

A Preliminary Study of the Fringillidae

Taxonomists have realized for years that the classification of the family Fringillidae was far from satisfactory. This paper is a report on preliminary studies of the family carried out under the direction of Drs. J. Van Tyne and George M. Sutton of the University of Michigan, and Dr. O. S. Pettingill, Jr. of the University of Michigan Biological Station. I am indebted to these men for helpful suggestions on methods of study and problems of interpretation of data.

Family Fringillidae

The family Fringillidae is made up of 426 species (Mayr, 1946a, p. 67) of birds variously called finches, sparrows, buntings, grosbeaks, etc. Sharpe (1909, p. 341) lists 139 genera in the family. However, the modern concept of larger genera in regard to included numbers of species would probably reduce this figure. The genera are grouped into three main subfamilies by most authors, with a fourth subfamily, the Fringillinae, proposed by Bushkin (1925, p. 256) and accepted by the current A.O.U. Check-list (1931, p. 318). The Fringillinae contains but one genus, Fringilla (Chaffinch and Brambling). The assemblage of finches peculiar to the Galápagos Islands may constitute a fifth subfamily, the Geospizinae. This is by no means certain, however, as Geospiza seems closely allied to Melanospiza, a Lesser Antillean emberizine genus (Bond, 1945, p. 150).

Ridgway (1901, p. 24) characterizes the Fringillidae as follows: "Conirostral, 'nine-primaried,' acutiplantar Oscines, with the commissure distinctly and more or less abruptly angulated or deflexed basally, or else with the

mandibular rami less than one-fifth as long as gonys, the mandibular tomium distinctly elevated (often angulated, sometimes toothed) post-medially, thence distinctly (usually abruptly) deflected to the rictus; rictal bristles obvious, usually distinct." The family is world-wide in distribution, except for the Australian Region and the extreme polar regions. Two fringillid genera, Acanthis and Plectrophenax, are probably the most northward ranging of all the passerines.

The Fringillidae present wide diversity in form and habit, but in general, possess stout conical bills adapted for seed-crushing. Since finches, as a group, tend to be less insectivorous than many other passerines, the Parulidae for example, they are on the whole, less migratory than the insect-eaters. Finches have invaded practically every type of terrestrial habitat, and as a result, they nest in a wide variety of situations. Some species nest on the ground only, some on the ground or at low elevations, and others in bushes or trees only. The nest may be only a crude platform of sticks (Pheucticus), a simple flimsy cup of grass (Passerherbulus henslowii), a substantial, well constructed cup (Acanthis), or even a spherical affair with a side entrance (Loxia passer, Tiaris). This latter type of domed nest is characteristic of many unrelated species of the New World tropics. In Jamaica, members of no less than three passerine families build globular nests. Sicalis flaveola, a South American finch which occurs (introduced?) in Jamaica, lays its spotted eggs in cavities in trees (Bond, 1947, p. 229). I know of no other similar case in the Fringillidae, though hole-nesting may be more common in Neotropical finches than

the literature indicates.

Since there is such diversity in structure and habits among the fringillid species, one might well ask if we are actually dealing with a single natural group of family rank. The conical bill is the only character which holds for all species in the family. In any birds, however, the bill is likely to become readily modified in evolution, owing, of course, to its great utility. Many families of passerine birds have, in fact, developed a conical seed-eating type of bill -- at least in some species. The Ploceidae are typically conirostral. In the Icteridae, Molothrus and Dolichonyx are familiar heavy-billed genera. Psittirostra, of the remarkable Drepaniidae, has a finch-like bill. The tanagers are a special problem -- they seem to grade into the finches in a manner that defies a natural delimitation of the families. When morphological characters are obscure or difficult to analyze, behavior patterns often give a clue to relationships. It must be remembered, however, that behavior itself is adaptive, and adaptive convergence in behavior in response to environment has been well documented (cf. Friedmann, 1946, pp. 395-398).

Subfamily Fringillinae

Within the Fringillidae there are, as already mentioned, four (or five) subfamilies. Of Fringillinae, containing but one genus (Fringilla), I know very little. Witherby et. al. (1938, pp. 104-107) say that both the Chaffinch (F. coelebs) and the Brambling (F. montifringilla) build well-constructed nests, that the female does all or most of the incubation, and that both sexes feed the young in the nest. The postjuvinal molt in both species is complete

except for the primary coverts, remiges, and rectrices. Both species are sexually dimorphic in color, though the duller female plumage is a result of decreased color-intensity and loss of certain patterns of the male plumage, rather than actual possession of characteristic patterns in its own right. Adults molt once a year, the breeding plumage being attained by wear. Juveniles resemble adult females.

I have not examined any skeletons of this group.

The Fringillinae are Palearctic in distribution, and if they are actually distinct from the Carduelinae and the Emberizinae, an Old World origin may be postulated for the group.

Subfamily Carduelinae

The subfamily Carduelinae is a predominantly Old World group, but one line (Spinus) apparently arrived early in America (Mayr, 1946b, p. 20), since a number of endemic species have developed even in South America, and since a closely related genus, Loximitris, is endemic in the Greater Antilles. Hesperiphona, with two species, is the only endemic North American cardueline genus, and it is closely related to Coccothraustes and, more especially, the Himalayan Mycerobas. The distribution of Hesperiphona clearly indicates an Asiatic origin. Hesperiphona vespertina has its center of abundance in the Northwest, while H. abeillii is a bird of the highlands of Mexico. Ridgway (1901, p. 38) gives the range of Hesperiphona as follows: "Western temperate North America, from British Provinces to highlands of Guatemala." The remainder of the North American carduelines belong to genera represented

in the Old World by closely related species or subspecies.

The North American species of the Carduelinae are arboreal as a group, at least more so than the Emberizinae. They all possess flight songs, and this is more remarkable when one considers that none of the species (except Leucosticte and, occasionally, Acanthis) are inhabitants of flat, treeless areas. Some North American emberizine species also have flight songs, but without exception they are forms dwelling in treeless plains, open fields, or tundra where elevated song perches are at a premium or else lacking. All North American carduelines build sturdy nests, although they are not necessarily of large size. Nests are placed in tall weeds, bushes, or trees at various elevations from the ground. Leucosticte (and occasionally Acanthis) nests on the ground, but ground nesting is not the general rule for the subfamily. Sexual dimorphism in color is strongly marked in most genera. However, Spinus pinus and S. notatus lack marked sexual dimorphism. In Carduelis, at least, of the Old World members of the group, males and females are also colored alike.

All adult carduelines have a complete postnuptial molt annually. Spinus tristis also has an extensive prenuptial body molt. Hesperiphona vespertina has (always?) a partial prenuptial molt of the head and neck (Magee, 1928, p. 149), while in Loxia, Acanthis, Pinicola, Spinus pinus, and Carpodacus purpureus there is probably no prenuptial molt (Forbush, 1929, pp. 6, 10, 14, 21, 26, and 30).

Juvenal Goldfinches (Spinus tristis) are unstreaked below, as are Evening Grosbeaks (Hesperiphona vespertina) and Pine Grosbeaks (Pinicola enucleator). In Loxia, Acanthis,

Spinus pinus, and Carpodacus purpureus the young are streaked below. According to Forbush (loc. cit.) the postjuvinal molt is complete except for the remiges, rectrices, and often the tertials and some wing coverts.

Of additional interest is the fondness for salt observed in the Evening Grosbeak, both crossbills (Loxia leucoptera and L. curvirostra), Pine Siskin (Spinus pinus), and Purple Finch (Carpodacus purpureus) (Roberts, 1936, p. 377). I have also noticed Pine Grosbeaks apparently eating dirt from recently salted roads near Morehouseville, in the Adirondack Mountains of New York, on January 2 and 3, 1942.

In contrast to the other fringillids with which I am familiar, it is noteworthy that the Goldfinch usually leaves the nest very dirty when the young leave. Weaver and West (1943, p. 502) report that in the Pine Siskin "the rim of the nest became fouled at the end of the nesting period." Dr. Sutton tells me that a Pine Siskin nest which he found in 1925 at Hull, Potter Co., Pennsylvania was also left in a run-down, untidy condition. As far as I know, this is not the case in either the Emberizinae or the Richmondinae.

Skulls of cardueline finches characteristically have a lateral projection of the anterior process of the palatines (see also Sushkin, 1925, pp. 257 and 258). One of the most notable features of the post-cranial skeleton is the relative shortness of the tarsometatarsus in comparison with that of non-cardueline finches. The humerus tends to be short and stocky, with the proximal end greatly dilated. The sequence of arrangement of

cardueline genera in the A.O.U. Check-list seems satisfactory to me, with two exceptions. First, I would reverse the positions of Carpodacus and Pinicola, since the former appears, on the basis of its bones, to be more closely related than the latter to Leucosticte. Second, the inclusion of Sporophila (1931, p. 321) in this subfamily is clearly erroneous. Regarding the position of Sporophila, Dr. A. Wetmore writes (in letter to J. Van Tyne, August 3, 1948) "..... I believe that I am responsible for removing it ~~/Sporophila/~~ from the position ~~/in the "Cardinalinae"/~~ given by Sushkin in his article in The Auk, 1925, p. 260..... Sporophila does not have the accessory palatine spine on either side of the palate that is found in the genera of Sushkin's subfamily 'Cardinalinae.' It belongs, therefore, in the Carduelinae....." Dr. Wetmore implies that mere absence of the accessory palatine spines of the Richmondinae (= Sushkin's Cardinalinae) indicates cardueline relationship. This is not true unless positive cardueline characters are present. Sporophila lacks the anterior laterad expansion of the palatines, does not have particularly short tarsometatarsi, and has humeri which definitely do not have cardueline conformation. Certainly the distribution of the genus -- "the whole of continental tropical America (southern Texas to Paraguay, etc.)" (Ridgway, 1901, p. 584) does not suggest Old World affinities. Sporophila is probably emberizine, although I am still uncertain about this.

Subfamily Emberizinae

The subfamily Emberizinae, which includes all of the North American "sparrows," towhees, longspurs, etc., is apparently of North American origin (Mayr, 1946b, p. 22).

There is considerable doubt as to which of the South American genera actually belong to the Emberizinae. Until this is determined, no final decision can be reached as to the origin of this, or the next subfamily, the Richmondinae. As Mayr suggests, there may have been a continuous faunal exchange between North and South America throughout the Tertiary (1946b, p. 22). If so, then it may prove impossible to determine definitely the centers of origin of the Emberizinae and the Richmondinae until or unless we find adequate early Tertiary fossil material.

One branch of closely related forms of the Emberizinae has reached the Old World. Over 30 endemic species have developed, but all belong to Emberiza or the doubtfully distinct Fringillaria, Milaria, or Melophus. Mayr regards this as evidence of an invasion of the Old World by the Emberizinae rather late in the Tertiary (1946b, p. 22).

The North American genera of the Emberizinae are more terrestrial as a group than either the Richmondinae or the Carduelinae. This is by no means without exception, however -- the cardueline genus Leucosticte is as terrestrial as any emberizine, while the richmondine (A.O.U. Check-list, 1931, p. 317) genus Spiza is also rather terrestrial. Spiza is a rather special case, however, because it is apparently an archaic genus with no marked affinities with any North American Fringillids (Sushkin, 1925, p. 281).

All North American species of the Emberizinae, with the possible exception of Spizella passerina, nest on the ground, at least some of the time. Nests not actually on the ground usually are placed at low elevations. Only four North American genera of the Emberizinae possess well-

developed flight songs (Rhynchophanes, Calcarius, Plectrophenax, and Calamospiza), although the Lark Sparrow (Chondestes grammacus) and probably others occasionally sing briefly while flying. Especially interesting is the fact that the four genera with flight songs also possess the most striking sexual dimorphism in color of the North American members of the subfamily. In the Red-eyed Towhee group (Pipilo erythrophthalmus and P. maculatus), the black of the male is replaced by brown in the female, but here again it is merely a matter of intensity of pigmentation. In Calamospiza, however, females have an entirely different pattern than do adult males -- as strikingly different as in the richmondine Rose-breasted Grosbeak (Pheucticus ludovicianus). In many other species of the Emberizinae, the males are brighter in color than the females, but with the same general patterns.

As I have already mentioned, nesting on or near the ground is the usual practice in this subfamily. Nests are fairly well constructed in most species, but in some, such as the Henslow's Sparrow (Passerherbulus henslowii) and the Vesper Sparrow (Poocetes gramineus), they are little more than loosely woven cups of grass, so flimsy that it is nearly impossible to collect a specimen.

All adult Emberizinae have a complete postnuptial molt annually. Some species, such as the Red-eyed Towhee (Pipilo erythrophthalmus) and the Song Sparrow (Melospiza melodia) have no prenuptial molt. Other species, such as the Swamp Sparrow (Melospiza georgiana), Chipping Sparrow (Spizella passerina), Field Sparrow (S. pusilla), Vesper

Sparrow, Lark Sparrow, Henslow's Sparrow, Savannah Sparrow (Passerculus sandwichensis), and Grasshopper Sparrow (Ammodramus savannarum) have a more or less extensive molt of the head in the spring (Sutton, unpubl. ms.).

Henslow's Sparrow is unstreaked below in the juvenal plumage (Sutton, 1935, p. 24), and is unique among Michigan Emberizinae in this respect. However, Leconte's Sparrow (Passerherbulus caudacutus), a member of the same genus, is sharply streaked below (see painting by Breckinridge, in Roberts, 1936, pl. 83). The postjuvenal molt is complete in the Grasshopper Sparrow and Henslow's Sparrow (as it is in the Cardinal (Richmondna cardinalis)), while the rest of the Michigan Emberizinae retain some or all of the remiges and rectrices during the first winter (Sutton, 1935, p. 9). In many, if not most, Emberizinae, the postjuvenal molt of body feathers begins before the juvenal flight feathers are fully grown. A "full" juvenal plumage is never attained in this case (ie. Red-eyed Towhee, Vesper Sparrow).

I do not know whether the male shares in incubation in most emberizines -- it certainly does not in many species (ie. Song Sparrow (Nice, 1937, p. 128) and Red-eyed Towhee).

In regard to osteology, the Emberizinae lack the lateral projection of the anterior process of the palatines which characterizes the Carduelinae. They differ from the Richmondeninae in lacking an accessory palatine process projecting posteriorly from the premaxillary lateral to the palatines. I am in doubt, however, as to the validity of this as a character for the Richmondeninae (see p. 14,

discussion of the osteological characters of the Richmondeninae). The palatines are not so massive in the Emberizinae as in the Richmondeninae.

Although a vast amount of work remains to be done on skeletons of this subfamily, I may make a few remarks on certain genera. Rhynchophanes is probably congeneric with Calcarius. Melospiza is, in my opinion, congeneric with Passerella (see also Linsdale, 1928, p. 339). It would be interesting to compare the bones of the large Aleutian Song Sparrow (Melospiza melodia sanaka) with those of a Fox Sparrow (Passerella iliaca) of equal size. The complex of genera composed of the "sharp-tailed" sparrows needs further study. Ammodramus probably is distinct. Passerculus seems to have no very close relatives. I do not believe, however, that Passerherbulus and Ammospiza can be separated on other than trivial characters. Indeed, Leconte's Sparrow seems closer to Nelson's Sparrow (Ammospiza caudacuta nelsoni) in many respects than to Henslow's Sparrow (see Ridgway, 1901, p. 212). The genus Aimophila contains a heterogeneous assemblage of species. Some of the Mexican and Central American species especially seem but distantly related to the North American species of the genus. This genus badly needs a thorough-going revisionary study.

Subfamily Richmondeninae

The subfamily Richmondeninae is apparently of South American origin (Mayr, 1946b, p. 25) although there is still some doubt about this (see discussion of origin of Emberizinae, p. 8). According to the A.O.U. Checklist (1931, pp. 312-317) only six genera of the Richmondeninae are resident within the limits of the United States, while

Tiaris, which is resident in Mexico and the West Indies, has been recorded as an accidental in this country (see discussion of position of Tiaris, p. 14).

The North American genera of the Richmondeninae are more arboreal as a group than the Emberizinae. They nest at various heights from the ground. The Indigo Bunting (Passerina cyanea) often builds in low bushes within a foot or two from the ground, while the Cardinal may nest in a tree as high as 30 feet. The Dickcissel (Spiza americana) is, as already mentioned, an aberrant species which frequently nests on the ground.

Nests of richmondenines are usually well-constructed, although the Rose-breasted Grosbeak (Pheucticus ludovicianus) makes a loose and openly built nest of rootlets, small twigs, and weed stalks. The nest of the Cardinal is only slightly more substantial.

As far as I know, most richmondenines do not have a well-developed flight song, although male Rose-breasted Grosbeaks and Indigo Buntings occasionally sing while flying. Tiaris olivacea, bicolor, and canora frequently deliver their buzzy songs while in flight -- at least in the West Indies. The Cardinal is unusual in that the female sings nearly, if not quite, as well as the male. Female Rose-breasted Grosbeaks and female Black-headed Grosbeaks (Pheucticus melanocephalus) also sing, although not as well as the males.

Sexual dimorphism in color is apparently the rule in this group. It is not as striking in some genera (ie. Pyrrhuloxia) as in others (ie. Pheucticus), yet there are no exceptions in the species found north of Mexico.

Of the Central and South American species we cannot be sure until their relationships are more fully understood. Regarding the subfamily as a whole, it probably would be wise not to be dogmatic until the limits of the group have been satisfactorily defined.

Adult richmondenines have one complete molt annually -- the postnuptial. Many, such as the Indigo Bunting and Rose-breasted Grosbeak, also have an extensive prenuptial molt of the body plumage. On the other hand, the Cardinal has no prenuptial molt whatever (Sutton, unpubl. ms.).

The Indigo Bunting has a more or less heavily streaked juvenal plumage. On the other hand, in the Rose-breasted Grosbeak the white natal down is followed by a juvenal plumage which is very lightly, if at all, streaked below. (It may be of interest to note here that the natal down of the Dickcissel is also pure white (Gross, 1921, p. 170)). The unstreaked juvenal plumage of the Cardinal is similar to the adult female.

The postjuvenal molt is complete in the Cardinal. Blue Grosbeaks (Guiraca caerulea), Dickcissels, and Rose-breasted Grosbeaks do not lose their wing and tail feathers in the postjuvenal molt (Forbush, 1929, pp. 112, 115), while Indigo Buntings may molt some or all of their tail feathers and sometimes five or six distal primaries (Dwight, 1900, p. 212).

Both sexes of the Rose-breasted Grosbeak incubate the eggs and brood the young. On the other hand, I doubt if the male Indigo Bunting ever visits the nest after the eggs are laid (Bradley (1948, p. 113) agrees with this), although the male often takes complete charge of the fledglings while the female starts another brood (Sutton,

unpubl. ms.). Male Cardinals do not incubate, but they do feed the young in the nest.

The Richmondinae is a difficult group to characterize osteologically. Most genera which I have examined (Richmondina, Pyrrhuloxia, Rhodothraupis, Saltator, Pheucticus, Melopyrrha, Cyanococcyz, Passerina, Spiza) are readily distinguished from other fringillids in that they have an accessory spine on either side of the palatines. This accessory spine occurs, however, in many tanagers. Indeed, Saltator seems closer to Piranga than to Richmondina! Sushkin (1924, p. 38) wrote that "Pitylus and Saltator are thick-billed Tanagers." Guiraca and Tiaris olivacea both lack the accessory spine, while it is present in Tiaris canora! Furthermore, some tanagers (Spindalis and Habia, for example) lack the accessory spine. The inconstancy of the presence of accessory palatine spines perhaps indicates that they are not reliable as taxonomic characters. I think it more likely, however, that the inconstancy indicates unreliability in our classification rather than in the taxonomic characters.

Although I am as yet unable to interpret the significance of the palate structure in the Richmondinae, the conclusion that they are closer to the Thraupidae than to the rest of the Fringillidae seems inescapable.

Conclusion

I have attempted to summarize in broad outline the relationships and habits of the Fringillidae. I am not yet certain enough of many points to propose any changes in the present A.O.U. classification, yet I am convinced that it is far from satisfactory. I dislike unnecessary changes in nomenclature -- changes, for instance, based on a bit

of obscure priority, yet I would be satisfied to see great violence done to the present system if it aided in reaching a better understanding of relationships.

If many of my statements seem dogmatic or to generalize too broadly, it is because I feel that excessive qualification of principles that are reasonably valid for a group as a whole tends to destroy the meaning of the principles. For instance, Chipping Sparrows very rarely nest on the ground -- indeed, they usually nest higher than Indigo Buntings. Yet the general statement that the Emberizinae as a group are more terrestrial than the Richmondininae is both valid and significant.

The classification of the Fringillidae is by no means complete. Except for some European and North American species, little is known of their life histories. Since it will be many years before adequate life history data are available, I believe that anatomical studies, correlated with life history data as they are made available, will enable us to formulate a more natural classification of this and related families in the shortest possible time.

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