THE WILSON BULLETIN

A QUARTERLY MAGAZINE OF ORNITHOLOGY

Published by the Wilson Ornithological Club

1946 Number 1

Vol. 58 MARCH ISSUE Pages 1–68

HISTORY OF THE NORTH AMERICAN BIRD FAUNA

BY ERNST MAYR

THE bird student cannot help becoming envious on observing with what accuracy and amazing detail the student of mammals reconstructs the history of that class. Rich finds of fossils have enabled the paleomammalogist to determine the probable region of origin not only of families but also of genera, sometimes even of species, and to trace past modifications in their ranges. The student of birds is far less fortunate. Bird bones, being small, brittle, and often pneumatic, are comparatively scarce in fossil collections. The majority of Tertiary species of birds described from North America belong to zoogeographically unimportant families of water birds. Even fewer fossil birds are known from South America. The absence of certain families or orders from the fossil record of either North or South America proves nothing as far as birds are concerned. Furthermore, the history of birds is more difficult to reconstruct than that of mammals for two other reasons. Birds seem to be a more ancient group than the mammals, many or most of the Recent families having been in existence at the beginning of the Tertiary. And secondly, since birds cross water gaps more easily than mammals, the isolation of a land mass does not necessarily result in the isolation of its bird fauna. It would seem on these premises that it would be almost impossible to trace the history of the components of a local bird fauna, but this is by no means the case. Indirect methods of faunal analysis lead to fairly reliable results, since most families of birds are rich in genera and species. A quantitative analysis is, of course, impossible in small families, and their place of origin (as, for example, that of the limpkins) can be determined only with the help of fossils. In a paper read in 1926 before the International Ornithological Congress at Copenhagen, Lönnberg (1927) demonstrated the productivity of the indirect method by applying it in an investigation of the origin of the present North American bird fauna. Although most of Lönnberg's conclusions are still valid today, so much additional knowledge has accumulated during the past 20 years that a fresh analysis seems timely.

BLUE-CROWNED MOTMOT

Momotus momota coeruliceps

The northernmost genus of the motmots, which belong by origin to the North American Element. From a water color made by George Miksch Sutton near Gomez Farias, Tamaulipas, Mexico, April 24, 1941.

Faunal and Regional Zoogeography

There have been trends and fashions in the science of zoogeography as in any other science. The zoogeography of the nineteenth century—the classical zoogeography of Schmarda (1853), Sclater (1858), and Wallace (1876)—was merely descriptive, essentially regional, and non-dynamic. It was based on the premise that different parts of the world are inhabited by different kinds of animals; and each of these major areas was called a zoogeographical region. This method seemed successful while knowledge of the distribution of animals was still incomplete. As far as the boundaries between these regions were concerned, it was recognized that they "depend upon climatic conditions, which are in a measure determined or modified by features of topography" (Allen, 1893:120). However, as the various parts of the world became better known, it became evident that the various regions proposed were of unequal value. This led to the proposal of new regions or to the fusion of previously separated regions into larger units. It is impossible to give here the history of the never-ending attempts to find a "perfect" zoogeographical classification. For example, it was soon found that the fauna of North America was somewhat intermediate between that of Asia and that of South America, which resulted in conflicting proposals concerning the zoogeographic position, or rank, of North America.

According to one school, North America was only part of a larger region combining North America, Europe, and north Asia. Gill (1875:254) called this region the Arctogaean, while Heilprin (at the suggestion of Newton) called it the Holarctic (Heilprin, 1883:270). This region (with the Palearctic and Nearctic as subregions) is perhaps even today the most frequently adopted zoogeographical classification of the northern hemisphere. Reichenow (1888:673 ff.) took emphatic exception to this classification. He showed that, as far as birds were concerned, North America was much closer to the "Neotropical" than to the Old World, and that North and South America should be combined in a "Western Zone" or "New World Region." This point is well substantiated by his statistics. J. A. Allen (1893:115) showed that the Old World element in the warm temperate parts of North America amounted to only 23 to 37 per cent of the genera, but he did not draw any conclusions from these figures. Subsequent writers almost completely ignored Reichenow's conclusions. Heilprin (1883) went to the opposite extreme. He refused to recognize the Nearctic even as a subregion. He drew a zoogeographic boundary right across North America, putting the northern half into the "Holarctic Region," the southern half in the "Neotropical Region." Wallace himself thought (1876:66) that it was a question "whether the Nearctic Region should be kept separate, or whether it should form part of the Palaearctic or of the Neotropical regions." The literature, particularly of the 1880's and 1890's, was filled with discussions of this question.

Eventually it was realized that the whole method of approach—*Fragestellung*—of this essentially static zoogeography was wrong. Instead of thinking of fixed regions, it is necessary to think of fluid faunas. As early as 1894, Carpenter said: "No zoological region can be mapped with the hard and fast line of a political frontier, and the zoologist must always think more of faunas than of geographical boundaries" (1894:57). The faunal approach made slow but steady progress in Europe and in America. In Europe it has led to such excellent studies as those of Stegmann (1938a) on the birds of the Palearctic and of Stresemann (1939) on the birds of the Celebes. In America it was E. R. Dunn who was the pioneer of this concept. In a spirited attack on the older, static, regional zoogeography, he stated (1922:336):

> There has been a constant search for some sort of scheme whereby ranges of animals might be reduced to a common denominator. . . .
>
> By far the most generally used of these philosophical methods is that of Realms, Regions and Zones. These are all based on the idea that large numbers of species have the same range, and that by picking out some of the conspicuous forms and mapping their ranges one has *ipso facto* a set of regions, to which other ranges may be referred, and with which other ranges should agree.
>
> This is, in some degree, true, but in nearly every case in which the ranges of any two species agree, the agreement is due to the geographic factors and not to the zoologic factors.
>
> It is obvious that the zoogeographical realms are nothing save and except the great land masses with lines drawn to corespond to the physiographic barriers. There is a great philosophical difference between such terms as Holarctic Fauna and Holarctic Region. In the first case we speak of zoological matters in terms of zoology, in the second of geographical matters in terms of mythology.
>
> The Palearctic fauna is an aggregate of species and may invade (in fact *has* invaded) Australia without forfeiting its name.

Following up these thoughts, Dunn (1931:107) analyzed the reptile fauna of North America and found that it could be classified into the following three groups:

> (1) A northern, circumpolar, modern element. This would be truly *Holarctic.*
>
> (2) A more southern, older element, which I shall call *Old Northern.* . . .
>
> (3) A still more southern, still older element, the original fauna of South America, with its analogues in the Australian or Ethiopian regions. This I shall call *South American,* as I wish to avoid the term Neotropical. . . .

I have attempted in the following sections to classify the North American bird fauna in a similar manner. This classification, tentative as it is under the circumstances, is very useful as a test of the various arrangements proposed by regional zoogeographers. It provides at least provisional answers to such questions as: "Is it justifiable to recognize a neotropical fauna and a nearctic fauna?" "Is the nearctic fauna, if it exists, part of a New World or of a holarctic fauna?" "Does North America have a fauna of its own, or is it merely an area of intergradation between the Eurasian and the South American faunas?" "Are the faunas of given geographical areas sufficiently homogeneous to justify

the recognition of zoogeographic regions, or does the delimitation of zoogeographic regions convey an erroneous impression?"

Recent Advances

We are in a much better position today to answer these questions than was Lönnberg 20 years ago. First, there has been a general advance in the whole field of zoogeography—a complete change in the concept of the functions of the science—signalized by the important publications of Simpson, Stegmann, and Stresemann. Classical zoogeography asked: What are the zoogeographic regions of the earth, and what animals are found in each region? The modern zoogeographer asks when and how a given fauna reached its present range and where it originally came from; that is, he is interested in faunas rather than in regions. In the light of this new concept of the science, such familiar terms as holarctic, nearctic, and neotropical acquire completely new meaning. Secondly, there have been many very specific recent additions to our knowledge, contributed partly by the paleontologist and partly by the taxonomist, which permit a more accurate analysis than Lönnberg could give.

Recent contributions of the paleontologist. The number of important discoveries of fossil birds has been greatly augmented in recent years, the Californian school and Alexander Wetmore having made the most valuable contributions. Finds of particular zoogeographic significance concern the following groups (Wetmore, 1940): 1. The Aramidae. The limpkin (*Aramus*) is the only living representative of this family; and, as Lönnberg said (1927:24), "if one has to judge only from the present distribution, [it] would certainly be regarded as South American"; but the fact that there are two extinct Tertiary genera (*Badistornis* and *Aramornis*) in North America favors a North American origin for the family. 2. The Old World vultures (Aegypiinae), which are now restricted to the Old World. Nobody would suspect the former occurrence in the New World of this subfamily of the Accipitridae if fossil remains of three extinct genera had not been found in the Miocene (*Palaeoborus*), Pliocene (*Palaeoborus, Neophrontops*), and Pleistocene (*Neogyps, Neophrontops*) of North America. No conclusion can be drawn, however, as to the origin of the family. 3. The New World vultures (Cathartidae), which Lönnberg (1927:22) listed as a South American family. The fact that Wetmore (1940 and 1944) has found several striking genera in the early Tertiary of North America indicates either a North American or pre-Tertiary origin for the family. 4. The Cracidae (curassows and guans), whose present center of distribution is in South America, where the vast majority of the species occur and where most of the genera are endemic. Even though seven Recent species occur in Central America and two genera are endemic

there (*Penelopina* and *Oreophasis*), this family would surely be considered a comparatively recent arrival in North America, were it not for the occurrence of two species in the Tertiary of North America (*Ortalis tantala* in the lower Miocene; *O. phengites* in the lower Pliocene) and for the occurrence in the Wyoming Eocene of the related (fossil) family Gallinuloididae.

Recent contributions of the taxonomist. Unsound classifications have caused much confusion in zoogeography, as ably pointed out by Simpson (1940b) in a discussion of the so-called evidence for an antarctic land bridge. Of particular zoogeographic significance are the following recent changes in the classification of birds.

"New World Insect Eaters." From a study of a number of South American genera it would seem that the tanagers (Thraupidae)—including the South American swallow-tanagers (Tersinidae), honeycreepers (Coerebidae), wood warblers (Parulidae—formerly "Compsothlypidae"), vireos (Vireonidae) — including the shrike-vireos (Vireolaniidae) and the pepper-shrikes (Cyclarhidae), blackbirds and troupials (Icteridae), and some of the finches (the subfamily Emberizinae) are closely related, constituting a single superfamily, perhaps the New World equivalent of the Old World family Muscicapidae of recent authors (J. T. Zimmer, verbal information).

Troglodytidae. Sharpe's Hand-list (vol. 4, 1903) and other older taxonomic works included among the wrens a considerable number of south Asiatic genera (*Pnoëpyga, Elachura, Spelaeornis, Sphenocichla,* and sometimes *Tesia*). Lönnberg (1927:9–10) consequently had considerable difficulty in proving an American origin for this family. Recent taxonomic work has clearly established the fact that none of the listed Asiatic genera (superficially wren-like babbling thrushes and Old World warblers) belongs to the Troglodytidae and that *Troglodytes troglodytes* is the only wren that occurs in the Old World. The strictly American character of the wren family is now beyond dispute.

"Chamaeidae." The Wren-tit (*Chamaea*) is not the sole representative of a separate family, but a member of the Paradoxornithinae (parrot bills and suthoras), and possibly not even generically separable from *Moupinia* of southwest China.

Fringillidae. The so-called finches are an assemblage (probably highly artificial) of seed-eating birds with cone-shaped bills. Three major groups can be distinguished within the fringillids that are established in North America: (a) Carduelinae—the cardueline finches; (b) Emberizinae—certain buntings and American sparrows; and (c) Richmondeninae—the cardinals, or South American finches. (See Sushkin, 1924 or 1925.) There is little doubt that the Carduelinae are Old World in origin; the Emberizinae North American, although some species are found in the Old World; the Richmondeninae South American, although some genera have become thoroughly established in

North America. (It should be noted that no final decision can be reached on the last two groups until it has been determined whether certain South American genera belong to the Emberizinae or to the Richmondeninae. A discussion of the characters of the fringillid subdivisions, as well as an incomplete listing of the genera, will be found in Sushkin.)

The Geological History of North America

The North America of today is connected with South America by an isthmus and is separated from Asia only by a narrow oceanic strait. These connections with the two adjoining faunal areas are of the greatest importance, and a study of their history, both geologically and climatically, is a prerequisite to full understanding of the faunal history of North America. There is also a loose connection directly with Europe through the arctic islands of the North Atlantic (Greenland, Iceland), but it is doubtful whether it ever played a greater role for land birds than it does today. The Wheatear (*Oenanthe oenanthe*) is one of the few birds that has come to us via this bridge.

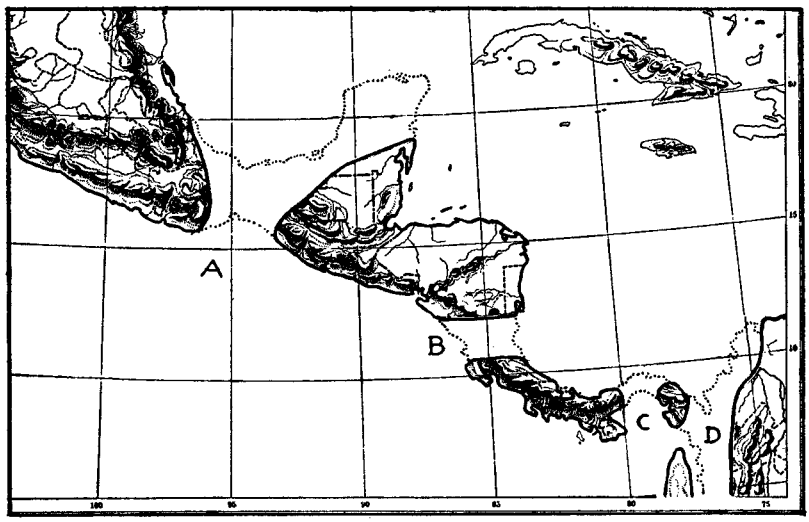

Figure 1. Tertiary water gaps between North and South America. A = Tehuantepec gap (late Miocene to middle Pliocene), B = Nicaraguan gap (late Eocene to middle Miocene), C = Panamanian gap (late Eocene to ? late Oligocene), D = Colombian gap (middle Eocene to late Miocene). (*Free reconstruction from various geological sources.*)

The coast line of North America in former geological periods was not always where it is today. There is, for example, good evidence for a former land connection across Bering Strait, as well as for oceanic gaps across what is now Central America (Figure 1). The extent of

these changes in the outlines of land areas is being debated rather vigorously by the geologists and paleogeographers, who tend to interpret the available evidence to fit the concepts of one of the following three schools. The oldest concept is that of a continuous large-scale change in the surface of the earth. Some land masses sink to the bottom of the ocean while others arise by buckling up. Old continents break to pieces as new ones are being formed. Today few authors believe in such violent upheavals. The prevailing theory today is perhaps that of "permanence of continents and oceans." The continents, as well as the major oceanic basins, are relatively stable according to this school of thought. "Sea bottoms" that dry up and lands that become submerged are merely the shallow "amphibious" zones on the continental shelves. The relative position of continents and oceanic basins has not changed materially, according to this theory, since Mesozoic times or even before. The third theory includes elements of the other two, but combines them in a very original way. It agrees with the second theory that continents will always remain continents and ocean bottoms will stay ocean bottoms, but denies that their relative positions are fixed. Rather it holds that the continents are floating on the magma of the earth like ice floes in the arctic sea and that they are continuously shifting their position (Wegener's theory of continental drift). As Simpson (1943a) and others have pointed out, the zoogeographical evidence is on the whole opposed to the theory of continental drift, at least for the Mesozoic and Tertiary periods.

Although some points are still controversial, the following facts seem to be well established:

(1) South America was separated from North America for the greater part of the Tertiary. The isthmus between Colombia and central Mexico was broken into a series of islands by several ocean channels between the Pacific and the Caribbean (Figure 1). A complete land connection between South and North America probably did not exist between the lower Eocene (50 to 70 million years ago) and upper Pliocene (about 2 million years ago).

(2) Asia and North America were repeatedly connected by dry land across Bering Strait during the Tertiary. There is no evidence that this bridge was ever much more extensive than the present shelf, nor is there any evidence for a complete land bridge to Asia across the Aleutians. The Bering Strait bridge may have existed as recently as the last ice age.

A few more words about the nature of these land bridges before we examine what faunal elements have reached or left North America on them. The ocean gaps between North and South America must have been considerable (perhaps even wider than shown in Figure 1), since they almost completely prevented an interchange of the mammals of

North and South America. Ground sloths were apparently the only South American mammals to reach North America during the period of separation; only raccoons (procyonids), with possibly also monkeys and opossums, crossed from North to South America (Simpson, 1940a:158). For birds, these ocean channels were much less of a hindrance, as will be shown below.

Most important for an understanding of the origin of the North American fauna is the fact, emphasized by Lönnberg (1927), Dunn (1931), and Simpson (1943b), that the whole southern half of North America was subtropical or tropical during most of the Tertiary, when it was separated from South America by oceanic gaps. Even in the later Tertiary, a tropical climate prevailed in the southernmost section of North America. This means that (with the exception of those animals that cross water gaps easily) there was not merely one tropical American fauna, the "Neotropical," but two quite distinct ones: one south of the ocean gaps, the other north of them. F. M. Chapman (1923) showed that the motmots (Momotidae), usually referred to as a "typically Neotropical" family, had actually originated in Middle America "where the ancestral forms of the existing genera were possibly developed during the Oligocene when this region consisted of scattered islands which would afford the isolation favorable to differentiation" (p. 58). Lönnberg (1927:12) states correctly that the same would probably be found to be true, if other families were examined as "thoroughly and masterfully" as the Momotidae were by Chapman. In the meantime, Dunn (1931), Simpson (1943b:428), and Hubbs (1944:271) have emphasized the importance of this Middle American (i.e. tropical North American) element among reptiles and fishes.

The mid-Tertiary fauna of North America was probably not only highly peculiar but also rather homogeneous. To visualize its composition, one must look at the South America of today. The temperate zone of South America, which admittedly is rather small because of the continent's triangular shape, does not have a fauna which is basically different from that of the tropical areas. It has its share of endemic species and even genera, but its fauna (although poorer) is composed more or less of the same families as that of the warmer portion. A similar faunal homogeneity was perhaps true for North America during Tertiary times, the faunas of the tropical, of the subtropical, and of the warm-temperate zones being very much alike in composition. The present-day contrast between the fauna of tropical-subtropical Central America and that of temperate North America, has two causes: (1) the climatic deterioration in the late Tertiary and Pleistocene, which eliminated all tropical elements then existing in North America, (2) the invasion (from South to North America) of a new tropical element after the closing of the Central American water gaps. This faunal mixing

during the late Pliocene and the Pleistocene led to a complete reshuffling of faunal elements. As far as birds are concerned, we can see only the final result of the opposing processes of range expansion on the one hand and extinction on the other. Simpson (1940a:158) has shown in detail what happened to the mammalian faunas. "Just before the two continents were united, South America had about 29 families of land mammals and North America about 27. With two doubtful exceptions [Didelphidae and Procyonidae], they did not then have any families in common. Shortly after the union of the continents, in the Pleistocene, they had 22 families in common, 7 of South American origin, 14 North American, and 1 doubtful." Considerable extinction and further migration have resulted in the Recent fauna, which consists of 38 families of land mammals, of which 14 are common to both continents, 15 confined to South America, and 9 confined to North America. Four North American families (tapirs, camels, peccaries, and short-faced bears) have become extinct in all or nearly all of their original home country, but are surviving in South America. Obviously it would be a zoogeographical error to classify such families, which were originally North American, with the truly autochthonous* South American families. Yet, nearly all the older zoogeographical treatises classify as "Neotropical" what is really a mixture of North and South American faunal elements. An effort has been made in the following classification to avoid this error. (In this paper zoogeographical North America is considered to extend southward to the edge of the tropical rain-forest.)

Classification of the Faunal Elements of the Americas

Three Tertiary land masses are the primary contributors to the present fauna of the Americas: South America, North America, and Eurasia. It would therefore appear that the simplest classification of faunal elements would be into the same categories: South American, North American, and Eurasian (or "Old World"). These three classes undoubtedly must be recognized, but they are not sufficient to cover all families and genera of birds. First, an additional category must be recognized for groups that cannot be analyzed for one reason or another (to be stated below). Second, there are certain groups ("holarctic," or "panboreal," elements) which have moved back and forth across Bering Strait so freely that they cannot be assigned with certainty to either continent. Others ("pan-American") crossed the Central American water gaps sufficiently freely to obscure their center of origin. Finally, there is an old tropical element ("pantropical") which is of such similar composition in the Old World and New World tropics that it is impossible at the present time to determine the original home.

* In this paper I have used the terms "endemic" and "autochthonous" as follows: Endemic = restricted to a given region; not found elsewhere. Autochthonous = having originated in a given region; now sometimes found beyond the borders of that region.

It is into these categories (Figure 2) that I have tried to classify all the families of birds known to occur in the Americas, whenever possible carrying the analysis even further: to subfamilies, genera, and occasionally to species. This is particularly necessary in the case of families that originated outside of North America, for parts of which North America became a secondary center of evolution (e.g. quails, jays, thrushes), and of those other families that reached North America repeatedly at different geologic periods (e.g. the swallows).

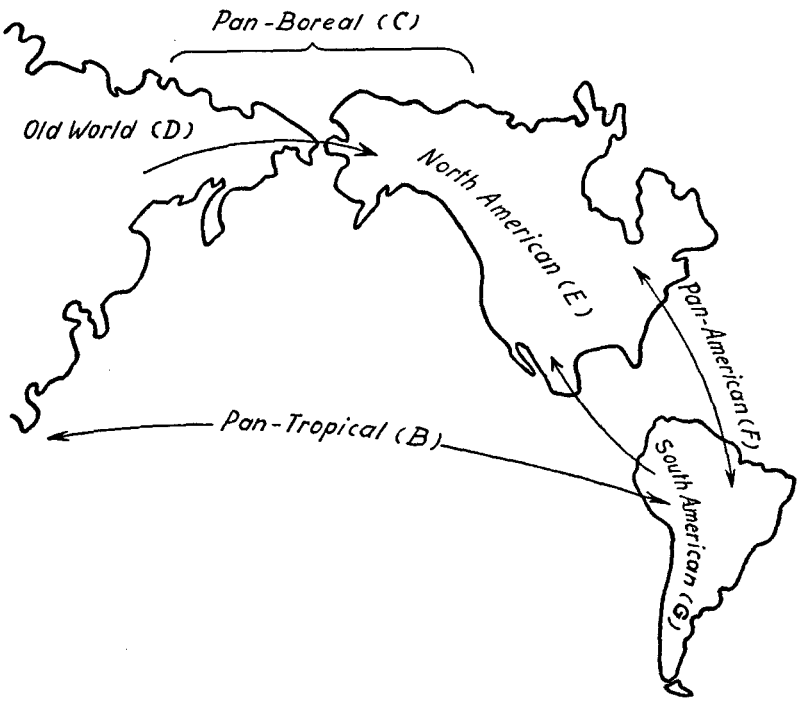

Figure 2. Diagram of the faunal elements of North America. The unanalyzed Element (A), whose geographical origin cannot be determined is, of course, omitted from the map.

Criteria

Unfortunately the bird geographer has, as stated above, relatively few fossils to guide him in his analysis. He is therefore forced to utilize indirect evidence, which is often difficult to evaluate. For example, both the Ruby-throated Hummingbird (*Archilochus colubris*) and the Horned Lark (*Otocoris alpestris*) are widespread North American birds. But the Horned Lark is obviously only a recent arrival in the New World; it is the only member of the Alaudidae, a typical Old World

family, to occur in North America and is not even an endemic species; whereas the hummingbird is clearly South American in origin. These cases indicate what evidence can be used. The larks are a family of more than 70 species and are represented in all parts of the Old World. Only certain subspecies of a single species occur in the New World. There can be no shadow of doubt concerning the family's Old World origin. Sometimes the distribution of the nearest relatives can be used as a clue. The gnatcatchers (Polioptilinae), for example, seem to be a branch of the rich Old World group of Insect Eaters (Muscicapidae) and they are without near relatives in the New World; these facts indicate an Old World origin for the subfamily.

These indirect methods are fully reliable only in richly developed families. The value of the evidence is uncertain in regard to families consisting of only one or merely a few species. Mammalogists like to cite in this connection the present distribution of the llamas (relatives of the camels) and the tapirs, two groups formerly widespread in North America but now surviving only in tropical or South America and (the tapir) in southeast Asia. However, both these groups would probably be considered northern elements, even without fossil evidence, because of the distribution of their relatives.

A. The Unanalyzed Element

The separation of land masses, which is responsible for the divergent development of terrestrial faunas, has little bearing on the evolution of sea bird faunas. Roughly, the oceanic birds can be classified into (1) a southern group: penguins (Spheniscidae) and sheath-bills (Chionidae); (2) a tropical group: tropic-birds (Phaëthontidae), boobies and gannets (Sulidae), frigate-birds (Fregatidae); (3) a northern group: skuas and jaegers (Stercorariidae); (4) a world-wide group: albatrosses, shearwaters, fulmars, and petrels (Tubinares), gulls and terns (Laridae). A further analysis and determination of the point of origin of these sea birds is outside the scope of this paper.

Equally obscure is the place of origin of the partly oceanic, partly fresh-water, families of the pelicans (Pelecanidae) and the cormorants (Phalacrocoracidae). Among the true fresh-water groups, a number of families are so evenly distributed in the Old and New World as to make determination of their centers of origin impossible. These include the grebes (Colymbidae), herons and bitterns (Ardeidae), storks and jabirus (Ciconiidae), ibises and spoonbills (Threskiornithidae), flamingos (Phoenicopteridae), the ducks, geese, and swans (Anatidae), and the rails, coots, and gallinules (Rallidae). With most of these, it is not simply the family as a whole that is widespread, but also the subfamilies, many of the genera, and frequently even the individual species. This point is well illustrated by the duck family, of which an up-to-date

classification is available (Delacour and Mayr, 1945). Of the nine recognized tribes (or "subfamilies"), only the monotypic torrent duck tribe (Merganettini) is restricted to a single continent. Of the 40 genera, no less than 18 are found on two or more continents. Many species are circumtropical or at least very widespread. For example, the White-faced Whistling Duck (*Dendrocygna viduata*): South America, Africa, Madagascar; the Fulvous Whistling Duck (*Dendrocygna bicolor*): America, Africa, India; the superspecies *Tadorna ferruginea* (which includes the four species formerly separated as *"Casarca"*): Europe, Asia, South Africa, Australia, New Zealand; the black duck–mallard group of river ducks (*Anas platyrhynchos–fulvigula*): spread over most of the world except South America; the superspecies *Aythya nyroca* (white-eyed ducks): Madagascar, Eurasia, east Asia, Australia, and New Zealand; the Muscovy Duck group (*Cairina,* including *"Pteronetta"* and *"Asarcornis"*): America, Africa, India; the mergansers (*Mergus,* including *"Mergellus"* and *"Lophodytes"*): Holarctic region, Brazil, Auckland Islands; the southern ruddy ducks (*Oxyura australis,* including *maccoa, ferruginea,* and *vittata*): South America, Africa, Australia.

Widespread genera and species are typical also of other families of fresh-water birds. A few examples are: the grebes (*Colymbus* [*Podiceps*]), which occur on all continents; the gray heron group (*Ardea cinerea–herodias*), the green heron group (*Butorides virescens –striatus*), the Egret (*Egretta alba*), the night heron group (*Nycticorax nycticorax–caledonicus*), and the bitterns (*Ixobrychus* and *Botaurus*), all of which are world-wide. Many additional examples could be cited from other fresh-water families, particularly from the rails.

Most of the families of shore birds also are so widespread as to make it impossible to trace their origin. This is particularly true for the oyster-catchers (Haematopodidae), the plover family (Charadriidae), avocets and stilts (Recurvirostridae), and thick-knees (Burhinidae). In the case of the snipes, woodcock, and sandpipers (Scolopacidae) an origin in the northern hemisphere appears probable.

Though all these families of fresh-water and shore birds cannot be analyzed at the present time, it seems certain that new evidence may bring us a good deal further. Most of them are composed of medium-sized and large forms, which we find represented in fossil recoveries to an ever-increasing extent. Furthermore, certain subdivisions within these families are sometimes clearly Old World, New World, or even more specifically South American. Finally, a study of their parasites might facilitate the finding of the center of origin, as Szidat (1940) has suggested.

Among the strictly terrestrial birds, there are eight families that are so widespread or so evenly distributed as to make analysis difficult at

the present time. These families are the hawks and eagles (Accipitridae), the osprey (Pandionidae), falcons and caracaras (Falconidae), nightjars (Caprimulgidae), swifts (Apodidae), woodpeckers (Picidae), and swallows (Hirundinidae). The evidence indicates that all of these families originated at such an early date (Eocene or Cretaceous) that subsequent shifts in distribution have obliterated most of the clues.

Indirect clues, however, permit a guess for two of these families. The Caprimulgidae may well be of New World origin, since this is the home not only of the entire subfamily nighthawks (Chordeilinae), but also of 10 of the 15 genera of goatsuckers (Caprimulginae). However, a comparison of the numbers of genera in the two regions does not give an entirely accurate picture, since the American birds are more finely split by the taxonomists. Students of New World Caprimulgidae employ 14 genera for 29 species, while Old World ornithologists recognize only 6 genera for 37 species. The woodpeckers (Picidae) are represented about equally well in the Americas and the Oriental regions. They are rather poorly developed in Eurasia and Africa and are absent from the Australian region and from Madagascar. This pattern of distribution suggests a New World (but very early) origin for the family, although the fact that their nearest relatives, the wrynecks (Jyngidae), are exclusively Old World would seem to indicate the opposite.

The swallows are also a very ancient family; it is particularly rich in species in South America and Africa but also extends to Madagascar and Australia. The place of origin of the family as a whole is uncertain, but it is fairly easy to determine where each of the (approximately) seven major subdivisions (Mayr and Bond, 1943) of the family first developed. The specialized mud-nest builders, *Hirundo* and *"Petrochelidon,"* as well as *Riparia,* are of Old World origin, being recent arrivals in America from the Palearctic. It is uncertain whether the family originated in South America, and retained one primitive branch in the Americas (*Progne–Atticora–Stelgidopteryx*), sending another branch to the Old World (*Psalidoprocne,* etc.) that gave rise to the specialized mud-nest builders and other Recent Old World forms, or whether the "old-American" swallows are descendants of early invaders from Asia. Parallel cases in other animal groups favor the second alternative.

B. The Pantropical Element

While representatives of the hawks, owls, and swifts are found in several climatic zones, there are certain other families which are also widespread but only within the tropical belt. For five families of freshwater birds (in some cases, partly marine), the area of origin is difficult to fix because each of them is found both in the Old World and New World tropics, though represented only by a single, or merely a

few, species. These families are the snake-birds (Anhingidae), sun-grebes (Heliornithidae), jacanas (Jacanidae), painted snipes (Rostratulidae), and the skimmers (Rynchopidae). All of them now have widely disrupted ranges, as can be easily seen from the map of the sun-grebes (Figure 3). It is also remarkable that the Recent Old World and New World representatives are often the members of a single species or superspecies (*Anhinga, Rostratula benghalensis, Rynchops*). This would indicate either extremely slow evolution or an enormous capacity for transoceanic dispersal.

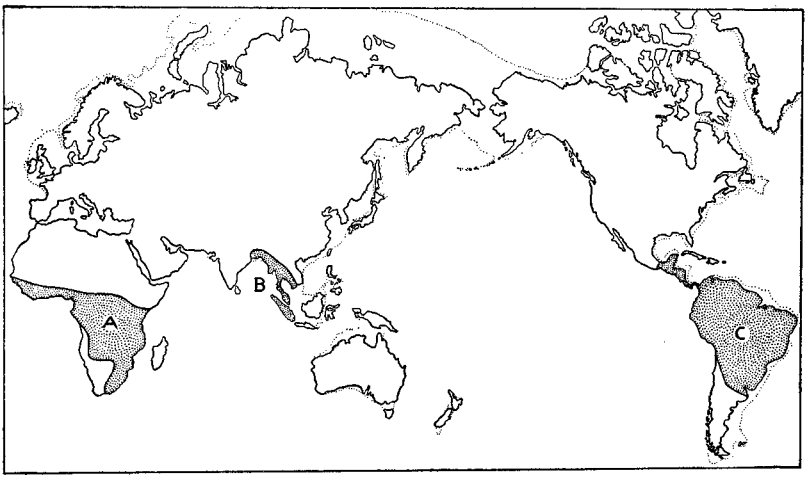

Figure 3. Present distribution of the sun-grebes (Heliornithidae), a typical family of the pantropical group. A = *Podica*, B = *Heliopais*, C = *Heliornis*.

Among the land birds, three families are pantropical. The barbets (Capitonidae) and the trogons (Trogonidae) have a notably similar distributional pattern. The ranges of both families are restricted to the humid tropics, and are bounded in the east by Wallace's Line. Fossil trogons have been found in the Eocene of France, and this fact, together with the scarcity of trogons in South America, has led most authors to assume an Old World origin for the family. On the other hand, trogons are much more diversified in Central America than in the Old World tropics; in fact, all the African and Indian species could be included in a single genus. Tropical North America or the Oriental region is the most likely place of origin. The barbets, with a similar distributional picture, are so much more richly developed in the Old World tropics than in the New that an Old World origin is probable (cf. Ripley, 1945:543–544).

The distribution of the parrots (Psittacidae) is considerably more extensive than that of the barbets and trogons. The parrots, with about

315 species, are one of the richest of all bird families, but about an equal number are found in the Old and the New World. However, most of the more aberrant types, such as the lories (Loriinae), cockatoos (Cacatuinae), and pigmy parrots (Micropsittinae), are found in the Old World, more specifically in the Australian region. It is, therefore, probable that the Psittacidae originated in the Old World, but the great number of endemic genera and species in America indicates a very early arrival in the New World. This might well have taken place before the Eocene separation of South America from North America.

The present ranges of these circumtropical families are widely disrupted, and they have therefore been used as "evidence" of former transatlantic or transpacific land connections by the advocates of such land bridges. We shall investigate in a later section how well founded their argument is.

C. The Panboreal Element

The loons (Gaviidae) among the fresh-water birds, the phalaropes (Phalaropodidae) among the shore birds, and the auk family (Alcidae) among the sea birds are typical of a large class of circumboreal birds. All three families are distributed in the arctic or in the north temperate zone and are about equally well represented in the Old and the New World. The auk family and the loons are known from the Tertiary of both North America and Europe. The temperate zones of Eurasia and America were in such direct contact for a good part of the Tertiary (by means of the Bering bridge) that it will be very hard to determine which of the two land masses was the giver and which the taker of the members of this temperate zone group. Among genera and species, this circumboreal element is much stronger than among families. Well over 80 per cent of the species of the circumboreal tundra zone belong to it, and it is impossible to determine their ultimate source. Stegmann (1938a) believes that Asia, more particularly Siberia, has probably made the greatest contribution to the group because it is the largest land mass in the temperate zone.

D. The Old World Element

It is generally admitted that the connection between Asia and North America across Bering Strait is very ancient (pre-Tertiary). As far as birds are concerned, a more or less active faunal exchange probably took place right through the Tertiary, even during periods when the two land masses were separated by water. This long-standing accessibility of North America to Old World immigrants is reflected in the taxonomic composition of the Old World element in America. According to the date of their immigration, these birds have either (1) not changed at all, e.g., the Alaska Yellow Wagtail (*Motacilla flava alascensis*), the Red-spotted Bluethroat (*Luscinia* [*"Cyanosylvia"*] *suecica*

robusta), and the Wheatear (*Oenanthe oe. oenanthe*); (2) they have become subspecifically distinct, e.g., Kennicott's Willow Warbler (*Phylloscopus* [*"Acanthopneuste"*] *borealis kennicotti*), the Northern Shrike (*Lanius excubitor borealis*), Brown Creeper (*Certhia familiaris americana*); or (3), if they arrived very early, they have evolved into separate species, genera, or even subfamilies—that is, America has become for them a secondary center of evolution.

The third case is true of the Old World pheasant family (Phasianidae), which has produced the American quails (subfamily Odontophorinae). And it is probably true of the cuckoos (Cuculidae). In this family, Peters (Check-list, vol. 4, 1940) recognizes six subfamilies. Three of these, the Cuculinae, the Couinae (Madagascar), and the Centropodinae, are restricted to the Old World; the Crotophaginae are American; the Neomorphinae have five genera in the New World, one in the Old; and the Phaenicophaeinae have nine in the Old World, three in the New. The evidence points toward an Old World origin of the family, and to tropical North America as a secondary center of evolution for three subfamilies.

It is highly probable that the typical owls (Strigidae) originally came from the Old World, since the closely related family Tytonidae is clearly of Old World origin (only one of its species occurring in the New World) and since in the Old World there are twice as many endemic genera of Strigidae as in the New World. However, this must have been a very early invasion, since there are now six endemic genera in the New World, and since four fossil species of the extinct family Protostrigidae are known from the Eocene of North America (Wetmore, 1940:66–67).

The gnatcatchers (subfamily Polioptilinae, comprising the three genera *Polioptila, Microbates,* and *Ramphocaenus*) offer a puzzling problem both to the taxonomist and the zoogeographer. They are usually treated as a subfamily of the Old World warblers ("Sylviidae"), but there seems little beyond the fine bill to support such a classification. They are surely one of the branches of the Old World Insect Eaters (Muscicapidae), but what their nearest relatives are is still obscure. Although more species of Polioptilinae are found in South than in Central America, it seems probable that tropical North America was the secondary evolutionary center of this group after its arrival from the Old World. Lönnberg (1927:17) expressed a similar opinion.

The pigeons (Columbidae) are world-wide in distribution—which indicates their great age. However, the rich development of the family in the Australian region, where the most aberrant members of the family occur (e.g., *Caloenas, Goüra, Otidiphaps,* and *Didunculus*), and the fact that most American species belong to just a few phyletic lines, prove an Old World origin. It seems probable that some species reached

South America as early as the middle Tertiary and established a second evolutionary center.

Both the crow family (Corvidae) and the thrushes ("Turdidae") are examples of Old World groups which have established minor secondary evolutionary centers in North America, particularly in the tropical part. For the Corvidae, Amadon (1944:16–20) has presented detailed evidence. The blue jay group (*Cyanocitta*) developed in America, but since there is not a single endemic genus in South America, it is obvious that the jays reached there only after the closing of the Central American water gaps in the late Tertiary. The genera *Corvus, Nucifraga,* and *Perisoreus* represent separate later invasions of the Corvidae into North America. In view of the early arrival of the jay group, it seems conceivable that some of the palearctic genera (*Perisoreus, Nucifraga, ? Garrulus*) evolved in America and crossed back to Asia by Bering Strait, but it would be impossible to prove this.

The thrush subfamily Turdinae (see Mayr, 1941:106) presents a very similar distributional pattern and probably had a similar history. Thrushes are rich in species in South America (where there are no less than 20 full species of *Turdus*), but all the genera (even the solitaires, *Myadestes*, and the nightingale-thrushes, *Catharus*) belong to a single natural group; and even with the two (not very pronounced) West Indian genera (*Mimocichla* and *Cichlherminia*), there are only a total of 12 genera in the New World—excluding the recent immigrants, *Oenanthe* (Wheatear) and *Luscinia* (the Bluethroat, *"Cyanosylvia"*). This compares with several dozen widely divergent genera of thrushes in the Old World, such as the Old World nightingales, redstarts, robins, and chats. There are about 244 Old World and 60 New World species. Since also all of the closer relatives of the Turdinae—babbling thrushes (Timaliinae) and Old World flycatchers (Muscicapinae)—are Old World in origin, there can be no question of the Old World origin of the subfamily. The interesting aspect of the American thrushes is, however, that they demonstrate very graphically the effect of the continuous availability of the Bering bridge. There was an early immigration of a *Turdus*-like stock which produced some of the endemic South and Central American genera; there was the later arrival of another group which gave rise to the solitaire, nightingale-thrush, and hermit-thrush groups (*Myadestes, Catharus, Hylocichla*); then the immigration that resulted in the bluebird genus *Sialia;* then additional members of the genus *Turdus,* which changed specifically but not generically; and finally the most recent immigrants, the Bluethroat (Alaska) and the Wheatear (Alaska and Labrador), in which not even subspecific differences have developed.

The cranes (Gruidae) are known from North America as far back as the middle Pliocene—perhaps even earlier (see Wetmore, 1940). However, they would seem to be an unquestionably Old World family

on the basis of their present distribution. There are 13 species (4 genera) in the Old World as compared with 2 species (one genus) in the New World.

The kingfishers (Alcedinidae) are a rich Old World family of which only one branch (Cerylinae) has reached the New World. This colonization cannot have been very recent, since a few species (the neotropical group *Chloroceryle*) are sufficiently distinct from their nearest Old World relatives to be considered by most authors a separate genus.

The cardueline subfamily of the Fringillidae is an Old World group, but one of the lines seems to have arrived in America rather early, since it has produced a number of endemic South American species (*"Spinus"*) and an endemic West Indian genus, *Loximitris* (Hispaniolan Siskin), which is closely related to *"Spinus."* *Hesperiphona* (Abeillé's and Evening Grosbeaks) is the only endemic North American genus, but it is closely related to the Himalayan *Mycerobas*—if at all separable from it. The purple and house finches (*Carpodacus*), pine grosbeaks (*Pinicola*), crossbills (*Loxia*), and rosy finches (*Leucosticte*) are even more recent arrivals from the Old World.

The Paridae (titmice) are a mainly Eurasian family, which has repeatedly invaded North America, where it has even developed two endemic genera, verdins (*Auriparus*) and bush-tits (*Psaltriparus*). But the latter genus seems closely related to the Asiatic genera *Aegithaliscus* and *Psaltria,* while the other American titmice are still more closely related to Asiatic species; some are even conspecific. They must have crossed Bering Strait during or after the late Pleistocene.

As stated above, the genus *Chamaea* (wren-tit) of the west coast of North America is not the sole representative of a separate family, but a member of the Paradoxornithinae (parrot-bills and suthoras) and probably congeneric with *Moupinia* of China. All the other genera of the Paradoxornithinae are palearctic, as are those groups of babbling thrushes (Timaliinae) which are the closest relatives of this subfamily.*

The wagtails and pipits (Motacillidae) are a definitely Old World family, about equally well represented in Africa and Asia. The family is a rather recent arrival in America but has developed six endemic species in North and South America.

Six additional Old World families (or subfamilies) have colonized the Americas so recently, and the New World representatives are still so similar to the Old World forms (congeneric or even conspecific), that North America cannot be considered, for them, a secondary evolutionary center. These are: barn owls (Tytonidae), larks (Alaudidae), nuthatches (Sittidae), creepers (Certhiidae), Old World warblers and

* As J. T. Zimmer has pointed out to me, it may be necessary to call the subfamily "Chamaeinae," a name first used by Baird in 1863. The name Paradoxornithidae seems to have been used first by Oates about 20 years later. However, I have not made a thorough investigation of this nomenclatural complication. Furthermore, it may not be possible to separate the group from the Timaliinae.

kinglets (Sylviinae), and shrikes (Laniidae). The Old World origin of most of these groups has been discussed by Lönnberg (1927) and earlier authors. Only two of them (the larks and barn owls) have reached South America, and that so recently that the South American representatives are no more than subspecifically distinct.

E. The North American Element

The fauna that developed in North America during the Tertiary, while this continent was separated from South America and connected with Asia only by the Bering Strait bridge, is of great zoogeographical importance. It was much neglected in the past, when some of its components were labelled "Holarctic," others "Neotropical." The greater part of the Tertiary North American continent had a subtropical or tropical climate, as mentioned above, and it is therefore not surprising that tropical families and genera are well represented in this North American element.

The reasons have already been stated why the New World vultures (Cathartidae) and the limpkins (Aramidae) have to be considered North American in origin. Lönnberg (1927:7–12) considered that the thrashers and mockingbirds (Mimidae), vireos (Vireonidae), wood warblers (Parulidae), the waxwings (Bombycillidae) with their relatives the silky flycatchers (Ptilogonatidae), the wrens (Troglodytidae), and motmots (Momotidae) are also North American in origin. The monotypic family palm-chats (Dulidae) also belongs to this group. In all these cases there are so many more endemic genera in North than in South America that no fault can be found with Lönnberg's conclusions. Among the Mimidae, for example, only two genera have reached South America, one of which, the mocking-thrush (*Donacobius*), is endemic. Five genera (three endemic) occur in Central America, five genera (four endemic) on the islands of the Caribbean, and four genera (two endemic) in North America. The tropical origin of the family is indicated by the fact that none of the United States species has entered the Canadian zone.

The vireos, shrike-vireos, and pepper-shrikes have six genera (two endemic—*Neochloe* and *Vireolanius*) in Mexico and Central America, as compared with four genera (none endemic) in South America. The single genus occurring in North America is rich in species (11), of which 2 (*solitarius* and *philadelphicus*) are at home in the Canadian zone. There are 7 endemic species in the Caribbean. Even though no less than 20 species are found in South America, the combined weight of the other facts favors a North American origin for the family.

The wood warblers (Parulidae) present a very similar picture. There are 16 genera in North America (many endemic) and only 6 in South America (none endemic). However, the genera *Myioborus* and

Basileuterus have respectively 6 and 17 endemic South American species. In the genus *Dendroica* alone there are about 20 endemic North American species, a good many of which are restricted to the Canadian zone coniferous forest. All the facts combined indicate a North American origin for the family.

A North American origin may also be postulated for the turkeys (Meleagrididae), grouse (Tetraonidae), dippers (Cinclidae), and the subfamily Emberizinae.

The evidence is unequivocal as far as the turkeys are concerned. The two Recent genera and the only known extinct one (*Parapavo*) have been found only in North America.

The grouse family presents a more difficult case. It has a wide distribution in the northern hemisphere, from Spain to Kamchatka, and from Alaska to Newfoundland and southward almost to Mexico. Absent from the subtropical and tropical belts of the Old and New World, the grouse show the typical distributional picture of a holarctic family. As both Lönnberg (1927:12) and Stegmann (1938a) have pointed out, there is much that favors an American origin for the family. Only three genera are endemic to the Old World (*Tetrao, Lyrurus,* and *Tetrastes*), all three being more or less Siberian taiga (moist coniferous forest) elements which have apparently radiated only quite recently into the western palearctic (Stegmann, 1932:396–397). The Old World has no equivalent of the American grassland genera *Tympanuchus, Pedioecetes,* and *Centrocercus*. Extinct genera of grouse have been reported from the Miocene and Eocene of North America.

The dippers (Cinclidae) are a family with only a single genus and too few species for a reliable analysis. There are three closely related species in the New World and two in the Old; one of the latter (*Cinclus pallasii*) is restricted to the eastern Palearctic. Relationship to the wrens (Troglodytidae), which is assumed by most authors, would indicate a North American origin.

The subfamily Emberizinae is apparently of North American origin, though (as mentioned above) no final decision can be reached without first determining which of the South American genera actually belong to the Emberizinae. Perhaps there was a continuous faunal exchange with South America throughout the Tertiary. One single branch of the Emberizinae, consisting of closely related forms, has reached the Old World. Even though more than 30 species are now found there, they all belong either to the genus *Emberiza* or to *Fringillaria, Miliaria,* and *Melophus,* which hardly deserve to be called more than subgenera. It can therefore be assumed that the invasion of the Old World by the Emberizinae must have taken place rather late in the Tertiary.

As stated in the preceding section, on the Old World element, North America became a secondary center of evolution for several Old World groups: American quails (Odontophorinae), the blue jay (*Cyanocitta*)

group of the family Corvidae, the *Myadestes–Catharus–Hylocichla* group of thrushes, and some others. In particular, the Odontophorinae, a whole subfamily restricted to North America, and known there as far back as the Miocene, well deserve to be included among the typically North American fauna. Part of the pan-American element (certain Icteridae), discussed below, has also now become sufficiently well established in North America to be considered part of the North American element.

F. The Pan-American Element

The water gaps that existed between North and South America from the lower Eocene to the late Pliocene produced an almost complete separation of the mammalian faunas of the two continents (Simpson, 1940a:157–163). The intervening chain of islands (Figure 1) permitted colonization by only a few groups especially adapted to "island hopping." On the whole, the geographical picture of this line of islands was apparently very similar to that of the Malay Archipelago, where colonization by mammals was almost completely prevented, even though the islands were more numerous and the water gaps comparatively small. For birds, these inter-island straits of the Malay Archipelago were much less of a barrier, as I have recently pointed out (Mayr, 1944a:171–194). The same is true for the inter-American island belt. It explains many of the difficulties of the bird geographer. There are quite a number of American families that are so rich, both in North and South America, in endemic genera and species that it is impossible to determine their primary country of origin without fossil evidence. It is rather obvious that these are the families able to utilize islands as stepping stones from one continent to the other. During the greater part of the Tertiary, the whole southern part of North America was apparently more humid, and certainly warmer, than it is today. It would have been more difficult for many of the species that developed in this climatic zone to enter the more temperate parts of North America than to cross into tropical South America. In the reverse direction, the same was true for species of tropical South America. This is one of the reasons that the contrast between the North and the South American Tertiary faunas is much less pronounced in birds than in mammals, and much less than one would expect on the basis of the length of separation of the two continents. On the other hand, the factor of age should not be left out of consideration. In the Eocene, when North and South America were connected, there were more bird families than mammal families with representatives on both continents.

Families almost certainly South American in origin, known to be successful transoceanic colonizers (West Indian fauna!), and rich in elements endemic to Central and North America, are the hummingbirds

(Trochilidae), the tyrant flycatchers (Tyrannidae), the tanagers (Thraupidae), and the blackbird–troupial family (Icteridae).

It is significant that not one of these families has crossed Bering Strait into the Old World although all four are rich in species and all four have at least a few species in temperate North America, some extending even as far as Alaska.

Among South American families of the suborder Mesomyodi, only the aggressive tyrant flycatchers (Tyrannidae) have penetrated far into North America. But many of these have reached the Canadian zone, and they were undoubtedly the first birds of this group to become established north of South America. There is every reason to believe that the invasion took place prior to the connection of the two continents in the late Pliocene. Nevertheless, their arrival must be considered comparatively recent. Of the 117 currently recognized genera of this family, only 10 are not indigenous to South America, and none of these is particularly distinctive; in every case the relationship to South American genera is more or less obvious, viz *Tolmarchus* (related to *Tyrannus*); *Hylonax, Deltarhynchus, Eribates,* and *Nesotriccus* (related to *Myiarchus*); *Blacicus* and *Nuttallornis* (related to *Contopus*); *Aechmolophus, Xenotriccus,* and *Aphanotriccus* (related to *Praedo*)—according to James Bond (*in litt.*).

The tanagers are more poorly represented in North America. There are a few genera in Central America; there are 5 endemic genera and 11 endemic species in the West Indies, but only one genus (*Piranga*) reaches the United States (with 4 species).

The blackbirds and troupials include 35 genera, of which no less than 16 are endemic to South America. There are two endemic genera in Central America, two in the West Indies (11 endemic species) and three in North America. (See also Lönnberg, 1927:10.) The family is well established in the temperate zone of North America with such hardy birds as the Bronzed Grackle (*Quiscalus quiscula*), Cowbird, (*Molothrus ater*), Meadowlark (*Sturnella*), Rusty Blackbird (*Euphagus carolinus*), and Red-wing (*Agelaius*). These species are so thoroughly at home in North America that a very early immigration is indicated.

Elements of the pan-American fauna that were perhaps originally North American are the curassow(Cracidae) and the cuckoo (Cuculidae) families. Both families are now richer in South, than in North, America, but both have relatives in the Old World (the mound-builders, family Megapodiidae, are at least distant relatives of the Cracidae). In the Cracidae, 5 out of 11 genera, 38 out of 46 species, are restricted to South America. On the other hand, the chachalaca *Ortalis* is known from the Pliocene and lower Miocene (Wetmore, 1940:42) of North America. The case of the Cuculidae has been discussed above in the section on the Old World element.

All of the families listed in this section have endemic genera or species in both North and South America. These are sufficiently peculiar to make it exceedingly unlikely that they could have developed in the short time since the re-establishment of the Panamanian land connections at the end of the Tertiary. They must have had as ancestors birds with the faculty of transoceanic colonization. On the other hand, there is not sufficient difference between the North American and the South American groups of genera to force us to assume an Eocene split of any of these families (by the separation of the two continents) into a northern and a southern section.

For the sake of completeness it will be useful to mention here those groups of Old World birds, discussed above, that arrived in North America at an early date and then crossed to South America with the help of the insular stepping stones. This includes, apparently, the pigeons (Columbidae), gnatcatchers (Polioptilinae), some thrushes (Turdinae), and some cardueline finches.

G. The South American Element

Certain families are very richly developed in all parts of South America, relatively scarce in Central America, even in the tropical parts, and extremely rare, or completely lacking, north of the tropics; and with these families, there can be no doubt about their South American origin. This is true for the tinamous (Tinamidae), potoos (Nyctibiidae), jacamars (Galbulidae), puff-birds (Bucconidae), toucans (Ramphastidae), oven-birds (Furnariidae), wood-hewers (Dendrocolaptidae), antbirds (Formicariidae) and two small related families, the ant-pipits (Conopophagidae) and tapaculos (Rhinocryptidae), the cotingas (Cotingidae), manakins (Pipridae), honey-creepers (Coerebidae), and the cardinal group (Richmondeninae). A South American origin is very probable also for the following families (though each contains less than five species, and some caution is therefore advised): rheas (Rheidae), screamers (Anhimidae), hoatzins (Opisthocomidae), trumpeters (Psophiidae), sun-bitterns (Eurypygidae), cariamas (Cariamidae), seed-snipe (Thinocoridae), oil-birds (Steatornithidae), sharp-bills (Oxyruncidae), and plant-cutters (Phytotomidae).

The cotingas (Cotingidae) may be cited to illustrate the distribution pattern characteristic of a typical South American family. Of the 31 genera of the family, only 12 reach Central America, and only one the United States; 19 genera are restricted to South America, not a single one to Central or North America; only one species (*Platypsaris niger*) has reached the West Indies (Jamaica). The oven-birds, wood-hewers, and antbirds are even more closely restricted to South America, and none of them has reached the West Indies.

The cardinals (Richmondeninae) apparently belong to the South American element, but, as already stated, nothing final can be said about this subfamily without first determining which genera belong to it.

As stated above, some of the families listed with the pan-American element are also of primary South American origin. This is reasonably certain for the hummingbirds (Trochilidae), tyrant flycatchers (Tyrannidae), tanagers (Thraupidae), and the blackbird–troupial family (Icteridae).

It is most remarkable that none of the families that are clearly South American in origin has developed any species that have crossed into the Old World. Old World families, on the other hand, have sent many branches into South America. Perhaps this means that a temperate zone family can more easily become adapted to the tropics than a tropical family to a temperate climate.

The above analysis is summarized in Table 1.

TABLE 1

ANALYSIS BY ORIGIN OF AMERICAN BIRD FAUNA

A. UNANALYZED ELEMENT

OCEANIC BIRDS
- Spheniscidae, *penguins*
- Procellariiformes, *tubinares*
- Chionidae, *sheath-bills*
- Sulidae, *boobies, gannets*
- Fregatidae, *frigate-birds*
- Phaëthontidae, *tropic-birds*
- Stercorariidae, *skuas, jaegers*
- Laridae, *gulls, terns*

SHORE BIRDS
- Haematopodidae, *oyster-catchers*
- Charadriidae, *plovers*
- Scolopacidae, *snipes, woodcock, sandpipers*
- Recurvirostridae, *avocets, stilts*
- Burhinidae, *thick-knees*

FRESH-WATER BIRDS (partly marine)
- Colymbidae, *grebes*
- Pelecanidae, *pelicans*
- Phalacrocoracidae, *cormorants*
- Ardeidae, *herons*
- Ciconiidae, *storks*
- Threskiornithidae, *ibises*
- Phoenicopteridae, *flamingos*
- Anatidae, *ducks, geese, swans*
- Rallidae, *rails*

LAND BIRDS
- Accipitridae, *hawks, eagles*
- Pandionidae, *osprey*
- Falconidae, *falcons, caracaras*
- N Caprimulgidae, *nightjars*
- Apodidae, *swifts*
- N Picidae, *woodpeckers*
- o Hirundinidae, *swallows*

B. PANTROPICAL ELEMENT

FRESH-WATER BIRDS (partly marine)
- Anhingidae, *snake-birds*
- Heliornithidae, *sun-grebes*
- Jacanidae, *jacanas*
- Rostratulidae, *painted snipes*
- Rynchopidae, *skimmers*

LAND BIRDS
- o Psittacidae, *parrots*
- N Trogonidae, *trogons*
- o Capitonidae, *barbets*

C. PANBOREAL ELEMENT
- Gaviidae, *loons*
- Alcidae, *auks, murres, puffins*
- Phalaropodidae, *phalaropes* (and many other groups of shore birds)

D. OLD WORLD ELEMENT

EARLY IMMIGRANTS
- Gruidae, *cranes*
- Columbidae, *pigeons*
- Cuculidae, *cuckoos*
- Strigidae, *typical owls*
- Corvidae, *crows, jays* (part)
- Turdinae, *thrushes* (part)

FAIRLY EARLY
- Alcedinidae, *kingfishers*
- Corvidae, *crows, jays* (part)
- Paridae, *titmice*
- Sittidae, *nuthatches*
- "Chamaeidae," *wren-tit*
- Motacillidae, *wagtails, pipits*
- Carduelinae, *cardueline finches* (part)

N = Probably originated in the New World. o = Probably originated in the Old World.

RECENT

Tytonidae, *barn owls*
Alaudidae, *larks*
Hirundinidae, *swallows* (part)
Certhiidae, *creepers*
Turdinae, *thrushes* (part)
Sylviinae, *Old World warblers, kinglets*
Laniidae, *shrikes*
Carduelinae, *cardueline finches* (part)

[Also of Old World origin are the Phasianidae, represented in the Americas by the quail (subfamily Odontophorinae); and the Muscicapidae, to which the American subfamily gnatcatchers (Polioptilinae) is undoubtedly related.]

E. NORTH AMERICAN ELEMENT

Cathartidae, *New World vultures*
Tetraonidae, *grouse*
Odontophorinae, *American quail*
Meleagrididae, *turkeys*
Aramidae, *limpkins*
Todidae, *todies*
Momotidae, *motmots*
Cinclidae, *dippers*
Troglodytidae, *wrens*
Mimidae, *mockingbirds*
Polioptilinae, *gnatcatchers*
Bombycillidae, *waxwings*
Ptilogonatidae, *silky flycatchers*
Dulidae, *palm-chats*
Vireonidae, *vireos, shrike-vireos, pepper-shrikes*
Parulidae, *wood warblers*
Emberizinae, *typical buntings*

[Some genera and species belonging to families listed under: A. (hawks, nightjars, woodpeckers, swallows); B. (trogons, barbets); D. (cuckoos, typical owls, pigeons, jays, thrushes, titmice, wren-tit, cardueline finches); are distinct enough to require mention under this heading.]

F. PAN-AMERICAN ELEMENT

APPARENTLY ORIGINALLY NORTHERN

Cracidae, *curassows, guans*

PROBABLY ORIGINALLY SOUTH AMERICAN

Trochilidae, *hummingbirds*
Tyrannidae, *tyrant flycatchers*
Thraupidae, *tanagers*
? Icteridae, *blackbirds, troupials*

[The cardinals (Richmondeninae) may have to be transferred from the South American group to this class.]

G. SOUTH AMERICAN ELEMENT

*Rheidae, *rheas*
Tinamidae, *tinamous*
*Anhimidae, *screamers*
*Opisthocomidae, *hoatzins*
*Psophiidae, *trumpeters*
*Eurypygidae, *sun-bitterns*
*Cariamidae, *cariamas*
*Thinocoridae, *seed-snipe*
*Steatornithidae, *oil-birds*
Nyctibiidae, *potoos*
Galbulidae, *jacamars*
Bucconidae, *puff-birds*
Ramphastidae, *toucans*
Dendrocolaptidae, *wood-hewers*
Furnariidae, *oven-birds*
Formicariidae, *antbirds*
Conopophagidae, *ant-pipits*
Rhinocryptidae, *tapaculos*
Cotingidae, *cotingas*
Pipridae, *manakins*
*Oxyruncidae, *sharp-bills*
*Phytotomidae, *plant-cutters*
Coerebidae, *honey-creepers*
Richmondeninae, *cardinals*

[Families marked with an asterisk contain less than five species, and their allocation is consequently somewhat doubtful. In most cases it is well supported by circumstantial evidence.]

Conclusion

The results of this analysis of the North American fauna can be summarized as follows: Most North American families and subfamilies are clearly either Old World in origin, South American in origin, or members of an autochthonous North American element that developed during the partial isolation of North America in the course of the Terti-

ary. Although many details of this analysis are still questionable, its major outlines are established facts. These facts are, however, merely descriptive raw material. It is only by correlating them with established concepts in related fields that their full significance becomes apparent. Such a correlation will be attempted in the following sections.

An Analysis of North American Bird Populations

In Table 2, the song birds of various areas in North America are analyzed according to their point of origin. The endemic North American genera among the swallows (Hirundinidae) and the blackbird–troupial group (Icteridae) were included with the North American element. It would have been most desirable to extend the type of analysis used in Table 2 to all the families of birds, but I failed in an attempt to do so. Many species of non-passerines were in the doubtful categories, *A*, *B*, and *C*, of Table 1; others belonged to the difficult families of cuckoos (Cuculidae), owls (Strigidae), and pigeons (Columbidae).

TABLE 2

Analysis by Geographical Origin of the Breeding Passerine Species of Several Districts of North America

	South American	North American	Old World
Yakutat Bay, southeast Alaska (Hudsonian Zone)[1]	3%	39%	58%
Oregon[2]	14	47	39
Nipissing area, southern Ontario, 46° N (Canadian Zone)[3]	13	57	30
New Jersey[4]	14	63	23
Florida[5]	20	59	21
Sonora, Mexico[6]	27	52	21

[1] Shortt, T. M. 1939. The summer birds of Yakutat Bay, Alaska. *Roy. Ont. Mus. Zool. Contr. No.* 17.

[2] Gabrielson, I. N., and S. G. Jewett. 1940. Birds of Oregon. Corvallis, Ore.

[3] Ricker, W. E., and C. H. D. Clarke. 1939. The birds of the vicinity of Lake Nipissing, Ontario. *Roy. Ont. Mus. Zool. Contr. No.* 16.

[4] Original data.

[5] Howell, A. H. 1932. Florida bird life. Tallahassee, Fla.

[6] van Rossem, A. J. 1945. A distributional survey of the birds of Sonora, Mexico. *La. State Univ. Mus. Zool. Occ. Paper No.* 21.

It might be claimed that the neglect of the non-passerines introduces so great a degree of uncertainty as to jeopardize the validity of the figures as indices of the composition of the North American fauna as a whole. This argument is not well founded for two reasons. One is that the families of Group A are composed of essentially the same mix-

ture of South American, North American, and Old World elements, in essentially the same proportions, as are the analyzed families as a whole. This is quite obvious from a cursory study of the hawks and rails, for example. The second reason is that most of the families of Group A (composed chiefly of large birds and other non-passerines) are comparatively rare. In faunal lists in which the species have equal value, these birds may constitute a significant percentage. But they are negligible if each species is weighed on the basis of numerical frequency. To determine the faunal composition of the bird population of a given type of forest, it would be necessary to analyze the total number of pairs instead of the total number of species. I suggested (Mayr, 1944b) that this should be done to test the validity of Wallace's Line, but no data were available for such an analysis. Fortunately, however, good census data are available for North American birds in the Audubon breeding-bird censuses initiated by William Vogt (Hickey, 1937–1944). Table 3 shows that the unanalyzed element is negligible. It becomes important only in aquatic habitats.

TABLE 3

ANALYSIS BY GEOGRAPHICAL ORIGIN OF THE BREEDING PAIRS REPORTED [1] FROM FIVE NORTH AMERICAN HABITATS

	South American	North American	Old World	Un-analyzed	Total Number of Pairs
Red and White Spruce in Maine (No. 27, 1941 [1938 data])	0.0%	73.0%	25.9%	1.1%	85
Northern Forest in Idaho (No. 27, 1944)	12.5	62.5	25.0	0.0	56
Beech-Maple in Ohio (No. 20, 1941)	23.0	52.5	23.0	1.5	131
Southern Hardwood in Alabama (No. 21, 1944)	25.8	54.8	16.2	3.2	62
Desert in southern California (No. 5, 1941)	37.1	48.6	14.3	0.0	35

[1] Audubon breeding-bird censuses (Hickey, 1937–1944).

If Table 2 (species analysis) is compared with Table 3 (pair analysis), a few interesting facts are apparent. One is the basic similarity of the figures. In both cases, the North American element makes up a large proportion of the total (47 to 63 per cent * in the species analysis, 48 to 73 per cent in the pair). The South American and the

* Unless one includes the marginal Yakutat Bay area (39 per cent).

Old World elements share the rest. However, the Old World element, largely consisting of permanent residents, is significantly lower in the pair, than in the species, tabulation, indicating a lower density. The South American element, on the other hand, composed mainly of hummingbirds (Trochilidae), tyrant flycatchers (Tyrannidae), tanagers (Thraupidae), and cardinals (Richmondeninae), is higher in the pair than in the species list.

A number of additional facts become obvious from a study of these tabulations. There is a decrease of the Old World element from the north to the south, but even as far south as Florida or Sonora, one-fifth of the species, or one-sixth of the pairs, are still of Old World origin. In mountainous western North America there is, naturally, a higher percentage of Old World elements than in a similar latitude in the lowlands of the eastern states. It is not justifiable, as far as birds are concerned, to include North America either in a "Neotropical" or in a "Holarctic" region, since the autochthonous North American element comprises up to 50 per cent, or even more, of the North American fauna in all habitats except the arctic. As is to be expected, from north to south, there is an increase of the South American element. However, even as far south as Sonora, only 27 per cent of the species are South American. Finally, it appears, again as is to be expected, that the faunal change from north to south is quite gradual—there are no "step clines" anywhere. Since each of the approximately 200 species involved in these analyses has different ecological requirements and a different distribution-pattern, it is not surprising that there is no sharp change in the gradient. The most rapid faunal change appears to occur near the northern tree limit.

The exact line, north of which more than 50 per cent of the bird species belong to the Panboreal and Old World element, has never been accurately drawn, but it runs somewhere through the middle of the Canadian coniferous forest. This 50:50 line does not by any means coincide with any major physiographic feature. There is, however, as stated above, a sharp drop in the percentage of American elements along timber line. Those who want zoogeographic regions may do well to follow the lead of the zoogeographers who recognize an Arctic (circumpolar) region as distinct from the Palearctic region. This was, I believe, first proposed by Schmarda (1853:225–226), later adopted by J. A. Allen (1871:381–382), by Reichenow (1888:673), and by the recent Russian zoogeographers (Stegmann, 1938a). Similarly, it will be advisable to include all the wooded parts of North America in the "North American region," even though the North American element might be slightly in the minority along the northern fringe. Since the only major avifaunal break occurs along the tree limit, it seems legitimate to accept the tree limit as a regional border.

The Arctic or tundra zone is inhabited by few land birds. The bird fauna consists almost entirely of sea birds, fresh-water birds, and shore birds. This fauna is strikingly different from that of the wooded parts of the continent, but it is practically identical on the two sides of Bering Strait. There are 104 species of birds that now breed in the arctic regions. Of these, only the following species seem to be restricted to the American continent: Canada Goose (*Branta canadensis*), Ross's Goose (*Anser rossi*), Bald Eagle (*Haliaeëtus leucocephalus*), Eskimo Curlew (*Numenius borealis*), Bristle-thighed Curlew (*Numenius tahitiensis*), White-rumped Sandpiper (*Ereunetes fuscicollis*), Stilt Sandpiper (*Micropalama himantopus*), Buff-breasted Sandpiper (*Tryngites subruficollis*), and the Surf-bird (*Aphriza virgata*). (Certain additional species usually considered exclusively North American I would include in superspecies that occur in both North America and Siberia.)

The same small number (nine species) are restricted to the Old World: Lesser White-fronted Goose (*Anser erythropus*), Red-breasted Goose (*Branta ruficollis*), Dotterel (*"Eudromias" morinellus*), Temminck's Stint (*Ereunetes temminckii*), Siberian Pectoral Sandpiper (*Ereunetes acuminatus*), Curlew Sandpiper (*Ereunetes ferrugineus*), Eastern Asiatic Knot (*Calidris tenuirostris*), Spoonbill Sandpiper (*Eurynorhynchus pygmeus*), and the Red-throated Pipit (*Anthus cervinus*). Thus, except for 18 species (of which 12 are shore birds), the arctic bird faunas of Asia and America are practically identical in composition. Furthermore, the arctic fauna is remarkable in that more than 50 per cent of its species are restricted to the Arctic zone, and in its almost complete difference from the fauna of the coniferous zone. The northern tree limit is, so far as birds are concerned, one of the clearest faunal boundaries on the earth.

I shall refrain from drawing any zoogeographical boundaries south of the timber line. Simpson (1943b:427–429) distinguishes five regions in America: Boreal, Middle, and Southern, in North America (including Mexico and Central America); Equatorial and Austral, in South America. It seems to me that this attempt to reconcile the historico-faunistic findings with descriptive-regional zoogeography is not entirely successful. As far as birds are concerned, none of the five regions mentioned by Simpson is well characterized by its present faunal contents, nor are the boundaries between the regions clear. Distinctive faunas develop only in isolation, and zoogeographic regions can retain their faunistic integrity only if they are separated from other regions by geographical or ecological barriers. The union of the North American and the South American tropical zones at the end of the Pliocene has resulted in such a mingling of the respective faunas that it seems futile to draw a line through Panama separating a tropical "Southern North America" from an "Equatorial South America." The faunas of the two "regions" are today essentially identical. If one wants zoo-

geographic regions, one may have to go back to the solution of the classical zoogeographers, who looked for a physiographic border line and found it in Mexico along the northern edge of the tropical rain-forest belt. This is where Wallace (1876:79) placed the border between his Neotropical and Nearctic regions. So far as I can see, it is along this line that the only major faunal break occurs in the warmer parts of North America. However, I agree with Dunn (1931) and Simpson (1943b) that the term Nearctic is misleading. To call the region north of the tropics (i.e. north of the tropical rain-forest) simply the North American region is probably the best solution.

Comparison of Birds with Other Animals and with Plants

On a walk through the woods in temperate North America, one encounters flowers and trees which differ but little from species found in temperate Asia. The admixture of tropical South American elements is negligible. The same is true for mammals. The porcupine and the armadillos are apparently the only South American elements in the present North American mammal fauna, compared with a 13 to 20 per cent South American element in the bird fauna, except at the northern fringe (Table 2). I do not know of any exact published figures, but I gather from the writings of mammalogists that more than 50 per cent of the temperate North American mammals are of Old World origin. (Is the percentage even higher in plants?) In birds (again excepting the northern fringe), it is only a third or less.

There are mainly two reasons why the Old World element is so much weaker among North American birds than among most other animal groups—or perhaps I should better say: why the South American and warm North American element in temperate America is so much stronger in birds than in other animal groups. One of these reasons is the ability of birds to cross water gaps. Thus, while the indigenous mammals were imprisoned in South America during the Tertiary separation of the two continents, several groups of South American birds crossed the water gap into the northern continent. Among the invading groups that became thoroughly established in North America are the blackbirds and troupials (Icteridae), tyrant flycatchers (Tyrannidae), and cardinals (*Richmondena, Hedymeles, Passerina,* etc.). Some of these genera and generic groups must have arrived in North America at a very early date. Pre-empting many ecological niches, the 40 or 50 species of these originally South American groups have helped stem the influx of Old World species.

A second and more important factor is bird migration. It enables many tropical or semitropical birds to include in their breeding range the areas of the temperate zone that have a hot summer season and move back into their tropical home when the cool season begins. An analysis of the mid-winter avifauna of temperate eastern North America shows that it is composed almost entirely of Old World elements. The

difference in migratory behavior between the autochthonous and the Old World elements is illustrated in the following statistics. Among the 28 species of permanent residents (excluding water birds and unanalyzable species) listed by Cruickshank (1942:25–26) for the New York region, no less than 23 (82.1 per cent) are of Old World origin. On the other hand, among 67 analyzable species of summer residents (which migrate south in the fall) only 8 (11.9 per cent) are of Old World origin. If the 95 species of the two categories are combined, it is found that of the 12 species of the South American element only one (8.3 per cent) is a permanent resident, of the 52 species of the North American element only 4 (8.3 per cent) are permanent residents, while of the 31 species of the Old World element no less than 23 (76.7 per cent) are permanent residents.* The Old World element, which, as Stegmann (1938a) has shown, developed for the most part in the always cold land mass of northern Siberia, is so thoroughly adapted to the cold that it can survive in this latitude without migration, whereas the autochthonous American element, most of which developed in a warm zone, survives the winter by avoiding it.

The combination of these two factors has resulted in the peculiar composition of the contemporary North American bird fauna. It is, therefore, obvious that no general zoogeographic scheme can be based on the distribution of birds, and that the ornithologist will find zoogeographical classifications inapplicable that are based on the distribution of mammals or reptiles. This difference between birds and other

* I present these analyses of Cruickshank's data merely as an illustration of a trend. Because the classification by origin of the birds of such populations (with different migratory status) involves weighing evidence and probabilities, such an analysis inevitably varies somewhat with the individual. For the benefit of students who may wish to make similar analyses of other populations and compare results, I give the following outline of my classification of the populations.

List of Permanent Residents. South American: Cardinal; North American: Ruffed Grouse, Bob-white, Carolina Wren, Song Sparrow; Old World: Sharp-shinned Hawk, Red-tailed Hawk, Bald Eagle, Marsh Hawk, Duck Hawk, Sparrow Hawk, Barn Owl, Screech Owl, Great Horned Owl, Barred Owl, Long-eared Owl, Short-eared Owl, Pileated Woodpecker, Hairy Woodpecker, Downy Woodpecker, Prairie Horned Lark, Blue Jay, Crow, Black-capped Chickadee, Carolina Chickadee, Tufted Titmouse, White-breasted Nuthatch, Goldfinch. (Not analyzed: Cooper's Hawk, Red-shouldered Hawk, Red-headed Woodpecker, Water birds; not considered truly permanent residents: Flicker, Meadowlark, Fish Crow, Swamp Sparrow, Field Sparrow.)

List of Summer Residents. South American (11 = 16.4%): Hummingbird, Kingbird, Crested Flycatcher, Phoebe, Acadian Flycatcher, Alder Flycatcher, Least Flycatcher, Wood Pewee, Scarlet Tanager, Rose-breasted Grosbeak, Indigo Bunting; North American (48 = 71.7%): Flicker, Tree Swallow, Rough-winged Swallow, Purple Martin, Short-billed Marsh Wren, Long-billed Marsh Wren, House Wren, Catbird, Brown Thrasher, Cedar Waxwing, White-eyed Vireo, Yellow-throated Vireo, Red-eyed Vireo, Warbling Vireo, Black and White Warbler, Worm-eating Warbler, Golden-winged Warbler, Blue-winged Warbler, Nashville Warbler, Yellow Warbler, Black-throated Green Warbler, Chestnut-sided Warbler, Pine Warbler, Prairie Warbler, Oven-bird, Louisiana Water-thrush, Kentucky Warbler, Yellow-throat, Yellow-breasted Chat, Hooded Warbler, Redstart, Meadowlark, Bobolink, Red-wing, Orchard Oriole, Baltimore Oriole, Purple Grackle, Cowbird, Towhee, Savannah Sparrow, Swamp Sparrow, Field Sparrow, Grasshopper Sparrow, Henslow's Sparrow, Sharp-tailed Sparrow, Seaside Sparrow, Vesper Sparrow, Chipping Sparrow; Old World (8 = 11.9%): Kingfisher, Bank Swallow, Barn Swallow, Fish Crow, Robin, Wood Thrush, Veery, Bluebird. (Not analyzed: First 31 species listed; added: 5 species from permanent-resident list.)

animal groups is the reason for much of the "New World" versus "Holarctic" controversy. Those who wanted to unite North and South America into a single "New World" based their conclusion mainly on a study of birds. Those who wanted to include North America with Eurasia in a "Holarctic" region based their conclusions on mammals or reptiles.

The History of the Pantropical Element

In a previous section I discussed a number of families which are more or less restricted to the tropics, but are found in the Old as well as in the New World. A similar distribution has been documented for various families and subfamilies of turtles (Simpson, 1943b), and other reptiles (Dunn, 1931), as well as for mammals (e.g. tapirs) and other groups. Various explanations have been advanced to account for this type of distribution. In a few exceptional cases, for example, the White-faced and Fulvous Whistling Ducks (*Dendrocygna viduata* and *D. bicolor*) and the Southern Pochard (*Netta erythrophthalma*), it is reasonably certain that transoceanic colonization is the answer. This explanation is, however, exceedingly improbable for most of the other groups, which have closely related representatives in the tropics of both the Old and the New World, for example, some of the snake-birds (Anhingidae), the sun-grebes (Heliornithidae), jacanas (Jacanidae), barbets (Capitonidae), trogons (Trogonidae), and parrots (Psittacidae) among the birds that I have classified with the Pantropical element; as well as some of the storks (Ciconiidae), ibises (Threskiornithidae), flamingos (Phoenicopteridae), nightjars (Caprimulgidae), woodpeckers (Picidae), and hawks (Accipitridae and Falconidae). A different explanation must be found for their movement from one continent to another.

The "land-bridge builders" considered this pattern of distribution as evidence of a former land connection across the Atlantic and Pacific. The objections to their theories were summarized by Matthew (1915), who showed that fossil finds indicate that many of these families formerly had much wider ranges (probably continuous across the Bering Strait bridge) in the temperate zones. A faunal agreement is particularly close between tropical-subtropical North America and the Old World tropics. It indicates that the present separation of the faunas is of comparatively recent date and that it must have been preceded by a long period of faunal exchange. Matthew (1915), Simpson (1943a:9), and others have postulated that the Bering Strait bridge was the pathway of this faunal exchange, which continued until late in the Tertiary (and, as far as non-tropical elements are concerned, down to the present). Stegmann (1938b) objects to this solution. He quotes considerable evidence from the field of paleobotany and paleoclimatology which indicates (p. 485): "that the climate in the region of Bering

Strait was at times warmer than it is now, but never reached tropical temperatures. Indeed it is quite certain that in northwestern America and in nearly all of Siberia the climate was never tropical or even subtropical during the entire Cenozoic and Cretaceous. . . . The Bering region was thus far outside the tropics during the entire period that needs to be taken into consideration for the evolution of Recent birds, so that it is without the slightest significance as a 'land bridge' for tropical groups." The records of American plant paleontologists support this contention. Chaney (1940) shows that as far back as the Eocene only a temperate climate existed in the countries east and west of the Bering Strait bridge. (See Figure 4.) One has to go as far south as the State of Washington on the American side, and to China on the Asiatic side, to find fossil plants that indicate even a subtropical climate.

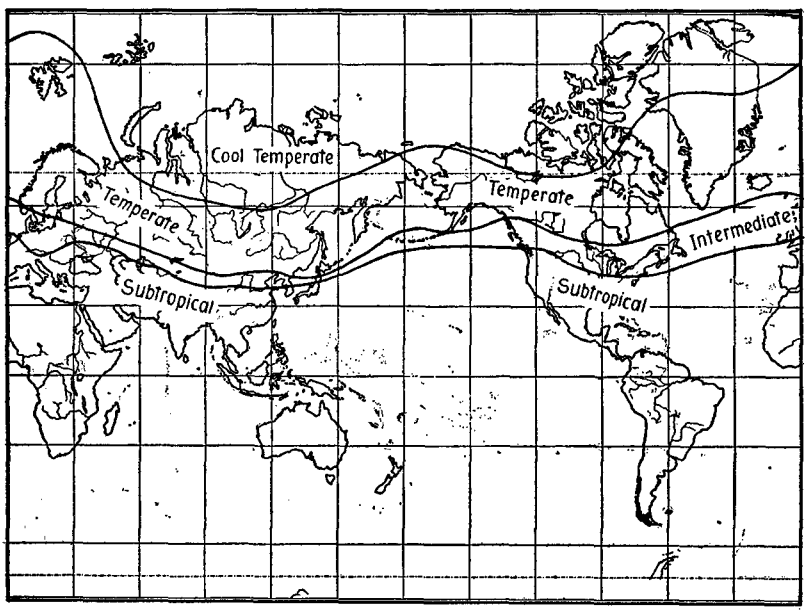

Figure 4. Eocene climatic zones as indicated by fossil plants. (*Based on Chaney, 1940.*)

A generation ago the opinion was widespread among paleogeographers that there were past periods during which a uniformly tropical climate prevailed all over the world. Reputed finds of Tertiary palms in Greenland seemed to strengthen this theory. However, these botanical reports have since been found to be erroneous; furthermore, certain geophysicists have made it abundantly clear that climatic zones must have always existed on the earth. This is a corollary of the earth's

curvature. Less radiated heat from the sun will reach a given area in the higher latitudes than will reach the equatorial districts, where at noon the sun is nearly overhead during the greater part of the year. Furthermore—and this is a factor strangely neglected in books on past climates—the axis of the earth is inclined at an angle of 23½° to the perpendicular to the plane of the ecliptic. This inclination causes our seasons. The northern hemisphere is turned away from the sun during the winter and turned toward the sun during the summer. Geophysicists believe that this angle of the ecliptic has not changed significantly during the geological past. This means that north of the Arctic Circle an Arctic winter night has existed at all times, including the so-called "warm periods" of the earth. The Arctic Circle goes exactly through Bering Strait, and there can be little doubt that an Arctic "winter" (in terms of daily sunlight) must have existed at least as far south as the Aleutians, in other words beyond the southern edge of the Bering shelf. Surely this would not be a favorable condition for tropical faunas and floras to pass freely back and forth between Asia and America.

Yet the close relationship between the Old and New World members of the Pantropical element, whose ranges are now widely discontinuous, proves that such a faunal exchange must have taken place, and this places the zoogeographer in a real quandary. The customary solution for the problem is to ignore it. Stegmann (1938b:492) and other authors of the Russian school (e.g. Wulff, 1943:173–196) attempt to solve it by suggesting a modified Wegenerian land connection across the North Atlantic lasting at least until the middle of the Tertiary. Simpson (1943a:20–22), however, objects to this proposal on the basis of the small number of early Tertiary mammalian forms that were common to Europe and North America. A similar objection comes from the field of botany. The Eocene floras of Europe and North America "were remarkably different" according to Reid and Chandler (1933:70–88). There could have been no direct land connection between the two areas. Additional indirect evidence against a transatlantic bridge is provided by the fact that the American fauna is much closer to the southeast Asiatic than to the European-African fauna.

In view of the improbability of a North Atlantic land connection, various attempts have been made to find new routes for the transpacific migration. I shall refrain from a discussion of the various proposed transpacific land bridges. They are faunistically possible, but find no geological support. There is, however, some evidence for considerable recent tectonic activity in and south of the Aleutian island region, as well as for a pronounced lowering of the floor of the Pacific as a whole. Malaise (1945) and other authors have therefore made the assumption that the Bering Strait bridge was formerly very much wider than it is now, wide enough, in fact, to reach southward into a tropical climate.

Another assumption sometimes made is that there was, during the Tertiary, a much stronger contrast than now on the Bering bridge between the warm climate of its southern shore and the temperate climate of the interior, owing to the shutting off of the Arctic Ocean and the stronger influence of the warm Japan Current. This theory can account for the strictly temperate climate character of all fossil plants found in the Bering bridge area only by assuming that they have come exclusively from inland stations. Also this theory necessarily minimizes the effects of the arctic winter season.

Strict adherents of the theory of permanence of oceans and continents will look for a different explanation of the intercontinental migration of tropical faunas. Perhaps the common ancestors of the tropical faunas in the Old and New Worlds were not so narrowly tropical as are their living descendants. Furthermore, many representatives of tropical families are not nearly so heat-loving as is generally assumed—although they live in equatorial latitudes, their habitat is not tropical. In the characteristically "tropical" family of trogons, for example, *Harpactes wardi* (Burma, Indochina) lives in the mountains between 2,500 and 3,000 meters; *Trogon personatus* and other South American species reach even higher altitudes. The climate at these altitudes is distinctly temperate. Most other "tropical" families of birds, particularly the parrots, have some members that live in an equable humid temperate climate. Species with similar ecological requirements might have been able to exist in the warm temperate parts of Bering Strait bridge, even during the rather dark winter days. It must not be overlooked that the tropical regions were apparently more arid at earlier geological periods than they are today. Perhaps the warm temperate zone was in the late Mesozoic to early Tertiary a refuge for species with a preference for an equable humid climate, just as the tropics are today.

These comments may suffice to indicate that the problems of the faunal exchange between Old and New World are by no means solved. However, the questions that need to be asked are beginning to crystallize, and the information needed to answer them is beginning to accumulate. We have advanced beyond the stage of pure speculation.

Faunal Zoogeography and Ecology

We are all familiar with the fact that among the birds of the northern coniferous woods there is a high percentage of recently immigrated palearctic species. The South American element, on the other hand, is almost non-existent in these forests. It would be a rewarding task to analyze the bird life of all the major North American habitats and determine their faunistic composition from the point of view of origin. To do this in detail would require much more space than can be given in this paper; furthermore, there are not enough reliable published tabulations of the characteristic species of the various habitats to pro-

vide the material for such a study. For example, I have looked in vain for a good tabulation of the typical birds of the chaparral or of some of the more specialized habitats in the Southwest. No comprehensive account of the breeding birds of the various types of prairie is available.

One of the striking features of North American faunal history is that not a single species of the originally South American fauna has crossed the Bering Strait bridge into the Old World. On the other hand, numerous Old World birds have been able to invade South America. Some became adapted to life in the tropics, for example, certain jays, thrushes, kingfishers, and cardueline finches. Others—the Short-eared Owl (*Asio flammeus*) and Horned Lark (*Otocoris alpestris*)—simply jumped the tropical gaps.

It would be tempting to reconstruct the climate on Bering Strait bridge throughout the Tertiary by analyzing the ecological requirements of the birds that passed this bridge at a given period. At present, for example, the bridge is passable only for birds of the tundra and of the coniferous belt (taiga = "Hudsonian"). Stegmann (1938b) lists the birds that could pass Bering Strait under climatic conditions similar to or slightly warmer than the present. But as we go further back in time, the analysis becomes more difficult. Again it seems that the Old World contributed more than the New. The only birds of North American origin that have spread into the Old World are the grouse (Tetraonidae), the finches of the subfamily Emberizinae, one species of wren (*Troglodytes troglodytes*), and—if these are indeed North American—two species of dippers (*Cinclus cinclus, C. pallasii*), and two species of waxwings (*Bombycilla garrula, B. japonica*). Even such richly developed North American families as the mockingbirds (Mimidae), vireos (Vireonidae), and wood warblers (Parulidae) * have not crossed for reasons that are difficult to understand. On the other hand, nearly every family of temperate Eurasia has entered North America, and most of them have sent at least one representative as far as South America.

It is conceivable that the fauna of each of the major habitats or ecological formations of North America would have its peculiar composition from the point of view of origin. However, a glance at Table 3 shows that there are no major differences, at least as far as forest habitats are concerned. What differences there are can be attributed mainly to latitude. Also there seems to be no striking difference from the point of view of origin between the faunas of climax and second growth. Among 159 breeding pairs listed in two years (1932, 1934) on a study area in a climax Maple-Beech-Hemlock forest Saunders (1938:32–33) records 10.0 per cent South American, 71.1 per cent North American, and 18.9 per cent Old World pairs. Among 104 pairs

* The Myrtle Warbler (*Dendroica coronata*) and the Northern Water-thrush (*Seiurus noveboracensis*) have recently crossed into Anadyrland.

(listed in 1932, 1933) in near-by second growth Cherry-Aspen there were 6.8 per cent South American, 71.1 per cent North American, and 22.1 per cent Old World pairs. The figures were thus almost identical.

In specialized habitats there are sometimes significant deviations from the faunal composition exemplified in Tables 2 and 3. For example, all of the species usually listed as typical for the mid-western prairie are of North American origin: Prairie Chicken (*Tympanuchus cupido*), Upland Plover (*Bartramia longicauda*), Burrowing Owl (*Speotyto cunicularia*), Western Meadowlark (*Sturnella neglecta*), Bobolink (*Dolichonyx oryzivorus*), Grasshopper Sparrow (*Ammodramus savannarum*), and Savannah Sparrow (*Passerculus sandwichensis*). This may mean that the great humidity of both the Bering and the Panama bridges prevented an influx of the faunas of the more arid habitat of Eurasia and South America. The ecological niche of the North American grasslands thus could be filled by the autochthonous North American element. The land birds of marshes also tend to be prevailingly (80 to 100 per cent) North American. For example, the Long-billed Marsh Wren (*Telmatodytes palustris*), Short-billed Marsh Wren (*Cistothorus stellaris*), Swamp Sparrow (*Melospiza georgiana*), Sharp-tailed Sparrow (*Ammospiza caudacuta*), Seaside Sparrow (*A. maritima*), Red-wing (*Agelaius phoeniceus*), and Yellow-headed Blackbird (*Xanthocephalus xanthocephalus*). The Old World element, on the other hand, is, as a rule, comparatively strong at the higher altitudes in the mountains.

It would be interesting to analyze in a similar manner other specialized habitats, such as the Californian chaparral, the creosote bush–mesquite thickets of the Southwest and the Caribbean mangroves, but adequate census data are not available. This brief discussion is to be considered merely as a hint at the interesting relationship between ecology and faunal history, which constitutes a fertile field for future investigators.

Literature Cited

Allen, J. A.

1871 On the mammals and winter birds of east Florida, with an examination of certain assumed specific characters in birds, and a sketch of the bird faunae of eastern North America. *Bull. Mus. Comp. Zool.*, 2, No. 3, pp. 161–450.

1893 The geographical origin and distribution of North American birds, considered in relation to faunal areas of North America. *Auk*, 10:97–150.

Amadon, Dean

1944 The genera of Corvidae and their relationships. *Amer. Mus. Novit. No.* 1251.

Carpenter, Geo. H.

1894 Nearctic or Sonoran? *Nat. Sci.*, 5:53–57.

CHANEY, RALPH W.
1940 Tertiary forests and continental history. *Bull. Geol. Soc. Amer.,* 51:469–488.

CHAPMAN, FRANK M.
1923 The distribution of the motmots of the genus Momotus. *Bull. Amer. Mus. Nat. Hist.,* 48:27–59.

CRUICKSHANK, ALLAN D.
1942 Birds around New York City. *Amer. Mus. Nat. Hist. Handbook Ser., No.* 13.

DELACOUR, JEAN, and ERNST MAYR
1945 The family Anatidae. *Wils. Bull.,* 57:3–55.

DUNN, EMMETT REID
1922 A suggestion to zoogeographers. *Science,* 56:336–338.
1931 The herpetological fauna of the Americas. *Copeia,* 1931:106–119.

GILL, THEODORE
1875 On the geographical distribution of fishes. *Ann. and Mag. Nat. Hist.* (Ser. 4), 15:251–255.

HEILPRIN, ANGELO
1883 On the value of the "Nearctic" as one of the primary zoological regions. Replies to criticisms by Mr. Alfred Russel Wallace and Prof. Theodore Gill. *Proc. Acad. Nat. Sci. Phila.,* 1883:266–275.

HICKEY, JOSEPH J.; MARGARET B. HICKEY
1937–1944 Bird-Lore's [Audubon Magazine's] breeding bird-census. 1–8. *Aud. Mag.* [formerly *Bird-Lore*], 39–46.

HUBBS, CARL L.
1944 [Review of "Studies in the genetics of Drosophila. III"]. *Amer. Nat.,* 78:270–271.

LÖNNBERG, EINAR
1927 Some speculations on the origin of the North American ornithic fauna. *Kungl. Svenska Vetenskapsakad. Handl.* Ser. 3, vol. 4, no. 6, pp. 1–24.

MALAISE, RENÉ
1945 Tenthredinoidea of southeastern Asia. *Opusc. Entom.,* suppl. 4.

MATTHEW, W. D.
1915 Climate and evolution. *Ann. N.Y. Acad. Sci.,* 24:171–318.

MAYR, ERNST
1941 List of New Guinea birds. Amer. Mus. Nat. Hist., New York.
1944a The birds of Timor and Sumba. *Bull. Amer. Mus. Nat. Hist.,* 83:123–194.
1944b Wallace's Line in the light of recent zoogeographic studies. *Quart. Rev. Biol.,* 19:1–14.

MAYR, ERNST, and JAMES BOND
1943 Notes on the generic classification of the swallows, Hirundinidae. *Ibis,* 85:334–341.

PETERS, JAMES LEE
1940 Check-list of birds of the world. vol. 4. Harv. Univ. Press, Cambridge, Mass.

REICHENOW, A.
1888 Die Begrenzung zoogeographischer Regionen vom ornithologischen Standpunkt. *Zool. Jahrb., Abtheilung für Systematik, Geographie und Biologie der Thiere,* 3:671–704.

REID, ELEANOR MARY, and MARJORIE ELIZABETH JANE CHANDLER
1933 The London clay flora. Brit. Mus. (Nat. Hist.), London.

RIPLEY, S. DILLON
1945 The barbets. *Auk,* 62:542–563.

SAUNDERS, ARETAS A.
1938 Studies of breeding birds in the Allegany State Park. *N. Y. State Mus. Bull. No.* 318.

SCHMARDA, LUDWIG K.
1853 Die geographische Verbreitung der Thiere. vol. 2. Vienna.

SCLATER, PHILIP LUTLEY
1858 On the general geographical distribution of the members of the class Aves. *Jour. Proc. Linn. Soc. London for Feb.* 1858, pp. 130–145.

SHARPE, R. BOWDLER
1903 A hand-list of the genera and species of birds. vol. 4. Brit. Mus. (Nat. Hist.), London.

SIMPSON, GEORGE GAYLORD
1940a Mammals and land bridges. *Jour. Wash. Acad. Sci.,* 30:137–163.
1940b Antarctica as a faunal migration route. *Proc. Sixth Pac. Sci. Congr.* (1939), vol. 2, pp. 755–768.
1943a Mammals and the nature of continents. *Amer. Jour. Sci.,* 241:1–31.
1943b Turtles and the origin of the fauna of Latin America. *Amer. Jour. Sci.,* 241:413–429.

STEGMANN, B.
1932 Die Herkunft der paläarktischen Taiga-Vögel. *Arch. f. Naturg.* (N.F.), 1:355–398. [Leipzig]
1938a Principes généraux des subdivisions ornithogeographiques de la région paléarctique. *Faune de l'URSS* (N.S. 19), *L'Oiseaux,* vol. 1, no. 2.
1938b Das Problem der atlantischen Landverbindung in ornithogeographischer Beleuchtung. *Proc. Eighth Internatl. Ornith. Congr.* (Oxford), 1934: 476–500.

STRESEMANN, ERWIN
1939 Die Vögel von Celebes. Teil 2. Zoogeographie. *Jour. f. Ornith.,* 87:312–425.

SUSHKIN, PETER P.
1924 [Résumé of the taxonomical results of morphological studies of the Fringillidae and allied groups]. *Bull. Brit. Ornith. Club,* 45:36–39.
1925 A preliminary arrangement of North American genera of Fringillidae and allied groups. *Auk,* 42:259–261.

SZIDAT, L.
1940 Die Parasitenfauna des Weissen Storches und ihre Beziehungen zu Fragen der Oekologie, Phylogenie und der Urheimat der Störche. *Z. Parasitenkunde,* 11:563–592.

WALLACE, ALFRED RUSSEL
1876 The geographical distribution of animals. vol. 1. Harper & Bros., New York.

WETMORE, ALEXANDER
1940 A check-list of the fossil birds of North America. *Smiths. Misc. Coll.,* 99, no. 4.
1944 A new terrestrial vulture from the upper Eocene deposits of Wyoming. *Ann. Carnegie Mus.,* 30:57–69.

WULFF, E. V.
1943 An introduction to historical plant geography. Chronica Botanica Co., Waltham, Mass.

THE AMERICAN MUSEUM OF NATURAL HISTORY, NEW YORK 24, N. Y.