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Speciation in Colombian Forest Birds West of the Andes

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INTRODUCTION

The Cordilleras of the northern Andes separate a narrow, humid, tropical lowland forest belt, along the Colombian Pacific coast, from the extensive Amazonian basin east of the mountains. The humid forest extends into Central America. This trans-Andean forest region² is characterized by a surprisingly large number of endemic birds. Chapman (1917, p. 106) called the fauna of the Pacific lowlands of Colombia "the most circumscribed and sharply defined, and possibly the most strongly characterized of any fauna of South America."

It is the thesis of the present paper that the faunas west of the Andes were more influenced by climatic changes during the Pleistocene and post-Pleistocene than by orogenic events. The isolation and differentiation of most trans-Andean species occurred after the early Pleistocene uplift of the northern Andes and probably under orographic conditions essentially the same as those that exist at the present time.

This paper is divided into two major parts. The distribution of tropical lowland forests in northwestern South America, the probable geo-

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² The tropical lowlands west of the Andes in Colombia and in Central America are designated in this paper as "trans-Andean" or "Pacific," and those east of the Andes as "cis-Andean" or "Amazonian." Geographically and historically (with respect to the evolution of the lowland bird faunas) this usage seems preferable to that of Chapman (1917, 1926) who sometimes referred to "cis-Andean" and "trans-Andean" in the opposite sense.

logical and climatic history, and the historic interpretation of the speciation of trans-Andean forest birds are given in the first part. In the second part I describe the results of my ornithological field work, especially with respect to the occurrence of narrow zones of allopatric hybridization in the Urabá region of northwestern Colombia. Multiple invasions into the trans-Andean region and an analysis of the Chocó fauna of western Colombia are also briefly discussed.

I spent a total of 23 months in the north Colombian lowlands when conducting geological field work in the area around the Gulf of Urabá, in the Atrato Valley, in Bolívar, and on the Guajira Peninsula during the years 1958 to 1966. A skin collection of approximately 1000 specimens made in these areas was divided between the Instituto de Ciencias Naturales, Universidad Nacional, in Bogotá, and the American Museum of Natural History, and has been discussed elsewhere (Haffer, 1959, 1961, 1962, and in press, a; Haffer and Borrero, 1965).

My thanks are due to Father A. Olivares, head of the Ornithology Department of the Instituto de Ciencias Naturales in Bogotá, who permitted me to use freely the collections and the library of the Instituto. I gratefully acknowledge critical comments and numerous helpful suggestions from Prof. Erwin Stresemann who kindly read the typescript. Mr. Eugene Eisenmann has patiently answered many questions concerning the distribution of Central American birds and discussed several aspects of this article with me. I wish to express my sincere thanks to him for his generous help and important suggestions. Dr. Ernst Mayr has read an early stage of the manuscript and also offered critical remarks. Dr. E. O. Willis kindly permitted me to include his unpublished observations on hybridization of manakins in northern Colombia. The following persons have furnished me with valuable information: Dr. Alexander Wetmore, Mr. Rodolphe M. de Schauensee, Mr. J. D. Macdonald, Dr. Maria Koepcke, Dr. H. Sick, Dr. Charles G. Sibley, and Mr. F. Vuilleumier. I must also thank my father, Dr. O. Haffer, who gave much of his time to prepare and send to Colombia copies and summaries of published articles not available to me. I am most grateful to Dr. Dean Amadon and Mr. Eisenmann for their painstaking help in the preparation of the manuscript for publication.

PRESENT DISTRIBUTION OF TROPICAL LOWLAND FORESTS IN NORTHWESTERN SOUTH AMERICA

The lowlands to the north, east, and west of the Colombian Andes are in part covered with extensive forests (fig. 1), although recent burning and clearing have reduced the drier woodlands to an alarming extent

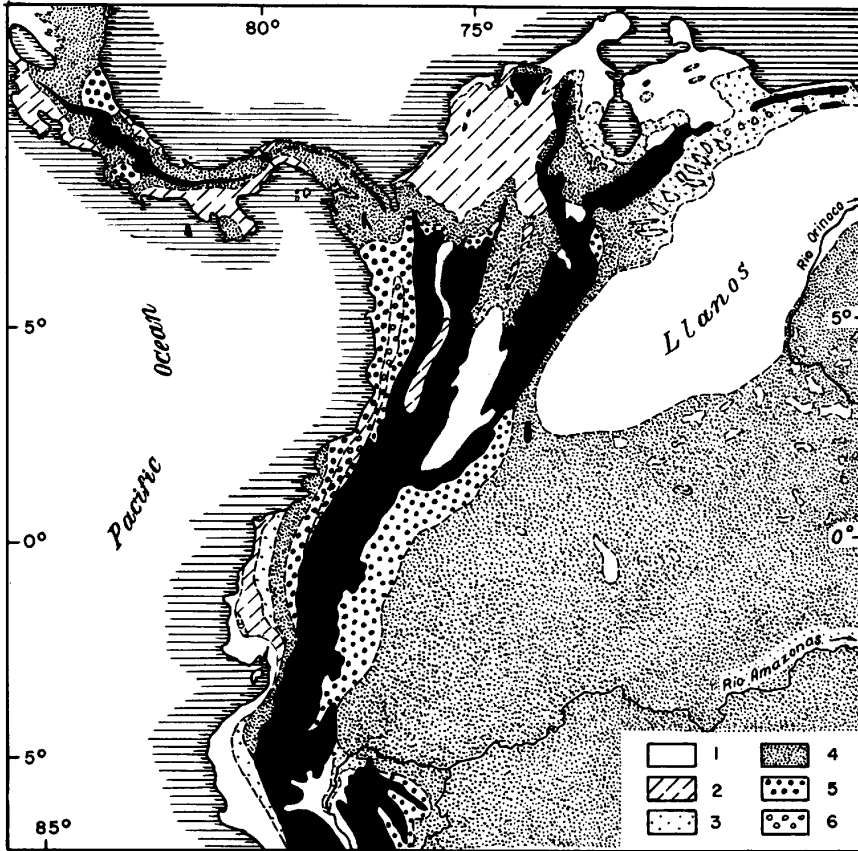


FIG. 1. Present distribution of tropical lowland forest in northwestern South America and southern Central America. The forests of the upper Orinoco region are influenced by the trade-wind climate and show characters of the Dry Tropical Forest (Hueck, 1966, p. 56). Elevations over 1000 meters are in black. Adapted from Chapman (1926), Hueck (1960), Koepcke (1961), Lauer (1959), Slud (1964), Eisenmann (*in litt.*), Espinal and Montenegro (1963), and author's observations in Colombia.

Key: 1. Dry open areas and natural savannas, i.e., llanos. 2. Artificial savannas and secondary growth with some remnants of Dry Forest (or of Moist Forest, chiefly in Caribbean Costa Rica and Panamá). 3. Dry Forest: 1000 to 2000 mm. of rain per year. 4. Moist Forest: 2000 to 4000 mm. of rain per year. 5. Wet Forest: 4000 to 8000 mm. of rain per year. 6. Pluvial Forest: More than 8000 mm. of rain per year.

in more accessible areas. The immense Amazonian forests of southeastern Colombia are still relatively untouched except at the foot of the Andes where large clearings exist around major villages and towns. Toward the

grass plains of the llanos these forests are interspersed with natural savannas of varying sizes. The forests continue northward along the foot of the Eastern Cordillera as a narrow band and cover the southern slope and foot of the Venezuelan Mérida Andes. The Maracaibo forests of the Catatumbo lowlands are directly connected with the forests on the western slope of the Serranía de Perijá. This forest connection is evident in the Montes de Oca at the northern end of the Serranía de Perijá. The open woods that originally covered the north Colombian plains have largely disappeared; only small remnants are still preserved in the valleys of low ranges close to the Caribbean coast (Serranía de San Jacinto). More extensive forests are found at the northern end of the Central and Western Cordilleras of Colombia and in the humid middle Magdalena Valley. These forests are broadly connected around the Gulf of Urabá with the wet and heavily forested region west of the Andes along the Pacific coast of Colombia and northwestern Ecuador. The trans-Andean humid forests continue northwestward into Middle America, covering most of the Caribbean slope from Panamá to Mexico and smaller portions of the Pacific slope, particularly in the Darién region of eastern Panamá and in southwestern Costa Rica.

It should be noted that large tracts of the more accessible forests have disappeared on account of the activity of man during the last centuries and are being destroyed daily. The more humid sections have suffered less from burning and clearing, and parts are currently being set aside as forest reserves in the hope of ensuring their preservation.

The above brief outline of the forest distribution in northwestern South America indicates a connection of the trans-Andean forests with the Amazonian basin, through narrow humid areas along the Caribbean slope at the northern foot of the mountain ranges in northern Colombia and northwestern Venezuela.

For a modern comprehensive treatment of the neotropical forests, see a recent work by K. Hueck (1966) which gathers the widely scattered literature and describes the ecology and distribution of the various plant formations of South America.

GEOLOGIC AND CLIMATIC HISTORY

TERTIARY

The Colombian cordilleras developed during Tertiary time when they were composed of low-lying, hilly, and in part swampy, country. The fauna of these Tertiary "Andes" of Colombia was probably poor, since the mountain chains were separated from one another and from the large land areas north and south of the present Amazon River by ex-

tensive shallow seas, lakes, and marshes, until the end of the Pliocene (fig. 2). During the Tertiary (Upper Eocene) an archipelago was formed in the region of present Central America, which allowed temporary exchange of some terrestrial forms (Simpson, 1950; Belding, 1955; Bürgl, 1961). The basalt ranges of the Colombian coastal cordillera, including the mountains of southeastern Darién in Panamá (Mt. Sapo, Mt. Pirri), probably formed part of this rather old archipelago (for a

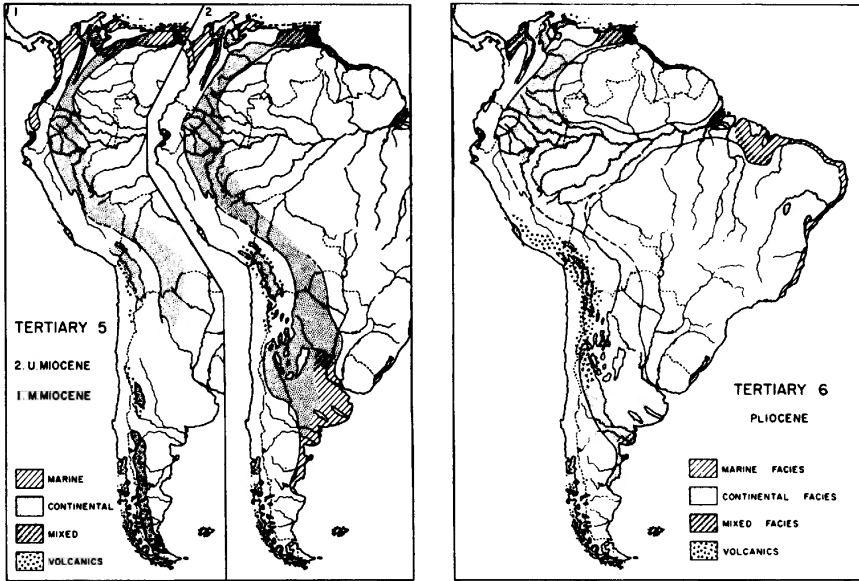


FIG. 2. Paleogeographic maps of South America during upper Tertiary time. *Left:* Middle and Upper Miocene. *Right:* Pliocene. After Harrington (1962).

discussion of the Central American ocean channels connecting the Pacific and Caribbean, see Darlington, 1957; Slud, 1960; Lloyd, 1963; Mayr, 1964).

The last gap separating Central and South America was probably not in Panamá but just south of the Gulf of Urabá in Colombia. This seaway connected the Caribbean Sea and the Pacific Chocó basin of western Colombia (Haffer, MS; Woodring and Thompson, 1949; Simpson, 1950). It was not closed until late Pliocene time.

PLEISTOCENE

The rather low mountain ranges of the Tertiary Colombian Andes were probably uplifted to about their present height at the beginning

of the Pleistocene. At the same time the surrounding lowlands of western and northern Colombia emerged, became forest covered, and thus habitable for the forest fauna of the Amazonian region. Extensive vestiges of the Pleistocene glaciations have been found in the Colombian Andes which are ascribed to the younger Riss and Würm glacials (Wilhelmy, 1957; van der Hammen and Gonzalez, 1960; Bürgl, 1961). The fact that no moraines of the older Günz and Mindel glaciations are known so far in Colombia has led some authors to assume that the northern Andes had not attained sufficient elevation at that time. However, more conclusive evidence is needed to substantiate this assumption.

A similar glaciation was recently discovered by Weyl (1956) in the highest peaks of the Cordillera de Talamanca of Costa Rica.

The glaciation of the South and Central American mountain ranges indicates a Pleistocene refrigeration in the tropics. The temperature reduction from that prevailing at present is believed to have amounted to approximately 3° to 4° C. in the lowlands (Mayr and Phelps, 1955; Wilhelmy, 1957), but reached 7° to 8° C. in the higher elevations of the mountains (van der Hammen and Gonzalez, 1960; van der Hammen, 1961). Under such circumstances the temperature gradient in at least parts of the tropics must have been greater during the cold glacial periods than it is today, possibly 0.8°–0.9° C. per 100 meters compared to the present 0.5°–0.6° C. per 100 meters (Mortensen, 1957), and the climatic transition from the tropical lowlands to the cool mountain zones would have been more abrupt. Also the transition zone from the tropics in South and Central America to the temperate zone in the southern United States was probably much narrower during the glacials than it is today, which means that the southward shift of the boundaries between glaciated to non-glaciated areas (arctic to temperate zone, temperate zone to subtropical zone, and subtropical to tropical zone) decreased progressively southward (toward the equator). In other words the tropical zone as such was only slightly reduced latitudinally and altitudinally by the southward-moving glaciers (and in the mountains from the downward moving glaciers). Certainly the reduction of the tropics was much less than one would assume from the southward push of the glaciated arctic zone alone. The faunas of the cool “temperate” and “subtropical” life zones on tropical mountains were able to extend their distributions considerably during the glacial periods, occupying relatively low ridges of only 1000 to 1200 meters and 400 to 600 meters in elevation, respectively, the latter being today completely within the hot tropical climate. Moreover, such low isolated ranges had a slightly higher elevation than they have today, owing to the Pleistocene lowering of the sea level, and these ranges

formed important stepping stones for at least part of the fauna of the cooler mountain zones across the lowlands (which remained in the tropical zone even at the height of the Pleistocene refrigeration).

A probable increase of the temperature gradient in Africa during the glacial periods of the Pleistocene is indicated by the data summarized by Mortensen (1957) and Moreau (1963). The reduction of the average temperature in this region was calculated by various authors at about 4° C. at sea level, and a drop of 6°, 7°, and 8° C. probably occurred

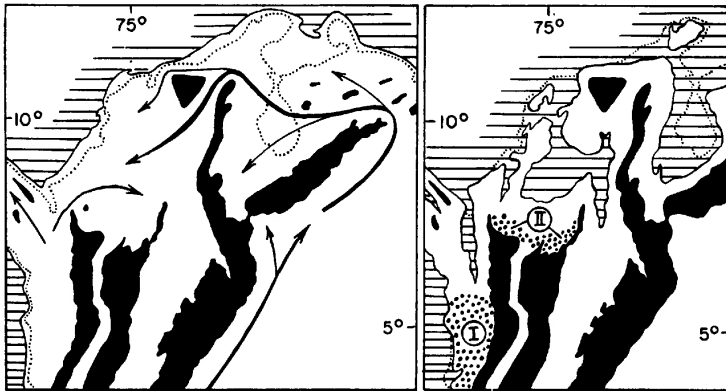


FIG. 3. Northern Colombia during the glacial and interglacial periods of the Pleistocene. The present coast line is dotted; elevations over 1000 meters are in black. *Left*: Glacials: Climate humid and sea level lowered by about 100 meters. Arrows indicate advancing cis-Andean and trans-Andean forest faunas. *Right*: Interglacials: Climate dry in northern half and sea level raised by 30 to 50 meters. I. Chocó Refuge; II. Nechí Refuge.

on Mt. Ruwenzori, Mt. Kilimanjaro, and in the highlands of Ethiopia, respectively.

The northern tip of South America (Guajira Peninsula) was in the tropical zone during the glacial periods (Wilhelmy, 1954), as were the lowlands of Colombia and great parts of Central America. That the tropical zone reached as far north as Mexico during the height of glaciation appears to be possible (Martin, 1958) but remains questionable.

The Pleistocene temperature changes were of much less importance to the fauna of the South American tropical lowlands than the periodic changes from dry to humid climates. The glacial periods were much more humid in tropical America than the interglacials. Wilhelmy (1954) has pointed out that there was an increase of precipitation in the tropics of South America during the glacials due to an extension of the equa-

torial rain belt and a corresponding compression of the dry trade-wind belt of the Northern Hemisphere. For this reason the north Colombian lowlands, including the now arid Guajira Peninsula, were forest-covered much more extensively during the humid glacial periods than they are today, thus providing a broad connection of the Amazonian faunal region with the trans-Andean faunal area of western Colombia and Central America. This effect was increased by the lowering of the sea level by approximately 100 meters. On the other hand, during the drier interglacials, the north Colombian connection of the cis- and trans-Andean forests was interrupted when the humid vegetation retreated southward, owing to a strengthened influence of the trade winds in this area, and the sea level rose by about 30 to 50 meters, thus flooding great parts of the Maracaibo basin and large portions of the north Colombian plains (fig. 3).

POST-PLEISTOCENE

The shifting of humid and dry zones and alternation of humid and dry periods in South and Central America continued during post-Pleistocene time (van der Hammen and Gonzalez, 1960; van der Hammen, 1961). Evidence for a more humid climate in the recent past in regions that at present are arid has been collected by Wilhelmy (1954). He found fossil valleys and peat deposits on the islands of Aruba and Bonaire, thick gravel beds in the Cesar Valley of northeastern Colombia, calcareous tufas, crusts, and limonite concretions on the Guajira Peninsula, and fossil red soils on Curaçao and near Maracaibo. These deposits could not have been formed in these areas under the present arid climate. On the other hand, Goosen (1964) described long, narrow sand dunes from the humid llanos of eastern Colombia. They run in a northeasterly direction of the trade winds and were formed during a sub-Recent period of drought. The widely scattered small patches of "campos cerrados" within the Amazonian forest region are also considered evidence for a previously much wider distribution of this plant formation when the forests were more restricted because of different climatic conditions (Hueck, 1966).

At present only the fact of repeated climatic changes and a corresponding shifting of the vegetation zones during the Pleistocene and post-Pleistocene can be demonstrated for the Neotropical Region. It is left for future investigators to study the distribution of forest and non-forest vegetation in different areas during each of the various climatic periods as is being done in Africa, where a great amount of detail has already been accumulated (Moreau, 1963).

TRANS-ANDEAN FOREST REFUGES AS CENTERS OF BIRD SPECIATION

FOREST REFUGES

The cis- and trans-Andean forests have been broadly connected in the north Colombian lowlands during the humid climatic periods of the Pleistocene and post-Pleistocene. An exchange of the eastern and western faunas around the northern tip of the Andes was further facilitated by the Pleistocene lowering of the sea level which resulted in a considerable expansion of the Caribbean lowlands north of the Andes. Amazonian forms that had come around the Andes in the north followed the Colombian Pacific coast southward, or occupied parts of Central America, or advanced in both directions (fig. 3).

During the interglacials and the post-Pleistocene dry climatic periods the humid forests were pushed southward on each side of the Andes and were replaced by drier types of vegetation. The Central American forests probably were also considerably reduced, with only parts of the north-eastern slope of the higher cordilleras left forest-covered. These forests received rains from the winds that, in blowing against the mountains, were sharply cooled by the abrupt slope. I believe, on the basis of the present rainfall pattern in the Urabá area (Schmidt, 1952; and West, 1957), that the connection of the Central American and the west-Colombian forests was interrupted in the Urabá-lower Atrato region during these dry periods when the effect of the trade winds was here more pronounced than at present. Even the lowlands of central and eastern Panamá were probably devoid of heavy forests in most areas (see also Haffer, in press, a).

Recently Reichel-Dolmatoff (1965, pp. 42-44) made a similar suggestion when discussing the immigration of prehistoric man into northern Colombia. He said "that climatic changes during Late Pleistocene times would have influenced the Darien landscape and that during drier periods the jungle growth would have largely disappeared and a route [for human migrations] would have presented itself," and "a southward shift of 2° of the present border of savannah climate in northern Colombia would clear the route to South America."

A number of forest refuges presumably existed during these dry periods which were effectively isolated from one another and from the great "Amazonian Refuge" east of the Andes. They may be named and briefly described as follows (fig. 4):

CENTRAL AMERICAN REFUGES

CARIBBEAN REFUGES: Several rather extensive refuges probably existed along the Caribbean slope of the Central American mountains in Guatemala, Hon-

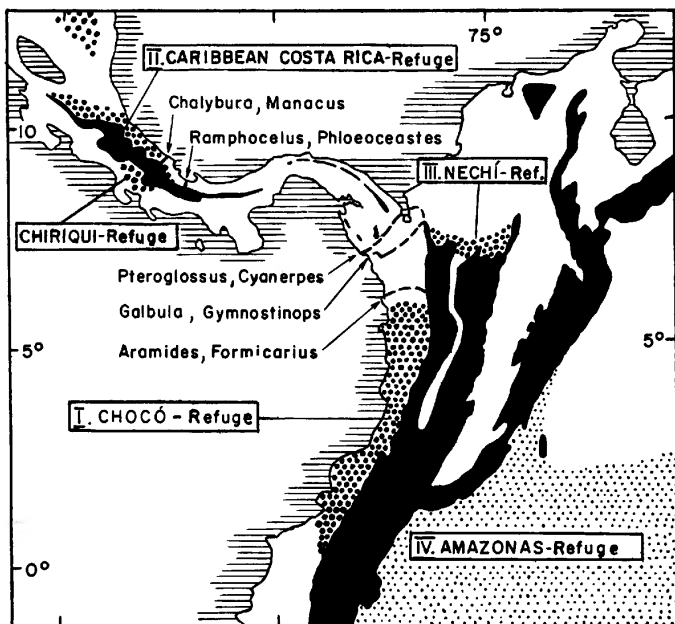


FIG. 4. Trans-Andean forest refuges during Pleistocene and post-Pleistocene periods of drought. Zones of secondary contact, possible overlap, or hybridization in Caribbean western Panamá and in the Urabá region are indicated by dashed lines (for species involved, see table 2). Other forest refuges existed along the Caribbean slope of Central America north of the area shown.

duras, Nicaragua, and Costa Rica. Many of the endemic bird forms of the Caribbean forests originated in these refuges. The southernmost refuge may be called the "Caribbean Costa Rica Refuge." It comprised the foothills and adjacent lowlands of the Guanacaste, Central, and Talamanca mountains of Costa Rica. Endemic forms of this refuge are: *Trogon clathratus*, *Tangara f. florida*, *Bangsia arcaei*, and *Heterospingus (xanthopygius) rubrifrons*.

CHIRIQUÍ REFUGE: This comprised the Pacific slope of southwestern Costa Rica and extreme western Panamá. The following forms differentiated in this area are so well marked that they must be considered semispecies, if not good species: *Trogon (viridis) bairdii*, *Pteroglossus (torquatus) frantzii*, *Thamnophilus bridgesi*, *Thryothorus (nigricapillus) semibadius*, and others.

COLOMBIAN REFUGES

CHOCÓ REFUGE¹: This comprised the central portion of the Pacific lowlands of Colombia. The bulk of the west-Colombian birds originated in this refuge area; a few are still restricted to its previous extent: *Columba (Oenoenas) goodsoni*,

¹ "Chocó" is the name of an Indian tribe inhabiting the lowlands of the Atrato and San Juan rivers (West, 1957). The Departamento Chocó comprises the northern half of the Pacific lowlands of Colombia.

Pittasoma rufopileatum, *Tangara johanna*, *Tangara florida auriceps*.

NECHÍ REFUGE¹: In forests along the northern foothills and adjacent lowlands of the Central and Western Cordillera of Colombia. The more important forms that probably originated here are: *Crypturellus (boucardi) columbianus*, *Crax alberti*, *Pionopsitta pyrilia*, *Trogon melanurus macroura*, *Brachygalba salmoni*, *Nonnula frontalis*, *Capito hypoleucus*, *Thamnophilus nigriceps*, *Dacnis viguieri*, *Tangara inornata*, *Habia gutturalis*, and *Gymnostinops guatimozinus*.

In addition other isolated forests may have existed on the northern or northeastern (or both) slopes of some of the mountain massifs of eastern Panamá (i.e., Mt. Pirri, Mt. Tacarcuna) and in the Serranía de Perijá.

An example of a forest refuge within the present trade-wind desert zone along the northern coast of South America is on the arid Guajira Peninsula of northeastern Colombia. The large plains of this peninsula are covered only with scattered cacti and scrub (Haffer, 1961). The low mountain range of the Serranía de Macuira (300 to 800 meters in elevation) close to the tip of the peninsula catches the winds from the Caribbean Sea. For this reason its northeastern flank is covered with a moist forest vegetation which is completely isolated from the woodlands at the base of the peninsula some 150 kilometers away. A number of bird species living in this forest belt in most cases are already differentiated as well-marked subspecies: *Ortalis ruficauda lamprophonia*,² *Momotus momota spatha*, *Thryothorus leucotis collinus*, *Turdus leucomelas cautor*, *Cyanerpes cyaneus gemmeus*, *Hylophilus flavipes melleus*, and *Arremon schlegeli fratruelis* (Wetmore, 1941, 1946, 1953).

During the dry climatic periods of the Pleistocene and post-Pleistocene the fauna of the more open and arid areas east of the Andes advanced into northern Colombia and followed the Magdalena Valley, which was devoid of heavy forest and more or less arid in its entire length; the un-forested regions around the Gulf of Urabá offered a pathway through Panamá into Central America. At the same time the fauna of the more arid portions of Middle America invaded northern South America. The return of more humid conditions interrupted the connection of the Central American and north Colombian open-country fauna which then retreated into several small dry refuges, i.e., along the Pacific coast of Central America, in the upper Magdalena Valley, the Patia Valley, and other intermontane valleys in the rain shadow of the surrounding mountains.³

¹ After the Rio Nechí, which flows down the northern slope of the Central Cordillera and joins the Cauca River at the village of Nechí.

² This subspecies was not recognized by Vaurie (1965) in his recent revision of *Ortalis*.

³ A historic interpretation of the differentiation of the non-forest faunas of north-western South America is given elsewhere (Haffer, in press, b).

SPECIATION

The bird populations of the trans-Andean forest refuges were isolated from one another and from the great population of the Amazonian basin. A gene exchange was prevented by the intervening arid areas and the mountain ranges. It is concluded that the numerous endemic forms of the Central American and west-Colombian lowland forests originated as peripheral isolates of the large Amazonian population.

The present situation is the result of several such processes of geographic isolation during the Pleistocene and post-Pleistocene. It is reasonable to assume that forms only weakly differentiated were isolated rather recently, and that strongly marked populations had been cut off west of the Andes much earlier. However, this situation may be reversed in conservative and plastic species, respectively.

ALLOPATRIC HYBRIDIZATION

The process of differentiation of an isolated bird population is gradual and progresses slower or faster according to various conditions such as the size of the population. For this reason every conceivable stage between the "subspecies" and "species" level was reached by trans-Andean isolates when they again came into contact with other trans-Andean refuge populations or with the Amazonian population during a later humid period. Those forms that had not developed sufficient pre-mating sexual isolating mechanisms (Mayr, 1963) hybridized along zones of secondary contact. The width of such belts of allopatric hybridization varies considerably (Mayr, 1942, 1963).

A broad zone of secondary intergradation is found between the Costa Rican wren *Thryothorus nigricapillus costaricensis* and *T. n. schottii* of western Colombia; it comprises the whole of central and eastern Panamá (Wetmore, 1959). In this species the chestnut-breasted form, *costaricensis*, probably originated in the Caribbean Costa Rica Refuge, whereas the subspecies *schottii*, with the anterior under parts barred black and white, was differentiated in the Chocó Refuge. Closer examination of those many forest species that are continuously distributed around the northern tip of the Andes will probably show in some cases that the trans- and cis-Andean populations are connected by broad zones of secondary intergradation, with stepped clines developed in northern Colombia or north-western Venezuela, or both.

Narrow zones of allopatric hybridization are developed along the eastern margin of the Caribbean Costa Rica Refuge and at the northern margin of the Chocó Refuge (fig. 4). In the first case Amazonian and

Chocó elements made contact with Central American forms that originated in one of the Caribbean refuges. In the second case Amazonian and Central American forms met Chocó elements in the Urabá region.

HYBRID ZONES ALONG EASTERN MARGIN OF CARIBBEAN COSTA RICA REFUGE: On the Panamá-Costa Rica border *Chalybura (urochrysis) melanorrhoea* intergrades with *C. u. isaurae* along a rather narrow zone (Eisenmann and Howell, 1962). Other allopatric "species" that meet or almost meet in the Caribbean lowlands of extreme western Panamá or adjacent Costa Rica include the following: *Manacus vitellinus* and *M. candei* (see below); *Ramphocelus flammigerus icteronotus*¹ and *R. passerinii*; *Phloeceastes melanoleucus* and *P. guatemalensis*. The partners of the latter two "species" pairs are known to replace each other abruptly in the lowlands at the Chiriquí lagoon of western Panamá (Peters, 1931).

HYBRID ZONES AT NORTHERN MARGIN OF CHOCÓ REFUGE: The partners of the two semispecies² pairs *Pteroglossus torquatus* and *P. (t.) sanguineus*, also *Galbula ruficauda* and *G. (r.) melanogenia* intergrade along narrow zones in the Urabá area (see detailed discussion in the second part of this paper). The following well-marked allopatric forms are still treated as "species" in formal lists, but they apparently meet and may also hybridize along narrow zones in this region. However, the zone of contact is not yet sufficiently known in these cases for a definite conclusion to be reached regarding their relationship: *Aramides cajanea* and *A. wolfei*, *Formicarius analis* and *F. nigricapillus*, *Glaucis hirsuta* and *G. aenea*, *Cyanerpes caeruleus* and *C. lucidus*, *Gymnostinops guatimozinus* and *G. cassini*.

Aramides cajanea inhabits the lower Atrato region (Rio Salaquí, Juradó), but *A. wolfei* is known from the central Chocó to the south. Both forms are reported from the Alto del Buey area which, however, does not prove sympatric breeding (for details of distribution in this case and the following, see de Schauensee, 1948-1952). The distribution of the *Formicarius* forms is very similar to that of *Aramides*: *F. nigricapillus* is found in the Chocó lowlands north to Nuquí and the Rio Jurubidá on the Pacific coast, and *F. analis* inhabits the Urabá region and the Atrato Valley. The nearest localities where these forms have been taken are approximately 80 kilometers apart. Both birds are inhabitants of the humid low-

¹ Sibley (1958) has shown that *R. flammigerus* (Jardine and Selby, 1833) of the Cauca Valley of Colombia hybridizes freely with *R. icteronotus* (Bonaparte, 1838) of the Pacific lowlands.

² Semispecies are defined as "populations that have acquired some, but not yet all, attributes of species rank" (Mayr, 1963, p. 671). As proposed by Lorković (1958), the name of the species of which a semispecies forms part is enclosed in parentheses. A semispecies may be monotypic or may consist of several clinal forms, which are designated as a "subspecies group" in this paper.

lands in western Colombia and may meet somewhere in the Alto del Buey area. *Glaucis aenea* occupies the Chocó lowlands north to Andagoya and Nuquí, whereas *G. hirsuta* was collected along the entire Atrato Valley south to Quibdó. The only locality at which both forms seem to have been taken is Santa Cecilia, Caldas.¹ The fact that both *Cyanerpes caeruleus chocoanus* and *C. lucidus isthmicus* have been taken along the Rio Juradó is no proof that they are sympatric breeders. However, so far no intergrades have been collected between any of the above-mentioned allopatric forms. The Nechí form *Gymnostinops guatimozinus* meets *G. cassini* in the Salaquí area. Two skins from this river are close in coloration to *G. guatimozinus*, "but the male shows a tinge of chestnut on the sides of the body. The head, upper mantle and underparts are glossed with green; this is not as intense as in *guatimozinus*. They are in a sense slightly intermediate between *guatimozinus* from Darién and *cassini* from the Rio Baudó" (R. M. de Schauensee, *in litt.*, and 1966). These birds may indicate the existence of a narrow hybrid zone between both forms in the lower Atrato Valley.

HYBRIDIZATION IN *Manacus* (FIG. 5): The cis-Andean white-breasted form *M. manacus* is represented west of the Andes by the yellow-breasted *M. vitellinus* (which extends through Panamá), and in Caribbean Central America by *Manacus candei*. These strictly allopatric forms have hitherto been considered specifically distinct from each other, although no detailed study of their zones of secondary contact has so far been undertaken. Recent observations by E. O. Willis at Caucaasia on the lower Rio Cauca (fig. 5, 1) indicate that *Manacus manacus abditivus* and *M. vitellinus milleri* hybridize freely where their ranges meet in northern Colombia: "At Caucaasia, in an isolated woodlot in the pastures four kilometers west of town and by the road, I found males of both types displaying in the same dancing ground, no more than ten meters apart. In between males of seemingly pure types in this same dancing ground, there were several intermediate or hybrid males displaying. Out of some ten males displaying in this small dancing ground, two at the north end were white, one or two at the south end were yellow and six or so in between were pale yellow in the parts of the plumage which differ in the two

¹ Santa Cecilia is at the foot of the Western Andes on the upper Rio San Juan. These *Glaucis* forms probably meet near this locality, because E. Eisenmann (*in litt.*) has compared one "male?" *aenea* (and apparently such) and one "female" (obviously immature, and agreeing with *G. hirsuta affinis*), both of which were collected near Santa Cecilia at 2400 feet on November 17 and 19, 1945, respectively. These specimens were kindly sent to Eisenmann by Mr. de Schauensee. The latter's statement (1966) that these forms "occur together commonly on the Pacific slope of Colombia" is still unproved.

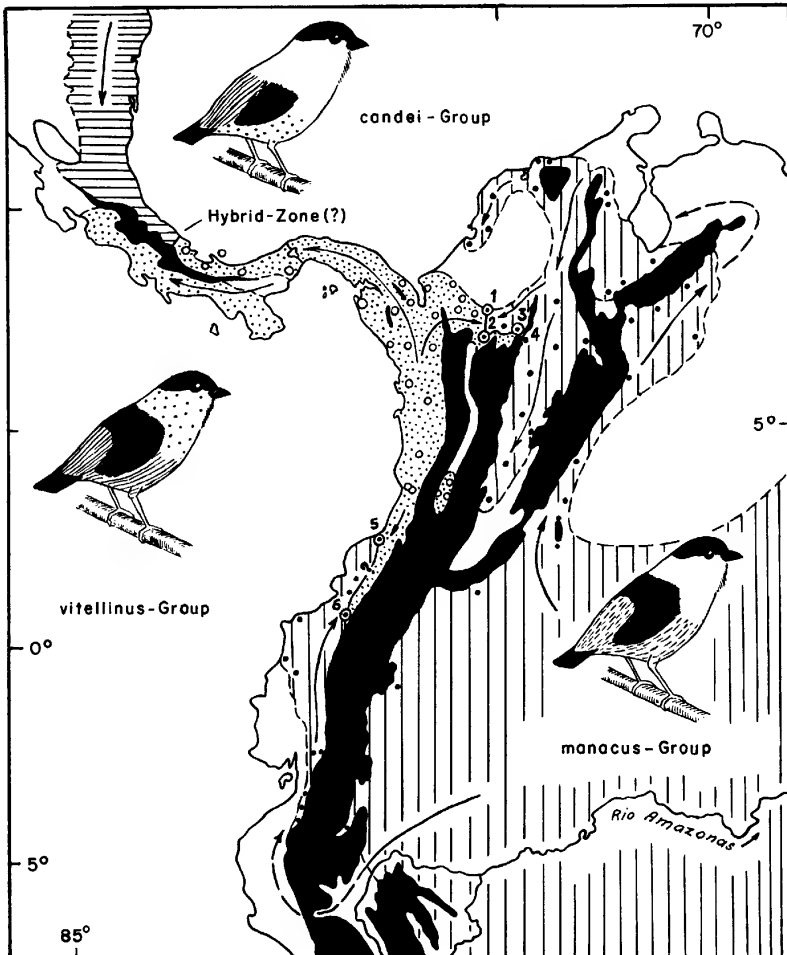


FIG. 5. Distribution of *Manacus manacus* (Linnaeus).

Key: Vertical lines, *Manacus manacus*; dotted area, *Manacus (manacus) vitellinus*; horizontal lines, *Manacus (manacus) candei*. Plumage color key: Dashed, gray; hatched, green; dotted, yellow; unmarked, white; solid, black. See text for numbered localities.

taxa. I collected one of the pale yellow birds (Museum of Vertebrate Zoology No. 148-593) and one of the white birds (MVZ No. 148-592), using mist nets set about four meters apart.

“Examination of the hybrid male from Cauasia and comparison with specimens of *Manacus vitellinus milleri* here at The American Museum of Natural History show that it is like *milleri* but much paler on the underparts and collar. The collar and cheeks are especially pale, being straw

yellow like the throat and breast rather than bright yellow. The collar is wider than in *milleri*, and the belly is tinged with much less yellow so that it looks grayish-green. The edges of the throat are especially pale, almost white. In all these respects it is almost exactly intermediate between *milleri* and the specimen of *Manacus manacus abditivus* which I took at Caucasia. The latter is white wherever *milleri* is tinged with yellow, and shows none of the yellowish tint seen in *M. m. flaveolus*. Unfortunately I did not get specimens of the bright yellow males at Caucasia, but I am sure that they were as bright as typical *milleri*. In summary, the hybrid is half way between *milleri* and *abditivus* in the amount of yellow which suffuses the plumage except in the black regions. Date for my specimens is 21 June 1962" (E. O. Willis, *in litt.*).

Other localities in the Cauca region where *manacus* and *vitellinus* come into contact are Puerto Valdivia (Chapman, 1917; see fig. 5, 2) and "Remedios." The village of Remedios is on the eastern slope of the Central Cordillera facing the Magdalena Valley (fig. 5, 4); Willis has found here only *M. manacus* during a two-week visit in 1962. For that reason it seems probable that the *vitellinus* specimens taken by T. K. Salmon during the last century actually came from just across the low divide of the Central Cordillera (fig. 5, 3). Two other "Remedios" males of *M. manacus abditivus* "have the white areas of the plumage very faintly tinged with yellowish" (Hellmayr, 1929, p. 68) and also may have been collected west of this village in the possible contact zone with *M. vitellinus*. The bird from Barranca Bermeja (Hacienda Monte Bello) reported by Borrero and Hernandez (1957) and Borrero, Olivares, and Hernandez (1962) as "*M. vitellinus*" is preserved in the Bogotá collection; upon re-determination it proved to be a female of *M. manacus abditivus*. The humid middle Magdalena Valley is inhabited exclusively by *M. manacus* which comes in contact with *M. vitellinus* only west of the northern tip of the Central Cordillera in the lower Cauca region.

A second zone of contact between *M. vitellinus* and *M. manacus* is in the Pacific lowlands of southwestern Colombia and northwestern Ecuador. *Manacus manacus* has crossed the Andes in northern Perú and has extended its range northward into the Pacific lowlands, meeting *M. vitellinus* at Guapi (fig. 5, 5) and near Paramba (fig. 5, 6). Olivares (1958) collected both forms in the environs of Guapi, and Hellmayr (1929, p. 70) described an intermediate bird from Paramba which was collected with normally colored specimens of *M. manacus*. This bird most probably is a hybrid. It should be noted that the courtship displays of *manacus* and *vitellinus* are in general identical, with only minor differences (Snow, 1962).

The Central American form *candei* is not known to be in contact with

M. vitellinus cerritus of extreme western Panamá on the Caribbean slope (Carriker, 1910; Wetmore, 1959). This, however, seems rather unlikely and needs confirmation in the field. Eugene Eisenmann wrote (*in litt.*), regarding the nature of *M. vitellinus cerritus*: It "is a very variable form ranging in the same locality (Almirante, Bocas del Toro) from individuals that in orange yellow color tone are like *vitellinus* to birds that are nearer to lemon yellow. To me *cerritus* suggests the result of some contact of *vitellinus* with *candei* in the past. . . . I believe it most likely that birds resembling *cerritus*, rather than true *candei*, will be found in the Costa Rican area just west of the Rio Sixaola."

It is concluded that *candei* and *vitellinus* originated as peripheral isolates of the Amazonian *manacus* in Caribbean Central America and in the Chocó Refuge, respectively. Apparently they have not reached full species status, still replacing each other geographically and hybridizing along narrow zones of secondary contact. It seems justifiable to speak of a *candei* and *vitellinus* "group" or of semispecies within the species unit *Manacus manacus* (Linnaeus).

GOOD SPECIES

Many trans-Andean forms developed sufficient sexual isolating mechanisms during geographic separation to permit the sympatric occurrence with the Amazonian parent population upon its re-invasion into the forest region west of the Andes. If the cis- and trans-Andean allies today still are separated by a distributional gap, their high degree of morphological difference often indicates that they are specifically distinct.

However, some pairs of such geographically isolated forms are variously treated by different authors as still being subspecies of a single unit or as having already reached species status, for example, the following trans-Andean birds: *Laterallus (melanophaius) albigularis*, *Leucopternis (schistacea) plumbea*, *Heliothrix (aurita) barroti*, *Myrmormis (torquata) stictoptera*, *Myiobius (barbatus) sulphureipygius*, *Myiornis (eaudatus) atricapillus*, *Cyphorhinus (aradus) phaeocephalus*, *Polioptila (guianensis) schistaceigula*, and *Tangara (nigrocincta) larvata*. In each case the specific name of the cis-Andean relative, which is also the older name, is in parentheses. A future comparison of the behavior and habitat patterns of these allies may facilitate a decision as to their systematic status.

Only a few characteristic examples, of a total of about 100 trans-Andean species, have been assembled in tables 1-4. The groups distinguished on the basis of their distribution pattern are briefly discussed below:

Group A (table 1) comprises trans-Andean species that are restricted

to the Chocó region or have extended their ranges into parts of Central America. In most cases a large gap separates the trans- and cis-Andean forms; however, *Pachyrhamphus cinnamomeus* and *P. castaneus* approach each other geographically in northwestern Venezuela. It would be interesting to study both forms in the possible zone of secondary contact. It should be noted that, in all three species pairs of the cotingid genera *Lipaugus*, *Rhytipterna*, and *Laniocera*, the trans-Andean representative changed its general plumage color from the gray of the Amazonian forms to rufous brown.

Group B (table 2) is composed of trans-Andean species that have variously differentiated populations both in Central America and in the Chocó region. Some of the Central American forms, all of which originated in the Caribbean Refuges, are still isolated from the Chocó population by a gap in Panamá or in northwestern Colombia, or in both (*Galbula* through *Gymnostinops*). This gap may be due to unsuitable ecologic conditions or simply lack of sufficient population pressure. The gap between species pairs in *Columba* (*Oenoenas*), *Trogon*, and *Pionopsitta* is in the lower Atrato Valley; between those in *Cotinga*, in western Panamá; and between those in *Gymnostinops*, in eastern Panamá.

Several Central American forms came into secondary contact with the Chocó population either in western Panamá or in the Urabá region (*Dysithamnus* through *Cyanerpes*). A narrow zone of sympatry seems to have been found only in *Dysithamnus* (Eisenmann, 1955; Slud, 1964). In the remaining cases both trans-Andean forms are either known to hybridize or are assumed likely to do so on the basis of their morphological similarity and strict geographic replacement. Some of the cis-Andean representatives in this group are partly sympatric with the trans-Andean form [*Columba* (*Oenoenas*) *subvinacea*, *Chalybura buffoni*]. In other cases a narrow zone of hybridization is either known to exist (*Galbula ruficauda*, *Manacus manacus*), or its existence seems very probable (*Glaucis hirsuta*).

Group C (table 3) comprises trans-Andean species without a representative in the Chocó region. They are restricted to Central America or, in a few cases, extended their range later into northwestern Colombia.

Group D (table 4), finally, comprises 14 trans-Andean genera; it should be noted that the generic separation of *Allocotopterus* and *Zarhynchus* is questionable (Hellmayr, 1929, 1937). One genus is restricted to Central America (not including *Chrysothlypis* which represents *Erythrothlypis*), and five are restricted to the Chocó region. Obviously these genera represent early trans-Andean isolates, of which the Amazonian representatives are, in most cases, unknown.

Another group of characteristic trans-Andean forest species are the

TABLE 1
 GROUP A: TRANS-ANDEAN SPECIES RESTRICTED TO THE CHOCÓ REGION
 OR EXTENDING THEIR RANGES INTO CENTRAL AMERICA
 (Species not connected by a symbol are separated by a distributional gap.)

Central American Elements	Chocó Elements	Amazonian Elements
^a ←—————	<i>Leucopternis semiplumbea</i>	<i>L. melanops</i>
	<i>Bucco noanamae</i>	<i>B. tamatia</i>
←—————	<i>Nystalus radiatus</i>	<i>N. chacuru</i>
	<i>Xenerpestes minlosi</i>	<i>X. singularis</i>
←—————	<i>Mitrospingus cassinii</i>	<i>M. oleagineus</i>
←—————	<i>Malacoptila panamensis</i>	<i>M. fusca</i>
←—————	<i>Myrmotherula fulviventris</i>	<i>M. leucophthalma</i>
←—————	<i>Hylophylax naevioides</i>	<i>H. naevia</i>
←—————	<i>Lipaugus unirufus</i>	<i>L. vociferans</i>
←—————	<i>Rhytipterna holerythra</i>	<i>R. simplex</i>
←—————	<i>Laniocera rufescens</i>	<i>L. hypopyrrha</i>
←—————	<i>Pachyrhamphus cinnamomeus</i>	<i>P. castaneus</i>
←—————	<i>Ceelus loricatus</i>	<i>C. grammicus</i>

^a Chocó elements advancing into Central America.

“Nechí elements” (see above, under Nechí Refuge). They are confined to northern Colombia, or have occupied additional portions of Panamá or northwestern Venezuela, or both.

CENTRAL AMERICAN ELEMENTS IN NORTHWESTERN COLOMBIA

During the extension of humid forests after dry climatic periods a northwardly directed invasion of Chocó elements and cis-Andean forms was noted in Central America. However, a smaller number of forest birds also advanced in a southern direction from Middle America into eastern Panamá and northern Colombia. Some met in this area their west-Colombian or Amazonian representatives, which had been isolated in the Chocó or Amazonian Refuge, respectively; i.e., *Pteroglossus t. torquatus* hybridizes with the Chocó form *P. (t.) sanguineus* in the Urabá region and approaches the range of its cis-Andean representative *P. pluricinctus* in northwestern Venezuela (fig. 11). Other species advancing into northwestern Colombia are still separated from their Chocó representatives by a gap: *Pionopsitta haematotis*, *Trogon m. massena*, and *Pittasoma michleri* (tables 2 and 4). “True” Central American forms without close relatives in northwestern Colombia that in part advanced even into the humid Magdalena Valley include the following (fig. 6): *Rhynchortyx cinctus*, *Hylomanes momotula*, *Gymnocichla nudiceps*, and *Oncostoma cinereigulare*. Others

TABLE 2
 GROUP B: TRANS-ANDEAN SPECIES WITH VARIOUSLY DIFFERENTIATED POPULATIONS
 BOTH IN CENTRAL AMERICA AND IN THE CHOCÓ REGION
 (Species not connected by a symbol are separated by a distributional gap.)

Central American Elements	Chocó Elements	Amazonian Elements
<i>a</i> ←	<i>Galbula (r.) melanogenia</i> —	<i>G. ruficauda</i> subsp.
←	<i>Glaucis (hirsuta) aenea</i> —	<i>G. hirsuta</i>
←	<i>Fornicarius nigricapillus</i> —	<i>F. analis</i> ^b
←	<i>Pipra mentalis</i>	<i>P. chloromeros</i> ^c
←	<i>Tangara florida</i> }	<i>T. schrankii</i>
	<i>Tangara johannae</i> }	
<i>Aramides cajaneus</i> subsp.	<i>A. wolff</i> —	<i>A. cajaneus</i> subsp.
<i>Neomorphus geoffroyi salvini</i>	<i>N. radiatus</i>	<i>N. geoffroyi</i> subsp.
<i>Pionopsitta haematotis</i>	<i>P. pulchra</i>	<i>P. barrabandi</i>
<i>Columba (Oenoceras) nigritrostris</i>	<i>C. (O.) goodsoni</i> }	<i>C. (O.) subvinae</i> subsp.
<i>d</i> ←	←	
<i>Trogon clathratus</i>	<i>T. comphus</i>	<i>T. melanurus</i>
<i>Trogon massena massena</i>	<i>T. massena australis</i> }	
<i>e</i> ←	←	
<i>Cotinga amabilis</i> + <i>C. ridgwayi</i>	<i>C. natterii</i>	<i>C. maynana</i>
<i>Platysaris algaiae</i>	<i>P. homochrous</i>	<i>P. minor</i>
<i>Gymnostinops montezuma</i>	<i>G. cassini</i>	<i>G. bifasciatus</i>
<i>Dysithamnus striaticeps</i> —	<i>D. puncticeps</i> —	<i>D. mentalis</i>
<i>Chalchura urochrysis melanorhoa</i> —	<i>C. urochrysis</i> subsp. —	<i>C. buffoni</i>
<i>Pteroglossus torquatus</i> + <i>P. (t.) frantzii</i>	<i>P. (torquatus) sanguineus</i>	<i>P. pluricinctus</i>
<i>Manacus (manacus) candei</i> —	<i>M. (manacus) vitellinus</i> —	<i>M. manacus</i> subsp.
<i>Tanagera anneae</i> —	<i>T. xanthogaster chocoensis</i>	<i>T. xanthogaster</i> subsp.
<i>Tanagera gouldi</i> + <i>T. imitans</i> —	<i>T. fuscicrissa</i>	<i>Tanagera</i> sp.

TABLE 2—(Continued)

Central American Elements	Chocó Elements	Amazonian Elements
<i>Ramphocelus passerinii</i> —————	————— <i>R. flammigerus icteronotus</i>	<i>Ramphocelus</i> sp.
<i>Chlorothraupis carmioli lutescens</i> —————	————— <i>C. olivacea</i>	<i>C. carmioli</i> subsp.
<i>Phloeocastes guatemalensis</i> —————	————— <i>P. melanoleucus malherbii</i>	<i>P. melanoleucus</i> subsp.
<i>Cyanerpes lucidus</i> —————	————— <i>C. caeruleus chocoanus</i>	<i>C. caeruleus</i> subsp.

←————— Ranges overlapping (sympatric): good species.

◊————— Hybrid zone proved: subspecies (or semispecies).

————— Ranges complementary (allopatric): relationship of the allies unknown (subspecies or species).
 ————— Ranges complementary (allopatric): relationship of the allies unknown (subspecies or species).

^a Chocó elements with an isolated, but not yet specifically differentiated, population in Central America.
^b *F. analis* and *F. nigricapillus* are locally sympatric on the Caribbean slope of Costa Rica and Panamá, apparently with some altitudinal replacement.

^c *P. erythrocephala* may form a superspecies with these *Pipra* forms; it seems to be allopatric with *P. mentalis* in eastern Panamá to northwestern Colombia, and with *P. chloromeros* in northeastern Perú, respectively. (For further details, see Hafer, in press, c.)

^d *C. (O.) subvinacea*, an Amazonian element, occurs in Chocó and Central America.

^e The Nechí form *T. melanurus macroura* advanced into central Panamá and the northern Chocó.

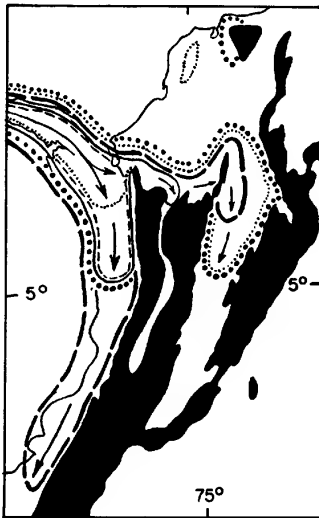


FIG. 6. How Central American elements advanced into northwestern Colombia.

Key: Heavy dashes, *Rhynchortyx cinctus*; fine dashes, *Hylomanes momotula*; heavy dots, *Oncostoma cinereigulare*; fine dots, *Gymnocichla nudiceps* and *Myrmornis torquata* (except near Caribbean coast); fine line, *Selenidera spectabilis*.

have closely allied forms in the Amazonian forest, such as *Selenidera spectabilis*, *Deconychura longicauda*, *Myrmornis (torquata) stictoptera*, and *Monasa morphoeus*. It should be emphasized that the southward invasion of some Middle American forms was apparently almost negligible compared to the main stream of northward-advancing Chocó and Amazonian elements during the humid climatic periods of the Pleistocene and post-Pleistocene.

AMAZONIAN ELEMENTS THAT CROSSED THE ANDES IN NORTHERN PERÚ

In the high mountain range of the Central Cordillera of the Colombian Andes, there is no pass below 2000 meters which could have permitted an exchange of the cis- and trans-Andean lowland faunas by a

TABLE 3
GROUP C: TRANS-ANDEAN FORMS RESTRICTED TO CENTRAL AMERICA OR EXTENDING THEIR RANGES INTO NORTHWESTERN COLOMBIA
(Species not connected by a symbol are separated by a distributional gap.)

Central American Elements	Chocó Elements	Amazonian Elements
<i>Selenidera spectabilis</i> —————→	^a	<i>S. reinwardtii</i>
<i>Deconychura longicauda</i> subsp. —————→		<i>D. longicauda</i> subsp.
<i>Aratinga finschi</i>		<i>A. leucophthalma</i>
<i>Piprites griseiceps</i>		<i>P. chloris</i>

^aCentral American elements advancing into northwestern Colombia.

TABLE 4
 GROUP D: TRANS-ANDEAN GENERA POSSIBLY REPRESENTED BY SOME OTHER GENUS
 IN AMAZONIA
 (Species not connected by a symbol are separated by a distributional gap.)

Central American Elements	Chocó Elements	Amazonian Elements
<i>Phlogothraupis sanguineus</i>		?
<i>Carpodectes nitidus</i> + <i>C. antoniae</i>	<i>C. hopkei</i>	<i>Xipholena</i> sp.?
<i>Pittasoma michleri</i>	<i>P. rufopileatum</i>	?
<i>Bangsia arcaei</i>	<i>B. rothschildi</i>	<i>Buthraupis</i> sp.?
<i>Heterospingus rubrifrons</i>	<i>H. xanthopygius</i>	<i>Tachyphonus</i> sp.?
<i>Chrysothlypis chrysomelas</i>	<i>Erythrothlypis salmoni</i>	<i>Thlypopsis</i> sp.?
	<i>Androdon aequatorialis</i>	?
	<i>Allocopterus deliciosus</i>	<i>Machaeropterus regulus</i>
	<i>Sapayoa aenigma</i>	?
	<i>Sipia berlepschi</i>	<i>Cercomacra</i> sp.?
	<i>Sipia rosenbergi</i>	
	<i>Xenomnis setifrons</i>	<i>Pygiptila</i> sp.?
^a ←	<i>Phaenostictus mcleannani</i>	<i>Phlegopsis</i> sp.
←	<i>Zarhynchus wagleri</i>	<i>Ocyalus latirostris</i>

^a Chocó elements advancing into Central America.

direct crossing of the mountains. The Colombian Andes have been a highly effective barrier to all lowland forest birds since the beginning of the Pleistocene. Only a few Chocó species seem to have crossed the rather low Western Cordillera to occupy the eastwardly adjoining Cauca Valley (i.e., *Manacus vitellinus viridiventris*; fig. 5). The Andalucia pass of the Eastern Cordillera probably did not serve as a pathway for Amazonian forest birds into the arid upper Magdalena Valley because of ecological reasons (Miller, 1952). Amazonian species advanced exclusively around the northern tip of the Colombian Andes, following the lowlands along the Caribbean coast; a direct crossing of the mountains in this area appears impossible. However, the narrowing Andes to the south seem to offer several pathways for Amazonian forms to reach the Pacific lowlands in northern Perú and southern Ecuador. The deeply incised valleys on each side of the mountain body in this region are mostly dry and devoid of heavy forest today, but must have been occupied to a large extent by lowland forest faunas during humid climatic periods of the past. Chapman (1917, 1926) and Koepcke (1961) have pointed out that an exchange of cis- and trans-Andean faunas probably took place at the low Porculla pass (2150 meters) in northern Perú ("Marañon route"). Chapman (1923) also discussed the possibility of a "Loja route" in south-

ern Ecuador. It seems very reasonable to assume that during humid periods certain Amazonian species "spilled over" to the west following various low passes in the narrow Andes of southern Ecuador and northern Perú. Particularly interesting examples are found in the *Trogon melanurus* group (fig. 15), in *Formicarius nigricapillus*, and in *Manacus manacus* (fig. 5) (Chapman, 1926, pp. 411, 536). The following west-Ecuadorian forms probably originated from small founder populations that crossed the Andes in this region:

Sittasomus griseicapillus aequatorialis

Pachyrhamphus spodiurus

Cacicus cela flavocrissus

Others have extended their range northward into the Chocó region, or in some cases even into Central America:

Crax rubra

Osculatia saphirina purpurata

Attila cinnamomeus torridus

Micromonacha lanceolata

Pipra mentalis

Gymnopithys leucaspis

Thamnistes anabatinus

Microrhopsis quixensis

These species either have their closest relatives in the upper Amazonian lowlands rather than in Venezuela, for example, *Crax globulosa*, *Osculatia s. saphirina*, *Pipra chloromeros*, or the cis-Andean population is restricted to the central and southern part of the Amazonian forest.

DISCUSSION

The amazing concentration of endemic forms in the forested lowlands west of the Andes is explained by the following facts: (1). Relatively small populations of Amazonian forest birds were repeatedly isolated in forest refuges west of the Andes during Pleistocene and post-Pleistocene periods of drought which broke forest connections and allowed the development of differences by selection and chance. (2). The repeated restoration of connection between the lowland forests west and east of the Andes during humid climatic periods allowed an increasing number of small Amazonian founder populations¹ to reach the forests west of the Andes in Central America and western Colombia. This led to a

¹ These founder populations contained "inevitably only a small fraction of the total variation of the parental species" (Mayr, 1963, p. 529). This was also of great importance for the rapid deviation of a trans-Andean form from its cis-Andean parent species (Mayr's "founder principle").

gradual accumulation of endemic trans-Andean forms. These are of very different age and have reached today various stages of taxonomic differentiation. (3). Owing to the repeated establishment of forest connections during humid periods, multiple invasions of the same Amazonian population into the region west of the Andes occurred in several cases.

The uplift of the northern Andes to their present height led to the formation of a very effective barrier to the lowland faunas on either side of the mountains. However, this event was only the indirect cause of the development of the numerous trans-Andean species. The direct cause was the repeated change of dry and wet climatic periods during the Pleistocene and post-Pleistocene which resulted in a corresponding reduction and expansion of the tropical lowland forests. Similar conclusions have been reached by other authors regarding different parts of the tropics (Stresemann and Grote, 1929; Stresemann, 1939; Darlington, 1957, p. 587; Keast, 1961; Mayr, 1963, p. 372; Moreau, 1963; Hall, 1963).

The above interpretation of the faunal differentiation west of the Andes contrasts sharply with Chapman's theory (1917, 1926). He assumed that part of a "pre-Andean" fauna was cut off west of the Andes by the rising mountain ranges of the northern Andes. However, the existence of a "pre-Andean" lowland fauna west of the Andes seems to me most unlikely, since these lowlands were covered by shallow seas before the uplift of the mountains. Island faunas existed on archipelagoes in the region of Middle America, but these permitted only a restricted immigration of Amazonian forms. The low cordilleras themselves were also separated from the Amazonian forest by shallow seas until the beginning of the Pleistocene. Moreover the separation of the lowlands, east and west of the Andes, by the Andean uplift was not complete; both regions remained narrowly connected north of the mountain ranges in northern Colombia and northwestern Venezuela, and a frequent exchange of the cis- and trans-Andean faunas was possible through Caribbean lowlands. These facts seem incompatible with Chapman's theory. Griscom (1932, 1935) in addition assumed that the Pleistocene refrigeration had forced the Central American lowland fauna to retreat southward into western Colombia, thus leading to the surprising concentration of endemic forms in the Chocó region. However, it is shown above that the temperature depression of the Pleistocene most probably did not affect the tropical lowland fauna of the central and southern part of Middle America.

Nevertheless the close relationship of the "Colombian Pacific fauna" and the Central American fauna stressed by Chapman (1926) remains a zoogeographic fact. It seems best explained by an intensive faunal ex-

change that took place between both regions during the humid periods. For that reason it appears useful to combine them in a zoogeographic classification as was done by Hershkovitz (1958). This author correctly interpreted the west-Colombian lowlands as the "South American root" of his Middle American province. The centers of the forest faunas of this Middle American province are represented by the former Caribbean Central American Refuges and the Pacific Chiriquí Refuge as well as the Chocó and Nechí refuges of Colombia.

A problem of particular interest is the age of the bird speciation west of the Andes. The range extensions that led to "allopatric" hybridization in western Panamá and in the Urabá region are probably of very recent age and may be only several thousand years old. However, we do not know for how long the hybridizing allies had been isolated. In cases such as *Glaucis (hirsuta) aenea*, *Galbula (ruficauda) melanogenia*, and *Formicarius nigricapillus*, in which the isolated west-Colombian and Central American populations are not even subspecifically distinct, the separation appears to be very recent and of post-Pleistocene age. However, in most other trans-Andean species no decision as to a Pleistocene or post-Pleistocene age can be made, although it seems reasonable to assume that more strongly differentiated genera¹ and species already had originated in early Pleistocene time.

In an excellently illustrated article on the morphology and distribution of the butterfly genus *Heliconius*, Emsley (1965) related the differentiation of this group of neotropical insects to the Tertiary paleogeographic history of northwestern South America. He was silent, however, about Pleistocene climatic changes and their possible effect on the distribution of the various species studied. I would assume that these climatic changes were equally important for the distribution of butterflies as they have been for that of birds. For this reason some of the speciation phenomena described by Emsley (1965) are perhaps better explained by the climatic, rather than the paleogeographic, history of the recent geologic past, particularly for the differentiation of some of the endemic species inhabiting the lowlands north and west of the Andes. Nevertheless, a few trans-Andean endemics in butterflies and birds may have originated on the isolated islands of the emerging northern Andes during middle and late Tertiary time and later extended their ranges onto the emerging lowlands west and north of the rising mountain chains. I assume, however, that the great majority of the forest species, inhabiting today the trans-Andean lowlands, advanced into these regions after the final connection

¹ These are mostly monotypic and nothing but strongly differentiated geographical isolates.

with the Amazonian lowlands was established at the end of Tertiary time and when dense forests developed around the rising mountain ranges. The differentiation of these trans-Andean populations was then related mainly to the Pleistocene climatic history of northern South America and of Middle America rather than to the Tertiary orogenic development of the northern Andes. On the other hand, the differentiation of the numerous Amazonian species of butterflies and birds did probably start earlier in the Tertiary and was influenced by the paleogeographic history of these areas, as well as by the Pleistocene climatic changes.

ALLOPATRIC HYBRIDIZATION AT THE NORTHERN MARGIN OF THE CHOCÓ REFUGE

When the forests of Central America and northwestern Colombia were united after a sub-Recent period of drought, previously isolated bird populations came into secondary contact as long as they followed the extending forests. Zones of allopatric hybridization resulted close to the eastern margin of the Caribbean Costa Rica Refuge and at the northern margin of the Chocó Refuge (fig. 4). For this reason the forests of Caribbean western Panamá and of the Urabá region of northwestern Colombia are of particular zoogeographic importance. Both areas have been treated in special publications (Peters, 1931; Eisenmann, 1957; Haffer, 1959), but no details of the secondary contact zone of any of the allopatric "species" pairs of these regions are known, except for the hybridization of *Chalybura (urochrysis) melanorrhoea* and *C. u. isaurae* in western Panama (Eisenmann and Howell, 1962).¹

Pteroglossus torquatus torquatus AND *Pteroglossus (torquatus) sanguineus*

The Collared Araçari (*Pteroglossus torquatus*) of Central America and northwestern South America is replaced in the Pacific lowlands of Colombia by the Stripe-billed Araçari (*P. sanguineus*). On the basis of marked differences in the coloration of the bill and hind neck, both forms were considered to be specifically distinct. However, they had never been found living in the same area. For this reason I collected material and made observations in the Urabá region, where they meet, to find out their relationship and taxonomic status.

¹ The distribution and interrelationship of *Crax rubra* and *C. alberti*, *Pipra mentalis* and *P. erythrocephala*, *Rhynchocyclus brevirostris* and *R. olivaceus* are discussed in a separate article (Haffer, in press, c). The allies of these pairs probably have reached species status and replace each other geographically on account of ecologic competition.

Both forms are similar in habits and coloration (fig. 10). *Sanguineus* is only slightly larger, and differs from *torquatus* in having a yellow tip to the bill, a black stripe along the upper mandible, and in lacking a chestnut band across the hind neck, which is characteristic of *torquatus*. The bill of the latter has a black tip and no black stripe. The neck band of *torquatus* from northern Colombia is light chestnut in males and dark maroon in females. Both "species" can be observed in the early morning

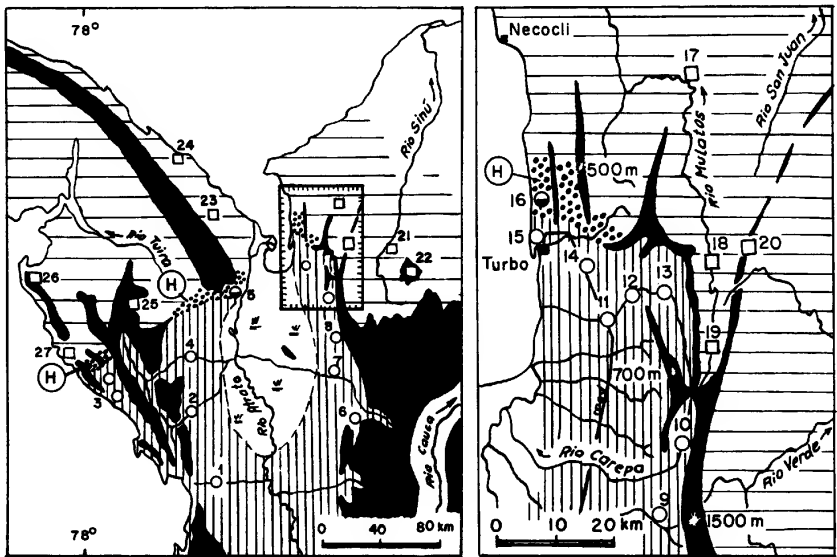


FIG. 7. Distribution of *Pteroglossus torquatus* and *Pteroglossus (torquatus) sanguineus* in the Urabá region, northwestern Colombia. Elevations over 300 meters are in black. The framed area east of the Gulf of Urabá is shown in more detail in the right-hand map. See text for numbered localities.

Key: Horizontal lines and quadrangles, *Pteroglossus torquatus torquatus*; vertical lines and circles, *Pteroglossus (torquatus) sanguineus*; heavy dots, hybrid zone (H).

and late afternoon in small groups of from five to 20 individuals along the river valleys in forested regions. Skutch (1958) described the habits of *P. torquatus* and of *P. (torquatus) frantzii*, a form closely allied to *P. torquatus* restricted to the Pacific coast of Costa Rica and western Panamá, which possesses a differently colored bill.

The distribution, as mapped in figure 7, is as follows:

EAST OF THE GULF OF URABÁ: The area of the upper Rio Sinú is inhabited by *torquatus* (de Schauensee, 1950). To the west I have collected 17 specimens of this form in the valley of the Rio Mulatos. These birds are typical for *torquatus*; they have the tip of the bill black and no stripe

on the upper mandible. The light (male) or dark (female) chestnut neck band is seen in all specimens, although narrow and not complete in three adult males. The rather small size of the Mulatos birds is also typical for *torquatus* (10 males: wing, 145.1; tail, 158.2; bill, 99.9 mm.).

Pteroglossus sanguineus inhabits the valleys at the western foot of the Serranía de Abibe (Rio Imamadó, Chigorodó, Carepa) and ranges north to the region of the Rio Currulao, Rio Guadualito, and Turbo (Haffer, 1959).

WEST OF THE GULF OF URABÁ: *Torquatus* is known in eastern Panamá from Cana (Griscom, 1929) and from the Rio Jesusito (Bangs and Barbour, 1922). Wetmore (*in litt.*) has collected typical specimens of this form at Jaqué and Armila. The only bird taken on the Colombian side is from the Rio Tanela (Haffer, 1959). *Sanguineus* is a common bird from about the Panamanian border of Colombia southward.

In more detail (as numbered on the map, fig. 7) the localities from which the two forms have been recorded are as follows:

Pteroglossus (torquatus) sanguineus: 1, Rio Napiquí (commonly observed); 2, Rio Truandó (de Schauensee, 1948-1952); 3, Juradó (one male, Bogotá, de Schauensee, 1948-1952) and upper Rio Juradó between mouth of Rio Jampavadó and Rio Antadó (seven males, five females); 4, Rio Salaquí (de Schauensee, 1948-1952); 5, Sautatá (one male, one male hybrid); 6, Alto Bonito (Chapman, 1917); 7, Pavarandocito (two males, one female); 8, Rio Imamadó (one male, one female); 9, Rio Chigorodó (five females); 10, Rio Carepa, 2 kilometers above mouth of Sucia Creek (five males, four females); 11, Rio Currulao at Turbo road (one male, one female); 12, Rio Currulao, mouth of Tia Lopez Creek (one female); 13, Rio Currulao, mouth of Limón Creek (one male); 14, Rio Guadualito (one male, one female); 15, Turbo (one female).

Hybrid Zone: 5, Sautatá (two males); 16, Rio Cope (11 males, nine females).

Pteroglossus torquatus torquatus: 17, Rio Mulatos, mouth of Umbito Creek (one male); 18, Rio Mulatos, camp II (eight males, four females); 19, Rio Mulatos, camp III (two males, two females); 20, Alto de Quimarí (14 specimens, de Schauensee, 1950); 21, Tierra Alta (three specimens, de Schauensee, 1950); 22, Murucucú (three specimens, de Schauensee, 1950); 23, Rio Tanela (one male, Haffer, 1959); 24, Armila (Wetmore, *in litt.*); 25, Cana (Griscom, 1929); 26, Rio Jesusito (Bangs and Barbour, 1922); 27, Jaqué (Wetmore, *in litt.*).

HYBRIDIZATION

While mapping the ranges of both strictly allopatric forms in the Urabá area, I found a hybrid population at the middle course of the small Cope River 8 kilometers north of Turbo in April, 1964 (fig. 7, 16). I collected 20 specimens (11 males, nine females) of this population in the immediate surroundings of our camp. These birds represent every conceivable stage between the *torquatus* and *sanguineus* extremes and show beyond doubt that both forms hybridize freely where they meet.

To facilitate the color analysis of the hybrids the hybrid-index system was applied. This method has been used frequently in recent years (Sibley and Short, 1959, 1964; Sibley and Sibley, 1964; Short, 1965) and requires no further description.

The index values for color characters of *Pteroglossus* forms are as follows:

Band across hind neck

- 0, missing, as from *sanguineus*
- 1, barely indicated
- 2, half developed
- 3, almost complete
- 4, complete, as in *torquatus*

Stripe along upper mandible

- 0, complete, as in *sanguineus*
- 1, almost complete
- 2, half developed
- 3, weakly developed
- 4, missing, as from *torquatus*

Tip of upper mandible

- 0, yellow, as in *sanguineus*
- 1, pale yellow
- 2, mixed yellowish and blackish
- 3, blackish
- 4, black, as in *torquatus*

The values for these characters are determined and totaled to give the hybrid index of each hybrid specimen. Pure *torquatus* specimens have the value 12, hybrids have indices of from 1 to 11, and pure *sanguineus* specimens have the value 0.

The histogram of the hybrid indices (fig. 8) shows the intermediate position of the Rio Cope population between *torquatus* and *sanguineus*. It bridges the morphological gap between these forms almost completely. In total it is slightly closer to *sanguineus*, since the mean hybrid index is only 4.7 and the measurements also agree with those of the larger Chocó form (table 5). In each character every stage between the *torquatus* and *sanguineus* extremes and every conceivable combination of these character stages are represented in the hybrid series. There are specimens with an almost pure bill of *torquatus* but without any indication of the chestnut band across the hind neck. Other specimens display a combination of an almost complete chestnut band with the pure bill of *sanguineus*. These numerous intermediate types indicate that the hybrids are fertile and that free crossing and backcrossing occur. It should be noted that pure parental types are lacking in the sample obtained.

TABLE 5
MEASUREMENTS OF *Pteroglossus* FORMS FROM NORTHWESTERN SOUTH AMERICA

	<i>N</i>	Wing Range (Mean \pm σ_m)	σ	<i>N</i>	Tail Range (Mean \pm σ_m)	σ	<i>N</i>	Bill Range (Mean \pm σ_m)	σ
<i>P. torquatus torquatus</i>									
Males	13	141-157 (147.7 \pm 1.35)	4.66	12	147-169 (159.0 \pm 2.07)	6.89	13	97-110 (102.6 \pm 1.3)	4.65
Females	5	147-152 (149.4)		5	157-173 (164.0)		5	95-101 (98.6)	
<i>P. (t.) sanguineus</i>									
Males	19	143-156 (151.5 \pm 0.88)	3.85	15	157-175 (166.3 \pm 1.77)	6.57	19	103-120 (111.5 \pm 0.94)	5.14
Females	19	143-157 (151.4 \pm 0.78)	3.42	16	154-172 (162.5 \pm 1.14)	4.55	19	95-113 (104.1 \pm 1.1)	4.37
<i>P. t. torquatus</i> \times <i>P. (t.) sanguineus</i> ,									
Rio Cope	11	145-157 (150.9 \pm 1.26)	3.78	11	160-178 (168.7 \pm 1.97)	5.9	10	108-120 (112.6 \pm 1.28)	3.61
Males									
Females	9	144-151 (148.6 \pm 0.77)	2.31	8	151-173 (163.2 \pm 2.42)	6.85	9	97-115 (103.3 \pm 1.9)	5.72
<i>P. pluricinctus</i>									
Males	6	149-159 (153.8)		6	158-181 (166.6)		6	105-130 (114.6)	
Females	5	150-157 (154.2)		5	154-172 (163.2)		5	102-111 (107.5)	
<i>P. castanotis</i>									
Males	8	157-170 (162.4)		8	146.5-161 (154.4)		8	114-130 (118.7)	

OCCURRENCE OF A HYBRID ZONE

Figure 7

A hybrid population was developed only when a *sanguineus* population and a *torquatus* population met without any orographic barrier. Contrary to my expectation, relatively low mountain ranges of from 300 to 500 meters in elevation prevent virtually any gene flow.

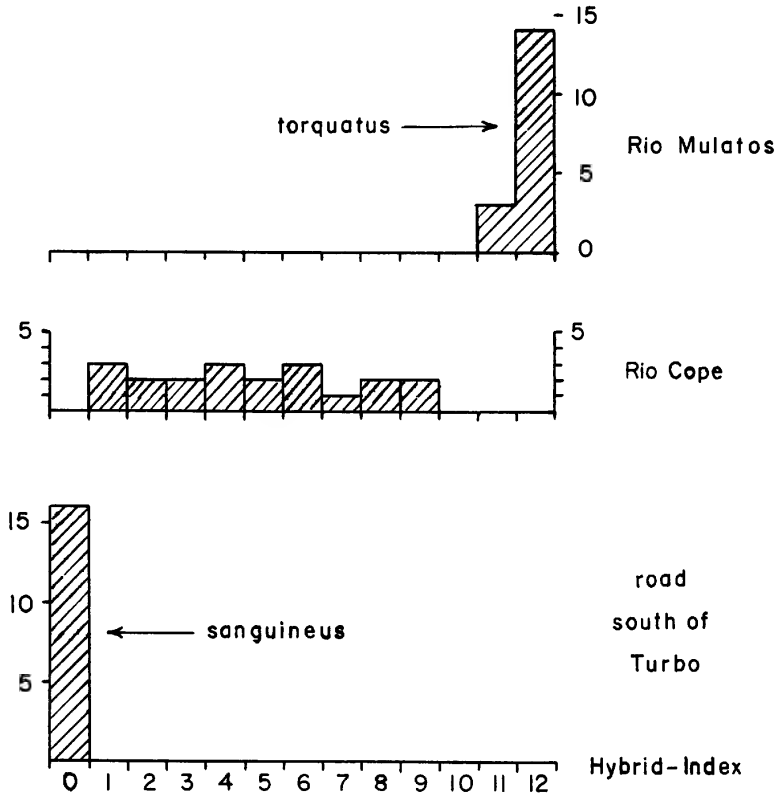


FIG. 8. Histogram of the hybrid indices of the Rio Cope population of *Pteroglossus*. Number of specimens is indicated at left and right, respectively.

EAST OF THE GULF OF URABÁ: The boundary of the ranges of both forms in this region is the divide of the rivers flowing west toward the Gulf and north to the Caribbean Sea, respectively. The watershed is formed in this area by chains of narrow, steep mountains that range in elevation from 300 to 700 meters. Acting as a highly effective barrier, they apparently prevent any visible gene flow, shown by the spatial proximity of a pure *sanguineus* population in the upper Carepa and Cur-

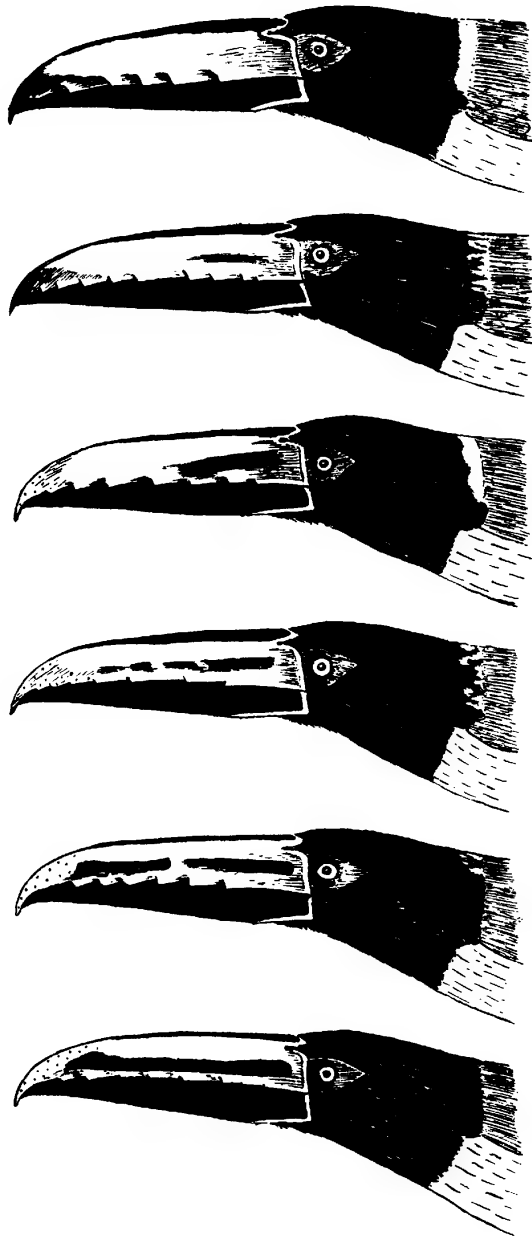


FIG. 9. *Pteroglossus torquatus torquatus* (top figure) and *Pteroglossus (torquatus) sanguineus* (bottom figure), with four hybrids from the Rio Cope (H-0281, 0280, 0271, 0270). Observe, from top to bottom, the disappearance of the chestnut collar across the hind neck; the replacement of the black tip of the bill by a yellow one; the development of a black stripe along the upper mandible; and the blackening of the red skin in front of the eye.

rulao valleys and of a pure *torquatus* population in the neighbouring Mulatos Valley far up the headwaters. The lack of hybridization in this area has no biological implications and may be entirely due to isolation by the mountains. The whole region is uniformly covered with "Moist Tropical Forest" (Espinal and Montenegro, 1963) that has been cleared around Turbo and along some of the major rivers. In three *torquatus* specimens of a total of 12 collected at camp II on the Rio Mulatos, the chestnut band across the hind neck is not quite completely developed. This fact may indicate a slight introgression of some *sanguineus* genes of the Currulao population across the divide which is here rather low; however, this must be confirmed by more material from this area.

Pteroglossus torquatus met the northward-advancing *sanguineus* just north of Turbo. The hybridization of both populations was not impeded in this area by the north-south mountain chains. Here both forms met in the intervening valleys and hybridized freely. Besides the Rio Cope area, further intergradation of these Araçari toucans probably takes place in the valleys of the Los Indios Creek and Turbo River. Unfortunately I did not find either form on a three-day trip along the Rio Turbo.

WEST OF THE GULF OF URABÁ: One of the two adult males that I collected at Sautatá on the lower Atrato River in 1959 is a hybrid with the hybrid index of 4. In this specimen the stripe of the upper mandible is only weakly developed and the tip of the bill is very pale yellow; there is no indication of a neck band. Another hybrid specimen was collected "near Juradó" and was mentioned by de Schauensee (1950) under *torquatus*. In this female, the "bill shows a rudimentary black stripe on the side of the upper mandible" (de Schauensee, *in litt.*). Probably it was collected some distance north of the village of Juradó in the headwaters of the Rio Jampavadó or Rio Juradó where both forms meet. All 12 specimens (seven males, five females) that I collected near the mouth of the Rio Jampavadó (at the Rio Juradó) in March, 1965, are pure *sanguineus*, as is a single male from "Juradó" in the Bogotá collections (collector K. von Sneidern, 1949). As well as the secondary intergradation of both forms in the upper Rio Juradó and in the Sautatá area, other small and restricted hybrid populations are probably to be found in the headwaters of the Tuirá River along the Panamanian/Colombian boundary.

A very narrow hybrid zone is indicated by the highly variable Rio Cope population and by the abrupt transition into a pure *sanguineus* population along the Turbo road. Probably the width is less than 20 kilometers.

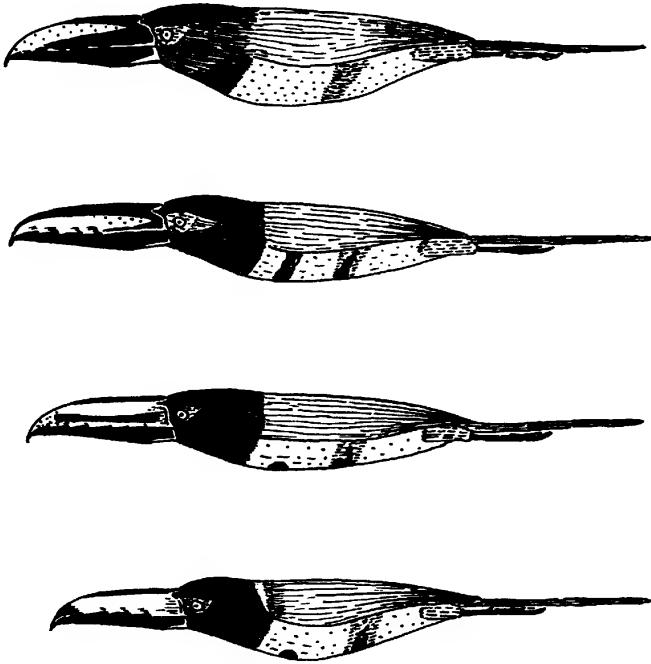


FIG. 10. Forms of *Pteroglossus* from northwestern South America. From top to bottom: *Pteroglossus castanotis*, *P. pluricinctus*, *P. (torquatus) sanguineus*, and *P. torquatus*.

CONCLUSIONS

1. No sufficient sexual isolating mechanisms have been developed during the geographic separation in Caribbean Central America (*torquatus*) and in the Chocó Refuge (*sanguineus*) to prevent free interbreeding of both forms where they meet today.

2. The occurrence of a hybrid zone is not correlated with ecological factors but depends strongly on orographic conditions.

3. The forms *sanguineus* and *frantzii*¹ are considered as semispecies within the species unit *Pteroglossus torquatus*.

4. The trans-Andean species *Pteroglossus torquatus* is subdivided in the following manner:

torquatus group: *Pteroglossus torquatus erythrozonus*, *Pteroglossus torquatus torquatus*, and *Pteroglossus torquatus nuchalis*

¹ This form of the Pacific slope of southern Central America probably meets *torquatus* in the Aguacate Mountains of Costa Rica (Slud, 1964).

frantzii group: *Pteroglossus (torquatus) frantzii*

sanguineus group: *Pteroglossus (torquatus) sanguineus* and *Pteroglossus (torquatus) erythropygus*

THE *Pteroglossus pluricinctus* SUPERSPECIES

Pteroglossus torquatus is the only trans-Andean member of the Amazonian genus *Pteroglossus* that ranges northward to Mexico and eastward to northern Venezuela. Its nearest cis-Andean representative is *Pteroglossus pluricinctus* which has a whitish upper mandible, black head, throat,

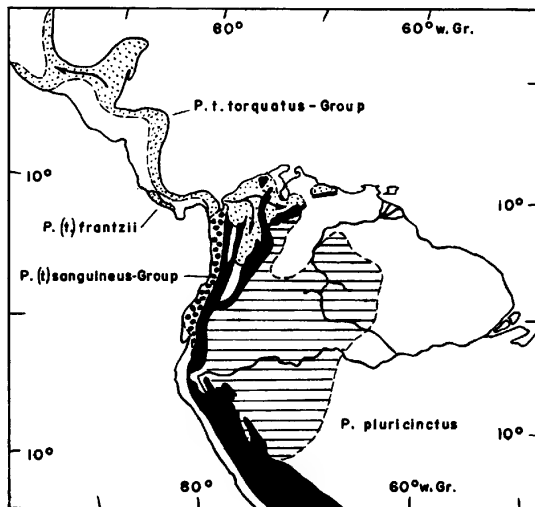


FIG. 11. Distribution of the *Pteroglossus pluricinctus* superspecies.

and breast, and a mixed black and red band across the upper abdomen; it is also similar in size and proportions (table 5). *Pteroglossus castanotis* is more distantly related, as shown by its different coloration and proportions (fig. 10). It seems justifiable to combine *Pteroglossus pluricinctus* and the trans-Andean forms of *Pteroglossus torquatus* into one superspecies. Both species approach each other closely in western Venezuela but remain separated by the dry area around Barquisimeto. *Pteroglossus torquatus* possibly originated from proto-*pluricinctus* stock that advanced into the trans-Andean region during one of the early humid periods and was isolated later in the Caribbean Central American Refuges (*torquatus*), in the Chiriquí Refuge (*frantzii*), and in the Chocó Refuge (*sanguineus*), respectively.

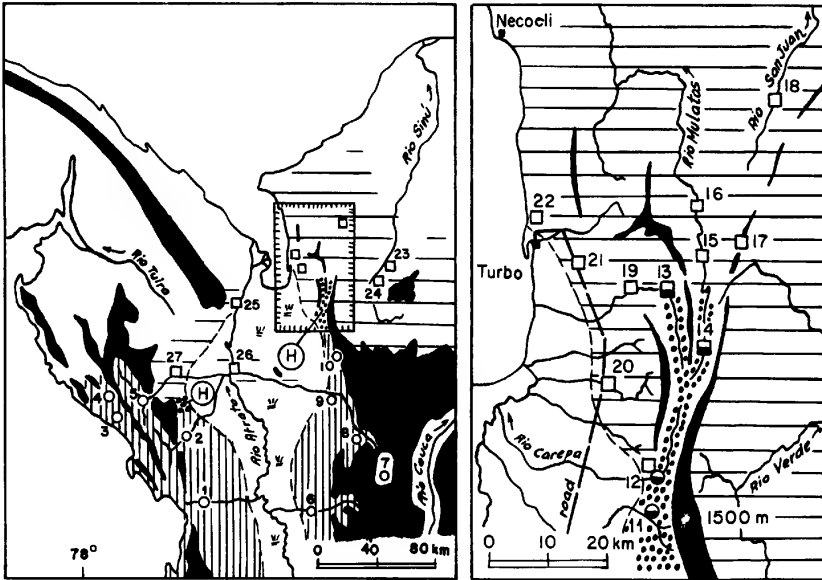


FIG. 12. Distribution of *Galbula ruficauda ruficauda* and *Galbula (ruficauda) melanogenia* in the Urabá region, northwestern Colombia. Elevations over 400 meters are in black. The framed area east of the Gulf of Urabá is shown in more detail in the right-hand map. See text for numbered localities.

Key: *Galbula r. ruficauda*, hatched horizontally and quadrangles; *Galbula (r.) melanogenia*, hatched vertically and circles; hybrid zones (H), dotted.

Galbula ruficauda ruficauda AND *Galbula (ruficauda) melanogenia*

The Rufous-tailed Jacamar (*Galbula ruficauda*) is a common neotropical bird that ranges from southern Brazil to Mexico. The trans-Andean form *melanogenia* inhabits tropical Middle America (except El Salvador) to western Panamá (Eisenmann, 1955) and the Pacific lowlands of Colombia and northern Ecuador. A peculiar hiatus in its range occurs throughout eastern and central Panamá where no individual of *Galbula* has ever been found (Griscom, 1935; Wetmore, *in litt.*; Eisenmann, *in litt.*).

The distribution in northwestern Colombia is mapped in figure 12, and the detailed records coincide with the numbers on the map, as follows:

Galbula (ruficauda) melanogenia: 1, Upper Rio Napipí (four males, one female); 2, Rio Truandó (five males, three females); 3, Juradó (de Schauensee, 1948-1952); 4, upper Rio Juradó (one male); 5, upper Rio Salaquí at mouth of Rio Jurachirá (one male, one female); 6, Rio Murri (1 female); 7, Frontino (T. K. Salmon collected a specimen of *Galbula* at this locality during the last century, which is cited in the literature under *ruficauda*; however, the Sucio Valley has

TABLE 6
 COLOR DIFFERENCES OF THE TRANS-ANDEAN AND
 CIS-ANDEAN FORMS OF *Galbula ruficauda*

	<i>G. (r.) melanogenia</i>	<i>G. r. ruficauda</i>
Throat	Clear white, chin dusky	White tinged with buffy, especially toward chin
Tail	First and second pair green, rest rufous	First pair green, second pair rufous, with only basal part of outer vane green, rest rufous
Tail and bill	Relatively short	Relatively long

access only to the Atrato plains inhabited by *melanogenia*, so the bird is almost surely *melanogenia*; 8, Alto Bonito (Chapman, 1917); 9, Pavarandocito (one male); 10, Rio Imamadó (one male).

Hybrid Zone (H): 11, Rio Chigorodó (one male, one female, one female juvenile); 12, Rio Carepa, 1 kilometer above mouth of Piedras Blancas Creek (one male, one female); 13, upper Rio Currulao, at mouth of Ahullamita Creek (one male); 14, Rio Mulatos, camp III (two males, two females).

Galbula ruficauda ruficauda: 15, Rio Mulatos, camp II (four males, two females); 16, Rio Mulatos, camp I (four males, five females); 17, Alto de Quimarí (four males, three females, de Schauensee, 1950); 18, Rio San Juan (two females); 19, Rio Currulao at mouth of Tia Lopez Creek (two males, two females); 20, Rio Apartadó (three males, one female); 21, Rio Guadualito (two males, three females); 22, Rio Cope (two males, one female); 23, Tierra Alta (one male, one female, de Schauensee, 1950); 24, Frasuquillo (one female); 25, Sautatá (one male, one female); 26, Riosucio (two males, 1 female juvenile); 27, Rio Salaquí (one male).

During the last century *ruficauda* has been reported from the Rio Nercua, the northern headwater of the Rio Truandó (Cassin, 1860). This determination seems doubtful, however, since I have collected *melanogenia* along the Rio Truandó and at the upper Rio Salaquí to the north of the Nercua River. Unfortunately Cassin's Nercua specimen cannot be found in the collections of the Academy of Natural Sciences of Philadelphia (de Schauensee, *in litt.*; see also Haffer, *in press*, a, for a discussion of this record and other doubtful ones from the lower Atrato Valley).

The ecological requirements of *G. r. ruficauda* and *melanogenia* are similar, although minor differences are noted. They live along shaded rivers and creeks in the tropical lowlands and nest in long tunnels which they excavate in soft banks (see the excellent life-history study by Skutch, 1963). *Melanogenia* requires a very humid climate in the Chocó region

TABLE 7
MEASUREMENTS OF *Galbula ruficauda ruficauda* AND *Galbula (r.) melanogenia* FROM THE URABÁ REGION

	<i>N</i>	Wing Range (Mean \pm σ_m)	σ	<i>N</i>	Tail Range (Mean \pm σ_m)	σ	<i>N</i>	Bill Range (Mean \pm σ_m)	σ
<i>G. (r.) melanogenia</i>									
Males	17	77.0-84.0 (81.1 \pm 0.45)	1.86	13	88.5-99.0 (94.3 \pm 0.87)	3.14	17	41.0-49.0 (45.5 \pm 0.58)	2.4
Females	6	78.5-84.0 (81.0)		6	87.0-97.0 (90.6)		5	43.0-45.5 (44.1)	
<i>G. r. ruficauda</i>									
Males	22	81.0-86.0 (82.8 \pm 0.3)	1.42	18	105.0-117.5 (110.0 \pm 0.73)	3.21	15	49.0-57.5 (52.7 \pm 0.67)	2.59
Females	16	79.0-85.0 (81.5 \pm 0.45)	1.79	15	97.0-110.0 (101.4 \pm 0.97)	3.78	12	46.0-53.0 (48.2 \pm 0.51)	1.75

and avoids the area with less than 3500 mm. of rainfall per year at the Gulf of Urabá. It is more confined to forest streams than *ruficauda*, occupying the overgrown forest border along the riverbanks and disappearing from an area once the forest has been cut. On the other hand, *ruficauda* is commonly found in secondary growth of *Calathaea* and bamboo in much-deforested and rather densely inhabited regions with less excessive rainfall. This ecologic difference is also apparent from the regional distribution pattern of *ruficauda*, which avoids the humid center of the Amazonian forest region. However, in Central America *melanogenia* apparently also inhabits second growth in only partially wooded areas (Slud, 1964).

HYBRIDIZATION

Long series of *ruficauda* (40 specimens) and *melanogenia* (21 specimens) from the Urabá region show that both forms differ in coloration and size consistently. A small and restricted hybrid population was found only in a few valleys southeast of Turbo. The hybrid specimens collected along the Rio Chigorodó, Carepa, Currulao, and Mulatos are proof of a limited gene flow between the two forms.

RIO CHIGORODÓ: One male (wing, 82; tail, 99; bill, 46.2 mm.), one female (wing, 82; tail, 89.5; bill, 44.5 mm.), one female juvenile. Measurements and color of chin and throat are typical for *melanogenia*. However, the inner vane of the second right tail feather of the male is extensively rufous, and the left second tail feather shows a rufous shaft streak. Also in the female a narrow rufous shaft streak is seen in the second pair of the tail feathers. This partial rufous coloring of the shiny green second tail feathers was never observed in any pure *melanogenia* specimen and suggests a definite introgression of *ruficauda* genes. The juvenile bird has a black chin and four of the central tail feathers are green; these are growing and are still too short (about 15 mm. long) to be checked for hybrid characters.

RIO CAREPA: One male (wing, 83; tail, 114; bill, 49 mm.), one female (wing, 79.5; tail, 91.5; bill, 45 mm.). This pair was apparently mated; it was collected near the mouth of the Piedras Blancas Creek. It is interesting to note that the female is *melanogenia* (the inconspicuous black chin may show a slight *ruficauda* influence), whereas the male phenotypically is a pure *ruficauda* with a few dark tips to the chin feathers. This bird apparently belongs to the *ruficauda* population inhabiting the rivers to the northwest of the Carepa locality. Unfortunately I did not find any jacamars in the north-south upper Carepa Valley, the original *Galbula* population of which was probably closer to *melano-*

genia. This genus must have left the area when the valley floor was deforested some 10 years ago.

UPPER RIO CURRULAO AT MOUTH OF AHULLAMITA CREEK: One male (wing, 80; tail, 102; bill, 48 mm.). In coloration of tail and in measurements this bird is intermediate; the color of chin and throat is of the *ruficauda* type. The rufous second tail feathers are extensively shiny green on the outer vane and on the distal portion of the inner vane. This specimen indicates that the population of the upper Currulao south of the mouth of Ahullamita Creek is intermediate between both forms.

UPPER RIO MULATOS, CAMP III: Two males (wing, 84, 82; bill, 50.5 mm.), two females (wing, 78.5, 77; tail, 100, 94; bill, 47 mm.). In coloration these birds are close to *ruficauda*; however, the chin is slightly dusky and the measurements are intermediate.

"QUIMARÍ": A female of *melanogenia* (wing, 78.5; tail, 95.5; bill, 44.5 mm.) labeled "Quimarí" is included in the collections of the Instituto de Ciencias Naturales, Bogotá (No. 8461). It shows a slight *ruficauda* influence by a weakly pronounced, dusky chin color. Mt. Quimarí is situated due east of Turbo and is less than 600 meters high. Seven *ruficauda* specimens have been reported from this locality by de Schauensee (1950). These were collected by hunters of von Sneider, probably in the general area of "Quimarí." The above female belonged to the same von Sneider collection and was presumably taken some distance south of Quimarí in the hybrid zone between *ruficauda* and *melanogenia*.

The hybrid populations southeast of Turbo occupy a very narrow area of approximately 40 kilometers from north to south comprising the valleys of the upper Chigorodó, Carepa, Mulatos, and Currulao rivers. The Serranía de Pavo (700 meters in elevation) just west of the Currulao and Carepa headwaters prevents any *melanogenia* influence on the pure *ruficauda* population along the Turbo road.

In the lower Atrato region pure *ruficauda* specimens have been taken at three different localities (Sautatá, Riosucio, lower Rio Salaquí). A very local hybrid zone may be found between the lower Salaquí and Truandó rivers. The birds taken along the upper Salaquí are pure *melanogenia*. This population is separated from *ruficauda* at the lower Salaquí by the steep and rugged Serranía de los Saltos and the narrow rocky canyon of the Salaquí River itself; probably no gene flow occurs along this river valley.

CONCLUSIONS

The northern limit of the range of *melanogenia* in the Chocó region more or less coincides with the 3500-mm. isohyet. It is here that *ruficauda*

hybridizes with the trans-Andean bird, forming very restricted and variable hybrid populations. For this reason *melanogenia* should be considered as a semispecies within the species unit *Galbula ruficauda* which is subdivided taxonomically as follows:

ruficauda group: *Galbula ruficauda ruficauda*, *Galbula ruficauda brevirostris*, and *Galbula ruficauda pallens*

melanogenia group: *Galbula (ruficauda) melanogenia*

rufoviridis group: *Galbula (ruficauda) rufoviridis* and *Galbula (ruficauda) heterogyna*

The range of the trans-Andean form *melanogenia* was presumably interrupted in Panamá and in the northern Chocó region during a period of drought in the recent past. Upon the return of more humid climatic conditions this gap was only partly closed, for our bird has never been taken in central or eastern Panamá (Griscom, 1935; Wetmore, *in litt.*). At the same time the Amazonian form occupied northern Colombia and the area around the Gulf of Urabá, which was left uninhabited by *melanogenia* because of ecological reasons.

DISCUSSION

The zones of allopatric hybridization at the northern margin of the former Chocó Refuge are characterized by very narrow width, great age, and an ecologically quite uniform environment.

THE NARROW WIDTH: On the basis of the data known in *Pteroglossus* and *Galbula* the hybrid zones are not broader than 20 to 40 kilometers. It must be assumed that hybrids are strongly selected against within the range of each ally. Possibly the small regional extent of the contact zones prevents, in these cases, widespread swamping despite the lack of isolating mechanisms (Short, 1965, p. 419).

THE GREAT AGE: The hybridization in the Urabá area was caused by natural range extensions of the allies, which occurred at least several thousand years ago. It has not been effectively influenced by any human activity in this region during the last few centuries.

THE ENVIRONMENT: A conspicuous climatic gradient is noted in the Urabá region by the increase of rainfall as one goes south. However, this gradient is not steep enough to account for the abrupt geographic replacement of the birds studied. Only the northern limit in the Chocó region of the range of *Galbula (r.) melanogenia* may also correspond with the ecologic limit of this population. *Galbula r. ruficauda*, as well as the *Pteroglossus* and *Manacus* forms, very probably would occupy at least part of the ally's range were it not for its presence across the zone of contact. The *Pteroglossus* and *Manacus* forms hybridize where they met on the re-

turn of sufficient forest growth in northern Colombia. In these cases the position of the hybrid zones changed probably very little since the time the allies came in contact. In other cases the shifting of the hybrid zone may have been more pronounced to achieve the present ecologically balanced situation.

It seems probable that similar cases of hybridization will be found when the contact zone of other "species" pairs are studied in more detail. The above examples show that large series from the critical area of geographic replacement and extensive field experience are needed for a correct evaluation of the relationship of closely related allopatric forms.

The hybridizations of the Urabá region appear to be comparable to the situation in the Carrion Crow (*Corvus corone*) of western Europe (Meise, 1928). They differ greatly, however, from those cases of narrow hybrid zones that are found along sharp ecological breaks such as rain forest and savanna (for examples, see Mayr, 1963). On the other hand, certain broad hybrid zones studied in the central part of the United States, in Mexico, and west of Cali, Colombia, by Sibley (Sibley and Short, 1959, 1964; Sibley and Sibley, 1964; Sibley, 1958) seem largely due to the recent activity of man, who provided artificial pathways for the dispersal of previously isolated, closely allied forms.

In a recent paper Bigelow (1965) criticized the emphasis on interbreeding in Mayr's species definition as opposed to "reproductive isolation," and redefined that term. Bigelow's modified species definition (which is intended to turn on the extent of gene flow) led him to consider as "good species" some forms that Mayr (1963) called "semispecies," or "subspecies" of a single species. If we followed Bigelow, the forms of *Pteroglossus* and *Galbula* here discussed would have to be considered as "reproductively isolated" entities (=species) because of the very narrow width of the hybrid zone. Unfortunately Bigelow did not discuss "semi-species," a very useful concept, which includes all transitional cases between two closely allied populations that are neither good sympatric species nor broadly intergrading subspecies. I feel that essentially allopatric forms that hybridize freely, even along a narrow zone only, should be distinguished nomenclaturally from good species living side by side. The semispecies concept of Mayr (1940), as subsequently emended by Lorković (1958), appears to serve this purpose very well.

MULTIPLE INVASIONS INTO THE TRANS-ANDEAN REGION

Owing to the fact that the cis- and trans-Andean forests became re-

peatedly connected during several humid periods, in a few cases the same Amazonian species was able to advance more than once into the lowlands west of the Andes. Such an advance led to the sympatric occurrence of the two consecutive invasions, if the first had already developed a sufficient number of sexual isolating mechanisms. The importance of multiple invasions for speciation, especially on islands and isolated mountain massifs, has been known for a long time (Stresemann, 1927-1934; Mayr, 1942, 1963).

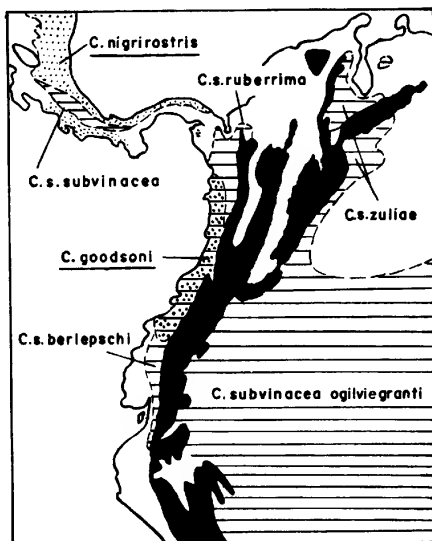


FIG. 13. Distribution of the *Columba (Oenoenas) subvinacea* species group. Recently the author has collected *C. goodsoni* at the northern end of the Western Andes, southeast of the Gulf of Urabá.

DOUBLE INVASIONS

PIGEONS OF THE *Columba (Oenoenas)* SPECIES GROUP

Figure 13

The *Oenoenas* group has been treated as a subgenus of *Columba* but was recently given generic status by Johnston (1962). *Oenoenas plumbea* and *Oenoenas subvinacea* are distributed over large areas of tropical South America. Only the latter form advances northward into the highlands of Costa Rica. *Oenoenas nigrirostris* and *Oenoenas goodsoni* are members of a superspecies and occupy small peripheral areas in Central America and western Colombia, respectively. Both are believed to be closer to *Oenoenas subvinacea* than to *Oenoenas plumbea*, mainly on the basis of the general body color and the cinnamon inner vanes of the primaries. A first invasion of proto-*subvinacea* led to the establishment of populations in Caribbean Central America and in western Colombia; here they were isolated

during the following periods of drought and were differentiated as *Oenoenas nigrirostris* and *Oenoenas goodsoni*, respectively. A second invasion of *subvinacea* made it sympatric with *Oenoenas goodsoni* in western Colombia (*Oenoenas s. berlepschi*); in Central America it occupied the higher mountain zones (*Oenoenas s. subvinacea*), thus being separated altitudinally from

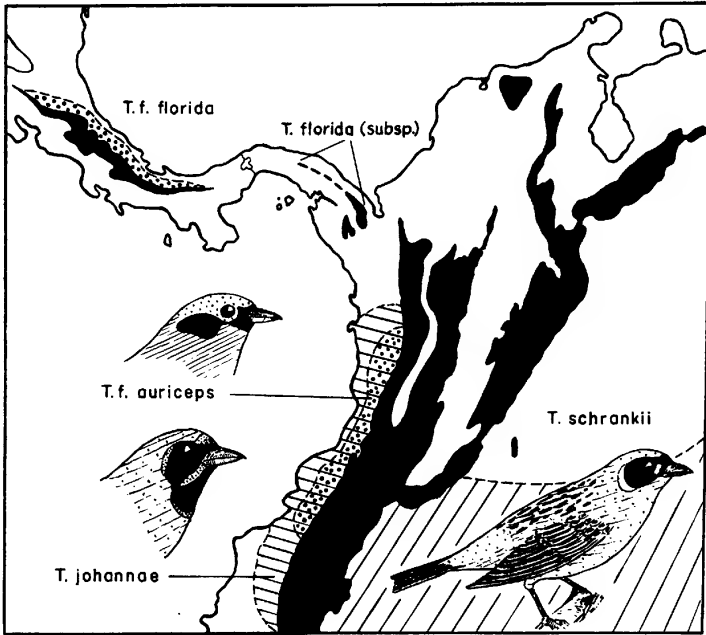


FIG. 14. Distribution of the *Tangara schrankii* species group. Recently the author has collected *T. johannae* at the northern end of the Western Andes, southeast of the Gulf of Urabá.

Plumage color key: Hatched, light emerald green; hatched and dotted, light gold-green; sparsely dotted, yellow; densely dotted, blue; solid, black.

the lowland species *Oenoenas nigrirostris*. It is of interest to note that the populations of both trans-Andean invasions deviate in the same manner from the Amazonian parent form: *Oenoenas goodsoni* and *Oenoenas subvinacea berlepschi* are smaller and lighter colored than the cis-Andean representatives, the latter form showing these characters less pronounced, because of the shorter period of isolation.

Tangara schrankii SPECIES GROUP

Figure 14

The trans-Andean representative of the Amazonian *Tangara schrankii*

is *Tangara florida*,¹ which is restricted essentially to the area of the former Caribbean Costa Rica Refuge and the Chocó Refuge. Eisenmann (*in litt.*) informs me that a population morphologically intermediate between *T. f. florida* and *T. f. auriceps*, but nearer to the latter, occurs on the Serranía del Darién in eastern Panamá, west to Cerro Azul, not far east of the Canal Zone. Hellmayr (1936) doubted that *T. schrankii* and *T. florida* are even specifically distinct. Another trans-Andean bird of this species group is *Tangara johannae*, the body coloration of which is very close to that of *T. schrankii*. The pattern of the head color, however, differs considerably from that of its relatives. It is assumed that *T. johannae* represents an earlier invasion of the same proto-*schrankii* stock and today is sympatric with the younger arrival *T. florida auriceps* in part of its range.

TRIPLE INVASION

THE *Trogon melanurus* SPECIES GROUP

Figure 15

In this group of closely related forms we count several trans-Andean species but only one (*T. melanurus*) in the Amazonian region. It seems possible that all trans-Andean forms originated from the same cis-Andean stock by three consecutive invasions.

The oldest and most restricted trans-Andean forms are *T. clathratus* and *T. comptus* of Caribbean Central America and western Colombia, respectively. These forms appear to be specifically distinct from each other and possibly represent the first trans-Andean invasion of proto-*melanurus*. Although *T. clathratus* today is still restricted to Caribbean Costa Rica and western Panamá (Caribbean Costa Rica Refuge), *T. comptus* has subsequently extended its range from the Chocó Refuge to include also the northern slope of the Western and Central Cordillera of Colombia.

Trogon massena, which may represent the second invasion of proto-*melanurus* stock, lives side by side with *T. clathratus* and *T. comptus* at the present time. The Central American (*T. m. massena*) and west Colombian (*T. m. australis*) populations are separated geographically by a gap in the Atrato region. Both are morphologically very close and are best considered still conspecific.

During a third, evidently rather recent, invasion, the cis-Andean population occupied northern Colombia, and part of it was isolated in the

¹*Tangara schrankii anchicayae* is a synonym of *Tangara florida auriceps*, as will be shown by Lehmann in a forthcoming publication.

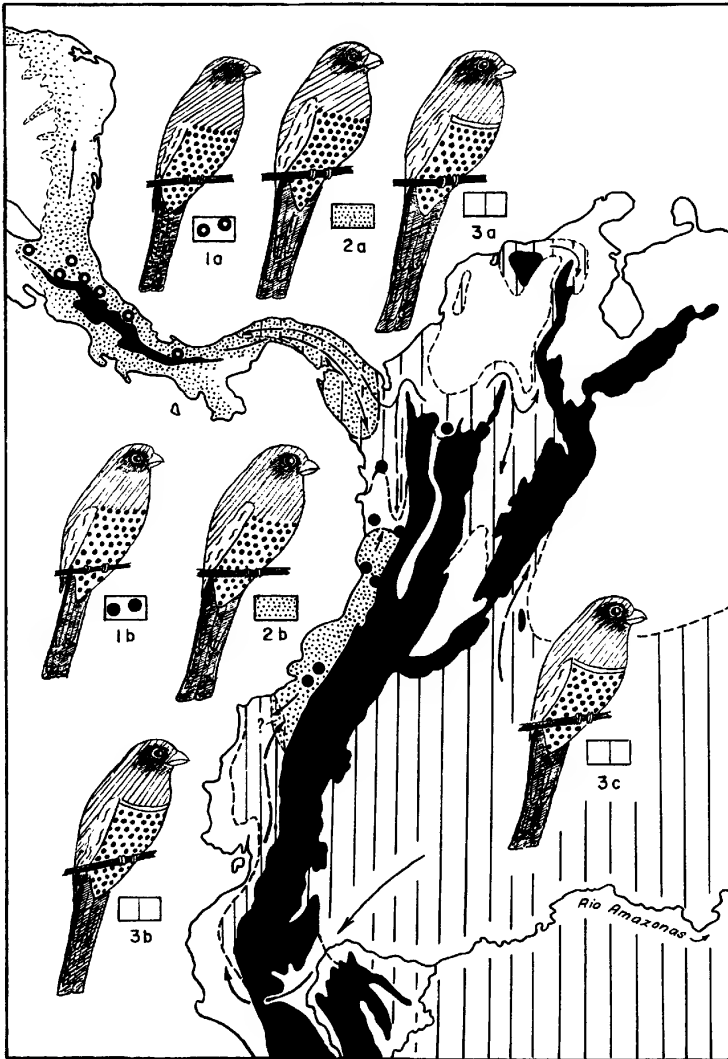


FIG. 15. Distribution and speciation of the *Trogon melanurus* species group. Several trans-Andean species originated from one Amazonian parent species by three consecutive invasions: First: 1a, *Trogon clathratus*; 1b, *T. comptus*. Second: 2a, *T. massena massena*; 2b, *T. m. australis*. Third: 3a, *T. melanurus macroura*; 3b, *T. m. mesurus*; 3c, *T. m. melanurus*.

Plumage color key: Dotted, red; broadly hatched, green; wavy lines, vermiculated black and white; narrowly hatched, wholly slaty or blackish (except 1a).

Nechí Refuge. It was here differentiated as *T. m. macroura*, a form that should be treated as conspecific with the cis-Andean *T. melanurus*. *Trogon*

TABLE 8
COMPARISON OF CIS-ANDEAN AND
TRANS-ANDEAN FOREST FAUNAS

	Number of Species in Southeast Colombia (Amazonian Forest)	Number of Trans- Andean Species ^a
Tinamidae	9	5 (1+1+3)
Cracidae	10	7 (7+0+0)
Galbulidae	12	3 (1+1+1)
Bucconidae	14	10 (5+2+3)
Ramphastidae	8	4 (4+0+0)
Formicariidae	74	35 (17+5+13)
Pipridae	13	11 (4+2+5)
Cotingidae	23	13 (7+1+5)

^a The three columns in the parentheses indicate (1) those that are specifically distinct, (2) those that are represented by a subspecifically distinct geographical isolate, and (3) those species that range continuously from east to west.

massena macroura has extended its range into central Panamá (where it is sympatric with *T. massena*) and into western Colombia. In the latter area the contact zone with *T. massena australis* in the upper San Juan Valley is not yet known.

Trogon melanurus has also crossed the Andes in the region of the Porculla pass, northern Perú. The west-Ecuadorian form *T. m. mesurus* still ranges today up into the subtropical zone (Chapman, 1926). It advanced northward along the Pacific coast and met *T. massena australis* near the Colombian boundary. Both forms may here be sympatric.

The above interpretation of the speciation within the *Trogon melanurus* group (subgenus *Curucujus*) is in accord with the current taxonomic treatment of the species involved and helps to solve certain problems as to the status of the west and north Colombian forms. Zimmer (1948) pointed out that the Chocó form *australis* might be specifically distinct from *T. massena* and should possibly be considered conspecific with *T. m. macroura*. However, in my opinion, each of these forms is best considered a member of two consecutive invasions of the same cis-Andean *melanurus* stock.

BRIEF ANALYSIS OF THE CHOCÓ FAUNA

The center of the area occupied by the "Chocó fauna" is the former Chocó Refuge. Today it also includes the forested lowlands of northwestern Ecuador and eastern Panamá. Western Panamá should be in-

cluded in the realm of the "Central American fauna," although it goes without saying that both faunas intermingle, and no fixed boundary can be drawn in the central portion of Panamá.

The fauna of northern Colombia and the humid middle Magdalena Valley is also strongly influenced by the Chocó fauna, but may be kept apart and designated as the "Nechí fauna" (Cauca-Magdalena fauna of Chapman, 1917) on account of several strongly differentiated species confined to this region.

In the following quantitative survey of the Chocó fauna 332 species have been considered (excluding all water and shore birds). One hundred thirty-one species and subspecies (126 + 5, see semitabular summary below), or 40 per cent of the total, are confined to the trans-Andean region. Those forms that are only subspecifically differentiated (35) are isolated by a gap from their cis-Andean relatives. Ninety forms are found in both western Colombia and Central America; of these 31 have isolated populations in the Chocó region and in Central America, and 59 range continuously from western Colombia into Middle America. In the latter group the majority show their derivation from the Chocó Refuge area by a rapidly decreasing abundance northward.

Twenty-two Central American forms have reached at least the northern Chocó area. Five of them have a geographical representative in western Colombia and six in the Amazonian region.

A small group of the Nechí fauna (10) advanced into the northern Chocó (lower Atrato Valley).

Another important element of the Chocó fauna is represented by those species that have reached the Pacific lowlands by crossing the Andes in northern Perú and southern Ecuador. Several of them are confined to the southern part of the Pacific lowlands, others occupied the entire Chocó region, and some even advanced into Central America.

Almost half of the Chocó fauna (43.1%) are "neutral" species. They are continuously distributed from the Amazonian to the trans-Andean lowlands, with no apparent major distributional break in northern Colombia. Since gene flow is not interrupted, only clinal variation is found in this group as one goes from Amazonia to western Colombia.

The composition of the Chocó fauna is in summary as follows:

Trans-Andean forms

Trans-Andean isolates (subspecies differentiation).....	35 (10.6%)
Chocó region only.....	9
Chocó region plus Central America	
Ranges discontinuous.....	2
Ranges continuous.....	24
Trans-Andean species (species differentiation).....	79 (23.8%)

Chocó region only.....	20	
Chocó region plus Central America		
Ranges discontinuous.....	25	
Ranges continuous.....	34	
Trans-Andean genera (genus differentiation).....	12	(3.6%)
Chocó region only.....	5	
Chocó region plus Central America		
Ranges discontinuous.....	5	
Ranges continuous.....	2	
Central American elements advancing into northwestern		
Colombia.....	22	(6.6%)
Without Chocó representative.....	11	
With Chocó representative.....	5	
With cis-Andean representative.....	6	
Nechí elements advancing into northern Chocó region.....	10	(3.0%)
Species reaching trans-Andean lowlands by crossing Andes		
in northern Perú and southern Ecuador.....	31	(9.3%)
Advancing into southern Chocó region.....	5	
Like above but also coming around Andes in north and		
found in northern Chocó region.....	10	
Occupying whole Chocó area and in part advancing		
into Central America.....	16	
“Neutral” species (cis- and trans-Andean populations in		
contact with each other in northern Colombia today).....	143	(43.1%)
Occupying the entire Chocó region.....	95	
Only advancing into the northern Chocó.....	48	
Total number of species.....	332	

The above survey differs sharply from Chapman's interpretation (1926, p. 58), especially by singling out those species and subspecies that are actually restricted to the trans-Andean region and designating as "neutral" those that are continuously distributed from east to west. Moreover, a much smaller percentage of the fauna appears to be of Central American origin. The large Chocó Refuge, with access for the Amazonian fauna from the north via the north Colombian lowlands and from the south across the Andes, has contributed much more to the Central American bird fauna than the other way around.

A comparison of the total numbers of cis-Andean and trans-Andean species within a given family is of particular interest, since the percentage of Amazonian species that reached the Pacific lowlands throws light on the problem of the efficiency of the Andes as a barrier to the cis-Andean birds. A few figures have been assembled in table 8. From these data it is obvious that at least half of the cis-Andean species, and often far more, advanced into the trans-Andean region (exception, the Galbulidae). Again, about 50 per cent of these were specifically differentiated from their cis-Andean parent species. Apparently, then, at least

half of the forest fauna of Colombian upper Amazonia was able to reach the trans-Andean lowlands. The efficiency of the northern Andes as a barrier to bird distribution was considerably reduced during the humid climatic periods of the Pleistocene and post-Pleistocene.

SUMMARY

The main uplift of the Colombian Andes took place at the beginning of the Pleistocene. At that time the present lowlands of southern Central America and along the Pacific and Caribbean coasts of Colombia emerged and were forest covered. The temperature gradient in at least parts of the tropical latitudes during the glacial periods of the Pleistocene was greater than it is today; for this reason the refrigeration affected the higher latitudes and altitudes more (7° – 8° C.) than the tropical lowlands (3° – 4° C.). The latitudinal extent of the tropical lowlands was not much less during the Pleistocene than it is today: the lowlands of Colombia and great parts of Central America remained in the tropical zone (notwithstanding an extensive glaciation of the Central and South American mountain ranges).

The faunas of the tropical lowlands were severely affected by sea-level fluctuations and by alternating wet and dry periods during the Pleistocene, caused by a contraction and expansion of the equatorial rain belt. These climatic changes continued through post-Pleistocene time. During the periods of drought the trans-Andean forest fauna was restricted to rather small humid refuges: (a) on the Caribbean slope of Central America (various refuges in Costa Rica, Nicaragua, Honduras); (b) on the Pacific slope of southwestern Costa Rica and adjacent Panamá ("Chiriquí Refuge"); (c) along the Pacific coast of Colombia ("Chocó Refuge"); and (d) at the foot of the northern slope of the Western and Central Andes of Colombia ("Nechí Refuge"). Strongly marked endemic forms originated in these refuges during periods of geographic isolation resulting from drought, at which time the connection of the trans- and cis-Andean forests was interrupted in the north Colombian lowlands.

It is concluded that the uplift of the Colombian Andes was only indirectly responsible for the development of the numerous Central American and west Colombian endemic species. The direct causation for their development was the repeated change of dry and humid periods during the Pleistocene and post-Pleistocene. These climatic changes permitted and interrupted repeatedly the contact of the trans- and cis-Andean populations in the north Colombian lowlands through the expansion and shrinkage of the forests. In this way an increasing number of small founder populations was able to reach the trans-Andean forests. The

high concentration of endemic species in the tropical lowland forests of western Colombia and Central America is explained by a gradual accumulation of isolates in the trans-Andean forest refuges.

Numerous Chocó elements extended their ranges to Central America, in some cases forming another isolate in the refuges along the Caribbean slope. On the other hand, only a few Central American species advanced into northern Colombia.

Zones of allopatric hybridization are developed at the eastern margin of the Caribbean Costa Rica Refuge in western Panamá and at the northern margin of the Chocó Refuge in the Urabá region of north-western Colombia. These zones are probably of very recent origin. The hybridization of *Pteroglossus t. torquatus* × *P. (torquatus) sanguineus* and of *Galbula r. ruficauda* × *G. (ruficauda) melanogenia* is described in detail.

Double invasions were responsible for the present co-existence of *Columbia (Oenoenas) goodsoni* and *Columbia (O.) subvinacea berlepschi* and of *Tangara johanna* and *T. florida* in western Colombia. A triple invasion caused the speciation within the black-tailed *Trogon melanurus* group.

The majority of the Amazonian forest birds that reached the trans-Andean lowlands came around the Andes from the north. However, a small group seems to have followed the upper Marañón Valley to cross the Andes in northern Perú or southern Ecuador (or both) during wet climatic periods of the past.

A quantitative analysis of the Chocó fauna is included. A comparison of the number of trans- and cis-Andean species of certain families of forest birds shows that at least half of the upper Amazonian fauna reached the trans-Andean forests.

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