A PRELIMINARY SURVEY OF TRENDS IN AVIAN EVOLUTION FROM PLEISTOCENE TO RECENT TIME

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In birds there has been little opportunity to observe evolution within individual groups. It is true that by means of the Jurassic archaeopterids the reptilian ancestry of the class as a whole has been made remarkably clear. And the toothed forms of the Cretaceous have brought to light the very early beginnings of adaptive modifications. Of the evolutionary lines of various avian orders or families, however, little can be said.

A few Eocene forms point to the common ancestry of certain closely related present-day families or subfamilies. The Hungarian *Eostega*, for example, apparently links the boobies and cormorants, and *Romainvillia* of France may have represented a group from which both ducks and geese were derived. But there are no avian fossils which provide a good consecutive series of evolutionary stages, such as have been found among the mammals in the horses, camels, and dogs.

Bird bones are extremely fragile, and as a consequence frequently have not survived the upheavals and metamorphic disturbances to which the older strata have been subjected. Rarely are the elements of a bird skeleton found associated. Dissociated elements are not a very satisfactory substitute, especially since, in the birds, there is nothing comparable to the dental battery of mammals which holds up well under fossilization and contributes the most valuable type of information on evolutionary progress.

Another difficulty encountered in attempting to study avian evolution is the apparent slowness with which changes have been effected in this group. Miocene birds, for example, can be assigned in many instances to modern genera, and the similarities of skeletal structure between Miocene and Recent birds are remarkable. This is a very different situation from that which obtains among the mammals, where each geologic epoch of the Tertiary brought its marked changes in structure. Among the birds, therefore, we are grateful for the slightest knowledge pertaining to evolutionary trends.

Approaching the Recent epoch, avian fossils become more abundant and in some of the Pleistocene deposits of the west coast, we have an opportunity to examine thousands of specimens. In spite of the dissociation of skeletal elements in these deposits, the great numbers of bones make possible secondary association which presents, with a fair degree of accuracy, an idea of the skeleton as a whole. Although in many instances the species which occur represent almost the end result in a long line of evolution which is obscured, it is now becoming evident that something of the evolutionary trend may be revealed by careful analyses of the large series available in contrast with series of skeletons of modern birds.

Examining the contents of these Pleistocene deposits, it is, of course, the extinct species (the forms which are obviously different from those of today) which first draw attention. Each record of a fossil locality centers around descriptions of new forms, with a few appended remarks on other species found. The great Pleistocene asphalt deposits of Rancho La Brea, for example, are noted for the occurrence of the huge vulture, *Teratornis*, the several species of strange eagles, the large stork, and others. These are naturally of interest and of importance in obtaining a knowledge of prehistoric bird life. But even more significant are the much less glamorous, although very much more abundant species which tie into our modern picture. At Rancho La Brea there are over 90 species which are almost or entirely indistinguishable from living birds, and only 15

which have left no modern descendants. Nearly 90 per cent, then, of the avian species in this typical Pleistocene deposit are a significant source of our present avifauna. This is in marked contrast with the mammalian assemblage from the same locality; over 40 per cent of the mammalian species recorded there are now completely extinct.

Surveying the Pleistocene avian picture of the entire west coast, the situation is very much the same. We find 36 species of birds which are so distinctive that they cannot possibly be considered ancestral to any living form. These include several water birds, a large number of raptors (mostly of large size), and a few other land birds. Some of the extinct forms represent groups which may have had a long history in our area, but are today found elsewhere. Such examples are: the Del Rey Gannet, *Moris reyana,* which was apparently one of the last of the sulids in California, where, since at least Miocene time, the Sulidae had been well represented; the "Pigmy Goose," *Anabernicula,* possibly of shelldrake affinity, which appears in the Pliocene of Arizona and in both California and Oregon in the Pleistocene; and the two aegypiine representatives, *Neophrontops americanus* and *Neogyps errans,* whose ancestors were known in America well back into the Miocene. Others appear and disappear with the Pleistocene, having left no clue, as yet discovered, as to their past.

The remainder of the fossil avifauna of the Pacific coast, some 150 species, is probably directly related to the avifauna of today. Among the members of this group there has been some shifting in local distribution in keeping with changing ecologic conditions, and, in certain instances, there has been slight structural change within individual species (or, perhaps we should say within the ancestral line of a species), but in general the Pleistocene picture, once the obviously extinct species are eliminated, is remarkably similar to that of today.

It is the occurrence of the slight structural changes which merits particular consideration. In a few instances it has recently been discovered that series of Pleistocene bones are not identical with comparable modern series and yet are so similar as strongly to suggest direct ancestral relationship. Some such instances have been discovered within groups thought at first to be identical with modern forms, and others have resulted in the combining of two species, one of which had been previously recorded as extinct, the other as modern. The present status of these "ancestral" Pleistocene forms is varied, about half bearing distinct names, the others classified under the name of the related living species. Their proper taxonomic treatment presents a problem which has been made the subject of a separate discussion by the present author (Auk, in press).

Turning now to a discussion of these occurrences which have recently been given attention, it is appropriate to consider first the raptorial birds. These, by reason of the character of the California asphalt deposits, are particularly well represented in the west coast Pleistocene record. There are, in addition to the extinct species, about 30 forms which are similar to birds of the Recent epoch. Some of these appear to be identical with the living representatives. Others, however, reveal small differences.

Outstanding among the raptors which have been found to differ slightly in their Pleistocene form are the California Condor and the Golden Eagle, both of which have been previously recorded from the Pleistocene by the scientific names today applied to the living birds. The condor now has been combined with a Pleistocene species described earlier from northern California, *Gymnogyps amplus* (Fisher, Condor, 46, 1944:289-290); the status of the eagle has not yet been decided. Careful studies were made of large series of skulls of each of these raptors from the Rancho La Brea asphalt deposits (Fisher, *loc. cit.*; and Howard, Auk, in press). These studies revealed structural differences from the modern birds, so slight as to have been unnoticed, or considered merely

variants from the norm, had there not been so large a number of specimens for examination. Although in only one or two instances actual measurements of the fossils fail to overlap similar measurements on the modern related species, ratios of one part of the skull to another widen the gap sufficiently to distinguish the two populations in each case. Only in the skull, however, are these distinguishing features marked. The rest of the fossil skeletons, except for slightly different size range and possible differences in proportions of leg to wing, appears to be structurally identical with the modern.

It seems logical to conclude that in this fossil representation we have the direct ancestors of the modern Golden Eagle and California Condor. A comparison of fossil with Recent specimens, therefore, reveals the minuteness of change which has taken place over a period of some 50,000 years or more. In the case of the eagle, we may postulate that the changes were adaptive. The strong jaws, and the musculature to operate them, which characterized the Pleistocene form, were appropriate for the day in which it lived—the day of larger mammals. As smaller forms began to dominate the scene, the need for heavy equipment to cope with larger prey would, presumably, have diminished. Possibly some similar explanation may account for the changes within the condor. In both of these birds we see reflected the trend toward smaller size (from Pleistocene to Recent time) which, in the over-all picture of the raptor group, is observable in the extinction of the larger eagles and vultures, and the increased abundance of the smaller hawks and owls.

In the Rancho La Brea Caracara (*Polyborus prelutosus*) the situation is slightly different. The characteristics of the bones of this bird tend to blend together those of both living species of *Polyborus* and also to resemble the Guadalupe Island species, extinct within historic time (Howard, Carnegie Inst. Wash., publ. no. 487, 1938:217-240). For this reason the earlier records of the bird referred it first to *Polyborus tharus,* and later to *P. cheriway,* with the suggestion, also, that possibly both species were represented.

Distinguishing characteristics are discernible in several skeletal elements in the Rancho La Brea Caracara, with, however, an overlap of the fossil form with all three Recent species. Whether or not the Pleistocene bird was actually ancestral to all of the Recent species is problematical. In view of the very slight changes observed in other groups, this is doubtful. There seems little question, however, that the Guadalupe Island bird was descended from Pleistocene stock very similar to the La Brea bird. The differences noted between the island species and the fossil bird are of about the same degree as those noted for the two populations of the Golden Eagle, or of the California Condor.

Among the nocturnal predators, it is likely that the Horned Owl may be included among the forms which have undergone some structural change since Pleistocene time. Measurements made some years ago on series of specimens from Rancho La Brea indicated that the fossil bird averaged larger than its modern representative, although, at the time, the great variability in size was stressed more than the larger average (Husband, Condor, 26, 1924:220-225). It has since been discovered that some of the specimens included in the measurements belong to another, somewhat smaller and more slender species, now described as distinct (*Strix brea* Howard, Condor, 35, 1933:66-69). Removal of these specimens from the series raises the average size of the Rancho La Brea Horned Owl, and, at least in the humerus, eliminates the smaller bones which had been previously compared with the minimum measurements of the modern owl. It is possible, also, that the large *Bubo sinclairi,* from the Pleistocene cave deposits of northern California, is only racially distinct from the Horned Owl of Rancho La Brea. Actually it exceeds only very slightly, if at all, the maximum size for the latter form. Both

the Rancho La Brea series and the specimens from northern California merit careful review.

Among aquatic birds there are two instances in which related modern and extinct forms were reported from the same Pleistocene deposit, namely, the lacustrine beds of Fossil Lake, Oregon. In each case the specimens, when assembled and examined as a whole, indicated the presence of a single species, varying from the related modern bird, but overlapping it as well (Howard, Carnegie Inst. Wash., publ. no. 551, 1946: 148-151, 182-183). The most outstanding of these instances is that of the Western Grebe (*Aechmophorus occidentalis*), of which excellent series of from 30 to 60 specimens for each element are available. The greatest difference between the Pleistocene and Recent grebe populations was found in the tarsometatarsus, the earlier form tending to have a longer, heavier-shafted bone, with, however, a narrower proximal end. Most other skeletal elements, too, showed an average greater length, although this was most marked in the leg elements.

The other species is the Coot (*Fulica americana*), the Pleistocene form of which averaged longer in the leg elements and shorter in the wing bones. It was upon the smallest of the wing bones that the separate species *Fulica minor* was erected. The proportions of leg to wing, however, were well within the variational limits of coots rather than of gallinules. Studying the series of bones of the grebe and of the coot left no doubt in my mind that the Pleistocene populations were ancestral to the living forms.

The foregoing survey, concerned with six examples of change within different avian forms from Pleistocene to Recent time, constitutes a preliminary step in the investigation of evolutionary trends by comparison of large series of specimens from contiguous geologic epochs. The occurrences cited are important to the student of evolution. The spottiness of the fossil record of life as a whole has tended to present a picture of evolution as a series of steps. These studies, which span but a single geologic epoch and which provide an opportunity for examination of large groups of individuals, give evidence of what goes on *between* steps.

The few examples already noted indicate that our modern avian forms did not spring abruptly from some unknown Tertiary ancestors, but that they have gradually assumed their present form through minute changes taking place over thousands of years. The examples cited here appear to demonstrate these changes, and in some instances, even to demonstrate trends of development within individual species. At the same time, however, they emphasize the minuteness of the change which can be expected over a period of 50,000 to 100,000 years. It is no wonder that we must go back several million years to observe any marked difference in avian forms—120 million years to the toothed birds of the Cretaceous, 150 million to *Archaeopteryx*.

It is regrettable that materials are not available to make possible comparisons of the kind discussed above between birds from some of the earlier geologic epochs. Possibly later discoveries may increase our collections from the Tertiary. The survey of the Pleistocene birds, however, will continue, and it is anticipated that many more instances of slight differences between Pleistocene and Recent forms will come to light. When all such occurrences can be examined together, they should, without doubt, add significantly to our understanding of the nature of evolutionary trends among birds.

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