of mensural characters. *Pholidornis* is not an estrildid. The classification of Goodwin (1982) was affirmed with these changes: Tribes should be dropped. The genus *Lepidopygia* should be lumped in *Lonchura*. Additional taxonomic changes are cautiously suggested.

Keywords: Wax-billed finches, Africa, Australia, southern Asia, Indo-Pacific islands

The finches studied here have variously been called waxbills, grass finches, manikins, munias, etc. They inhabit Africa, Australia, southern Asia, and the Indo-Pacific islands, and have been widely kept and studied in aviaries worldwide. From 108–140 species of Estrildidae, arranged in 15–40 genera, are recognized by recent authorities. Three tribes (or subfamilies) are usually recognized, although several genera have been moved back and forth amongst those tribes. External anatomy (including patterns of mouth spotting in nestlings), behavioral patterns, presence or absence of nessoptiles, appendicular myology, chromosomal configurations, and chemical analysis of proteins and DNA (both nuclear and ribosomal) have been used as characters for classification of species, genera, and tribes. Biochemical studies were those of Kakizawa & Watada (1985), Christidis (1987), Sorenson & Payne (2001, 2002), Payne & Sorenson (2003), Sorenson et al. (2004), and Van der Meij et al. (2005). The addition of a set of skeletal characters should help clarify relationships.

Complete classifications which may be called modern were these: Delacour (1943) recognized 15 genera and 108 species, grouping them into three tribes, Estrildae, Poephilae, and Lonchurae. (Hereafter, these tribal names are more correctly spelled Estrildini, Poephilini, and Lonchurini.) Wolters (1957) recognized 31 genera. Steiner (1960) recognized 9 tribes and 33 genera. Mayr (1968) recognized 25 genera, but did not list every species; he utilized Delacour's three tribes, but moved four genera to different tribes. Mayr, Paynter & Traylor (1968) recognized three tribes and 27 genera. Goodwin (1982) recognized 27 genera and 132 species—not quite the same genera as in Mayr et al., for he split one of their genera (*Lonchura*) and lumped another (*Padda*); he did not explicitly recognize tribes. Sibley & Monroe (1990) recognized 29 genera, although they mentioned as generic characters only the DNA work of Sibley & Ahlquist (1990) on three genera and four species and the protein electrophoresis work of Christidis on 16 genera. In a series of papers, Sorenson & Payne (2001, 2002), Payne & Sorenson (2003), and Sorenson et al. (2004), using mitrochondrial DNA, studied 74 species and 26 genera (also 12 more genera they recognized, but which Goodwin 1982 did not). Sorenson et al. (2004) grouped the family into two major clades, a primarily African one (= Estrildini) and a primarily Australasian one (= Poephelini and Lonchurini); the former they divided into three clades and the latter into two or three in their next two steps.

Systematic studies at the generic level but omitting several genera included: Wolters (1950, 1966) reviewed the African genera. Güttinger (1970) revised *Lonchura* using behavioral characters. Ziswiler, Güttinger & Bregulla (1972) revised *Erythrura* using behavioral and external anatomic characters. Güttinger (1976) reviewed two genera using behavioral characters. Bentz (1979) studied 23 genera using appendicular muscle characters. (Bentz raised the taxonomic level of the three tribes to subfamilies.) Kakizawa & Watada (1985) studied protein electrophoresis of 20 genera; they reduced the number of tribes from three to two, lumping Poephilini with Lonchurini. Christidis (1986, 1987) studied the chromosomes and proteins of 16 genera; he recognized the three tribes but moved *Aidemosyne* to a different one. Baptista et al. (1999) studied seven genera using protein eletrophoresis, palate markings of nestlings, neossoptile distribution, bill shape, and six behavioral characters; they split *Lonchura* into two genera, lumped *Padda* into one of these, and moved *Amadina* from Lonchurini to Estrildini. Schodde & Mason (1999) reclassified the 20 Australian species into eight genera; they lumped *Aegintha*, *Aidemosyne*, *Chloebia*, and *Padda* into various genera, but split *Emblema* into two genera (*Emblema* and *Stagonopleura*) and *Poephila* into two genera (*Poephila* and *Taeniopygia*). Also, they split *Heteromunia* off from *Lonchura*. Van der Meij et al. (2005) studied 12 genera using mitochondrial and nuclear DNA.

Many workers have investigated the relationships of the Estrildidae to other major suprageneric groups. Sibley & Ahlquist (1990) gave a thorough summary. Sushkin (1927) concluded that the waxbills were most closely related to the whydahs (*Vidua*), but belonged as a subfamily in the Ploceidae. Tordoff (1954) on the basis of skull characters placed the Estrildinae in the Ploceidae, near the Carduelinae. Friedmann (1960, 1962) concurred with Sushkin. Ziswiler (1967) studied the structure of the alimentary canal of various seed-eating birds (including two species of whydahs and nine species of eight genera of estrildids). He found estrildids uniform among themselves and distant from Ploceidae (including Viduinae) and Fringillidae. Foelix (1970) studied the salivary glands of seed-eating birds (not including any whydahs); he found the estrildids uniform among themselves and distinct from Ploceidae and Fringillidae. Ziswiler (1979) from a study of the stiffening devices of the tongue confirmed his earlier position that the Emberizidae, Ploceidae, and Estrildidae had evolved the seed-eating adaptation separately. Christidis (1986, 1987) on the basis of chromosome and protein electrophoresis work placed the estrildids closer to the Ploceidae than to any other group. Sibley & Ahlquist (1990) and Sibley & Monroe (1990) on the basis of their DNA studies placed the estrildids and whydahs (two species studied) in one subfamily of Passeridae and the sparrows and weavers in other subfamilies. Cramp & Perrins (1994) characterized the Estrildidae, Passeridae, and Ploceidae, placing the Bubalornithinae in Ploceidae and Viduinae in Estrildidae. Schodde & Mason (1999) included several skeletal characters in their characterization of Estrildidae. Sorenson & Payne (2001, 2004) on the basis of mitochrondrial DNA studies, concluded that the estrildids and viduins had evolved together, separate from the ploceids and passerids. Lahti & Payne (2003), followed by Fry & Keith (2004) moved *Anomalospiza* from Ploceidae to Estrildidae, Viduinae, on the basis of anatomy and behavior, concluding that it was a fairly close relative of *Vidua*.

From all of the literature review above, one poorly-known genus, *Pholidornis*, which has sometimes been placed in Estrildidae, has been excluded (Traylor 1968, Vernon & Dean 1975, Sefc et al. 2003).

METHODS

Skeletons of 401 individuals belonging to 103 species and 27 genera of Estrildidae were examined. In addition, 23 skeletons of eight species of Viduinae and 52 skeletons of 22 species of 13 genera of Ploceidae (two genera of Bubalornithinae, five of Passerinae, and six of Ploceinae) were compared. The classification of Goodwin (1982) is used in this paper for Estrildidae except where otherwise stated. Outside Estrildidae, the classification of Moreau & Greenway (1962) in *Check-list of Birds of the World* is used, except for the genera *Pholidornis* and *Anomalospiza*.

Fifty-one characters (measurements, ratios between measurements, and shapes of bony parts) were tabulated for each specimen. Of course, as a result of broken or missing bones or my inadvertence, a few data on some specimens were not recorded. On arithmetical characters the figure used for a species is a mean of the specimens measured. Of these, 20 characters were arithmetical and complete enough to be used in a principal components

Table 1.—Best generic characters observed in Estrildidae. For explanation, see text, pages 92–94.

Genus	Caudal basibranchial shape: D = depressed, N = not depressed	Maxillary process of nasal shape: A = broad & heavy, B = moderately broad, C = fairly slender, D = slender	Transpalatine process shape: length/width	Palatine process pre-maxilla: O = absent, sf = slight flange, f = broad flange, —extra process: 0 = absent, number = width	Pneumotricipital fossa: See text page 94	Parasphenoidal rostrum keel: P = prominent, S = slight, R = absent, N = not observed	Tibiotarsus length measured: (mm)
Parmoptila	N	C	3.8	O & sf—0	A&E&F	S&P	20.3
Nigrita	D or N	B&C	3.0–7.3	sf&f—0–0.3	A&F&DO	S	21.8–25.0
Nesocharis	Not	B&C&D	2.8–3.0	sf&f—0–0.3	A&E&F	N	19.0–23.8
Pytilia	D or N	B&C	1.3–1.8	f—0–0.2	A&F	S	22.9–24.3
Mandingoa	N	A&B&C	2.2	f—0.2	A&F	N	22.5
Cryptospiza	N	B&C	2.0–2.6	f—0.05–0.2	A&F	P	25.0–25.9
Pyrenestes	N	A	1.0–1.6	f—0.1–0.2	A&E&F	R	25.0–27.8
Spermophaga	N	A&B	1.2–1.5	f—0.05–0.2	A&E&F&DO	S&R	28.9–29.8
Clytospiza	N	C	1.3	f—0	A&E&DT	S	25.0
Hypargos	D or N	B&C	1.3	f—0	A&E	S	24.1
Euschistospiza	D or N	C&D	1.6	f—0.1	A	N	23.0
Lagonosticta	N	B&C	1.2–1.4	f—0–0.1	A&E&F	S&P	18.2–21.1
Uraeginthus	D or N	C&D	1.2–1.8	f—0–0.2	A&E&F	S&P	21.0–24.8
Estrilda	N	B&C&D	1.3–3.8	f—0–0.2	A&E&F&DO	S	18.9–21.3
Amandava	N	B&C&D	1.2–2.1	f—0–0.1	A&E&F	S&P	17.4–21.6
Ortygospiza	D or N	C&D	1.5–2.4	f—0.2	A&E&F	S&R&P	20.2–20.6
Aegintha	N	C	1.6	f—0.05	A	N	22.4
Emblema	D or N	A&B&C&D	0.8–3.5	f—0–0.2	A&F&DT	S&R	20.7–25.7
Neochmia	D or N	A&C	1.0–1.2	f—0.1–0.2	A&E&F	S&P	20.9–21.9
Poephila	D or N	B&C	0.4–0.9	f—0.1–0.2	A&F&DO	S&P	20.2–22.7
Erythrura	D or N	A&B&C	2.0–4.5	f—0.1–0.2	A&E&F&DO	S&R&P	21.7–24.6
Chloebia	D or N	A&B&C	2.2	f—0.2	E&F	S&P	22.9
Aidemosyne	D	C	1.0	f—0.2	A	P	22.0
Lonchura	D or N	A&B&C&D	0.7–3.0	f—0–0.2	A&E&F	P	19.0–26.7
(Padda)	D	A&B&C	1.6–1.8	f—0–0.1	A&E&F	P	26.2–27.8
Lepidopygia	N	B&C	2.2	f—0.1	A&F	P	18.4
Amadina	N	C	1.1–1.3	f—0.1	A&E&F	P	23.2–24.6

analysis (PCA) ordination for the 127 species (Table 2 and Figs. 1–14). All data were converted to ranks to avoid problems associated with distributions of ratios and lack of normality and to give all variables equal weight. Analyses were performed using PC-ORD (MjM Software 2002).

The specimens and species examined are listed in Appendix 1. The 35 species and one genus not studied are listed in Appendix 2. One taxon (*Estrilda melanotis quartinia*) which was listed as a subspecies by Goodwin (1982) was analyzed separately because it was recognized as a full species by Sibley & Monroe (1990) and Fry & Keith (2004). Eight more taxa split as full species by Sibley & Monroe but lumped as subspecies by Goodwin (1982) were not examined, nor were five more species added by Payne & Sorenson (2004) and Fry & Keith (2004).

Ortygospiza (= *Paludipasser*) *locustella* could not be studied because no skeleton exists in the world's museums (Wood & Schnell 1986). The only one listed by Wood & Schnell could not be found in the Brodkorb collection.

GENERA OF ESTRILDIDAE

The following 15 characters provided the best separation of genera. See Table 1 for a convenient comparison. *Padda* is included for convenience, but it was reduced to a subgenus by Goodwin (1982). They are arranged below

Table 1.—Extended.

Skull length measured: (mm)	Interorbital septum: C = completely ossified, S = small gap, L = large gap, N = not observed	Ectethmoid foramina: D = double, P = pinched, S = single, T = triple. Lateral/medial	Interpalatine process: 0 = absent length/width	Tarsometatarsus shape: length/width	Compression of rostral basibranchial: height/width	Fusion of mediopalatines: % fused	Premaxilla shape: length/width
15.6	C&S&L	D&P 1.1	0.2	9.6	3.0	40	1.9
16.0–18.4	C&S&L	D&P&T 1.3–1.8	0.3–1.7	8.6–9.1	2.2–3.0	27–62	1.4–1.6
13.8–18.4	S	D&P 2.0	0–1.0	9.6–9.9	3.1–3.2	25–100	1.3–1.6
16.2–17.0	C&S	D&P 1.3–3.3	0.2–1.2	8.2–9.4	2.2–2.7	25–58	1.5–1.7
16.6	C	D 2.1	0.2	8.3	3.2	90	1.6
17.5–17.6	C&S&L	D 1.8–1.9	0	10.0–10.2	3.5	29–42	1.6–1.7
18.6–21.0	C	P&S 6.0–14.0	0	8.2–9.4	4.0–4.9	0	1.1–1.2
19.6–21.2	C&S&L	D&P&S&T 3.7–4.5	0.2–0.3	9.4–9.8	3.8–4.2	0–5	1.4–1.5
17.2	C&L	D&P 1.6	0.8	9.2	3.0	66	1.5
17.3	C	D&P 1.3	0.2	8.9	3.6	0	1.4
16.8	N	P&S 1.3	0.8	8.9	2.8	23	1.8
14.5–16.2	C&S&L	P&S 1.0–2.0	0.5–2.5	8.5–9.2	2.1–3.5	10–50	1.3–1.7
15.3–17.0	C&S&L	D&P&S 1.0–1.2	0.2–2.0	9.1–9.8	2.1–3.3	15–75	1.4–1.6
14.0–15.4	C&S&L	D&P 1.6–5.7	0–1.0	9.5–11.1	2.3–3.4	15–100	1.4–1.7
13.0–15.2	C&S&L	D&P&S&T 1.3–1.7	0.4–1.2	8.6–10.1	2.5–2.8	33–58	1.4–1.5
13.8–15.1	C&S&L	D&P&S 1.0–1.7	0.7–1.0	9.0–9.4	2.5–3.0	18–25	1.2–1.4
15.5	C&S	D&P&T 2.3	0	9.8	3.3	86	1.3
15.6–17.4	C&S&L	D&P 1.5–4.0	0.4–2.5	8.7–9.6	3.0–3.4	16–50	1.2–1.7
15.8–16.2	C&S&L	D&T 4.5–7.0	0.4–1.8	8.6–8.7	3.1–3.7	22–61	1.3–1.4
15.0–16.4	C&S&L	D&P 1.9–4.2	0–0.4	8.6–9.8	2.3–3.7	33–94	1.3–1.4
16.6–18.0	C&S&L	D 1.1–2.3	0	7.6–9.3	2.5–4.1	30–88	1.3–1.6
15.9	C&S	D 2.0	0.1	7.8	3.5	60	1.2
15.6	L	D 1.9	0.3	9.1	3.2	65	1.3
13.3–18.8	C&S&L	D&P&S 1.3–10.0	0–1.6	8.1–10.9	2.7–4.6	30–100	1.0–1.7
18.3–19.5	C&S&L	D&P 4.0–6.8	0.8–1.8	8.3–9.0	4.1–4.5	50–60	1.4–1.6
13.8	C	P 2.5	0	9.3	3.3	62	1.2
17.2–18.3	C&L	D&P&T 2.7–3.3	0.6–1.5	7.8	2.9–3.3	10–43	1.3–1.4

in approximately their order of usefulness—that is, the order in which they separate the most genera.

(1) *Shape of caudal basibranchial:* The basilbranchial (= urohyal) was flattened dorsoventrally (depressed) in some species, but slender, not depressed, in others.

(2) *Shape of maxillary process of nasal:* It was only broad and heavy or some broad and heavy and some moderately broad, in *Pyrenestes*, *Spermophaga*, *Erythrura trichroa* (one of the seven species in the genus), and two of the 29 species of *Lonchura*.

(3) *Shape of transpalatine process:* The transpalatine process, at the latero-caudal corner of the palatine bone, was measured as the ratio of its length over its width. It was elongated, 3.3 or more, in *Parmoptila*, two species of *Nigrita*, two species of *Estrilda*, *Emblema oculatum*, and *Erythrura prasina*. It was blunt, under 1.6, in eight genera and parts of eight more.

(4) *Palatine process of premaxilla:* The palatine process of the premaxilla was present as a lateral flange (except in one specimen of *Parmoptila*), but with no suture evident between it and the palatine bone (Tordoff 1954; Bock 1960). Often an additional extension, or process, was present, extending caudally from the lateral edge of the process; sometimes this additional process was as long as 0.3 of the width of the entire lateral flange plus palatine

at that point. The lateral flange was small or slight in *Parmoptila* (absent in one specimen), two species of *Nigrita*, *Nesocharis shelleyi*, and in one specimen of *Clytospiza*; in all other species it was broad. The additional process was lacking in three genera and some specimens or species of 19 more genera.

(5) *Pneumo-tricipital fossa:* The pneumotricipital fossa of the humerus was always double, and usually combined. The various shapes were categorized as they were for Icteridae (Webster 2003): A—Combined dorsal and ventral fossae equally deep, bottom translucent, separation by medial bar incomplete. F—Dorsal and ventral fossae equally deep, but a low, rounded ridge extends distally from the internal tuberosity clear across, separating the fossae. DT—Dorsal and ventral fossae equally deep and translucent-bottomed, but a prominent partition or medial bar extends distally from the internal tuberosity, separating the fossae. E—Dorsal fossa opaque-bottomed, 70–90% as deep as the translucent-bottomed ventral fossa; separation between the fossae a step-down. DO—As in E, but dorsal fossa only 40–60% as deep as the ventral fossa. Only two specimens (of *Clytospiza* and *Emblema guttatum*) were DT.

(6) *Ventral surface of parasphenoidal rostrum:* The base of the parasphenoidal rostrum bore a narrow ventral keel (Sushkin 1927) in some specimens.

(7) *Tibiotarsus length.*

(8) *Skull length:* Measurement was from the caudal end of the external nare. Maximum was 21.2 mm in *Spermophaga ruficapilla*; minimum was 13.0 in *Amandava subflava.*

(9) *Interorbital septum.*

(10) *Ectethmoid foramina:* The ectethmoid (= orbitonasal) foramina were single, pinched, double, or in a few cases triple. However, these divisions were rather erratic within genera or even within species. The relative size of these foramina was fairly consistent within species and genera; it was recorded as size of the lateral foramen over the medial foramen. This was not clear in individuals with a single foramen; if triple foramina were present, the two lateral ones were added together as the numerator.

(11) *Interpalatine process:* The interpalatine process varied from absent to well-developed. It was absent or only a slight bump in five genera and in three species of *Estrilda*, *Poephila bichenovii*, and eight species of *Lonchura*. All other species showed a well-developed process; the maximum of 2.5 was in *Lagonosticta nitidula* and *Emblema oculatum.*

(12) *Tarsometatarsus shape:* The tarsometatarsus varied in stoutness.

(13) *Compression of rostral basibranchial:* The rostral basibranchial (basihyal) was invariably compressed, but the degree of compression (ratio of height to width at the midpoint) varied. This character was omitted from the PCA because so many specimens (all specimens of seven species) lacked the bone.

(14) *Fusion of mediopalatines:* The dorsal walls of the choanal fossa of the paired palatine bones (= mediopalatines) were fused or sutured together in the midline for part (usually) or all of their length, except in *Pyrenestes* and *Hypargos* and a few scattered specimens (no entire species) in other genera. The condition was recorded as the percentage of the length fused (or sutured) of the length where the paired palatines were close to the midline.

(15) *Shape of premaxilla:* The premaxillae varied in their taper, measured as length over width at the caudal end of the external nares. (Of course with the rhamphotheca removed.)

Principal component analysis.—A summary is in Table 2, showing factor loadings. Seven of the best intergeneric chracters are omitted because they are not quantitative (six) or lack complete data (one). On the PCA figures, axis 1 is heavily weighted to long bone ratios between wing and leg—positive correlation to humerus/femur and ulna/tarsometatarsus and negative correlation to tibiotarsus/humerus and tibiotarsus/ulna. Thus species positive on this axis have relatively long wings and short legs; negative values are the opposite. Axis 2 is heavily weighted positively to more slender humerus and broader cranium and negatively to larger lateral ectethmoid foramen and longer postorbital process. Axis 3 is heavily weighted to skull length and tibiotarsus length (measurements of total size); negative values are bigger species.

The following 12 additional characters showed consistency within species, but individually provided only a little in the way of intergeneric variation, or generic characters (all of them were used in the PCA analysis, along with eight of the nine arithmetical characters already discussed): (1) ratio of cranium

Table 2.—Principal component analysis of rank transformed data.

Variable	PC Axis 1	PC Axis 2	PC Axis 3
Skull length	0.071	0.094	−0.554
Premaxilla length/width	0.020	0.293	−0.041
Cranium width/interorbital width	0.061	0.368	0.132
Tibiotarsus length/ulna length	−0.392	−0.040	−0.100
Tibiotarsus length/humerus length	−0.381	−0.127	−0.026
Tibiotarsus length/femur length	−0.234	0.016	0.124
Ulna length/femur length	0.297	0.064	0.186
Humerus length/femur length	0.305	0.193	0.183
Length/width of interpalatine process	0.050	0.080	−0.344
Length/width of transpalatine process	−0.058	0.095	0.158
Length/width of zygomatic process	0.139	−0.245	0.008
Tarsometatarsus length/femur length	−0.265	0.218	0.155
Length/width of tarsometatarsus	−0.337	0.059	0.164
Tarsometatarsus length/skull length	−0.231	0.296	−0.042
Ectethmoid foramina	−0.117	−0.380	−0.083
Ulna length/tarsometatarsus length	0.394	−0.097	0.028
Postorbital process	−0.080	−0.312	−0.130
Mediopalatines joining	−0.083	−0.255	0.213
Tibiotarsus length	0.006	0.107	−0.558
Humerus length/width	−0.108	0.411	−0.027
Eigenvalue	5.668	3.682	2.294
Variance explained	0.283	0.184	0.115
Cumulative variance explained	0.283	0.468	0.582

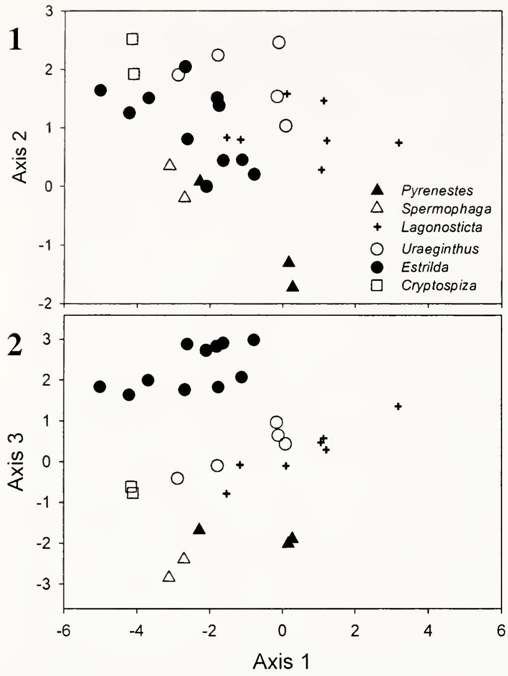
width–interorbital width, (2) shape of the zygomatic process of the squamosal bone, (3) relative length of the postorbital process, (4) ratio of tibiotarsus length–ulna length, (5) ratio of tibiotarsus length–humerus length, (6) ratio of tibiotarsus length–femur length, (7) ratio of ulna length–femur length, (8) ratio of ulna length–tarsomatatarsus length, (9) ratio of humerus length–femur length, (10) ratio of tarsometarsus length–femur length, (11) ratio of tarsometatarsus length–skull length, (112) ratio of humerus length–width.

The PCA analysis (Table 2 and Figs. 1–10) shows these points of generic similarities and differences: *Nesocharis* is very close to *Parmoptila* on both Figs. 1 and 2, but those genera are far from the close cluster of *Nigrita* in both figures. *Cryptospiza*, *Mandingoa*, and *Spermophaga* are the only genera of Estrildini which are separate from all others on all Figs. 1–6. *Estrilda*, *Uraeginthus*, and *Lagonosticta* are separate from one another on Fig. 4, but not on Fig. 3. *Spermophaga* is close to *Pyrenestes*, especially *P. minor*, on both Figs. 3, 4. The twinspots, *Clytospiza*, *Hypargos*, and *Euschistospiza*, but not *Mandingoa*, are close to one another in Figs. 5, 6. *Ortygospiza* is not close to *Amandava* on either Fig. 5 or 6, and the three species of *Amandava* are not well clustered on either figure. *Pytilia* is rather widely split, with *P. melba* far from the other three species in both Figs. 1, 2. *Estrilda* is well clustered, despite the large number of species, in both Figs. 3, 4.

The genera *Aegintha*, *Emblema*, *Neochmia*, and *Poephila* (= *Poephilini*) are all separate from one another in Fig. 8. In Fig. 7, *Aegintha* is within *Emblema* and *Emblema* partly overlaps *Poephila*. *Emblema* is radically split in both figures, with *E. guttatum* and *E. pictum* close to one another and *Poephila* and *E. oculatum* and *E. bellum* near or around *Aegintha*. All five species of *Poephila* are grouped together in both figures. *Aidemosyne* is close to *Neochmia* in both figures.

The genus *Lonchura* is well clustered for such a large group in Fig. 9, and *Aidemosyne* is within it; *Lonchura*, *Padda*, *Erythrura*, *Chloebia*, and *Amadina* are separate from one another, although *Chloebia* is near *Erythrura*. In Fig. 10 of the same genera, *Chloebia* and *Amadina* are separate from the others and each other, but *Aidemosyne*, *Padda* and *Erythrura* overlap *Lonchura*; *Amadina* is outside all the other genera of Estrildidae and not particularly close to any of them on both Figs. 9, 10 and the complete figures (Figs. 11 and 12, where not labeled).

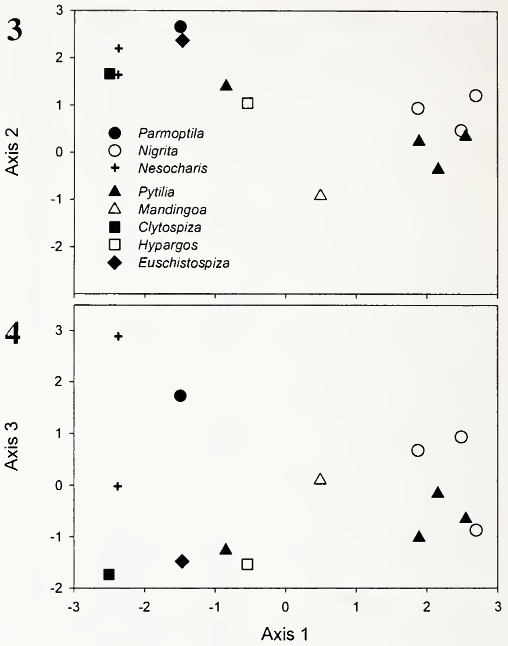
Unused characters.—Twenty-four more characters were tabulated for each specimen, but then abandoned. Of these, nine were too inconsistent within species to be useful: Shape of the lateral margin of the ectethmoid plate, size of the supraotic fenestra, relative lengths



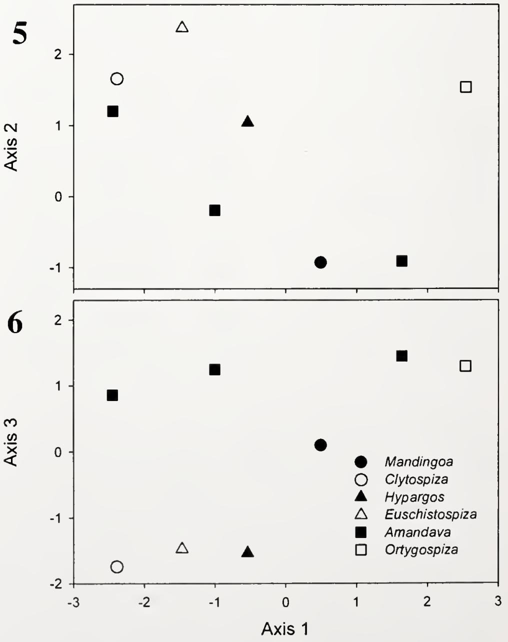
Figures 1, 2.—Results of a principal components analysis (PCA) of 127 species of Estrildidae and Ploceidae, but with all but 6 genera removed. Axis 1 is heavily weighted to long bone ratios between wing and leg. Axis 2 is heavily weighted to certain skull and humerus proportions. Axis 3 is heavily weighted to measurements of total size in mm.

of the metatarsal trochleae, shape of the maxillopalatine bones, shape of the internal (= medial) process of the mandible, presence and nature of the Pocock foramina (Pocock 1966), the degree of the distal bend of the tarsometatarsus, degree of the medial curve of the rostral palatine, and presence and shape of a manubrium-sternum bridge.

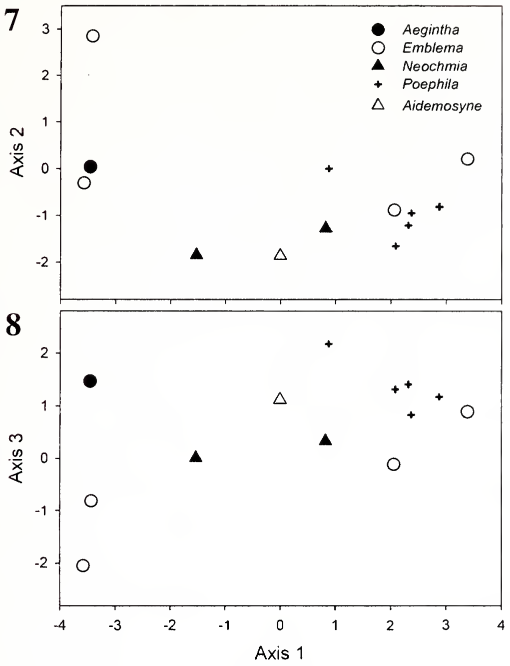
Fifteen characters showed too little variation within the family—were too consistent—to be useful: Degree of ossification of the nasal septum, degree of ossification of the nasal conchs, presence or absence of a horizontal flange of the nasal septum (= floor of the nasal capsule), rostral palatines twisted or not, shape of orbital process of quadrate bone, shape of retroarticular process of mandible, completeness of rostral palate, shape of process 7b of mandible, shape of pseudotemporal process of mandible, presence or absence of a free lacrimal bone, degree of fusion of pterygoid-palatine junction, ratio of ulna length: humerus length, ratio of tibiotarsus length: tar-



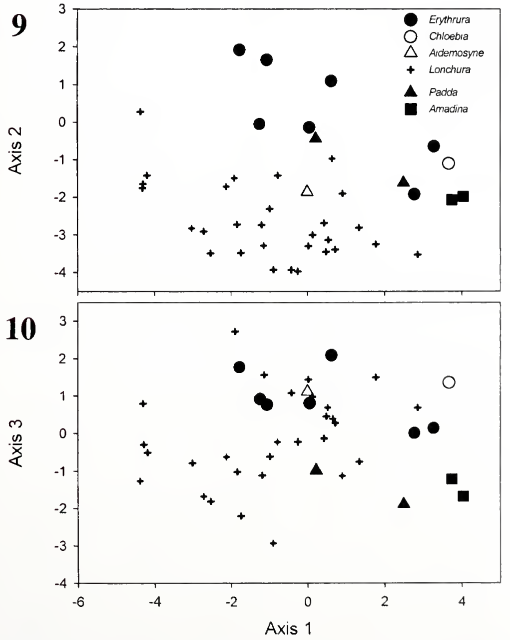
Figures 3, 4.—Results of PCA of 134 species of Estrildidae and Ploceidae, but with all but eight genera removed. Axes as in Figures 1 and 2.



Figures 5, 6.—Results of PCA of 134 species of Estrildidae and Ploceidae, but with all but six genera removed. Axes as in Figures 1 and 2.



Figures 7, 8.—Results of PCA of 134 species of Estrildidae and Ploceidae, but with all but five genera removed. Axes as in Figures 1 and 2.



Figures 9, 10.—Results of PCA of 134 species of Estrildidae and Ploceidae, but with all but six genera removed. Axes as in Figures 1 and 2.

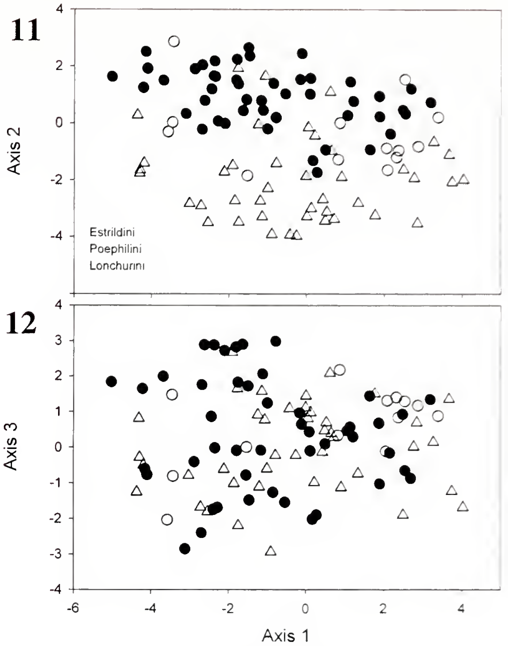
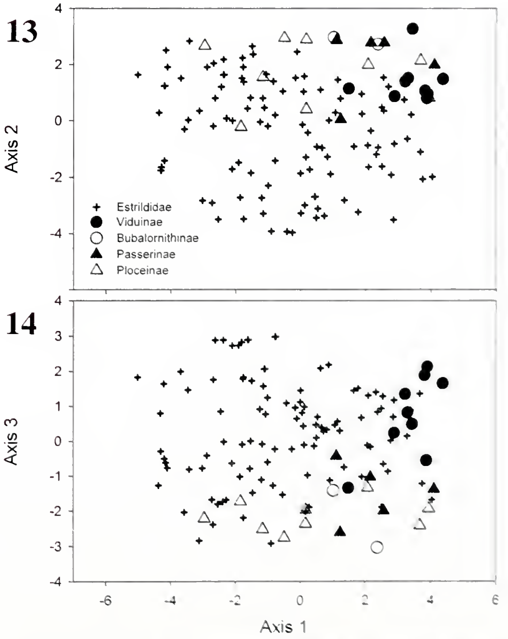
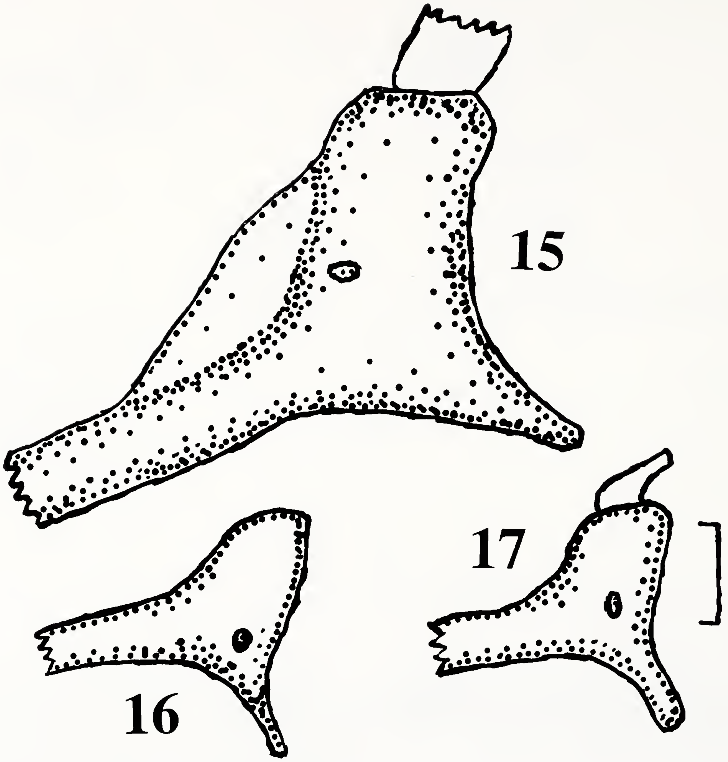


Figure 11, 12.—Results of PCA of 134 species of Estrildidae and Ploceidae, but with the Ploceidae removed, leaving only the 103 species of Estrildidae to compare supposed tribes. Axes as in Figures 1 and 2.



Figures 13, 14.—Results of PCA of 134 species of Estrildidae and Ploceidae, complete. Axes as in Figures 1 and 2.



Figures 15–17.—15. *Poephila guttata*, CAS90110; 16. *Passer domesticus*, HA3059; 17. *Vidua fischeri*, MI217526. Right lateral views of the rostral end of the vomer. Rostral to the right, dorsal up in each case. All are drawn with the aid of a camera lucida to the same scale, the 1 mm scale beside 17. In Figs. 15 and 17 the unstippled dorsal projection is a nasal conch fused to the vomer. The smallest species of the three has much the largest vomer.

sometatarsus length, degree of squamosal inflation, shape and size of the rostral end of the vomer.

Boundary of *Lonchura*.—Because there have been so many taxonomists who have split the large genus *Lonchura*, but in a variety of ways, it was analyzed in detail for the 51 tabulated osteological characters (including *Lepidopygia*). For these the maximum and minimum one or two species within the genus were recorded; if three or more tied, it was recorded as no extreme. Altogether, 24 of the 29 examined species were extreme for one or more characters. There were no extremes for 15 characters; there was either no minimum or no maximum extreme for 12 more characters.

Results were: Extreme on nine characters—*Lonchura cantans*. Extreme on seven characters—*L. vana*, *L. monticola*. Extreme on six characters—*L. melaena*. Extreme on four characters—*L. striata*. Extreme on three characters—*L. cucullata*, *L. nevermanni*, *L. teerinki*, *L. pectoralis*. Extreme on two characters—*L. griseicapilla*, *L. bicolor*, *L. fringilloides*, *L. grandis*, *L. hunsteini*, *L. leucosticta*, *L. fuscans*, *L. spectabilis*, *L. flaviprymna*. Extreme on one character—*Lepidopygia nana*, *L. leucogastroides*, *L. tristissima*, *L. malacca*, *L. caniceps*.

The genus *Padda* has been lumped with *Lonchura* by several workers (Delacour 1943; Goodwin 1982; Baptista et al. 1999; Schodde & Mason 1999). When compared with the 29 species of *Lonchura* for the 51 osteological characters, there were these results: both species of *Padda* were beyond the variation in *Lonchura* on three characters. *Padda fuscata* was beyond the variation in *Lonchura* when *Padda oryzivora* was not in three more characters. *Padda oryzivora* was beyond the variation in *Lonchura* when *Padda fuscata* was not in three more characters. The three characters in which both species of *Padda* were outside *Lonchura* were ratio of humerus length to femur length, ratio of ulna length to femur length and caudal basibranchial shape. It is concluded that osteological characters indicate the same as external structural characters—*Padda* may either be retained as a weakly characterized genus or lumped as a subgenus within *Lonchura*.

In the same way, *Euodice*, a subgenus in the Goodwin (1982) classification, was compared with the variation in *Lonchura*. The two species examined, *L. cantans* and *L. griseicapilla*, were not both outside the variation in the rest of *Lonchura* on any character. Similarly, *Spermestes*, another subgenus in the Goodwin (1982) classification, was compared. The three species, *Lonchura cucullata*, *L. bicolor*, and *L. fringilloides* were outside the variation in the rest of *Lonchura* on only one character (shape of the zygomatic process). On two other characters, all but *fringilloides* were outside. As noted above, *Lepidopygia nana* was outside *Lonchura* variation on only one character, length of tibiotarsus. *Lonchura pectoralis* has been split from the large genus as a montypic genus *Heteromunia* by several workers. On osteological characters, then, *Lepidopygia*, *Spermestes* and *Euodice* are not valid genera; and *Heteromunia* is but weakly separate.

Other genera which are weakly characterized on the basis of their skeletons are *Aegintha* (from *Emblema*), *Chloebia* (from *Erythrura*), and *Mandingoa* (from *Pytilia*). Two genera, *Pytilia* and *Emblema*, seem composite osteologically. There is some osteological evidence for the lumping of *Clytospiza*, *Hypargos*, and *Euschistospiza* as Goodwin (1982) suggested.

SUPRAGENERIC TAXA

Tribes.—The Family Estrildidae was divided into three tribes by Delacour (1943) and these were recognized by most subsequent workers. Osteological data don't support a division of the family into three tribes or into two tribes, much less their elevation into subfamilies. In fact, the most distinct groups osteologically (See Table 1) are *Pyrenestes* (with *Spermophaga*) and *Parmoptila* (with *Nesocharis* and *Nigrita*). The PCA (Figs. 11, 12) shows on Fig. 11 about ⅓ of Estrildini overlapping ⅓ of Lonchurini, with both of those tribes mostly overlapping Poephilini. In Fig. 12 there is nearly complete overlap of all three tribes. Different tribal placement of *Amadina* and *Aidemosyne* does not change this point.

Subfamilies.—Osteological data are equivocal as to whether the Viduinae belong in Estrildidae or Ploceidae or in a separate family by themselves. Seven species (21 specimens) of *Vidua* (the whydahs and indigo birds) and two specimens of *Anomalospiza imberbis* (the Cuckoo Finch) were examined, with the results in comparison to the Estrildidae presented in Table 3.

Only the first two characters in Table 3 show consistent differences between Estrildidae and the other two genera. The next five characters show *Anomalospiza* within Estrildid variation, but some or all *Vidua* outside. The last three characters show *Vidua* within Estrildid variation but *Anomalospiza* outside, as noted by Lahti & Payne (2003). Those authors also noted a large median groove in the premaxilla. This observation in *Anomalospiza* is confirmed but not enough Estrildidae were compared with rhamphotheca removed. (Most of the specimens of Estrildidae had been returned to their owners before this comparison.) Not a large enough series of skeletons of any species was examined to speak to their character of delayed pneumatization of the skull.

In summary, *Vidua* and *Anomalospiza* are each more distinct from the 26 genera of estrildids on osteological characters than is any genus within that group except, perhaps, *Pyrenestes*. However, *Vidua* and *Anomalospiza* bear about the same weight of osteological distinction from the other subfamilies of Ploceidae as they do from Estrildidae.

Families.—Sushkin (1927) listed skeletal differences between the Estrildidae (excluding Viduinae) and Ploceidae (Bubalornitinae, Passerinae, and Ploceinae). Findings in this more extensive study are listed in Table 4, with an asterisk (*) marking that mentioned by Sushkin. Only the first character is consistent: the other 11 show some overlap. Presumably the large vomer in Estrildidae functions in seed hulling (Figs. 15–17; *cf* Ziswiler 1979).

Eight more family-differentiating characters mentioned by Sushkin (1927) were found useless. In seven of these Sushkin did not realize the variability within Estrildidae because he

Table 3.—Subfamily characters.

Character	Estrildinae (or Estrildidae)	Viduinae	
		Anomalospiza	*Vidua*
Vomer (Figs. 15–17)	Large, horns broad	Small, horns narrow	Small, horns broad or narrow
Pseudotemporal process of mandible	More ventral	More dorsal	More dorsal
Humerus length: femur length	0.9–1.1	1.1	1.2
Ectethmoid foramina, lateral: dorsal	1.0–14.0	—	0.4–3.8
Tibiotarsus length: ulna length	1.2–1.6	1.3	1.1–1.2
Tibiotarsus length: humerus length	1.4–1.9	1.5	1.3–1.4
Process 7b of mandible	Smaller, sloping except 3% flat-topped	Smaller, sloping	Smaller, sloping except 19% flat-topped and larger in one
Manubrium-sternum bridge	Absent, minute, or small	Very large	Absent or minute
Rostral end of pterygoid	Not expanded except slightly in *Pyrenestes*	Large, heavy, expanded	Not expanded
Caudal end of jugal	Not expanded	Expanded	Not expanded

Table 4.—Family characters. Viduinae excluded. *Noted in Suskin (1927).

Character	Estrilidae	Ploceidae (Bubalornithinae, Passerinae, and Ploceinae)
Vomer (Figs. 15–17)	Large; horns long and broad	Small; horns usually short and narrow
Rostral palatines	Twisted 90°–120°	Not twisted (12 species) or twisted (eight species)
Palatine process of premaxilla (Tordoff 1954, Bock 1960)	Lateral flange, usually prominent	Not a flange, often separated by a suture (12 species) or slight flange (seven species) or prominent flange (one species)
Lateral wall of nasal capsule*	Not ossified	Bone in seven species of four genera
Lateral ectethmoid foramen: medial foramen	1–14, usually high	0.3–9.5, usually low
Interpalatine process, length: width	0–2.5, often absent	0.8–5.2, usually long
Postorbital process of squamosal	0.3–0.7 of way to jugal arch	0.1–0.3 except *Euplectes* 0.4
Pseudotemporal process of mandible	0.4–1.8, usually below 1.0	0.8–4.7, usually over 1.0
Pneumotricipital fossa of humerus	A, E, F, DO, or DT; 3% DO or DT	A, E, F, DO, DT, or DS; 31% DO or DT or DS
Tibiotarsus length: tarsometatarsus length	1.3–1.7	1.3–1.5
Tibiotarsus length	17.4–29.8 mm	23.7–46.0 mm (eight of 20 species over 29.8)
Skull length	13.0–21.2 mm	17.3–27.4 mm (10 of 20 species over 21.2)

lacked specimens of *Parmoptila*, *Nigrita*, *Nesocharis*, and several other genera. These characters were: position of the club of the maxillopalatine, medial curvature of the rostral palatine, length of the interpalatine space, position of the palatal crests, shape of the rostral end of the vomer in ventral view, nature of the pterygoid-palatine joint, and size or presence of an interorbital fontanel. One character mentioned by Sushkin, the constriction of the rostral palatine in its caudal region in a direct ventral view is better expressed as the twist of the bone at that point, as described by Tordoff (1954) and above. The actual relative width of the palatine at that point varies little from species to species.

Schodde & Mason (1999) included five skeletal characters in their characterization of the family Estrildidae. Of these, three are evidently the same as those listed above, although the terminology is different. One was noted, but not tabulated—"vestigially toothed mandibular angle." One, "vestigial maxillopalatine process," was too variable within Estrildidae, even within species, to be useful.

The PCA figures show a broad overlap between Estrildidae and Ploceidae (four subfamilies, with *Anomalospiza* in Viduinae) in Fig. 14 and a lesser overlap between Estrildidae and Ploceidae of three of these subfamilies (Passerinae, Viduinae, and Bubalornithinae) in Fig. 13.

In five more tabulated characters there was some difference in a few species between Estrildidae and Ploceidae, but there were large areas of overlap: size of the retroarticular process of the mandible, shape of the caudal basibranchial, presence and size of a manubrium-sternum bridge, ratio of tarsometatarsus length to skull length, and ratio of humerus length to femur length.

DISCUSSION

Traylor (1968) put *Pholidornis rushiae* (Cassin) in Estrildidae as a genus *incertae sedis*. Apparently there is no complete skeleton in the world's museums (Wood & Schnell 1986), but the lone skull in the British Museum was examined. It is certainly not an estrildid; it exceeds the variation in that family on 11 of the 26 tabulated osteologic characters of the skull. The premaxilla is too long and slender, there is no palatine process of the premaxilla, there is no bone in the nasal septum, the vomer bears no horns, and the rostral palatines aren't twisted, etc. However, with neither a hyoid or a humerus a more specific family identification is unwise. Sefc et al. (2003) placed *Pholidornis* in the Sylvioidea, close to Cisticolidae.

The small, slender, rostral tongue bone figured by Ziswiler (1979) and called hypentoglossum in Estrildidae was not clear in most dried skeletons. It was clear, however, in a few specimens of four different genera. No doubt its presence or absence must be ascertained in fresh or spirit-preserved material for an analysis.

Schodde & Mason (1999) revised the genera of Australian Estrildidae. They put *Aegintha* into *Neochmia*, segregated *Emblema bellum*, *E. oculatum*, and *E. guttatum* into *Stagonopleura*, and left *E. pictum* as the only species in *Emblema*. Also they moved *Aidemosyne* into *Neochima* and split *Poephila* into *Taeniopygia* with *guttata* and *bichenovii*, leaving *Poephila* including only *P. personata*, *P. acuticauda*, and *P. cincta*. *Chloebia* they lumped into *Erythrura*. Of these changes, osteologic characters do not agree with their disposition of *Aegintha*—rather it should be put in *Stagonopleura*. *Emblema guttatum* should be left in *Emblema*, which would then require changing the name *Stagonopleura* to *Zonaeginthus*. The placement of *Aidemosyne* in *Neochmia* agrees with osteology. The split of *Poephila* is quite unnecessary—the five species form a close group on osteologic evidence. The placement of *Chloebia within Erythrara* is equivocal on osteologic characters. Moving of the genus *Amadina* to a position within the almost strictly African Estrildini as advocated by Walters (1957), Goodwin (1982), Baptista et al. (1999), and Fry & Keith (2004) is neither supported nor denied by osteologic data.

Evolutionary history within Estrildidae has been studied by several workers. Delacour (1943) and Steiner (1960) nominated *Clytospiza* as most like an ancestral form. Mayr (1968) was not explicit, but seemed inclined toward either *Clytospiza* or *Parmoptila* as nearest an ancestral form. Goodwin (1982) suggested that *Amandava* was probably nearest to an ancestral estrildid. Of the several molecular studies (Kakizawa & Watada 1985; Christidis 1987; Baptista et al. 1999; Sorenson & Payne 2001, 2002; Payne & Sorenson

2003; Sorenson et al. 2004; Van der Meij et al. 2005) only Sorenson & Payne studied nearly all of the genera and a majority of the species. All of these workers found an ancient divergence between the African Estrildini and the primarily Australasian Lonchurini plus Poephelini. However, Kakizawa & Watada found Australasian *Erythrura* and *Chloebia* within the African group, and Christidis found African *Amadina* within the Australasian group, near *Lonchura*. Sorenson & Payne (2001, 2002) found *Ortygospiza locustella* (= *Paludipasser locustella*) distinct and representing a group ancestral to all other estrildids. (That species was examined by none of the other molecular workers nor was a skeleton available for this study.)

The recent treatment of Estrildidae by Sorenson & Payne (2001, 2002), Payne & Sorenson (2003), and Sorenson et al. (2004) should be compared with this work. Actually, there are only these distinct differences: (1) There are no skeletal data on *Paludipasser* (= *Ortygospiza*) *locustella* to compare. (2) They recognize 13 more genera than this work, including a split of *Lonchura* into six genera; most of these were subgenera in the Goodwin (1982) scheme.

Relationships of *Vidua* and *Anomalospiza* to Estrildidae have been variously hypothesized. Most systematists who have studied the question—Chapin (1917, 1929, 1954), Sushkin (1927), Delacour (1943), Tordoff (1954), Wolters (1957, 1960), Friedman (1960, 1962), Bentz (1979), Sibley & Ahlquist (1990), Lahti & Payne (2003), and Fry & Keith (2004)—placed the whydahs closer to their hosts, the waxbills, than to any other systematic group. On the other hand, Beecher (1953), Steiner (1960), Nicolai (1964), Ziswiler (1967), Mayr (1968), Mayr et al. (1968), and Goodwin (1982) placed the whydahs closer to one or another ploceid group than to the waxbills. Recent studies of *Anomalospiza* by Sorenson & Payne (2001) and Lahti & Payne (2003) placed that genus close to *Vidua*. Cramp & Perrins (1994) and Fry & Keith (2004) separated Passeridae as a separate family from Ploceidae.

The family Estrildidae is a relatively homogenous group on osteologic characters, contrasting with Emberizinae (Webster & Webster 1999) and Icteridae (Webster 2003) in this respect. No taxonomic changes in the arrangement in Goodwin (1982) above the species level are recommended except the deletion of *Pholidornis*, the dropping of tribes, and the lumping of *Lepidopygia* with *Lonchura*. Probably, also, the genera *Clytospiza* and *Euschistospiza* should be united with *Hypargos* following the suggestion by Goodwin (1982). Probably the genus *Zonaeginthus* should be recognized to include *Emblema bellum*, *Emblema oculatum*, and *Aegintha temporalis*. Probably *Aidemosyne modesta* should be transferred to *Neochmia*. Recognition of the genera *Padda* and *Heteromunia* (splits from *Lonchura* not recognized by Goodwin (1982) are equivocal, as is the lumping of *Chloebia* with *Erythrura*. Whether the subfamily Viduinae should be transferred from Ploceidae to Estrildidae or segregated as a separate family is not clarified by osteology.

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Appendix 1.

Specimens examined. Museum designations: AM, American Museum of Natural History. CAS, California Academy of Sciences. CM, Carnegie Museum of Natural History. FL, Florida State Museum. FM, Field Museum of Natural History. HA, Hanover College. KS, University of Kansas Museum of Natural History. LAC, Los Angeles County Museum. LSU, Louisiana State Museum of Science. MI, University of Michigan Museum of Zoology. RO, Royal Ontario Museum. BM, The Natural History of Museum of the United Kingdom. US, United States National Museum. YP, Peabody Museum of Natural History of Yale University.

Estrildidae:

Parmoptila woodhousei, 5 FM385327, US292451, US292452, BM S/1980. 6.2, AM24935
Nigrita fusconota, 4 FM313270, FM3835328, US322542, US292481
Nigrita bicolor, 3 US 347578, US292479, US292480
Nigrita canicapila, 5 FM356422, KS70888, US291136, US292478, YP9410
Nesocharis shelleyi, 2 US318625, US318626
Nesocharis capistrata, 1 MI201774
Pytilia phoenicoptera, 3 AM12715, AM12829, BM S/1966. 39.20
Pytilia hypogrammica, 3 AM12268, AM14084, AM16495

Appendix 1.

Continued.

Pytilia afra, 3 AM12346, AM12660, AM12347
Pytilia melba, 5 US430316, US429100, US558781, LAC89770, LAC89768
Mandingoa nititula, 6 AM13700, AM13698, AM13701, MI1214380, MI207779, BM1981.82.2
Cryptospiza reichenovii, 2 BM S/1992.27.1, S/992.27.2
Cryptospiza salvadorii, 5 FM356455, FM356459, FM356458, KS70941, KS70942
Pyrenestes sanguineus, 4 AM13696, AM13759, AM13697, BM S/1993.38:1
Pyrenestes ostrinus, 4 AM12686, AM17105, AM17104, MI232532
Pyrenestes minor, 2 MI214379, MI214378
Spermophaga haematina, 6 US347593, US322435, US322434, CAS71723, MI2221317, MI1221316
Spermophaga ruficapilla, 4 MI223525, MI208342, US499894, YP13765
Clytospiza monteiri, 4 MI201775, MI201776, MI232533, AM24947
Hypargos niveoguttatus, 4 CAS71724, AM11819, KS80654, CAS71724
Euschistospiza dybowskii, 3 AM14260, AM14261, AM14263
Lagonostica rara, 3 CAS71727, CAS71726, CAS71727

Appendix 1.

Continued.

Lagonostica rufopicta, 4 AM14304, AM14046, MI221300, MI221308

Lagonostica nitidula, 2 MI203301, BM S/958.19.1

Lagonosticta senegala, 4 US430652, US502062, CAS83508, CAS71730

Lagonostica rubricata, 6 CAS84857, AM14082, AM13205, AM13204, BMS/1986.75.26, BM S/5.24

Lagonosticta rhodopareia, 3 US430676, US430807, BM S/1982.77.3

Lagonosticta larvata, 3 AM14135, MI221311, MI221312

Uraeginthus angolensis, 5 US558782, US431594, US430001, BM S/1982.136.5, BM S/982.136.2.

Uraeginthus bengalus, 5 CAS71738, CAS85089, LAC89787, LAC89790, YP9272

Uraeginthus cyanocephalus, 4 AM8759, AM8809, AM8767, CAS90061

Uraeginthus granatina, 6 CAS71734, MI222633, MI220363, MI233565, BM S/1991.1.27, BMS/991.1.28

Uraeginthus ianthinogaster, 4 AM11915, AM'12086, AM12087, BM S/1987.23.15

Estrilda caerulescens, 4 CAS42861, US347286, US557890, CAS42861

Estrilda perreini, 1 BM S/1962.18.1

Estrilda melanotis, 3 MI218669, CAS90031, CAS90030

Estrilda melanotis quartinia, 1 MI218670

Estrilda paludicola, 3 FM362222, FM362221 FM362220

Estrilda melpoda, 4 CAS71735, MI223530, MI223531, BM 1891.7.20.188

Estrilda rhodopyga, 3 AM11812, AM11832, CAS90074

Estrilda troglodytes, 5 AM11829, AM11818, AM12173, BM S/1966.39.10, BM S/1966.39.8

Estrilda astrild, 5 US490778, US490874, US490779, BM S/1990.3.3, BM S/1990.3.2

Estrilda nonnula, 3 LAC89798, LAC90692, LAC89800

Estrilda atricapilla, 3 FM385352, FM358204, FM313281

Estrilda erythronota, 4 CAS71422, MI222628, MI233264, CAS90073

Amandava amandava, 6 US556164, US5556156, FM96103, CAS90068, CAS90026, BM S/1962.12.2

Amandava formosa, 3 LAC90694, FM106437, BM S/1986.75.38

Amandava subflava, 5 US322525, US432034, US322505, KS31150, CAS90027

Appendix 1.

Continued.

Ortygospiza atricollis, 5 AM1410, AM14141, AM14138, BM S/1998.48.73, CAS90105

Ortygospiza species, 2 BM S/1967.5.1, FL31619 (incomplete data, measured by Auth)

Aegintha temporalis, 5 MI204457, MI205437, MI205436, FM105467, FM105492

Emblema pictum, 6 CAS57594, CAS60370, AM12831, AM11814, BM S/1954.7.1, CAS60371

Emblema bellum, 3 RO186380, RO136166, RO136378

Emblema oculatum, 2 FM104083, FL31621 (incomplete data, measured by Auth)

Emblema guttatum, 6 CAS84574, CAS57637, AM10737, AM10331, BM1867.7.8.16, BM1865.5.20.13

Neochmia phaeton, 4 CAS60372, AM12964, AM12966, BM S/1998.48.52

Neochmia ruficauda, 4 CAS83891, CAS71740, BM S/1984.28.1, CAS71738

Poephila guttata, 8 MI220494, MI205109, MI219070, KS83369, KS83322, KS80636, CAS90110, CAS90058

Poephila bichenovii, 4 US620269, US343821, US620270, BM S/1983.129.1

Poephila personata, 5 MI205599, MI205598, MI119233, FM104058, FM96083

Poephila acuticauda, 5 US345241, US354284, US344878, BM S/1984.28.10, BM S/1984.28.11

Poephila cincta, 5 CAS43603, MI119234, FM96152, FM105362, KS80879

Erythrura hyperthra, 4 CAS85132, AM11846, AM11844, BM S/1984.27.1

Erythrura prasina, 6 US344594, US344497, US614130, CAS71753, BM S/1989.2543, BM S/1987.23.20

Erythrura viridifacies, 3 BM S/1982.104.1, BM S/1983.133.1, BM S/1984.30.1

Erythrura trichroa, 5 MI210799, MI209458, MI210798, FM104454, FM104172

Erythrura psittacea, 5 CAS48970, MI221643, MI220930, KS80964, KS80963

Erythrura tricolor, 2 CAS90129, CAS No #

Erythrura pealii, 4 CAS42707, CAS90118, BM S/1993.16.4, FL31650 (incomplete data, measured by Auth)

Chloebia gouldiae, 7 US321161, US501540, CAS71477, CAS84820, BM S/1954.1.1, BM S/1981.91.2, CAS60949

Aidemosyne modesta, 3 CAS57865, MI205612, MI205613

Lepidopygia nana, 2 MI208433, BM1897.5.10.48

Appendix 1.

Continued.

Lonchura cantans, 3 AM12913, AM11994, AM12263
Lonchura griseicapilla, 5 CAS85726, FM362202, FM362201, KS70556, KS70524
Lonchura cucullata, 3 US556170, US556174, US556076
Lonchura bicolor, 3 US347586, US347587, US347585
Lonchura fringilloides, 3 LSU160452, LSU111948, AM16453
Lonchura striata, 5 CAS84020, CAS85461, FM315110, FM104099, CAS71540
Lonchura leucogastroides, 3 CAS85105, CAS85712, BM S/1985.32.1
Lonchura fuscans, 2 KS41000, KS41118
Lonchura molucca, 5 US557491, US557484, US557485, US557489, US557483
Lonchura punctulata, 4 CAS85727, MI235135, MI207365, LAC89840
Lonchura leucogastra, 3 MI206402, MI206399, MI206401
Lonchura tristissima, 5 MI21585, LSU101032, YP9000, YP8999, YP8998
Lonchura leucosticta, 3 AM12832, AM11796, AM12834
Lonchura quinticolor, 4 CAS85108, CAS90081, CAS90050, CAS90049
Lonchura malacca, 4 KS31144, KS41357, CAS84904, CAS No #
Lonchura maja, 4 CAS85109, CAS85728, US345468, US344591
Lonchura grandis, 3 LSU101033, YP8977, YP8978
Lonchura vana, 1 KS41113
Lonchura caniceps, 4 LAC89850, LAC89849, FM290944, YP6190
Lonchura nevermanni, 3 AM12948, AM12657, AM11835
Lonchura spectabilis, 7 CAS85111, KS81180, US489252, US289250, YP8987, YP8991, YP8985
Lonchura hunsteini, 3 LSU85929, LSU86921, LSU86928
Lonchura flaviprymna, 3 FM105853, FM105901, FM314884
Lonchura castaneothorax, 4 CAS85309, FM343031, FM96143, CAS90080
Lonchura teerinki, 2 CAS90147, CAS90159
Lonchura monticola, 1 AM5820
Lonchura melaena, 1 BM S/1961.11.48
Lonchura pectoralis, 5 AM12906, MI214327, KS83207, CM7240, CM7242
(Padda) fuscata, 3 CAS85729, CAS90085, CAS90059
(Padda) oryzivora, 4 CAS58654, CAS71539, CAS85747, CAS85314

Appendix 1.

Continued.

Amadina erythrocephala, 4 US429108, US429109, US429107, BM S/2003.4.3
Amadina fasciata, 8 CAS85625, CAS85536, AM11963, AM11965, LAC89852, LAC102979, YP102898, YP103284

Hyliidae:

Pholidornis rushiae, 1 BM 1930.12.3.11

Ploceidae, Viduinae:

Vidua chalybeata, 3 MI222621, MI218102, MI222620
Vidua funerea, 2 CM9573, CM9571
Vidua funerea purpurascens, 2 MI223739, MI223738
Vidua fischeri, 3 BM S/1993.30.1, MI217526, MI212960
Vidua regia, 2 MI204760, MI222615
Vidua macroura, 2 MI212961, MI136012
Vidua paradisaea, 5 MI222619, MI224501, RON149481, RON126721, BM 1982.54.1
Vidua orientalis, 2 CAR9570, CAR9569
Anomalospiza imberbis, 2 MI217511, MI219072

Ploceidae, Bubalornithinae:

Bubalornis albirostris, 2 RON156913, US430787
Dinemiellia dinemelli, 2 KS70745, KS70744

Ploceidae, Passerinae:

Plocepasser mahali, 1 KS70632
Pseudonigrita arnaudi, 2 CM7266, CM7267
Passer domesticus, 9 HA3056, HA3059, HA3205, records lost of 6
Passer montanus, 1 MI119071
Petronia xanthocollis, 2 KS70447, KS70773
Sporopipes frontalis, 4 KS70628, YP13245, YP13250, US490719

Ploceidae, Ploceinae:

Amblyospiza albifrons, 3 CM789, CM785, US322509
Ploceus ocularis, 2 RO114496, RO114466
Ploceus melanogaster, 1 KS71003
Ploceus cucullatus, 5 YP9413, YP7500, MI221231, MI221191, MI221216
Ploceus philippinus, 1 YP9828
Malimbus rubricollis, 2 YP9412, YP9411
Malimbus malimbicus, 1 US291132
Malimbus rubriceps, 2 RO114571, RO114577
Quelea quelea, 7 RO12076, RO120766, MI219934, MI219943, MI219949, MI219953, MI219958
Foudia madagascariensis, 1 US432205
Euplectes orix, 2 CM1575, CM16514
Euplectes ardens, 2 KS71020, KS71019

Appendix 2.

Species of Estrildidae whose skeletons were not studied. An asterisk (*) means that no skeleton exists in the world's museums, according to Wood & Schnell (1986). Thirteen species recognized by various recent workers but not by Goodwin (1982) are included.

Parmoptila rubrifrons
*Nigrita luteifrons**
*Nesocharis ansorgei**
Pytilia lineata
Cryptospiza jacksoni
*Cryptospiza shelleyi**
Spermophaga poliogenys
Hypargos margaritatus
Euschistospiza cinereovinacea
*Lagonsticta landanae**
Lagonosticta virata
Lagonosticta vinacea
Estrilda thomensis
Estrilda rufibarba
*Estrilda nigriloris**
*Estrilda charmosyna**
Estrilda polioparia
Estrilda kandti
*Ortygospiza gabonensis**
*Ortygospiza locustella**
*Oreostruthus fuliginosus**
*Erythrura coloria**
Erythrura papuana
Erythrura regia
*Erythrura kleinschmidti**
Erythrura cyaneovirens
Lonchura malabarica
Lonchura nigriceps
Lonchura kelaarti
Lonchura ferruginosa
*Lonchura pallida**
Lonchura forbesi
Lonchura nigerrima
Lonchura stygia
*Lonchura montana**