

ORIGIN OF THE BIRD FAUNA OF THE WEST INDIES

BY JAMES BOND

ALTHOUGH our knowledge in ornithology of the West Indies (which include the Antilles, Cayman and Swan Islands, St. Andrew and Old Providence, and the Bahama Islands) far surpasses that in any other natural science, there has been no comprehensive zoogeographic study of the bird life of the region. During the present century many important data have been gathered, chiefly through taxonomic research and field work, enabling us to understand more clearly the relationships of a number of West Indian genera and species, and forcing us to revise our concepts of their origin.

WEST INDIES CONSIDERED AS OCEANIC ISLANDS

Most students of West Indian zoogeography now consider the islands oceanic, at least in the sense that their vertebrate fauna was received across the sea. It seems probable that no land-bridge has connected any of the islands with the mainland since Oligocene time, when, geologists believe, the Antilles were almost entirely submerged (Schuchert, 1924: 593-595). The earliest land mollusks known from the West Indies are Miocene (H. A. Pilsbry, verbal information), although certain Antillean groups may have survived from an earlier period (Pilsbry, 1930: 222-223).

Referring to mammals, Simpson (1940:154) states that "in the West Indies the Pleistocene land mammals included only peculiar rodents, insectivores and ground sloths, without any of the ungulates, carnivores, and other groups abundant on all adjacent continental areas. This fauna, too, is inexplicable as a result of normal filtering on a land-bridge." Simpson suggests that mammals reached the West Indies by adventitious migration, because this theory explains "simply and completely, facts that the land-bridge theory does not explain" (p. 156). Some mammals have been introduced in the West Indies by man. I have seen *Procyon*, *Dasyprocta*, and the West Indian endemics, *Capromys* and *Geocapromys*, in captivity, and on a number of occasions have partaken of their flesh. Such animals are sometimes carried about in order to provide a supply of fresh meat. Chapman (1892:326) considered that the discovery of a *Geocapromys* on "Swan Island" (= Little Swan Island) "differing but slightly if at all from the Jamaican species,¹ points strongly towards the former extension of land in this direction." However, *Geocapromys* was presumably brought to this remote islet "by aborigines or by rafting" (Allen, 1942:111).

¹ The existing Jamaican form (*G. brownii*) is slightly larger and darker than that from Little Swan Island.



Snowy Egret (Leucophoyx thula). Photographed by Allan D. Cruickshank at Aransas Refuge, Texas, April 1948.

In discussing the origin of the herpetological fauna of the Antilles, Emmet Dunn states (*in litt.*): "I don't believe in land connections at all, except during glacial periods between islands on the same (40 fathom) bank; and I see no explanation of this fauna possible on terms of land connection with either Central or South America. I can point to Cuban genera which could only have come from Florida; from Europe; from Africa; from Central America; from South America. No conceivable juggling around of mainland forms in past times could have got that lot together at one time and place for a land-bridge or a close oversea hop. And Cuba has *by far* the best representation of mainland genera. This is a prime fact in the herpetological situation."

As a result of his study of West Indian land mollusks Pilsbry (1930:222) states that "it does not seem likely that there has been a direct connection between Cuba or Jamaica and any part of Yucatan or Central America later than Paleocene or Eocene."

But, to my mind, the strongest case in favor of considering the West Indies as oceanic islands is that presented by Myers (1938:356), who states that "the most striking feature of the fresh-water fish fauna of the West Indies is the complete absence of members of the primary division of fresh-water fishes, in particular the Ostariophysii, which swarm in all the waters of North, Central, and South America." He believes that these aggressive fishes, had they reached the Antilles, would have thrived and that nothing short of complete submergence of the larger islands would have destroyed them. Hence he concludes (p. 362) that "the only conceivable continental connection of a Greater Antillean land mass is one with Central America at a time when neither the North American nor the South American Ostariophysii had invaded much of Middle America. . . . Finally, if we are to suppose that all the South American Ostariophysii originally wended their way southward through Central America, I believe we should have to push any such continental bridge back into the Mesozoic, if indeed it ever existed at all."

Mayr (1944:186) considers that "the majority of the land bridges postulated during the past 50 years are to be rejected." He writes (*in litt.*) that since "the distances between the various Antilles are so much shorter than the well-substantiated jumps made by Pacific birds, I would not hesitate to accept transoceanic dispersal for the whole Antillean [Region] bird fauna without any major change of the present geographical contours."

I shall show that birds probably reached the West Indies over water, for the most part at times when the water gaps were smaller, as during the glacial periods of the Pleistocene. The former proximity of Jamaica to Honduras is indicated by contour maps of the Caribbean Sea. The shallow, submarine shelf is seen to extend to the Rosalind

Bank, far to the eastward of Honduras. A smaller shelf extends south-westward from Jamaica to the Pedro Bank. In the intervening area is a relatively deep (600–700 fathom) channel that may have been the only important water barrier separating Jamaica from Honduras.

For birds (as also for bats, reptiles, amphibians, and invertebrates) the problem of oversea transportation is obviously simpler than for mammals and fresh-water fishes. Nevertheless, numerous families of birds are remarkably sedentary, among which are the Galliformes which are absent, except by introduction, from the West Indies. True, there is a Bob-white (*Colinus virginianus cubanensis*) in Cuba and the Isle of Pines, but it has been suggested by Gundlach (1893:171) that the species was introduced in this Republic about the close of the eighteenth century.² In this connection it is of interest that the Rufous-tailed Chachalaca (*Ortalis ruficauda*), which has been introduced on two of the Grenadines, has evidently thriven on these islands. It is also noteworthy that there are no jays (Garrulinae) in the West Indies, although crows (Corvinae) are well represented in the Greater Antilles. Jays are much more sedentary than crows. For example, it is unusual to find jays on any of the islands off the coast of Maine (even such large islands as Mt. Desert and Grand Manan) during any season of the year, although the Blue Jay (*Cyanocitta cristata*) and (in the colder months) the Canada Jay (*Perisoreus canadensis*) are not rare on the adjacent mainland.

Under normal conditions a stretch of open water, such as a channel or strait, presents a very effective barrier over which, as I have stated (1942:97), "only the more aggressive birds are wont to cross." I should have added "if and when they are subjected to a physiological urge to do so." If a sedentary mainland species is found on an oceanic island its presence there must be regarded as having probably been brought about through purely fortuitous circumstances. A hurricane may sometimes be responsible, as suggested by Darlington (1938:278).

The dispersal of forms of life apart from winged creatures is brought about in a different manner. Flotsam must be a major factor in the spreading of plants, invertebrates, and probably of mammals. After heavy rains in the mountains the larger rivers in the West Indies bring down debris, part of which, on reaching a relatively calm sea, might not be affected by salt water, and yet be transported by winds and currents from one island to another. Thus, it seems to me that even delicate invertebrates, susceptible to salt water, might be carried some distance across a sea or ocean. Mayr (1944:182) states that "it has been found that even strictly oceanic islands in the Pacific may have rather rich faunas of snails, flightless insects, lizards, and other animals which were formerly believed to be able to spread only with help of

² Cuban "quail" are certainly of mixed stock, and although those from the Isle of Pines are supposed to be true *cubanensis*, an adult male that I collected there can almost be matched with Florida individuals.

land bridges." He adds that "the most successful colonizers among the beetle fauna of eastern Polynesia are small flightless species that breed in dead twigs."

There is general agreement that South America and North America have been separated during most of the Tertiary. The two continents are believed to have been united last in middle or upper Pliocene when the Isthmus of Tehuantepec emerged and, of course, have remained united ever since. According to Mayr (1946:9) a previous connection is thought to date back to lower Eocene. During the Miocene there existed between North and South America a group of Central American and Antillean islands which I call the Caribbean Archipelago. During the existence of the Caribbean Archipelago the southern half of the North American continent was tropical and possessed a fauna distinct from that of South America. There is evidence that this "tropical North American fauna" existed at an early date in Central America and thence spread sporadically to the West Indies. This dispersal was doubtless accelerated by hurricanes. It is also apparent that in Pleistocene time a number of birds from southeastern North America established themselves on the West Indies, and it is noteworthy that all but one of these species are indigenous to Florida. The single exception is the boreal White-winged Crossbill (*Loxia leucoptera*), which I shall discuss later. It appears likely that all these birds became part of the indigenous fauna of the islands at times when they were not subject to a migratory urge. Unfavorable climatic conditions in the north not only forced birds south of their normal breeding ranges, but also apparently caused the extensive migrations from North America to the West Indies, Central America, and South America that we see today.

ANALYSIS OF THE AVIFAUNA

Irrespective of the manner by which the indigenous West Indian birds were originally established on the islands, it is obvious that the West Indian avifauna is fundamentally tropical North American. The same is true of the Central American avifauna, although here the northern element is much restricted, due primarily to competition that has resulted from the influx of South American species following the formation of the Central American isthmus. Chiefly as a result of such invasions, approximately 25 families of birds are indigenous to Central America (between Chiriquí, Panama, and the Isthmus of Tehuantepec) that are not represented in the West Indies.

There are certain important differences between the tropical North American element of the avifauna of the West Indies and that of Central America. In Central America there are motmots (Momotidae), a family believed to have arisen in northern Central America (Chapman, 1923:58); but there are no motmots in the West Indies, where they are replaced by the todies (Todidae). Again, the silky flycatchers (Ptilonotidae), which constitute a characteristic, but probably not

autochthonous,³ Central American element, are absent from the West Indies, where they are presumably represented by palm-chats (*Dulidae*). The todies and palm-chats may have developed as families in the Greater Antilles, but I am inclined to believe that *Dulus*, which is a sturdy, strong-flying, bird and among the most abundant of Hispaniolan species, is a relict that developed on the mainland. If it were an ancient West Indian form we should expect representation of the genus on other of the larger islands. In regard to the todies, the most primitive of West Indian birds, it is noteworthy that there is only one genus in this family, whereas there are six genera of motmots, and five of these inhabit Guatemala. The most significant difference between the tropical North American elements in the avifauna of Central America and the West Indies is the apparent absence of native gallinaceous birds from the islands.

According to my "Check-list of Birds of the West Indies" (1945), there are in the West Indies 175 indigenous Recent genera, representing 58 families. Of these no less than 50 (representing 21 families) are endemic (i.e., not found elsewhere), of which number, 41 are found in the Greater Antilles, 14 in the Lesser Antilles, and 7 in the Bahama Islands (Table 1).⁴ In contrast, the entire group of East Indian islands on the continental shelf, situated to the west of the "Wallace Line," possesses at most 7 endemic genera. It is thus evident that the West Indies constitute a well defined Subregion of the North American Region, with rather distinct Greater Antillean and Lesser Antillean Provinces. I include the Bahama Islands in the former.

Much has been written to show the homogeneity of various other faunas of the Greater Antilles, the veritable "heart-land" of the West Indies, but it is apparent that the same can hardly be shown for the bird fauna. The localized distribution of most West Indian genera in these islands indicates that Cuba, Jamaica, Hispaniola, and Puerto Rico have long been separated. An analysis of the endemic West Indian genera that inhabit the four important Greater Antilles reveals that 12 of the 19 found in Cuba are unknown from the other major islands; 11 of 18 found in Hispaniola and 11 of 17 found in Jamaica have not been reported from Cuba; 8 are found in Hispaniola but not in Jamaica, and 7 in Jamaica but not in Hispaniola. Nine West Indian endemic genera inhabit Puerto Rico, of which one (*Nesospingus*) is restricted to Puerto Rico, and two, both widespread in the Lesser Antilles, have not been definitely reported from the other three large islands. Only four of the West Indian endemic genera (*Todus*, *Saurothera*, *Tolmarchus*, *Spindalis*) occur on all four islands (Table 2).

³ Jean Delacour informs me that the genus *Hypocolius*, of Asia Minor and northeastern Africa, may be a member of this family.

⁴ Although the number of genera here recognized is excessive according to modern generic concepts, it is less than are recognized in the "Catalogue of Birds of the Americas." A narrow generic concept is useful in zoogeographic studies.

TABLE 1
DISTRIBUTION OF BIRD GENERA ENDEMIC TO THE WEST INDIES

	Endemic to Bahamas and Greater and Lesser Antilles	Endemic to Bahamas and Greater Antilles	Endemic to Greater Antilles	Endemic to Greater and Lesser Antilles	Endemic to Lesser Antilles
RALLIDAE			Cyanolimnas		
COLUMBIDAE			Geotrygon Starnoenas		
CUCULIDAE		Saurothera	Hyetornis		
STRIGIDAE			Gymnoglaux Pseudoscops		
CAPRIMULGIDAE			Siphonorhis		
APODIDAE			Tachornis		
TROCHILIDAE			Trochilus Mellisuga	Sericotetes ⁴ Orthorhyncus ⁴	Cyanophaea Eulampis
TROGONIDAE			Temnotrogon Priotelus		
TODIDAE			Todus		
PICIDAE			Nesocleus Xiphidiopicus Nesocittes		
TYRANNIDAE		Tolmarchus			

HIRUNDINIDAE		Callichelidon	Lamprochelidon	
TROGLODYTIDAE			Ferminia	
MIMIDAE	Margarops ¹			Allenia Cinlocerthia Ramphocinclus
TURDIDAE	Mimocichla			Cichlherminia
DULIDAE			Dulus	
COEREBIDAE			Euneornis	
PARULIDAE			Microligea Teretistris	Catharopeza Leucopeza
THRAUPIDAE		Spindalis ³	Pyrrhuphonia Phaenicophilus Nesospingus Calyptophilus	
ICTERIDAE			Ptiloxena Nesopsar	
FRINGILLIDAE	Loxigilla ²		Loxipasser Melopyrtha Loximitris Torreornis	Melanospiza
TOTALS	3	4	32	9 [50]

1. Also inhabits some islands in the southern Caribbean Sea.
2. Recorded on questionable evidence from British Guiana (Hellmayr, 1938:167, footnote; Bond, 1945:152, footnote).
3. Also inhabits Cozumel Island, off Yucatán.
4. Predominantly Lesser Antillean.

Approximately half of the endemic West Indian genera belong to cosmopolitan families of more or less doubtful origin. The remainder, excluding the todies (*Todus*) and palm-chats (*Dulus*), are members of tropical North American, or of South American, families.⁵ I wish particularly to discuss the "South American" element as represented by the hummingbirds (Trochilidae), tyrant flycatchers (Tyrannidae), honey-creepers (Coerebidae), and tanagers (Thraupidae). Of these the tyrannids are unquestionably South American, while the remainder are presumably so. All these families are now found in North America.

In the latest classification of the Trochilidae (Peters, 1945) 123 genera are recognized, of which as many as 24 are confined to North and Middle America. In spite of the strikingly specialized forms of hummingbirds in South America, we can only assume that the family originated on that continent. It is possible that in North America hummingbirds were formerly more widely distributed than they are now. At present the more northern species are among the least specialized. Specialized forms would be greatly influenced by any change of climate, such as occurred during the Ice Age, affecting the flowering plants on which they depend. In spite of their aggressiveness many hummingbirds have a restricted range; for example, the beautiful little Bahaman Woodstar (*Calliphlox evelynae*), found on virtually every island and cay of the Bahamas, has not become established elsewhere. The West Indies possess numerous and notable species of this family, in particular the Streamer-tail (*Trochilus polytmus*) of Jamaica, and the tiny Bee Hummingbird (*Mellisuga* ["*Calypte*"] *helenae*) of Cuba, the smallest bird in the world.

Honey-creepers (Coerebidae), a heterogeneous group related to finches, tanagers, and wood warblers, comprise another family largely dependent on flowers. Currently, 10 genera are recognized, though certain of these (e.g., *Conirostrum*) should, perhaps, be placed with the wood warblers (Parulidae). Six of the genera are found north of South America, but only one genus (in fact, one species) is endemic to Middle America. This is the aberrant Jamaican Orangequit (*Euneornis*), considered by some ornithologists as worthy of family rank. The internal structure of the three genera of Coerebidae found in the West Indies (*Coereba*, *Cyanerpes*, and *Euneornis*) was studied by Lucas (1894). He considered them more nearly related to the Australasian honey-eaters (Meliphagidae) than to the New World Parulidae or Thraupidae, usually held to be their nearest relatives, basing his conclusions primarily on the form of the tongue and pattern of the palate; but this likeness probably is superficial and merely reflects their similar feeding habits.

⁵ South America has the richest bird fauna of any of the world's continents, whereas North America has the most impoverished.

TABLE 2
DISTRIBUTION OF ENDEMIC WEST INDIAN GENERA IN THE GREATER ANTILLES

	Cuba	Hispaniola	Jamaica	Puerto Rico	Cuba	Hispaniola	Jamaica	Puerto Rico
Cyanolimnas	x	-	-	-	x	-	-	-
Geotrygon	-	-	x	-	x	-	-	-
Starnoenas	-	-	-	-	-	-	-	x
Hyetornis	-	x	x	-	x	-	-	x
Saurothera	x	x	x	x	-	-	-	-
Gymnoglaux	x	-	-	-	-	-	-	-
Pseudoscops	-	x	x	-	x	-	-	-
Siphonorhis	-	x	x	-	-	-	-	-
Tachornis	x	x	x	-	x	-	-	-
Sericoteles ¹	-	-	-	-	x	-	-	x
Trochilus	-	-	x	-	-	-	-	-
Mellisuga	x	x	x	-	-	-	-	x
Temnotrogon	-	x	x	-	-	-	-	-
Priotelus	x	-	-	-	x	-	-	-
Todus	x	x	x	x	-	-	-	-
Nesocelus	x	x	-	-	-	-	-	-
Xiphiopicus	x	-	-	-	-	-	-	x
Nesocittes	-	x	-	-	-	-	-	-
Tolmarchus	-	x	-	-	x	-	-	-
Lamprochelidon	x	x	x	-	x	-	-	-
Callichelidon								
Ferminia								
Margarops ^a								
Mimocichla ^a								
Dulus								
Euneornis								
Microligea								
Teretistris								
Pyrrhuphonia								
Spindalis								
Phainicophilus								
Nesospingus								
Calyptophilus								
Ptiloxena								
Nesopsar								
Loxipasser								
Loxigilla								
Melopyrrha								
Loximitris								
Torreornis								

1. Has merely a toe hold in extreme eastern Puerto Rico. Another Lesser Antillean hummingbird genus (*Orthorhyncus*) inhabits nearby Vieques Island.

2. Not known to inhabit Hispaniola proper, although found on Beata, one of the nearby coastal islands.

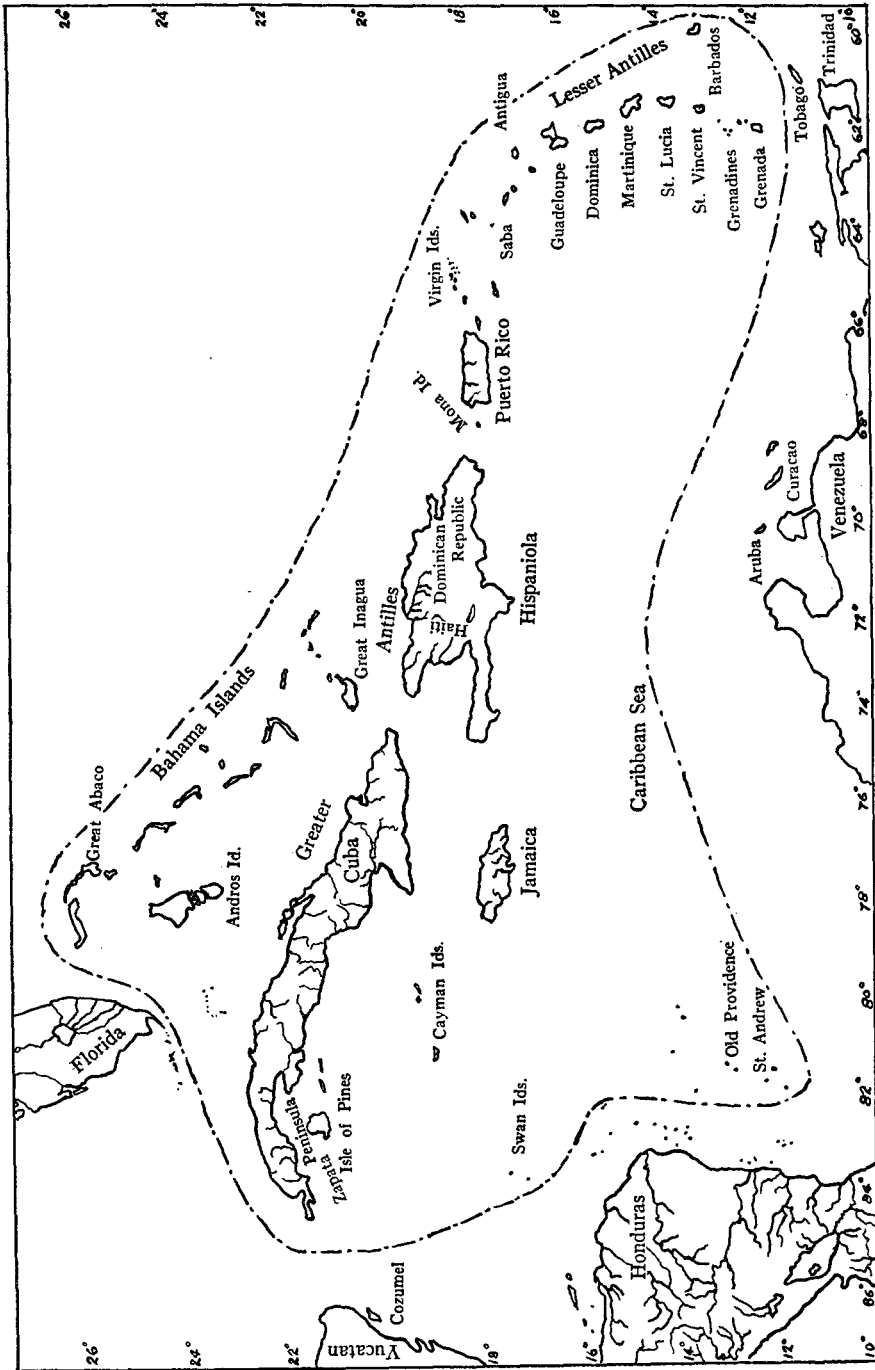
3. The Grand Cayman Thrush (*Mimocichla ravidia*) is probably a representative of an extinct Jamaican species of this genus.

There are as many as five ⁶ endemic West Indian genera of tanagers (Thraupidae), a so-called South American family. I feel, however, that tanagers may have developed independently, from similar fringillid stock, in tropical North America and in South America. It must be remembered that these birds are very close to the Richmondeninae, an American subfamily of "finches." As Griscom (1945:167) has pointed out: "With a number of tropical American birds there is no way to settle whether they shall be called tanagers or finches." If the tanagers are considered of purely South American origin, the numerous genera (some very distinct) found in the West Indies indicate that the family is highly aggressive, far more so than the tyrant flycatchers (Tyrannidae); yet the A.O.U. "Check-list of North American Birds" (1931) lists only one tanager genus, in comparison with 11 genera of tyrant flycatchers, as occurring in North America north of Mexico. This situation may be due to ecological factors rather than to remoteness of the region of family origin.

The troupial family (Icteridae) is more sharply marked than the tanager family (Thraupidae). There are some 30 icterid genera represented in South America, and 20 in North and Middle America. Many of these genera are restricted to one region or the other, and it seems futile to speculate on the continent of primary origin. The two genera confined to the West Indies, the Cuban *Ptiloxena* and the Jamaican *Nesopsar*, are closely related to widespread mainland genera, respectively *Dives* and *Agelaius*. In fact, recent study of the Cuban Blackbird (*Ptiloxena atroviolacea*) indicates that this species may be congeneric with continental blackbirds of the genus *Dives*.

The tyrant flycatchers (Tyrannidae) are the only unquestionably South American family of birds with endemic genera in North and Middle America. The tyrannids belong to a large group or suborder (Mesomyodi) of the Passeres, found in both the Old and New Worlds, but best represented in South America. How the Mesomyodi reached that continent is one of the great ornithological mysteries. They may have been derived from the west (via Antarctica?), since the tapaculos (Rhinocryptidae), with their center of abundance in Chile, are evidently allied to the New Zealand wrens (Acanthisittidae), and may represent the last successful mesomyodian invasion into South America. The Mesomyodi obviously arrived rather recently in North and Middle America. The northward spread was spearheaded by the comparatively aggressive tyrannids, of which a number of species have reached Canada. Other, more or less sedentary, mesomyodian families probably did not become established in Central America until later, since they have no endemic genera in Middle America and since only one species, the Jamaican Becard (*Platypsaris niger*), has arrived in the West Indies (where it is confined to Jamaica). It is of interest to note

⁶ One of these (*Spindalis*) is also found on Cozumel Island, Yucatán.



that the genus *Platypsaris* has reached the southern border of the United States and, except for the tyrannids, is the northernmost of mesomyodian genera. It is not surprising that the long-isolated Jamaican form, *P. niger*, is specifically distinct from its mainland relatives, whereas the form found on the Tres Marias Islands, off the western coast of Mexico, is conspecific with mainland birds.

There are 117 currently recognized genera of Tyrannidae, of which 10 are not indigenous to South America. Three of these are West Indian, and are certainly not well marked. Two so-called genera of the West Indies ("*Hylonax*" and "*Blacicus*") I have long discarded, while a third (*Tolmarchus*) might well be united with *Tyrannus*, from which it differs chiefly in the absence of attenuated outer primaries, a character of questionable value generically. Indeed, it seems likely that the Loggerhead Flycatcher (*Tolmarchus caudifasciatus*) reached the West Indies later than the Gray Kingbird (*Tyrannus dominicensis*), for the latter species, together with the Black-whiskered Vireo (*Vireo altiloquus*), has the now apparently unnecessary habit of migration to South America from the northern and western parts of its range. North and Central American genera of Tyrannidae, not indigenous to South America, are more or less closely related to South American genera; viz., *Deltarhynchus*, *Eribates*, and *Nesotriccus* are related to *Myiarchus*; *Nuttallornis* to *Contopus*; *Aechmolophus*, *Xenotriccus*, and *Aphanotriccus* to *Praedo* and to *Mitrephanes*. All are monotypic.

West Indian families believed of tropical North American origin (Mayr, 1946)⁷ include the Troglodytidae, Mimidae, Vireonidae, and Parulidae. There are only two genera (one endemic) of wrens in the West Indies, but there are numerous thrashers, vireos, and wood warblers there, and the West Indian species in these families are more closely related to North and Central American, than to South American, forms. Numerous species of the northern subgenus *Vireo* (in which I include "*Laletes*" and "*Lawrencia*") are found in the West Indies, but none of the widespread southern genus *Hylophilus*, though it occurs in Trinidad and Tobago. Again, there are 8 indigenous West Indian species of the northern wood warbler genus *Dendroica*, but none of the southern *Basileuterus*.

The trogons, a pantropical group, are considered by Mayr (1946: 16) as probably of tropical North American or of Oriental origin. There are two endemic West Indian genera, one of which (*Temnotrogon*) is barely separable from the mainland genus *Trogon*. Two other West Indian families, the New World vultures (Cathartidae) and the limpkins (Aramidae), are considered by Mayr (p. 6) as of probable North American origin. This seems to be warranted by fossil evidence,

⁷The reader will find on pages 26 and 27 of this work by Mayr a classification by origin of all the families of birds of the Americas.

but their inclusion in the North American element is purely tentative, since there are few avian fossils known from South America.⁸

Relationships of species belonging to genera that are indigenous, but not endemic, to the West Indies are usually more or less obvious. Northern forms are characteristic of the West Indies, even among the water birds. Thus we find among genera occurring in both North and South America the Great Blue Heron (*Ardea herodias*), not the Cooi Heron (*A. cocoi*); the Green Heron (*Butorides virescens*), not the Black-crowned Heron (*B. striatus*); the White Ibis (*Guara alba*), not the Scarlet Ibis (*G. rubra*); and the remarkable South American genera of the Ardeidae and Threskiornithidae are absent. All of the West Indian land bird genera, exclusive of endemics, are found in North America (including Mexico) with the exception of two hummingbird genera (*Glaucis* and *Calliphlox*), both known from Central America. Of course the Antillean hermit (*Glaucis*), found in the West Indies only on Grenada, was derived from South America, but the Bahaman Woodstar (*Calliphlox evelynae*) has its nearest relative (*bryantae*) in Costa Rica and western Panama.

There is reason to believe that very few West Indian species of birds (and no West Indian genera) have invaded North or South America. The aggressive grackles probably originated in southern North America, and thence spread to Central America, the West Indies, and (recently) to extreme northern South America. Perhaps the most primitive of Central American grackles is the Nicaraguan species (*Quiscalus* ["*Cassidix*"] *nicaraguensis*), which bears a remarkable resemblance to certain races of the Lesser Antillean *Quiscalus* ["*Holoquiscalus*"] *lugubris*. The latter has now a toe hold in South America, where it is virtually confined to towns and settlements, occurring in an association or ecological niche not occupied by any other icterid.

Of the recent (probably Pleistocene) arrivals in the West Indies, a number were obviously derived directly from North America, e.g., a crane (*Grus*),⁹ flicker (*Colaptes*), and crows (*Corvus*); others apparently from Central America, e.g., a rail (*Porzana*), jacana (*Jacana*), and potoo (*Nyctibius*). The most extraordinary of the recent northern immigrants is the Hispaniolan White-winged Crossbill (*Loxia leucoptera megaplaga*). Probably this Canadian and Hudsonian Zone species, which on the mainland of North America does not now breed south of

⁸ Of the 15 species of birds known in the West Indies only from subfossil bone fragments, the most interesting are two Bahaman eagles (*Calohierax* and *Titanohierax*), a peculiar rail (*Nesotrochis*), and the giant barn owls (*Tyto pollens* and *T. ostologa*). This material is not very enlightening, except as an indication of the former abundance of small mammals on these islands.

⁹ The family Gruidae is considered of Old World origin by Mayr (1946: 19-20). He states that cranes "are known from North America as far back as the middle Pliocene—perhaps even earlier"; but Wetmore (1940: 48-50) records as many as 7 species of Gruidae from the Eocene. The Sandhill Crane (*G. canadensis*), the only species found in the West Indies, is reported from the Pliocene.

the Adirondacks of New York, reached the West Indies fortuitously during the Ice Age when it must have ranged farther south than at present. Finding climatic and ecological conditions (viz., pine forest) suitable, the bird has thrived in the mountains of Hispaniola at altitudes above 4,000 feet.¹⁰ However, it is the other North American or "Holarctic" species, the Red Crossbill (*L. curvirostra*), that has spread southward into Central America.

Most of the recent arrivals in Cuba reached the island from the north. On the other hand, most of those inhabiting Jamaica were probably derived from the west, and some of these (e.g., the rail *Porzana flaviventer*, and Gray Potoo, *Nyctibius griseus*) have spread to Hispaniola. I am inclined to believe that two emberizine species, the Grasshopper Sparrow (*Ammodramus savannarum*) and the Andean Sparrow (*Brachyspiza capensis*) reached the Antilles from the west. The former does not breed in Cuba, where conditions seem favorable to its existence, and where it occurs as a rather rare but regular winter resident. The species is widespread in North and Central America, and is found in northwestern South America south to Ecuador. A closely related genus (*Myospiza*) occurs in South America. The only other indigenous species of this subfamily in the West Indies is the peculiar Zapata Finch (*Torreornis*), confined to a remote part of the Zapata Swamp in Cuba.¹¹ It is difficult to account for the dearth of members of this subfamily of finches in the West Indies, since the Emberizinae are well represented in both North and South America; and 17 genera, including both *Ammodramus* and *Brachyspiza*, inhabit Central America.

The Andean Sparrow (*Brachyspiza capensis*) is absent from North America (i.e., from north of the Isthmus of Tehuantepec), and is known in the West Indies only from Hispaniola, where it has a more circumscribed range than any other species (with the exception of the La Selle Thrush, *Turdus swalesi*), being confined to the Cordillera Central of the Dominican Republic. The Central American races of *Brachyspiza* likewise inhabit only the hills and mountains, but at the height of refrigeration of the Ice Age presumably occurred at low elevations (Griscom, 1932:25). During this period the species may well have inhabited Jamaica. Certain South American forms, such as the race found on Curaçao and Aruba, have become adapted to tropical,

¹⁰ Hispaniola is the only island in the West Indies with a distinct subtropical bird fauna, and even here few species are restricted to the Subtropical Zone, notably *Loxia leucoptera* and the Andean Sparrow (*Brachyspiza capensis*). In Cuba every species characteristic of the higher altitudes in the Sierra Maestra also occurs elsewhere at or near sea level, while all the species of other islands are known from elevations as low as 2,000 feet.

¹¹ The three genera of birds that are confined to the Zapata Swamp (*Cyanolimnas*, *Ferminia*, and *Torreornis*), are highly specialized in their adaptation to the conditions under which they occur, indicating that such habitats have existed for a long period in Cuba.

even arid tropical, conditions. I feel confident that *Brachyospiza* was developed in South America, probably during late Pliocene or early Pleistocene, and subsequently worked its way northward. The original stock that gave rise to *Brachyospiza* may have been derived from North America, where closely related genera (viz., *Zonotrichia*, *Melospiza*, and *Passerella*) exist today. If the Andean Sparrow had spread southward, as contended by Chapman (1940), we should expect the West Indian and Central American races to be the most differentiated because of long isolation, but this is not the case. The migratory form, *australis*, that breeds in southern South America, is the most distinct of the many races of this species. Again, if a North American *Brachyospiza* had been so "exceptionally well qualified" to colonize (the genus occurs in the Tropical, Subtropical, Temperate, and Puna Zones of South America), one would expect some representation of the species on the northern continent. Chapman was convinced that a southward movement took place in "postglacial" times, a period estimated by geologists as comprising 25,000 to 30,000 years; but it is unlikely that geographic variation such as exists among South American forms of this species could have developed in so short a period, for Wetmore (1933:238) believes that since the close of the Tertiary "there have arisen only some of the slight differences of color and size that distinguish the less well marked subspecies." I agree with Chapman (1940:385) that *Brachyospiza* is a poorly differentiated genus and consider that the widespread *B. capensis* should be regarded as congeneric with some, if not all, of the forms now included in the North American genera mentioned above. At present, however, it seems premature to call it, as Chapman does, a *Zonotrichia*.

VULNERABILITY OF INSULAR BIRDS

Decreased competition and comparative scarcity of predators tend to cause vulnerability in island populations. The individuals simply do not retain the traits necessary to the existence of their mainland representatives. For example, on Cozumel Island the Black Catbird (*Melanoptila glabrirostris*) is abundant and remarkably tame, whereas the same bird on the adjacent mainland is rare and very shy (Griscom, 1926:11). I have little doubt that if Black Catbirds from Cozumel were released in Yucatán they would soon perish, but that those from the mainland would survive if brought to Cozumel.

Although one species native to the West Indies has become established in South America (the grackle *Quiscalus lugubris*), it is unlikely that a genus peculiar to these islands could invade any continental area. It is axiomatic that a genus now confined to the West Indies is not necessarily of West Indian origin; that the occurrence of a genus both in the West Indies and in some part of the South or North American continents is an indication of its mainland origin.

Even the so-called West Indian genus *Tiaris* (the grassquits), one of the most abundant and widespread genera in the West Indies, but of local distribution in other parts of tropical America, probably originated in North or South America.

The Galápagos finches (geospizids), by far the most primitive of Galápagos land birds, are believed by Lack (1945:7) to be allied to the grassquits. I do not disagree, but consider that *Melano-spiza*, a rare relict and monotypic genus confined to St. Lucia, is more closely related. Lack states (pp. 6-7) that the only diagnostic feature of the so-called subfamily "Geospizinae" is the presence of long, fluffy feathers on the lower back; and this timaliid-like character is as fully developed in the St. Lucian Black Finch (*Melano-spiza*), the adult male of which bears a remarkable resemblance to the Medium Ground-finch (*Geospiza fortis*). Ridgway (1901:544), an astute taxonomist, noted the affinity of *Melano-spiza* to *Tiaris* ["*Euethia*"].¹² It is possible that the St. Lucian Black Finch represents a primitive stock that invaded the Galápagos Islands and the West Indies, but has been extirpated on the mainland due to stress of competition. The geospizids of the Galápagos doubtless survived through lack of competition with mainland species and the absence of important predators.

In the West Indies it is unusual to find more than one species of a genus on any small island: where two such species associate, one is always dominant. Such conditions do not necessarily prevail on the mainland, nor even in Trinidad or on the four large islands of the Greater Antilles which offer diverse ecological habitats. As many as three resident species of *Dendroica* inhabit the pine forest of Grand Bahama and Abaco, but each appears to occupy a separate ecological niche. All may be found in the same tree, but the Olive-capped Warbler (*D. pityophila*) is apt to forage nearer the ground than the Pine Warbler (*D. pinus*); and the Yellow-throated Warbler (*D. dominica*), unlike the other species, may often be seen probing for food behind crevices in the bark, its long, narrow bill being well adapted to this method of feeding.

Recent arrivals in the Lesser Antilles include the Yellow-bellied Elaenia (*Elaenia flavogaster*). Previously, there had evidently been two invasions of the genus into the West Indies; the first (probably from Central America) represented by the Greater Antillean Elaenia (*E. fallax*), which inhabits Jamaica and Hispaniola; the second (possibly from Central America) represented by the Caribbean Elaenia (*E. martinica*), a species that has a most extraordinary range. Confined to the West Indies and other Caribbean islands, including mangrove islets off the coast of Yucatán, the Caribbean Elaenia is more numerous in the Lesser Antilles than elsewhere. It does not inhabit

¹² In the latest classification of the Fringillidae (Hellmayr, 1938), *Melano-spiza*, *Tiaris*, and the geospizids are placed in three separate subfamilies.

Puerto Rico nor other islands to the westward, except the Cayman Islands and some Caribbean islands off South and Central America. The species is exceedingly like *E. flavogaster* morphologically, but differs considerably in behavior, and may readily be identified in the field. Obviously, one would expect considerable competition between such closely related ("sibling") species where their ranges overlap. This is, indeed, the case. On Grenada, *E. flavogaster* has completely ousted *martinica* from the lower, hotter parts, and these two flycatchers now occur on this island as representative forms, one (*martinica*) inhabiting the mountains, the other (*flavogaster*) the lowlands. In the Grenadines only *flavogaster* is found at the present time. On St. Vincent, however, both *flavogaster* and *martinica* occur together near sea-level, with the former decidedly dominant.

It is apparent that a continental form arriving in the West Indies ousts its insular representative. Where, however, more than one species of a genus has entered this region from the mainland a different situation exists. In this case it appears that the first to become established on a small island will tend to keep out any allied form. This is well illustrated in the Apodidae by the distribution of Lesser Antillean swifts of the genus *Chaetura*. Three South American species have invaded the Lesser Antilles, but not more than one is known to occur on a given island.¹³ Thus, the Gray-rumped Swift (*Chaetura cinereiventris*) is the Grenada species; the Short-tailed Swift (*Ch. brachyura*), the St. Vincent species; while the Lesser Antillean Swift (*Ch. martinica*) inhabits St. Lucia, Martinique, Dominica, and Guadeloupe. All of the above, in addition to two other species of *Chaetura*, have been recorded from Trinidad. Two of these Lesser Antillean swifts have been noted on islands northwest of Guadeloupe, where their occurrence must be considered accidental or casual. It is evident that these islands are too small to maintain even a single species of swift, and therefore fail to constitute "stepping stones" for the spread of these aggressive birds to Puerto Rico.

DERIVATION OF THE LESSER ANTILLEAN AVIFAUNA¹⁴

Most, if not all, birds that have arrived in the West Indies from South America have entered the region via Jamaica or Grenada, but it is astonishing that so few South American species have spread into these islands. Every ornithologist who has visited Grenada and Trinidad has been amazed at the difference between their avifaunas. The difference is even more marked if we compare the bird life of St. Lucia

¹³ Although I have never found more than one species of *Chaetura* on St. Vincent and Grenada, it is quite possible that a second species exists on one or both of these islands.

¹⁴ The Lesser Antilles comprise islands from Grenada north and northwest to the Anegada Channel. They do not include the Virgin Islands, although these have a Lesser Antillean element in their avifauna.

with that of the continental islands of Trinidad or Tobago. The inclusion of the latter islands as part of the West Indies would more than double the number of indigenous genera of land birds and add as many as 15 families to this Subregion.

Among the earliest birds to invade the Lesser Antilles from South America were hummingbirds (Trochilidae), for it is virtually certain that the Lesser Antillean genera *Orthorhyncus* (Antillean Crested Hummingbird) and *Sericotes* (Emerald-throated Hummingbird) were derived from the south, since only on the southernmost islands do we find racial variation: it would be futile to speculate whence came the others—the Garnet-throated Hummingbird (*Eulampis*) and Blue-headed Hummingbird (*Cyanophaia*). Of the recent arrivals (i.e., birds identical with, or not specifically distinct from, those of northern South America), as many as 14 are not found north of St. Vincent. One South American species, the Bananaquit (*Coereba flaveola*) is known to be highly aggressive. There is a record of the Trinidad race (*luteola*) from Grenada, a record of the Dominican race (*dominicana*) from Martinique, and I have seen the species at sea at least two miles off the coast of Antigua. The Glossy Cowbird (*Molothrus bonariensis minimus*) was unknown in the Lesser Antilles until 1899, but has since become established on these islands as far north as St. Lucia. Another example of an aggressive South American species is the Blue-black Grassquit (*Volatinia*), which inhabits Grenada and has been observed at sea between this island and Trinidad (Chapman, 1894:33). One important fact to remember is that all of the South American genera that have recently invaded the Lesser Antilles have likewise spread northward into Central America, or at least now inhabit Central America.

Northern elements in the Lesser Antilles include wrens (Troglodytidae), thrashers (Mimidae), thrushes (Turdidae), vireos (Vireonidae), and wood warblers (Parulidae). Among these families the genera and species endemic to the Lesser Antilles are, I believe, relicts, and were formerly more widespread in the West Indies. For example, the range of the Pearly-eyed Thrasher (*Margarops fuscatus*) is significant: primarily Lesser Antillean, this species ranged west to Mona Island, where it is abundant. It is also found on many of the southern Bahama Islands, but is not known to occur beyond Mona in the Greater Antilles except on the little island of Beata, off the southern coast of the Dominican Republic.

The genera endemic to the West Indies and found in the Lesser Antilles belong to five families, namely the hummingbirds, thrashers, thrushes, wood warblers, and the finches. St. Lucia has the richest, Grenada and Barbados the poorest, representation of these genera (Table 3), while as many as seven (three strictly Lesser Antillean) inhabit the small and geologically recent island of Saba.

The distinctness of the avifauna of the Lesser Antilles is probably due to their geographical isolation, affording the birds compara-

TABLE 3
DISTRIBUTION OF ENDEMIC WEST INDIAN GENERA ON THE LARGER LESSER ANTILLES

	Guade- loupe	Domi- nica	Marti- nique	St. Lucia	St. Vincent	Gren- ada	Barb- ados
Cyanophaia	—	x	x	—	—	—	—
Eulampis	x	x	x	x	x	—	—
Sericotes	x	x	x	x	x	x	x
Orthorhyncus	x	x	x	x	x	x	x
Allenia	x	x	x	x	x	x	x
Margarops	x	x	x	x	—	—	?
Cinclocerthia	x	x	x	x	x	—	—
Ramphocinclus	—	—	x	x	—	—	—
Mimocichla	—	x	—	—	—	—	—
Cichlherminia	x	x	?	x	?	—	—
Catharopeza	—	—	—	—	x	—	—
Leucopeza	—	—	—	x	—	—	—
Melanospiza	—	—	—	x	—	—	—
Loxigilla	x	x	x	x	x	x	x

tive freedom from competition. Scarcity of winter resident land birds on these islands is also a factor favoring the survival of the relicts. North American migrants abound in the Greater Antilles and the Bahamas and have certainly had a deleterious effect on the indigenous bird life. Thus, in Cuba, Jamaica, and Hispaniola, the Golden Warbler (*Dendroica petechia*) is chiefly restricted to mangrove swamps, whereas in the Lesser Antilles this warbler also inhabits secondary growth. The primitive Arrow-headed Warbler (*Dendroica pharettra*), of Jamaica, is confined to mountain forest, and is relatively less widespread than its ally, the Lesser Antillean Plumbeous Warbler (*D. plumbea*).

DERIVATION OF THE BAHAMAN AVIFAUNA

It is the accepted opinion that the present Bahama Islands were submerged during Pliocene and (early ?) Pleistocene times, and have never been connected with any other land area (Schuchert, 1935: plate 16). All Bahaman birds must therefore be regarded as more or less recent arrivals, and this is soon evident to any student of the avifauna. The most notable Bahaman species are the Bahaman Woodstar (*Calliphlox evelynae*) and the Bahaman Swallow (*Callichelidon cyaneoviridis*). The former, as I have pointed out, has its nearest relative in Central America, the genus having evidently been extirpated in the intervening area. The latter comprises an ill-defined monotypic genus not entirely restricted to the Bahamas, since individuals evidently winter in Cuba. There is a decided Floridian element, including a Brown-headed Nuthatch (*Sitta pusilla*), on the northwestern islands of the group, but most of the birds have come from Cuba, probably having reached the islands as a result of hurricanes. Such storms may have carried Thick-billed Vireos (*Vireo crassirostris*) and bananaquits

(*Coereba*) to the Bahamas from the Cayman Islands. Neither is known to occur in Cuba, perhaps because their ecological niches had been filled by the Cuban Vireo (*Vireo gundlachii*) and Blue Honey-creeper (*Cyanerpes cyaneus*) respectively, although this honey-creeper and the bananaquit live side by side in tropical continental areas. The proximity of the Bahamas to Cuba in periods of glaciation is indicated by the extensive and extremely shallow Great Bahama Bank. The narrow gap presented by the Old Bahama Channel would not have prevented an influx of numerous Cuban birds into the northern islands.

Although some Bahaman forms (e.g., the Bahaman races of *Mimocichla plumbea* and *Spindalis zena*) are very distinct from those in Cuba, there is little variation in birds on these islands, only seven species breaking up into minor geographical races. For example, only one form of the highly plastic bananaquit (i.e., *Coereba flaveola bahamensis*) is found in the Bahamas.

It seems to me possible that the Bahaman forms of the Greater Antillean Bullfinch (*Loxigilla violacea*) and Black-faced Grassquit (*Tiaris bicolor*) may have been derived from Cuba, although neither species occurs there at present. Taking their place in Cuba are the Cuban Bullfinch (*Melopyrrha nigra*) and the Cuban Grassquit (*Tiaris canora*). In support of this theory, I might mention that Black-faced Grassquits of Hispaniola and Jamaica are identical, whereas Bahaman individuals represent a quite distinct subspecies. Indeed, one cannot mention a single land bird that can be said without question to have reached the Bahamas from Hispaniola. Perhaps the explanation is that the high mountainous "backbone" of this island is sufficient to dissipate a hurricane moving up from the Caribbean, even such a storm as that which devastated the southern coast of the Dominican Republic on September 3, 1930, one of the worst ever recorded in the West Indies. Probably as a result of this hurricane, four species reached Mona Island, and at least three of these, a Sparrow Hawk (*Falco sparverius dominicensis*), the White-winged Dove (*Zenaida a. asiatica*), and the Smooth-billed Ani (*Crotophaga ani*) are now established there as residents (Bond, 1946:2).

One of the most remarkable cases of bird distribution in the West Indies is that of the Bahaman Mockingbird (*Mimus gundlachii*), a species that is most nearly allied to South American forms of the genus. Its range is very circumscribed in Jamaica, where it is confined to arid sections near the southern coast. It also inhabits islets off the northern coast of Cuba and is widespread in the Bahamas, but is absent from Grand Bahama and Great Abaco, although present on the little mangrove cays north of these islands.

CONCLUSIONS

The West Indies are a group of oceanic islands, at least in the sense that their vertebrate fauna (mammals, birds, reptiles, amphibians,

and fresh-water fishes) did not reach this region by way of a land bridge. The islands comprise a Subregion of the North American Region, and may be divided into two provinces—the Greater Antillean Province (including the Bahama Islands) and the Lesser Antillean Province.

The avifauna of the West Indies is fundamentally and predominantly tropical North American, derived from the north and from the west. The South American element, which entered through Jamaica and the Lesser Antilles, is of comparatively recent arrival and comprises only members of aggressive families. The West Indies give us a rather clear picture of a tropical North American avifauna, which has been largely eradicated in Central America since the formation of the Central American isthmus, which permitted an influx of a great many more or less sedentary South American forms, for the most part of mesomyodian families. What is left of the tropical North American element in Central America is not unlike that which is present in the West Indies, but it is significant that there are no jays nor, apparently, any indigenous species of gallinaceous birds on these islands. A few West Indian genera (e.g., *Corvus*, *Sitta*, *Loxia*) are of Palaearctic origin, but these are also represented in North America.

The only so-called "South American" families with numerous endemic genera in the West Indies are the Trochilidae (hummingbirds) and Thraupidae (tanagers). The Trochilidae are probably, but not unquestionably, South American in origin; and the Thraupidae may have arisen independently and simultaneously from primitive fringillid stock in tropical North America and in South America, through parallel evolution due to specialized feeding habits.

The avifauna of the Bahama Islands was almost entirely derived from Cuba and Florida, with the Cuban element older and predominant.

There can be no doubt that dispersal of birds in the West Indies has been largely brought about by hurricanes, but the prevailing easterly trade winds have had little effect on bird distribution.

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