DISTRIBUTION OF THE FAMILIES OF BIRDS

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THE division of the world into six faunal regions by Alfred Russel Wallace (1876) is familiar to most zoölogists. Wallace used chiefly the distribution of mammals in arriving at the extent and boundaries of his regions but he was greatly indebted to the British ornithologist, Philip Lutley Sclater, for the latter had announced in 1858 a division of the globe into six regions based on his study of the distribution of birds. Sclater had proposed the following regions: Palaearctic, Ethiopian, Indian, Australian, Neotropical and Nearctic; and they were adopted almost exactly by Wallace with the exception of a change of name of the Indian region to Oriental as being more descriptive. Other zoögeographic divisions of the world have been advanced but Wallace's is undoubtedly the best known.

Mayr (1935) has estimated that there are approximately 27,000 named species and subspecies of birds known today, a great increase over the number known to Sclater and Wallace. Continued study of their relationships has resulted in the creation of many new families while other groups, which once enjoyed the family rank, have been consolidated. The most recent work of this type is Wetmore's 'A Systematic Classification for the Birds of the World' (1934). In this classification, 166 families of Recent birds were recognized and it has been followed closely in this paper, the sole change being a consolidation of the families Loriidae and Psittacidae made necessary by an unfortunate confusion existing in the nomenclature of these two groups. This of course reduced the number of families to be considered here to 165. Mr. Rudyerd Boulton of the Field Museum suggested to me that it would be a worthwhile project to map the distribution of each of the families of birds according to Wetmore's classification and then to classify each family as belonging to one or more of Wallace's regions. This I did, basing the maps mainly on data from Peters's 'Check-list of Birds of the World', Knowlton and Ridgway's 'Birds of the World' and Stresemann's 'Aves' in Kükenthal's 'Handbuch der Zoologie'. When the maps had been completed, an attempt was made to form a table showing the distribution of all the families of birds among Wallace's regions. However, it soon became apparent that certain families could not be placed fairly in any of the regions as defined by Wallace so they were omitted from the table. The families thus eliminated were as follows: Spheniscidae (penguins), Diomedeidae (albatrosses),

Procellariidae (shearwaters and fulmars), Hydrobatidae (storm petrels), Pelecanoididae (diving petrels), Phaëthontidae (tropic-birds), Fregatidae (frigate-birds), Chionidae (sheath-bills) and Stercorariidae (skuas and jaegers). These are all waterbirds and most of them nest on islands and range widely over the oceans between breeding seasons.

Several other families were also eliminated because they are limited to oceanic islands, which do not fit well into Wallace's scheme. The families thus removed were as follows: Apterygidae (kiwis) and Xenicidae (New Zealand wrens) of New Zealand; Mesoenatidae (roatelos, monias), Leptosomatidae (cuckoo-rollers and ground-rollers), Philepittidae (asities), Hypositidae (coral-billed nuthatches) and Vangidae (vanga shrikes) of Madagascar; Rhynochetidae (kagus) of New Caledonia; Raphidae (dodos, solitaires) of the Mascarene Islands; Todidae (todies) and Dulidae (palm-chats) of the West Indies; Drepanididae (Hawaiian honey-creepers) of the Hawaiian Islands.

The elimination of the 21 families noted above left 144 families to be considered and their distribution is shown in Table 1.

NOTE: X denotes presence of family in region; x denotes presence of family in region but not a typical member.

TABLE 1

DISTRIBUTION OF FAMILIES OF BIRDS AMONG WALLACE'S REGIONS

Family	*Region*					
	Palaearctic	*Ethiopian*	*Oriental*	*Australian*	*Neotropical*	*Nearctic*
Struthionidae, ostriches	x	X				
Rheidae, rheas					X	
Casuariidae, cassowaries				X		
Dromiceiidae, emus				X		
Tinamidae, tinamous					X	
Gaviidae, loons	X					X
Colymbidae, grebes	X	X	X	X	X	X
Pelecanidae, pelicans	X	X	X	X	X	X
Sulidae, gannets	X	X	X	X	X	X
Phalacrocoracidae, cormorants	X	X	X	X	X	X
Anhingidae, snake-birds	x	X	X	X	X	X
Ardeidae, herons, bitterns	X	X	X	X	X	X
Cochleariidae, boat-billed herons					X	
Balaenicipitidae, whale-headed storks		X				
Scopidae, hammerheads		X				
Ciconiidae, storks, jabirus	X	X	X	X	X	x

TABLE 1—(*Continued*)

Family	*Region*					
	Palaearctic	*Ethiopian*	*Oriental*	*Australian*	*Neotropical*	*Nearctic*
Threskiornithidae, ibises, spoonbills	X	X	X	X	X	X
Phoenicopteridae, flamingos	X	X	X		X	x
Anhimidae, screamers					X	
Anatidae, ducks, geese, swans	X	X	X	X	X	X
Cathartidae, New World vultures					X	X
Sagittariidae, secretary-birds		X				
Accipitridae, hawks, Old World vultures, harriers, ospreys	X	X	X	X	X	X
Falconidae, falcons, caracaras	X	X	X	X	X	X
Megapodiidae, megapodes			X	X		
Cracidae, curassows, guans, chachalacas					X	
Tetraonidae, grouse	X					X
Phasianidae, quails, pheasants, peacocks	X	X	X	X	X	X
Numididae, guinea-fowl		X				
Meleagrididae, turkeys					X	X
Opisthocomidae, hoatzins					X	
Turnicidae, bustard-quails	X	X	X	X		
Pedionomidae, collared hemipodes				X		
Gruidae, cranes	X	X	X	X		X
Aramidae, limpkins					X	x
Psophiidae, trumpeters					X	
Rallidae, rails, coots, gallinules	X	X	X	X	X	X
Heliornithidae, sun-grebes		X	X		X	
Eurypygidae, sun-bitterns					X	
Cariamidae, cariamas					X	
Otididae, bustards	X	X	X	X		
Jacanidae, jacanas		X	X	X	X	x
Rostratulidae, painted snipe	x	X	X	X	X	
Haematopodidae, oyster-catchers	X	X	X	X	X	X
Charadriidae, plovers, turnstones, surf-birds	X	X	X	X	X	X
Scolopacidae, snipe, woodcock, sandpipers	X	X	X	X	X	X
Recurvirostridae, avocets, stilts	X	X	X	X	X	X
Phalaropodidae, phalaropes	X					X
Dromadidae, crab-plovers		X	X			
Burhinidae, thick-knees	X	X	X	X	X	
Glareolidae, pratincoles, coursers	X	X	X	X		
Thinocoridae, seed-snipe					X	
Laridae, gulls, terns	X	X	X	X	X	X
Rynchopidae, skimmers		X	X		X	X
Alcidae, auks, auklets, murres	X					X
Pteroclidae, sand-grouse	X	X	X			
Columbidae, pigeons, doves	X	X	X	X	X	X

TABLE 1—(*Continued*)

Family	*Region*					
	Palaearctic	*Ethiopian*	*Oriental*	*Australian*	*Neotropical*	*Nearctic*
Psittacidae, parrots, macaws, lories	x	X	X	X	X	x
Musophagidae, plantain-eaters		X				
Cuculidae, cuckoos, roadrunners, anis	X	X	X	X	X	X
Tytonidae, barn owls	X	X	X	X	X	X
Strigidae, owls	X	X	X	X	X	X
Steatornithidae, oil-birds					X	
Podargidae, frogmouths			X	X		
Nyctibiidae, potoos					X	
Aegothelidae, owlet-frogmouths				X		
Caprimulgidae, goatsuckers	X	X	X	X	X	X
Micropodidae, swifts	X	X	X	X	X	X
Hemiprocnidae, crested swifts			X	X		
Trochilidae, hummingbirds					X	X
Coliidae, colies		X				
Trogonidae, trogons		X	X		X	
Alcedinidae, kingfishers	X	X	X	X	X	X
Momotidae, motmots					X	
Meropidae, bee-eaters	X	X	X	X		
Coraciidae, rollers	X	X	X	X		
Upupidae, hoopoes	X	X	X			
Phoeniculidae, wood-hoopoes		X				
Bucerotidae, hornbills		X	X	X		
Galbulidae, jacamars					X	
Bucconidae, puff-birds					X	
Capitonidae, barbets		X	X		X	
Indicatoridae, honey-guides		X	X			
Rhamphastidae, toucans					X	
Picidae, woodpeckers, piculets	X	X	X	x	X	X
Eurylaimidae, broadbills		X	X			
Dendrocolaptidae, wood-hewers					X	
Furnariidae, ovenbirds					X	
Formicariidae, ant-thrushes					X	
Conopophagidae, ant-pipits					X	
Rhinocryptidae, tapaculos					X	
Cotingidae, cotingas					X	
Pipridae, manakins					X	
Tyrannidae, tyrant flycatchers					X	X
Oxyruncidae, sharp-bills					X	
Phytotomidae, plant-cutters					X	
Pittidae, pittas		X	X	X		
Menuridae, lyre-birds				X		
Atrichornithidae, scrub-birds				X		

TABLE 1—(*Continued*)

Family	*Region*					
	Palaearctic	*Ethiopian*	*Oriental*	*Australian*	*Neotropical*	*Nearctic*
Alaudidae, larks	X	X	X	X	x	X
Hirundinidae, swallows	X	X	X	X	X	X
Campephagidae, cuckoo-shrikes		X	X	X		
Dicruridae, drongos	X	X	X	X		
Oriolidae, Old World orioles	X	X	X	X		
Corvidae, crows, magpies, jays	X	X	X	X	X	X
Paradiseidae, birds of paradise				X		
Paradoxornithidae, parrot-bills, suthoras	X		x			
Paridae, titmice	X	X	X	X		X
Sittidae, nuthatches	X		X	X		X
Certhiidae, creepers	X	X	X	X		X
Chamaeidae, wren-tits						X
Timeliidae, babbling thrushes	X	X	X	X		
Pycnonotidae, bulbuls	X	X	X	x		
Cinclidae, dippers	X		X		X	X
Troglodytidae, wrens	X		X		X	X
Mimidae, thrashers, mockingbirds					X	X
Turdidae, thrushes	X	X	X	X	X	X
Zeledoniidae, wren-thrushes					X	
Sylviidae, Old World warblers	X	X	X	X	X	X
Regulidae, kinglets	X					X
Muscicapidae, Old World flycatchers	X	X	X	X		
Prunellidae, accentors, hedge sparrows	X					
Motacillidae, wagtails, pipits	X	X	X	X	X	X
Bombycillidae, waxwings	X					X
Ptilogonatidae, silky flycatchers					X	X
Artamidae, wood-swallows		X	X	X		
Laniidae, shrikes	X	X	X	X		X
Prionopidae, wood-shrikes		X	X	X		
Cyclarhidae, pepper-shrikes					X	
Vireolaniidae, shrike-vireos					X	
Sturnidae, starlings	X	X	X	X		
Melithreptidae, honey-eaters		x		X		
Nectariniidae, sunbirds	x	X	X	X		
Dicaeidae, flower-peckers			X	X		
Zosteropidae, white-eyes	X	X	X	X		
Vireonidae, vireos					X	X
Coerebidae, honey-creepers					X	
Compsothlypidae, wood warblers					X	X
Ploceidae, weaver finches	X	X	X	X		
Icteridae, blackbirds, troupials					X	X
Procniatidae, swallow-tanagers					X	

TABLE 1—(*Continued*)

Family	*Region*					
	Palaearctic	*Ethiopian*	*Oriental*	*Australian*	*Neotropical*	*Nearctic*
Thraupidae, tanagers					X	X
Catamblyrhynchidae, plush-capped finches					X	
Fringillidae, grosbeaks, finches, buntings	X	X	X		X	X
Number of families per region	69	79	78	72	86	62
Number of endemic families	1	7	0	7	31	1
Per cent of endemic families	1.4	8.9	0	9.7	36.1	1.6

NOTE: X denotes presence of family in region; x denotes presence of family in region but not a typical member.

An inspection of the table reveals that some further qualifications seem advisable. Some families, typical of a certain region, are found represented just over the border in an adjoining region by one or two species. This fact is indicated in Table 1 by a small 'x', denoting the family's occurrence in the invaded region. The element of personal opinion thus entered into the making of decisions as to whether a border-line case should be considered as a typical family of a given region. I have been guided in this matter by the judgment of Mr. Boulton, to whom I am indebted and grateful for help on this and many other points.

Of the 144 families listed in Table 1 almost one-fourth, 33 in fact, are found in all of Wallace's regions. They are about equally divided between terrestrial and aquatic families. The total number of families in any given region does not differ greatly from the number in any other region. The range between the 62 families of the Nearctic and the 86 families of the Neotropical is not very great. However, one is struck by the great variation in the number of endemic families, ranging from none in the Oriental to 31 in the Neotropical, a figure which is expressive of the distinctive character of the Neotropical region. The Ethiopian and Australian regions and the Palaearctic and Nearctic regions are close parallels in the matter of endemic families, a fact which will be recalled for consideration later. The Oriental region appears to have acted as a meeting point for Ethiopian, Palaearctic and Australian families of birds so the lack of endemic families is not surprising. Figures to show the degree of relationship between the Oriental and the three other regions mentioned above will be given later.

Almost as instructive as the endemic families are those groups of birds that occur in five of Wallace's regions but are missing from one region. Here again the Neotropical is most distinctly set off for it lacks the following families: Gruidae, Paridae, Certhiidae and Laniidae. The place of the Gruidae appears to be filled by the Psophiidae, a closely related family, in the Neotropical. The Paridae and Certhiidae appear to be families of northern origin which have not yet penetrated the Neotropical. The family Laniidae is mainly Old World in distribution. In addition, the family Alaudidae is poorly represented in the Neotropical. Larks are plains birds, dwellers in open country, and are evidently filtering into South America by way of the *paramos* of the Andes Mountains. They are restricted in their eastward distribution by the presence of the great tropical rain-forests of the Orinoco and Amazon River systems but they may be expected to spread out over the broad llanos and pampas of southern South America in the future.

The Nearctic region lacks the Rostratulidae and Burhinidae, two families which probably occurred there in the past but have been driven out or exterminated. The Ciconiidae are very sparingly represented in the southern part of the Nearctic by the Wood Ibis alone. The Wood Ibises, which include three Old World species, have been thought by some taxonomists to be worthy of family rank.

The Australian region lacks the Phoenicopteridae and Fringillidae. The absence of such an ancient group as the flamingos is difficult to explain satisfactorily. The Fringillidae is a very successful family which may be expected to become established in the Australian region eventually. The Picidae are just over the line in the Australian for they occur in some of the Moluccas. It seems quite possible that in the course of time they may occupy more of the Australian region although the isolation of the continent of Australia coupled with the fact that the woodpeckers are not very strong fliers may delay their establishment there for a long time.

A further inspection of Table 1 shows that there are certain families which are confined to two regions and are found nowhere else. This may be taken as evidence of close faunal relationship, at least as far as families of birds are concerned. There is no need to list these families for they can be easily abstracted from Table 1 but the figures are interesting: Palaearctic-Ethiopian, 1; Palaearctic-Oriental, 1; Palaearctic-Nearctic, 6; Ethiopian-Oriental, 3; Oriental-Australian, 4; Neotropical-Nearctic, 11. If one were to estimate degree of faunal relationship solely on this basis, then one would say that the Neotropical-Nearctic pair are most closely allied. But it

seems to me that there is a difference in the quality of the relationship between members of different pairs of regions. In the Palaearctic-Nearctic pair it is difficult to determine which families are predominantly Palaearctic, which Nearctic, a point in favor of combining the two and calling it the Holarctic region. Another relationship is indicated between the members of the Ethiopian-Oriental pair where there has been a fairly even exchange, the Indicatoridae being Ethiopian in origin and the Eurylaimidae of Oriental origin. The third type is the one-sided relationship existing between the Neotropical and the Nearctic where most of the families are Neotropical in origin, judging from the number of genera and species found there in contrast to the number of genera and species of the same families in the Nearctic. On this basis the Trochilidae, Tyrannidae, Mimidae, Ptilogonatidae, Vireonidae, Icteridae and Thraupidae are almost certainly of Neotropical origin. To estimate the closeness of relationship between the Neotropical and Nearctic, or between any two regions, solely on the basis of peculiar families in common seems unfair. It should be supplemented by a comparison of the number of families common (not necessarily peculiar) to the two regions. Table 2 does this for all the combinations of Wallace's regions.

TABLE 2

A NUMERICAL COMPARISON OF THE FAMILIES OF BIRDS IN EACH PAIR OF WALLACE'S REGIONS

Regions	*Total no. of families in two regions*	*No. of families common to two regions*	*Per cent of common families*
Palaearctic-Ethiopian	90	58	64.4%
Palaearctic-Oriental	85	61	71.2%
Palaearctic-Australian	87	54	62.1%
Palaearctic-Neotropical	116	39	33.6%
Palaearctic-Nearctic.	83	48	57.8%
Ethiopian-Oriental	87	70	80.5%
Ethiopian-Australian	91	60	65.9%
Ethiopian-Neotropical	123	42	34.1%
Ethiopian-Nearctic	100	41	41.0%
Oriental-Australian	86	64	74.4%
Oriental-Neotropical	120	44	36.7%
Oriental-Nearctic	96	43	44.8%
Australian-Neotropical	122	36	29.5%
Australian-Nearctic	95	39	41.1%
Neotropical-Nearctic	98	50	51.0%

According to the figures given in Table 2, the Ethiopian and Oriental regions are most closely related with 80.5 per cent of their families in common. The Oriental-Australian regions with 74.4 per cent and the Palaearctic-Oriental regions with 71.2 per cent of their families in common come next on the list. The fact that the Oriental region appears in all three of these most closely related combinations of regions is indicative of the lack of distinction in its fauna previously mentioned in connection with its lack of endemic families. Since the Ethiopian and Oriental regions were probably connected in the past, it is not surprising that they should be so closely related. One might expect the Neotropical and the Nearctic to show close affinities and indeed they do in the possession of 11 families found nowhere else, but as Table 2 shows, only 51 per cent of their families is common to both. We must, therefore, recognize that the Nearctic and Neotropical regions do differ to a considerable degree in spite of the comparatively large number of families peculiar to the two regions.

Table 2 might be applied to answer such a question as whether the Oriental region is more closely related to the Palaearctic region, with which it lies in contact on the north, or with the Australian region lying to the southeast. According to Table 2 the relationship is closer with the Australian and this conclusion is supported by the fact that the Oriental has four families in common with the Australian which are found nowhere else while it has only one peculiar family in common with the Palaearctic. Table 2 should be employed with some caution, I believe, and taken as indicating in a broad manner the degree of relationship between Wallace's regions. This is particularly true in those groups ranking near the bottom of the list, for any two regions, even at opposite ends of the earth, may be expected to show a certain percentage of common families as a result of the fact, previously noted, that there are 33 families which are cosmopolitan in their distribution and eight which are absent from only one of the six regions.

Sclater placed his four Old World regions in one group, Palaeogaea, and the two New World regions in another group called Neogaea. There are fourteen families found in all four of the Old World regions; they are: Turnicidae, Otididae, Glareolidae, Meropidae, Coraciidae, Dicruridae, Oriolidae, Timeliidae, Pycnonotidae, Muscicapidae, Sturnidae, Nectariniidae, Zosteropidae and Ploceidae. On the other hand, the New World has eleven families which are present in both the Nearctic and the Neotropical and are absent from the Old World. These families are: Cathartidae, Meleagrididae, Arami-

dae, Trochilidae, Tyrannidae, Mimidae, Ptilogonatidae, Vireonidae, Compsothlypidae, Icteridae and Thraupidae.

The Meropidae (bee-eaters) appear to fill an ecological niche in the Old World which is occupied by the Galbulidae (jacamars) of the New World. Other ecological equivalents might be mentioned: Muscicapidae (Old World flycatchers) and Tyrannidae (tyrant flycatchers), Nectariniidae (sunbirds) and Trochilidae (hummingbirds). It seems likely that the Nectariniidae, as an example of ecological equivalence, could exchange places with the Trochilidae, provided they could reach the New World. But the two families are separated by the Atlantic Ocean, making it extremely improbable that such an exchange will ever occur. Here we have an example of one of the barriers to the distribution of land birds, the ocean.

In addition to the ecological equivalents just mentioned there are some families in the Old World which are morphologically very close to certain of the New World families. The Zosteropidae (white-eyes) are structurally very close to the Vireonidae (vireos) and Compsothlypidae (wood warblers). Also the Ploceidae (weaver finches) resemble the Icteridae (blackbirds and troupials) and Thraupidae (tanagers) in that they are all specialized finches.

The Phoenicopteridae (flamingos) are found in the Ethiopian and Neotropical regions, in the southern Palaearctic, western Oriental and southeastern Nearctic. It is evidently an ancient group for the Phoenicopteridae are well represented by fossils, the oldest of these forms coming from the upper Cretaceous of Denmark. Other forms have been found in the middle and late Tertiary of Europe and a single Pliocene form from central Oregon, according to Knowlton and Ridgway.

The distribution of the Sittidae (nuthatches) seems to be in accord with Matthew's (1915) theory of the dispersal of vertebrates from a Holarctic center of origin. The nuthatches inhabit the forested areas of the Palaearctic, Oriental, Australian and Nearctic regions. From this distribution it would appear that the family arose somewhere in the Palaearctic and spread south through the Oriental and Australian regions and east across the Bering Strait into the Nearctic. It is probable that the desert character of most of northern Africa has prevented the family from entering the Ethiopian region. Its absence from the Neotropical can best be explained by the likelihood that the Sittidae have not had sufficient time to penetrate this region.

Two families, the Cinclidae (dippers) and Troglodytidae (wrens), show this distribution: Palaearctic, Oriental, Nearctic, Neotropical.

The dippers are found only where there are swift mountain streams and appear to have originated in the Palaearctic. They followed the mountains of the Palaearctic west to the Atlantic Ocean and east to Bering Strait, which they crossed, entering the Nearctic. They then came down the long chain of mountains extending from Alaska almost to the southern tip of South America. The dippers might flourish in the Appalachian Mountains of the eastern Nearctic but there are approximately 2,000 miles of mountainless country intervening. They occur in the Atlas Mountains of Africa but are prevented by the Sahara Desert from reaching the equatorial mountains of central Africa, where they might find suitable habitats. This distribution shows mountain chains acting as highways for birds but in a slightly different manner from that in which the highlands of the Andes are furnishing a road for the penetration of the Neotropical by the larks. The Troglodytidae are regarded as having their center of distribution in the Neotropical, whence they have spread into the Nearctic, Palaearctic and Oriental. They have not reached the Ethiopian and Australian regions although they are close to Wallace's Line in the Oriental and probably will spread into the Australian region in the future.

Still another combination of regions is that in which the Rynchopidae occur. The skimmers are found in the Ethiopian, Oriental, Neotropical and Nearctic regions along the coast and occasionally penetrate into the interior by means of large rivers, such as the Amazon of the Neotropical and the Congo of the Ethiopian. In the Nearctic they are found around the Gulf of Mexico and breed north to New Jersey and Long Island. This may be due to the warm Gulf Stream along that portion of the coast of the Nearctic.

The case of the Spheniscidae (penguins) offers a somewhat similar instance of an ocean current influencing the distribution of a group of birds. The penguins are typically birds of the Antarctic, but a single species occurs on the Galapagos Islands, which lie on the equator off the west coast of South America. Their presence here is believed due to their following the cold waters of Humboldt's Current, which parallels the west coast of the Neotropical. Thus we have the range of a tropical family extended by a warm current in the case of the skimmers and that of an Antarctic family by a cold current in the ocean in the case of the penguins. The Fregatidae (frigate-birds) and Phaëthontidae (tropic-birds) appear to illustrate the restriction of the range of families through temperature barriers for, although they are found around the world, they are restricted to tropical and subtropical seas.

The families Pterocletidae (sand grouse), Upupidae (hoopoes) and Pycnonotidae (bulbuls) are found in the Palaearctic-Ethiopian-Oriental group of regions. The sand grouse dwell in that great belt of desert and semi-desert country stretching across Africa from the western Sahara, the Syrian and Arabian deserts and the deserts of Asia to the Gobi. Their distribution is dependent on the presence of open country for they shun forests. They have advanced from the Sahara in Africa down the east coast of that continent and are found in the desert area of southwestern Africa. They have probably been prevented from populating the great desert tracts of Australia by the dense forests of southeastern Asia as much as by the distances involved. This is a case of the forest acting as a barrier to the distribution of a desert form.

Families peculiar to the Ethiopian-Oriental-Australian complex are: Bucerotidae (hornbills), Pittidae (pittas), Campephagidae (cuckoo-shrikes), Artamidae (wood-swallows), Prionopidae (wood-shrikes) and Nectariniidae (sunbirds). Most of these families are sparsely represented in the semi-desert regions of southwestern Asia; they are forest-dwellers by preference.

Another combination of regions is the Ethiopian-Oriental-Neotropical with three families not found elsewhere. These are the Heliornithidae (sun-grebes), Trogonidae (trogons) and Capitonidae (barbets). Their rather peculiar distribution seems best explained on the basis of Matthew's theory. This is supported by the fact that a fossil trogon is known from the Miocene of France, indicating a more northern distribution in the past.

The Oriental-Australian regions have four peculiar families: Megapodiidae (megapodes), Podargidae (frogmouths), Hemiprocnidae (crested swifts) and Dicaeidae (flower-peckers). The Hemiprocnidae are residents of the monsoon forest and tropical rain-forest of southeastern Asia and the East Indies. The absence of such a forest in Australia may explain their absence from that continent.

The Palaearctic-Nearctic regions have six families not found elsewhere. These are Gaviidae (loons), Tetraonidae (grouse), Phalaropodidae (phalaropes), Alcidae (auks), Regulidae (kinglets) and Bombycillidae (waxwings). The Gaviidae are known from the lower Miocene of France and the Pliocene of England yet in spite of this antiquity have not spread into the Southern Hemisphere. It would seem that there is a temperature barrier beyond which they do not pass. An illustration of a temperature barrier in members of another family, Laridae, was discovered by R. C. Murphy (1924). He mapped the lines of average over-surface temperatures in the North

Atlantic in June and found that the isotherm of 70 degrees Fahrenheit coincided with the southern boundary of the Common Tern, *Sterna hirundo,* while the isotherm of 80 degrees Fahrenheit coincided with the northern boundary of the breeding range of the Noddy Tern, *Anous stolidus.* It is quite possible that an isotherm might be found south of which loons do not breed.

The Alcidae are of interest as being ecological equivalents of the Spheniscidae of the Antarctic. Like them they nest on the coasts of polar regions and obtain their food from the sea. The Great Auk, now extinct, was an excellent example of convergence in evolution for, like the penguins, its wings were so reduced that the bird was flightless.

The Regulidae is a family of very small birds which seem to prefer the coniferous forest as a breeding ground. This, coupled with temperature, may determine their distribution.

In any discussion of the dispersal of birds the origin and fossil record of the group should be taken into account. It is generally accepted that the avian stock split off from a group of reptiles known as the pseudosuchians in the Triassic. The first birds appeared in the fossil record in the Jurassic and their primitive character is shown especially by the fact that they possessed teeth.

The most generally accepted theory today of the evolution and dispersal of land vertebrates is that of W. D. Matthew (1915). Two of his important conclusions are: (1) secular climatic change has been an important factor in the evolution of land vertebrates and the principal cause of their present distribution; (2) the principal lines of migration in later geological epochs have been radial from holarctic centers of dispersal.

In my description and discussion of the distribution of the families of birds, I mentioned several cases where the fossil record and present distribution seem to indicate a dispersal from the Holarctic into the subtropical and tropical areas. A search through the fossil record showed that the first genera of birds which still exist appeared in the middle Eocene. A few examples might be given of genera which once existed to the north of the region to which they are now confined. *Sarcoramphus,* now found only in Central America, is known from the California Pliocene; *Agriocharis,* now found in Yucatan, is known from the Pliocene of Arizona; *Jabiru* and *Geranoëtus* from the Pleistocene of the West Indies are now confined to Central and South America.

In comparison with the mammals, birds are rare as fossils and this leaves many gaps in the record, making a complete explanation

of their dispersal more difficult. I do not believe that the presence of the large number of families in the Neotropical region can be explained by assuming that they were all pushed down into that region from the Nearctic by a change in climate. Undoubtedly some of the richness of the Neotropical region in families of birds is due to the fact that it has acted as a haven for families driven down from the north by climatic changes. This is true also of the Ethiopian and Australian regions. However, the large number of endemic families in the Neotropical seems best explained by assuming that most of them arose there and this explanation would apply also to the endemic families of the Ethiopian and Australian. The number of endemic families in any region seems to me to be the result of the interaction of various factors among which are the following: (1) number of ecological niches into which different types of birds might evolve; (2) length of time during which climatic conditions have remained relatively stable, that is, without marked changes which would eliminate the families once formed; (3) degree of geographical isolation, which would tend to hinder the dispersal of families from the region in which they arose; (4) degree of freedom from predators.

The relative weight of these factors has undoubtedly differed among the different regions. For example, the Ethiopian and Australian regions each have seven endemic families but the isolation and predation factors are certainly of different value in the two regions. To judge from the results, the Neotropical has had an unusually favorable combination of factors influencing the formation and preservation of endemic families, the Ethiopian and Australian a distinctly less favorable combination, and the Palaearctic and Nearctic a still less favorable combination.

CONCLUSIONS

1. Birds as a class arose from reptilian stock in the Holarctic and spread out from this region.

2. Some families which arose in the Holarctic are now found only in tropical regions.

3. Other families, particularly some of those endemic to the Neotropical, Ethiopian and Australian, probably originated in those regions from more primitive families which may have had their origin in the Holarctic.

4. Other families, tropical in origin, have migrated in later geological times to regions lying to the north, e. g., some of the families peculiar to the Neotropical-Nearctic regions.

In the description of the distribution of certain families of birds a number of influential factors were mentioned, for example, ocean currents, separation of continents before the families had attained their present status and specialization to inhabit a certain type of vegetation. The confinement of whole families of birds to certain regions in spite of the fact that birds are the most mobile of terrestrial vertebrates seems sufficient reason for the division of the earth into faunal regions. Although Wallace's 'regions' are of unequal value, particularly with regard to endemic families, I believe that the division made is as fair as any that could be conceived without multiplying the number of regions to such an extent as to obscure the fact that there are broad faunal areas over the face of the earth as a consequence of its past history.

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