SKELETONS AND THE GENERA OF SPARROWS (EMBERIZINAE)

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Abstract.—Based on comparisons of skeletons from 228 species of sparrows (Emberizinae), we detected 24 characters that were useful for generic separations. Of these, 19 quantitative characters were used in a detrended correspondence analysis (DCA) ordination. Presence or absence of a lacrimal bone, degree of inflation of the squamosal area, length of the lateral process of the laterosphenoid, ratio of ulna length to femur length, length of the skull, and premaxilla length-to-width ratio were the most informative characters. The first two axes of the DCA clearly grouped most genera. Based on our analysis of these skeletal characters, we recommend the following changes to the classification of Paynter (1970): *Sporophila obscura* belongs in *Tiaris; Emberizoides ypiranganus* is a valid species; *Pselliophorus* and *Pezopetes* should be lumped with *Atlapetes;* and *Torreornis* and *Oriturus* should be lumped with *Aimophila.* In addition, a different sequence of genera should be adopted. Two groups of genera are distinct: seedeaters and North American sparrows. A third group, South American grassland finches, overlaps with the first two groups. *Received 17 February 1998, accepted 15 March 1999.*

The subfamily Emberizinae constitutes a large (279 species in 65 genera) group of songbirds adapted for eating seeds during at least part of the year. Most species occur only in the Western Hemisphere, but two are Holarctic, and four genera are confined to the Eastern Hemisphere. The last comprehensive classification of the Emberizidae was by Sharpe (1888), although Ridgway (1901) characterized the North and Middle American forms and some of the South American genera. Hellmayr (1938) listed all of the Western Hemisphere forms, noting the characters of some genera. Vaurie (1959) and Cramp and Perrins (1994) reviewed the Eurasian species, and Meyer de Schauensee (1970a) and Ridgely and Tudor (1989) listed the South American species and provided characterizations. Hall and Moreau (1970) reviewed the African species. Paynter (1970) listed all of the forms and their geographic ranges in the most recent complete classification based on specimens, but he did not include characterizations; we follow his classification in this paper except where noted otherwise. Sibley and Monroe (1990) listed the genera and species with their ranges; they did not include characterizations, and their classification was based on DNA-DNA hybridization studies (Sibley and Ahlquist 1990) of 22 (34%) genera and 24 (9%) species. Sibley and Mon-

roe's most striking innovation was transferring 52 of the 65 genera (a group they called the "tanager finches") to the Thraupini (=Thraupinae of most authors) based on DNA evidence from only 9 of the 52 genera involved.

Comparative studies of the skeletal elements of emberizines were conducted by Parker (1878), Shufeldt (1888), Sushkin (1924), Linsdale (1928), Beecher (1953), Tordoff (1954), Berger (1957), Bock (1960, 1962), Bowman (1961), George (1962, 1968), Robins and Schnell (1971), Wolf (1977), Webster and Goff (1979), Steadman (1982), Zink (1982), Moreno (1984), Rising (1988), Webster (1993), and Patten and Fugate (1998). Of these studies, Tordoff's is based on the largest number of species. Bowman's (1961) study of the 14 Galapagos species is the most intensive skeletal study but does not include other species.

Overall, classification of the emberizine genera and species has been rather thoroughly studied for North American and European taxa. Knowledge of the systematics of Asian, South American, and some of the Middle American forms, however, is modest and poorly coordinated with that of the better-known groups. Here, we provide additional information on the skeletons of nearly all species of emberizines and suggest changes in current classification of emberizines where skeletal evidence is clear. For convenience and clarity, we

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have followed Paynter's classification (1970) throughout most of the paper.

MATERIALS AND METHODS

Our strategy was to be extensive rather than intensive. We tried to examine skeletons of all species of Emberizinae and their close relatives and were able to study 794 specimens of 228 species in 62 genera (Table 1). Thirty-nine of the 50 species and all three of the genera (i.e. *Latoucheornis, Oreothraupis, Charitospiza*) that we did not examine apparently do not exist in the world's museums (Wood and Schnell 1986). The species recognized by Paynter (1970) that we did not examine are listed in the Appendix 1. On each specimen we made 15 measurements (two of angles and 13 of distances) and 27 other observations. Thirty-nine characters were tabulated, 12 of these as ratios of two measurements. A few specimens were broken or incomplete, so all measurements could not be performed on some specimens.

We also examined the following skeletons that do not belong to Paynter's (1970) Emberizinae: Parulidae, 26 genera and 109 species; Thraupinae, 57 genera and 195 species; Tersininae, 1 species; Catamblyrhynchinae, 1 species; Cardinalinae, 8 genera and 22 species; Icteridae, 22 genera and 79 species; Fringillidae, 15 genera and 24 species.

Nineteen quantitative characters (Table 2) of the total 39 tabulated characters were used in a detrended correspondence analysis (DCA) ordination (Gauch 1982) for the 224 species for which we had complete data. The four omitted species for which our data were incomplete because of missing or broken bones were *Emberiza yessoensis, Incaspiza laeta, Camarhynchus pauper,* and *Atlapetes citrinellis.* The only quantitative character not included in the DCA was the degree of mobility of the craniofacial hinge. It was omitted because several more species would then have had to be omitted for lack of data, and variation between species and genera was slight. All data were converted to ranks to avoid problems associated with distributions of ratios and lack of normality (Atchley et al. 1976, Conover and Iman 1981). However, analyses of nontransformed data produced qualitatively similar results to those presented here. Analyses were performed using PC-ORD (McCune and Mefford 1997).

In nearly all of the emberizine genera we examined, a slender process projects rostro-ventrally from the lateral margin of the laterosphenoid bone into the orbital space. It does not seem to have been named (Baumel 1993); for convenience, we call it the lateroventral process of the laterosphenoid (Fig. 1).

RESULTS

Twenty-four characters proved useful for generic distinctions among the Emberizinae and are listed and described below.

1. *Lacrimal bone.*—A fairly clear distinction among the 228 species was provided by the presence or absence of a lacrimal bone. In all specimens of 42 genera, the lacrimal was not free, being either fused or absent (the fused and absent conditions usually were not distinguishable). Single specimens in each of five other genera (*Zonotrichia, Spizella, Aimophila, Pipilo,* and *Pezopetes*) showed a free lacrimal, which we consider to be unusual variants. In eight other genera, all from South or Central America or South Atlantic islands, a free lacrimal was always present (*Melanodera, Haplospiza, Acanthidops, Rowettia, Nesospiza, Lophospingus, Idiopsar,* and *Xenospingus*). In three other South American genera, the lacrimal usually was free, but it was missing in a few specimens that we judged had lost it postmortem (*Diuca, Gubernatrix, Paroaria*). In 2 of the 27 examined species of *Emberiza,* 4 of the 9 species of *Phrygilus,* 3 of the 10 species of *Poospiza,* and 2 of the 3 species of *Catamenia,* the lacrimal was present in the specimens examined but not in the other species of those genera. Presumably, these four genera are composite and diphyletic. The species in these four genera that have a free lacrimal are *Emberiza flaviventris, E. bruniceps, Phrygilus atriceps, P. gayi, P patagonicus, P. unicolor, Poospiza thoracica, P. lateralis, P. torquata, Catamenia analis,* and *C. inornata.*

2. *Inflation of the squamosal area.*—The squamosal area was described by Tordoff (1954) as an informative character. It is not peculiar to grassland species (as suggested by Tordoff), and Wolf (1977) was unable to relate the extreme inflation of *Aimophila* to function. We classified the specimens as did Tordoff (1954), and reached the same groupings that he did with a few exceptions (Appendix 2).

3. *Lateroventral process of laterosphenoid.*—The lateroventral process of the laterosphenoid (Fig. 1) was consistent in length in most species. In 38 genera it was always short, no more than 0.4 as long as the zygomatic process just lateral to it. In 13 genera it was always or nearly always long, 0.8 to 1.3 as long as the zygomatic process (*Calamospiza, Zonotrichia, Junco, Pooecetes* [moderate length in one specimen], *Chondestes* [moderate length in one specimen], *Torreornis, Oriturus, Pipilo, Melozone, Arremon* [moderate length in one specimen], *Atlapetes, Pezopetes, Pselliophorus*). In no genus was the process always of moderate size (0.5 to 0.7 as

TABLE 1. Taxa of Emberizinae recognized by Paynter (1970).

Genus	Total species	No. examined	No. not examined	No. specimens
Melophus	1	1	0	4
Latoucheornis	1	0	1	0
Emberiza	38	27	11	75
Calcarius	4	4	0	15
Plectrophenax	1	1	0	8
Calamospiza	1	1	0	5
Zonotrichia	9	9	0	53
Junco	3	3	0	14
Ammodramus	10	10	0	36
Spizella	6	6	0	28
Pooecetes	1	1	0	5
Chondestes	1	1	0	5
Amphispiza	2	2	0	9
Aimophila	2	13	1	37
Torreornis	1	1	0	5
Oriturus	1	1	0	5
Phrygilus	10	9	1	29
Melanodera	2	2	0	7
Haplospiza	2	2	0	11
Acanthidops	1	1	0	2
Lophospingus	2	2	0	9
Donacospiza	1	1	0	3
Rowettia	1	1	0	2
Nesospiza	2	1	1	1
Diuca	2	2	0	12
Idiopsar	1	1	0	2
Piezorhina	1	1	0	5
Xenospingus	1	1	0	3
Incaspiza	4	4	0	7
Poospiza	15	10	5	31
Sicalis	11	8	3	23
Emberizoides	1	2[a]	0	8
Embernagra	2	1	1	7
Volatinia	1	1	0	5
Sporophila	31	19	12	50
Oryzoborus	2	2	0	9
Amaurospiza	2	1	1	6
Melopyrrha	1	1	0	5
Dolospingus	1	1	0	1
Catamenia	4	3	1	10
Tiaris	4	4	0	13
Loxipasser	1	1	0	4
Loxigilla	3	3	0	10
Melanospiza	1	1	0	3
Geospiza	6	6	0	20
Camarhynchus	6	5	1	15
Certhidea	1	1	0	8
Pinaroloxias	1	1	0	9
Pipilo	7	7	0	30
Melozone	3	3	0	8
Arremon	5	4	1	13
Arremonops	4	3	1	11
Atlapetes	22	17	5	42
Pezopetes	1	1	0	7

TABLE 1. Continued.

Genus	Total species	No. examined	No. not examined	No. specimens
Oreothraupis	1	0	1	0
Pselliophorus	2	1	1	4
Lysurus	1	1	0	1
Urothraupis	1	1	0	1
Charitospiza	1	0	1	0
Coryphaspiza	1	1	0	1
Saltatricula	1	1	0	6
Gubernatrix	1	1	0	4
Coryphospingus	2	2	0	10
Rhodospingus	1	1	0	3
Paroaria	5	4	1	19
Totals	278	228	50	794

ᵃ Includes a recently described species (see Discussion).

long as the zygomatic process), but in 11 genera the process varied: *Calcarius* (always short except one specimen moderate); *Ammodramus* (six species long; *caudacutus* long and moderate; *savannarum, humeralis,* and *aurifrons* short); *Spizella* (*arborea* long; five species short); *Amphispiza* (*bilineata* long, *belli* long and short); *Aimophila* (nine species short, *stolzmanni* long and short, *ruficeps, notosticta,* and *rufescens* long); *Phrygilus* (eight species short, *patagonicus* long); *Oryzoborus* (*crassirostris* short, *angolensis* short, moderate, and long); *Loxigilla* (*portoricensis*

moderate, *violacea* long, *noctis* short); *Geospiza* (*magnirostris* moderate, five species short); *Camarhynchus* (four species short, *crassirostris* short to moderate); and *Gubernatrix* (short and moderate).

Several years ago, we supplied M. A. Patten with data on the lateroventral process of the laterosphenoid (LVP), which were published in Patten and Fugate (1998: appendix 1). We offer the following additions as a result of our study but do not correct some typographical errors: *Dolospingus fringilloides* (LVP short, 1 specimen

TABLE 2. Results of detrended correspondence analysis ordination. Values are the scores of the skeletal characters on each of the DCA axes. The bottom rows indicate the eigenvalues of the axes and coefficients of determination of the correlations comparing ordination distances between bird species and distances in the original data.

Variable	Axis 1	Axis 2	Axis 3
Skull length	4	−12	71
Premaxilla length:width	6	60	−98
Cranium width:interorbital width	25	−11	−165
Tibiotarsus length:ulna length	−106	67	91
Tibiotarsus length:humerus length	−73	138	108
Tibiotarsus length:femur length	90	255	58
Ulna length:humerus length	216	149	50
Ulna length:femur length	235	115	7
Humerus length:femur length	233	90	−16
Length:width of interpalatine process	17	−114	59
Length:width of transpalatine process	79	94	273
Length:width of zygomatic process	163	37	15
Length:width of retroarticular process of mandible	45	−4	−116
Length:width of pseudotemporal process of mandible	7	−62	164
Angle of internal tuberculum of humerus with shaft	150	32	165
Tarsometatarsus length:femur length	31	245	35
Tibiotarsus length:tarsometatarsus length	199	−99	91
Length:width of tarsometatarsus	−16	168	55
Tarsometatarsus length:skull length	−64	100	−10
Eigenvalue	0.125	0.046	0.027
Coefficient of determination	0.620	0.130	0.030
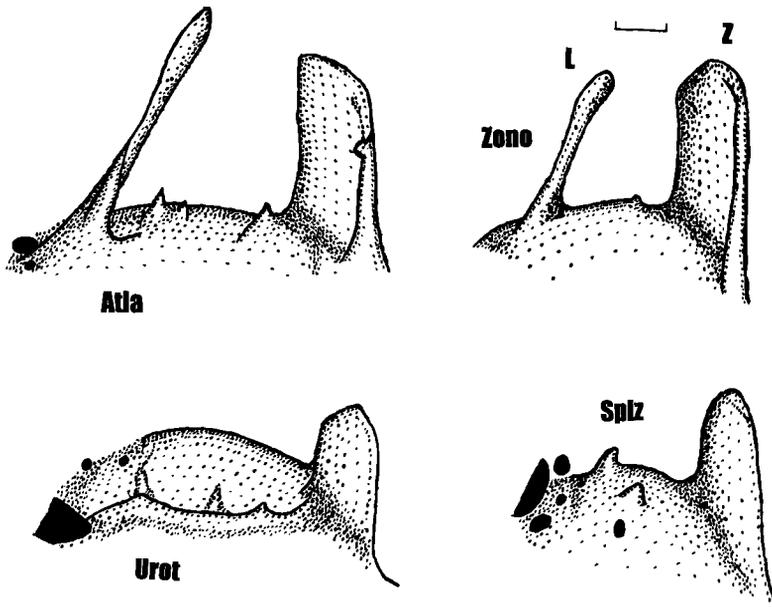
FIG. 1.   Camera lucida drawings of emberizid lateroventral process of the laterosphenoid. Atla = *Atlapetes pallidinucha* (LSUMNS 90178); Zono = *Zonotrichia albicollis* (UWZM 30588); Urot = *Urothraupis stolzmanni* (LSUMNS 84153); Spiz = *Spizella passerina* (UWZM 27252). L denotes the lateroventral process of the laterosphenoid, and Z denotes the zygomatic process of the squamosal. Each view is almost dorsal (slightly rostral and slightly lateral) and of the right side. The scale depicted above Zono is 1 mm and is the same for all drawings. The lateroventral process is long in *Atlapetes* and *Zonotrichia* and short in *Urothraupis* and *Spizella*.

examined); *Geospiza scandens* (LVP short, 5 specimens); *Camarhynchus pallidus* (LVP short, 3 specimens); *Arremon taciturnus* (LVP long, 4 specimens); *Arremon flavirostris* (LVP long, 3 specimens); and *Urothraupis stolzmanni* (LVP short, 1 specimen).

4. *Length of ulna and femur.*—One of the better generic separations was the ratio of the ulna length to the femur length. The highest values were 1.6 for *Emberiza striolata*; 1.5 for *Emberiza tahapisi*, *Calcarius mccownii*, and *C. ornatus*; and 1.3 to 1.4 for *Melophus*, the other two species of *Calcarius*, *Plectrophenax*, *Pooecetes*, *Chondestes*, *Melanodera*, *Melophyrrha*, *Loxipasser*, *Paroaria*, 17 more species of *Emberiza*, *Ammodramus* [*Passerculus*] *sandwichensis*, *Spizella passerima*, five species of *Phrygilus*, *Haplospiza rustica*, seven species of *Sicalis* (all except *taczanowskii*), 16 species of *Sporophila*, *Oryzoborus crassirostris*, two species of *Tiaris*, *Loxigilla noctis*, and *Geospiza fortis*.

Most species were 1.1 or 1.2; low at 0.8 to 1.0 were *Torreornis*, *Oriturus*, *Donacospiza*, *Emberizoides*, *Embernagra*, *Melozone*, *Arremonops*, *Pezopetes*, *Lysurus*, *Urothraupis*, *Coryphaspiza*, six species of *Zonotrichia*, *Junco vulcani*, four species

of *Ammodramus*, 10 species of *Aimophila*, two species of *Poospiza*, three species of *Incaspiza*, *Diuca speculifera*, six species of *Pipilo* (all except *fuscus*), and 16 species of *Atlapetes* (all except *schistaceus*). Of these taxa, the lowest value was 0.8 for *Aimophila rufescens*.

5. *Length of skull.*—Skull length was used as a general size comparison and separated a few genera and species from the rest of the list. The largest value was 27.7 mm for *Geospiza magnirostris*; also large at 25.0 to 25.6 mm were *Rowettia*, *Idiopsar*, *Pezopetes*, and two species of *Pipilo*; large at 24.1 to 24.8 mm were *Oriturus*, *Embernagra*, *Aimophila rufescens*, *Incaspiza ortizi*, three species of *Pipilo*, *Arremonops conirostris*, and five species of *Atlapetes*. Most species were 17.0 to 23.9 mm; small at 15.4 to 16.9 mm were *Volatinia*, 10 species of *Sporophila*, *Catamenia analis*, and two species of *Tiaris*. Species with the smallest skulls were *Tiaris canora* (15.1 mm) and *Sporophila minuta* (14.8 mm). Rising and Sommers (1989) found that tibiotarsus length was the best single measurement for size in Savannah Sparrows (*Passerculus sandwichensis*), although skull length was second best. For our

purposes, with so many genera involved, skull length seemed the better measure of general size. Most taxa lacked adequate data on body mass.

6. *Premaxilla.*—The length-to-width ratio of the premaxilla corresponded only moderately with epidermal bill shape. Measurement ratios of length : width were *Pinaroloxias* and *Acanthidops,* 2.5; *Certhidea,* 2.4; *Zonotrichia* [*Melospiza*] *georgiana, Ammodramus maritimus, Haplospiza rustica, Donacospiza, Rowettia, Idiopsar, Xenospingus,* two species of *Incaspiza,* and two species of *Geospiza,* 1.9 to 2.3; most species, 1.3 to 1.8; *Dolospingus* and two species of *Sporophila,* 1.0. Also low at 1.1 to 1.2 were *Spizella atrogularis,* 14 more species of *Sporophila, Oryzoborus, Amaurospiza,* and *Catamenia analis.*

7. *Cranium width : interorbital width.*—The ratio of the cranium width to the interorbital width is a measure of skull strength supporting the upper maxilla. It was lowest in *Geospiza magnirostris* (2.0). Next lowest were *Sporophila peruviana* and *Oryzoborus crassirostris* (2.6) followed by 13 species of *Sporophila, Oryzoborus angolensis, Melopyrrha, Dolospingus, Loxigilla, Tiaris fuliginosa,* two species of *Geospiza, Camarhynchus crassirostris,* and *Gubernatrix* (2.8 to 3.5). Values for most species ranged from 3.6 to 5.4. Values for *Junco vulcani,* three species of *Ammodramus, Aimophila notosticta,* two species of *Phrygilus, Incaspiza,* two species of *Poospiza,* four species of *Atlapetes,* and *Urothruapis* ranged from 5.5 to 6.1. The highest values (6.3 and 6.4) were for *Certhidea* and *Xenospingus.*

8. *Ectethmoid foramen.*—The arrangement of the ectethmoid foramen was stated by Beecher (1953) to be a family or subfamily character in the oscines. In fact, as Webster (1994) noted for the Thraupinae, it is quite variable in the Emberizidae. Within the subfamily, it was variable within some genera, especially those with many species (e.g. *Emberiza*), but was consistent within most species and some genera. The presence of a single foramen was consistent in 16 genera: *Calamospiza, Junco, Pooecetes, Torreornis, Donacospiza, Rowettia, Nesospiza, Embernagra, Amaurospiza, Melopyrrha, Pinaroloxias, Pselliophorus, Lysurus, Urothraupis, Coryphaspiza,* and *Saltatricula.* A pinched foramen was the only type found in *Loxipasser,* and a double foramen occurred in the lone specimen of *Dolospingus.* The foramen was either single or pinched in 26 genera: *Zonotrichia, Ammodramus,*

Spizella, Amphispiza, Oriturus, Haplospiza, Lophospingus, Acanthidops, Piezorhina, Xenospingus, Diuca, Incaspiza, Volatinia, Oryzoborus, Loxigilla, Catamenia, Melanospiza, Geospiza, Certhidea, Pipilo, Melozone, Arremonops, Atlapetes, Pezopetes, Coryphospingus, and *Rhodospingus.* In the other 18 genera, the foramina were either double or pinched; single or double; or single, pinched, or double.

9. *Ossification of nasal septum.*—Ossification of the nasal septum and the nasal conchs was recorded along with the development of a solid bony palate rostral to the caudal tip of the maxillopalatines. An extensive bony palate, formed from various bones (see below), occurs in several emberizines (generally those with heavy, stubby bills). Such a palate was depicted by Tordoff (1954: figures 24, 36, 38, 56), but he did not comment on it except for the palatomaxillary (=palatal process of premaxilla) part.

We classified emberizine skeletons into five groups for this set of characters. (1) No ossification of the nasal septum, no ossification of the nasal conchs, and no extensive bony rostral palate occurs in any specimen of 13 genera: *Chondestes, Amphispiza, Melanodera, Acanthidops, Donacospiza, Rowettia, Idiopsar, Xenospingus, Embernagra, Amaurospiza, Catamenia, Pezopetes,* and *Pselliophorus.* (2) In 33 genera, there was never an extensive bony rostral palate, but sometimes the nasal septum and (rarely) the nasal conchs were ossified. (3) *Zonotrichia* [*Passerella*] *iliaca* subspecies *iliaca* and *chilkatensis* (but not other species of that genus) frequently possessed an extensive bony rostral palate (as in Tordoff 1954: figure 56), usually accompanied by a partially ossified nasal septum but not by ossified nasal conchs. (4) In 10 genera, the nasal septum always had some ossification, the nasal conchs sometimes were ossified, but there was never an extensive bony rostral palate: *Melophus, Lophospingus, Nesospiza, Melopyrrha, Dolospingus, Loxipasser, Melanospiza, Lysurus, Coryphaspiza,* and *Urothraupis.* (5) Maximum development of bone in the palate and nose occurred in only five genera: *Sicalis, Sporophila, Oryzoborus, Loxigilla,* and *Geospiza.* Only one of the three specimens of *Sicalis taczanowskii* that we examined had a bony palate that we called extensive, as well as a bony nasal septum and nasal conchs; both of the other specimens lacked the extensive bony palate, and one lacked bony nasal conchs. Each of the other seven species of *Sicalis*

lacked the extensive bony palate and bony nasal conchs, but a few specimens had a partially bony nasal septum. In *Loxigilla*, we termed the palate extensive in both of the *L. portoricensis*, one of three *L. noctis*, and four of the five *L. violacea* that we examined. The bony palate was formed by widening of the premaxillae, maxillae, and palatines in *L. portoricensis* and *L. noctis*. In addition, the bony nasal septum in *L. violacea* was broadened horizontally slightly dorsal to the plane of the palatines. In *Geospiza*, (except for one *difficilis*), the nasal septum was partly bony, and the bony nasal conchs were always absent. An extensive bony palate occurred only in *G. magnirostris* (Tordoff 1954: figure 24), where it was formed by the premaxillae, palatine processes of the premaxillae, maxillae, and palatines. Finally, still more bony development of this region was found in *Sporophila* and *Oryzoborus* (Tordoff 1954: figures 37 and 38). In all specimens of 14 species of *Sporophila* (*schistacea, intermedia, plumbea, americana, torqueola, collaris, luctuosa, albogularis, leucoptera, peruviana, simplex, ruficollis, castaneiventris,* and *telasco*), and in *Oryzoborus crassirostris*, an extensive bony palate of two layers was formed by the premaxillae, palatine process of the premaxillae, and palatines ventrally, and by an extensive horizontal shelf of the nasal septum dorsally. To the last were fused or ankylosed the horns of the vomer; the nasal septum was at least partly bony, but the nasal conchs were only erratically bony. Similar structure was present in five of the six specimens of *Oryzoborus angolensis* and a majority of the specimens of *Sporophila lineola, S. nigricollis,* and *S. minuta*. All four specimens (two each) of *Sporophila obscura* and *S. caerulescens* lacked an extensive bony palate (*obscura* was moved to *Tiaris* by Steadman [1982], Ridgely and Tudor [1989], and Bates [1997], as suggested by Paynter [1970]).

10. *Palatine process of premaxilla.*—This process (cf. Tordoff 1954, Bock 1960) was noted for each specimen in the categories described by Tordoff (1954). In most cases, our assessment agreed with Tordoff's, but we had many more species and in some cases more specimens (Appendix 3). However, in *Geospiza*, our observations disagreed with those of Tordoff. We recorded for the six species Pa1, Pa2, and Pa3, although his depiction looks like Pa2. Symbols in Appendix 3 follow Tordoff (1954:35): Pa1, palatine process of premaxilla free of palatine; Pa2, process adjacent to, but not fused with, palatine; Pa3, process fused with palatine but suture present; and Pa4, process completely fused.

Two additional observations regarding this process are of interest. In *Melanospiza richardsoni*, a species not available to Tordoff or Bock, not only is the process long and free (=Pa1) of the palatine (also noted by Steadman 1982), but an extra bone is caudal to it that articulates with it by a ligament. The extra bone is slender, about the same size and length as the ordinary bone rostral to it, and it extends caudally to the level of the base of the transpalatine process. This structure was identical in all three specimens of *M. richardsoni*. Also, one of the three specimens of *Loxigilla noctis* approached this condition. In this specimen, the palatine process of the premaxilla is free but long and slender, although it is not divided into two bones.

In both species of *Oryzoborus* and 14 species of *Sporophila* (all except *lineola, luctuosa, obscura, caerulescens,* and *telasco*), the palatines appeared to be broadened rostrally (palatine process of premaxilla with a lateral flange) as they are in the Carduelinae. Tordoff (1954) stated that the condition is characteristic only of carduelines, although he depicted it in *Oryzoborus*. Bock (1960) for *Oryzoborus* also noted the similarity to the Carduelinae. As Bock showed, the palatine process of the premaxilla has little value in showing relationships between families or subfamilies of passerines. Within the Emberizinae it appears to be of modest use in generic distinctions.

11. *Interpalatine process.*—The interpalatine process did not prove very useful in distinguishing among genera. It was consistently small or absent only in the monotypic genera *Loxipasser* and *Melanospiza*. Also, it was more often small or absent in some of the tropical genera of seedeaters (*Oryzoborus,* 88% of specimens; *Loxigilla,* 90%; *Camarhynchus,* 88%; *Certhidea,* 75%; *Pinaroloxias,* 56%) than in the others (37% or fewer). The "small or absent" variant occurred occasionally in 20 other genera, but never in 35 genera.

12. *Manubrium-sternum bridge.*—Webster (1993) reported that the manubrium-sternum bridge was absent, minute, small, or large, but erratic in distribution in the Emberizinae. With the study of many additional genera and species,

this statement need not change. In no case was a very large bridge present (as in some Fringillidae), and a small or a large bridge was present in a minority of specimens in 15 genera: *Ammodramus, Junco, Spizella, Oriturus, Haplospiza, Incaspiza, Sporophila, Melanospiza, Geospiza, Camarhynchus, Pipilo, Arremon, Arremonops, Pselliophorus,* and *Paroaria.* Only in *Certhidea* did a majority (six of eight) of specimens have a large or a small bridge. If minute bridges were added to the record, 14 more genera were included, and bridges became more common in the first 15 genera. Still, only in four genera, *Volatinia* (four of five), *Melanospiza* (two of three), *Certhidea* (seven of eight), and *Paroaria* (17 of 19), was any bridge present in a majority of specimens.

13. *Lateral process of nasal bone.*—We categorized the lateral process of the nasal bone as broad and heavy, moderate, fairly slender, or slender. It was uniformly broad and heavy only in *Oryzoborus* and *Melopyrrha,* but half or more of the specimens of *Torreornis, Loxigilla,* and *Gubernatrix* also fit that class, as did a few specimens in 13 more genera. The lateral process of most of the genera, species, and specimens was moderate or fairly slender, but a few specimens in seven genera, and most of those in *Certhidea* and *Saltatricula,* had slender processes.

14. *Retroarticular process of mandible.*—A long retroarticular process of the mandible is correlated with power to depress the mandibles. We measured it as the ratio of the length to width at base. This value exceeded 1.9 in nine species of *Emberiza, Calcarius ornatus,* two species of *Zonotrichia, Junco vulcani,* two species of *Ammodramus,* four species of *Spizella,* two species of *Aimophila, Phrygilus unicolor, Donacospiza, Rowettia,* three species of *Poospiza, Emberizoides ypiranganus, Pipilo chlorurus, Melozone biarcuatum,* 10 species of *Atlapetes, Pselliophorus,* and *Saltatricula;* the highest values were 2.5 in *Donacospiza* and 2.4 in *Emberiza hortulana, Atlapetes rufinucha,* and *A. albofrenatus.* The lowest value was 0.8 for *Oryzoborus angolensis* and *Geospiza magnirostris,* which were the only species with a value below 1.1.

15. *Pseudotemporal process of mandible.*—The pseudotemporal process of the mandible was long (i.e. more than 3 times as long as wide) in *Calamospiza, Chondestes, Torreornis, Oriturus, Rowettia, Emberiza tristrami,* three species of *Zonotrichia,* six species of *Ammodramus,* nine

species of *Aimophila, Phrygilus patagonicus, Poospiza hypochondria, Sicalis lutea, Oryzoborus angolensis,* two species of *Pipilo,* two species of *Melozone,* three species of *Arremon,* two species of *Arremonops,* and seven species of *Atlapetes.* Of these, the maximum value was 5 times as long as wide in *Aimophila humeralis* and *Atlapetes leucopterus;* the others varied from 3.1 to 4.3. Values for most taxa were between 1 and 3, and the shortest processes (0.4 to 0.9 times as long as wide) occurred in *Certhidea, Melanospiza,* six species of *Emberiza, Sporophila albogularis, Catamenia homochroa, Geospiza fortis,* and *Camarhynchus crassirostris.*

16. *Length of tibiotarsus and femur.*—The ratio of the length of the tibiotarsus to the length of the femur distinguished several genera. The highest values were *Certhidea* (2.0) and *Acanthidops, Donacospiza, Nesospiza, Piezorhina, Xenospingus, Camarhynchus, Pinaroloxias, Pselliophorus, Urothraupis, Emberiza yessoensis,* two species of *Spizella,* four species of *Phrygilus, Haplospiza rustica,* four species of *Poospiza,* two species of *Catamenia,* three species of *Geospiza,* four species of *Atlapetes,* and *Paroaria coronata* (1.8 to 1.9). The values for most species ranged from 1.6 to 1.7; low at 1.5 were *Coryphaspiza, Emberiza cabanisi,* two species of *Ammodramus,* three species of *Aimophila,* and *Poospiza garleppi.* The lowest value was 1.3 for *Ammodramus* [*Passerculus*] *sandwichensis.*

17. *Length of tarsometatarsus and femur.*—The ratio of tarsometatarsus length to femur length separated several genera from others. *Certhidea* had the highest value at 1.5; also high at 1.3 to 1.4 were *Acanthidops, Donacospiza, Nesospiza, Xenospingus, Melanospiza, Camarhynchus, Pinaroloxias, Pselliophorus, Urothraupis, Junco vulcani,* three species of *Spizella,* three species of *Phrygilus, Incaspiza watkinsi,* five species of *Poospiza,* two species of *Catamenia, Loxigilla noctis,* two species of *Arremon,* four species of *Geospiza,* and eight species of *Atlapetes.* Values for most species fell between 1.1 and 1.2, with the lowest (1.0) occurring in *Coryphaspiza, Emberiza cabanisi,* and *Aimophila sumichrasti.*

18. *Length of tarsometatarsus and skull.*—The ratio of tarsometatarus length to skull length distinguished several genera from others. The highest value was 1.3 for *Junco vulcani, Rowettia,* and *Pezopetes.* Also high at 1.2 were *Nesospiza, Embernagra, Certhidea, Ammodramus maritimus,* two species of *Phrygilus, Incaspiza ortizi, Poospi-*

za garleppi, Camarhynchus crassirostris, Pipilo ocai, Melozone leucotis, Arremon aurantiirostris, Arremonops conirostris, 12 species of Atlapetes, and Paroaria coronata. Values for most species were from 1.0 to 1.1, with the lowest being 0.8 to 0.9 in Volatinia, Oryzoborus, Amaurospiza, Melopyrrha, Dolospingus, five species of Emberiza, Ammodramus henslowii, Spizella passerina, Lophospingus pusillus, Sicalis columbiana, 15 species of Sporophila, three species of Tiaris, and two species of Geospiza.

19. Length of tibiotarsus and humerus.—The ratio of tibiotarsus length to humerus length separated several genera from the others. The highest value at 2.1 was for Atlapetes citrinellus and A. pallidinucha; also high at 1.8 to 2.0 were Acanthidops, Donacospiza, Nesospiza, Xenospingus, Certhidea, Pinaroloxias, Pezopetes, Pselliophorus, Urothraupis, five species of Zonotrichia, Junco vulcani, Ammodramus maritimus, two species of Aimophila, Phrygilus patagonicus, two species of Incaspiza, four species of Poospiza, two species of Catamenia, Tiaris olivacea, two species of Camarhynchus, two species of Pipilo, two species of Arremonops, and 14 other species of Atlapetes (all species of Atlapetes were high except albiceps). Values for most species ranged from 1.5 to 1.7; low values (1.3 to 1.4) occurred in Melophus, six species of Emberiza, three species of Calcarius, Spizella passerina, Pooecetes, Chondestes, two species of Phrygilus, Lophospingus pusillus, Sicalis uropygialis, and two species of Sporophila.

20. Length of tibiotarsus and ulna.—The ratio of tibiotarsus length to ulna length separated a few genera from the others. The highest values were 2.0 for Atlapetes pallidinucha and 1.9 for Pezopetes, Urothraupis, Diuca speculifera, and Atlapetes pileatus. Also high at 1.8 were Xenospingus, Certhidea, two species of Zonotrichia, Ammodramus maritimus, two species of Aimophila, Incaspiza ortizi, two species of Pipilo, and 10 species of Atlapetes. Values for most species ranged from 1.3 to 1.7; the lowest value was 1.0 for Emberiza striolata. Also low (1.1 to 1.2) were Melophus, Pooecetes, Chondestes, Loxipasser, nine species of Emberiza, three species of Calcarius, Spizella passerina, Phrygilus carbonarius, four species of Sicalis, six species of Sporophila, and Oryzoborus crassirostris.

21. Length of humerus and femur.—The ratio of humerus length to femur length distinguished several genera. The highest value (1.2) occurred

in Pooecetes, five species of Emberiza, three species of Calcarius, Phrygilus carbonarius, and two species of Sporophila. Values for most of the species were from 1.0 to 1.1; the lowest value (0.8) was for Pezopetes, Atlapetes citrinellus, and A. pallidinucha. A low value (0.9) also occurred in Torreornis, Melozone, Atlapetes (the other 15 species), Pselliophorus, Urothraupis, Zonotrichia [Melospiza] lincolnii, Junco vulcani, two species of Ammodramus, six species of Aimophila, three species of Incaspiza, Emberizoides herbicola, Poospiza garleppi, two species of Pipilo, and Arremonops rufivirgatus.

22. Tarsometatarsus.—The ratio of the length to width of the tarsometatarsus separated a few genera from the others. Certhidea was highest at 12.7; next highest was Geospiza scandens at 11.9; also high at 11.0 to 11.8 were Acanthidops, Xenospingus, Rhodospingus, Junco vulcani, two species of Spizella, Amphispiza bilineata, Poospiza garleppi, two species of Catamenia, and six species of Atlapetes. Values for most species ranged between 8.5 and 10.9, with the lowest (8.1 to 8.4) measured in Plectrophenax, two species of Emberiza, two species of Sicalis, and Sporophila plumbea.

23. Transpalatine process.—The shape of the transpalatine process was quite consistent in each species and separated a few genera in each of two features. The process was flared (broader distally than proximally) in the following genera and species: Calamospiza, Chondestes, Torreornis, Oriturus, Oryzoborus, Melopyrrha, Dolospingus, three species of Emberiza, three species of Zonotrichia, two species of Ammodramus, three species of Aimophila, Sicalis taczanowskii, 18 species of Sporophila (all except obscura), two species of Loxigilla, four species of Geospiza, two species of Pipilo, and Arremon abeillei. In all other species, the process was wider proximally than distally or the same width in both dimensions. We measured the process as the ratio of length to width at the base. This ratio was highest (7.0) in Atlapetes leucopterus and ranged from 3.3 to 6.0 in two species of Emberiza, Ammodramus henslowii, Spizella pusilla, Phrygilus patagonicus, seven species of Sporophila, Amaurospiza, Pipilo erythrophthalmus, Melozone biarcuatum, two species of Atlapetes, and Pselliophorus. In most species the value ranged from 0.9 to 3.2. It was lowest (0.4) in Poospiza thoracica and P. boliviana and ranged from 0.5 to 0.8 in Melophus, three species of Em-
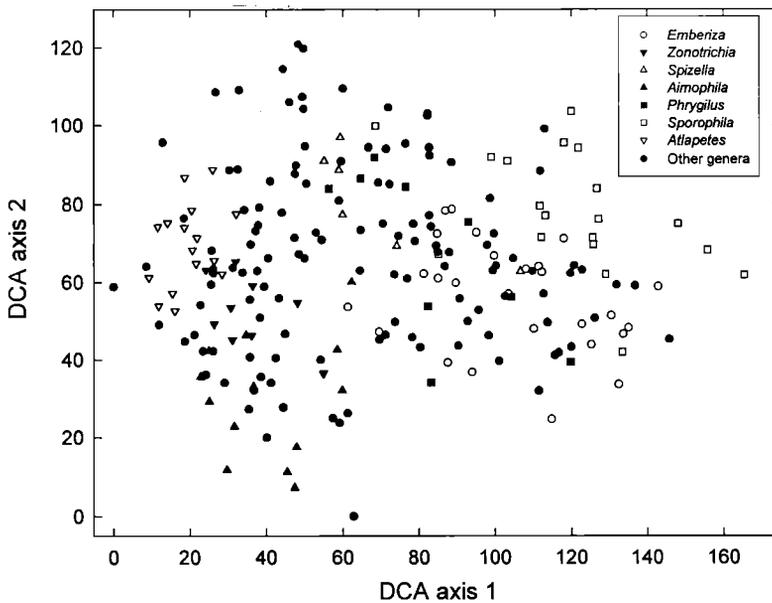
FIG. 2.   Results of detrended correspondence analysis (DCA) of 224 species of Emberizinae showing the first two DCA axes. Several larger genera are shown with individual symbols.

beriza, *Idiopsar, Xenospingus,* two species of *Si-calis, Catamenia analis,* and *Certhidea.*

24. *Zygomatic process of squamosal.*—The shape of the zygomatic process of the squa-mosal, as described by its length-to-width ra-tio, separated a few genera and species. It was highest in *Nesospiza* (2.5) and high (2.0) in *Row-ettia* and *Emberiza citrinella.* Values for all other species were between 0.9 and 1.7 except for *Melopyrrha, Poospiza garleppi,* and *Pipilo aberti,* which had the lowest value at 0.8.

Additional characters.—We recorded the fol-lowing features for all or nearly all specimens. Some were too variable to be useful in distin-guishing species or genera: shape of the lateral margin of the palatine posteriorly, shape of the rostral part of the lateral process of the man-dible, shape of the internal process of the man-dible, angle between internal tuberculum of humerus and shaft of humerus, degree of distal bend of the tarsometatarsus, shape of the ros-tral end of the vomer, shape of the maxillopa-latine, shape of the lateral margin of the ecteth-moid plate (cf. Beecher 1953, where used as a family character). Some characters were too uniform within the subfamily to serve as spe-cies or generic distinctions: length and shape of the orbital process of the quadrate, shape of the basihyoid, degree of mobility of the craniofa-

cial hinge, nature of the tricipital fossa of the humerus, ratio of length of ulna to humerus, ratio of length of tibiotarsus to tarsometatar-sus, and relative lengths of the metatarsal trochleae.

Results of the DCA ordination (Table 2) in-dicated that the first axis was related to the rel-ative lengths of the wings and legs. Species with high values on axis 1 were those with rel-atively long wings and short legs. Most species of *Sporophila* had high values on axis 1, and all species of *Atlapetes* had low values on this axis (Fig. 2). On axis 2, high values indicated species with relatively short femora compared with the rest of the leg. All species of *Camarhynchus* had high values on axis 2, and most species of *Aim-ophila* had low on this axis (Fig. 2). Axis 3 was related to skull characteristics. Species with low values on axis 3 tended to have slender bills, whereas species with higher values on axis 3 tended to have stubby bills. Examples of species with low scores on axis 3 were two spe-cies of *Calcarius* (*pictus* and *ornatus*), although the other two *Calcarius* were intermediate on axis 3 (*lapponicus* and *mccownii*). Some species of *Emberiza* and *Phrygilus* were low on axis 3 (Fig. 3), especially *E. striolate, E. poliopleura,* and *P. alaudinus. Sicalis uropygialis* had a low score on axis 3, although other members of this genus
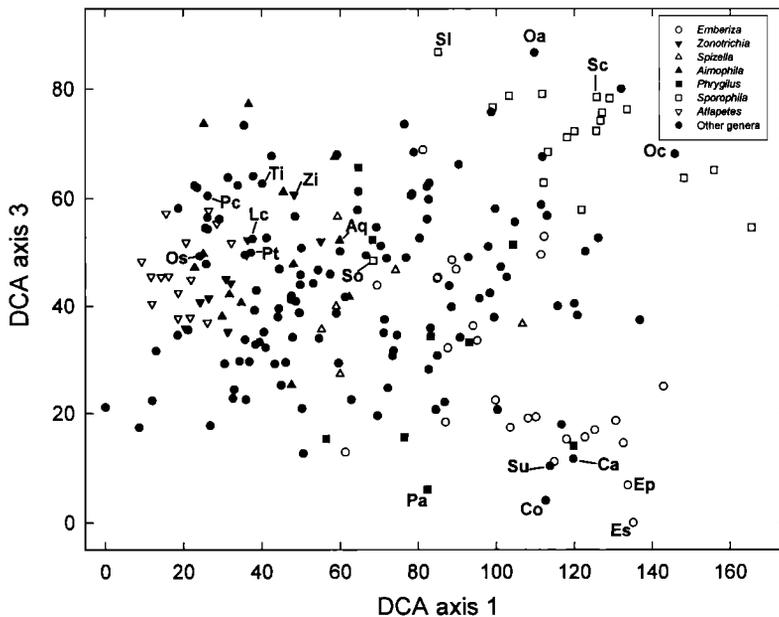
FIG. 3. Results of detrended correspondence analysis (DCA) of 224 species of Emberizinae showing the first and third DCA axes. Larger genera are shown with individual symbols. Sc = *Sporophila caerulescens*; Sl = *S. luctuosa*; So = *S. obscura*; Oa = *Oryzoborus angolensis*; Oc = *O. crassirostris*; Ti = *Torreornis inexpectata*; Zi = *Zonotrichia iliaca*; Pc = *Pezopetes capitalis*; Os = *Oriturus superciliosa*; Pt = *Pselliophorus tibialis*; Lc = *Lysurus castaneiceps*; Aq = *Aimophila quinquestriata*; Ca = *Calcarius pictus*; Co = *C. ornatus*; Su = *Sicalis uropygialis*; Ep = *Emberiza poliopleura*; Es = *E. striolata*; Pa = *Phrygilus alaudinus*.

had intermediate scores. Species with high values on axis 3 included most species of *Sporophila* (especially *luctuosa* and *caerulescens*). Also, both species of *Oryzoborus* (especially *angolensis*) and some species of *Aimophila* had high values on axis 3. Species scores on axes 1 to 3 are shown in Figures 2 and 3; Figures 4 to 6 are extracts from Figure 2 for specific groups of genera.

DISCUSSION

Paynter (1970) recognized *Sporophila obscura* but noted that the species might belong in *Tiaris*. Steadman (1982), Ridgely and Tudor (1989), and Kaiser (1992) moved it to *Tiaris*. Skeletal anatomy confirmed that disposition. In addition, the single-layered bony palate of *Sporophila caerulescens* does not fit with the structure of the other 17 species of *Sporophila* examined; its generic placement is doubtful. Bates (1997) also placed *S. obscura* in *Tiaris*, citing various characters in support of the move. As to the skeleton, Bates quoted a manuscript by A. Wetmore and W. H. Phelps, Jr., describing the na-

ture of the palatine process of the premaxilla, which agrees with *Tiaris* rather than *Sporophila*. Our observations agree with this assessment. *Sporophila obscura* is a clear outlier from other *Sporophila* on DCA axis 1 (Fig. 4) and also is the extreme low value for the genus on axis 3 (Fig. 3). Scores of *S. obscura* generally were close to those for species of *Tiaris* (Fig. 4). *Sporophila luctuosa* also was an outlier on axes 1 and 3, and *S. caerulescens* fell well within range of the genus on all three DCA axes (Figs. 3 and 4).

Emberizoides ypiranganus is much smaller than *E. herbicola* (skull length 20.9 mm vs. 22.3 mm, respectively), which supports the position of Eisenmann and Short (1982) that the two taxa are distinct species. We did not examine any specimens of *E. duidae*.

The merging of *Sporophila* and *Oryzoborus* (Olson 1981a, b; Wetmore et al. 1984) is not indicated by the skeletal features that we studied. The thinness of the ectethmoid plate in *Oryzoborus* is distinctive, which contrasts not only with *Sporophila*, but also with all of the other genera of nine-primaried oscines. In two other characters (degree of mobility of the craniofa-
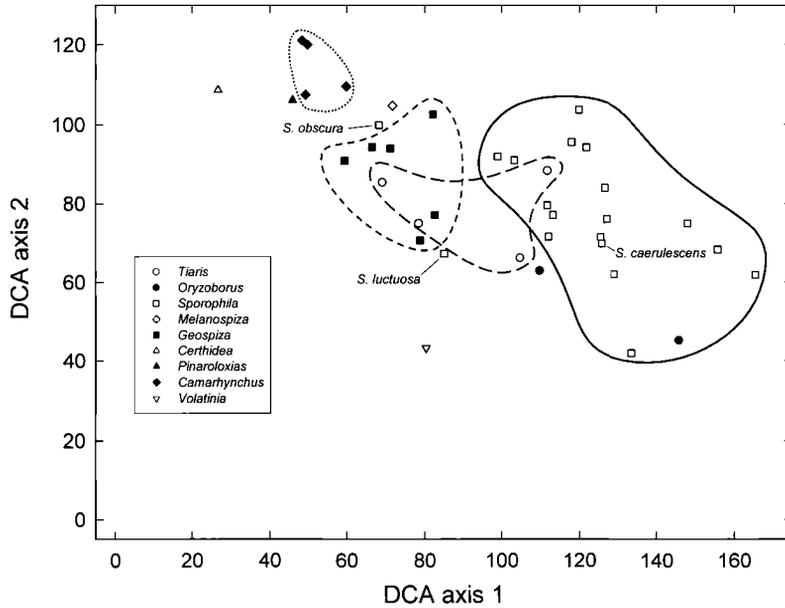
FIG. 4.   Results of detrended correspondence analysis (DCA) of 224 species of Emberizinae showing only several genera of seedeaters (including Darwin's finches) on the first two DCA axes. Dotted line = *Camarhynchus*; short dashed line = *Geospiza*; long dashed line = *Tiaris*; and solid line = *Sporophila*.
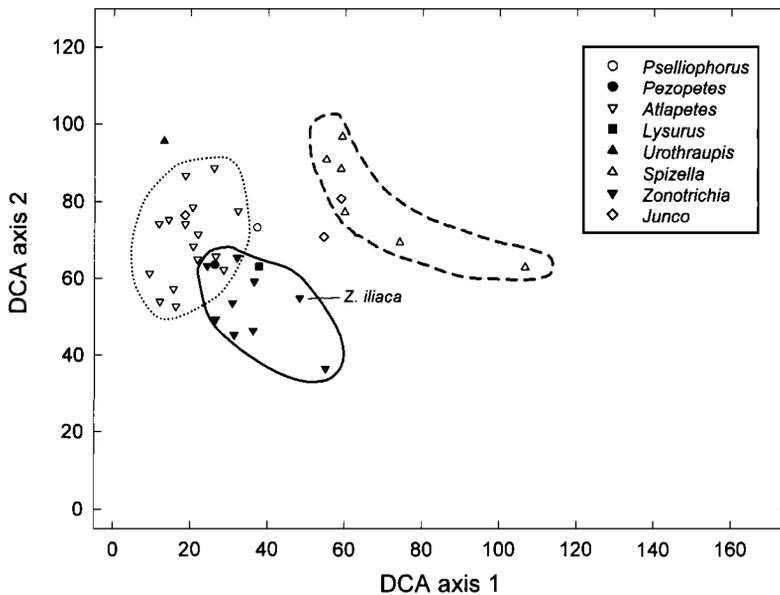
FIG. 5.   Results of detrended correspondence analysis (DCA) of 224 species of Emberizinae showing only *Atlapetes* and related genera and *Zonotrichia* and supposedly related genera on the first two DCA axes. Dotted line = *Atlapetes*; dashed line = *Spizella*; and solid line = *Zonotrichia*.
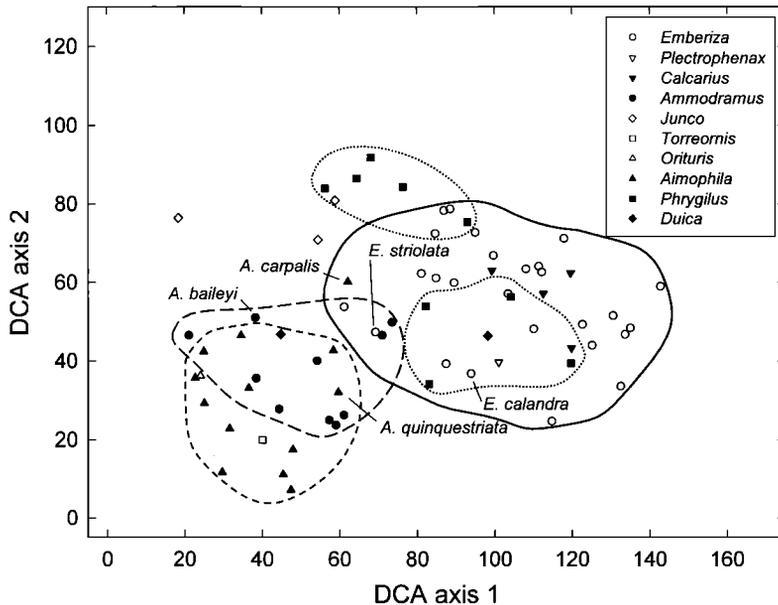
FIG. 6. Results of detrended correspondence analysis (DCA) of 224 species of Emberizinae showing only some miscellaneous genera on the first two DCA axes. Dotted line = *Phrygilus*; solid line = *Emberiza*; long dashed line = *Ammodramus*; and short dashed line = *Aimophila* exclusive of *A. carpalis*.

cial hinge and width of the lateral process of the nasal), all specimens of *Oryzoborus* lie outside the range of variation in *Sporophila*; also in nine more characters some specimens of *Oryzoborus* lie outside the range of variation in *Sporophila*. Meyer deSchauensee (1970b) showed that *Oryzoborus* included a third species, *O. maximiliani*, which we have not seen. The DCA did not differentiate the two genera. Both species of *Oryzoborus* examined scored within the range of *Sporophila* on all three DCA axes. Skeletons of 12 species of *Sporophila* were unavailable.

The genera *Emberizoides* and *Embernagra* are rather similar to one another in most skeletal features. However, all specimens of *Embernagra* lie outside the range of variation within *Emberizoides* in 9 of the 39 tabulated characters; fusion of the two genera seems premature.

Piezorhina and *Diuca* also are similar to one another in most skeletal features. However, *Piezorhina* lies outside the range of variation within *Diuca* in 12 of the 38 tabulated characters. One of these, at least, is probably important: the lacrimal was missing or fused in all specimens of *Piezorhina*, but present and free in 10 of the 12 specimens of *Diuca*. In the DCA, the two species of *Diuca* differed more from each other

than either did from the species of *Piezorhina* on axis 1, and *Piezorhina* was not much different on axes 2 and 3.

The large genus *Atlapetes* and the genera *Pezopetes* (monotypic), *Lysurus* (monotypic), and *Psellioporus* (two species) are close to one another in skeletal anatomy. Paynter (1970) placed them in close proximity and acknowledged in a footnote that *Pezopetes* was possibly congeneric with *Atlapetes*. On tabulation, *Pselliophorus* lies slightly outside the range of variation in *Atlapetes* in two characters, and two specimens show variation beyond *Atlapetes* in two other features. *Pezopetes* lies slightly outside the range of variation in *Atlapetes* in five characters, and two specimens show variation beyond *Atlapetes* in two more features. *Lysurus* lies outside the range of variation in *Atlapetes* in seven characters; one of these, the lateroventral process of the laterosphenoid, is probably important. In the DCA, all three genera were within the range of *Atlapetes* on all three axes except that *Lysurus* was higher on DCA axis 1, and *Pezopetes* was higher on axis 3 (Figs. 3 and 5). Based on skeletal characters, then, *Pselliophorus* definitely should be lumped with *Atlapetes*, *Pezopetes* probably should be lumped, and *Lysurus* should be retained as monotypic.

In a later treatment, Paynter (1978) recognized two additional species of *Atlapetes* (*virenticeps* and *atricapillus*) that he had previously included in *A. torquatus*. On this basis, the two skeletons we examined of *A. torquatus* were *A. virenticeps*, and we did not see *A. torquatus* (sensu stricto) or *A. atricapillus*. *Urothraupis* is not far from *Atlapetes* in skeletal features, but it lies outside the range of variation in *Atlapetes* in 11 of the tabulated characters and in axes 2 and 3 of the DCA.

Hackett (1992) provided DNA and allozyme evidence for splitting *Buarremon* from *Atlapetes*. Remsen and Graves (1995) followed Hackett on this action, although noting that the external morphological separation (bill shape) was weak. We found that skeletal evidence for this split was essentially lacking; in only one character (premaxillary length-to-width ratio) did both species of *Buarremon* lie outside the range of variation within *Atlapetes*; in two more characters one but not both species of *Buarremon* exceeded the variation within *Atlapetes*. Hackett's (1992) allozyme and DNA work indicated that *Pselliophorus* and *Pezopetes* were closely related to most species of *Atlapetes* and that *Lysurus* was closely related to the *Buarremon* group.

The limits of *Zonotrichia* have been well studied. Paynter (1964, 1970) advocated a large genus, and various authors have proposed splitting the group into two, three, or four genera. The AOU (1998) recognizes three genera in the group (*Passerella*, *Melospiza*, and *Zonotrichia*). On the basis of skeletal characters, we would use the broad concept of Paynter (the single genus *Zonotrichia*), or recognize *Passerella* as the most distinct genus and place the other eight species (three *Melospiza* and five *Zonotrichia*) in *Zonotrichia*. Zink (1982) and Zink and Blackwell (1996) gave skeletal, allozyme, and DNA evidence for including *Junco* within *Zonotrichia* (sensu latu) and for showing that *Passerella* [*Zonotrichia*] *iliaca* was the most disparate (or phylogenetically distant) member of the group. They did not include the Middle American species of *Junco* in their studies. Their skeletal data comprised 40 different measurements but differed from ours in excluding ratios (although body proportions were indirectly implied). Our study agrees with Zink's (1982) on all points except the position of *Junco*. We found 19 characters in which at least one species of *Junco* (*pallatus*, *phaeonotus*, or *vulcani*) was outside the

range of variation within *Zonotrichia*. As detailed above, *J. vulcani* differed in more characters from the other two species than the latter two did from one another. The three species of *Junco* were well separated from *Zonotrichia* on DCA axis 2, and *Zonotrichia* [*Passerella*] *iliaca* was distinct from other *Zonotrichia* only on axis 3 (Figs. 3 and 5).

The genus *Ammodramus* as recognized by Paynter (1970) includes *Xenospiza* and *Passerculus* (AOU 1998), as well as *Myospiza* from South America. Based on skeletal characters, Robins and Schnell (1971) advocated the recognition of two genera for the group; unfortunately they omitted three species (*baileyi*, *humeralis*, *aurifrons*) from their study. Our results suggest that either one, two, or three genera might be recognized on osteological characters: (1) a broad single genus with 10 species, as recognized by Paynter (1970). (2) *Ammodramus* for *savannarum*, *humeralis*, and *aurifrons*, with the other seven species together as *Ammospiza*. (3) Recognition of *Passerculus* for *sandwichensis*, *Ammospiza* for six species, and *Ammodramus* for three species as in (2) above. *Ammodramus baileyi* (=*Xenospiza*) is very close in skeletal features to *A. henslowii* and *A. bairdii*. The DCA showed no consistent separations among the 10 species of *Ammodramus* (sensu latu), including *A. baileyi* (Figs. 3 and 6).

The genus *Aimophila* has generated much dispute among ornithologists. Wolf (1977) included the Five-striped Sparrow (*A. quinquestriata*) in the genus with some misgivings, suggesting that it might belong in *Melozone* instead. He did not mention *Torreornis inexpectata* or *Oriturus superciliosus* and did not study *Aimophila strigiceps* or *A. stolzmanni*. We, too, were unable to study a skeleton of *A. strigiceps*, but the skeleton of *A. stolzmanni* was similar to those of *A. ruficauda* and *A. humeralis*. The skeletons of *Torreornis* and *Oriturus* are similar to those of *Aimophila*; we see no osteological basis for maintaining those monotypic genera. In the DCA, *A. quinquestriata*, *Torreornis*, and *Oriturus* were well within the range of the genus *Aimophila* on all axes (Figs. 3 and 6). The most disparate species of the group is *A. carpalis*, which is quite distinct in Figure 6.

Cramp and Perrins (1994) considered *Milaria calandra* to belong to a different genus from *Emberiza*. Doubtless this is justified on characters of behavior and external anatomy as detailed in

that work, but our skeletal data yielded few characters to confirm such a separation. Only in two characters, length of skull and relative proportions of the palatine process of the premaxilla, did *Milaria* lie outside the range of variation in the 26 other species of *Emberiza* that we examined. *Emberiza striolata,* in contrast, represented an extreme for the genus (that is, beyond the range of variation in the other 26 species) in six characters. The DCA showed *Emberiza* to be widely scattered but without any obvious separations. *Emberiza [Milaria] calandra* was near the extreme on axis 2, and *E. striolata* had a low score on axis 1 (Fig. 6). However, skeletons of 11 species of *Emberiza* were not available for study.

Three genera are so heterogenous in skeletal structure that they must be diphyletic and surely ought to be divided: *Emberiza* (whether or not *Milaria* be split off), *Phrygilus,* and *Sporophila* (if *obscura* and *caerulescens* are included). *Sicalis* (cf. Hellmayr 1938, Ridgely and Tudor 1989) and *Geospiza* (cf. Bowman 1961) each has one large-billed species that seems out of place (*S. taczanowskii* and *G. magnirostris*) but probably should stand as they are.

The first two axes of the DCA clearly show *Phrygilus* in two groups: *unicolor, atriceps, patagonicus, plebejus,* and *gayi* in a group with higher scores on axis 2; and *alaudinus, fruticeti, erythronotus,* and *carbonarius* in another group (Fig. 6). However, these groups are not evident on axis 3 (Fig. 3). The presence or absence of the lacrimal bone is not consistent within either group. Whereas all members of the second group lack a free lacrimal, and four species of the first group possess one, *P. plebejus* belongs in the first group (based on Fig. 6) but lacks a free lacrimal. Skeletons of *P. dorsalis* and *P. coracinus* (Fjeldså 1993) were not available for study.

Skeletal characters suggest three distinct groups of emberizine genera: (1) North American sparrows; (2) South American grassland finches (several genera of the first group range into South America and several genera of the second group range into Middle America or are endemic there); (3) and Middle and South American seedeaters, including Darwin's finches. These are, more or less, the seven groups noted by Paynter and Storer (1970: vii–viii), but groups 1 and 6, 2 and 3, and 4 and 5, respectively, are combined. Six genera (including the

three we did not examine) remain as group 4, incertae sedis. The DCA shows a fairly clear separation of the North American grassland group and the seedeaters on axes 1 and 2 (Fig. 7). The North American species tend to fall on the lower left of Figure 7; i.e. they have relatively longer femora and shorter wings. The seedeaters tend to have shorter femora and longer wings and fall on the upper right of Figure 7. The South American grassland group broadly overlaps the other two groups. *Emberiza,* which makes up the largest group of uncertain species, mostly falls in with the seedeaters; *E. tristrami, E. fucata, E. capensis,* and *E. cabanisi* fall in more with the North American grassland species. *Melophus lathami* is also in with the seedeaters, and *Volatinia jacarina* is an outlier from the other seedeaters (Fig. 7). *Coryphaspiza melanotis,* of the South American grassland species, is much lower on the DCA axis 2 than are the others in the group (Fig. 7).

Table 3 lists the emberizid genera in these four groups. In each of the first three groups, we placed a superscript "a" after the genera that do not fit quite so well as the others into their respective groups. At the same time, within each group we have attempted to begin with the most generalized forms and proceed to more specialized genera, while keeping presumably closely related genera near one another. Generic departures from Paynter's (1970) list are those recommended above: *Milaria* is added; *Torreornis* and *Oriturus* are merged into *Aimophila;* and *Pezopetes* and *Pselliophorus* are merged into *Atlapetes.*

Distinction between the Emberizinae and Fringillinae is difficult. Zusi (1978) and other workers failed to cite informative skeletal characters, and we were no more successful in this regard. Comparing *Fringilla* (manubrium-sternum bridge examined in 14 specimens of 3 species; all other characters examined in 5 specimens of 2 species) with the Emberizinae, we found these slight differences (1) The manubrium-sternum bridge is very large in *F. coelebs* and *F. teydea* but small in *F. montefringilla;* no emberizine species has a very large bridge, and no emberizine genus has a bridge in 100% of the specimens (Webster 1993, this study). (2) In shape of the maxillopalatine bone, no emberizine has the slender club and gradual curve of the pedicel seen in one specimen of *F. coelebs.* (3) The ratio of ulna length to humerus length of
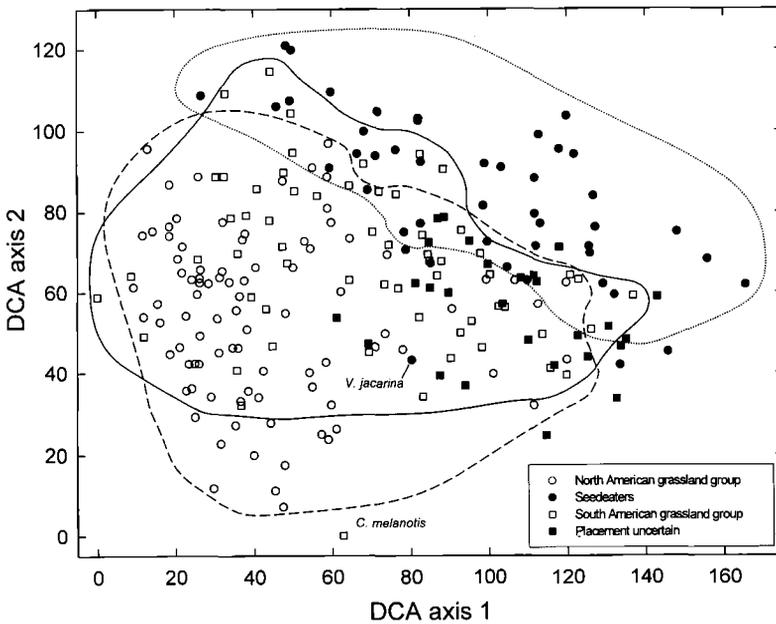
FIG. 7. Results of detrended correspondence analysis (DCA) of 224 species of Emberizinae showing the first two DCA axes with symbols indicating the four groups of genera listed in Table 3. Dashed line = North American grassland group; dotted line = seedeaters; solid line = South American grassland group.

TABLE 3. Suggested order of genera in the Emberizinae. Generic changes reflect recommendations in this paper.

North American grassland	Seedeaters	South American grassland	Placement uncertain
Ammodramus	Tiaris	Embernagra[a]	Emberiza
Spizella	Geospiza	Emberizoides[a]	Milaria
Junco	Camarhynchus	Donacospiza[a]	Melophus
Zonotrichia	Certhidea[a]	Coryphaspiza[a]	Latoucheornis
Pooecetes	Pinaroloxias	Sicalis	Oreothraupis
Chondestes	Melanospiza[a]	Phrygilus[a]	Charitospiza
Calamospiza	Loxigilla[a]	Haplospiza	
Calcarius[a]	Loxipasser[a]	Acanthidops	
Plectrophenax[a]	Melopyrryha	Lophospingus	
Amphispiza	Dolospingus	Melanodera	
Aimophila[a]	Amaurospiza[a]	Rowettia	
Arremon	Volatinia[a]	Nesospiza	
Arremonops[a]	Sporophila	Diuca	
Melozone	Oryzoborus	Piezorhina	
Pipilo		Idiopsar	
Atlapetes		Xenospingus	
Lysurus[a]		Catamenia	
Urothraupis[a]		Poospiza	
		Incaspiza	
		Saltatricula	
		Gubernatrix[a]	
		Paroaria	
		Coryphospingus	
		Rhodospingus	

[a] Placement in this column less certain.

1.3 in *F. montefringilla* is beyond the range found in Emberizinae. Actually, in 29 of the 39 skeletal characters we tabulated, the species of *Fringilla* were about average for the genera of Emberizinae; in six other characters other than the three just mentioned, one or both species were in the high or low parts of the range for Emberizinae but not in the extreme. Distinction among *Fringilla* (or Fringillinae) and Emberizinae and Carduelinae is clear on the basis of the structure of the salivary glands (Foelix 1970) and the digestive tract (Ziswiler 1967).

Separation of Carduelinae from Emberizinae is clear based on the double-walled interorbital septum of the former (Zusi 1978). We found no exceptions among the specimens we examined. The shape of the palatine process of the premaxilla, however, is not a consistent distinction. This process has the same form in *Oryzoborus* and in most species of *Sporophila* as it does in Carduelinae. The short tarsometatarsus of Carduelinae has been cited as another subfamilial distinction (Tordoff 1954). Tordoff noted overlap in this character; our data show that most species from both groups are in the region of overlap, leaving only a few separable extremes.

Bowman (1961) recognized separate genera (*Platyspiza* and *Cactospiza*) for *Camarhynchus crassirostris* and *C. pallidus*, as lumped by Lack (1947) and Paynter (1970). On the other hand, Steadman (1982) lumped all of these genera, as well as *Certhidea*, *Pinaroloxias*, and *Volatinia*, with *Geospiza*. Whether or not *Volatinia* (as Steadman argued) was ancestral to the various island species (Cocos and Galapagos Islands), the lumping of forms as diverse as *Pinaroloxias*, *Certhidea*, *Camarhynchus* (sensu latu), and *Geospiza* is idiosyncratic. Generic lumping should be done with the systematics of the rest of the family thoroughly compared. Steadman's conclusions have already been questioned by Barrowclough (1983), Baptista and Trail (1988), and Grant (1986), although favored by Ratcliffe and Boag (*in* Lack 1983) and Wetmore et al. (1984). The DCA of Darwin's finches indicated that the four genera and the 12 species available for study generally are in the same regions on DCA axes 1 and 2 (Fig. 4) and also on axis 3. In both cases, *Geospiza* and *Camarhynchus* overlap except on axis 2, and *Certhidea* and *Pinaroloxias* are outliers. *Tiaris* overlaps *Geospiza* on all three axes. *Melanospiza* is within or very near

the range of *Geospiza* on all three DCA axes, and *Volatinia* is quite separate from these groups on DCA axis 2 (Fig. 4).

An analysis of Steadman's work on osteology (Steadman 1982:284–288) is necessary. Steadman studied only 22 of the 65 genera and 36 of the 279 species of Emberizinae, which yielded an incomplete view of variation within the subfamily; his comparative material of other families and subfamilies was even more inadequate. Most of the characters he used to differentiate Darwin's finches from other groups are correct within the species studied, but they are not to be understood as osteologically informative characters within the family. For instance, the retroarticular process is stated to be smaller in Emberizinae than in *Coereba*, larger in Emberizinae than in Fringillidae (apparently he meant Fringillinae + Carduelinae, but he examined only *Carpodacus* and *Carduelis*), and smaller in Emberizinae than in Icteridae. We measured the proportions (length : width) as 1.0 to 2.5 in Emberizinae, 0.3 to 1.1 in Fringillinae + Carduelinae, 1.2 to 6.5 in Icteridae, and 1.0 to 2.5 in various races of *Coereba flaveola*. The size of the process compared with the rest of the mandible was extremely variable in both Emberizinae and Fringillinae + Carduelinae, but we did not measure it. The angle at the jugal-maxillary junction was stated to be more acute in Emberizinae than in Parulidae and Thraupinae; we found the opposite, whether the vertical or the horizontal plane was viewed. We did not record thickness and curvature of the dentary and surangular. Steadman (1982) referred to fusion of the prepalatine bar to the jugal (not in Emberizinae), but we did not record any such fusion in any nine-primaried oscine. Probably, Steadman meant the fusion of the lateral-flange type of palatine process of the premaxilla, as sometimes occurs in *Carduelis* (Tordoff 1954, Bock 1960).

Steadman (1982:286–287) distinguished between the skeletons of Darwin's finches and certain other Emberizinae. Most of these distinctions seem valid, although some ignore *Certhidea* and *Pinaroloxias*. The palatine process of the premaxilla (=palatomaxillary) of *Melanospiza richardsoni* was stated to be "long and slender," but the second bone was not mentioned. For *Poospiza nigrorufa*, it was stated "maxillo-palatine process located ventrally," which is probably erroneous as an informative

character. Sometimes the pedicel of the maxillopalatine in Emberizinae (and other nine-primaried oscines) is bent in various directions; apparently, it is rather flexible during the drying process of skeleton preparation.

Steadman (1982:287–288) compared the skeletons of Darwin's finches with those of *Volatinia, Tiaris* (including *T. obscura*), and *Melanospiza*. We analyzed the same species based on the 39 characters noted above and found that for 28 characters, *Volatinia, Tiaris* (at least one species), and *Melanospiza* were within the range of variation within the four genera of Darwin's finches. In nine characters, *Volatinia* was outside the range of the Darwin's finch genera, but *Tiaris* (at least one species) and *Melanospiza* were within that range. In two characters, *Melanospiza* was outside the range of the Darwin's finch genera, but *Volatinia* and *Tiaris* (at least one species) were within the range. At least one species of *Tiaris* was within the range of the Darwin's finches in all 39 characters. We conclude, using a different suite of osteological characters than used by Steadman, that *Volatinia* is the least likely and *Tiaris* the most likely to be an ancestor of Darwin's finches. However, this is not very decisive. The ancestor of Darwin's finches is unidentified, although *Tiaris, Volatinia, Melanospiza*, or some extinct genus are possible candidates. The proper taxonomic procedure is to recognize all seven (or nine) genera. In fact, *Certhidea* is osteologically the most divergent genus within the Emberizinae.

We were unable to clarify several important aspects of emberizine systematics. First, the boundaries between Emberizinae and Cardinalinae and between Emberizinae and Thraupinae remain unclear. Second, the proposal by Sibley and Ahlquist (1990) and Sibley and Monroe (1990) to move 52 genera from Emberizini (=Emberizinae) to Thraupini (=Thraupinae) is neither supported nor disputed. However, two genera whose DNA they did not examine, *Paroaria* and *Gubernatrix*, belong with the South American grassland finches on the basis of skeletal characters (*Paroaria* clearly, *Gubernatrix* probably), regardless of whether that group is allied with the tanagers or the North American sparrows. Sibley and Monroe (1990) placed these genera with the North American sparrows. Last, *Emberiza*, the largest genus, remains amorphous and unwieldy.

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APPENDIX 1.   Species of Emberizinae recognized by Paynter (1970) but not examined in our study.

*Latoucheornis siemsseni, Emberiza leucocephala, E. jankowskii, E. buchanani, E. cineracea, E. impetuana, E. socotrana,
E. chysophrys, E. affinis, E. kaslowi, E. sulphurata, E. variabilis, Aimophila strigiceps, Phrygilus dorsalis, Nesospiza
wilkinsi, Poospiza alticola, P. erythrophrys, P. rubecula, P. baeri, P. caesar, Sicalis citrina, S. luteocephala, S. auriventris,
Embernagra longicauda, Sporophila frontalis, S. falcirostris, S. ardesiaca, S. melanops, S. nigrorufa, S. bouvreuil, S.
insulata, S. hypoxantha, S. hypochroma, S. palustris, S. cinnamomea, S. melanogaster, Amaurospiza concolor, Catamenia
oreophila, Camarhynchus heliobates, Arremon schlegeli, Arremonops tocuyensis, Atlapetes leucopis, A. flaviceps, A.
fuscoolivaceus, A. pallidiceps, A. semirufus, Oreothraupis arremonops, Pselliophorus luteoviridis, Chaitospiza euco-
soma, Paroaria baeri*

APPENDIX 2. Inflation of the squamosal area in the Emberizinae. Symbols in parentheses follow Tordoff (1954).

High inflated (S3, or S2 + S3)

Calamospiza, Zonotrichia[b], *Junco, Ammodramus*[b], *Spizella, Pooecetes, Chondestes, Amphispiza*[a], *Aimophila, Torreornis, Oriturus, Phrygiluls*[a], *Melanodera, Rowettia, Diuca*[a], *Catamenia*[a], *Pipilo, Melozone, Arremon, Arremonops, Atlapetes, Pezopetes*

Moderately inflated (S2, or S1 + S2)

Melophus, Calcarius, Haplospiza, Acanthidops, Idiopsar, Incaspiza, Nesospiza, Lophospingus, Piezorhina, Poospiza, Emberizoides, Embernagra, Sicalis, Volatinia[a], *Sporophila, Oryzoborus*[a], *Melopyrrha, Tiaris, Loxipasser, Loxigilla, Geospiza, Camarhynchus, Pselliophorus, Lysurus, Urothraupis, Coryphaspiza, Saltatricula, Gubernatrix*[a], *Coryphospingus, Rhodospingus, Paroaria*

Slightly inflated (S1)

Donacospiza, Xenospingus, Amaurospiza, Dolospingus, Melanospiza, Certhidea, Pinaroloxias

Inflation variable (S1, S2, or S3)

Emberiza[a], *Plectrophenax*[a]

[a] Observations disagree with those of Tordoff (1954).
[b] Observations disagree with those of Tordoff (1954) in his appendix but agree with his text.

APPENDIX 3. Form of the palatine process of the premaxilla in the Emberizinae. Symbols follow Tordoff (1954).[a]

Prominent (Pa1 or Pa2 in all specimens of a taxon)

4 species of *Emberiza, Sporophila obscura*, 3 species of *Tiaris, Loxipasser, Melanospiza*, 3 species of *Geospiza*[b], 2 species of *Camarhynchus*

Sometimes prominent (Pa1 or Pa2 in some specimens of a taxon but P3 in others)

Melophus, 10 species of *Emberiza*[c], 2 species of *Calcarius*[b,c], *Spizella pusilla*, 2 species *Phrygilis*[b], *Haplospiza unicolor, Diuca diuca, Poospiza hispaniolensis, Melopyrrha, Amaurospiza, Loxigilla noctis*, 2 species of *Camarhynchus*, 3 species of *Geospiza*[b], 3 species *Altapetes*[b], *Pselliophorus*[b], *Paroaria gularis*

Moderate or slight (Pa2 in some specimens of a taxon but Pa4 in others)

Emberiza poliopleura, Plectrophenax[b], *Melanodera melanodera, Sporophila nigricollis, Certhidea, Pinaroloxias, Gubernatrix, Paroaria dominicana*[b]

Slight (all specimens Pa3 and/or Pa4)

The remaining 37 genera and other species in the genera noted above

[a] Pa1, palatine process of premaxilla free of palatine; Pa2, palatine process of premaxilla adjacent to, but not fused with palatine; Pa3, palatine process of premaxilla fused with palatine but suture present; Pa4, palatine process of premaxilla completely fused.
[b] Our observations exhibit more variation than recorded by Tordoff (1954), with the process sometimes more prominent.
[c] Our observations exhibit more variation than recorded by Bock (1960).