REMARKS ON THE ORIGIN AND DISTRIBUTION OF THE ZONOTRICHIAE.

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IN practically all parts of the globe are found the Fringillidae, perhaps the largest and most cosmopolitan group of birds generally recognized as a family. Yet in the great number of species, certain well defined subgroups may be recognized, and approximate lines of division and general characterizations may be made for each. One of these groups is that containing the Crossbills, Pine Grosbeaks, Purple Finches, House Finches, Longspurs and their allies. This group is of circumpolar distribution, and, from the fact that many more species are found in Asia than in America, it is generally regarded as having originated in the Palearctic Region, invading North America through Alaska. A no less interesting group is that of which the Buntings of Europe are typical.

We call our melodious White-throat a "Sparrow," and Song Sparrow and Fox Sparrow are well recognized names. Nevertheless "Sparrow" in the strict sense should be applied only to that group of which the House Sparrow, (*Passer*), is typical, and our White-throated and Song and Fox Sparrows are, in their relationships, Buntings.

I have no new races to propose, or ranges to extend, but I wish merely to suggest an interpretation of the origin and dispersal of that group of genera which Ridgway has called the Zonotrichiae, together with certain Asiatic genera placed in the Emberizinae by Sharpe.

The material for this study has been drawn from the data in such standard works of reference as Ridgway's 'Birds of North and Middle America,' Sharpe's 'Fringillidae' of the British Museum Catalogue, Brabourne and Chubb's 'Checklist of South American Birds', Hartert's 'Die Vögel der paläarktischen Fauna,' and Reichenow's 'Die Vögel Afrikas.' The revisions

[1] Read at the Pittsburgh meeting of the American Ornithologists' Union November, 1924.

of *Buarremon, Junco* and *Arremonops* by Dr. Chapman, Dr. Dwight and Mr. Todd respectively, have also been consulted.

The Zonotrichiae are found practically throughout North and South America, and as many as nineteen genera are found north of Panama. While the lines of generic division are admittedly tentative, the relationships of the genera are fairly well established, and the possible future restriction or amplification of certain of these or the suppression of others will make little difference in such a problem as this. On plotting the ranges of each species and subspecies, one cannot fail to notice that by far the greater number of forms and individuals are found at a point about midway between the extremes of the range, namely at the southern end of the Mexican tableland. To the north are found those genera which in pattern of coloration more or less closely resemble one another, a pattern of brown, buff, gray and black streakings. Such are *Junco, Zonotrichia, Plagiospiza, Aimophila, Amphispiza, Spizella, Melospiza* and *Passerella,* while *Brachyspiza* extends south along the Andes to Tierra del Fuego. South of the Mexican plateau are found those genera which are characterized by more brilliant coloration and more diverse pattern, their plumage being green, yellow, chestnut, black and grey, and the areas of color in masses rather than in streaks. Such genera are *Melzone, Arremonops, Arremon, Buarremon, Lysurus, Atlapetes, Pselliphorus* and *Pezopetes,* while two, *Pipilo* and *Oberholseria* venture northward. The genera with which this paper is primarily concerned are those of the first group which are found principally in the Nearctic Region.

In the Old World is found a rather uniform genus, *Emberiza,* in which, in the Palearctic Region alone, Dr. Hartert places twenty-nine species. This genus ranges from northeastern Asia west through Europe and south to India and Africa. It is not found in the Indo-Malayan or Australian Regions. On the whole the various species of *Emberiza* are rather small Buntings, generally smaller than any member of the genus *Zonotrichia,* either brownish and streaked, with various patterns of white, brown, black and yellow about the head as in *Zonotrichia,* or brilliant yellow below. Those forms which are yellow below are better developed in Europe and Africa, and one of the principal characters on which the

Emberizinae is founded, the development and swelling of the palate, is most pronounced in *Miliaria*, a European and western Asiatic species, which is recognized by some as a monotypic genus, but by Dr. Hartert, placed in the genus *Emberiza*. *Fringillaria* found in the southern part of the Palearctic Region and in the Ethiopian Region differs, together with *Miliaria*, from the New World forms and less so from *Emberiza*, by having the mandibular and maxillary tomium curled inwards, which in conjunction with the development of the palate must form a most efficient instrument for cracking hard seeds.

Before proceeding with any discussion of point of origin or dispersal, I will state my hypothesis and then discuss in more detail the various reasons for believing it to be probable. The Zonotrichiae, at least the ancestral stem of the group, arose somewhere in Central America, probably between Panama and central Mexico, in the early Tertiary. One branch extended southward differentiating into that group of genera which has already been mentioned. The other branch extended to the north, crossed to Asia by way of Behring Straits, and gave rise to the group now known as the genus *Emberiza*.

First let us look at the geographical conditions which prevailed in the Tertiary Period in the Western Hemisphere. According to W. D. Matthew, from the end of the Cretaceous to the beginning of the Pliocene, North America was separated from South America at the Isthmus of Panama, and during the middle Eocene there were further divisions at Tehuantepec and at Nicaragua. Likewise, from the end of the Miocene to the end of the Pliocene, Alaska was connected with Asia across Behring Sea. In the Pleistocene however, the advance and retreat of the Great Ice Cap may have been connected with the repeated uplift and downwarp of the continental masses. The exact number of advances of the Ice Cap and the bridging of the eastern and western hemispheres at Alaska during this period is a matter of dispute among geologists today, but there is fairly good evidence that Siberia and Alaska were in much closer relation to each other during the Pleistocene, if not actually continuous.

The climate of the Tertiary period is equally interesting, for as Matthew says, "Climate and environment are more important

in the dispersal of birds, than are geographical barriers." At the end of the Cretaceous Period, there was a long era of warm, moist climate. Through the succeeding periods the temperature fell gradually at first and more rapidly later, culminating finally and abruptly in the Ice Age of the Pleistocene. Cockerell may be quoted as saying that "the climate of Colorado in the Miocene was warm and moist with no heavy snows during the winters, although the altitude was about the same as now." During the Pleistocene, a marked change occurred, periods of extreme cold being followed abruptly by periods of warm, moist climate. The interglacial periods, the Gunz-Mindel in particular were of greater duration than the glacial periods and the climate was probably warmer even than it is today. A period of rapid climatic and environmental change is much more favorable for the evolution and differentiation of species than is a monotonous environment, even though favorable, and it is during one of these interglacial periods, I believe, that the ancestors of *Emberiza* crossed from Alaska to Asia.

But why, I am sure you ask, did this extension of range take place from east to west, instead of from west to east as so many other migrations through Alaska are supposed to have done? It would of course be foolish to assume that during the period of connection there was no interchange of faunas from the two continents,—to say definitely that all movement was from America to Asia. An examination of the more distant relatives of the group Zonotrichiae discloses my reasons for thinking that it is not of Asiatic origin. The Tanagridae and Fringillidae have so many connecting links that no one has yet been able to draw a line dividing the two families which was satisfactory to all of his contemporaries. On the other hand, the closest relatives of the Fringillidae in the Old World, the Ploceidae, while admittedly an old group as shown by their retention of a primitive tenth primary, are nevertheless quite distinct. In the New World the Fringillidae have on one side the Icteridae and on the other, the Tanagridae, Mniotiltidae and Coerebidae which merge almost imperceptibly one into the other.

There are two rather radically opposed views in explaining the origin and dispersal of animals. Briefly, the two schools differ

on the following point: one postulates the theory that the most primitive forms are found farthest from their center of origin, the other that the most advanced and specialized forms are found farthest from the center of origin. It would be difficult to find two theories attempting to explain the same thing, more different than these. Personally I believe that neither one nor the other is invariable. The conditions under which the species evolved, certainly must be the controlling factors. If the environment at the center of dispersal was radically changeable, the ancestral forms would be forced to seek more favorable conditions and would be found at the periphery of the range. If the environment at the center of dispersal was uniform, then the outlying members of a species would either be driven back to their original place of origin, or would be modified to adapt themselves to new conditions, and the most specialized forms would then be found at the periphery of the range.

C. C. Adams has formulated ten criteria for the determination of centers of dispersal, and while I do not believe that set rules will solve any particular problem, it is interesting to apply these to the question in hand.

The first criterion is the location of the greatest differentiation of type, and the area where the greatest number of species is found. This most certainly is in southern Mexico where over forty species and subspecies belonging to ten genera occur within several hundred miles. Four genera occur only to the north and four only to the south.

Second, is the dominance or greatest abundance of individuals. This I believe also to be in southern Mexico.

Third is the location where the most closely related species are to be found. In northwestern Asia there are many species of *Emberiza* which differ only slightly one from another. Moreover they differ but little more from *Zonotrichia* which extends up the eastern side of the Pacific to Alaska. Some of the species in coloration and pattern might well be taken for *Zonotrichiae* and one was even described in *Junco* so similar is it to the latter genus. This seems to be an indication of the close relationship of these groups, the environment in the northern Hemisphere during the Quartenary having been such as not to have caused

radical differentiation. The primary center of closely related species seems to be, however, in southern Mexico, where within any one of the ten genera before mentioned, the species and subspecies occurring near Mexico City differ only in slight degrees of color and measurements.

The fourth criterion is the location of maximum size of individuals. The largest individuals are found in the genera *Miliaria, Zonotrichia* and *Buarremon.* In the case of the first two it seems to be a specialization for cold weather and migratory habit, while in *Buarremon* it may be a sign of senescence or due to uniform favorable environment.

Fifth is the location of greatest production. This cannot be answered from the data at hand, but it seems probable that the greatest production takes place in colder regions where almost universally the number of eggs laid is larger than in the tropics.

Sixth, is the continuity or convergence of the lines of dispersal. In the western states and the Canadian Rockies, *Spizella, Junco, Melospiza, Passerella, Zonotrichia, Amphispiza,* and *Pipilo* have their point of greatest differentiation, while in South America *Buarremon, Arremon, Arremonops,* and *Atlapetes* are most greatly differentiated in Colombia, Bolivia and Ecuador, and *Brachyspiza* occupies with its three species and thirteen subspecies the length of the Andes. It seems that the lines of dispersal are in general north and south, converging in southern Mexico, while in Asia the line of dispersal seems to run from northeastern Siberia through Europe to Africa, using as characters the development of the palate and tomium, and the change from streaked underparts and upperparts to the more uniform yellow of these areas. Under this same discussion should go the seventh criterion, the continuity and directness of individual variation and modification radiating along highways of dispersal.

The eighth criterion, is the direction indicated by annual migration routes. This is probably so modified by present climatic conditions, that little remains of the original line of dispersal. The Yellow Wagtail, the Wheatear, and the Willow Warbler, breeding in Alaska migrate back to Asia, and the Greenland Wheatear migrates to Africa through Europe. There is no trace of such migration among the Emberizinae, but they have probably

been resident in Asia a much longer time than have the Wagtail and Wheatear been in Alaska. In this connection, even though the general trend of migration is from north to south, it is interesting to note that the three races of *Zonotrichia leucophrys* may be found in winter in Lower California, and that, in general, the members of the genera breeding in the far North migrate farther south than is apparently necessitated by climatic conditions.

The ninth criterion, the location of least dependence on restricted habitat, and the tenth, the direction of dispersal indicated by biogeographical affinities, I have not been able to apply in the present case.

In conclusion, I believe that the evidence presented indicates that the group *Zonotrichiae* originated somewhere between Panama and the Rio Grande, that one branch spread south, differentiating into the group of genera characterized by *Buarremon* but retaining the general type of coloration and structure of its tanagrine-fringilline ancestor, that another group spread north, typified by *Zonotrichia*, and crossing Behring Sea at a time when favorable climate and land connection existed, probably in the early Pleistocene, gave rise to *Emberiza*.

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From pencil drawing by W. Rowan

HYBRID GROUSE (A) (*Tympanuchus a. americanus* × *Pedioecetes phasianellus*).