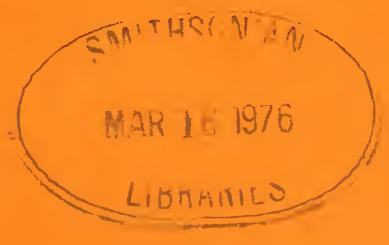
# AVIFAUNA OF NORTHWESTERN COLOMBIA, SOUTH AMERICA

by

JÜRGEN HAFFER

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## 1. Introduction

The lowlands of northwestern Colombia connect the isthmus of Panamá with the mainland of South America. This largely forested area is today the meeting place of various Middle and South Americans faunas. Many bird species advanced into northwestern Colombia from Amazonia by following the Caribbean lowlands north of the Andes. A lesser number extended their range southward and eastward from Middle America. In the forests around the Gulf of Urabá of northwestern Colombia some of these forms made contact with their strongly differentiated representatives of the Chocó region of western Colombia and of the Nechí region along the northern base of the Colombian Andes. These zones of contact reveal striking faunal discontinuities in a continuous forest environment.

I studied the bird fauna of this interesting part of the Neotropical Region from 1958 to 1967. I collected birds and made observations during the course of geological field work as professional duties permitted. Several previously published articles dealt with particular aspects of the distribution of certain birds and with portions of my collection. In the present publication I summarize the information obtained and give a complete list of birds that I encountered. I specially emphasize the secondary contact zones of parapatric species and hybridizing subspecies in northwestern Colombia. In the introductory portion of this publication, I deal with general aspects of the ecology and zoogeography of the avifauna of northwestern Colombia as they relate toward elucidating the relationships of this forest fauna with other trans-Andean [1]) faunas and with the Amazonian fauna.

## 2. Acknowledgments

I am grateful to my field companion Donald A. Beattie who, during the early years of my field work, helped collect birds and prepare study skins. Manuel Montes obtained many specimens and provided much useful information on the natural history of the forest and its inhabitants. The ornithologists at the Instituto de Ciencias Naturales, Universidad Nacional, Bogotá, Professor José I. Borrero (now in Cali), Father Antonio Olivares (deceased) and Dr. Jorge Hernandez C., permitted me to use freely the skin collection and the library of the Instituto and discussed with me many ornithological aspects of Colombia during my stay in that country from 1957 to 1961 and from 1963 to 1967.

I am also much indebted to Dr. Eugene Eisenmann, New York, who answered numerous questions since the inception of my work in Colombia and generously

[1]) The tropical lowlands and their faunas west of the Andes and in Middle America are designated 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.

gave his time to discuss ornithological problems and particular specimens of my collections. Mr. R. Meyer de Schauensee, Philadelphia, and Dr. A. Wetmore, Washington, kindly identified a number of skins and sent me important information on several species. I thank Drs. E. R. Blake (Chicago), K. C. Parkes (Pittsburgh), F. C. Novaes (Belém), H. Sick (Rio de Janeiro) and G. E. Watson (Washington) for distributional data on certain species based on material in their respective collections. Dr. E. O. Willis (Brazil) kindly reviewed an early version of the manuscript and permitted me to include some of his observations made in the upper Sinú region in recent years. I also thank Professor J. I. Borrero, Departamento de Biología, Universidad del Valle, Cali (Colombia), who furnished the photographs of Colombian birds mostly taken near Buenaventura on the Pacific coast. The curators of the Departments of Ornithology at the American Museum of Natural History (New York), Dr. W. Lanyon, and at the Academy of Natural Sciences (Philadelphia), Mr. R. M. de Schauensee and Dr. F. Gill, kindly permitted me to use the collections under their care.

## 3. Topography

The Andes are a narrow compact mountain range over most of their huge extension along the west coast of South America. They develop a more diverse relief near their northern end in Colombia, where three cordilleras are separated by deep tropical valleys (from west to east): Western Cordillera, Cauca Valley, Central Cordillera, Magdalena Valley, Eastern Cordillera, Llanos (Fig. 1). The Eastern Cordillera continues northeastward into Venezuela (Mérida Andes) and follows the Caribbean coast decreasing progressively in height. The Central Cordillera of Colombia ends before reaching the Caribbean coast but can be traced through the isolated Sierra Nevada de Santa Marta and the low mountains of the outer Guajira Peninsula into the island chain of the Netherlands Antilles. Exten-

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Fig. 1: Present distribution of humid lowland forest in northern South America and southern Middle America. Modified from Hueck & Seibert (1972, South America) and Lauer (1968, Middle America).

*Explanation:* Shaded — Evergreen forest (Wet and Pluvial Forest). Shaded and dashed vertically — Seasonal forest (Moist and Dry Forest) near savanna regions. Blank — Grass savanna and gallery forest along rivers in the Llanos of eastern Colombia, southern Venezuela and Guyana; agricultural areas in northern Colombia-Venezuela, in Pacific Middle America, and in western Ecuador. „Savannas" are often artifical and include secondary growth with remnants of Dry and Moist Forest. Scrubby vegetation exists on the southeastern Colombian table mountains in the Amazonian forest. Small open circles — Xerophytic vegetation on the Caribbean peninsulas Guajira and Paraguaná, in inter-Andean valleys, and in Pacific lowlands of northwestern Perú. Areas outlined in northwestern Colombia are shown in more detail in Figures 3 and 4, respectively.

Mountains above 1000 m elevation are in black. 1 — Mountains of Costa Rica and western Panamá. 2 — Serranía del Darién. 3 — Cerro Pirre. 4 — Alto del Buey (Serranía del Baudó). 5 — Western Cordillera. 6 — Central Cordillera. 7 — Eastern Cordillera of Colombia. 8 — Sierra de Perijá. 9 — Sierra Nevada de Santa Marta. 10 — Mérida Andes. 11 — Sierra de la Macarena. 12 Table mountains of southeastern Colombia. 13 — Table mountains of southern Venezuela ("Pantepui").

sive low lying plains in northern Colombia are drained by the lower portions of the rivers Magdalena, Cauca, San Jorge, and Sinú, which flow northward into the Caribbean Sea.

The Western Cordillera forms several mountain ridges and ranges of hills near its end in northwestern Colombia. The Serranía de Abibe to the southeast of the Gulf of Urabá forms a high northern spur of the Western Andes (Fig. 2). It reaches 2200 m elevation at the Alto de Carrizal and drops in a northern direction to 1000 m east of Chigorodó. Still farther north, in the area east of the Gulf of Urabá between Turbo and the upper Río Sinú, there are chains of narrow steep ridges, 200 to 700 m in elevation, which represent the last extensions of the Serranía de Abibe. The elevations given for the Alto de Carepa and Alto de Quimarí in this area on official maps are erroneous, as both peaks are under 1000 m high.

East of the upper Sinú River, a complex of sandstone ridges forms Mt. Murucucú (1270 m elevation). Further north, between Montería and Planeta Rica, series of low hills represent the northern extension of the Western Andes. These hills rise again in the Serranía de San Jacinto near the Caribbean coast to attain elevations of around 600 m or even 800 m (Cerro Maco).

A rugged basalt range, 100 to 300 m in elevation, forms the western shore of the Gulf of Urabá and many small islands dot the coastal waters. A

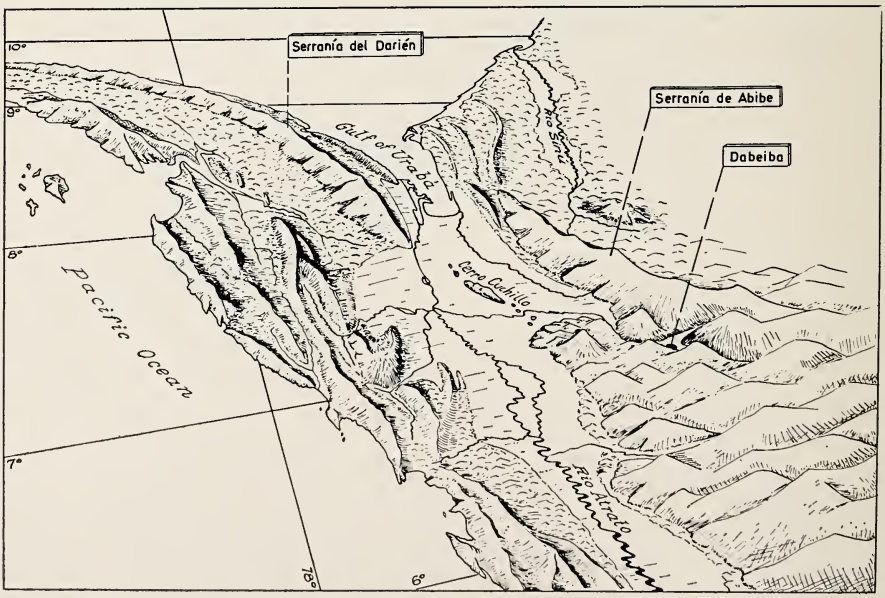


Fig. 2: Northwestern Colombia and adjoining parts of eastern Panamá. View over the region where Central America joins the South American continent.

rough sea beats the rocky coast line during the trade wind season, from December to March. The Serranía del Darién rises farther inland to elevations of 1900 m at Mt. Tacarcuna (Fig. 2). This mountain range forms the Colombian-Panamanian border and terminates abruptly southwest of the Gulf of Urabá. Its geological continuation in a southeastward direction underneath and across the wide swampy lower Atrato Valley is indicated by a series of isolated forested hills which rise from the immense Atrato swamps. Cerro Cuchillo is the highest oft these hills. It has an average elevation of around 500 m with the highest peak possibly reaching 600 m. Other low hills to the northwest (Loma Aislada) and southeast of Cerro Cuchillo complete the discontinuous connection of the Serranía del Darién with the Andes of Colombia („Cuchillo bridge", Fig. 2). The size, elevation, number and exact location of these hills are not yet indicated on any published map. The hills stand out very clearly from the densely forested swampy plains of the Atrato Valley and are easily viewed from the foothills of the Serrania de Abibe to the east.

The Atrato River forms an extensive delta on the southwestern shore of the Gulf of Urabá. This delta deposits into the Gulf through numerous small mouths which are blocked by bars of depths of two meters or less. Sandy, mangrove-covered cays line the head of the Gulf north to Turbo.

A series of steep and rugged basalt ranges follow the Pacific coast of Colombia (Serranía de Baudó, Serranía de los Saltos), continuing into eastern Panamá (Mt. Sapo, Mt. Pirre). The elevation of Mt. Pirre is about 1550 m (Myers 1969). The Serranía de los Saltos averages 300 to 600 m in elevation and is crossed by the upper Río Salaquí and Río Truandó in narrow rocky canyons with numerous impassable rapids. The divide between the rivers which flow east towards the Río Atrato and those which flow west to the Pacific Ocean is formed by another somewhat lower basalt range that also joins the Pirre massif at the Panamanian border (Alturas de Nique). Near the headwaters of the Río Napipí the divide between the Atrato plains and the Pacific slope is low and narrow, but it rises steeply to the south to form the Serranía de Baudó which culminates in the Alto del Buey (1070 m elevation; higher values given on published maps are erroneous).

The eastern border of the Atrato Valley is formed by the steep flank of the Western Cordillera which often rises quite abruptly from the swampy and heavily forested plains.

The first descriptions of parts of the country around the Gulf of Urabá and along the Atrato Valley were given during the last century by Trautwine, Michler, Selfridge, Wyse, and Collins who explored the feasibility of an inter-Ocean ship canal in this region. Troll (1930), Hubach, Vallejo, Murphy, and Ossa published more detailed information on the area (references in Haffer 1970 b). A second and third effort to study the possibility

of a canal connecting the Gulf of Urabá and the Pacific Ocean along the Atrato-Truandó route led to the publication of a „Special Report" in 1949 and an „Interim Geologic Report" by the U. S. Corps of Engineers in 1967. Topographic and engineering studies in conjunction with the construction of the Panamerican highway system have been conducted in Darién and south of the Gulf of Urabá (Guardia 1957). The first regional geographic account of the entire Pacific lowlands of Colombia, including the Urabá region, was prepared by West (1957) who concentrated his main field work on the Chocó area. Vann (1959) studied the delta of the Atrato River in detail. The distribution of different types of soil in the lower Atrato Valley and around the Gulf of Urabá was mapped on the basis of air photographs by Goosen et al. (1962). Interesting accounts of the Sinú region were published by Gordon (1957) and Parsons (1952). The latter author (1960) commented on the rediscovery of the ruins of the old Spanish town Santa María la Antigua at the northern margin of the Atrato delta. It was from this village that Vasco Núñez de Balboa set out to discover the Pacific Ocean in 1513. For additional information on the Urabá region the reader is referred to Parsons (1967) and Haffer (1970 b).

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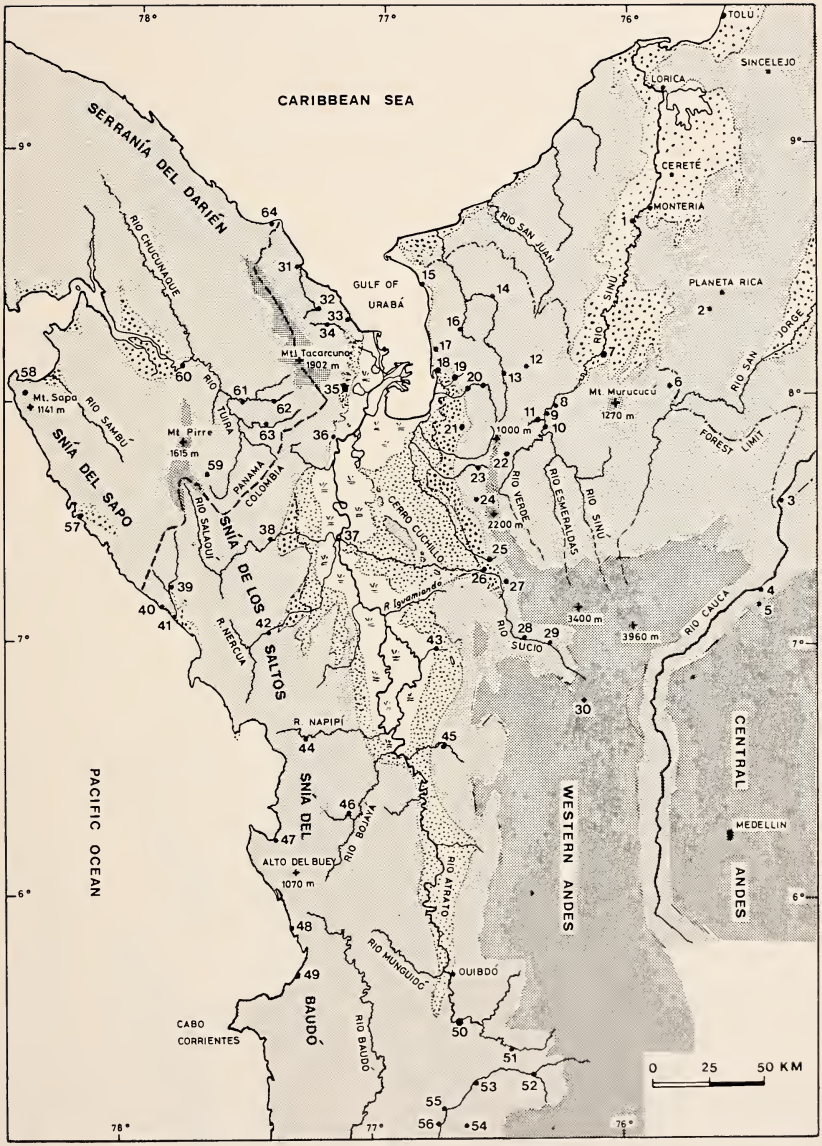
Fig. 3: Collecting stations in the lowlands of northwestern Colombia and eastern Panamá.

*Explanation:* Shaded dark — mountains above 1000 m. Shaded light — hill and mountain areas under 1000 m. Dotted — alluvial plains and terraces (largely deforested along the Turbo road southeast of the Gulf of Urabá, along the Caribbean coast, and in the Sinú Valley). Stippled — swamp forest (periodically flooded). Dashed — grass and palm swamps, marshes, and lagoons. The dashed-dotted line east of the Gulf of Urabá marks the approximate limit of forests during the mid-sixties. Rapid deforestation continually pushes this line southward and southwestward. *Colombia:* 1 Jaraquiel. 2 Catival; an old Indian name for a site southwest of Planeta Rica and a few miles northwest of Ciénaga San Lorenzo. There is no village (misplaced by Haffer 1967-b, Fig. 3, no. 10). 3 Cáceres. 4 Puerto Valdivia. 5 Valdivia and nearby La Frijolera (1 500—1 600 m). 6 Quebrada Charrura. 7 Tierra Alta. 8 Frasquillo. 9 Tucurá. 10 Socorro (Socarré). 11 Río Naín. 12 Alto de Quimarí, approximately 700 m (not 1 600 or even 2 000 m as shown on some maps). 13 upper Río Mulatos. 14 lower Río Mulatos. 15 Necoclí. 16 Río Tulapa. 17 Río Cope. 18 Turbo. 19 Río Guadualito. 20 Río Currulao. 21 Apartadó. 22 Quebrada Saisa. 23 upper Río Chigodoró. 24 upper Río Imamadó. 25 Villa Arteaga. 26 Pavarandocito. 27 Mutatá. 28 Alto Bonito. 29 Dabeiba. 30 Frontino (1330—1550 m). 31 Acandí. 32 Río Tolo. 33 Titumate. 34 upper Río Tanela. 35 Unguía. 36 Sautatá. 37 Riosucio. 38 Río Salaquí. 39 Río Juradó. 40 Punta Ardita. 41 Juradó, village. 42 Río Truandó. 43 Murindó. 44 upper Río Napipí. 45 Río Murrí. 46 Río Uva, near its mouth into Río Bojayá. 47 Mutis (Bahía Solano). 48 Jurubidá. 49 Nuquí. 50 El Tambo and Yuto. 51 Bagadó (Río Andagueda). 52 Santa Cecilia. 53 Tadó (Río San Juán). 54 Condoto. 55 Istmina. 56 Andagoya.

*Eastern Panamá:* 57 Jaqué. 58 Río Jesusito, north slope of Mt. Sapo. 59 Cana. 60 El Real. 61 Pucro. 62 Quebrada Tapalisa. 63 Paya. 64 Puerto Obaldía.



## 4. Climate

The tropical climate of northwestern Colombia is characterized by a long rainy season from April to November (barely interrupted by a drier spell in June) and a dry season from December to March. The dry season results from the southward shift of the northern tradewind belt to include the lowlands of northern Colombia during the northern winter. A steady northeasterly wind blows in the Urabá region during the winter months south to about the Río Napipí. I experienced occasional strong winds somewhat to the south of this river in the Río Uva Valley. Still farther south, the influence of the northern tradewinds terminates. The rains fall without major breaks in the central Chocó region where the climate is extremely humid (average annual rainfall in Quibdó 10 545 mm).

The tradewinds, in crossing the lower Atrato Valley in a southwesterly direction, cause a conspicuous southwestward bulging of the isohyets (Fig. 5). The winds are strongly felt on the Pacific coast around Juradó, where the coastal waters are smooth as a gentle lake during the months when the tradewinds blow off the land.

The climate grows rapidly less humid in a northeasterly direction from the Gulf of Urabá in northern Colombia, where the drying influence of the tradewinds is strongly felt from December through March. Locally increased precipitation occurs over the isolated Serranía de San Jacinto west of the lower Río Magdalena (Fig. 4. & 5).

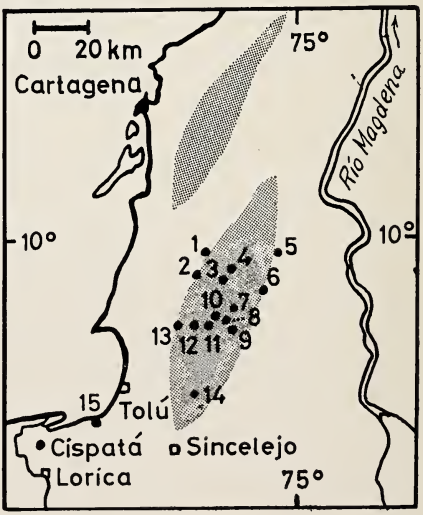



Fig. 4: Northern Colombia, Departamento Bolivar. Index map showing collecting stations in the Serrania de San Jacinto (shaded). For location of map see Fig. 1.

*Explanation:* 1 María La Baja. 2 Arroyo Playón. 3 San Cristóbal. 4 Arroyo Cacao, 5 San Juán Nepumuceno. 6 San Jacinto. 7 San Isidro. 8 Cansona. 9 San Carlos. 10 Arroyo Camaroncito. 11 Lázaro. 12 Arroyo Tigre. 13 Palmira. 14 Colosó. 15 Coveñas.

Schmidt (1952) discussed the rainfall distribution in Colombia and included the Urabá region in the „tradewind area" of northern Colombia which is confirmed by the data given above. More recent summaries of rainfall measurements were published by West (1957) and Trewartha (1962). The great detail shown on the rainfall map by Trojer (1958) is based on relief interpretation, but is not backed by corresponding field data. The high rainfall area near Villa Arteaga southeast of the Gulf of Urabá (Fig. 5 & 6) probably is connected with the very humid region along the western base of the Western Andes to the south rather than representing a small humid „island" as mapped by Trojer (1958) who located Villa Arteaga too far north on his map. The forest and climate grow increasingly more humid as one goes south from this village along the western slope of the mountains.

The Atlas de Colombia (1969: 67—71) gives a useful summary of climatic information on the country as a whole.

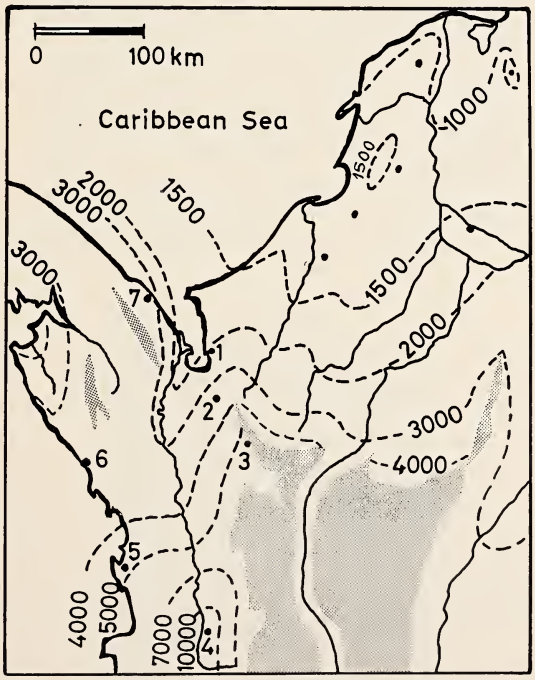



Fig. 5: Annual rainfall (mm) in northwestern Colombia. Modified from Schmidt (1952) and West (1957).

*Explanation:* Black dots — weather stations listed by Schmidt (1952), as follow: 1 Turbo; 2 Chigorodó; 3 Villa Arteaga; 4 Quibdó; 5 Bahia Solano; 6 Juradó; 7 Acandí. Rainfall is not mapped in the dry inter-Andean calleys. See also legend of Fig. 6. Gray shading — mountains above 1000 m elevation.

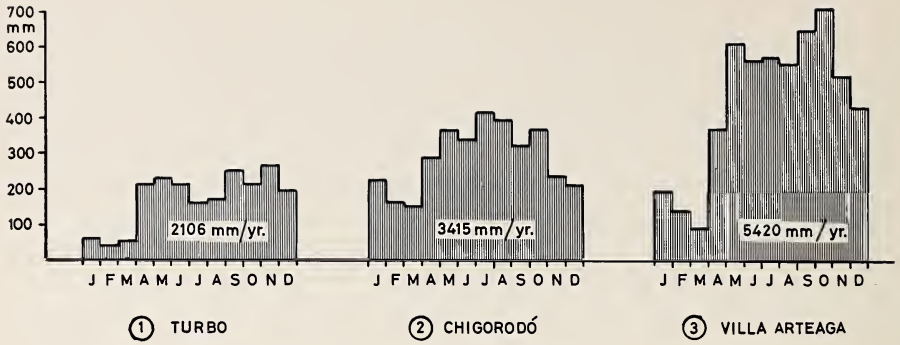



Fig. 6: Average monthly rainfall (mm) in the Urabá region, NW Colombia. Data from Parsons (1967, Table 1).

*Explanation:* 1 Turbo, airport 1931—1960, 13 years incomplete. 2 Chigorodó, 1951—1954, 1960. 3 Villa Arteaga, 1952—1957, 1959—1960. The average annual rainfall at other stations as numbered on Fig. 5 is estimated as follows: no. 4, Quibdó 10 545 mm; no. 5, Ciudad Mutis, Bahía Solano 4501 mm; no. 6, Juradó 4376 mm; no. 7, Acandí 3280 mm.

## 5. Vegetation

The lowlands around 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 in the more accessible areas. The open woods or Dry Tropical Forest that originally covered the northern Colombian plains have largely disappeared; only small remnants are still preserved in the valleys of low ranges close to the Caribbean coast, e. g. Serranía de San Jacinto. More extensive humid forests exist along the northern base of the Central and Western Andes as well as in the humid middle Magdalena Valley. These forests are broadly connected around the Gulf of Urabá with the wet forests in the Pacific lowlands of Colombia and northwestern Ecuador. The trans-Andean humid forests continue into Middle America where they cover 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.

*Evergreen Rain Forest (Pluvial and Wet Forest):* No pronounced dry season; precipitation 4 000 to over 10 000 mm per year. Heights of trees 30 to 40 meters. Almost daily showers keep the forest humid including the understory and the forest floor. Natural clearings are rare. Schematic vegetation profiles across a forest river in its upper, middle, and lower course (Fig. 7) indicate that an appreciable interruption of the forest habitat is

Plate 1

Fig. 1: Evergreen rainforest along the middle Río Salaquí, Dep. Chocó, lower Atrato Valley. March 1964. For location see Fig. 3, no. 38.

Fig. 2: Evergreen rainforest along the middle Río Truandó, Dep. Chocó, lower Atrato Valley. March 1964. For location Fig. 3, no. 42.

Fig. 3: Evergreen rainforest at the Río Tasidó, Dep. Antioquia; bridge of Turbo road. August 1963; 12 km south of Mutatá (Fig. 3, no. 27).

Plate 2

Fig. 1: Evergreen rainforest 5 km southwest of Mutatá, Dep. Antioquia, August 1966. For location see Fig. 3, no. 27.

Fig. 2: Clearing in seasonal forest, upper Río San Jorge Valley, Quebrada Charrura, Dep. Córdoba. May 1960. For location see Fig. 3, no. 6.

noticeable only along the lower portion. The forest is most luxuriant along the middle course, where the forest canopy from opposite river banks tends to close the gap of the river (see also Plate 1, Fig. 1 and 2). Due to occasional flooding of the widened lower river valley, there are fairly extensive *Heliconia* thickets and secondary growth characterized by *Cecropia* trees which grade backward into the rainforest.

This forest assumes a wide distribution in the Pacific lowlands of Colombia and northwestern Ecuador as well as along the northern base of the Western and Central Andes and along the slopes of some mountain ranges in Darién.


Fig. 7: Schematic vegetation profiles across a forest river in its upper part (above); middle course (center); and lower course (below); northwestern Colombia.


Fig. 8: Forest clearing of a settler along a river course in northwestern Colombia.

*Evergreen Seasonal Forest (humid monsoon forest; Moist Forest):* Some trees lose their leaves during the dry season from December to March (Plate 2, Fig. 2). Annual precipitation is about 2 000 to 4 000 mm. This forest covers large areas in the Urabá region where many settlers established extensive clearings and plantations. Fig. 8 illustrates a typical forest clearing along a river course in this area, see also Plates 3 and 4.

*Semi-evergreen Seasonal Forest (dry monsoon forest; Dry Forest):* A large percentage of the trees lose their leaves during the pronounced dry season. Annual precipitation is 1 000 to 2 000 mm. Height of the trees is only around 20 meters and the occurrence of bottle-shaped tree trunks (water storage) increases.

This forest originally covered extensive areas in northern Colombia but has been largely destroyed by man in agricultural regions.

*Cloud Forest:* The steep mountain ranges in easternmost Panamá (Darién) are covered from 750 m upward with cloud forest, as these ridges are enveloped in mist and cloud almost daily. The crest of the highest ranges (Mt. Pirre, Mt. Tacarcuna) is characterized by a cold, dense, low, mossy forest thicket, the Elfin Woodland (Myers 1969). On low mountain ranges 30 to 40 kilometers southeast of Turbo and to the east of the head of the Gulf of Urabá (Serranía de Pavo, 750 m; Alto de Carepa, 800 m elevation) I found cool misty forest along the crests and all trees heavily covered with moss. Cloud forest probably exists along the Serranía de Abibe and on some of the peaks of the Serranía de Baudó to the south.

Summary information on the vegetation of the Urabá region and Colombia as a whole are given by Cuatrecasas (1958), the Atlas de Economía Colombiana, 3rd part (1962), and the Atlas de Colombia (1969: 74—81) besides general works on the vegetation of South America (e. g. Hueck 1966).

Plate 3

Figures 1 and 2: Indian settlement in evergreen seasonal forest at the Río Esmeraldas near its mouth into the Río Sinú, Dep. Córdoba. June 1963.

Plate 4

Fig. 1: Evergreen seasonal forest along the upper Río Sinú, near mouth of the Río Esmeraldas, Dep. Córdoba. June 1963.

Fig. 2: Small farm with corn field in evergreen seasonal forest along the upper Río Sinú, Dep. Córdoba. June 1963.

### 6. Ornithological Exploration

Northwestern Colombia received comparatively little attention ornithologically. Chapman (1917) summarized the results of the field work of early expeditions into this area, such as the Michler expedition in 1858 to study the feasibility of a ship canal from the Gulf of Urabá to the Pacific Ocean. Birds were collected during this survey expedition by Arthur C. V. Schott and the brothers W. S. and C. J. Wood along the lower Atrato, Truandó and Nercua Rivers as well as near Turbo (Cassin 1860[1])). Mrs. Elizabeth L. Kerr worked in the lower Atrato Valley between 1909 and 1912; Boyle and Miller visited the Alto Bonito region west of Dabeiba in 1915; Anthony, Ball and Richardson travelled in eastern Panamá, reaching the Colombian slope of the Serranía del Darién in 1915 (Chapman 1917). Frank M. Chapman, Curator of Birds at the American Museum of Natural History, New York, directed, between 1910 and 1930, these and other expeditions to Colombia, Ecuador and portions of Venezuela and Peru, which represented the first systematic ornithological explorations of northwestern South America. Chapman's interpretations of the results, published in several classic accounts (e. g. 1917, 1926), were aimed at a broad biological and ecological understanding of the bird faunas and their evolution.

Kjell von Sneidern made bird collections for the Academy of Natural Sciences, Philadelphia, in the upper Río Sinú region (De Schauensee 1950 a, b) and in the Atrato Valley (records included in De Schauensee's catalogue, 1948—1952). The mammalogist P. Hershkovitz collected game birds in northwestern Colombia (Blake 1955). M. A. Carriker, Jr. travelled widely in northern Colombia collecting for the U. S. National Museum, Washington, and A. Wetmore published notes on some of the more interesting species (Wetmore 1951, 1955, 1958, 1959, 1962, 1965, 1968, 1972). The published results of continued explorations by Dr. A. Wetmore (1965, 1968, 1972) in Panamá, including the Darién region, have been particularly useful in comparing the data I obtained in adjacent parts of Colombia.

I visited the lowlands of northwestern Colombia from January to September 1958 and from January to March 1959, when conducting geological field work in the Sinú region and in the area around the Gulf of Urabá. I collected birds and made observations as professional duties permitted. I returned to northwestern Colombia during May-June 1963, March-April 1964, and January-March 1965. During these periods I worked in the upper Sinú and Mulatos Valleys, along several eastern and western tributaries

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[1]) The identification of a number of birds in Cassin's report seems doubtful, e. g. *Ara militaris, Galbula r. ruficauda, Hypnelus ruficollis, Rhynchocyclus brevirostris,* as discussed in the respective species accounts below.

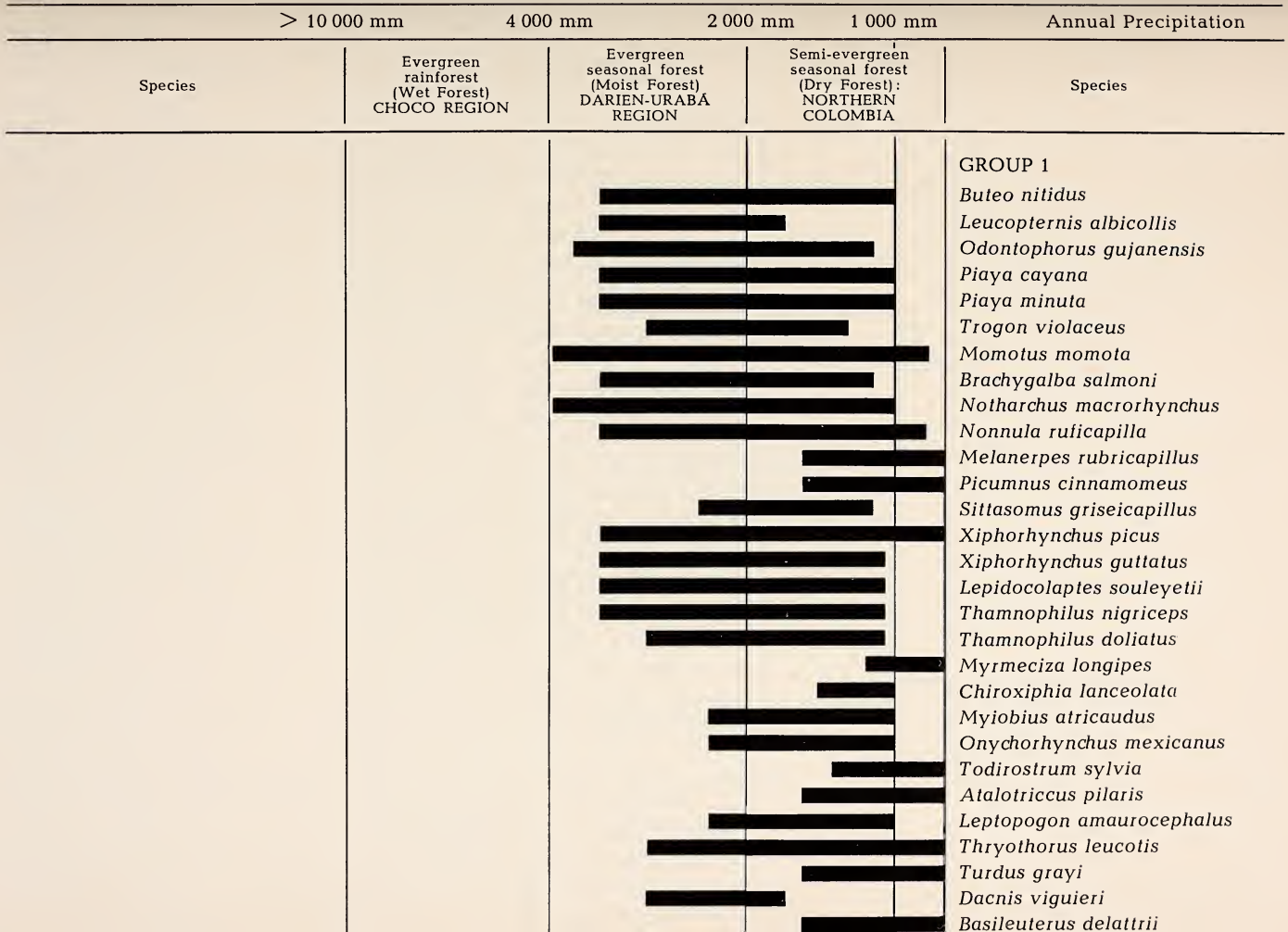
of the middle and lower Río Atrato and also along the northern Colombian portion of the Pacific coast around Juradó. In August 1966 I had an opportunity to work in a particularly interesting part of the area not visited before: The lowlands near Mutatá, 100 km southsoutheast of the Gulf of Urabá, where I collected 205 specimens near the base of the Serranía de Abibe (Haffer 1967 c). Data on 316 specimens taken in the Serranía de San Jacinto near the Caribbean coast (Fig. 1) and in the upper San Jorge Valley have been published by Haffer & Borrero (1965) and are summarized in the species accounts below. I made additional bird collections outside the area under consideration, e. g. on the remote arid Guajira Peninsula of northeastern Colombia (Haffer 1961 a) and in the semiarid upper Patía Valley of southwestern Colombia (Haffer MS). I spent a total of 26 months on expeditions in the northern and western Colombian lowlands in 1958—1961 and 1963—1967. During these years, I was stationed in the capital city of Bogotá and also undertook shorter field trips to the lowlands east of the mountains as well as to various portions of the northern Andes. This report, based on the results of my field work, builds upon and extends Chapman's (1917) analysis of the avifauna of northwestern Colombia.

## 7. Ecology

7.1. *Ecological distribution of forest birds in northwestern Colombia:* The ecological range of tropical birds varies over similarly broad limits as in birds of higher latitudes. There are widely distributed forest species which live in superhumid rainforest as well as in moist and dry seasonal forests often showing only clinal variation in color or size as one goes from one ecological forest type to another. A second group of forest birds confine themselves to a particular type of forest, such as Pluvial Forest or dry tropical forest, or occur only in certain seasonal forests. It remains unknown which ecological factors delimit the occurrence of these species. However, these environmental factors are directly or indirectly related to the amount of annual precipitation which we utilize as an ecological indicator.

The following table summarizes qualitatively the ecological distribution of characteristic forest species of northwestern Colombia. Notes taken during field work in dry Caribbean forests south to the wet forests in the Pacific lowlands form the basis for this subjective interpretation. It is quite obvious from this tabulation that there are three main ecological groups of birds in this region. First, those species that inhabit the wet Chocó forest, often extending their ranges for varying distances into the less humid forests. Second, species that remain restricted to dry or seasonal forests and avoid the wet Pacific forests. Third, those birds that are represented in the wet and seasonal forests by well differentiated allies which meet in the Urabá region.

Table 1: Ecological distribution of forest birds in northwestern Colombia



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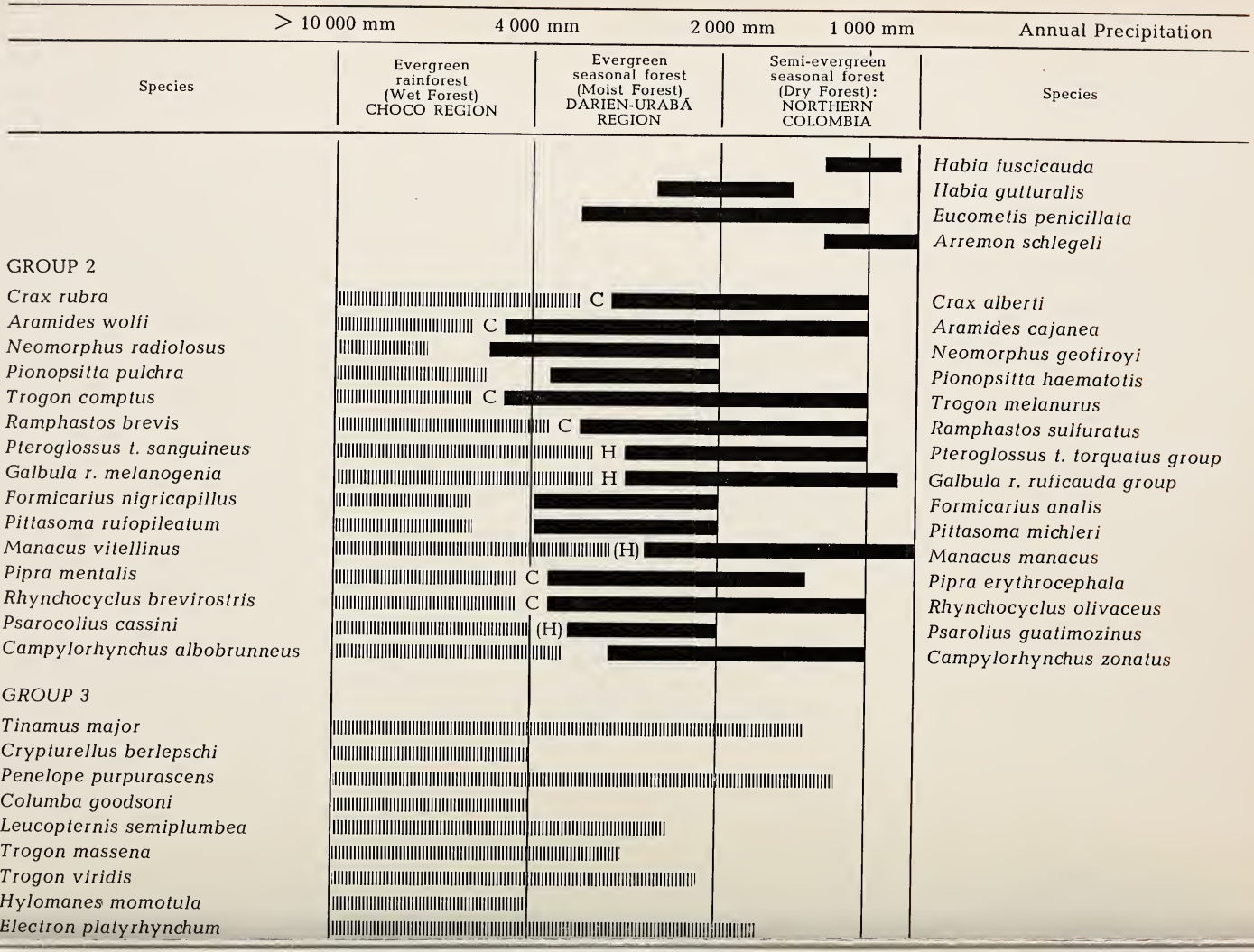

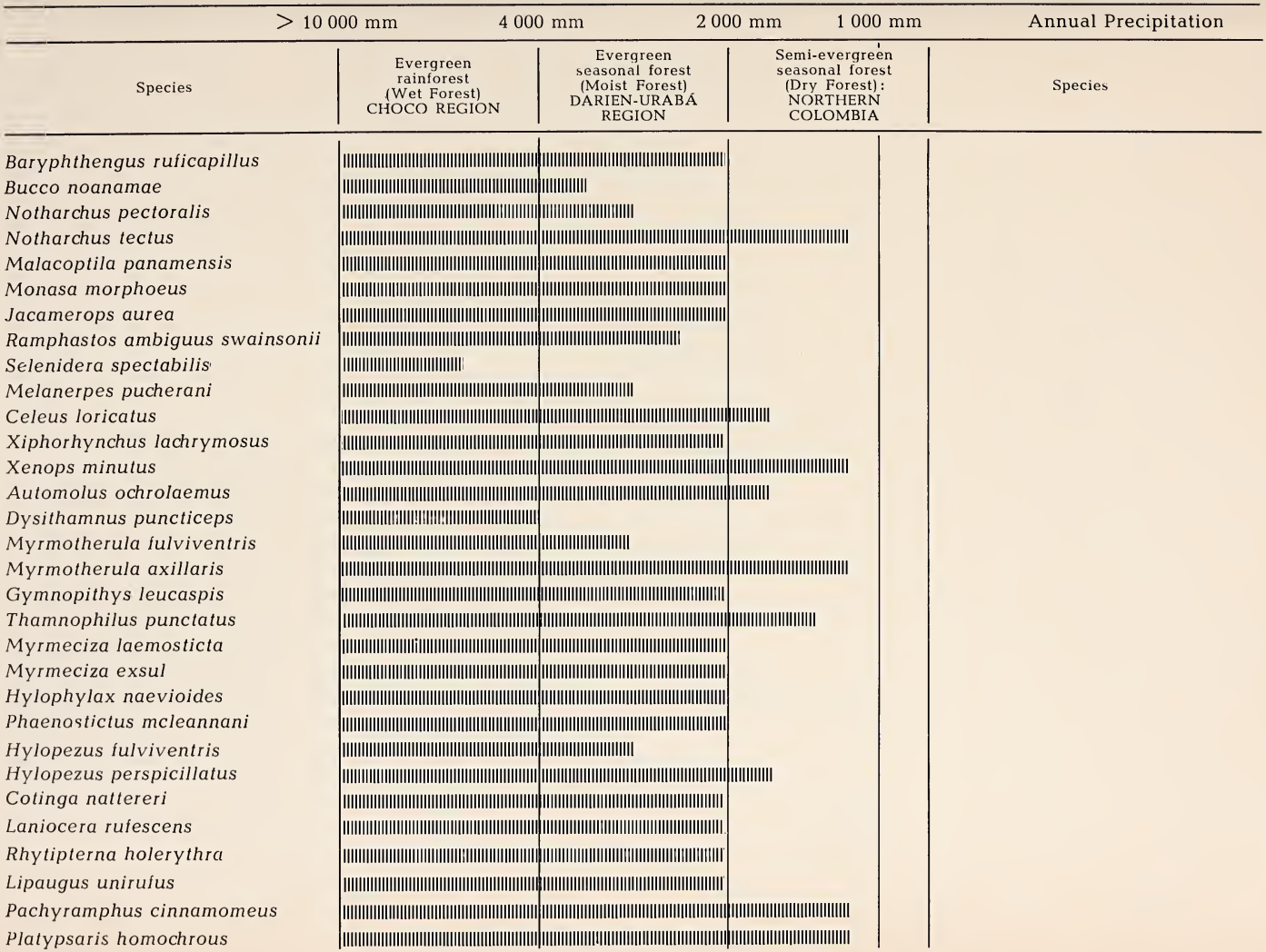

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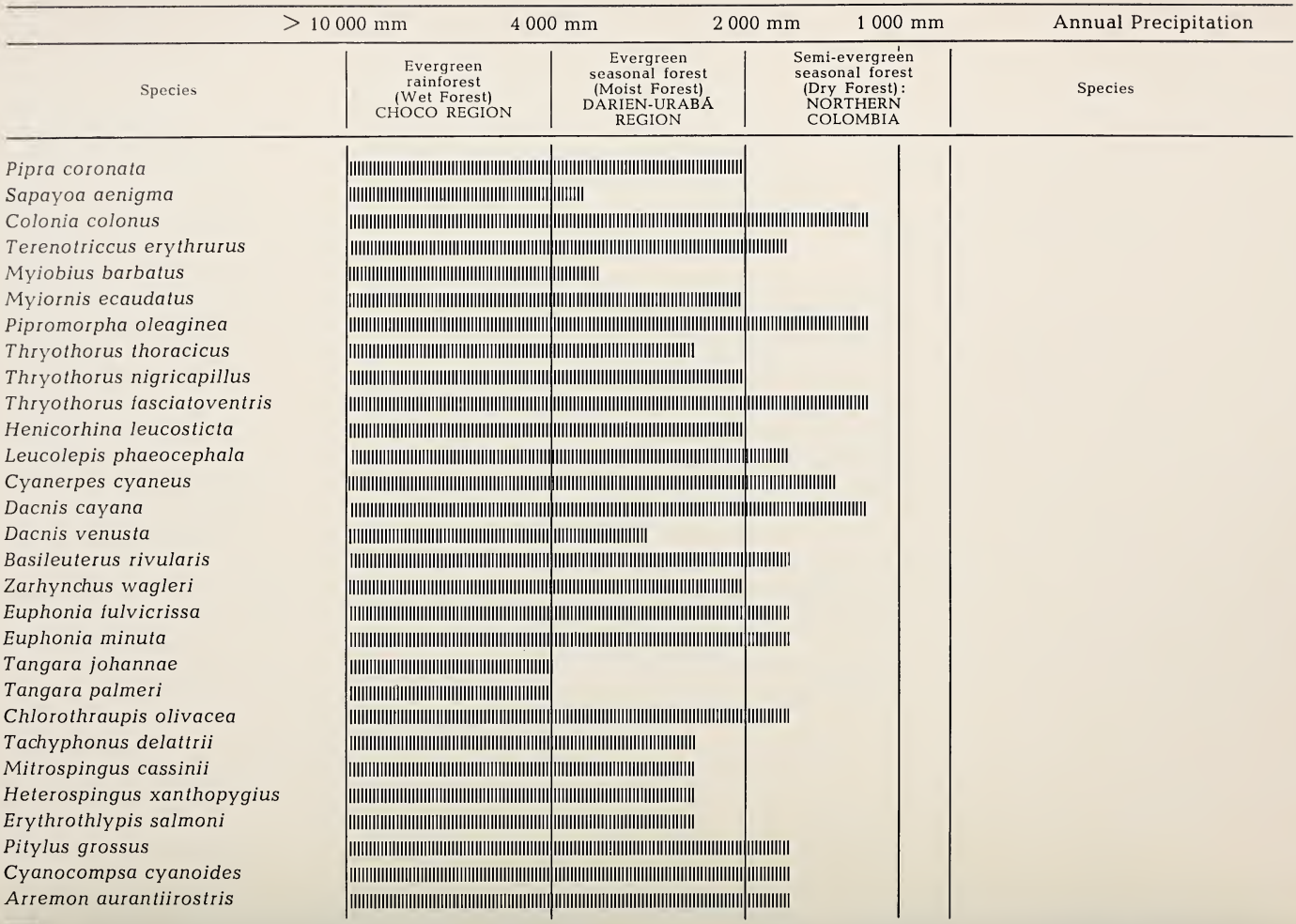


C — Contact without hybridization (H) — Contact with restricted hybridization H — Contact with unrestricted hybridization

7.2. *Occurrence of bird species inside the forests of northwestern Colombia:* Most species inhabit more or less well defined zones in the forest, such as forest floor, low or high understory, canopy. The vertical stratification of the forest habitat probably is an important factor in contributing to the stratified sympatric occurrence of the numerous tropical forest birds. In the following paragraphs I list the typical forest habitats with their characteristic species based on my field notes (Fig. 9). The classification is that proposed by Slud (1960) and Karr (1971: 218) for the forest bird fauna of Costa Rica and Panama, respectively. Other workers in South America, such as Brosset (1964) for western Ecuador, Davis (1953) for Guyana, Novaes (1973) for lower Amazonia and O'Neill & Pearson (1974) for eastern Perú prepared similar lists.

*Forest floor:* The tinamou *Tinamus major*, the curassow *Crax rubra*, the wood-quail *Odontophorus gujanensis*, the Quail-dove *Geotrygon veraguensis* (in humid areas only), the Ground-cuckoo *Neomorphus geoffroyi*, the antbirds *Formicarius analis* (light forest, forest border, and adjoining second growth), *Hylopezus perspicillatus*.

*Understory.* Low (1 to 2 meters above the ground): the hummingbird *Phaethornis longuemareus*, the antbirds *Myrmeciza exsul*, *Gymnopithys leucapsis*, *Hylophylax naevioides*, *Phaenostictus mcleannani*, the wrens *Henicorhina leucosticta* (in humid areas), *Cyphorhinus aradus*, the finches *Cyanocompsa cyanoides* and *Arremon aurantiirostris*. High (2 to 5 metres above the ground): several hummingbirds, the trogon *Trogon rufus*, the motmots *Momotus momota* and *Electron platyrrhynchum*, the puffbirds *Malacoptila panamensis* and *Nonnula frontalis*, the woodcreeper *Xiphorhynchus guttatus*, the antbirds *Thamnophilus punctatus*, *T. nigrescens*, *Myrmotherula fulviventris*, and *M. axillaris*, the manakins *Pipra coronata*, *P. erythrocephala*, *P. mentalis*, and *Sapayoa aenigma*, the mourner *Rhytipterna holerythra*, many flycatchers such as *Terenotriccus erythrurus*, *Myiobius barbatus*, *Platyrinchus coronatum*, *Rhynchocyclus olivaceus*, *Pipromorpha oleaginea*, the tanagers *Tachyphonus delattrii* and *Chlorothraupis olivacea*.

*Middle forest:* Several species of birds of prey like *Leucopternis semiplumbea*, and the noisy *Daptrius americanus*, the trogons *Trogon melanurus* and *T. viridis*, the puffbird *Monasa morphoeus*, the jacamar *Jacamerops aurea*, the woodpecker *Celeus loricatus*, the cotingids *Lipaugus unirufus* and *Querula purpurata*, the tanagers *Tachyphonus luctuosus* and *T. delattrii* (also high understory).

*Canopy:* The guan *Penelope purpurascens*, the parrots of the genera *Ara* and *Amazona*, the toucans *Pteroglossus torquatus*, *Ramphastos sulfuratus*, *R. ambiguus swainsonii*, the caciques *Psarocolius decumanus*, *Zarhynchus wagleri*, *Psarocolius guatimozinus*, the honeycreepers *Dacnis cayana* and *D. viguieri*, several tanagers which are seen in low fruiting trees on forest clearings and at forest borders, such as *Euphonia xanthogaster*, *E. fulvicrissa*, *E. minuta*, *E. laniirostris*, *Tangara nigrocincta*, *T. inornata*, and *T. lavinia*.

*Thickets and overgrown forest edges:* The tinamou *Crypturellus soui*, the rail *Aramides cajanea* (near rivers), the chachalaca *Ortalis garrula*, the squirrel-cuckoos *Piaya cayana* and *P. minuta*, the trogon *T. viridis*, the jacamars *Brachygalba salmoni* and *Galbula ruficauda*, the woodcreeper *Glyphorhynchus spirurus*, the antbirds *Myrmeciza exsul*, *Cymbilaimus lineatus*, *Taraba major*, *Thamnophilus doliatus*, *Cercomacra nigricans*, *Gymnocichla nudiceps*, and *Hylopezus fulviventris*, the cotingids *Pachyramphus cinnamomeus*, the manakin *Manacus vitellinus*, the

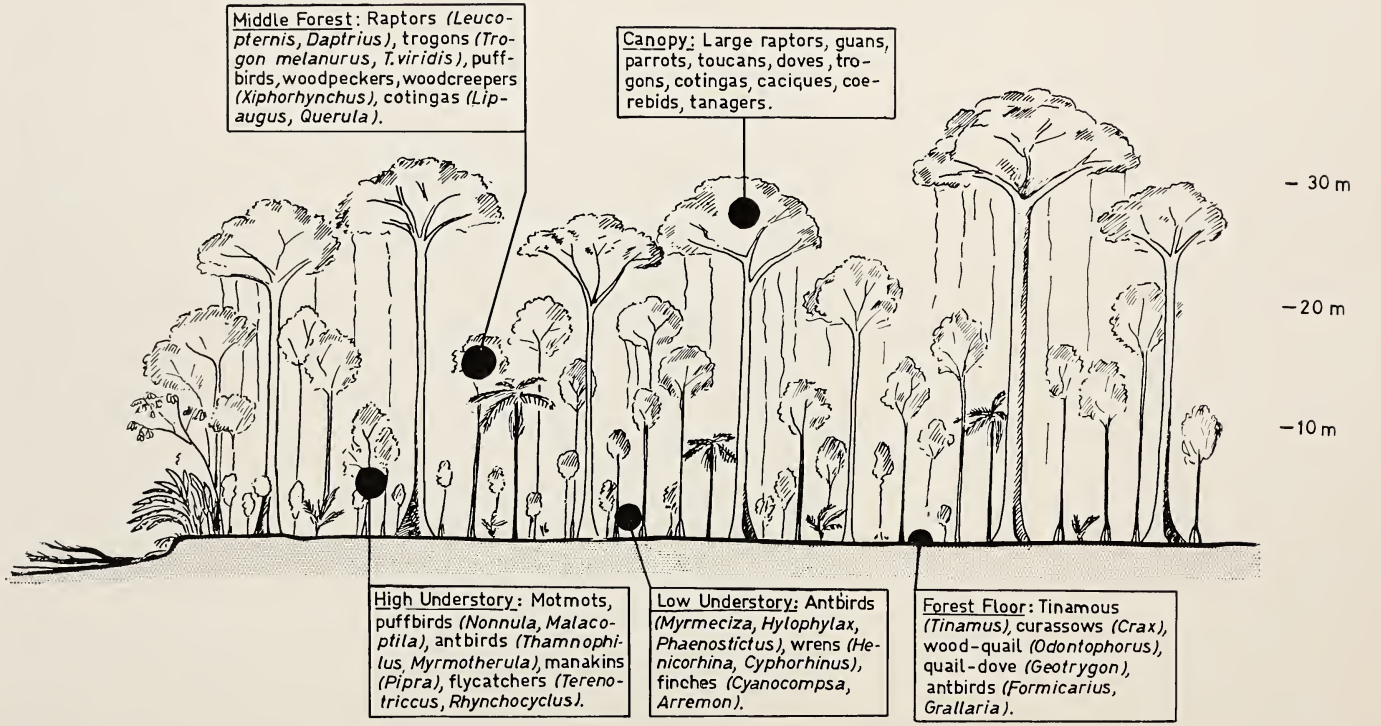


Fig. 9: Occurrence of birds inside the forest of the Urabá region, northwestern Colombia. A river bed on the left side of this schematic drawing.

flycatchers *Myiodynastes maculatus, Todirostrum cinereum,* and *Tyrannulus elatus,* the cacique *Amblycercus holosericeus,* the tanagers *Thraupis episcopus, Ramphocelus dimidiatus* and *R. icteronotus, Mitrospingus cassinii,* the wrens *Thryothorus leucotis, T. fasciatoventris, T. nigricapillus, Campylorhynchus albobrunneus, C. zonatus* (northeast of Turbo), the finch *Arremon conirostris.*

*Forest rivers and creeks:* The finfoot *Heliornis fulica,* the sunbittern *Eurypyga helias,* the kingfishers *(Megaceryle, Chloroceryle),* the flycatcher *Pitangus lictor,* and the terrestrial warbler *Basileuterus fulvicauda.*

7.3. *Flocking in forest birds:* One may walk through a Colombian forest for hours without noticing any bird. Then suddenly a noisy mixed species flock of birds may travel through the branches overhead or may follow a swarm of army ants near the forest floor. Other mixed species assemblages can be observed near fruiting trees. Gregarious parrots form flocks during the nonbreeding season and are often seen flying over the forest canopy. Courtship parties of manakins *(Manacus manacus, M. vitellinus, Pipra erythrocephala)* as well as singing assemblies of the hummingbird *Phaethornis longuemareus* in the undergrowth of the forest are of a different nature than the mixed species flocks mentioned above.

Although I have not studied mixed species flocks in detail, I watched them often in the Urabá forests and confirm as „professional" attendants of swarms of army ants in this area the following antbirds: *Hylophylax naevioides, Gymnopithys bicolor, Phaenostictus mcleannani,* and the woodcreeper *Dendrocincla fuliginosa,* among other species. Willis (1967, 1972, 1973) recently gave excellent accounts of the biology of these birds based on studies in Panamá and Colombia. Willis & Oniki studied antfollowing antbirds in Amazonia, where species of *Rhegmatorhina, Pithys, Phlegopsis,* and other Amazonian species of *Gymnopithys, Hylophylax,* etc. replace the trans-Andean ant-followers mentioned above.

Certain mixed species flocks that exploit fruiting trees, such as the tanager-honeycreeper associations, were studied by Moynihan (1962) in Panamá. I observed near Mutatá the following species as members of such flocks: *Cyanerpes caeruleus, Chlorophanes spiza, Dacnis cayana, Dacnis venusta, Tangara johannae, Tangara lavinia,* and *Erythrothlypis salmoni.*

Bird flocks that wander through the lowland forest at medium levels are typically composed of insectivorous birds, such as the antwrens *Myrmotherula axillaris, M. fulviventris,* and *Microrhopias quixensis* (see also Slud 1960, 1964; Skutch 1969; Wiley 1971). Among other species joining such flocks are *Xenops minutus, Xiphorhynchus guttatus* and occasionally the woodpecker *Celeus loricatus.* Some of the species attending swarms of army ants join at times with flocks of wandering birds or, conversely, a wandering flock joins temporarily a mixed flock over a swarm of army ants. It remains unknown whether interspecific flocking primarily helps to protect the birds against predation or mainly increases foraging efficiency.

## 8. Zoogeography

### 8.1. Analysis of the trans-Andean lowland forest avifauna

In order to interpret the nature of the northwestern Colombian forest avifauna and to understand some of its characteristic aspects, it is necessary to broaden the scope of our study and to incorporate in our analysis the tropical avifauna of the entire trans-Andean lowland forest region of which northwestern Colombia forms a small part. The Middle American landbridge is of zoogeographic importance as a connecting link and extensive, yet narrow, transition zone between the nearctic and neotropical realm (Simpson 1950, Darlington 1957, Stuart 1964). Griscom (1942), Mayr (1946, 1964) and Howell (1969) discuss general zoogeographic aspects of the entire avifauna of Middle America. The publications of Stuart (1966), Duellman (1966), and Savage (1966) provide important information on the ecology, composition, and history of the Central American herpetofauna and those of Baker (1963) and Ryan (1963) on the Middle American mammalian faunas.

In a zoogeographic study of the Middle American avifauna it is advantageous to separate initially analyses of the lowland and montane faunas and to distinguish between forest and nonforest elements. A future synthesis of the results of these separate studies will lead to an understanding of the composition and history of the Middle American avifauna as a whole. The Middle American mountains harbor many endemic species and permit the southward penetration into low latitudes of a number of northern elements which are lacking in the tropical lowlands of Middle America (Howell 1969; Haffer 1974, Fig. 8.3).

We are here concerned exclusively with an analysis of the avifauna of the trans-Andean humid lowland forests (Dry, Moist, Wet and Pluvial Forest in the Holdridge classification), which cover the Caribbean slope of Middle America from northwestern South America to southeastern Mexico (Fig. 1). Extensive forests along the drier Pacific slope of Middle America occur only in eastern and western Panamá as well as in the Golfo Dulce region of southwestern Costa Rica (Fig. 1). Whereas the avifauna of seasonal (monsoon) forests is included in the following discussion, the faunas of cloud forest and coniferous forest are excluded.

The close relationships of the trans-Andean forest fauna with the avifauna of Amazonia emphasized by previous authors (Chapman, Griscom, Mayr) indicate a fairly recent direct connection of these faunal areas. This contrasts with the situation found in the Middle American nonforest fauna whose relationships with the cis-Andean nonforest avifauna are rather weak (Mayr 1964, Haffer 1967 d).

Amazonian forest birds probably reached the trans-Andean lowlands in large numbers during humid climatic periods of the geological past, as discussed below, coming around the northern tip of the Andes and following the Caribbean lowlands westward to enter Middle America and Pacific Colombia via the Urabá region. A smaller group of Amazonian forest birds probably reached the Pacific lowlands of Ecuador-Colombia by crossing the Andes in northern Perú, where the locally narrow mountains offer a number of relatively low passes (Loja route, Marañón route; Chapman 1926, Haffer 1967 a). Extensive faunal interchange within the trans-Andean forest region led to the immigration of Middle American elements into northwestern South America and of northern and western Colombian species into Middle America, thus "blurring" to a certain extent the zoogeographic distinctness of the distribution centers (core areas) of the trans-Andean forest fauna analysed below.

8.1.1. *Size:* In order to elucidate the zoogeographic characteristics of the trans-Andean lowland forest avifauna, a broad definition of "forest species" should be applied. I designate as forest species birds of the forest interior as well as species inhabiting forest edges, riparian vegetation in forested areas, and species that are generally restricted to forested regions and disappear from an area once the forest has been cut. Water and swamp birds as well as aerial feeders such as swifts and swallows are excluded.

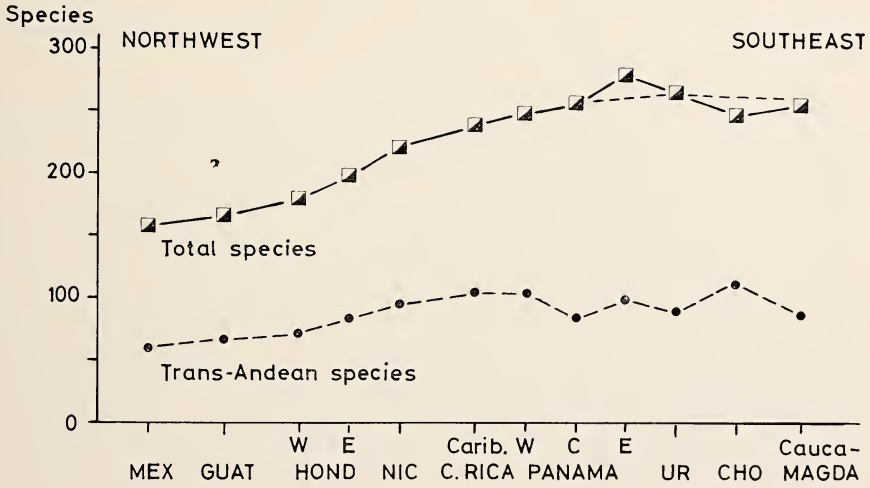


Fig. 10: Total number of forest bird species in the humid trans-Andean lowlands (upper curve) and number of exclusively trans-Andean forest species (lower curve). See Table 2 for details.

*Explanation:* MEX — Mexico. GUAT — Guatemala. HOND — Honduras (western and eastern). NIC — Nicaragua. Carib. C.RICA — Caribbean Costa Rica. PANAMA — Panamá (western, central, eastern). UR — Urabá region. CHO — Chocó region. CAUCA-MAGDA — Cauca-Magdalena region.

Based on these criteria, I have compiled the following data: The total number of species in the forested trans-Andean lowlands ranges from 280 in eastern Panamá to 156 species in southeastern Mexico (Fig. 10 and Table 2). The total number of species decreases gradually along the Middle American isthmus, presumably because of ecological reasons, more effective isolation from the Amazon basin, as well as a regional filter effect of the reduced available land area. The rate of reduction in species number is particularly high in Nicaragua, where pine savannas reduce the width of the rainforest belt (Howell 1971) and in Honduras, where steep mountains reach close to the coast, thus narrowing the humid lowlands appreciably (Monroe 1968). Also, the Middle American forests probably grow progressively less complex structurally and in plant species composition going northward. Through the reduction in the number of available niches, this situation may lead to the successive northward reduction in the number of forest bird species. There are, however, no field studies to substantiate this assumption (see also discussions by Slud, 1960: 141, and Howell, 1971: 231).

The northward reduction in species numbers of different avian families varies considerably (Fig. 11). Species-rich families suffer greater reduction on a percentage basis than families represented by only a few species like the toucans and jacamars. The decrease in species numbers of the more strictly forest-adapted antbirds (Formicariidae) is particularly conspicuous. Howell (1969) illustrated and discussed the varying species numbers of avian families along the Middle American isthmus combining, however, lowland and montane birds.

The locally higher and lower than expected total number of lowland forest species in eastern Panamá and in Pacific Colombia, respectively (Fig. 10), may be explained as follows: Environmental conditions in the Chocó region are more extreme, i. e. the climate is excessively humid and the vegetation cover is a solid blanket of Wet and Pluvial Forests. This may lead to some reduction in the number of widely distributed forest birds in the Chocó region, perhaps through the absence of certain feeding trees, of old tree trunks providing nest cavities and/or the absence of openings in the forest or forest edge situations, etc. Thus only six parrots are known from the central Chocó region compared to eleven species in the Urabá region and 13 parrots in the Cauca-Magdalena area of northern Colombia. Similarly, there are more Bucconidae (8 versus 6 species), Dendrocolaptidae (10 versus 7 species), Tyrannidae (27 versus 20 species), etc. in the Urabá region than in the Chocó area, presumably also because of the ecologically more extreme conditions in Pacific Colombia. On the other hand, these conditions lead to the presence, in the latter area, of the largest number of endemic trans-Andean birds, as discussed below.

Eastern Panamá combines, to a certain extent, ecological conditions of the Chocó and Urabá regions. Very humid forests extend northward from the

Table 2: Distributional analysis of the trans-Andean lowland forest avifauna [1])

| | SE-Mexico | Guatemala | W-Honduras | E-Honduras | Nicaragua | Pacific Costa Rica | Caribbean Costa Rica | Western Panamá | Central Panamá | Eastern Panamá | Urabá region | Chocó region | Cauca-Magdalena region | NW-Venezuela |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| A. Species of Caribbean northern Middle America (7 species) | 6 | 6 | 6 | 6 | 1 | | | | | | | | | |
| B. Species od Caribbean southern Middle America (14 species) | | | | 4 | 8 | 3 | 14 | 12 | 3 | 3 | 1 | | | |
| C. Species of Pacific southern Middle America (12 species) | | | | | | 12 | | 4 | | | | | | |
| D. Species of the Cauca-Magdalena region (14 species) | | | | | | | | | 2 | 7 | 8 | | 13 | 2 |
| E. Species of Pacific Colombia (32 species) | | | | | | | | | | 6 | 5 | 32 | 2 | |
| F. Middle American species (35 species) | 30 | 33 | 35 | 35 | 35 | 14 | 31 | 24 | 12 | 9 | 4 | 1 | 3 | 2 |
| G. Species of northwestern South America and southern Middle America (54 species) | | 3 | 6 | 12 | 22 | 10 | 32 | 37 | 45 | 52 | 51 | 54 | 47 | 6 |
| H. Species occupying most of the trans-Andean forest region (27 species) | 24 | 24 | 26 | 27 | 27 | 23 | 27 | 27 | 25 | 23 | 22 | 25 | 21 | 7 |
| Number of trans-Andean species | 60 | 66 | 73 | 84 | 93 | 62 | 104 | 104 | 87 | 100 | 91 | 112 | 86 | 17 |
| (Percent of total species) % | *39* | *41* | *40* | *42* | *43* | *38* | *44* | *41* | *34* | *35* | *34* | *45* | *34* | |
| Number of cis-Andean species undifferentiated or only sub-specifically differentiated in trans-Andean lowlands | 96 | 99 | 107 | 115 | 127 | 100 | 135 | 147 | 171 | 180 | 176 | 135 | 170 | |
| (Percent of total species) % | *61* | *59* | *60* | *58* | *57* | *62* | *56* | *59* | *66* | *65* | *66* | *55* | *66* | |
| Total species | 156 | 165 | 180 | 199 | 220 | 162 | 239 | 251 | 258 | 280 | 267 | 247 | 256 | |

1) *A total of 195 forest bird species are restricted to the trans-Andean lowlands. Of these birds 112 and 104 species are found in Pacific Colombia and Caribbean Costa Rica, respectively.*

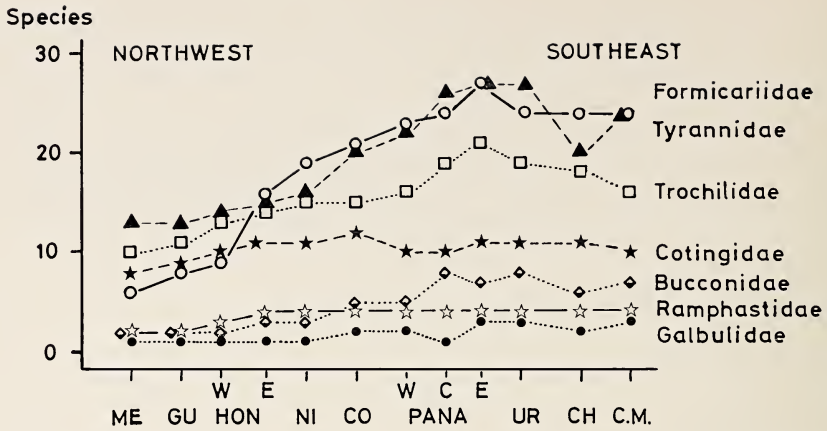


Fig. 11: Decrease of species numbers in selected bird families from northwestern Colombia along the Caribbean lowlands of Middle America to southeastern México.

*Explanation:* ME — southeastern Mexico. GU — Guatemala. HON — Honduras (western, eastern). NI — Nicaragua. CO — Costa Rica. PANA — Panamá (western, central, eastern). UR — Urabá region. CH — Chocó region. C.M. — Cauca-Magdalena region. Open circles — Formicariidae. Solid triangles — Tyrannidae.

Chocó along the mountains of Darién harboring Chocó birds like *Cryptturellus kerriae, Xenornis setifrons, Carpodectes hopkei, Tangara palmeri* to mention only a few that are missing from central Panamá and farther north. At the same time, less humid conditions comparable to those prevailing in northern Colombia and in the Urabá region are found in parts of eastern Panamá permitting the occurrence of forest birds that are missing from the Chocó probably because of ecological reasons. Thus the greater ecological range of forest habitats in the relatively small area of eastern Panamá probably explains the locally increased species diversity in this region.

Table 3 provides details of the size of various regional trans-Andean and Amazonian forest avifaunas. This table also compares the number of birds in each family at three individual forest sites studied in detail (La Selva, Costa Rica; Yarinacocha and Balta, both in eastern Perú). The size of the rich forest avifaunas of Pacific Colombia and of humid Caribbean Costa Rica is fairly similar, viz. 247 and 239 species, respectively. Trans-Andean birds represent 45 % and 44 % of these faunas. The rest of the species are shared with Amazonia. The Chocó fauna has usually one or two more species in each family than the Caribbean Costa Rican fauna. This, however, is reversed in the parrots, owls, motmots, woodcreepers, and finches which are represented by less species in the Chocó region. In the case of the owls the total of four species for the Chocó fauna may

Table 3: Composition of the trans-Andean and cis-Andean lowland forest avifaunas. Comparison by families; exclusive of water birds and aerial feeders such as swifts and swallows.

| Family | Number of sympatric species 1) | | | | | | |
|---|---|---|---|---|---|---|---|
| | Trans-Andean Avifauna | | | Cis-Andean Avifauna | | | |
| | La Selva, Costa Rica | Caribbean Middle America | Pacific Colombia | SE-Colombia | Surinam | Yarina Cocha | Balta, E-Peru |
| Tinamidae | 3 | 3(1) | 4(2) | 6(4) | 4(1) | 6 | 9 |
| Accipitridae | 9 | 20(1) | 18(2) | 17(2) | 17(2) | 11 | 8 |
| Falconidae | 6 | 7(0) | 8(1) | 8(1) | 7(1) | 7 | 7 |
| Cracidae | 2 | 2(2) | 3(3) | 6(6) | 3(3) | 3 | 3 |
| Phasianidae | 2 | 2(2) | 2(2) | 1(0) | 1(0) | 1 | 2 |
| Psophiidae | 0 | 0(0) | 0(0) | 1(1) | 1(1) | 0 | 1 |
| Eurypygidae | 1 | 1(0) | 1(0) | 1(0) | 1(0) | 1 | 1 |
| Columbidae | 6 | 10(4) | 11(5) | 7(1) | 7(1) | 7 | 6 |
| Psittacidae | 6 | 10(6) | 6(3) | 16(10) | 15(7) | 11 | 13 |
| Cuculidae | 2 | 2(0) | 3(1) | 4(1) | 3(1) | 4 | 6 |
| Nyctibiidae | 1 | 1(0) | 2(0) | 3(0) | 2(0) | 2 | 2 |
| Caprimulgidae | 1 | 2(0) | 2(0) | 3(2) | 3(2) | 2 | 4 |
| Strigidae | 5 | 7(1) | 4(1) | 6(2) | 5(2) | 6 | 5 |
| Trochilidae | 13 | 16(9) | 18(12) | 23(16) | 10(7) | 12 | 12 |
| Trogonidae | 4 | 4(2) | 4(2) | 6(1) | 5(0) | 6 | 4 |
| Alcedinidae | 5 | 5(0) | 5(0) | 5(0) | 5(0) | 5 | 5 |
| Momotidae | 2 | 4(2) | 1(0) | 3(0) | 1(0) | 3 | 3 |
| Galbulidae | 2 | 2(0) | 2(0) | 7(6) | 6(5) | 4 | 3 |
| Bucconidae | 4 | 5(1) | 6(4) | 8(7) | 5(3) | 8 | 8 |
| Capitonidae | 0 | 0(0) | 3(3) | 3(3) | 1(0) | 2 | 2 |
| Ramphastidae | 4 | 4(3) | 4(3) | 7(6) | 5(4) | 7 | 8 |
| Picidae | 6 | 6(5) | 9(7) | 14(10) | 11(8) | 14 | 10 |
| Dendrocolaptidae | 7 | 11(4) | 7(3) | 12(6) | 12(6) | 11 | 14 |
| Furnariidae | 5 | 5(2) | 7(3) | 22(17) | 10(7) | 8 | 19 |
| Formicariidae | 17 | 21(11) | 24(13) | 66(53) | 37(28) | 27 | 43 |
| Conopophagidae | 0 | 0(0) | 0(0) | 2(2) | 2(2) | 0 | 2 |
| Rhinocryptidae | 0 | 0(0) | 0(0) | 1(1) | 0(0) | 0 | 1 |
| Cotingidae | 12 | 12(8) | 11(7) | 19(14) | 19(16) | 16 | 15 |
| Rupicolidae | 0 | 0(0) | 0(0) | 1(1) | 1(1) | 0 | 0 |
| Pipridae | 4 | 4(3) | 7(4) | 10(4) | 9(4) | 7 | 5 |
| Tyrannidae | 18 | 20(6) | 20(4) | 28(12) | 20(14) | 20 | 25 |
| Corvidae | 0 | 1(1) | 1(1) | 1(1) | 1(1) | 1 | 1 |
| Troglodytidae | 7 | 7(5) | 7(5) | 4(3) | 3(2) | 5 | 4 |
| Turdidae | 1 | 1(0) | 1(0) | 2(0) | 2(0) | 2 | 2 |
| Sylviidae | 2 | 2(0) | 3(1) | 2(1) | 2(1) | 2 | 0 |
| Vireonidae | 3 | 4(2) | 4(1) | 6(4) | 6(2) | 3 | 5 |
| Icteridae | 3 | 3(2) | 3(2) | 8(6) | 2(1) | 4 | 9 |
| Parulidae | 2 | 2(1) | 2(1) | 1(1) | 2(1) | 0 | 1 |
| Coerebidae | 3 | 5(2) | 6(2) | 8(4) | 5(0) | 6 | 4 |
| Thraupidae | 14 | 19(15) | 21(15) | 24(16) | 16(12) | 19 | 21 |
| Fringillidae | 7 | 9(3) | 7(1) | 5(1) | 6(2) | 3 | 4 |
| Total | 189 | 239(104) | 247(111) | 377(226) | 273(148) | 256 | 297 |

1) *Added to the total number of sympatric birds is in parentheses the number of species endemic in the trans-Andean region (two left columns) and in Amazonia (two right columns). The number in parentheses, of course, includes the species endemic to each individual area.*

be incomplete. The motmots originated in Middle America and are represented by four species in Caribbean Costa Rica and by only one species in the central Chocó.

Southeastern Colombia harbors 377 forest species, although only 250 to 300 species may be found at any single locality. However, long term observations in this region have not been conducted. O'Neill (1974) and O'Neill et al. (1974) recently provided complete lists of the birds at two localities in eastern Peru, viz. Balta, Río Curanja (headwater region of the Rio Purus) and Yarinacocha in the valley of the Río Ucayali (Table 3). The bird fauna of the Balta forest is extremely rich; e. g. nine species of tinamous (Tinamidae), eight species of toucans (Ramphastidae), and 43 species of antbirds (Formicariidae) are sympatric there, probably the largest numbers of allies in these families to be found together at a single locality anywhere in the tropics of South America. O'Neill (1974) provided interesting discussions on the "ecological sorting mechanisms" by which sympatric congeneric species avoid, or at least reduce, ecological competition. I consider 297 birds of the Balta fauna and 257 species of the Yarinacocha fauna as forest species. Applying a somewhat more restrictive definition, O'Neill (1974) accepts only 251 species as primarily forest-inhabiting at Balta. These figures compare with a total of 189 forest birds at La Selva, Costa Rica (Table 3). I compiled the latter figure from the lists published by Slud (1960).

8.1.2. *Composition:* The trans-Andean lowland forest avifauna has a pronounced Amazonian character, as mentioned above. 55 to 66 % of the species composing the trans-Andean fauna are either undifferentiated or at most subspecifically distinct from the representative Amazonian populations (Table 2). Even among the 195 endemic trans-Andean forest species many are closely related to their Amazonian representatives and are just at or barely above the level of species differentiation (Figs. 12, 13; Table 4). In these cases the northern Andes and the extensive grass plains (Llanos) of central Venezuela and eastern Colombia separate the trans-Andean and Amazonian representatives. Only few of them have later extended their ranges and made contact in narrow forest corridors along the base of the Venezuelan or northern Colombian mountains.

The most distinct and perhaps oldest elements of the trans-Andean fauna are 30 species, which belong to 22 or 23 endemic trans-Andean genera 15 or 16 of which are monotypic (Table 5). Their cis-Andean representatives are, in most cases, unknown and are probably extinct.

I analysed the geographical distribution of the 195 trans-Andean species, first, by calculating a "faunal resemblance factor" for various trans-Andean forest avifaunas and, second, by considering individual species ranges and establishing several distribution centers or core areas. In calculating the

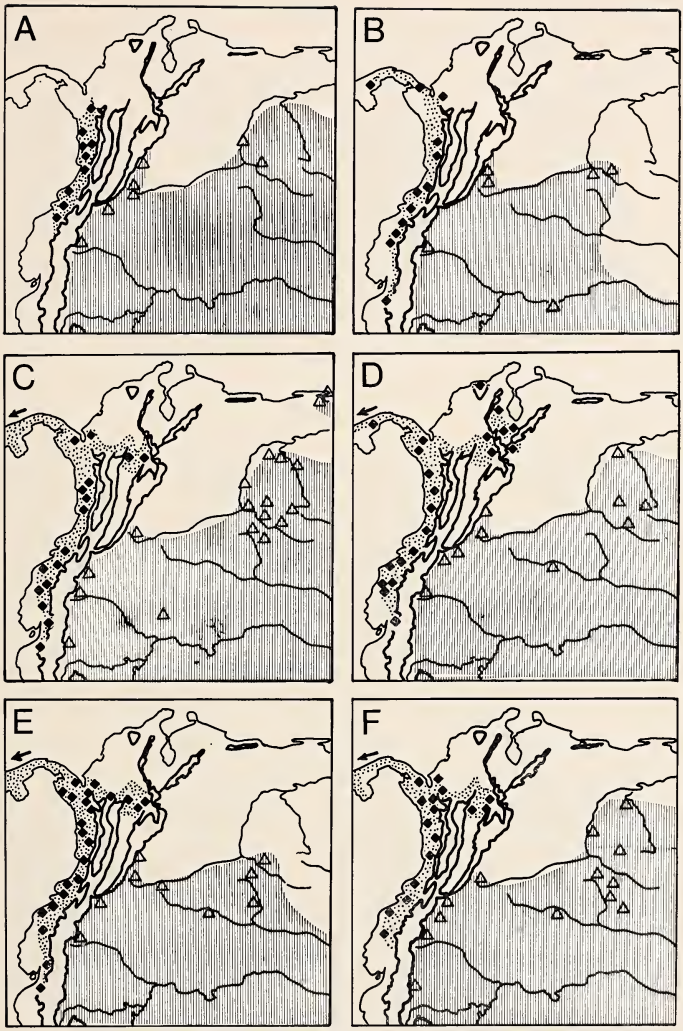


Fig. 12: Distribution of selected trans-Andean forest birds and their Amazonian representatives. Note separation of allies by northern Andes.

*Explanation:* Heavy black line delimits mountain ranges above 1000 m elevation. Arrow indicates that range extends into northern Middle America. The Pacific representative (locality records shown as solid squares, range stippled) is listed first, its Amazonian ally second (selected locality records shown as open triangles, range shaded): **A** Tinamous *Crypturellus berlepschi* — *C. cinereus.* **B** Forest hawks *Leucopternis plumbea* — *L. schistacea.* **C** Hummingbirds *Heliothryx barroti* — *H. aurita.* **D** Hummingbirds *Threnetes ruckeri* — *T. leucurus.* **E** Puffbirds *Malacoptila panamensis* — *M. fusca.* **F** Antbirds *Hylophylax naevioides* — *H. naevia.*

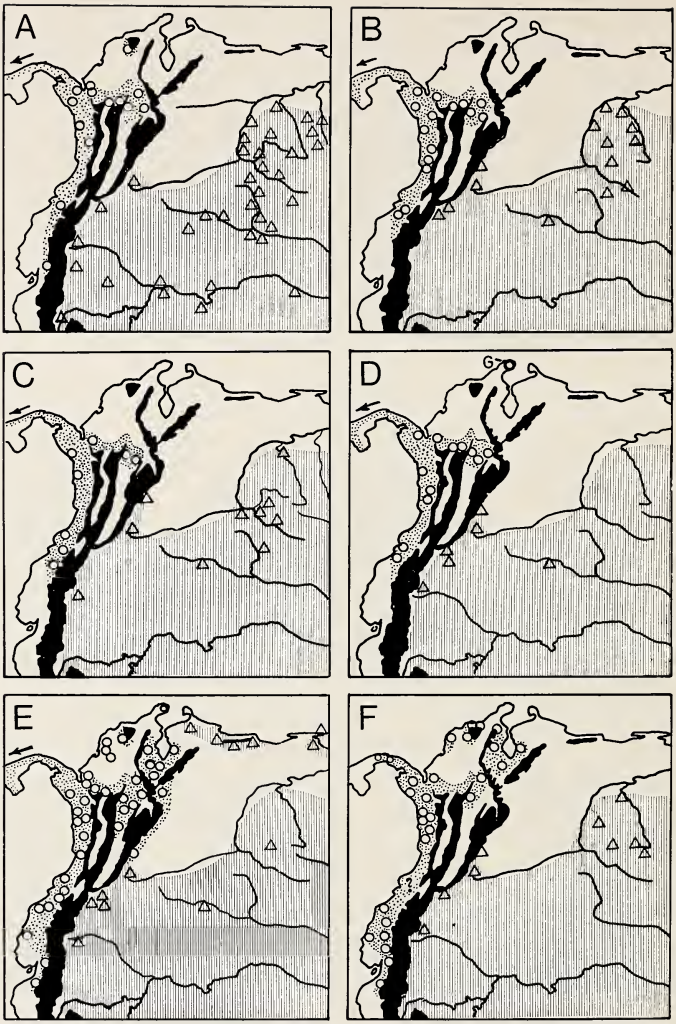


Fig. 13: Distribution of selected trans-Andean forest birds and their Amazonian representatives. Note separation of allies by northern Andes, except in E.

*Explanation:* Andes mountains above 1000 m elevation are in black. Arrow indicates that range extends into northern Middle America. The Pacific representative (locality records shown as open circles, range stippled) is listed first, its Amazonian ally second (selected locality records shown as open triangles, range shaded): **A** Woodpeckers *Celeus loricatus* — *C. grammicus*. **B** Mourners *Rhytipterna holerythra* — *R. simplex*. **C** Mourners *Laniocera rufescens* — *L. hypopyrrha*. **D** Pihas *Lipaugus unirufus* — *L. vociferans*. **E** Becards *Pachyramphus cinnamomeus* — *P. castaneus*. **F** Becards *Pachyramphus homochrous* — *P. minor*; in this group, *P. aglaiae* is the representative in northern Middle America.

Table 4: Some trans-Andean isolates of the forest fauna at or near the species level of differentiation, with their cis-Andean representatives. Modified from Haffer (1974 b). See also Figures 12 and 13.

| Family | Trans-Andean Elements | Cis-Andean Elements |
|---|---|---|
| Tinamous | *Crypturellus berlepschi* *) | *C. cinereus* |
| Hawks | *Leucopternis semiplumbea* | *L. melanops* + *L. kuhli* |
| | *Leucopternis plumbea* *) | *L. schistacea* |
| Falcons | *Micrastur plumbeus* | *M. gilvicollis* |
| Rails | *Laterallus albigularis* *) | *L. melanophaius* |
| Parrots | *Pionopsitta pulchra* + *P. haematotis* | *P. barrabandi* + *P. caica* + *P. vulturina (Haffer 1970 a)* |
| Hummingbirds | *Heliothrix barroti* *) | *H. aurita* |
| | *Threnetes ruckeri* | *T. leucurus* |
| Puffbirds | *Bucco noanamae* | *B. tamatia* |
| | *Nystalus radiatus* | *N. chacuru* |
| | *Malacoptila panamensis* | *M. fusca* |
| Woodpeckers | *Celeus loricatus* | *C. grammicus* + *C. undatus* |
| Furnariidae | *Xenerpestes minlosi* | *X. singularis* |
| Antbirds | *Hylophylax naevioides* | *H. naevia* |
| | *Myrmotherula fulviventris* | *M. leucophthalma* |
| | *Myrmornis stictoptera* *) | *M. torquata* |
| Cotingas | *Cotinga nattereri* + *C. ridgwayi* + *C. amabilis* | *C. maynana* + *C. cotinga* + *C. maculata* |
| | *Lipaugus unirufus* | *L. vociferans* |
| | *Pachyramphus cinnamomeus* | *P. castaneus* |
| | *Pachyramphus homochrous* | *P. minor* |
| Flycatchers | *Rhytipterna holerythra* | *R. simplex* |
| | *Laniocera rufescens* | *L. hypopyrrha* |
| | *Myiobius sulphureipygius* *) | *M. barbatus* |
| | *Myiornis atricapillus* *) | *M. ecaudatus* |
| Wrens | *Cyphorhinus phaeocephalus* *) | *C. arada* |
| Gnatcatchers | *Polioptila schistaceigula* | *P. guianensis* |
| Oropendolas | *Psarocolius montezuma* + *P. cassini* + *P. guatimozinus* | *P. bifasciatus (incl. yuracares)* |
| Warblers | *Basileuterus fulvicauda* *) | *B. rivularis* |
| Tanagers | *Mitrospingus cassinii* | *M. oleagineus* |
| | *Tangara larvata* *) | *T. nigrocincta* |

*) Trans-Andean forms marked with an asterisk (*) are variously treated by authors as subspecies of the cis-Andean population or as separate species.

Table 5: Trans-Andean isolates of the forest fauna at the genus level of differentiation, with their presumed cis-Andean representatives. The ranges of several examples are shown in Figures 21 and 22.

| Family | Trans-Andean Genera | Cis-Andean Allies [1] |
|---|---|---|
| Quails | *Rhynchortyx cinctus* (m) [2] | —— |
| Hummingbirds | *Androdon aequatorialis* (m) | ? |
| | *Damophila julie* (m) | ? |
| | *Microchera albocoronata* (m) | ? |
| Motmots | *Hylomanes momotula* (m) | —— |
| Antbirds | *Sipia berlepschi* and *S. rosenbergi* | *Cercomacra* sp. |
| | *Clytoctantes alixi* (m) | ? |
| | *Xenornis setifrons* (m) | *Pygiptila* sp. |
| | *Gymnocichla nudiceps* (m) | ? |
| | *Phaenostictus mcleannani* (m) | *Phlegopsis* sp. |
| | *Pittasoma michleri* and *P. rufopileatum* | ? |
| Cotingas | *Carpodectes nitidus*, *C. antoniae*, and *C. hopkei* | *Xipholena* sp. |
| Manakins | *Allocotopterus deliciosus* (m) | *Machaeropterus* sp. |
| | *Sapayoa aenigma* (m) | ? |
| Flycatchers | *Oncostoma cinereigulare* and *O. olivaceum* | ? |
| | *Aphanotriccus capitalis* and *A. audax* [3] | ? |
| Wrens | *Uropsila leucogastra* (m) | —— |
| Icterids | *Zarhynchus wagleri* (m) | *Ocyalus latirostris* |
| Tanagers | *Phlogothraupis sanguinea* (m) | —— |
| | *Erythrothlypis salmoni* (m) | *Thlypopsis* sp. |
| | *Heterospingus rubrifrons* and *H. xanthopygius* | *Tachyphonus* sp. |
| | *Bangsia arcaei*, *B. rothschildi* (three additional species in montane forest of western Colombia) | *? Wetmorethraupis sterrhopteron* |

[1] A dash indicates that the trans-Andean ancestor probably never reached the Amazonian region. A question mark indicates that the cis-Andean representative is unknown or possibly extinct.

[2] m — monotypic.

[3] *A. audax* is often separated generically from *Aphanotriccus* as the monotypic genus *Praedo*.

faunal resemblance factor (FRF) I used the method proposed by Duellman (1966: 710):

$$FRF = \frac{2\ C}{N_1 + N_2}$$

Where $N_1$ and $N_2$ are the numbers of species (here trans-Andean species) in any two given faunas, and C is the number of trans-Andean species common to both faunas. The actual number of trans-Andean species in any given fauna, the number of trans-Andean species in common between any two faunas, and the faunal resemblance factor for each faunal comparison are tabulated (Table 6). Because of the continuity of the lowland forests from northwestern Colombia along the Caribbean slope of Middle America north to Mexico, no distinct faunal breaks occur. This impression would be strengthened if we included in our tabulation the Amazonian species which represent over half of the trans-Andean forest avifauna and decrease in numbers northward (Fig. 10). Changes in species composition of the forest fauna are gradual along the Middle American isthmus. For example, of the 104 trans-Andean species occurring in Western Panamá, 93 species inhabit Caribbean Costa Rica and 76 species are found in Caribbean Nicaragua. We notice in Table 6 also that 24 species of a total 112 trans-Andean

Table 6: Comparison of avifaunal assemblages in humid tropical lowlands west of the Andes, exclusive of Amazonian species. Distributional analysis of 195 endemic trans-Andean species.

| Faunal Resemblance Factor | Trans-Andean Species in Common | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|
| | Southwestern Mexico | Caribbean Honduras | Caribbean Nicaragua | Caribbean Costa Rica | Western Panamá | Central Panamá | Eastern Panamá | Chocó lowlands | Cauca-Magdalena region |
| Southwestern Mexico | **60** | 59 | 57 | 54 | 46 | 34 | 29 | 24 | 19 |
| Caribbean Honduras | .82 | **84** | 79 | 73 | 63 | 48 | 43 | 39 | 32 |
| Caribbean Nicaragua | .75 | .89 | **93** | 87 | 76 | 57 | 53 | 48 | 42 |
| Caribbean Costa Rica | .66 | .78 | .88 | **104** | 93 | 65 | 63 | 58 | 46 |
| Western Panamá | .56 | .67 | .77 | .89 | **104** | 68 | 67 | 62 | 51 |
| Central Panamá | .46 | .56 | .63 | .68 | .71 | **87** | 81 | 69 | 64 |
| Eastern Panamá | .36 | .47 | .55 | .62 | .66 | .87 | **100** | 79 | 74 |
| Chocó lowlands | .28 | .40 | .47 | .54 | .57 | .69 | .75 | **112** | 66 |
| Cauca-Magdalena region | .26 | .38 | .47 | .48 | .54 | .74 | .80 | .66 | **86** |

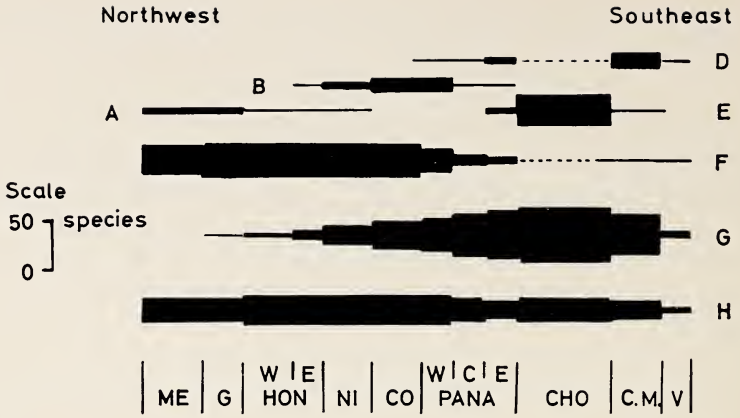


Fig. 14: Distributional analysis of the 195 exclusively trans-Andean lowland forest bird species. Species groups are labelled following Table 2 (see text for species lists).

*Explanation:* ME — Mexico. G — Guatemala. HON — Honduras (western, eastern). NI — Nicaragua. CO — Caribbean Costa Rica. PANA — Panamá (western, central, eastern). CHO — Chocó region. C. M. — Cauca-Magdalena region. V — nordwestern Venezuela. Stippled line indicates that species group is not represented.

species in the Chocó region range north into southwestern Mexico [1]). Since a total of 60 trans-Andean species occur in southwestern Mexico, the balance of 36 species indicate the existence of a strong Middle American element which, however, cannot be studied with the method of faunal analysis under discussion. The same probably applies to the herpetofaunas of the Middle American lowland forests as tabulated by Duellman (1966: 712). For example, of the total of 125 species recorded from Central Panamá only 38 species occur in southwestern Mexico. Here the total fauna comprises 93 species thus indicating the existence in Mexico of 55 Middle American species which are unknown in Panamá and replaced by southern Middle American or South American representatives. Centers of endemism in the trans-Andean humid tropical lowlands are not conspicuous in the avifauna or the herpetofauna. However, such centers do exist and are of importance for an understanding of the differentiation of the trans-Andean lowland forest faunas.

We observe local concentrations of endemic trans-Andean bird species in the forests of Pacific Colombia (112 species, 45 % of the local forest

[1]) Table 6 further illustrates the close relationships of the Nechí fauna (Cauca-Magdalena fauna) with the fauna of eastern and central Panamá which have more trans-Andean species in common and, therefore, a higher faunal resemblance factor (0.80 and 0.74, respectively) than the Chocó fauna and the Nechí fauna (FRF=0.66).

fauna) and of Caribbean Costa Rica (104 species, 44 % of the local forest fauna); see Fig. 10. Analysing the distribution of those 195 bird species that are restricted to the humid trans-Andean lowlands, we distinguish on the basis of their geographic distribution several distinct groups (Fig. 14 and Table 2; the species of Groups A, B, C, D, and E are listed and discussed on p. 51 ff.):

A. Species of Caribbean northern Middle America: 7 species (Fig. 15).

B. Species of Caribbean southern Middle America: 14 species (Fig. 15).

C. Species of Pacific southern Middle America: 12 species (Fig. 15).

D. Species of the Cauca-Magdalena region, northern Colombia: 14 species (Fig. 16).

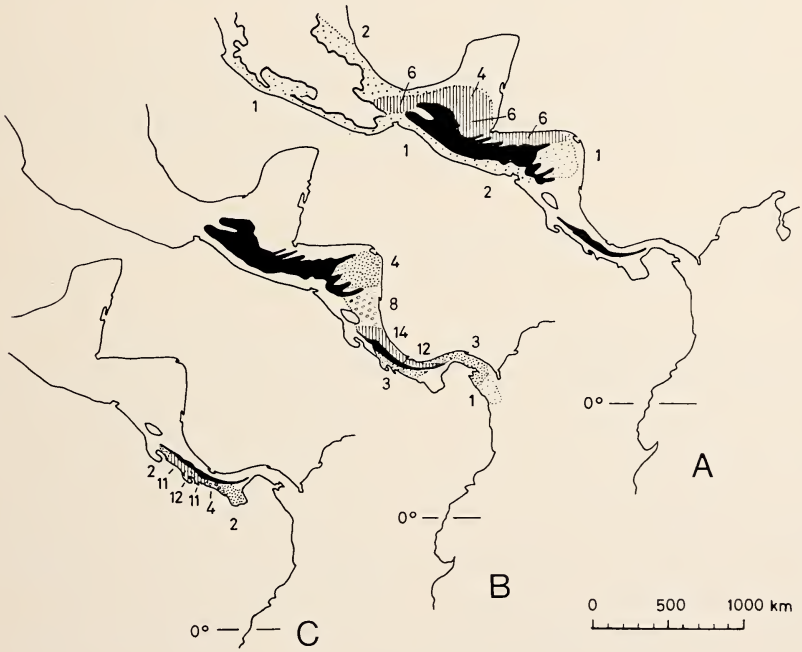


Fig. 15: Distribution centers *(core areas)* of the Middle American lowland forest avifauna. **A** Caribbean northern Middle American center. **B** Caribbean Costa Rica center. **C** Pacific Costa Rica center.

*Explanation:* Superimposed ranges of 7 endemic species in A; of 14 endemic species in B; and of 12 endemic species in C (Groups A, B, and C of Table 2, respectively). Numbers indicate totals of species recorded. See text for species lists and for further details. Mountains above 1000 m elevation are in black.

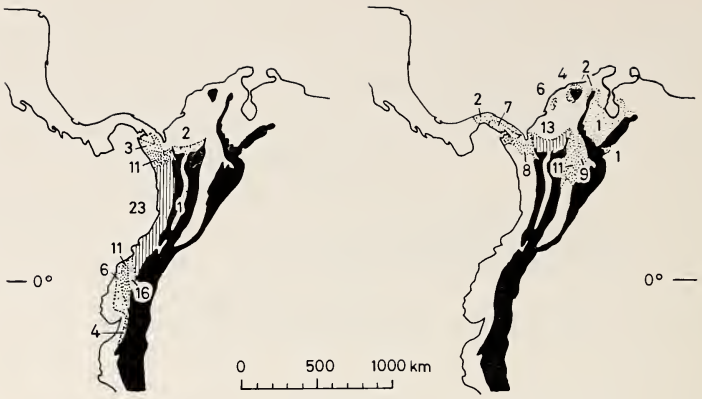


Fig. 16: Distribution centers *(core areas)* of the northwestern Colombian lowland forest avifauna. Left — Pacific Colombian (Chocó) center. Right — Cauca-Magdalena (Nechí) center.

*Explanation:* Superimposed ranges of 32 endemic species (left) and of 14 endemic species (right); Groups E and D of Table 2, respectively. Numbers indicate totals of species recorded. See text for species lists and for further details. Andes mountains above 1 000 m elevation are in black. Note: Number 2 in northern Colombia of left map should read 3.

E. Species of Pacific Colombia, Chocó region: 32 species (Fig. 16).

F. Middle American species: 35 species (Fig. 17):

*Crypturellus boucardi* (M, C) [1])
*Columba nigrirostris* (M, P)
*Pionopsitta haematotis* (M, Col)
*Aratinga astec* (M, P)
*Pionus senilis* (M, P)
*Chlorostilbon canivetii* (M, C)
*Hylocharis eliciae* (M, P)
*Amazilia candida* (M, C)
*Hylomanes momotula* (M, Col)
*Electron carinatum* (M, C)
*Ramphastos sulfuratus* (M, V)
*Piculus simplex* (H, P)
*Celeus castaneus* (M, P)
*Phloeoceastes guatemalensis* (M, P)
*Dendrocincla anabatina* (M, P)
*Xiphorhynchus flavigaster* (M, C)
*Gymnocichla nudiceps* (G, Col)
*Cotinga amabilis* (M, C)
*Carpodectes nitidus* * (H, P) [2])
*Pachyramphus aglaiae* * (US, C)
*Piprites griseiceps* (G, C)
*Manacus candei* (M, C)

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[1]) The range of each species in this and the following lists is indicated by giving the northernmost and southernmost area inhabited. Abbreviations are as follows: M Mexico, G Guatemala, H Honduras, N Nicaragua, C Costa Rica, P Panamá, Col Colombia, V Venezuela, E northwestern Ecuador, Pe northwestern Peru.

[2]) Species in this and the following lists marked with an asterisk (*) are treated by some authors as conspecific with an allopatric ally restricted to other portions of the trans-Andean lowlands.

*Oncostoma cinereigulare* • (M, P)
*Ornithion semiflavum* • (M, C)
*Smaragdolanius pulchellus* (M, V)
*Hylophilus decurtatus* (M, P)
*Psarocolius montezuma* (M, P)
*Cyanerpes lucidus* (M, Col)
*Euphonia lauta* (M, P)
*Euphonia gouldi* (M, P)
*Ramphocelus passerinii* (M, P)
*Phlogothraupis sanguinolenta* (M, P)
*Habia fuscicauda* (M, Col)
*Saltator atriceps* (M, P)
*Caryothraustes poliogaster* (M, P)

These 35 species are widely distributed along the humid Caribbean lowlands of Middle America from southeastern Mexico usually to the Almirante region of western Panamá (Fig. 17). Fourteen species also occupied the Pacific forests of southwestern Costa Rica. Nine and four species reached eastern Panamá and the Urabá region, respectively. One species, viz. *Hylomanes momotula,* entered the northern Chocó region and three birds recur in the Serranía de San Jacinto of northern Colombia near the Caribbean coast, viz. *Gymnocichla nudiceps, Habia fuscicauda,* and *Ramphastos sulfuratus.* The latter toucan's eastward advance was checked in the forest west of Lake Maracaibo, where it came in contact with its competitor *R. vitellinus. Gymnocichla nudiceps* also occurs along the humid northern base of the Serranía de Macuira on the arid outer Guajira Peninsula and is the only species of this Middle American group found in the humid middle Magdalena Valley of central Colombia.

G. Species of western Colombia and southern Middle America: 54 species (Fig. 18):

*Leucopternis plumbea* ǂ (P, Pe) [3])
*Leucopternis semiplumbea* (H, E)
*Odontophorus erythrops* (H, E)
*Rhynchortyx cinctus* (H, E)
*Geotrygon veraguensis* (C, E)
*Ara ambigua* (H, E)
*Touit dilectissima* (P, V)
*Popelairia conversii* (C, E)
*Glaucis aenea* (N, E; except central Panamá to northern Chocó)
*Amazilia amabilis* (N, E)
*Damophila julie* (P, E)
*Threnetes ruckeri* (G, E)
*Chalybura urochrysia* (N, E)
*Notharchus pectoralis* (P, E)
*Nystalus radiatus* (P, E)
*Capito maculicoronatus* (P, Col)
*Selenidera spectabilis* (H, E)
*Celeus loricatus* (N, E)
*Xiphorhynchus lachrymosus* (N, E)
*Xenerpestes minlosi* (P, Col)
*Dysithamnus puncticeps* (P, E)
*Myrmotherula fulviventris* (H, E)
*Myrmeciza exsul* (N, E)
*Myrmeciza laemosticta* (C, V, E)
*Hylophylax naevioides* (H, E)
*Phaenostictus mcleannani* (H, E)
*Myrmornis stictoptera* ǂ (N, Col)
*Formicarius nigricapillus* (C, E; except central Panamá to Urabá)

[3]) Species of this and the following lists marked with a dagger (ǂ) are treated by some authors as conspecific with a cis-Andean ally.

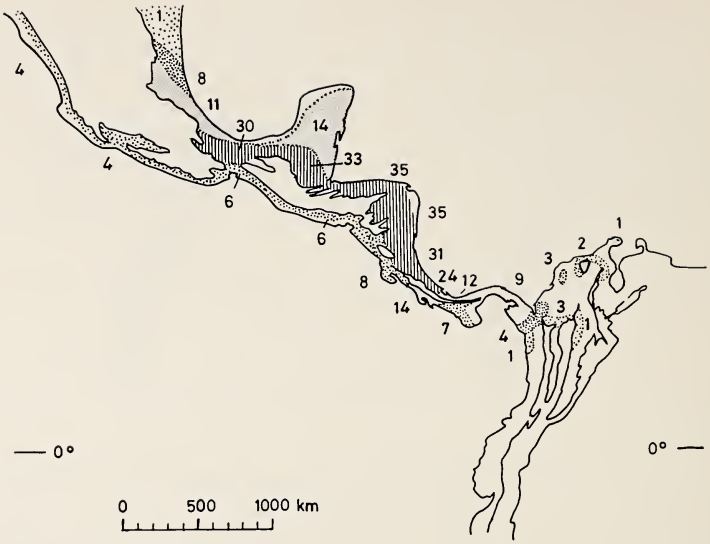


Fig. 17: Distribution of Middle American lowland forest birds.

*Explanation:* Superimposed ranges of 35 Middle American species (Group F of Table 2); numbers indicate totals of species recorded. See text for species list. Black line delimits mountains above 1000 m elevation.

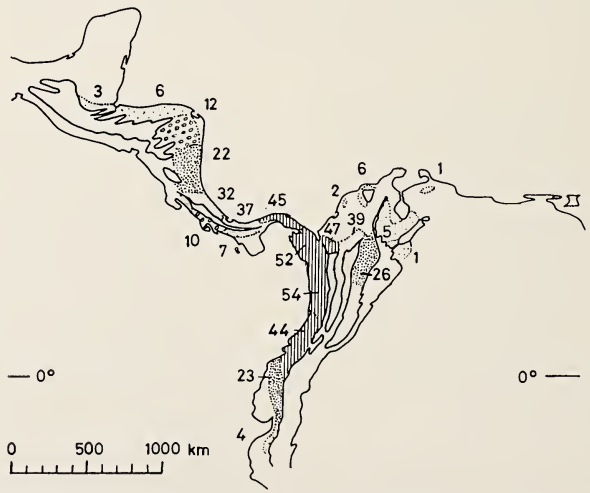


Fig. 18: Distribution of lowland forest birds of western Colombia — southern Central America.

*Explanation:* Superimposed ranges of 54 species (Group G of Table 2). Numbers indicate totals of species recorded. See text for species list. Black line delimits mountains above 1000 m elevation.

*Hylopezus perspicillatus* (N, E)
*Cotinga nattererii* (P, V, E)
*Laniocera rufescens* (G, E)
*Pachyramphus homochrous* • (P, V, Pe)
*Manacus vitellinus* (P, Col)
*Sapayoa aenigma* (P, E)
*Ornithion brunneicapillum* • (C, E)
*Myiornis atricapillus* † (C, E)
*Cyphorhinus phaeocephalus* † (H, E)
*Campylorhynchus albobrunneus* (P, Col)
*Thryothorus fasciatoventris* (C, Col)
*Thryothorus nigricapillus* (N, E)
*Thryothorus leucopogon* • (P, E)
*Polioptila schistaceigula* (P, E)
*Cyanocorax affinis* (C, Col)
*Hylophilus minor* (P, E)
*Dacnis venusta* (C, E)
*Tangara inornata* (C, Col)
*Tangara lavinia* (G, E)
*Tangara florida* (C, Col)
*Tachyphonus delattrii* (N, E)
*Chlorothraupis olivacea* (P, E)
*Ramphocelus icteronotus* (P, E)
*Ramphocelus dimidiatus* (P, V)
*Heterospingus xanthopygius* (P, E)
*Mitrospingus cassini* (C, E)

Because of the continuity of the forests, these 54 species extended their ranges from Pacific Colombia for varying distances into the Cauca-Magdalena region and into Middle America, thus occupying the combined distribution areas of species groups B, D, and E.

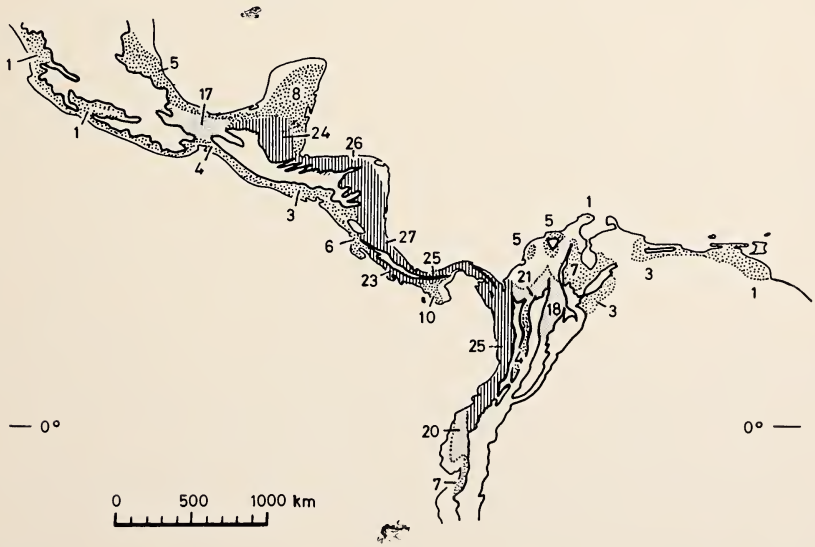


Fig. 19: Distribution of wide ranging trans-Andean lowland forest birds.

*Explanation:* Superimposed ranges of 27 trans-Andean species (Group H of Table 2). Numbers indicate totals of species recorded. See text for species list. Black line delimits mountains above 1000 m elevation.

H. Wide ranging trans-Andean forest birds: 27 species (Fig. 19):

*Penelope purpurascens* (M, V, E)
*Crax rubra* (M, E)
*Ciccaba nigrolineata* † (M, V, Pe)
*Leptotila plumbeiceps* (M, Col; except central Panamá to Urabá)
*Leptotila cassinii* (M, Col)
*Heliothryx barroti* † (M, E)
*Amazilia tzacatl* (M, V, E)
*Trogon massena* (M, E)
*Malacoptila panamensis* (M, E)
*Pteroglossus torquatus* (M, V)
*Melanerpes pucherani* (M, E)
*Xiphorhynchus erythropygius* (M, E)
*Dendrocincla homochroa* (M, V)
*Synallaxis brachyura* (H, E) [1])
*Sclerurus guatemalensis* (M, E)
*Pachyramphus cinnamomeus* (M, V, E)
*Rhytipterna holerythra* (M, E)
*Lipaugus unirufus* (M, E)
*Gymnopithys bicolor* † (H, E)
*Pipra mentalis* (M, E; except eastern Panamá to Urabá)
*Rhynchocyclus brevirostris* (M, E; except lowlands eastern Panamá to Urabá region)
*Myiobius sulphureipygius* † (M, E)
*Campylorhynchus zonatus* (M, E; except central Panamá and Pacific Colombia)
*Geothlypis semiflava* (M, E; except Panamá to Urabá region)
*Tangara larvata* † (M, E)
*Zarhynchus wagleri* (M, E)
*Amaurospiza concolor* (M, E)

These 27 species occupy most of the trans-Andean forests from western Colombia or northwestern Ecuador north to Guatemala — southeastern Mexico (Fig. 19). Only 18 of them inhabit the humid middle Magdalena Valley and seven species reached the Maracaibo basin of northwestern Venezuela. The occurrence of *Lipaugus unirufus* on the outer Guajira Peninsula needs confirmation. The widespread trans-Andean guan *Penelope purpurascens* advanced east to the mouth of the Orinoco River. The forests of northern and northwestern Venezuela represent zoogeographically a wide transition zone between the trans-Andean and the cis-Andean faunal regions.

Most of the trans-Andean species (groups F, G, H; 116 species or 60 % of the total of 195 species; Fig. 14) are widely distributed testifying to the ecological uniformity of the forests in the lowlands west of the Andes. The species of group F probably originated somewhere in Middle America (Guatemala or Costa Rica region). Conversely, most or all species of group G probably spread from western Colombia northward. The wide distribution of group H prevents any interpretation as to their possible area of origin in the trans-Andean lowland region. On the other hand, the species comprising groups A, B, C, D, and E are very restricted geographically and characterize conspicuous distribution centers *(core areas)*, which may represent the differentiation and dispersal centers for the entire trans-Andean lowland forest avifauna. These centers are discussed in detail in the following section.

[1]) *Synallaxis brachyura jaraguana* of southern Goiás, east-central Brasil, may represent a distinct species (De Schauensee 1966: 246).

8.1.3. *Distribution centers:* In a comparative study of the distribution areas of animal species inhabiting a given region, geographically-ecologically related species are recognized. By superimposing outline maps of the breeding ranges of these species, centers of distribution or core areas, which all or most member species inhabit, become apparent. Several authors working on the Palearctic region (Hultén, Reinig, Stegmann, de Lattin), North America (Miller, Udvardy, Mengel), and Africa (Winterbottom) analysed distribution centers and used them in their interpretations, as summarized by Udvardy (1969: 283 ff.).

Haffer (1967 a, 1969, 1974) and Müller (1973) applied this method to the zoogeographic study of the neotropical fauna. In an effort to interpret the history of core areas, Haffer (l. c.) also analysed the population structure of a number of species and superspecies and mapped the location of clusters of secondary contact zones of parapatric [1]) species and of hybridizing subspecies. These clusters of contact zones fall between centers of distribution thus indicating that the core areas have acted as centers of differentiation and dispersal in the past. In conjunction with the results of palynological and geomorphological studies, Haffer (l. c.) and Müller (l. c.) interpreted neotropical core areas as faunal and floral refugia during adverse climatic periods in the past and as dispersal centers, from which range expansion took place during following favorable climatic-vegetational phases. I emphasized previously the zoogeographic importance of secondary contact zones and of earth science studies to reveal the historical nature of distribution centers.

I recommend designating as *distribution centers or core areas (nuclear areas)* the geographically restricted centers of the superimposed ranges of all or most species of a given region [2]), labelling several geographically-historically related centers as a group of distribution centers. I avoid the use of the category "subcenter" (de Lattin, Müller) if the analysis permits the interpretation that such "subcenters" have functioned as independent refugia or dispersal centers in the past. For example, Müller

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[1]) *Parapatric* species occur in non-overlapping geographical contact, with no or only very limited interbreeding. I use "parapatric" mostly for species which exclude each other geographically in ecologically uniform environments. Species that meet along sharp ecological breaks, such as forest/savanna, remain outside our discussion, although they also qualify as parapatric. *Allopatric* populations also occupy mutually exclusive areas but are not in geographical contact. Therefore, the decision whether allopatric populations are still subspecies or have reached the level of species differentiation, in many cases will be highly subjective.

[2]) Therefore, core areas will be determined mainly by more or less coincident ranges of localized species. It is often difficult to explain why these species have remained geographically restricted in distribution despite the continuity of the environment far beyond the range of these species. Unrecognized competitors may form ecological barriers, particular feeding trees may be similary restricted in distribution, etc.

(1973: 83, 179) designated the vast area of upper Amazonia as the "Amazon centre" with two subcenters (Napo and Ucayali). In this case a conspicuous cluster of secondary contact zones of forest birds between the above "subcenters" indicates that the Napo refuge and the group of eastern Peruvian refugia (Haffer 1969, 1974) probably acted as separate centers of differentiation and dispersal. To indicate the varying importance of dispersal centers in the history of Amazonia, I distinguished between large *"primary refugia"* of general significance and *"secondary refugia"* of smaller size and of less significance for faunal differentiation (Haffer 1970: 288).

I purposely exclude from zoogeographic analyses the "subspecies" category unless the nature of a given "subspecies" is known. This is in contrast to many authors, notably Müller (1973) on the Neotropical Region. "Subspecies" formally recognized by taxonomists are artificially delimited populations and are not units of evolution (Mayr 1959, 1963). An arbitrarily defined "subspecies" may constitute either part or all of a geographical isolate, it may be a stage in a clinal population continuum or in two or more clinal continua, or it may represent a hybrid population, or part of it, along a secondary contact. Such subspecies are all identical from a nomenclatural standpoint and are often delimited and defined following widely varying arbitrary standards. Unless the nature of "subspecies" of wide ranging bird species is discussed and specified in detail, subspecies should not be used indiscriminately in zoogeographic studies. Only those "subspecies" which are shown to have originated in geographic isolation could be used to interpret a given core area as a center of differentiation and dispersal. The subspecies as such is not a useful category in the analysis of the history of a given fauna or taxon. The following somewhat exaggerated statement underscores this position even more strongly "... many avian systematists are now convinced that the subspecies category is unsatisfactory, if not worthless ..." (Selander 1971: 75).

Savage (1966, Fig. 1) subdivided the Middle American lowland forest herpetofauna ("Eastern Lowland Herpetofauna") into the Veracruzian, Caribbean, Isthmian, Golfo Dulcean, and Chocoan faunas. He stated (1966: 755) "Each of these units is represented today by a center of species differentiation that reflects a common distributional history". Savage (l. c.) did not, however, support this statement by an analysis of the various species characterizing the forest herpetofaunas and a discussion of their ranges. As far as the trans-Andean lowland forest avifauna is concerned, I did not recognize a center of species differentiation in Honduras-Nicaragua ("Caribbean herpetofauna" of Savage), which area represents an extensive avifaunal "suture zone", as discussed in detail below.

### Caribbean Northern Middle American Center

Seven species characterize the avifauna of the Caribbean forests of southeastern Mexico-Guatemala-Honduras, as follow (Group A of Fig. 14):

*Campylorhynchus curvipennis* (M, H)
*Amazilia luciae* (H)
*Synallaxis erythrothorax* (M, H)
*Uropsila leucogastra* (M, H)
*Thraupis abbas* (M, N)
*Lanio aurantius* (M, H)
*Arremonops chloronotus* (M, H)

The superimposed breeding ranges of these species are shown in Fig. 15 A. Seven species are found in Honduras (one exclusively) but not more than six are sympatric in the forests of southeastern Mexico, Guatemala and Honduras; one species reached Nicaragua. Three species, viz. *Synallaxis erythrothorax, Uropsila leucogastra,* and *Thraupis abbas,* also occupied portions of the Pacific lowlands, where sufficient vegetation cover permits their existence. Most of the 150 (southeastern Mexico) to 190 (northeastern Honduras) members of the forest avifauna of Caribbean northern Middle America are widely distributed and their ranges include other core areas in southern Middle America as well (Table 2). 24 Middle American species of Group F characterize a Middle American species group ranging from Mexico south to western Panamá (Fig. 17).

The Caribbean Northern Middle American center (Caribbean Guatemala Center) was discussed by Haffer (1974: 65) and corresponds to the "Central American rain-forest centre" of Müller (1973: 10). Of the species listed by Müller as characterizing this distribution center, we cite *Dasyprocta mexicana, Heliconius hortense,* and *Liomys heterothrix.* Other species he mentioned are widely distributed, hence cannot be assigned to any of the Middle American core areas without more detailed studies. Müller's analysis of the avifauna of northern Middle America probably needs revision in the light of the data presented above. The latter author claimed without further discussion that there are 59 species and 111 subspecies (faunal elements) that are still restricted to the Central American rainforest center. However, he did not give any details as to the names, distribution or population structure of these birds.

### Caribbean Costa Rica center

The following fourteen species characterize as faunal elements the heavy forests along the lower Caribbean slope and the lowlands along the base of the mountains of Costa Rica — western Panamá (Group B of Fig. 14; Fig. 15 B):

*Aratinga finschi* (N, P)
*Touit costaricensis* (C, P)
*Microchera albocoronata* (H, P)
*Trogon clathratus* (C, P)
*Dysithamnus striaticeps* (H, C)
*Pittasoma michleri* (C, Col)
*Procnias tricarunculata* (H, P)
*Aphanotriccus capitalis* (N, C)
*Thryothorus thoracicus* (N, P)
*Thyothorus atrogularis* (N, P)
*Euphonia anneae* (C, P)
*Bangsia arcaei* (C, P)
*Lanio leucothorax* (H, P)
*Heterospingus rubrifrons* (C, P)

Some of these species extended their ranges northward into Nicaragua and, in four cases, even reach the Olancho forests of easternmost Honduras (Fig. 15 B). Only one species, viz. *Pittasoma michleri,* entered northwestern Colombia. Since the forests of Caribbean Costa Rica extend uninterrupted into Nicaragua and throughout Panamá, as well as beyond, the reasons why the species listed above have such restricted ranges remain obscure. "Obvious barrier-zones" in southern Nicaragua and in central Panamá, invoked without further discussion by Müller (1973: 23), do not seem to exist. Some of the species like *Trogon clathratus* and *Bangsia arcaei* are adapted to the forests of broken hill country and may not range into Nicaragua and central Panamá because there the hills grade into more level lowlands. Other species, e. g. *Dysithamnus striaticeps, Pittasoma michleri, Euphonia anneae,* and *Heterospingus rubrifrons* probably are halted along their southern range limits by competition with their parapatric representatives *D. puncticeps, P. rufopileatum, E. xanthogaster* and *H. xanthopygius,* respectively, as discussed more fully below.

### Pacific Costa Rica center

Twelve species represent faunal elements of this core area, their ranges being confined to southwestern Costa Rica around Golfo Dulce and adjacent parts of western Panamá (Group C of Fig. 14; Fig. 15 C):

*Amazilia boucardi* (C, mangove)
*Trogon bairdii* * (C, P)
*Pteroglossus frantzii* * (C, P)
*Melanerpes chrysauchen* * (C, P)
*Thamnophilus bridgesi* (C, P)
*Cotinga ridgwayi* * (C, P)
*Carpodectes antoniae* * (C, P)
*Manacus aurantius* (C, P)
*Thryothorus semibadius* * (C, P)
*Euphonia imitans* (C, P)
*Habia atrimaxillaris* (C)
*Lanio melanopygius* * (C, P)

The absence of humid forests along the Pacific slope beyond southwestern Costa Rica and western Panamá prevents further range extension of these forms. Those marked with an asterisk in the above list may not yet have reached the level of species differentiation, possibly still representing geographically isolated "subspecies" of wide ranging species of the forests along the Caribbean slope of Middle America.

Other names of the Pacific Costa Rica center are Chiriquí center (Haffer 1967 a, Müller 1973) or Dulce center (Haffer 1974). Müller (l. c.) considered the core areas along the Caribbean and Pacific slopes of the Costa Rican mountains as "subcentres" of one "Costa Rica centre". Since both core areas are well separated from each other by the central mountain range and are each characterized by several very distinct birds, I designate both as distribution centers, even though they are located close together geographically. The separation apparently is less obvious in the case of amphibia, 35 species of which characterize the combined Caribbean and Pacific Costa Rica centers according to Müller (1973).

## Nechí center

The ranges of 14 bird species define a distribution center along the forested northern base of the Western and Central Andes of Colombia (Group D of Fig. 14; Figures 16 and 20):

*Crypturellus columbianus* (Col)
*Crax alberti* (Col)
*Pionopsitta pyrilia* (P, V)
*Brachygalba salmoni* (P, Col)
*Nonnula frontalis* (P, Col)
*Capito hypoleucus* (Col)
*Melanerpes pulcher* (Col)
*Thamnophilus nigriceps* (P, Col)
*Clytoctantes alixi* (Col, V)
*Aphanotriccus audax* (P, Col)
*Oncostoma olivaceum* * (P, Col)
*Psarocolius guatimozinus* (P, Col)
*Dacnis viguieri* (P, Col)
*Habia gutturalis* (Col)

Extensive deforestation in the northern Colombian lowlands reduced the range of most of these species considerably during the last one hundred years. Six species, viz. *Crypturellus columbianus, Crax alberti, Nonnula frontalis, Brachygalba salmoni, Thamnophilus nigriceps,* and *Aphanotriccus audax,* still inhabit the transitional forests in the isolated Serranía de San Jacinto near the Caribbean coast. Four reached the forests along the western base of the Sierra Nevada de Santa Marta, east of the mouth of the Río Magdalena. Two species, *Pionopsitta pyrilia* and *Clytoctantes alixi,* reached the Maracaibo basin of northwestern Venezuela. No species is endemic to the Santa Marta forests *(Crax "annulata"* cited by Müller, 1973: 30, is a color phase of *C. alberti;* cf. Vaurie 1967); the nature of the "subspecies" restricted to this area remains unstudied. In many cases the subspecies of the Santa Marta lowland forests may merely represent stages in clinally varying populations and thus be without historical significance.

## Colombian Pacific center

32 species characterize the zoogeographically distinctive Chocó fauna of western Colombia (Group E of Fig. 14; also Figures 16 and 21—22):

*Crypturellus berlepschi* † (Col, E)
*Crypturellus kerriae* (P, Col)
*Micrastur plumbeus* † (Col, E)
*Aramides wolfi* (Col, E)
*Penelope ortoni* (Col, E)
*Columba goodsoni* (Col, E)
*Leptotila pallida* (Col, E)
*Pionopsitta pulchra* * (Col, E)
*Neomorphus radiolosus* (Col, E)
*Androdon aequatorialis* (P, E)
*Phaethornis yaruqui* (Col, E)
*Hylocharis grayi* (P, E)
*Amazilia rosenbergi* (Col, E)
*Trogon comptus* (Col, E)
*Bucco noanamae* (Col)
*Capito squamatus* (Col, E)
*Capito quinticolor* (Col)
*Ramphastos brevis* (Col,E)
*Xenornis setifrons* (P, Col)
*Sipia berlepschi* (Col, E)
*Sipia rosenbergi* (Col, E)
*Pittasoma rufopileatum* (Col, E)
*Carpodectes hopkei* * (P, Col)
*Allocotopterus deliciosus* (Col, E)

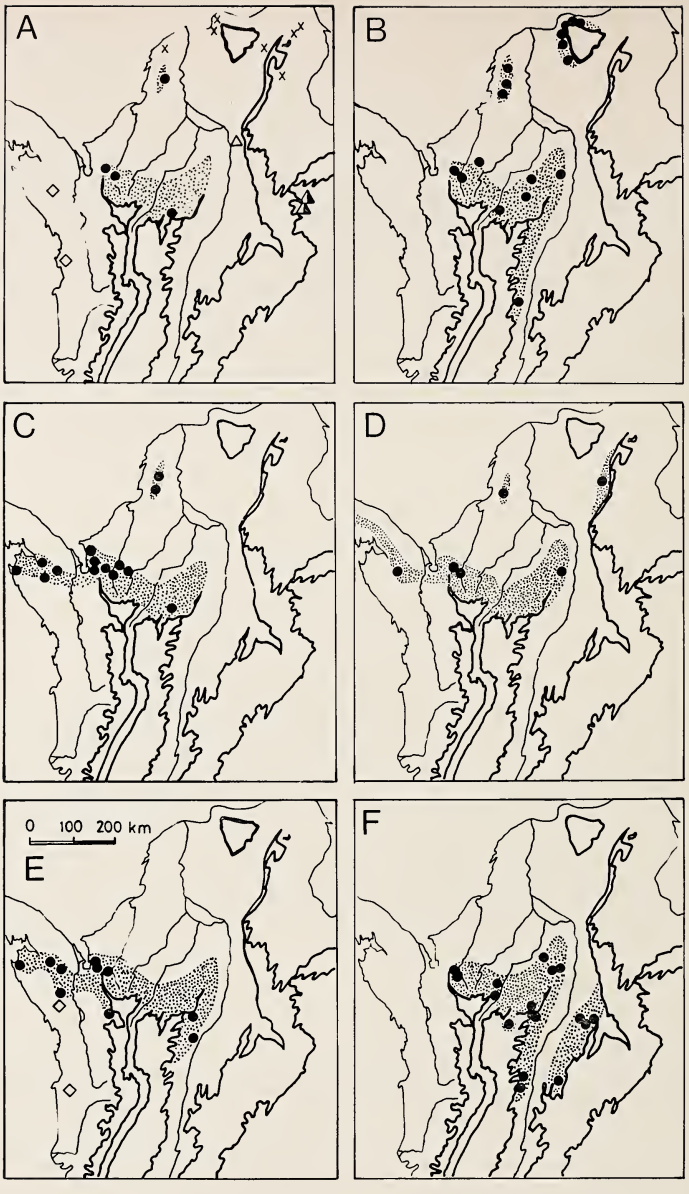


Fig. 20: Distribution of forest birds endemic to northern Colombia — eastern Panamá. Ranges (stippled) were probably more extensive in the Caribbean lowlands prior to large scale deforestation during the last one hundred years. *Explanation:* Solid circles indicate locality records. Heavy black line delimits Andes mountains above 1000 m elevation. **A** Tinamous *Crypturellus columbianus* (solid circles); *C. saltuarius* (Open triangle); *C. kerriae* (open squares); *C. idoneus* (crosses); and *C. duidae* (semisolid triangles). **B** *Crax alberti*, a currassow; the Pacific representative is *C. rubra* and the eastern ally is *C. daubentoni*. **C** *Brachygalba salmoni*, a short-tailed jacamar, representing *B. goeringi* of northwestern Venezuela. **D** *Aphanotriccus audax*, a flycatcher; an additional record west of the area shown is from Puerto Antonio near Chepo. **E** Oropendolas *Psarocolius guatimozinus* (solid circles) and *P. cassini* (open squares). **F** *Habia gutturalis*, an ant-tanager.

*Psarocolius cassini* (Col)
*Dacnis berlepschi* (Col, E)
*Chlorophonia flavirostris* (Col, E)
*Tangara johannae* (Col, E)
*Tangara palmeri* (P, E)
*Bangsia rothschildi* (Col, E)
*Bangsia edwardsi* (Col, E)
*Erythrothlypis salmoni* (Col, E)

Chapman (1917: 106) stated that the Colombian-Pacific fauna may be "... the most circumscribed and sharply defined, and possibly the most strongly characterized of any fauna of South America". Its geographically isolated location and the extreme environmental conditions of the Pacific Colombian lowlands probably are among the chief factors responsible for the existence in this area of the highest number of trans-Andean species (112 species, 45 % of the local forest avifauna). Many of the species of Group G (Table 2) probably also originated in the Chocó region having later extended their ranges into Central America. Another name for this distribution center is Chocó center (Haffer 1967 a).

Some of the 32 endemic Chocó species whose ranges have been superimposed in Fig. 16 are very localized in distribution and no more than a total of 23 species are found sympatrically in any given area. Similarly, only three of the six species which entered eastern Panamá actually occur in the same general area. Three Chocó birds, viz. *Androdon aequatorialis, Trogon comptus* and *Erythrothlypis salmoni,* followed the northern slopes of the Western Andes of Colombia and reached the lower Río Cauca region (Fig. 21 and 22).

## 8.2. Secondary contact zones

Many taxonomically related neotropical forest birds exclude each other geographically with or without hybridization along conspicuous zones of secondary contact or they narrowly overlap their ranges. These contact zones are clustered in a few fairly restricted areas of the neotropical lowlands (Haffer 1974 b). They are located between distribution centers (core areas). Remington (1968) designated as *"suture zones"* areas of faunal fusion and overlap characterized by clusters of secondary contact zones. In the trans-Andean lowlands, the "Honduras-Nicaragua suture zone" is located between the core areas of Caribbean Northern and Caribbean Southern Middle America. The "Panamá-northwestern Colombia suture zone" is recognized between the Caribbean Costa Rica center, the Colombian Pacific center and the Nechí center.

Analyses of zones of secondary contact are not only of importance for an historical study of a given fauna but also help in elucidating genetic aspects of the speciation process as well as details of the community structure and species diversity of neotropical faunas. Ecological and behavioral studies of non-hybridizing populations in contact (parapatric species) are especially needed to facilitate an understanding of the

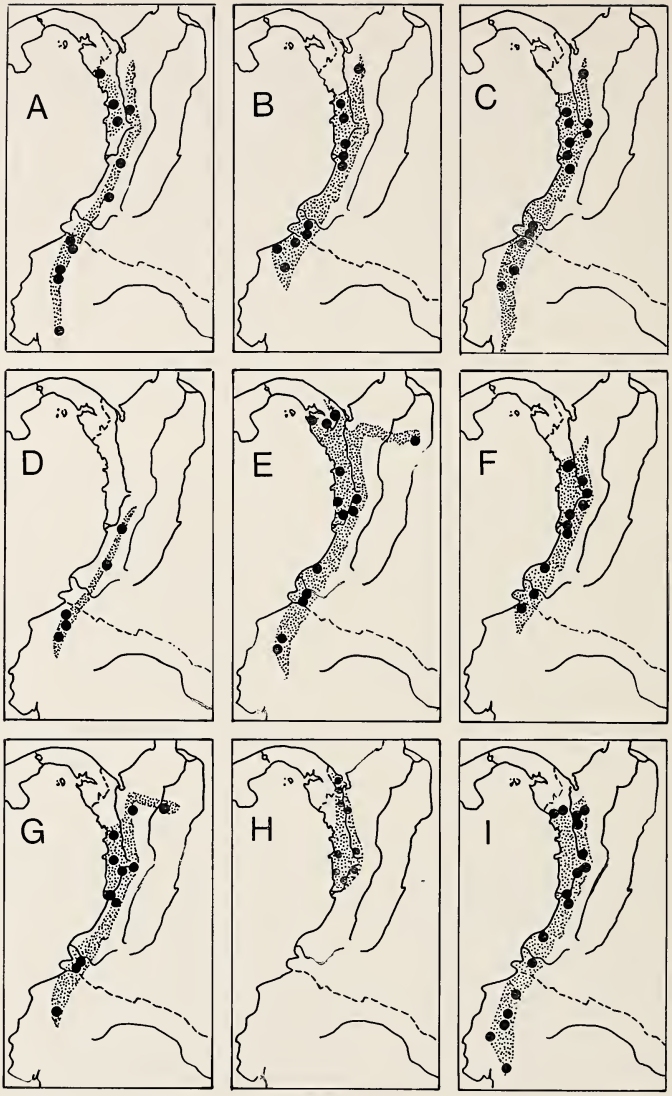


Fig. 21: Distribution of selected Pacific Colombian forest birds.

*Explanation:* Range is stippled, solid circles indicate locality records. **A** *Penelope ortoni*, a guan. **B** *Columba goodsoni*, a pigeon. **C** *Pionopsitta pulchra*, a parrot. A record from El Chiral, western Ecuador, falls just south of the area shown. The Middle American representative is *P. haematotis*. **D** *Neomorphus radiolosus*, a ground-cuckoo. The Middle American ally *N. geoffroyi salvini* ranges into northwestern Colombia south to the central Chocó region. **E** *Androdon aequatorialis*, a monotypic humming bird genus. **F** *Amazilia rosenbergi*, a hummingbird. **G** *Trogon comptus*, a trogon. **H** *Bucco noanamae*, a puffbird. **I** *Ramphastos brevis*, a toucan. Dashed lines indicate political boundaries (Panamá/Colombia; Colombia/Ecuador).

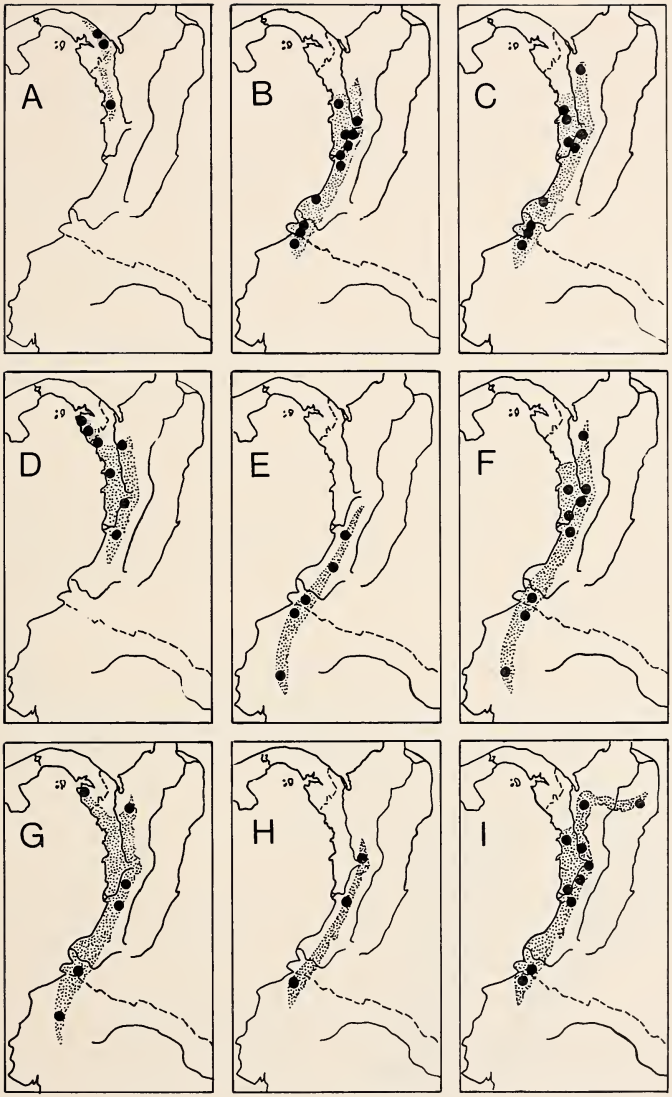


Fig. 22: Distribution of selected Pacific Colombian forest birds. Most species are members of trans-Andean genera some of which are monotypic (A, E, I).

*Explanation:* Dashed lines indicate the boundaries of Panamá-Colombia and Colombia-Ecuador, respectively. Solid circles represent locality records. **A** *Xenornis setifrons,* an antshrike. **B** *Sipia berlepschi,* an antbird. **C** *Pittasoma rufopileatum,* an antpitta; the parapatric ally *P. michleri* enters Colombia from Panamá; see Fig. 42. **D** *Carpodectes hopkei,* a snowy white cotinga. **E** *Allocotopterus deliciosus,* a manakin. **F** *Tangara johannae,* a tanager. **G** *Tangara palmeri,* a tanager. **H** *Bangsia rothschildi,* a tanager. **I** *Erythrothlypis salmoni, a tanager.*

maintenance of parapatric situations. Several species that exclude each other geographically in a more or less uniform forest environment are common enough in northwestern Colombia to make such studies feasible, e. g. manakins, tanagers, and toucans. If indeed ecologic competition keeps parapatric species apart, it should be determined which resources are in short supply and/or what competitive behavioral interactions take place. One may speculate that immature birds of parapatric species, during an early phase in life, learn to avoid the competitor along the contact zone. Therefore, interactions of the adults might be comparatively rare or inconspicuous, particularly in view of the fact that some of these tropical forest birds may have rather long lives. Snow (1962 a, b; 1974) determined an annual mortality rate of only 10 % in the manakins *Manacus manacus* and *Pipra erythrocephala* on Trinidad. Also, the question remains unanswered "Why can't these supposedly competing species eventually overlap their ranges maintaining interspecific territories?" This situation would appear to be an ecological alternative to parapatry. Detailed studies of the birds along secondary contact zones should be undertaken before increasing forest destruction will alter the natural situation which is still more or less preserved in many cases in the Urabá region and other parts of the neotropical lowlands.

### Honduras — Nicaragua suture zone

Differently colored, yet closely related birds of wide distribution replace each other abruptly in northern Honduras or Nicaragua, as listed in Table 7.

Table 7: Members of species and subspecies pairs in secondary contact in Honduras and Nicaragua.

| Northern Elements | Southern Elements |
|---|---|
| Honduras: | |
| *Ortalis vetula* | *O. cinereiceps* |
| *Aramides cajanea albiventris* | *A. c. pacifica* |
| *Synallaxis erythrothorax* | *S. brachyura* |
| *Formicarius analis intermedius* | *F. a. umbrosus* |
| *Lanio aurantius* | *L. leucothorax* |
| *Caryothraustes p. poliogaster* | *C. p. scapularis* |
| *Arremonops chloronotus* | *A. conirostris* |
| Nicaragua: | |
| *Thraupis abbas* | *T. palmarum* |
| *Habia fuscicauda salvini* | *H. f. fuscicauda* |

Monroe (1968) discussed these pairs and illustrated the distribution of some of the parapatric forms in Honduras. Details of the interactions of the allies along the contact zones are not known in any of these cases. Whereas some of these allies probably have reached the level of good species, others are assumed to hybridize extensively and therefore are listed as "subspecies". No details of the interaction of the forms that meet in Nicaragua are known either.

### Panamá — northwestern Colombia suture zone

Populations in secondary contact or separated by a distributional gap occur from the Almirante region of westernmost Panamá throughout the isthmus and the Darién region into northwestern Colombia (Table 8 and Fig. 23). I interpret this entire region as one extensive area of fusion

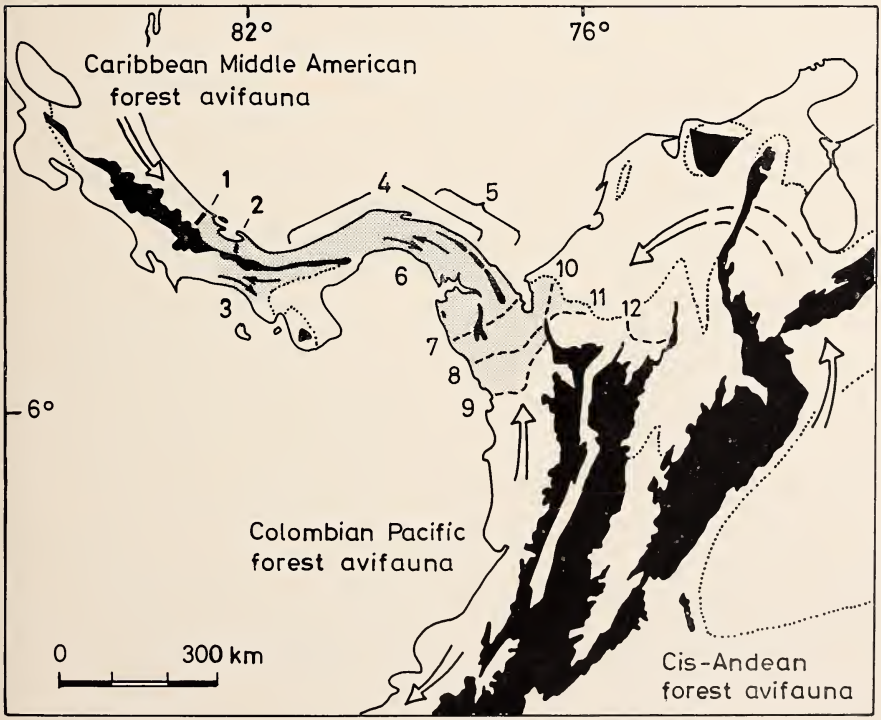


Fig. 23: The Panamá-northwestern Colombia suture zone (shaded), an area of interaction between the Middle American, Pacific Colombian, and Amazonian forest avifaunas.

*Explanation:* Secondary contact zones are numbered following Table 8 which lists the species and subspecies pairs in contact. The stippled line indicates the limit of humid forest. Mountains above 1000 m elevation are in black.

between the lowland forest avifaunas of Middle America and those of trans- and cis-Andean South America [1]). Species that barely extended their ranges into Panamá from northern Middle America or from South America as well as conspicuous gaps in Panamá in the ranges of several widespread species or between close allies support this conclusion. Details on some of the contact zones near the Costa Rica/Panamá border and in northwestern Colombia have been summarized previously (Haffer 1967 a, 1974 b [2]) ). Additional species and subspecies pairs are listed in Table 8 and are briefly discussed below.

The jaçanas may be separated by a distributional gap on the Caribbean slope of westcentral Panamá but overlap their ranges along a portion of the Pacific slope in Chiriquí and Veraguas. Hybridization probably occurs to a small extent in the area of overlap (Wetmore 1965: 372; Betts 1973). The broad zone of secondary intergradation between the chestnut-breasted wren of Caribbean Costa Rica *(Thryothorus nigricapillus costaricensis)* and the barred *T. n. schottei* of Pacific Colombia includes the whole of central and eastern Panamá, as discussed in detail by Wetmore (1959).

A number of allies are separated by distributional gaps of varying width in central and eastern Panamá. Similar gaps also occur in this area between several conspecific populations of Middle America and South America. In some cases the cis-Andean ally occupied all or part of the gap in Panamá *(Glaucis hirsuta, Rhynchocyclus olivaceus, Pipra erythrocephala, Galbula r. ruficauda).* In other cases no explanation is forthcoming why the gaps in the ranges have not been closed despite the continuity of the forests. To quote Griscom (1935: 285) "What, so to speak, is the matter with the (intervening) forest" such that the allies of *Cotinga, Carpodectes, Oncostoma, Psarocolius,* etc. are not in contact? Why do not the Middle American forms range farther east and the South American allies farther west in Panamá? Ecological reasons such as the absence of certain feeding trees or habitat differences may be responsible. In other cases the allies may be still expanding their ranges and may meet in the future.

A number of geographical representatives inhabiting the forests of Amazonia, western Colombia and/or Middle America are in contact in the forests of northwestern Colombia (Table 8, Fig. 23). These allies probably have somewhat different ecological preferences, each form being better adapted to different ranges or sets of ecologic influences, such as

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[1]) The hill forests in the upper tropical and subtropical zone along the mountains of western and eastern Panamá harbor several endemic forms which remain outside our discussion. They probably originated in isolated montane forests (Darién refuges) which persisted when most of the Panamanian lowlands were unforested or only sparsely forested during arid climatic periods.

[2]) In these publications I treated these areas as two separate zones of faunal integration. Further study convinced me that the *entire* Panamanian and northwestern Colombian lowlands together form one extensive faunal suture zone.

Table 8: Members of species and subspecies pairs in secondary contact in Panamá and northwestern Colombia (and their presumed origin [1]) characterizing a conspicuous „suture zone". Gaps in the ranges between widespread conspecific populations and between close allies also occur in this region.

| Western or Northern Elements | Eastern or Southern Elements |
|---|---|
| 1. *Chalybura u. melanochroa* (M) | *C. u. urochrysia* (CH) |
| *Dysithamnus striaticeps* (M) | *D. puncticeps* (CH) |
| *Manacus candei* (M) | *M. vitellinus* (CH) |
| 2. *Phloeoceastes guatemalensis* (M) | *P. melanoleucus* (C) |
| *Ramphocelus passerinii* (M) | *R. icteronotus* (CH) |
| 3. *Jacana spinosa* (M) (overlap) | *J. jacana* (C) |
| 4. *Thryothorus nigricapillus costaricensis* (M) (intergradation) | *T. n. schottii* (CH) |
| 5. *Psarocolius montezuma* (M) (range gap) | *P. guatimozinus* (N) |
| Range gap comprising larger portions of Panamá: | |
| *Touit costaricensis* | *T. dilectissima* |
| *Galbula r. melanogenia* | *G. r. ruficauda* |
| *Cotinga amabilis* | *C. nattererii* |
| *Carpodectes antoniae* | *C. hopkei* |
| *Oncostoma olivaceum* | *O. cinereigulare* |
| *Thryothorus thoracicus* | *T. leucopogon* |
| *Geothlypis semiflava bairdi* | *G. s. bairdi* |
| *Caryothraustes poliogaster* | *C. canadensis* |
| 6. *Pipra mentalis* (CH) (overlap) | *P. erythrocephala* (C) |
| 7. *Pteroglossus t. torquatus* (M) | *P. t. sanguineus* (CH) |
| *Cyanerpes lucidus* (M) | *C. caeruleus* (C) |
| *Euphonia anneae* (M) | *E. xanthogaster* (C) |
| *Chlorothraupis olivacea* (CH) | *C. carmioli* (C) |
| *Smaragdolanius pulchellus* (M) | *S. eximius* (N) |
| *Heterospingus rubrifrons* (M) | *H. xanthopygius* (CH) |
| *Cochlearius c. panamensis* (M) | *C. c. cochlearius* (C) |
| 8. *Ramphastos sulfuratus* (M) | *R. brevis* (CH) |
| *Galbula r. melanogenia* (CH) | *G. r. ruficauda* (C) |
| *Psarocolius cassini* (CH) | *P. guatimozinus* (N) |
| 9. *Aramides wolfi* (CH) | *A. cajanea* (C) |
| *Pionopsitta haematotis* (M) | *P. pulchra* (CH) |
| *Pittasoma michleri* (M) | *P. rufopileatum* (CH) |
| *Formicarius nigricapillus* (CH) | *F. analis* (C) |
| *Pipra mentalis* (CH) | *P. erythrocephala* (C) |
| *Rhynchocyclus brevirostris* (CH) | *R. olivaceus* (C) |
| 10. *Crax rubra* (CH) | *C. alberti* (N) |
| 11. *Ramphastos sulfuratus* (M) | *R. vitellinus citreolaemus* (N) |
| 12. *Manacus vitellinus* (CH) | *M. manacus* (C) |

[1]) Numbers refer to Fig. 23 which illustrates the location of the contact zones. The presumed geographical origin of these forms (see text) is indicated in parentheses: CH = Chocó refuge, N = Nechí refuge, M = Middle American refuges, C = Cis-Andean refuges.

temperature, humidity, vegetation, etc. However, for most of these species there are no indications that they reach their limit of tolerance for environmental conditions at the zone of contact. It seems that many of the parapatric species would occupy at least part of the range of their allies were it not for the presence of the latter across the zone of contact. Apparently they exclude each other as a result of eologic competition. The northern range limits of many or most Chocó elements may correspond to the ecologic limits of these birds which are adapted to the extremely humid climatic conditions of the Pacific lowlands. These forms reach their northern range limit in the lower Atrato Valley, where the annual rainfall decreases considerably and ecologic conditions change correspondingly. This is mainly due to a northward increasing influence of the drying tradewinds which blow into the Urabá region and lower Atrato Valley from the northeast during the winter dry season (December to April). Although this conspicuous climatic gradient is responsible for important faunal differences between the Urabá and Chocó regions, it is not steep enough to account for the abrupt geographic replacement of members of species pairs. Probably a balanced situation exists today with each form at a competitive advantage over its ally in the area occupied.

Restricted or unrestricted hybridization along the contact zone has been proven in a few instances, in forms of the aracari-toucan *Pteroglossus torquatus* (Fig. 37), of the jacamar *Galbula ruficauda* (Fig. 35), in the manakins *Manacus manacus* and *M. vitellinus,* and in the oropendolas *Psarocolius cassini* and *P. guatimozinus* (Fig. 47).

Haffer (1974 a, b) discussed other areas in the Neotropical Region in which clusters of secondary contact zones of forest birds indicate that entire faunas overlapped and partly fused, e. g., in central Amazonia and in upper Amazonia.

Summarizing, we recognize in the trans-Andean forest region the distribution centers of Caribbean northern Middle America, Caribbean and Pacific Costa Rica; Pacific Colombia-Ecuador, and the Cauca-Magdalena center. They are separated from one another by the Honduras-Nicaragua suture zone and the Panamá-northwestern Colombia suture zone of faunal intergradation (Fig. 24). "Boundaries" between these zoogeographic areas are always broadly transitional, never sharply defined. I derived the extent of the various core areas using the maps shown in Figures 15 and 16 in conjunction with the location of clusters of secondary contact zones between distribution centers (Tables 7 and 8; Fig. 23).

Each of the distribution centers acted as a "refuge" and differentiation center for portions of the trans-Andean lowland forest avifauna during arid climatic periods of the past (as discussed in more detail below). Therefore we may speak of the Carribbean Northern Middle American lowland forest avifauna, the Caribbean and Pacific Costa Rica lowland

forest avifauna, the Pacific Colombia-Ecuador forest avifauna (Chocó fauna) and the Cauca-Magdalena forest avifauna (Nechí fauna) to designate the groups of species and subspecies of birds that originated in the various forest refugia (centers) [1]). These different avifaunas intermingled when the forests expanded during humid climatic periods and also mixed with Amazonian faunal elements, in this way establishing the present composition of the trans-Andean lowland forest avifauna. Many trans-Andean faunal elements occupied wide distribution areas because of the ecological uniformity of the trans-Andean lowland forests. This prevents these species to be assigned to a particular trans-Andean fauna.

I distinguish between distribution type and faunal type as defined above. Animal species which originated in the same forest refuge are elements of the same fauna, yet may exhibit different distribution patterns due to varying dispersal distance from their common center of origin. Conversely, species with the same distribution pattern did not necessarily originate in the same forest refuge and, therefore, may represent elements of different faunas. For example, the species showing distribution patterns illustrated in Figures 15 and 16 can be assigned as faunal elements to particular trans-Andean avifaunas, whereas those species with a distribution shown in Figures 17 to 19 cannot be assigned to particular avifaunas, except the broad "trans-Andean" group. About half of the species of Group F (Fig. 17) may have originated in the Caribbean Northern Middle American forest refuge and the other half of them (or more) probably spread from the Carribbean Costa Rica refuge. The species of Group G (Fig. 18) probably represent mostly Chocó faunal elements that occupied various portions of southern Central America. The species of Group H (Fig. 19) range through most of the trans-Andean lowland forests and, for this reason, cannot be assigned as faunal elements to any particular local trans-Andean fauna. Group H probably is a mixture of elements of four or all five trans-Andean lowland forest avifaunas.

### 8.3. Lowland avifaunas of western and northern Colombia

The two major ecological formations found in the tropical lowlands of South America are "forest" and "nonforest" vegetation. Both cover immense terrain in Colombia and are inhabited by bird faunas of widely different aspect; numerous species are confined to each. The term "nonforest" refers

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[1]) A "fauna" as here defined consists of the kinds of animals (faunal elements) that originated in a given area during past periods of geographic-ecologic isolation spreading into other areas and intermingling with species of other such "faunas" upon the termination of isolation. For other definitions and further discussions of "faunas" see Mayr (1965).

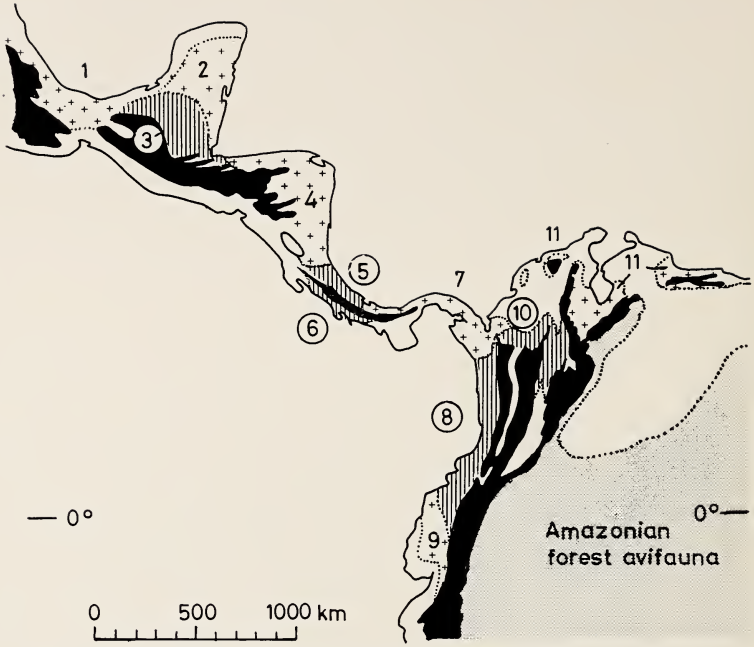


Fig. 24: Zoogeography of the trans-Andean lowland forest region.

*Explanation:* Hatched vertically — distribution centers (core areas) characterized by strong endemic faunal element. Crosses — areas inhabited by fauna of mixed origin derived from adjacent and more distant centers. Small core areas probably also exist along the mountain slopes of areas 7 and 11 (see text for details). 1 southeastern Mexican forest region. 2 Yucatan forest region. 3 Caribbean northern Middle America center. 4 Honduras-Nicaragua suture zone. 5 Caribbean Costa Rica center. 6 Pacific Costa Rica center. 7 Panamá-northwestern Colombia suture zone. 8 Pacific Colombia (Chocó) center. 9 Northwestern Ecuador forest region. 10 Cauca-Magdalena (Nechí) center. 11 Caribbean forest region (Santa Marta, Maracaibo, northern Venezuela). Mountains above 1000 m elevation are in black. Blank lowland areas represent nonforest regions (see Fig. 1).

to open areas such as grassland savanna, dry open woodland, cactus plains, thorn scrub, etc.

The distribution of forest birds in northwestern Colombia permits one to distinguish the zoogeographic Chocó region (Pacific Colombia-northwestern Ecuador) from the Darién-Urabá region. Historically, the Chocó region represents the center of origin of the Chocó fauna, whereas the Darién-Urabá region forms part of the Panamá-northwestern Colombia suture zone, as discussed above. The range limits of species confined to either one of these areas form a fairly well defined "boundary" or narrow transition zone in the lower Atrato Valley extending from Mutatá south-

ward and thence swinging westward across the Atrato River between the Río Napipí and Río Uva to reach the Pacific coast at the Gulf of Cupica (Haffer 1967 c). Many endemic Chocó birds, east of the lower Atrato River, extend their ranges further north than on the western side of this river, probably because of ecological reasons. Wet forests follow the base of the Western Andes north to the area of Mutatá and Chigorodó, as the influence of the drying tradewinds is here felt less than on the opposite side of the Atrato River, where seasonal forests increasingly replace evergreen forests from the Río Truandó to the north.

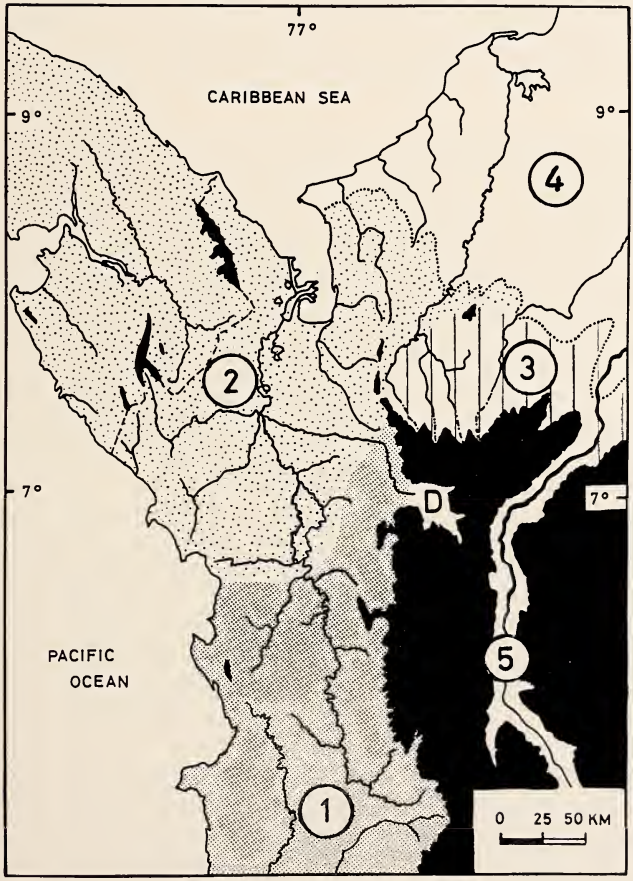


Fig. 25: Ornithogeographic areas of northwestern Colombia.

*Explanation:* Forest regions: 1 Pacific Colombian rainforest region (Chocó region). 2 Eastern Panamá-northwestern Colombia rainforest region (Darién-Urabá region). 3 Cauca-Magdalena forest region (Nechí region). Nonforest regions: 4 Northern Colombian nonforest region. 5 Arid Cauca Valley. D Arid Dabeiba Valley. Mountains above 1000 m elevation are in black.

The Darién-Urabá region is in broad connection with the Cauca- Magdalena region (Nechí center) to the east. The "boundary" between the two areas in the upper Sinú region, of course, is broadly transitional and inconspicuous. I have used on Figure 25 the contact zone between the Middle American toucan, *Ramphastos sulfuratus*, and the Nechí form, *R. vitellinus citreolaemus*, to separate schematically the Darién-Urabá region from the Cauca-Magdalena region. Faunal resemblance based on a distributional analysis of trans-Andean species is somewhat greater between the Darién and Cauca-Magdalena faunas than between the Chocó and Cauca-Magdalena faunas (Table 6).

Table 1 indicates the faunal differences between the Chocó region and the Darién-Urabá region and lists the many birds restricted to the wet Pacific forests of Colombia-northwestern Ecuador (see also p. 53).

Chapman's (1917; pl. 26) interpretation of the life zones and faunas of northwestern Colombia is similar to that discussed above and served as a basis for my analysis. He distinguished the Colombian-Pacific fauna and the Cauca-Magdalena fauna including the birds of the Urabá - lower Atrato region with the latter and those of the Darién region with the former. However, Chapman (1917: 119) emphasized that these faunas merge "so completely .... that any attempt to map their respective boundary lines in this region must be purely arbitrary". It is interesting to note that Hernandez (1969) considered the combined Darién-Urabá-lower Cauca region as the "area of integration between the Pacific-Central American and the Brazilian Provinces". This interpretation corresponds to our concept of a "Panamá-northwestern Colombia suture zone".

Seasonal forests similar to those of the Urabá area occur also in northwestern Ecuador and are inhabited by a number of endemic species. Several birds of the Darién-Urabá fauna that are missing in the Chocó forests recur in northwestern Ecuador such as *Ara ararauna*, *Ara ambigua*, *Piaya minuta*, *Phaethornis superciliosus*, *Damophila julie*, *Trogon violaceus*, *Momotus momota*, *Notharchus macrorhynchus*, *Sittasomus griseicapillus*, *Lepidocolaptes souleyetii*, *Sclerurus guatemalensis*, *Cacius cela*, and *Arremon conirostris*.

The avifauna inhabiting the very reduced forests in the Serranía de San Jacinto near the Caribbean coast of northern Colombia is of mixed origin (Haffer et al. 1965). Amazonian species that are widespread both east and west of the Andes occur there together with trans-Andean forms that originated in the Chocó region or in Middle America, e. g. *Penelope purpurascens*, *Ramphastos sulfuratus*, *Pteroglossus torquatus*, *Notharchus tectus*, *Gymnocichla nudiceps*, *Pachyramphus cinnamomeus*, and *P. homochrous*. Of particular interest in the Serranía de San Jacinto are several endemic northern Colombian species of the Cauca-Magdalena fauna: *Crypturellus columbianus*, *Crax alberti*, *Trogon melanurus macroura*, *Non-*

*nula frontalis, Brachygalba salmoni, Thamnophilus nigriceps,* and *Aphanotriccus audax.* The dry transitional forests near the coastal city of Cartagena have largely disappeared. Due to a northward decrease in humidity of the climate and a less luxuriant vegetation the original forest bird fauna in the hills near Cartagena studied by Dugand (1947) is less varied than that of the Serranía de San Jacinto. A number of species found in the latter range have not been encountered by Dugand (1947) during his long extended explorations in the hills to the north, such as *Crypturellus columbianus, Crax alberti, Trogon violaceus, Brachygalba salmoni, Notharchus tectus, Picumnus olivaceus, Sittasomus griseicapillus, Xenops minutus, Thamnophilus nigriceps, Cercomacra nigricans, Colonia colonus, Myiobius atricaudus, Onychorhynchus mexicanus, Leptopogon amaurocephalus, Pipromorpha oleaginea, Thryothorus fasciatoventris, Basileuterus delattrii,* and *Euphonia laniirostris.*

The seasonal forests along the northern and western base of the isolated Sierra Nevada de Santa Marta, in the Maracaibo basin and near the coastal mountains of northern Venezuela (Fig. 1) are inhabited by an avifauna of mixed trans-Andean and Amazonian origin. Most of the trans-Andean species listed above for the Serranía de San Jacinto also reached northern or at least northwestern Venezuela. Several endemic subspecies and species (e. g. *Picumnus cinnamomeus)* occur in the Caribbean lowland forests characterizing the Catatumbo and North Venezuelan distribution centers (Haffer 1967 b, 1974 a, b). However, it remains to be determined which of the endemic subspecies in these forests represent clinal forms of species spreading from distant centers of origin (and thus are of no direct historic zoogeographic significance) and which may have originated in reduced forest refugia of this region during arid climatic periods (see below).

The nonforest avifauna of northern Colombia has direct connections with that of northern Venezuela and harbors only few endemic species, e. g. *Ortalis garrula, Columba corensis, Leucippus fallax, Lepidopyga goudoti, Hypnelus ruficollis, Poecilurus candei, Sakesphorus melanonotus, Inezia tenuirostris, Miozetetes inornata, Campylorhynchus nuchalis, Icterus icterus, Pyrrhuloxia phoenicea, Saltator orenocensis,* and *Arremon schlegeli.* Most members of the Colombian-Venezuelan nonforest avifauna are closely related to representatives inhabiting the nonforest regions of central Brazil and eastern Bolivia. There are no endemic genera in northern Colombia-Venezuela; of the two examples listed by Haffer (1967 d: 321), *Quiscalus* is also represented in North America and *Hypnelus* has been merged with *Bucco* by Cottrell (1968); however, De Schauensee (1966) retained this genus. About half of the nonforest species of the Caribbean lowlands of northern South America recur in the dry Pacific lowlands of Panamá. On the other hand, the faunal relationships of the densely forested Caribbean slope of Panamá lie with the humid Pacific lowlands of northwestern South America. Dunn (1940) emphasized this peculiarity of Pana-

manian zoogeography (the "Panamanian X") for the herpetofauna; it is equally conspicuous in the case of the lowland avifaunas.

The area in northern Colombia occupied by the nonforest fauna has been enlarged greatly through forest destruction in the last centuries. The cultivated area on both sides of the lower Sinú River was covered originally by seasonal evergreen and dry tropical forests. Continued forest clearing in northwestern Colombia pushes the limit of more or less unbroken forest rapidly southward and southwestward in the direction of the Gulf of Urabá, where large clearings have also appeared along the Turbo road (Fig. 3). Many populations of forest birds in northern Colombia are separated by extensive artificial savannas from the larger populations inhabiting the forested base of the Colombian Andes and form isolated populations confined to remnant forests. Most of them will undoubtedly disappear within a few years on account of the progressive clearing and burning of the forests, which is underway all over northern Colombia.

The dry intermontane valleys of the Colombian Andes have been populated from the Caribbean lowlands to the north. Endemic forms of the Magdalena, Cauca, and Patía Valleys have reached the subspecies level of differentiation and some are markedly different (Haffer 1967 d).

### 8.4. Historical interpretation of bird speciation and distribution patterns

At the present time the tropical lowland forests extend without interruption (not taking into consideration recent changes through the activity of man) from the base of the northern Andes in Colombia throughout Middle America, covering mainly the Caribbean slope north to Mexico. This continuity of the forests, however, represents only a temporary stage in the vegetational history of these areas as suggested by the climatic changes which affected the northern part of the Neotropical Region during the Pleistocene and post-Pleistocene. Hammen & Gonzales (1960) and Hammen (1961, 1974) have shown, by analyzing the pollen contents of lake and bog deposits of the highlands of the Eastern Andes of Colombia, that the Pleistocene and Holocene climate of the northern Andes was characterized by a succession of wet and dry phases. Several periods correlate closely with contemporaneous phases known from North America and Europe. In contrast to the situation in highlands of tropical mountains, the surrounding lowlands probably were only weakly affected by the Pleistocene temperature changes. However, the variation of average rainfall and cloud cover during these climatic periods seems severely to have influenced the distribution of tropical lowland forests and nonforest vegetation. The presently continuous lowland forest zone of northwestern South America and Middle America probably was broken up into a number of more or less isolated forests which acted as *"refugia"* for the forest fauna and have been

named as follows (Haffer 1967 a, 1969, 1974): Caribbean Middle American refugia (Guatemala, Caribbean Costa Rica); Pacific Costa Rica refuge; Chocó refuge; Nechí refuge; and others. The distribution centers (core areas) analysed above probably remained forested during arid periods and acted as centers of differentiation of the forest fauna. Many trans-Andean species probably originated in these forest refugia and extended their ranges upon the expansion of forests during later humid periods.

I suggested (Haffer 1967 a), on the basis of the present rainfall pattern in the Urabá region, that the connection between the Middle American and the western Colombian forests was interrupted in the Urabá-lower Atrato region during dry climatic 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 [1]). Direct palynological evidence from these areas is not yet available; however, Wijmstra (1967) discussed post-Pleistocene vegetational changes in the lower Magdalena Valley of northern Colombia.

The isolated forests of the refugia rejoined and again formed a continuous forest zone during humid climatic phases. Great numbers of Amazonian forest birds probably advanced through these continuous forests into northern and western Colombia and into Middle America, coming around the northern tip of the Andes and following the lowlands along the Caribbean coast (Fig. 26). Upon the return of more arid conditions, many of the trans-Andean forest birds survived in the forest refugia mentioned above. These various refuge populations north and west of the Andes would have been modified in isolation from their Amazonian parental populations and from one another. They must have reached many different levels in the speciation process before, in some cases, they made contact again during a later humid phase with one of their representatives which also would have been evolving in some other forest refuge. These processes of isolation and rejoining of forest and nonforest bird populations were repeated several times (see Haffer, 1974, for further details).

A number of birds that probably originated in the Chocó Refuge of western Colombia established contact with their Middle American or Amazonian representatives in the Urabá region upon the return of more favorable climatic conditions, possibly only several thousand years ago. However, details are not yet known. The Urabá region is therefore of particular interest for the study of zones of secondary contact of forest birds at various stages of speciation. Several cases of allopatric hybridization and of geographic exclusion of parapatric, nonhybridizing species are known to occur (see above).

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[1]) Montane forests probably remained, however, along the slopes of the mountain ranges of Darién, where several endemic subtropical species may have originated.

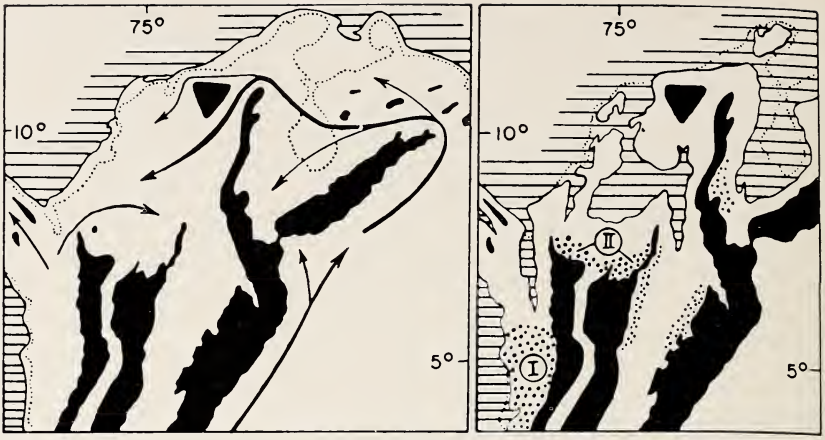


Fig. 26: Northern Colombia during the Pleistocene (after Haffer 1967 a).

*Explanation:* The present coast line is dotted; mountain areas presently over 1000 m elevation are in black. *Left:* During glacial periods. The sea-level was lowered by about 100 m. Arrows indicate immigration routes of cis-Andean and trans-Andean forest avifaunas which advanced during these periods. *Right:* During interglacial periods. The sea-level was about 30 to 50 m higher than today, and the climate was dry, at least in the northern half of the area shown. Birds of the humid forest found refuges (stippled) in the Chocó area (I) and Nechí area (II).

From the brief discussion of the zoogeography of northwestern Colombia, the Urabá region emerges as a transit area for the faunas of the more open and drier vegetation during dry climatic periods of the past and as an important meeting place of various Recent Central and South American forest faunas (Fig. 26).

Past climatic-vegetational changes in Middle America help understanding certain peculiar distribution patterns observed in trans-Andean birds today: Small isolated populations of several South American species presently inhabit restricted areas in northern Middle America and are widely separated from their South American "mother" population. Examples are the isolated Mexican populations of the Green Macaw *(Ara militaris),* of the Bicolored Wren *(Campylorhynchus griseus),* and the Tufted Jay *Cyanocorax dickeyi* as well as the species of *Granatellus;* the isolated Nicaraguan population of the Pearl Kite *(Gampsonyx swainsonii).* The more widely distributed species *Burhinus bistriatus* and *Pyrocephalus rubinus* are missing from southern Middle America. These isolated populations probably have been connected with the main species range in the past when favorable vegetational conditions permitted the range extension. The connecting populations may have disappeard when ecologic conditions changed in the intervening area. Some other trans-Andean birds show peculiar gaps in their range comprising portions of northwestern Colombia

and Panamá, e. g. *Galbula ruficauda melanogenia* and *Pipra mentalis*. These gaps are presently occupied partially or entirely by a competing or hybridizing ally (*P. erythrocephala* and *G. r. ruficauda,* respectively). In these cases the gap in the range of the trans-Andean ally probably originated during an adverse climatic-vegetational period and was occupied by the competing cis-Andean ally before the trans-Andean ally could do so (Haffer 1967 b).

Summarizing, the concentration of endemic forms in the trans-Andean lowland forests is explained by the following facts: 1) Relatively small populations of Amazonian forest birds were repeatedly isolated in forest refugia 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 Amazonian founder popoulations [1]) to reach the forests west of the Andes in Middle America and western Colombia. This led to a 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 parent population into the region west of the Andes occurred in several cases.

Our historical interpretation contrasts with that given previously by Chapman (1917: 89). He assumed that a pre-Andean forest fauna was split, by the rising Andes mountains, into a Pacific and an Amazonian portion. Chapman (l. c.) stated "The specific identity of many birds common to both areas is evidence that ... in such cases evolution has, so to speak, been at a standstill" since the time their ranges were disconnected. We would suggest today that these forms immigrated from the Amazonian lowlands more recently than thoroughly differentiated subspecies and endemic species of Pacific Colombia. Chapman (1926: 59, 62) later emphasized a Middle American origin of many western Colombian and Ecuadorian forms. Griscom (1932: 75, 1935: 285) suggested that the origin of the Middle American and western Colombian fauna was due to the Pleistocene refrigeration which, he supposed, had forced the Middle American lowland fauna to retreat southward into western Colombia and Ecuador, thus leading to the surprising concentration of endemic forms in the Chocó region. However, the Pleistocene temperature depression probably did not effect the tropical lowland fauna of most of Middle America because forest birds survived arid periods in a number of forest refugia. The northward decrease

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[1]) These founder populations contained "inevitably only a small fraction of the total variation of the parental species" (Mayr 1963: 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,* 1942).

in species diversity of the Middle American forest avifauna probably has ecological rather than historical reasons. The close relationship between many western Colombian and Middle American subspecies and species very probably is due to immigration of South American forms into Middle America from the Chocó region rather than the other way around. Thus, while I agree with Chapman's and Griscom's general statement that the trans-Andean forest avifauna was derived from Amazonia and spread into Pacific Colombia and north to Mexico, our interpretations regarding the Pleistocene distributional history of this avifauna differ considerably.

No simple answer can be given to the question of why the trans-Andean forest fauna is so uniform in composition and similar to the Amazonian fauna (Mayr 1964). Possibly the restricted early Pleistocene forest refuges of Middle America permitted only few members of the Tertiary northern forest fauna to survive such as, e. g., the motmots Momotidae. A flood of southern colonists invaded Middle America when the forests reexpanded during humid climatic periods forming a geographically continuous forest zone from South into Middle America.

Climatic and vegetational changes during the Pleistocene and Holocene probably also determined important zoogeographic aspects of the trans-Andean reptile and mammalian faunas which several previous authors attempted to explain in terms of the Tertiary paleogeographic history of Middle America. The extensive Quaternary faunal differentiation must be investigated before a study of the evolution of neotropical animals during the preceding Tertiary period can be undertaken successfully.

### 9. Breeding and Molting Seasons

As I worked in the lowlands of northern Colombia during only portions of successive years, my records are not nearly complete enough to establish the existence of definite seasons in the annual cycle of the avifauna of this part of South America. However, there are strong indications of a pronounced peak in breeding activity during the months of March and April extending into June and of molting occurring in the latter half of the year. A conspicuous number of male birds collected during March and April had enlarged testes: 44 specimens of 35 species in March and 22 males of 21 species in April. These figures contrast with only 8 males taken in February and 9 in June that had enlarged testes. A few breeding records of northern Colombian jacamars, puffbirds, and toucans also refer to the months of April, May, and June (Haffer 1968).

A large percentage of birds which I collected near Mutatá, southeast of the Gulf of Urabá, during the month of August were found to be in full wing and tail molt and many immature birds with an unossified skull were taken at this locality, as listed by Haffer (1967 c). Only a few species appeared to be still breeding in this area in August. Specimens of *Galbula*

*ruficauda* from northern Colombia that I found to be in wing and tail molt were taken between August and December. Over 50 specimens of this bird in the Bogotá collection taken in northern Colombia between January and July did not molt their wing and tail feathers. The molt of toucans in northwestern Colombia extends into the months of January through April (Haffer 1968).

The above data are in agreement with the summarizing statements of Eisenmann (1952) who found that the greatest number of birds in central Panamá seem to breed between March and June and of D. & B. Snow (1964) who reported the months April-June as the height of the breeding season in Trinidad and that molting is at its height in the months July-October. Friedmann & Smith (1955) obtained similar results in northeastern Venezuela.

The annual cycle of the avifauna probably is adjusted to the climatic regime which is similar over northern South America. Food probably becomes scarce during the dry season from December to March. With the return of the equatorial rain belt to more northern latitudes rains again begin to fall in March/April and the food supply increases sharply when breeding is at its height (see D. & B. Snow, 1964, for detailed discussions).

## 10. List of Collecting Stations

The following alphabetical list summarizes information on collecting stations in the lowlands of northern and northwestern Colombia. All places are below 200 meters elevation (except the Río Imamadó, 350 m). Numbers of the following list refer to Figure 3 which illustrates the location of the collecting stations except for those in the Serranía de San Jacinto, which are shown in Figure 4. The time of my visit and the number of specimens collected at each locality are also given.

Information on additional collecting stations in our study area and in other parts of Colombia can be obtained from the detailed gazetteer prepared by De Schauensee (1948—1952, pp. 278—342 and 1124—1139). Nicéforo Maria & Olivares provided a useful list of Colombian locality records published since the appearance of De Schauensee's catalogue (Nicéforo Maria et al. 1964: 5—6).

*Acandí, Dep. Chocó* (no. 31): A small town on the western shore of the Gulf of Urabá. Collections come from the forested hills and partially cleared lowlands near the town. March 1959 (33 specimens).

*Catival, Dep. Córdoba:* An old Indian name for a site southwest of Planeta Rica and a few miles northwest of Ciénaga San Lorenzo. Only remnants of forest remain today along some of the hills in this open area.

*Cerro Quía:* The forested ridge that forms the boundary between Departamento Chocó, Colombia, and Panamá at the southern end of Cerro Pirre. Dr. P. Galindo here collected birds for the U. S. National Museum, Washington.

*Charrura, Quebrada (=creek), Dep. Córdoba* (no. 6): A small western tributary of the upper Río San Jorge and approximately 80 km south of Montería. Located near the present northern limit of forests that connect the Urabá-Sinú forests with those of the humid middle Magdalena Valley (Pl. 2, Fig. 2). May 1960 (41 specimens).

*Colosó, Dep. Bolivar* (Fig. 4): A village near the southern end of the Serranía de San Jacinto, about 30 km east of Tolú.

*Frasquillo, Dep. Córdoba* (no. 8): A small village on the eastern bank of the upper Río Sinú above the first rapids; about 12 km below the mouth of the Río Verde and close to the larger village of Tucurá. The area is rapidly being deforested along the banks of rivers and creeks, although much of the hilly and mountainous terrain remains forested (Pl. 3 and 4). 7—19 June 1963 (53 specimes).

*Jaraquiel, Dep. Córdoba:* A small village on the west bank of the Río Sinú, about 10 km south of Montería, where M. A. Carriker, Jr. collected for the Carnegie Museum, Pittsburgh, in 1916. No forests remain in this area today.

*La Raya, Dep. Bolivar:* A village on the right bank of the lower Río Cauca in open country. Partially wooded hills are found around Ciénaga de La Raya; more extensive forests exist 30 km to the east, in the Serranía de San Lucas.

*Mutatá, Dep. Antioquia* (no. 27): A small village on the Turbo road located at the western base of the Serranía de Abibe about 100 m above sea level. Large areas have been deforested around this village. Hills and mountain slopes are still covered with unbroken forest. A road in a northwesterly direction to Pavarandocito, following the western bank of the Río Sucio, was under construction at the time of my visit and was traverseable through uninhabited forest for about 5 km (Pl. 2, Fig. 1). A collection totaling 205 specimens (77 species) was made along this road (130 m above sea level) between 4 and 16 August 1966.

*Nazaret, Dep. Córdoba:* A collecting station of M. A. Carriker, Jr. in partially cleared country of the upper Sinú Valley, 19 km northwest of Tierra Alta (De Schauensee 1948—1952: 1133).

*Pavarandocito, Dep. Antioquia* (no. 26): Birds were taken opposite this village about 1 to 3 km south of the Río Sucio, in unbroken forest. 2—5 February 1965 (29 specimens).

*Quebrada Salvajín, Dep. Córdoba:* A small Indian farm and collecting station of M. A. Carriker, Jr. on the west bank of the Río Esmeraldas, near the mouth of the Quebrada Salvajín and a short distance above the point where the Río Esmeraldas joins the Río Sinú (Charriker 1955: 63; Wetmore 1965: 460). The area is densely forested.

*Río Chigodoró, Dep. Antioquia* (no. 23): Birds were collected close to the base of the steep slope of the Serranía de Abibe in forested country with only a few scattered clearings. 2—8 April 1964 (45 specimens). Five kilometers below our camp the river reaches the extensive banana plantations of the deforested plains along the Turbo road.

*Río Cope, Dep. Antioquia* (no. 17): A small river emptying into the Gulf of Urabá about 8 kilometers north of Turbo. The river valley is covered with dense second growth and plantations, while the surrounding hills are forest-covered. 17—20 April 1964 (44 specimens).

*Río Currulao, Dep. Antioquia* (no. 20): Six skins were collected where this river leaves the forested hills and reaches the deforested level plains near the Turbo road. February 1959.

*Río Guadualito, Dep. Antioquia* (no. 19): A small river about 10 kilometers southeast of Turbo. Collections were made in the forested hills, where the river reaches the open level plains near the Turbo road. February 1959 (56 specimens).

*Río Imamadó, upper Río León, Dep. Antioquia* (no. 24): A small collection was made in the foothills of the densely forested Serranía de Abibe at an elevation of around 350 meters above sea level. The area is partially cleared. 9—12 April 1964 (43 specimens).

*Río Juradó, Dep. Chocó* (no. 39): The forest is more or less cleared along this river from just above the mouth of the Río Jampavadó to the village of Juradó which is located on the coast. The upper part is a rough forest stream with numerous short rapids and only widely scattered small clearings and Indian dwelling sites along the banks. The surrounding rugged basalt ridges are heavily forested down to the coast line. I crossed the rather low range that separates the upper Río Juradó and upper Río Salaquí on a foot trail in about five hours. Birds were collected mainly close to the mouth of the Río Jampavadó in forests and partially cleared land. 21—27 March 1965 (30 specimens).

*Río Mulatos, Dep. Antioquia* (nos. 13 and 14): In 1959, it remained in its middle and upper course a lonely forest stream; the banks are now being deforested by settlers coming in from the north. A few clearings are already found in the headwaters southeast of Turbo. January 1959 (30 specimens); 21—29 January 1965 (41 specimens).

*Río Murrí, Dep. Chocó* (no. 45): The small village of La Playa is located on the lower part of this river in the swampy Atrato Valley. The river is uninhabited in the forested foothill zone of the Western Cordillera. Several birds were collected in these foothills close to the mouth of the Río Pavarandó, a small northern tributary. 15—16 March 1965 (11 specimens).

*Río Napipí, Dep. Chocó* (no. 44): The banks of this small and narrowly meandering river are cleared by rice-growing settlers far upstream. I camped for several days at the upper part close to the mouth of the Río Doguadó, where the Napipí leaves the rugged basalt ridges to the west. These densely forested ridges represent the southern extension of the Serranía de los Saltos and separate the headwaters of the Río Napipí from the Pacific coast. The country along the upper Napipí River is forested with only a few small clearings along the river banks inhabited by Chocó Indian families. 26 February—2 March 1965 (45 specimens).

*Río Salaquí, Dep. Chocó* (no. 38): The uppermost portion, flowing southward, follows the western base of the Serranía de los Saltos and forms a forested swampy valley which is still uninhabited. The basalt ridge of the Serranía de los Saltos rises northward to connect with the Mt. Pirre massif across the Panamanian border. The Río Salaquí crosses the basalt ridge in a narrow rocky canyon just below the mouth of the Río Jurachirá. Farther east the river splits into numerous small channels, where it reaches the swamps and marshes of the lower Atrato Valley. Birds were taken in the forests at the eastern base of the Serranía de los Saltos near the last westernmost clearings encountered along the Río Salaquí (Pl. 1, Fig. 1). 4—8 March 1964 (30 specimens).

*Río Tanela, Dep. Chocó* (no. 34): A river on the eastern slope of the Serranía del Darién which, in its upper half, flows through uninhabited forests. Collections come from the forest in the area where the trail to the Río Tolo leaves the bed of the Tanela River. Elevation is around 100 meters in this area. March 1959 (93 specimens).

*Río Tarazá,* Dep. Antioquia: A small river that joins the lower Río Cauca opposite Cáceres in the Municipio Ituango.

*Río Tolo, Dep. Chocó* (no. 32): A river on the eastern slope of the Serranía del Darién that empties into the Gulf of Urabá near the town of Acandí. March 1959 (10 specimens).

*Río Truandó, Dep. Chocó* (no. 42): The headwaters of this river are close to the Pacific Ocean near Cupica. It is joined from the north by the Río Nercua just before cutting through the Serranía de los Saltos in an easterly direction. After crossing this basalt ridge in a rocky canyon it reaches the extensive Atrato swamps. Except for a lumber camp no houses or clearings are encountered until one reaches La Nueva, a small village in the swamps close to the Atrato River. Birds were collected in the forests at the eastern base of the Serranía de los Saltos (Pl. 1, Fig. 2). 11—15 March 1964 (41 specimens).

*Río Tulapa, Dep. Antioquia* (no. 16): A few settlers had opened small clearings in the semi-evergreen forest covering the hilly terrain northeast of Turbo during the time of my visit in January 1959 (15 specimens).

*Río Uva, Dep. Chocó* (no. 46): A rough forest stream, on the eastern slope of the Baudó Mountains, with many rapids along its course. The area is densely forested. A few Indian families live in widely scattered small clearings. At one such dwelling site near the Río Bojayá I camped for a week. 7—12 March 1965 (66 specimens).

*Ríosucio. Dep. Chocó* (no. 37): A village on the eastern bank of the Atrato River at the mouth of the Río Sucio, surrounded by large swamps. Behind the village, firm ground with secondary forest and abandoned plantations exists for some distance. 2—3 March 1965 (10 specimens).

*Sautatá, Dep. Chocó* (no. 36): An abandoned sugar plantation. The extensive clearings are now devoted to cattle raising. Collections were made mostly along the Río Sautatá above the Hacienda in forested terrain and around the clearings. March 1959 (67 specimens).

*Serranía de San Jacinto, Dep. Bolivar* (Fig. 4): A series of hills and low mountains, 600 to 800 m elevation, representing the northernmost extension of the Western Andes. Rainfall here is considerably higher than in the surrounding open plains and may reach 1 500 mm per year. Remnants of the original forest cover (Moist to Dry Tropical Forest) remain along some of the deeply incised valleys. Coffee forests with the Avocado tree *(Persea americana* Mill.) used as shade cover for the coffee bushes are found in parts of the area. The rest of the country has been fairly well cleared, although in many places it has grown back as entangled and low second growth. We collected 230 specimens in this range in September 1960 and from January through March 1961. Collecting stations are (Fig. 4): María La Baja; Arroyo (=creek) Playón; San Cristóbal; Arroyo Cacao; San Juán Nepomuceno; San Jacinto; San Isidro; Cansona; San Carlos; Arroyo Camaroncito; Lázaro; Arroyo Tigre; Palmira.

*Socarré (Socorro), Dep. Córdoba:* A collecting station of M. A. Carriker, Jr. and P. Hershkovitz on the upper Río Sinú, about 2.5 km below the mouth of the Río Verde, in forested hilly terrain.

*Tenche, Dep. Bolivar:* A village on the left bank of the lower Rio Cauca some 75 kilometers from its confluence with the Río Magdalena. The area is largely cleared and devoted to cattle raising. However, on small hills along the right river bank the original forest vegetation (which covers the mountains to the east) is still preserved. July 1960 (21 specimens).

*Tierra Alta, Dep. Córdoba* (no. 7): A village on the eastern bank of the Río Sinú, near the southern end of the wide cultivated valley. Forested hills and mountains occur several kilometers to the south of Tierra Alta.

*Tilupo, Dep. Chocó:* Five specimens were collected along the Tilupo River, 10 kilometers north of Sautatá (no. 36). February 1959.

*Titumate, Dep. Chocó* (no. 33): A small fishing village on the rocky western shore of the Gulf of Urabá. March 1959 (7 specimens).

*Turbo, Dep. Antioquia* (no. 18): A small town behind the mangroves lining the southern portion of the Gulf of Urabá and surrounded by extensive clearings and open plantations. 33 specimens were collected along the beaches, in remnant humid forest, and in open country. February 1959.

*Unguia, Dep. Chocó* (no. 35): A village at the base of the forestcovered Serranía del Darién just west of the Atrato delta. Collections were made in the forested hills west of the village. March 1959 (35 specimens).

*Villa Arteaga, Dep. Antioquia* (no. 25): A village on the Turbo road, 70 km SSE of the Gulf of Urabá. This forested area is partly cleared along the Turbo road and the lower slopes of the Serranía de Abibe.

*Yatí, Dep. Bolivar:* A village on the bank of the Brazo de Loba (lower Río Magdalena), 15 kilomters north of the town of Magangué, and located in the open and partially inundated plains along the lower Río Magdalena. March 1961 (24 skins).

## 11. Annotated List

The bird collection treated below consists of 1418 specimens from the tropical lowlands of northwestern Colombia and was assembled by the author between 1959 and 1966. Four hundred specimens have been deposited at The American Museum of Natural History, New York. The Instituto de Ciencias Naturales, Universidad Nacional, in Bogotá (Colombia) received 397 specimens taken in the Urabá region and 316 specimens from northern Colombia. 205 specimens from Mutatá, Dep. Antioquia and 100 specimens from the Urabá region have been deposited in the Zoologische Staatssammlung, München, Germany. Preliminary lists of parts of the collection have been published by Haffer (1959, 1967 c) and Haffer & Borrero (1965). This information is here summarized and treated together with the data obtained between 1963 and 1965. Additional species recorded from northwestern Colombia which I did not collect, have been listed by De Schauensee (1948—1952, 1950 b).

The length and width of the larger testis for males and the diameter of the largest follicle for females, e. g. ♂ (5 x 3 mm), ♀ (2 mm), is indicated for each specimen of the Urabá collection assembled between 1963 and 1965. No dates of collection are mentioned in the species accounts, because I remained only a few days at each collecting station. These dates can be found in the preceding list of localities. English names and the sequence of species follow De Schauensee (1970).

I stated above (p. 50) my position regarding the ambiguous nature of "subspecies". Nevertheless, I used trinomials throughout the species list below following current tradition. Whenever possible I provided some information on the population structure of the various species and on the nature of "subspecies" under discussion. Subspecific names are nothing but labels for convenient cataloguing by the taxonomist and convey very little biological information other than the indication that a particular "subspecies" differs from another population (or populations) designated by another subspecies name. "Subspecies" proved useful in breaking away from the typological tradition of the species concept and "is a convenient means of classifying population samples in geographically variable species, in particular in those with phenotypically distinct geographical isolates" (Mayr 1963: 349). The subspecies concept is basically still typological if the erroneous assumption is made that subspecies represent uniform subdivisions of species and can be defined objectively. To further our understanding of species, i. e. their composition and interaction, we must study population structure and superspecies, not "subspecies" as Ernst Mayr (1959, 1963) has emphasized repeatedly. A new level of taxonomic insight is only reached if subspecific determination is no longer considered an end in itself. We need analyses of continuous or stepped clines in Colombia, of hybrid zones, geographical isolates, etc. Labeling the various differing populations of a given species by means yet to be devised (e. g. letters, numbers, ratios, etc.) may eventually replace, or be combined with, the less flexible system of "subspecies".

A large number of species listed below also occur in Middle America. For this reason the publications of Chapman (1928, 1929, 1935, 1938), Eisenmann (1952) and Wetmore (1965, 1968, 1972) on Panamá as well as Skutch (1954, 1960, 1969, 1972) and Slud (1964) on the avifauna of Costa Rica should be consulted for data on general behavior, nesting, voice, and other biological aspects of many species of northwestern Colombia. The books by Chapman (1929, 1938) on the bird life of Barro Colorado Island in the Panamá Canal Zone provide an excellent introduction to the avifauna of the trans-Andean lowlands.

## Tinamidae

Common species in northwestern Colombia are the **Great Tinamou,** *Tinamus major saturatus* (Río Mulatos 1 ♂; Río Tanela 1 ♂, 1 ♀), of the forest floor and the **Little Tinamou,** *Crypturellus soui,* which inhabits dense thickets along river valleys and around clearings. Specimens of the latter species from west of the Gulf of Urabá (e. g. Acandí 1 ♀, *C. s. harterti)* have the chest more intensively colored and less ferruginous than birds from east of the Gulf (Río Multatos 1 ♀, *C. s. caucae;* additional records of this form from northwestern Colombia are given by De Schauensee 1948—1952, 1950 b and Blake 1955). The population inhabiting the hills along the lower

Río Cauca is typical of *C. s. caucae* (specimens from Norosí and La Raya in the Bogotá collection). A male which I collected near the base of the Serranía de San Jacinto at San Juán Nepomuceno, Dep. Bolivar, has buffy underparts and less rufescent wing coverts. It is phenotypically close to the pale form *C. s. mustelinus* which inhabits the dry hilly area near the Caribbean coast including portions of the Guajira Peninsula (Marinkelle 1970). The population near San Juán Nepomuceno may be intermediate between typical *caucae* and *mustelinus*, as another bird from this locality has been referred to *caucae* by Blake (1955) and presumably is more intensively colored than our specimen.

A widespread species of the superhumid forest in the Pacific lowlands of Colombia is dark gray **Berlepsch's Tinamou** *(Crypturellus berlepschi)*, a representative of the Amazonian species *C. cinereus* (Fig. 12 A). I have heard frequently the song of what was most probably *C. berlepschi* in the forest near Mutatá; Blake (1955) reported this species from Villa Arteaga, not far from Mutatá. Berlepsch's Tinamou is missing from the less humid Urabá region and from northern Colombia.

Another western Colombian endemic species is the **Chocó Tinamou** *(Crypturellus kerriae)*, which had been known until recently only from a male and a female collected in the Baudó Mountains of the central Chocó region (Wetmore 1950). Wetmore et al. (1972) identified it also in the hills along the Panamanian border with Colombia (Cerro Quía, Fig. 15 A). I did not collect this rare species in the Urabá region.

The **Colombian Tinamou** *(Crypturellus columbianus)* is restricted to the deciduous woodland and seasonal forests of northwestern Colombia (Nechí Valley, upper Sinú Valley, Serranía de San Jacinto; Fig. 20 A; De Schauensee 1950 b, Blake 1955). It is missing from the humid Pacific forests. *C. columbianus* was thought to be related to *C. noctivagus* and *C. cinnamomeus* by De Schauensee (1950 b) and to *C. boucardi* of Middle America by Blake (1955). P. Schwartz, E. Blake and E. Eisenmann (pers. comm.) now believe this form to be a race or close ally of *C. erythropus* of northern Amazonia and Venezuela being connected by *C. idoneus* and *C. saltuarius* of northern Colombia (Fig. 20 A). Carriker (1955) also reached the conclusion that the northern Colombian species *C. columbianus, saltuarius,* and *idoneus* are very closely related based on the identical or very similar mallophagan fauna. Wetmore (1950) originally thought *C. saltuarius* to be related to *C. kerriae* and Mayr (1957) designated it a subspecies of *C. kerriae.*

## Water and Sea Birds

Birds observed along the sea shores and water courses of northwestern Colombia include the following: *Sula leucogaster* was common along the rocky Pacific coast. I saw this bird frequently in March 1965 on and around the islets that dot the coastal waters from Bahia Solano north to Juradó.

It was also found at the western coast of the Gulf of Urabá near Titumate and Acandí. A nesting colony exists on Isla Tonel near the Panamanian border (Wetmore 1965 b: 58).

The cormorant *Phalacrocorax brasilianus* is very common along all rivers, wide or small, of the region. *Anhinga anhinga* is also frequently seen but appears to be restricted to large rivers such as the Río Atrato and the Río Sinú.

Among the egrets, storks, and bitterns, I observed or collected in the Urabá region and along the Sinú River *Ardea cocoi, Butorides v. virescens* (Turbo 1 ♂, imm., 10 February 1959), *B. s. striatus* (Turbo 1 ♀), *Florida caerulea caerulescens* (common, Turbo 1 ♂), *Casmerodius albus egretta* (common), *Leucophoyx t. thula, Mycteria americana* (Sinú Valley), *Bubulcus ibis* (Sautatá 1 ♀; this immigrant species has occupied almost all open areas in Colombia); *Tigrisoma lineatum* (observed along several forest streams of the Urabá region).

The **Boat-billed Heron** *(Cochlearius cochlearius)* occurs locally along rivers in northwestern Colombia; I did not obtain specimens. The *zeledoni* subspecies group of this heron is known throughout Panamá, except along the Río Jaqué in southwestern Darién, and extended its range eastward across the Colombia border at least to Acandí *(C. c. panamensis;* see Wetmore 1965). On the other hand, the South American subspecies, *C. c. cochlearius,* has been collected along the Pacific coast at Nuquí and Río Jaqué, Darién. It remains unknown whether or not both groups are in contact and, if so, whether they hybridize. Middle American *zeledoni* and South American *cochlearius* may have to be considered specifically distinct (De Schauensee 1948—1952: 364, 1145).

The **Northern Screamer** *(Chauna chavaria;* Sautatá 1 ♀) is quite common in the marshes of the lower Magdalena and Sinú Valleys as well as in the extensive marshes and swamps of the lower Atrato Valley, where I encountered frequently pairs on low trees or feeding on the ground only several hundred meters apart. This species had not been reported by previous authors from the Atrato region.

*Aramus g. guarauna* (Sautatá 1 ♂) was observed occasionally in the Sinú Valley, along the Río Atrato, and near Unguía.

Among the woodrails, *Aramides c. cajanea* (upper Río Sinú, mouth of Río Naín 1 ♂, 9 × 3 mm) is a fairly common bird which I heard along the Ríos Mulatos, Naín, and near Unguía and Acandí. Its characteristic call, usually uttered as a duett in the early morning and in the evening, is a loud series *gitigak gitigak gitigak* .... repeated five to ten times and followed by a subdued *googoogoo* .... The local name in the Urabá region is Cheleka. This species appears to be much rarer along clear forest streams, for I have not heard its voice along rivers in the Pacific forest, e. g. the

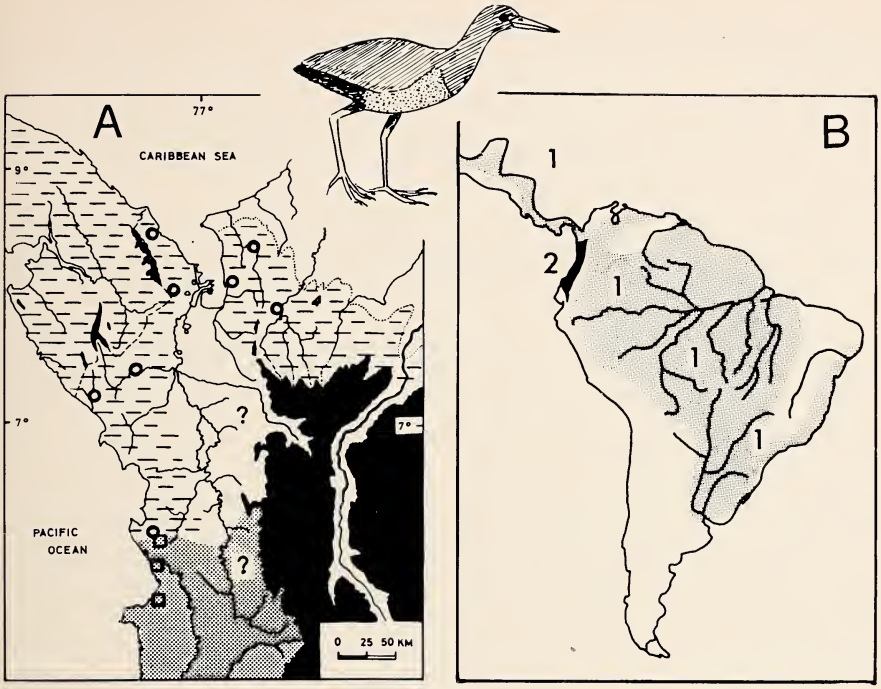


Fig. 27: Distribution of the woodrails, *Aramides cajanea* superspecies.

*Explanation:* **A** Distribution of *A. cajanea* and *A. wolfi* in northwestern Colombia and easternmost Panamá [1]). Dashed area and open circles — *A. c. cajanea.* This bird is common in eastern Panamá, where no individual records are plotted. Shaded area and open squares — *A. wolfi.* **B** Generalized distribution of *A. cajanea* (1, shaded area) and *A. wolfi* (2, solid area).

upper Río Truandó, Río Uva or the Río Murrí. It has been reported in the lower Atrato Valley from the Río Salaquí and from the Alto del Buey region in the Baudó Mountains (De Schauensee 1948—1952). *A. cajanea* is widespread east of the Andes and in Middle America but is replaced from the central Chocó region to the south by its close relative *Aramides wolfi,* a form also recorded from the Alto del Buey in the central Chocó (Fig. 27). This, however, does not prove sympatric breeding of these two allied species. A detailed study of their zone of contact is needed to clarify their interrelationship and taxonomic status. *A. wolfi* has a somewhat heavier bill and a more richly colored back, which is chestnut brown or olivaceous brown in *wolfi* and olive in *cajanea.*

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[1]) Locality records shown on this and the following maps are taken from Wetmore (1965—1972) for eastern Panamá and from De Schauensee (1948—1952) and Haffer (this publication) for northwestern Colombia. Mountains above 1000 m elevation are in black. The stippled line east of the Gulf of Urabá indicates the present eastern limit of humid forest.

*Laterallus exilis* is known from a few scattered localities in Colombia (Nicéforo-Maria 1948: 202, de Schauensee 1948—1952: 170). I found a pair and collected the female in an extensive open marsh in the lower Atrato Valley, 5 km upstream from Sautatá. *Porphyrula martinica* (Sautatá 1 ♀) was also encountered in this region, where *Jacana jacana hypomelaena* is very common (Atrato, Sinú River).

I observed *Heliornis fulica* in a small pond of the Río Doguadó which empties into the upper Río Napipí in densely forested terrain. Another specimen was caught near Riosucio on the lower Río Atrato.

The **Sunbittern** *(Eurypyga helias major)* is fairly common in forested areas of northwestern Colombia, where I observed it east of the Gulf of Urabá along the Ríos Mulatos, Guadualito, Currulao, Grande, Zungo, near Mutatá (1 ♂) as well as near Titumate on the western shore of the Gulf. It is missing from the forest of the Chocó region.

*Vanellus chilensis* is common in the open Sinú Valley and was occasionally observed near Turbo. Migrating waders seen or collected on the beaches around Turbo include *Squatarola squatarola, Charadrius semipalmatus, Tringa flavipes, T. solitaria, Actitis macularia, Catoptrophorus semipalmatus, Arenaria interpres,* and *Calidris mauri* (see Haffer 1959).

## Cathartidae

The common species in and around villages and towns is *Coragyps atratus. Cathartes aura* is seen frequently along the forest streams. In March 1959, I saw large flocks of this species composed of over 100 individuals along the Río Tolo near Acandí on the western side of the Gulf of Urabá. These flocks may have been migrating birds of the northern nominate subspecies. The **King Vulture** *(Sarcoramphus papa)* is also widespread; I observed it near Turbo and along the rivers Mulatos, Tulapa, and Broqueles as well as at other localities in the upper Río San Jorge and lower Río Cauca Valleys.

## Accipitridae

Among the species of hawks observed or collected are the following: *Elanus leucurus* was seen in February 1959 over pastures near Turbo. This species has expanded its range considerably and has become much more common in Middle America in recent years (Eisenmann 1971).

*Gampsonyx swainsonii leonae* (Turbo 1 ♂, Mutatá ♂), *Rostrhamus s. sociabilis* (Unguía 1 ♂); *Ictinia plumbea* (Unguía 1 ♂, 1 ♀; Quebrada Charrura 1 ♂); *Buteo magnirostris insidiatrix* (Río Tulapa 1 ♂, Turbo 1 ♂) is common along edges of forest and thickets; *Buteo n. nitidus* (Sautatá 1 ♀, Río Tanela 2 ♀, Mutatá 1 ♂, Quebrada Charrura 1 imm.); *Leucopternis semiplumbea* (Río Tulapa 1 —); *Heterospizias m. meridionalis* (Río Guadua-

lito 1 —); *Buteogallus u. urubitinga* (Río Mulatos 1 ♂); *Buteogallus anthracinus* (Río Guadualito 1 ♂, Unguía 1 ♀); *Harpia harpyja* (Río Napipí 1 ♀, Río Mulatos 1 ♀). I did not obtain specimens of two interesting hawks, *Leucopternis albicollis* and *L. plumbea,* which De Schauensee (1950 b) reported from Quimarí in the upper Sinú region (Fig. 12 B).

*Helicolestes hamatus* (Temminck) **Slender-billed Kite**

*Specimens:* Unguía 1 —; Río Truandó 1 ♀ (1.5 mm); in both specimens iris yellow, cere and feet orange. *Taxonomy:* Monotypic. Spottily distributed from Amazonia to eastern Panamá.

The status of the Slender-billed Kite, of spotty distribution in northern Colombia, is not yet known. According to Hellmayr & Conover (1949) only one record from Antioquia was extant when I collected a specimen near Unguía, west of the mouth of the Atrato River (Haffer 1959). The female from the Río Truandó is the third specimen collected in Colombia. Meanwhile Wetmore (1962, 1965 b) recorded two individuals of this hawk from the upper Tuira basin in extreme eastern Panamá near the Colombian border. It now appears that this interesting species is not excessively rare along some of the swampy forest streams of the lower Atrato Valley and in the adjacent Tuira basin. I encountered this species along shady banks of forest rivers sitting about two meters high on horizontal branches. The lower Atrato Valley appears to be ecologically similar to the area in Surinam, where Haverschmidt (1959) observed the breeding of this species, although the open swamps and the swamp forest are more extensive in northwestern Colombia.

## Falconidae

A noisy and conspicuous bird of the forests around the Gulf of Urabá is the **Red-throated Caracara** *(Daptrius americanus;* Río Tanela 1 ♀), which I observed also in the Serranía de San Jacinto and near Coveñas on the Caribbean coast in open hilly terrain with only small scattered patches of secondary growth. The loud calls *cacáo* . . . *caca* . . . *cáo* . . . remind one more of a gallinaceous bird than a raptor. De Schauensee (1950 b) reported the forest falcons *Micrastur mirandollei* and *M. ruficollis* from Quimarí in the upper Sinú region.

Species of unforested areas that followed large clearings and entered the forested Urabá region include, e. g., *Herpetotheres cachinnans* (Plate 5, Fig. 1), *Milvago chimachima* (Turbo 1 ♀), *Falco rufigularis petoensis* (Turbo 2 ♂, 1 ♀), and *F. sparverius* (Río Guadualito 1 ♀, 1 —; Río Mulatos 1 ♀).

## Cracidae

*Ortalis cinereiceps chocoensis* De Schauensee **Gray-headed Chachalaca**

*Specimens:* Sautatá 1 ♂, 1 ♀; Juradó 1 ♀ (4 mm). *Taxonomy:* Middle American *O. cinereiceps* consists of a series of clinally related subspecies *O. c. frantzii-*

Plate 5

Fig. 1: Laughing Falcon, *Herpetotheres cachinnans,* at a large forest clearing. Foto J. I. Borrero.

Fig. 2: Lemon-browed Tanager, *Chlorothraupis olivacea,* inhabits the understory of the trans-Andean forests. Foto J. I. Borrero.

*cinereiceps-mira-chocoensis* (Vaurie 1965). Allopatric with *O. garrula* of northern Colombia.

The Gray-headed Chachalaca is quite common in thickets and secondary growth around the large clearings of Sautatá on the lower Atrato River. I also observed flocks of ten to twenty individuals around Titumate and Acandí near the western shore of the Gulf of Urabá as well as at Juradó on the Pacific coast. De Schauensee (1950 a) reported this bird from the Río Salaquí and I saw a group of five birds along the Río Napipí, presently the southernmost record of this species in western Colombia (Fig. 28).

*Ortalis garrula* (Humboldt) **Chestnut-winged Chachalaca**

*Specimens:* None. *Taxonomy:* Monotypic and endemic in northern Colombia; parapatric with *O. ruficauda;* allopatric with *O. cinereiceps* (Fig. 28).

I have frequently heard and observed this noisy bird in the upper Sinú Valley. It gives a conspicuous, loud, far-carrying chorus which starts low and increases in loudness and may end rather abruptly. According to the local people the female asks the male "Se cae la casa?" and the male answers "No se cae, no se cae!' in rapid succession, which imitates the song rather well.

The Chestnut-winged Chachalaca is common in dense thichets and tall second growth of northern Colombia (Fig. 28), entering clearings in the upper Sinú Valley. As of 1966 it had not yet reached the Río Verde, a western headwater stream of the Río Sinú. No chachalaca is found in the

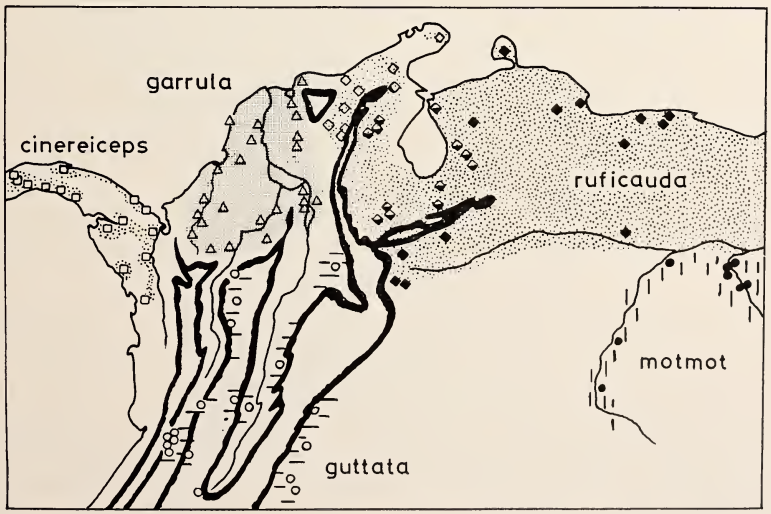


Fig. 28: Distribution of the Chachalacas, *Ortalis motmot* superspecies, in northwestern South America (modified from Vaurie 1965). Mountains above 1000 m elevation are outlined in black.

forest region between the Sinú River and the Gulf of Urabá. The situation may change in the near future, as these forests are rapidly being destroyed, leading to a great range expansion in the Sinú population of *O. garrula*.

I saw chachalacas, but unfortunately did not obtain specimens in 1964 and 1965 near Turbo and near Currulao, east of the Gulf of Urabá where large clearings appeared during the banana boom of 1962—1965. I assume that these are advance colonists of *garrula* that may have followed cleared land along the Caribbean coast. Or they might be colonists of *cinereiceps* from across the Atrato River.

The tall swamp forest and dense palm and grass swamps found south of the Gulf of Urabá probably are ecologically unsuited to any chachalaca. I believe that *cinereiceps* and *garrula* are essentially separated by a distributional gap, which, however, is rapidly being bridged. The Obaldía specimens and the "intermediate" bird from Tierra Alta on the upper Río Sinú discussed by De Schauensee (1950 b), Vaurie (1965) and Wetmore (1965 b: 306) may indicate occasional introgression. However, I think these specimens can be used neither as evidence for overlapping ranges of good species (as by Wetmore) nor as evidence for the existence of a broad "zone of secondary intergradation" (as by Vaurie). There simply are no chachalacas in the area where they are supposed to overlap or hybridize. I think *cinereiceps* and *garrula* represent two allopatric populations whose designation as subspecies or species cannot be based on existing field evidence. The birds themselves may answer this problem once they are in broad contact after continued clearing of the forests in Urabá.

If *Ortalis ruficauda* of northern Venezuela and *Ortalis garrula* are considered specifically distinct (both must be in direct contact in northeastern Colombia, yet must remain parapatric), the same treatment should be given *Ortalis cinereiceps* and *O. garrula,* particularly if the similarity and dissimilarity, respectively, of the voice is also taken into consideration. Certainly, *cinereiceps* and *garrula* originated in widely separated areas.

I suspect that the single male collected by Marinkelle (1970) at the base of the Serranía Macuira, Guajira Peninsula, represents *O. ruficauda lamprophonia* Wetmore (1953) rather than *O. garrula* as reported.

*Penelope purpurascens aequatorialis* Salvadori & Festa **Crested Guan**

*Specimens:* Mutatá 1 ♂, 1 ♀. *Taxonomy: P. p. aequatorialis* is a clinal form of this trans-Andean species. Parapatric with *P. jacquaçu* of Amazonia.

A fairly common species in the forests of northwestern Colombia but much hunted for its meat. This widespread guan occupied the entire trans-Andean forest region north to Mexico and east to the mouth of the Orinoco River.

The smaller Baudó Guan *(P. ortoni)* is a species of the Chocó forests and has not been found near the Gulf of Urabá (Fig. 21 A).

*Crax alberti* Fraser **Blue-billed Curassow**

*Specimen:* San Juán Nepomuceno 1 ♂. *Taxonomy:* Monotypic. Endemic species of northern Colombia. In contact with *C. rubra* (Fig. 29).

The Blue-billed Curassow is the northern Colombian allospecies of the *Crax ruba* superspecies and inhabits parts of the upper Sinú region (Socarré, Quimarí), where it meets *C. ruba* (Fig. 29). *C. alberti* is known also from the upper San Jorge Valley (Catival), the lower Cauca region (Río Nechí, Valdivia), the western side of the humid Magdalena Valley (Volador and 20 km west of Honda) as well as from isolated forests near the Caribbean coast, such as those along the northern base of the Sierra

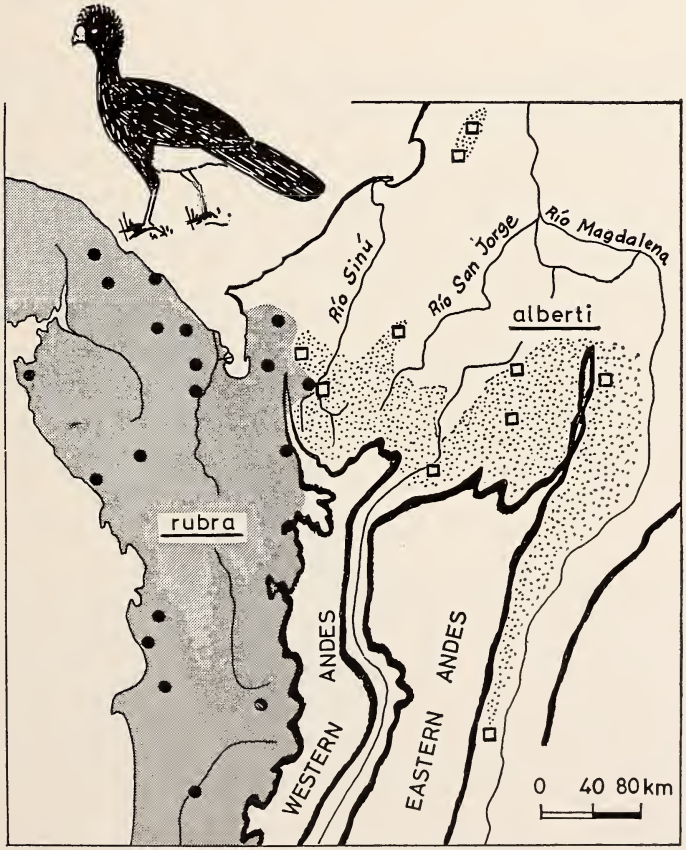


Fig. 29: Distribution of the Black Curassows, *Crax rubra* superspecies, in northwestern Colombia.

*Explanation*: Solid circles and shaded area — *C. rubra*. Open squares and stippled area — *C. alberti*.

Nevada de Santa Marta and in the Serranía de San Jacinto (Fig. 20 B); see Vaurie (1967). It is still present in small numbers in the Serranía de San Jacinto but is becoming very rare. We collected an adult male west of San Juán Nepomuceno and Blake (1955) reported this curassow from Colosó, in the southern portion of the Serranía de San Jacinto.

*Crax "annulata"* of the Santa Marta region is a color phase of female *C. alberti*, not a separate species (Vaurie 1967).

*Crax rubra rubra* (L.) **Great Curassow**

*Specimens:* Río Mulatos 1 ♀; Río Tanela 1 ♀; Río Salaquí 1 ♂, 1 ♀. *Taxonomy:* This trans-Andean species forms clines of decreasing size and of female coloration northward in Middle America (Vaurie 1967). In contact with *C. alberti* in the Sinú region.

The Great Curassow is hunted wherever settlers cut new clearings. It soon becomes shy and retiring. The bird is found throughout the humid lowlands of Middle America and western Colombia to northwestern Ecuador. It also inhabits the eastern shores of the Gulf of Urabá, where it is known from several localities in the valleys of the Río Mulatos, Río Currulao, and Río Naín (Blake 1955, Haffer 1967 b). Farther east in the upper Sinú-Mulatos region, *C. rubra* meets the parapatric *Crax alberti*, a close relative of the northern Colombian forests (Fig. 29, 20 B). These species were reported from localities only a few kilometers apart without indication of interbreeding. It has been claimed that their ranges overlap in the upper Sinú region (Vuilleumier 1965) which, however, is not known to be the case. Presumably, *Crax rubra* and *C. alberti* exclude each other geographically as a result of ecologic competition. Field evidence is needed to substantiate this assumption.

## Phasianidae

The **Marbled Wood-Quail** *(Odontophorus gujanensis)* forms coveys consisting of 5 to 8 birds on the forest floor in the lower Atrato Valley and in the Urabá region, but does not range south into the wet Chocó region possibly because of ecological reasons. The southernmost records of this species in the Atrato Valley are from the Río Salaquí, Murindó (De Schauensee 1948—1952), and the Río Truandó, where I heard the characteristic *"corco-vao"* call. Skutch (1947) published a life history study of this wood-quail.

Two other species of northwestern Colombia are *Odontophorus erythrops* (known from Juradó) and *Rhynchortyx cinctus* reported from the Pacific lowlands and eastward to Murucucú, Tarazá, and Volador in the Magdalena Valley (De Schauensee 1950 b, Wetmore 1965 b). I did not collect these wood-quails.

## Columbidae

*Columba cayennensis pallidicrissa* Chubb **Pale-vented Pigeon**

*Specimen:* Frasquillo 1♂ (14 mm). *Taxonomy: C. c. pallidicrissa* comprises populations from Mexico to northern Venezuela and Trinidad; probably clinally related to the Chocó form *C. c. occidentalis.*

Large flocks were observed occasionally near Sautatá and in the upper Sinú Valley near Frasquillo.

*Columba goodsoni* Hartert **Dusky Pigeon**

*Specimen:* Mutatá 1♂ (7×4 mm), deposited at Acad. Nat. Sci. Philadelphia. *Taxonomy:* Monotypic (?). Endemic species of western Colombia—northwestern Ecuador.

The Dusky Pigeon is a bird of the humid Pacific forests (Fig. 21 B and 30). I found it in the lower Atrato Valley north only to Mutatá, where it was quite common in August 1966 (Haffer 1967 c). The typical call *hóó-goo-goo*

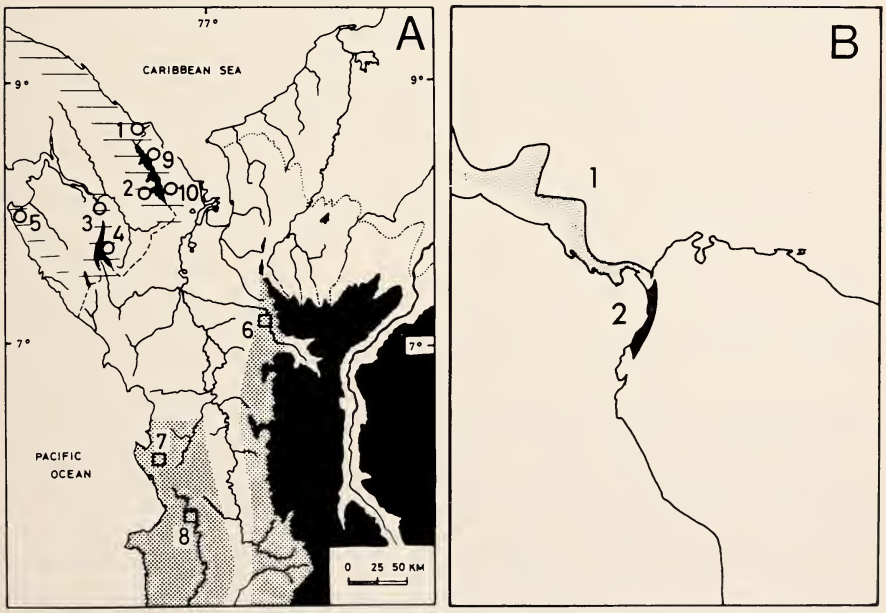


Fig. 30: Distribution of the *Columba nigrirostris* superspecies.

*Explanation:* **A** Distribution of *Columba nigrirostris* and *C. goodsoni* in northwestern Colombia and eastern Panamá. Dashed area and open circles — *C. nigrirostris:* 1 Puerto Obaldía, 2 Cerro Mali, 3 El Real, 4 Cerro Pirre, 5 Cerro Sapo, 9 Forest west of Acandí, 10 Headwaters of Río Cuti. Shaded area and open squares — *C. goodsoni:* 6 Mutatá, 7 Alto del Buey, 8 Río Baudó, **B** Generalized distribution of *C. nigrirostris* (1, stippled area) and *C. goodsoni* (2, solid area).

was heard frequently from the tree tops on sunny mornings. Mr. De Schauensee (pers. comm.) examined my specimen and concluded that it may belong to an undescribed subspecies because of certain color characters (underparts more gray, crown darker, rest of upper parts more liver color and less tinged reddish than in specimens from the central Chocó region).

The Middle American representative of *C. goodsoni* is the Short-billed Pigeon *(Columba nigrirostris,* Fig. 30) whose call Wetmore (1968) rendered as *oh-whit-mo-gó* and Eisenmann (1952) as *ho, cu-cu-cooo.* This species ranges from southeastern Mexico to Panamá inhabiting the lowlands and lower slopes of the mountains. It enters Colombian territory on the eastern slope of Mt. Tacarcuna (Wetmore 1965 a, 1968). *C. nigrirostris* and *C. goodsoni* may be separated by a distributional gap, as I have not found either of these pigeons in the less humid forests around the Gulf of Urabá.

A close relative of the species discussed above is *Columba subvinacea* which is a rare inhabitant of the northwestern Colombian forests. I did not encounter this species or *Columba plumbea* reported by De Schauensee (1950 b) from Quimarí.

*Columbina talpacoti rufipennis* (Bonaparte) **Ruddy Ground-Dove**

*Specimens:* Turbo 1 ♂; Unguía 1 ♀; Serranía de San Jacinto (Lázaro 1 ♀; Cansona 1 ♀). *Taxonomy:* This subspecies comprises populations from Mexico to Trinidad. The species is missing in the Chocó region.

This ground-dove is restricted to open areas in fairly humid regions, where it is quite common.

*Leptotila verreauxi verreauxi* (Bonaparte) **White-tipped Dove**

*Specimens:* Sautatá 1 ♀; Serrania de San Jacinto (San Carlos 1 ♂). *Taxonomy:* This subspecies comprises populations from Nicaragua to Trinidad; not in contact with *L. v. decolor* of southwestern Colombia to northern Peru.

Common in fairly humid regions, where this dove inhabits thickets, secondary forest and forest borders.

I did not collect *Leptotila c. cassinii,* which is known from several localities in northwestern Colombia.

*Geotrygon veraguensis* Lawrence **Olive-backed Quail-Dove**

*Specimens:* Río Napipí 2 ♂ (8×4, 7×4 mm). *Taxonomy:* Monotypic. Endemic species of the trans-Andean region (Costa Rica—Ecuador).

A trans-Andean quail-dove of the dark forest floor. Dr. E. O. Willis (pers. comm.) found it in wet ravines of the upper Río Verde region. The species is missing from the less humid forests around the Gulf of Urabá but it ranges along the wet foothills of the Western Andes to the lower Cauca Valley.

## Psittacidae

Six species of **macaws** *(Ara)* occur in northwestern Colombia as follow: *Ara ararauna, A. militaris, A. ambigua, A. macao, A. chloroptera,* and *A. severa.* They are at least partially sympatric except for the two green macaws *Ara militaris* and *A. ambigua.* There is no definite specimen record of *A. macao* from the Urabá region. I observed *A. severa* in fairly open areas near Sautatá on the lower Atrato River. Like other Amazonian species, the macaws avoid the Wet and Pluvial Forests of the central Chocó region and none of them has been found south of the Baudó Mountains and the Nuquí region. I observed *A. ararauna* in the Atrato Valley south to the Río Salaquí. Isolated populations of *A. ararauna* and *A. ambigua* recur south of the Chocó region in the less humid seasonal forests of western Ecuador.

The green macaws *Ara militaris* and *A. ambigua* form a superspecies (Fig. 31). The differences betweeen these species are not conspicuous but constant over their respective ranges. These differences may be summarized as follows (De Schauensee 1970, Forshaw 1973): *Ara ambigua* inhabits humid forests and has a larger bill than *A. militaris;* more yellowish green plumage; paler blue rump and uppertail coverts; basal part of central tail feathers more orange; forehead and feathered lines on lores scarlet, not red as in *A. militaris.* Forshaw (1973) reported the following measurements for 12 males of *A. a. ambigua, left,* and for 10 males of *A. m. militaris,* right:

| | | | |
|---|---|---|---|
| wing | 356—422 (391.6) | against | 345—347 (360.1) mm |
| tail | 330—468 (399.1) | against | 375—419 (387.9) mm |
| exposed culmen | 65— 81 ( 71.6) | against | 53— 59 ( 56.9) mm |

Wetmore (1968: 67) reported even longer tail feathers in seven males of *A. a. ambigua:* 387—481 (430) mm.

The above differences between *A. ambigua* and *A. militaris* in plumage color and measurements are also apparent in examples of these species from the Urabá region and from the Western Andes of Colombia, respectively, which I compared in New York (AMNH) and in Philadelphia (ANSP). *A. ambigua* and *A. militaris* may be in contact in the lower Cauca region of northwestern Colombia (Fig. 31), although this is not known to be the case [1]). Therefore it also remains unknown whether both species hybridize

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[1]) De Schauensee (1950 b: 120) reported by a slip of the pen *„Ara militaris militaris"* from the upper Sinú Valley (Quimarí and Murucucú) together with *Ara ambigua.* Actually, De Schauensee's intention (pers. comm.) was to record *Ara chloroptera* (instead of *A. militaris)* in the cited publication. The collections at Philadelphia contain a male and a female of *Ara chloroptera* from Quimarí but no specimens of *A. militaris* at all from Colombia.

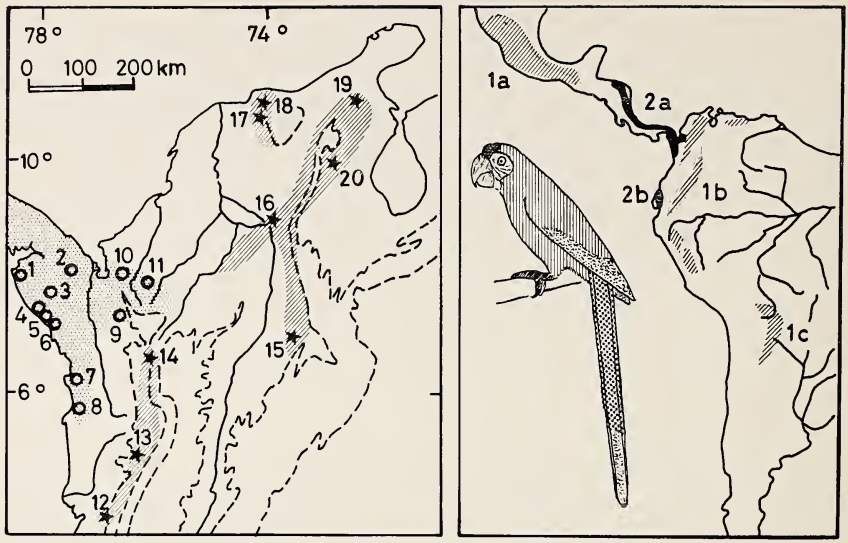


Fig. 31: Distribution of the Green Macaws, *Ara militaris* superspecies.

*Left:* Distribution of *Ara ambigua* and *A. militaris* in northern Colombia and easternmost Panamá. Open circles and stippled area — *Ara a. ambigua.* Panamá: 1 Garachiné; 2 Cerro Mali, Río Tacarcuna; 3 Cerro Pirre; 4 upper Río Jaqué. Colombia: 5 Juradó; 6 Río Nercua; 7 Baudó Mountains; 8 Nuquí; 9 Villa Arteaga (2 spec., USNM Washington); 10 Quimarí; 11 Murucucú. Closed stars and hatched areas — *Ara m. militaris.* Colombia: 12 Cisneros; 13 Silencio; 14 Antioquia; 15 Chucurí; 16 El Banco; 17 Riofrio and Orihueca; 18 Bonda and Las Nubes. Venezuela: 19 Montes de Oca and El Bosque; 20 La Sierra. Dashed line delimits the Colombian Andes above 1000 m elevation.

*Right:* Generalized distribution of *Ara militaris* (hatched areas) and *Ara ambigua* (solid areas). 1 a *Ara militaris mexicana.* 1 b *A. m. militaris.* 1 c *A. m. boliviana.* 2 a *A. a. ambigua.* 2 b *A. a. guayaquilensis.* Both species are mostly green or yellowish green with a red or scarlet forehead, blue wings and orange red central tail feathers which are tipped with blue.

along a potential contact zone or whether they remain parapatric as a result of ecologic competition. Since their ecologic requirements differ to some extent (see below), they may not actually meet anywhere in northern Colombia.

The Green Macaws, *Ara militaris* superspecies, are widespread but of local occurrence. They have disappeared from large areas due to human activity and are now confined to the more remote forest districts. *Ara ambigua* inhabits humid lowland forests and lower montane forests in western Ecuador *(A. a. guayaquilensis;* Chapman 1926) and in northwestern Colombia to Nicaragua probably also ranging into Honduras *(A. a. ambigua;* Monroe 1968, De Schauensee 1970). *A. militaris* occupies a wide

range of habitats from dry forest, open woodland to gallery forest in arid regions. Generally it avoids humid forests which, by contrast, are the home of *A. ambigua* [1]).

*Ara militaris* forms a series of more or less isolated populations along the eastern slope and foothill zone of the Andes in northern Argentina and Bolivia, in eastern Peru, Ecuador, and southeastern Colombia, in the coastal mountains of Venezuela and in northern Colombia (Fig. 31). In the latter area it is known from the Santa Marta region and the Magdalena Valley. It also ranges along the Western Andes of Colombia south to Silencio and Cisneros, where specimens of *A. militaris* have been obtained (Chapman 1917). In some of these regions, the Military Macaw may only be a temporary visitor, as this species is known to migrate over some distance. Flocks of *A. militaris* have been observed to cross the Andes in northwestern Perú from the Marañón Valley during certain months of the year (Koepcke 1961). According to information on the labels of specimens of *A. m. boliviana* from Province Sara, eastern Bolivia (AMNH, New York) flocks of 30 to 40 birds "appear in this area from January onward".

The Military Macaw is missing from most of Middle America (where *A. ambigua* occurs) but an isolated population inhabits Mexico. *A. militaris* is here widely distributed in arid and semi-arid regions ranging up to 2 500 meters in pine and oak forest (Blake 1953). Similarly isolated populations of South American birds are the Mexican forms *Campylorhynchus griseus chiapensis,* a wren, *and Cyanocorax dickeyi,* a jay (Fig. 45).

De Schauensee (1950 b) reported *Aratinga pertinax* and *Pyrrhura picta* from Quimarí and Murucucú in the upper Sinú region. I did not collect these latter species.

*Brotogeris jugularis jugularis* (Müller) **Orange-chinned Parakeet**

*Specimens:* Río San Juán 1 ♂; Titumate 1 ♂. *Taxonomy:* The widespread trans-Andean nominate subspecies may not be in contact with *B. j. exsul* of western Venezuela. This species forms a superspecies with parapatric *B. cyanoptera* and *B. chrysopterus.*

A fairly common species in semi-open areas of northwestern Colombia. It has also been collected at Quimarí and Murucucú (De Schauensee 1950 b).

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[1]) A specimen of *A. ambigua* collected by the Michler expedition in the humid forests of the Río Nercua Valley, west of the lower Atrato River and close to the village of Juradó, was reported by Cassin (1860: 137) as *"Ara militaris"*. The bird is preserved in Washington "U. S. N. M. 17820, marked ♀, and now identified as *Ara ambigua"* (A. Wetmore, pers. comm.). De Schauensee (1948—1952: 472) listed the "Río Nercua" under both species, *A. ambigua* and *A. militaris,* although probably only the female specimen mentioned above is available from this river valley.

*Pionopsitta pulchra* Berlepsch **Beautiful Parrot**

*Specimens:* Mutatá 1 ♂, 1 ♀. *Taxonomy:* Monotypic. Endemic species of western Colombia to Ecuador.

For comments see under following species.

*Pionopsitta haematotis coccinicollaris* (Lawrence) **Brown-hooded Parrot**

*Specimens:* Unguía 1 ♂. *Taxonomy:* A Middle American species which entered northwestern Colombia. *P. h. coccinicollaris* intergrades with the nominate subspecies in westcentral Panamá.

The two *Pionopsitta* parrots *P. pulchra* and *P. haematotis* form a trans-Andean superspecies. *P. pulchra* is known north to the Baudó Mountains and to Mutatá (Fig. 21 and 32). Its Middle American representative, *P.*

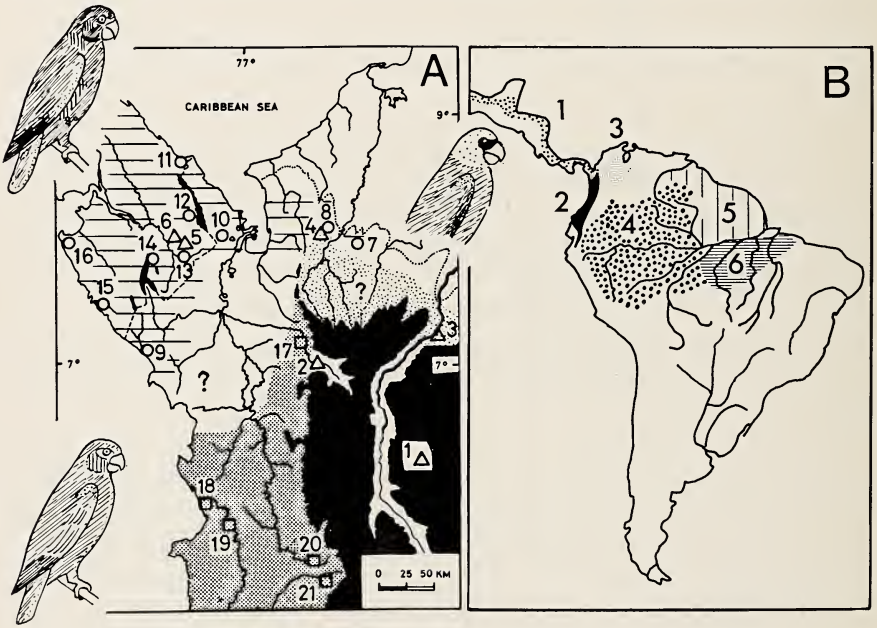


Fig. 32: Distribution of the *Pionopsitta caica* species group.

*Explanation:* **A** Distribution of *P. haematotis, P. pulchra,* and *P. pyrilia* in northwestern Colombia and eastern Panamá. Open triangles and stippled area — *P. pyrilia* (status in northwestern Colombia uncertain; see text). 1 Santa Elena. 2 Alto Bonito. 3 Puerto Valdivia. 4 Quimarí. 5 Tapalisa. 6 Cituro. Open circles and hatched area — *P. haematotis coccinicollaris.* 7 Murucucú. 8 Quimarí. 9 Juradó 10 Unguía. 11 Puerto Obaldía, Permé, 12 Río Tacarcuna. 13 Boca de Paya. 14 Cerro Pirre. 15 Jaqué. 16 Cerro Sapo and Jesusito. Open squares and shaded area — *P. pulchra.* 17 Mutatá. 18 Río Jurubidá. 19 Río Baudó. 20 Andagueda. 21 La Selva. **B** Generalized distribution of the *P. haematotis* superspecies (1 *P. haematotis,* 2 *P. pulchra),* 3 *P. pyrilia,* and *P. caica* superspecies (4 *P. barrabandi,* 5 *P. caica,* and 6 *P. vulturina).*

*haematotis,* has been taken near Unguía, Juradó, and in the upper Sinú Valley (Quimarí, Murucucú, De Schauensee 1950 b). I did not find either species in the lower portion of the Atrato Valley, where they may or may not be in contact.

The *P. haematotis* superspecies represents, together with *P. pyrilia* of northern Colombia-Venezuela, the Amazonian *P. caica* superspecies (Fig. 32 B), as discussed in more detail by Haffer (1970 a). The color pattern of the wings and tail are of particular importance in this group, whereas the coloration of the head is a rather variable and taxonomically less important character to demonstrate interspecific relations.

*Pionopsitta pyrilia* (Bonaparte) **Saffron-headed Parrot**

*Specimens:* None. *Taxonomy:* Monotypic. Endemic to northwestern Venezuela and northern Colombia.

The Saffron-headed Parrot is closely related to the two preceding species. Whether or not they are sympatric breeders in peripheral parts of their ranges remains unknown. *P. pyrilia* is widespread in the forests along the northern base of the Andes, in the humid middle Magdalena Valley, and in northwestern Venezuela. Isolated records indicate its temporary (?) presence in western Colombia (Quimarí, Alto Bonito, Noanamá, De Schauensee 1948—1952, 1950 b) and in the Tuira Valley of easternmost Panamá (2 specimens; Griscom 1935, Wetmore 1968). I did not collect this parrot.

*Pionus mentruus rubrigularis* Cabanis **Blue-headed Parrot**

*Specimens:* Unguía 1 ♂; Mutatá 1 ♀. *Taxonomy:* This trans-Andean subspecies is not in contact with the Amazonian nominate form.

This is a common parrot in the forests of northwestern Colombia and usually observed in large flocks.

*Amazona*

Three species of this genus have been taken in the Urabá region, viz. *A. ochrocephala* (Turbo 3 ♂, Unguía 1 ♂), *A. autumnalis,* and *A. farinosa* (Sautatá 1 —). I observed *A. ochrocephala* also in the Serranía de San Jacinto.

## Cuculidae

*Piaya cayana thermophila* Sclater **Squirrel Cuckoo**

*Specimens:* Sautatá 1 ♂; Río Tanela 1 ♂; Acandí 1 ♂.

The Squirrel Cuckoo is represented west of the Gulf of Urabá by the Middle American form *P. c. thermophila* which ranges south to Sautatá and the Río Salaquí. *P. c. mehleri* is found east of the Gulf of Urabá in the Mulatos and Sinú regions north to the Serranía de San Jacinto (De Schauensee 1950 b, Haffer 1959, Haffer et al. 1965). This species avoids the

densely forested Pacific lowlands south of the Salaquí River. It has been taken along the slope of the Western Andes above the lowland forests.

*Piaya minuta panamensis* Todd **Little Cuckoo**

*Specimens:* Acandí 1 ♀; Río Tanela 1 ♀; Sautatá 1 ♂, 1 ♀; Riosucio 1 ♀; upper Río Sinú, mouth of Río Naín 1 ♀ (2 mm). *Taxonomy: P. m. panamensis* is clinally related to *P. m. gracilis* of northern and central Colombia. The isolated population of western Ecuador is also grouped under the name *P. m. gracilis*.

The specimen from Riosucio on the lower Río Atrato is identical with the specimens of *P. m. panamensis* taken along the western shore of the Gulf of Urabá, while the bird from the upper Sinú River is slightly paler on the breast and belly. Thus this bird approaches in color *P. m. gracilis* of the Magdalena and Cauca Valleys.

Wetmore (1968: 121) reported *P. m. panamensis* from Unguía and Villa Arteaga.

*Piaya minuta* is missing from the Pacific lowlands of Colombia but is common in western Ecuador (Chapman 1926). It may have reached this isolated area during a drier climatic period of the past, when it ranged continously from the Urabá region southward along peripheral portions of the Chocó refuge.

*Crotophaga major* Gmelin **Greater Ani**

*Specimens:* Acandí 1 ♂, 1 ♀. *Taxonomy:* A widespread monotypic species.

Observed occasionally in flocks along rivers near Acandí, Titumate, Sautatá, and the Río Zungo, southeast of Turbo.

*Crotophaga ani* L. **Smooth-billed Ani**

*Specimens:* None. *Taxonomy:* A widespread monotypic species.

Common in open areas and even remote clearings of otherwise unbroken forest. I did not confirm the presence of *C. sulcirostris* in our area.

*Tapera naevia* (L.) **Striped Cuckoo**

*Specimens:* None.

Common in open regions of northern Colombia. I heard its melancholic whistled call also in cleared portions of the Urabá region near Turbo and Sautatá.

*Neomorphus geoffroyi salvini* Sclater **Rufous-vented Ground-Cuckoo**

*Specimens:* Río Tanela 1 ♂. *Taxonomy:* The subspecies is a trans-Andean isolate (Nicaragua—Colombia) that is widely separated from the Amazonian main species range.

This large ground-cuckoo keeps to the forest floor rarely rising a few meters into the understory. It is a shy bird which I encountered only once

in the hilly forests of the upper Tanela River. It has been collected also near Juradó, at Quimarí in the upper Sinú region, and south to the Baudó Mountains. E. O. Willis (pers. comm.) observed this species near Tucurá on the upper Sinú River, along the upper Rio Verde and the upper Rio San Juán northeast of Turbo.

The representative Chocó species *N. radiolosus* is known from only a few localities along the Pacific foothills of the Western Andes in Colombia and northwestern Ecuador (De Schauensee 1948—1952, Lehmann 1960; see Fig. 21 D).

## Strigidae

We collected only rarely at night and consequently have few data on owls of the study area. A specimen of *Otus choliba* from San Carlos in the Serranía de San Jacinto had a wing (chord) measurement of 155 mm and a tail length of 86 mm; it agrees in color intensity with material of *O. c. crucigerus* from the interior of Colombia. We had no secimens of the paler form *O. c. margaritae* of northern Venezuela and Colombia for comparison. De Schauensee (1950 b) reported *Lophostrix cristata* and *Ciccaba virgata* from the upper Sinú region.

*Pulsatrix perspicillata chapmani* Griscom **Spectacled Owl**

*Specimens:* Sautatá 1 ♂; Tilupo 1 ♂; Serranía de San Jacinto (Arroyo Playón 1 ♂).
*Taxonomy:* The various subspecies of this widespread owl show little differences in color and size and are clinally related.

The Spectacled Owl is fairly common in the forests and is seen occasionally at day time. The specimens from Sautatá and Tilupo agree in color intensity with a topotype of *P. p. chapmani* from the Río Juradó as does the bird from the Serranía de San Jacinto in northern Colombia. Kelso (1938) in describing *P. p. "ecuatoriana"* (here considered a synonym of *chapmani)* mentioned this form from Jaraquiel (near Montería), Dep. Córdoba; El Tambor, Dep. Santander; and Murindó, Dep. Antioquia, in the lower Atrato Valley. These records from northern Colombia have been overlooked in the recent literature.

The populations inhabiting the dry Caribbean forests *(P. p. perspicillata)* are paler. Recent records are from Los Pendales, Dep. Atlántico, and from the base of the Santa Marta Mountains. Occasionally, darker colored specimens occur in the latter area (Kelso 1938).

The Spectacled Owl ranges from Middle America and the Pacific forests of Colombia across northern Colombia into Venezuela. It was not known from the humid middle Magdalena Valley until J. I. Borrero (Haffer & Borrero 1965) saw a mounted specimen in the Colegio de San José, Medellín; this bird is said to have come from Ambalema, Dep. Tolima.

## Caprimulgidae

*Nyctidromus albicollis albicollis* (Gmelin) **Pauraque or Bujío**

*Specimens:* Río Tulapa 1 —; Quebrada Charrura 1 ♂; Serranía de San Jacinto 1 ♂. *Taxonomy:* The widespread nominate form probably is clinally related with the paler northern Colombian subspecies *N. a. gilvus.*

The Bujío is a common bird in sufficiently humid areas of northern Colombia, where it inhabits openings and artifical clearings. The characteristic call *bo-éé-o bo-éé-o* was heard frequently around our camps at dusk and dawn. Skutch (1972) published a life history study of this goatsucker.

*Caprimulgus maculicaudus* (Lawrence) **Spot-tailed Nightjar**

*Specimens:* Sautatá 1 ♂; Tilupo 1 ♂. *Taxonomy:* Monotypic. A widespread species of spotty distribution.

I encountered this rare goatsucker only in and around the cattle farms of Sautatá and Tilupo at the base of the Serranía del Darién. The bird is known in Colombia from only a few widely scattered localities in the Llanos and at the lower Río Sinú (Loríca).

## Trochilidae

*Glaucis hirsuta affinis* Lawrence **Rufous-breasted Hermit**

*Specimens:* Río Guadualito 1 ♂; Serranía de San Jacinto (Arroyo Camaroncito 1 ♀; San Carlos 1 —). *Taxonomy:* Possibly hybridizes with *G. aenea* in central Panamá and western Colombia.

This species occurs in northern Colombia and ranges in the Atrato Valley south to Quibdó, where *G. hirsuta* meets its parapatric representative *G. aenea.* This bird is somewhat smaller in size and coppery bronze above instead of iridescent green. Both species have been collected in western Colombia near Santa Cecilia at the base of the Western Andes on the upper Río San Juán (Eisenmann in Haffer 1967 a, p. 14). The statement by de Schauensee (1966, p. 158) that these species "occur together commonly on the Pacific slope of Colombia" is still unproved. *Glaucis aenea* recurs in Middle America and meets *G. hirsuta* in western Panamá. Details of this contact are apparently unknown (Wetmore 1968). D. & B. Snow (1973) published biological accounts of *Glaucis hirsuta.*

The following species were also collected: *Phaethornis longuemareus striigularis* Frasquillo 1 ♂; *Ph. l. nelsoni* Mutatá ♂; *Florisuga mellivora* Río Tanela 1 ♂; *Thalurania furcata fannyi* Titumate 1 ♂; *Anthracothorax n. nigricollis* Tenche 1 ♀ (also often seen in the Serranía de San Jacinto); *Eutoxeres aquila munda* Río Napipí 1 ♂ (4x2 mm); *Damophila julie panamensis* Río Tanela 1 ♀; Acandí 1 ♂; *Amazilia a. amabilis* Río Uva 1 ♂ (3x2) mm); *Amazilia rosenbergi* Río Uva 1 ♀ (see distribution map, Fig. 21 F); *Amazilia saucerottii warscewiczi* San Carlos (Serranía de San Jacinto) 1 —; *Amazilia t. tzacatl* Mutatá 1 ♂; *Chalybura u. urochrysia* Río Tulapa

1 ♂; Río Uva 1 ♂ (2x1 mm); *Heliothrix barroti* Río Guadualito 1 ♀; Río Tanela 1 ♂; Río Uva 1 ♀, 1 — (imm.). The last species represents the Amazonian *H. aurita* (Fig. 12 C).

## Trogonidae

Six trogons occur in the lowlands of northwestern Colombia but no more than four have been found living in the same area; five are sympatric in eastern Panamá. The *Trogon melanurus* group is composed of species with a red belly: Two species are sympatric in eastern Panamá *(T. melanurus, T. massena)* and western Colombia *(T. massena, T. comptus);* most of the dry and moist forests in northern and central Colombia harbor only one species *(T. melanurus).* Of the yellow-bellied species, *T. viridis* and *T. rufus* are widespread, whereas *T. violaceus* avoids the wet Pacific forests.

*Trogon massena hoffmanni* (Cabanis & Heine) **Slaty-tailed Trogon**

*Specimens:* Río Tanela 1 ♂. *Taxonomy:* Middle American *T. m. hoffmanni* is not in contact with the Colombian Pacific isolate *T. m. australis.*

This trogon is sympatric with *T. melanurus macroura* in eastern and central Panamá (Wetmore 1968) ranging in western Colombia south to the Río Truandó (de Schauensee 1948—1952). A large distributional gap in the Atrato Valley probably separates the ranges of *T. m. hoffmanni* and its southern representative *T. m. australis.* Like *T. m. hoffmanni,* this form also lacks the white chest band which characterizes *T. melanurus.* The central rectrices are bluish in *T. m. australis* instead of brass green as in the northern group of subspecies of *T. massena. T. m. australis* inhabits the central Chocó region north at least to Quibdó (Haffer 1967 c) and to the Río Jurubidá (Wetmore 1968). A female from Quibdó originally was referred to *"T. melanurus macroura"* by Todd (1943), but it is very probably an example of *T. m. australis* instead. M. A. Carriker, Jr. collected four males and a female of this form for the Smithsonian Institution at Nuquí and along the Río Nuquí, another female on the Río Jurubidá, and a male farther south at Puerto Muchimbo on the Río Juán, Dep. Valle (Wetmore pers. comm.). *T. melanurus macroura* was also reported from the Río Jurubidá. However, it remains unknown whether *T. massena* and *T. melanurus* are parapatric near Jurubidá or sympatric at least in a restricted portion of the central Chocó region. *T. melanurus macroura* is missing from the upper Atrato Valley and most of the Pacific lowlands possibly because another species *(T. comptus)* is sympatric with *T. massena* in this area.

*Trogon melanurus macroura* Gould **Black-tailed Trogon**

*Specimens:* Unguía 2 ♂; Río Tanela 3 ♂; Acandi 1 ♀; Río Salaquí 1 ♂; Río Juradó 1 ♀; Río Napipi 1 ♂ (6×4 mm); Pavarandocito 2 ♂ (8×5, 7×4 mm); Río Tulapa 1 ♂, 1 ♀; Frasquillo 1 ♂; Quebrada Charrura 1 ♂; Tenche 1 ♂; Serrania de San Jacinto (San Cristobal 2 ♂). *Taxonomy: T. m. macroura* is a geographical isolate widely separated from Amazonian *T. m. melanurus* and western Ecuadorian *T. m. mesurus* (see Haffer 1967 a, Fig. 15).

A large trogon with a red belly and a white chest band. 13 males from northern Colombia measure as follows: Wing (flat) 165—179 (172), tail 171—187 (177.8), and bill 25—28 (26.9). I heard and observed this trogon fairly commonly in the forests of northwestern Colombia including the Serranía de San Jacinto. It even inhabits small patches of forest in generally cleared regions (e. g. Tenche, T of Fig. 33) and usually stays in the canopy level. The bird is common in the lower Atrato Valley (Pavarandocito, Murindó, Río Salaquí, etc. Fig. 33) and in eastern Panamá (Wetmore 1968), where it is sympatric with *T. massena*. *T. melanurus* ranges

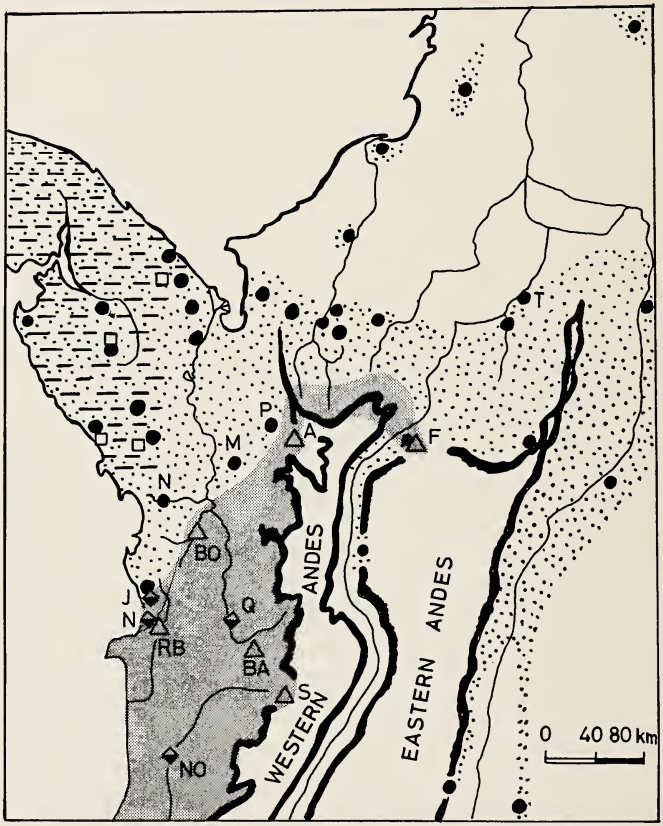


Fig. 33: Distribution of the red-bellied trogons, *Trogon melanurus* species group, in northwestern Colombia.
*Explanation:* Solid circles and stippled area — *T. melanurus macroura*. Open triangles and shaded area — *T. comptus*. Open squares and dashed area — *T. massena hoffmanni*. Half-solid squares and shaded area — *T. massena australis*. Note geographic exclusion of *T. melanurus macroura* and *T. comptus*. *T. massena* is sympatric with both these species. Because of extensive deforestation in northern Colombia, the occurrence of *T. melanurus macroura* has become very localized in this region.

along the Pacific coast south to the Río Jurubidá (one male, one female compared by De Schauensee, pers. comm., and Zimmer 1948). The presence of *T. comptus* and *T. massena australis* in the Chocó region may prevent the southward advance of *T. melanurus macroura* (Fig. 33).

*Trogon comptus* Zimmer **Blue-tailed Trogon**

*Specimen:* Upper Río Bojayá (10 km below mouth of Río Uva) 1♂ (6.5×4.5 mm). *Taxonomy:* Monotypic; endemic in western Colombia and northwestern Ecuador.

The only specimen collected measures wing (flat) 158, tail 146, bill 26 mm. The sides of the head and the throat are black; the upperparts including the central tail feathers show a strong blue hue. These characters, together with its smaller size, serve to distinguish *T. comptus* from *T. massena,* with which it is sympatric in the central Chocó region.

I found *T. comptus* along the Río Bojayá, where we heard a number of males calling. They were spaced several hundred meters at the river banks formed by heavily forested steep slopes and sandstone bluffs up to 60 meters high. A single bird I heard along the Río Uva in the rugged Baudó Mountains probably belonged also to this species. The call of *T. comptus* differs slightly from that of *T. melanurus macroura:* The interval between the *hoo's* is slightly longer and the call is slightly lower pitched; otherwise it sounds very similar.

*Trogon comptus* inhabits wet forests in hilly terrain of Pacific Colombia ranging south into northwestern Ecuador (Gyldenstolpe 1951) and eastward to the north slope of the Central Andes of Colombia (La Frijolera, F of Fig. 33, 21 G). A female from Alto Bonito, 25 km south of Mutatá, originally reported by Chapman (1917, p. 319) under "*T. massena australis*" actually belongs to *T. comptus* (Haffer 1967 c).

*Trogon comptus* is parapatric with *T. melanurus macroura* and with *T. m. mesurus* in the Atrato Valley and in northwestern Ecuador, respectively.

*Trogon viridis chionurus* Sclater & Salvin **White-tailed Trogon**

*Specimens:* Río Tanela 5♂, 3♀; Río Juradó 1♀ (2 mm); Río Truandó 1♀ (4 mm); Mutatá 2♂; Quebrada Charrura 1♂, 2♀. *Taxonomy:* This subspecies is a geographical isolate in western Colombia—Panamá and widely separated from the main Amazonian range of the species (Fig. 34).

It is a common species in northwestern Colombia, where I heard and observed it at many additional localities such as Río Carepa, Río Chigorodó, Río Imamadó, Pavarandocito, and Río Napipí. This bird is missing, however, from the isolated forests of the Serranía de San Jacinto near the Caribbean coast.

The White-tailed Trogon sits even more tamely than the other trogons; it remained several times motionless only two or three meters overhead when we passed noisily along a trail with our pack animals. *T. viridis* is


Fig. 34: Distribution of the *Trogon viridis* superspecies.

*Explanation: Trogon viridis* (1, 2, 3). Dashed area and dotted circles — *T. v. melanopterus* (1). Stippled area and open circles — *T. v. viridis* (2). Hatched horizontally — *T. v. chionurus* (3). Solid area — *T. bairdii*. Hatched vertically — *T. melanocephalus*. Dotted area — *T. citreolus*. Andes mountains above 2000 m elevation are in black. *Plumage color:* Upper parts blue-black, increasingly dull black in the species of northern Middle America. Belly yellow except in *T. bairdii* with orange-red underparts.

mostly seen inside lighter forest or in patches of secondary growth sitting four to ten meters high. The call differs from that of the other trogons in the area and resembles the song of *Thamnophilus* antbirds without the characteristic note at the end.

The White-tailed Trogon is widely distributed in South America from southeastern Brazil throughout Amazonia to northern Venezuela, Colombia, and Panamá (Fig. 34). The Middle American representatives *T. bairdii* of Pacific Costa Rica and western Panamá as well as *T. melanocephalus* and *T. citreolus* of northern Middle America very probably are specifically distinct. They are not in direct contact with each other or with *T. viridis* and may be combined to form one zoogeographic species, the *Trogon viridis* superspecies (Fig. 34).

*Trogon rufus cupreicauda* Chapman **Black-throated Trogon**

*Specimens:* Río Chigorodó 1 ♂ (3×2 mm), 1 ♀ (2 mm); Pavarandocito 1 ♂ (5×4 mm), 1 ♀ (4 mm). *Taxonomy:* Middle American *T. r. tenellus* and western Colombian *T. r. cupreicauda* may be in secondary contact in the lower Atrato Valley. Both are widely isolated from the main Amazonian range of the species.

Both pairs collected were in breeding condition. The male from the Río Chigorodó had at least 5 cm of the rectrices worn off. In the male from Pavarandocito the fresh tail feathers are rich golden coppery, as is typical for *T. r. cupreicauda,* the form which advanced into the humid middle Magdalena Valley. The Middle American form *T. r. tenellus* is known in northwestern Colombia from Acandí, Unguía (Wetmore 1968), Sautatá, Juradó, and Río Truandó (De Schauensee 1948—1952) and presumably intergrades with *cupreicauda* in the region of the Río Napipí.

Skutch (1959) published details of the biology of this trogon based on observations made in Costa Rica.

*Trogon violaceus caligatus* ≷ *concinnus* **Violaceous Trogon**

*Specimens:* Río Tulapa 1 ♀; Serranía de San Jacinto (San Cristobal 2 ♂, 2 ♀; Lázaro 1 ♂). *Taxonomy:* The two trans-Andean forms are clinally related and isolated from the Amazonian main range of the species.

The populations inhabiting northern and northwestern Colombia as well as eastern Panamá belong to the broad zone of intergradation of *T. v. concinnus* and *caligatus,* since the extent of blue color on the crown and upperparts varies considerably in the specimens available. The posterior part of the crown is extensively blue in the male from Lázaro similar to examples of typical *caligatus* from the middle Magdalena Valley. In the two males from San Cristóbal, however, the top of the head is black as in *concinnus.* Similar observations were published by de Schauensee (1950 b) on birds from the upper Sinú region and by Wetmore (1968: 419) on specimens from the Darién region of eastern Panamá.

*Trogon violaceus* is found in Middle America east to the Caribbean coast of Darién (Griscom 1935, Wetmore 1968) but was never recorded from Pacific Colombia (de Schauensee 1964, p. 165 listed it from that area without, however, discussing any proof). The species does occur in northwestern Ecuador, and, possibly, avoids the humid forests of Pacific Colombia because of ecologic reasons. The isolated western Ecuadorian population may have originated from immigrants that ranged along peripheral parts of the Chocó Refuge during a dry climatic period of the past. In the Urabá region I found it only once along the Río Tulapa. The bird is more common in the drier forest and shady secondary growths of the Serranía de San Jacinto. Skutch (1972) described the biology of the Violaceous Trogon based on observations in Costa Rica.

## Alcedinidae

The following widely distributed kingfishers are commonly found along the rivers of the Urabá region: *Ceryle torquata, Chloroceryle amazona,* and *C. americana.* The large *Ceryle torquata* is common along the wide Río Salaquí, while the smaller species were seen here less frequently. On the other hand, along the narrower Río Truandó, the most conspicuous species was *Chl. amazona. C. torquata* was seen much less often. The tiny *Chl. aenea* enters also small creeks not inhabited by its larger relatives.

## Momotidae

*Hylomanes momotula obscurus* Nelson **Tody Motmot**

*Specimen:* Río Imamadó 1 ♀ (2 mm). *Taxonomy:* A Middle American species which barely entered northwestern Colombia; composed of several clinal subspecies *(H. m. chiapensis, momotula, obscurus).*

A rare bird in northwestern Colombia restricted to forests along the Andean foothills in northern Chocó east to the lower Cauca River. Known from only a few additional localities: Dabeiba, Alto del Buey, Nuquí (De Schauensee 1948—1952); upper Río Sinú Valley (Socarré, Quebrada Salvajín) and lower Cauca River (Valdivia) as reported by Wetmore (1968). Dr. E. O. Willis (pers. comm.) observed it along the Saisa trail crossing the Serranía de Abibe from the upper Río Verde.

*Electron platyrrhynchum columbianum* De Schauensee **Broad-billed Motmot**

*Specimens:* Río Tulapa 1 ♀; Río Mulatos 1 ♂ (2.5×1.5 mm); Quebrada Charrura 1 ♂. *Taxonomy:* Several clinal subspecies occur west of the Andes; an isolated population *(E. p. pyrrholaemum)* lives in upper Amazonia.

The characters of this race, particularly the blue chin spot, are well marked in these specimens. This motmot is widespread in the forests of the upper Sinú region, but has not occupied the drier forests near the Caribbean coast. See Skutch (1971) for a life history study of this and the following species of motmot.

*Baryphthengus ruficapillus semirufus* (Sclater) **Rufous Motmot**

*Specimen:* Río Uva 1 ♀ (3 mm). *Taxonomy:* This trans-Andean subspecies is widely isolated from the Amazonian population.

The Rufous Motmot is found in the more humid forests of the central Chocó region and avoids the lighter forests inhabited by *M. momota. B. ruficapillus* probably also ranges along the humid northern foothill zone of the Western Andes and of the Central Andes, where it has been taken at Mt. Murucucú (De Schauensee 1950 b) and at Puerto Valdivia, etc. (Chapman 1917). I did not encounter this bird in the less humid lowland forests east of the Gulf of Urabá, where *M. momota* is common.

*Momotus momota* (L.) **Blue-crowned Motmot**

*Specimens: M. m. conexus* Thayer & Bangs: Río Juradó 1 ♀ (2 mm); Sautatá 1 ♂; Unguía 1 ♀; Río Tanela 1 ♂, 1 ♀; Río Guadualito 1 ♀. *M. m. conexus* ≧ *subrufescens* Sclater: Quebrada Charrura 1 ♂, 2 ♀, Serranía de San Jacinto (San Carlos; Cansona; San Jacinto; Arroyo Tigre; San Cristobal; Lázaro) 3 ♂, 2 ♀, 1 —. *Taxonomy:* The populations of eastern Panamá and northern Colombia form a color cline from more intensively colored *conexus* to pale *subrufescens*.

In comparing color intensity of specimens from northern Colombia, those from the Urabá region are darkest *(conexus),* followed by the Charrura birds and the population of the Serranía de San Jacinto, which are still more rufescent below and above than the pale populations inhabiting the dry forests near the Caribbean coast of northern Colombia *(M. m. subrufescens).* Wetmore (1968: 454) discussed the variation in plumage color of this motmot in eastern Panamá and northwestern Colombia synonymizing *M. m. reconditus* with *M. m. conexus.*

*Momotus momota* ranges in the Atrato Valley south only to the Río Napipí, where I have heard and observed it several times. While missing in the central Chocó region it recurs in western Ecuador *(M. m. argenticinctus).* Chapman (1926: 272) believed that it may "have reached western Ecuador over the Marañón route" from Amazonia.

The Blue-crowned Motmot is quite common in the seasonal forests of northwestern Colombia. The soft *coot hoot* of these birds is often heard before sunrise. Skutch (1964) wrote a detailed field study of this species.

## Galbulidae

*Brachygalba salmoni* Sclater & Salvin **Dusky-backed Jacamar**

*Specimens:* Río Guadualito 1 ♂, 1 ♀; Frasquillo 2 ♀; Río Mulatos 3 ♂ (5×3.5, 7×4, 8×4 mm), 2 ♀ (0.5, 0.5 mm); Quebrada Charrura 1 ♂, 1 ♀; Serranía de San Jacinto (Arroyo Camaroncito; Arroyo Tigre; Lázaro; San Cristobal) 3 ♂, 4 ♀, 1 — (imm.). *Taxonomy:* Monotypic. Endemic in northern Colombia and eastern Panamá; not in contact with nearest ally *B. goeringi.*

Previously a rare bird in collections my specimens together with the material collected by M. A. Carriker in northwestern Colombia (upper Sinú Valley and Necoclí, Haffer 1962) indicates that the Dusky-backed Jacamar is fairly widespread in forested areas of northwestern Colombia and the Darién region (Fig. 20 C). However, the bird avoids the humid Chocó forests. It is usually found at small clearings with low second growth along forest streams, where it is seen flycatching from dry horizontal branches of small trees. It probably breeds in burrows dug in river banks or ravines as does its close relative of northwestern Venezuela *B. goeringi* (Skutch 1968).

Minor color differences and a slight curvature of the bill thought by Haffer (1962) to distinguish the presently isolated population near the Caribbean coast have been found duplicated by Wetmore (1968) in more complete material. The species of *Brachygalba* replace each other geogra-

phically in peripheral portions of Amazonia and form the *B. albogularis* superspecies (Haffer 1974 b). *B. salmoni* represents this superspecies west of the northern Andes.

*Galbula ruficauda* Cuvier **Rufous-tailed Jacamar**

*G. r. ruficauda* and *G. r. melanogenia. Specimens:* 65 specimens of both subspecies from northwestern Colombia. *Taxonomy:* These forms hybridize along a zone of secondary contact in the Urabá region. *G. ruficauda* is a member of a widespread neotropical superspecies of medium-sized jacamars (Haffer 1974 a, b).

*Galbula r. ruficauda* and *melanogenia* differ in the number of the green rectrices (4 in *melanogenia,* 2 in *ruficauda),* in the color of the chin (black in *melanogenia,* buff in *ruficauda)* as well as in measurements. The contact zone is located in the Chigorodó area and perhaps between the lower Río Salaquí and the Río Truandó (Fig. 35). Limited geneflow between these two subspecies is seen in the material collected southeast of Turbo (see Haffer 1967 a for a detailed discussion of the distribution and hybridization of these jacamars). Wetmore (1968: 460) mentioned intermediate specimens

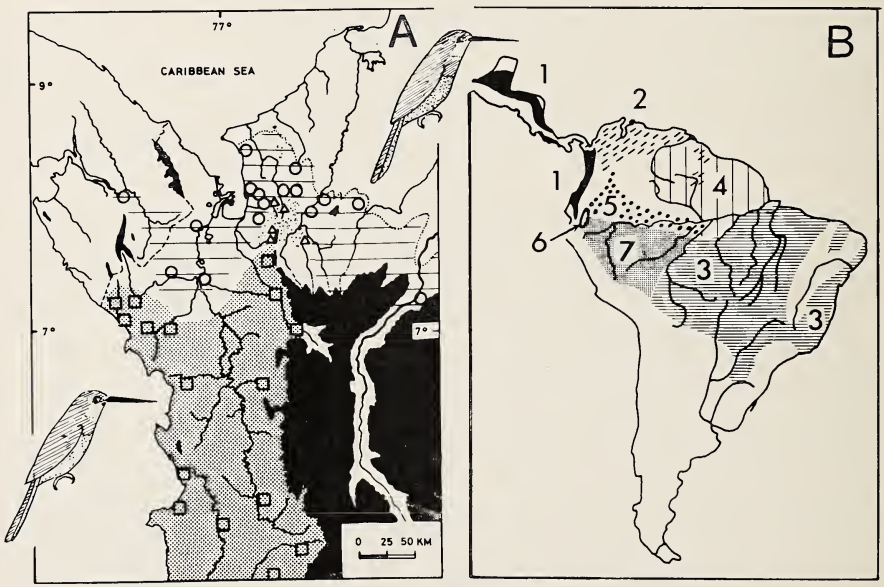


Fig. 35: Distribution of the Green Jacamars, *Galbula galbula* superspecies.

*Explanation:* **A** Distribution of *G. r. ruficauda* and *G. r. melanogenia* in northwestern Colombia and eastern Panamá. Modified from Haffer (1967 a). Hatched area and open circles — *G. r. ruficauda.* Shaded area and open squares — *G. r. melanogenia.* Stippled area and open triangles — hybrid zone. **B** Generalized distribution of *G. r. melanogenia* (1, solid area); *G. r. ruficauda* (2, dashed area); *G. r. rufoviridis* (3, area hatched horizontally); *G. galbula* (4, area hatched vertically); *G. tombacea* (5, dotted area); *G. pastazae* (6, open oval); *G. cyanescens* (7, area shaded dark). Modified from Haffer (1974 b).

from Necoclí, Nazaret (upper Rio Sinú region), and Quebrada Salvajín (Río Esmeraldas).

*Galbula r. ruficauda* advanced into the Darién region, where W. B. Richardson collected two females near El Real on the lower Río Tuira in 1914 (specimens in the American Museum of Natural History, New York). This occurrence has been confirmed recently by P. N. Slattery who found a nest burrow and collected two nestlings along the Río Pirre in the same area of El Real (Wetmore 1968: 460).

Cassin (1860) reported one specimen as "*Galbula ruficauda,* Cuvier" from the Río Nercua, a headwater of the Río Truandó. I collected *G. r. melanogenia* along the Río Truandó and also along the upper Río Salaquí, north of the Nercua river. Judging from these records it seems likely that Cassin's specimen ("in bad condition") actually belonged to *G. r. melanogenia.*

The Rufous-tailed Jacamar is a common bird along forest streams and enters even fairly open areas in northern Colombia and Venezuela, where it may be found in light second growth and dry thickets. I collected 2 ♂


Fig. 36: Distribution of the Great Jacamar, *Jacamerops aurea.*

*Explanation:* a *J. a. penardi;* b *J. a. isidori;* c *J. a. aurea;* d *J. a. ridgwayi.* Andes Mountains above 2000 m are in black.

and 3 ♀ of the pale subspecies *G. r. pallens* in rather dry habitats of the Serranía de San Jacinto.

*Jacamerops aurea penardi* Bangs & Barbour **Great Jacamar**

*Specimens:* Acandí 1 ♂; Unguía (observation); Río Tanela (observation); Río Chicorodó 1 ♂ (5×3 mm); Río Truandó 1 ♂ (4.5×3.5 mm). *Taxonomy:* This subspecies is a geographical isolate of this widespread Amazonian species (Fig. 36).

The Great Jacamar is an inhabitant of intermediate levels of the forest interior but not often seen in northwestern Colombia.

## Bucconidae

*Notharchus macrorhynchus hyperrhynchus* (Sclater) **White-necked Puffbird**

*Specimens:* Río Tanela (observation); Acandí (observation); Río Mulatos 1 ♂, 1 —; Quebrada Charrura 1 ♂; Serranía de San Jacinto (San Cristóbal 1 ♂). *Taxonomy:* This subspecies is widely distributed in northwestern South America and in Middle America; in secondary contact with the nominate form in eastern Venezuela (Orinoco delta). Cottrell (1968) merged *Notharchus* with *Bucco*.

I have found the White-necked Puffbird on both sides of the Gulf of Urabá, where it is not rare. It is missing in the wet Chocó forests but recurs in the seasonal forests of extreme southwestern Colombia (Olivares 1957) and western Ecuador (Chapman 1926).

*Notharchus tectus subtectus* (Sclater) **Pied Puffbird**

*Specimens:* Río Guadualito 1 ♀; Frasquillo 1 ♂ (2.5×1.5 mm), 1 ♀ (1.5 mm); Río Chigorodó 1 ♂ (5×2.5 mm), 1 ♀ (2 mm); Serranía de San Jacinto (San Juán Nepomuceno 1 ♀). *Taxonomy:* A widespread trans-Andean isolate of this Amazonian species.

The pair taken at Frasquillo on June 10, 1963 was excavating a hole in a termite nest 4 meters above the ground in a tree surrounded by low second growth, close to a large clearing (Plate 7, Fig. 2). The record from the Serranía de San Jacinto extends the known range of this bird considerably to the north in Colombia.

*Bucco noanamae* Hellmayr **Sooty-capped Puffbird**

*Specimens:* Río Tanela 1 ♀; Riosucio 1 ♀. *Taxonomy:* Monotypic. Endemic species in northern Chocó region.

The bird from the Río Tanela was in high forest, whereas that from Riosucio was taken in rather low second growth forest adjoining an abandoned cacao plantation just east of the village.

This puffbird probably originated in the Chocó refuge and has extended its range northward to the western shore of the Gulf of Urabá (Fig. 21 H). Its Amazonian representative is probably *Bucco tamatia,* which is very close in the coloration of the upperparts. Both species are similar in body size but *B. noanamae* has a larger bill (21—32 mm) compared to that of *B. tamatia* (25—27 mm).

A bird reported as *"Bucco ruficollis"* from the Río Truandó by Cassin (1860) may have been an example of the present species, as discussed below.

*Nystalus radiatus* (Sclater) **Barred Puffbird**

*Specimens:* None. *Taxonomy:* Monotypic; however, the pale population of the upper Magdalena Valley probably deserves taxonomic recognition. The species is restricted to the trans-Andean lowlands. Cottrell (1968) merged *Nystalus* with *Bucco.*

Although widely distributed in the trans-Andean lowlands, I did not encounter this puffbird which, according to Wetmore (1968: 478), inhabits forest borders, edges of forest trails and thickets in open plains. The bird is rare in the Urabá and upper Sinú regions (Quimarí, De Schauensee 1950 b). It advanced into the humid middle Magdalena Valley southward to the region around Carmen de Apicalá and Melgar, where the country is fairly dry and open. Six females from the latter area in the collection of the Instituto de Ciencias Naturales (Bogotá) are white or buffy white underneath indicating that this population is paler than the population of more humid areas and may deserve taxonomic recognition as a clinal subspecies (see also Chapman 1917: 342, Haffer 1967 d: 322, Wetmore 1968: 479).

*Hypnelus ruficollis ruficollis* (Wagler) **Russet-throated Puffbird**

*Specimens:* Serranía de San Jacinto (west of San Jacinto 1 ♂); Tenche 2 ♂; Yatí 1 ♂, 1 —. *Taxonomy:* Endemic to northern Colombia—Venezuela. The *ruficollis* and *bicinctus* subspecies groups hybridize in the Maracaibo region. Cottrell (1968) merged the monotypic genus *Hypnelus* with *Bucco.*

Inhabits thickets and scrub in the open Caribbean lowlands of northern Colombia and Venezuela. The species reaches its western range limit in the lower Sinú Valley, where I observed it near Lorica and Coveñas and along the lower Cauca River (Tenche).

Cassin (1860: 134) reported *"Bucco ruficollis"* from the Truandó River in the humid lower Atrato Valley, where subsequently it has never been taken again. The occurrence of this bird in the humid Pacific region seems very unlikely. 27 species listed by Cassin (l. c.) were collected in 1858 by members of the Michler expedition near Cartagena and 6 species came from both Cartagena and the Urabá region. For this reason one might surmise that the above specimen of *"B. ruficollis"* was actually obtained near Cartagena, where this species is quite common. However, the collector of this specimen specifically stated "Seen once only, at the first camp on the Truandó, after leaving the Atrato". Probably the specimen was in rather bad condition, as Cassin said "For all I can see this is the young of *B. bicincta,* Gould, as above . . ." It seems reasonable to assume, therefore, that the Truandó bird represented some other species, possibly *Bucco noanamae,* which was described by Hellmayr much later (in 1909)

and which I have taken near Riosucio close to the mouth of the Río Truandó.

*Malacoptila panamensis* Lafresnaye **White-whiskered Puffbird**

*Specimens: M. p. chocoana* De Schauensee: Río Imamadó 1 —; Pavarandocito 1 ♂ (5×3 mm), 1 ♀ (1.5 mm); Río Salaquí 1 ♀; Río Truandó 1 ♀ (1 mm); Río Napipí 1 ♂ (17×7 mm); Mutatá 2 ♂, 2 ♀. *M. p. panamensis* Lafresnaye: Acandí 1 ♀, Río Tanela 2 ♂, Frasquillo 1 ♂ (5×4 mm), Quebrada Charrura 1 ♂. *Taxonomy:* Several clinal subspecies of this trans-Andean bird are recognized which differ mainly in details of plumage coloration.

The birds from the lower Atrato Valley, including the specimen from the Río Imamadó, agree closely with a topotype of *chocoana* from the Río Juradó. The White-whiskered Puffbird is commonly encountered at low levels inside the forest of northwestern Colombia, where it represents the Amazonian *Malacoptila fusca* (Fig. 12 E). While of similar body size (wing length 87—91 mm), *M. panamensis* has a larger bill (30—33 mm versus 27—28 mm) and a longer tail (70—78 mm versus 65—67 mm). Their zonal representative in the subtropical zone of the Andes is *M. mystacalis* which is much closer to the trans-Andean *M. panamensis*.

*Nonnula frontalis* (Sclater) **Gray-cheeked Nunlet**

*Specimens: N. f. frontalis* (Sclater): Frasquillo 1 —, 1 ♂; Río Sinú, mouth of Río Naín 1 ♀. *N. f. stulta* Wetmore: Acandí 1 ♂, 1 ♀, 1 —; Pavarandocito 1 ♀ (1 mm); Río Salaquí 1 ♀; Río Napipí 1 ♂ (3×2 mm). *N. f. pallescens* Todd: Serranía de San Jacinto (Cansona; Arroyo Camaroncito; San Juán Nepomuceno 4 ♂, 2 ♀. *Taxonomy:* A northern Colombian species which varies clinally under changing climatic conditions; *N. f. pallescens* of the Caribbean littoral is the palest form.

The birds from the lower Atrato region agree more closely with *stulta* than with the small series of *frontalis* from the upper Sinú region. In *stulta* the throat and breast are somewhat deeper colored, the upper surface is slightly less rufescent and the crown is duller brown (Wetmore 1953). The Urabá region is inhabited by *stulta*. For that reason the occurrence of rather pale colored birds near Unguía west of the mouth of the Río Atrato is puzzling. Wetmore (1953, 1968) mentioned specimens from this locality which he referred to *pallescens* (the pale northern Colombian form). I have also collected one bird near Unguía in 1959 that has a pronounced grayish crown and is less intensively colored on the throat and breast than birds from Acandí and the lower Atrato Valley.

*Monasa morphoeus* (Hahn & Küster) **White-fronted Nunbird**

*Specimens: M. m. pallescens* Cassin: Unguía 1 ♂, 1 ♀, 1 —; Sautatá 1 ♀. *M. m. sclateri* Ridgway: Río Mulatos 3 ♀; Río Tulapa 1 ♂; Quebrada Charrura 2 ♂, 1 ♀, 1 — (imm.). *Taxonomy:* These clinal subspecies differ in details of plumage coloration and are widely separated from conspecific populations in Amazonia.

The White-fronted Nunbird has a dark gray and gray plumage and a red bill. It is fairly common at intermediate levels of the forest and usually encountered in small family groups of four to six birds. The

unusual social habits including chorus singing by such groups make this a particularly interesting member of the puffbird family (Skutch 1972).

## Capitonidae

*Capito maculicoronatus rubrilateralis* Chapman **Spot-crowned Barbet**

*Specimens:* Acandí 2♂, 1♀; Río Juradó 1♂ (8×5 mm), 1♀ (2 mm); Río Guadualito 1♂; Mutatá 1♀. *Taxonomy:* Endemic species of northwestern Colombia and Panamá. The nominate subspecies of the Caribbean slope of central Panamá forms the end of a cline and has the streaks on the flanks orange-red instead of bright red as in *C. m. rubrilateralis.*

## Ramphastidae

*Pteroglossus torquatus* (Gmelin) **Spot-chested Aracari**

*Specimens: P. t. torquatus* (Gmelin) and *P. t. sanguineus* Gould; 60 specimens of both forms from the Urabá region. *Taxonomy:* This trans-Andean toucan forms a widespread superspecies with its cis-Andean relatives of the *P. aracari* superspecies (Haffer 1974 b).

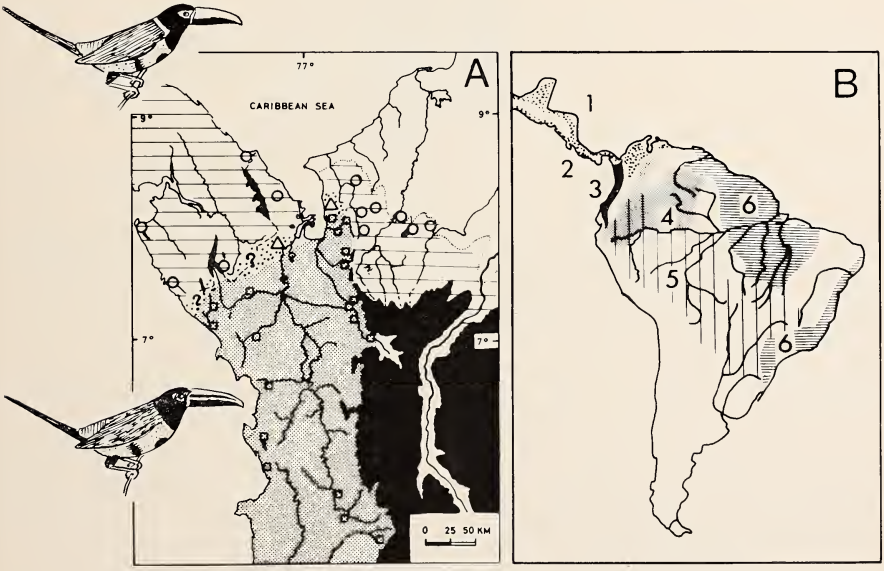


Fig. 37: Distribution of the *Pteroglossus aracari* superspecies.

*Explanation:* **A** Distribution of *Pteroglossus t. torquatus* and *P. t. sanguineus* in northwestern Colombia and easternmost Panamá. Modified from Haffer (1967 a). Hatched area and open circles — *P. t. torquatus.* Shaded area and open squares — *P. t. sanguineus.* Stippled area and open triangles — hybrid zone. Note difference in bill color and presence or absence of rufous nuchal collar in these birds. **B** Generalized distribution of *P. t. torquatus, P. t. erythrozonus, P. t. nuchalis* (1, stippled area); *P. t. frantzii* (2, dotted coastal area of Pacific Costa Rica and western Panamá); *P. t. sanguineus* and *P. t. erythropygius* (3, solid area); *P. pluricinctus* (4, shaded area); *P. castanotis* (5, area hatched vertically); *P. aracari* (6, area hatched horizontally).

The well differentiated subspecies of this trans-Andean aracari-toucan hybridize freely in several areas around the Gulf of Urabá, where they meet (Fig. 37), A highly variable and very restricted hybrid population occurs in the Río Cope Valley, 8 km north of Turbo (see Haffer 1967 a for a detailed discussion). *P. t. torquatus* and *sanguineus* differ mainly in the presence or absence of a chestnut nuchal collar; in the color of the facial skin and in the color of the bill.

Usually groups of three to ten individuals of these slender toucans are seen along the river valleys and their high-pitched sibilant calls are often heard: *pit psit pitsit* ... Skutch (1958) published biological data on this species based on observations on *P. t. frantzii* of southwestern Costa Rica and western Panamá.

*Selenidera spectabilis Cassin* **Yellow-eared Toucanet**

*Specimens:* None. *Taxonomy:* Monotypic. Restricted to trans-Andean lowlands and forms superspecies with Amazonian allies (see Haffer 1974 b).

I saw this small toucanet once only at the upper Río Tanela, west of the Gulf of Urabá. It is apparently quite rare in northwestern Colombia. It prefers wet hill forests of the Chocó region and also occurs in the northern foothill zone of the Andes (Murucucú, La Frijolera). Norton et al. (1972) recently reported this species from northwestern Ecuador.

*Ramphastos vitellinus citreolaemus* Gould **Channel-billed Toucan**

*Specimens:* None; upper Río Verde Valley (E. O. Willis, observ.); Cerro Murucucú (De Schauensee 1950 b). *Taxonomy:* Northern Colombian isolate of the Amazonian *R. vitellinus*. Hybridizes with *R. v. culminatus* in Maracaibo basin but is parapatric with *R. sulfuratus* in northern Colombia.

For comments on this species see below under *R. brevis*.

*Ramphastos sulfuratus brevicarinatus* Gould **Keel-billed Toucan**

*Specimens:* Río Tanela 1 ♂; Río Naín 1 ♂; Quebrada Charrura 1 ♂; also commonly seen in the Serranía de San Jacinto. *Taxonomy:* This subspecies is the southern clinal form of Middle American *R. sulfuratus*, which forms a superspecies with *R. brevis*, *R. vitellinus*, and *R. dicolorus*.

For comments of this species see below under *R. brevis*.

*Ramphastos brevis* De Schauensee **Chocó Toucan**

*Specimen:* Mutatá 1 ♂ (7×3 mm), wing 210, tail 154, bill 151.4 mm. *Taxonomy:* Endemic species of Colombian Pacific forests; monotypic. Forms superspecies with *R. sulfuratus*, *R. vitellinus*, and *R. dicolorus* (see Haffer 1974 b).

*Ramphastos sulfuratus* and *R. brevis* have a keeled bill, very similar plumage color and croaking vocalizations *krik ... krik ... krik ...* but differ in bill color. The ecological requirements of both species apparently are so similar that they compete ecologically and, for this reason, exclude each other geographically where they come into contact in the lower

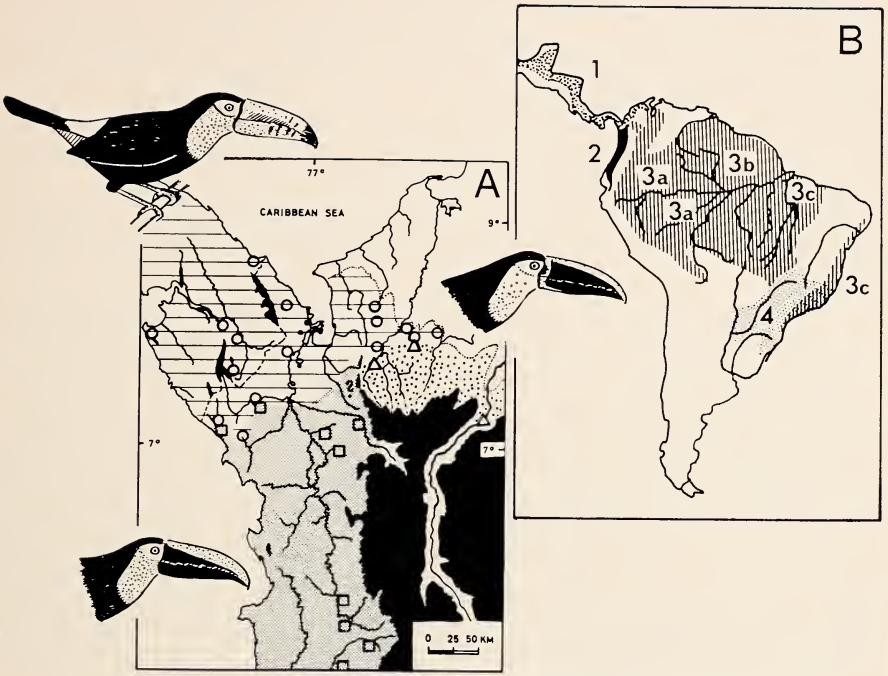


Fig. 38: Distribution of the *Ramphastos dicolorus* superspecies.

*Explanation:* **A** Distribution of *R. sulfuratus, R. brevis,* and *R. vitellinus* in northwestern Colombia and easternmost Panamá. Hatched area and open circles — *R. sulfuratus brevicarinatus.* Shaded area and open squares — *R. brevis.* Stippled area and open triangles — *R. vitellinus citreolaemus.* Note difference in bill color. **B** Generalized distribution of *R. sulfuratus* (1, stippled area); *R. brevis* (2, solid area); *R. vitellinus* (3, area hatched vertically; 3 a *R. v. culminatus,* 3 b *R. v. vitellinus,* 3 c *R. v. ariel; R. v. citreolaemus* inhabits the middle Magdalena and lower Cauca Valleys of Colombia); *R. dicolorus* (4, area lightly stippled).

Atrato Valley and in the forests of the upper Sinú region (Fig. 38). Van Tyne (1929) and Skutch (1971 b) presented detailed life history studies of *R. sulfuratus.* Little is known on the biology of *R. brevis,* a typical Chocó form, confined to the Pacific lowland forests of western Colombia and northwestern Ecuador (Fig. 21 I). *R. sulfuratus* is widely distributed in Middle America, northern Colombia, and extreme northwestern Venezuela. Both species have been taken near Juradó and along the Río Salaquí (Fig. 38). This, however, does not prove sympatric breeding of the secies but simply denotes the area of contact.

*Ramphastos sulfuratus* and *R. vitellinus citreolaemus* meet in the upper Sinú Valley; I found the former species along the Río Naín and Quebrada Charrura and De Schauensee (1950 b) reported it from Quimarí, Murucucú and Tierra Alta. *R. v. citreolaemus* occurs in the Río Verde Valley (E. O.

Willis, pers. comm.) and at Cerro Murucucú (De Schauensee 1950 b). There is no indication of hybridization between these parapatric species. Sight records of *C. v. citreolaemus* near the Gulf of Urabá mentioned by Haffer (1959) are considered invalid.

*Ramphastos ambiguus swainsonii* Gould **Yellow-throated Toucan**

*Specimens:* Río Tanela 1 ♂; Unguía 1 ♀; Río Chigorodó 1 ♂, 1 ♀, 1 — (imm.). *Taxonomy:* This subspecies represents a previously isolated trans-Andean population that is in secondary contact with *R. a. abbreviatus* in the Magdalena Valley (Haffer 1974 b).

This large toucan inhabits the canopy level and is fairly common in the forests of northwestern Colombia, including the humid middle Magdalena Valley but does not enter the dry forests along the Caribbean coast. Its voice is a yelping *Díos . . . te . . . dé . . . te . . . dé . . . díos . . . te . . . dé* (May God give you!). Throughout its range *R. a. swainsonii* is sympatric with the smaller species *R. brevis, R. sulfuratus,* or *R. vitellinus citreolaemus* in their respective distribution areas. The size and vocalizations distinguish *R. a. swainsonii* from the group of smaller black toucans which have croaking calls. *Swansonii* is usually considered specifically distinct but it probably intergrades with *R. a. abbreviatus* around the middle Magdalena Valley and represents this form in the trans-Andean lowlands (Haffer 1974 b). Skutch (1972) published biological data on *R. a. swainsonii* in Costa Rica.

## Picidae

*Picumnus cinnamomeus* Wagler **Chestnut Piculet**

*Specimens: P. c. cinnamomeus* Wagler: Yati 1 ♂. *P. c. persaturatus* Haffer: Serranía de San Jacinto (San Isidro 1 ♀; Palmira 1 ♀; west of San Jacinto 1 ♀, 1 — (imm.); San Juán Nepomuceno 3 ♂). *Taxonomy:* An endemic species of northwestern Venezuela and northern Colombia. *P. c. persaturatus* is restricted to the Serranía de San Jacinto.

The population of the Chestnut Piculet inhabiting the Serranía de San Jacinto has a deep chestnut plumage and was described by Haffer (1961 b) under the proposed new name *P. c. persaturatus.* The forehead is Ivory Yellow as in *P. c. cinnamomeus.* However, the tail is extensively Mikado Brown rather than restricted whitish and the secondaries are broadly edged with Burnt Sienna rather than narrowly margined whitish, as in the other subspecies. The specimens from Palmira and from west of San Jacinto are identical with the type from San Isidro. In the three males from San Juán Nepomuceno, the inner vane of the central rectrices is light buffy colored rather than Mikado Brown and the coloration of the abdomen is intermediate between *persaturatus* and *cinnamomeus.* However, in their deeply colored chest and back they are closer to *persaturatus.* It seems that *P. c. persaturatus* is confined to the Serranía de San Jacinto and intergrades with the paler nominate form in the surrounding lowlands.

The Chestnut Piculet is a bird of dry thickets, scrub, and edges of forest. It is missing from the humid Urabá region. The range of this species comprises the lower Magdalena Valley (e. g. Yatí, see above), the Departamento Atlántico (Dugand 1947), the Santa Marta region, the Guajira Peninsula (Marinkelle 1970) and south to the Río Nechí Valley (De Schauensee 1948—1952) and to Gamarra on the Río Magdalena (Carriker 1955).

*Picumnus olivaceus malleolus* Wetmore **Olivaceous Piculet**

*Specimens:* Upper Río Sinú, mouth of Río Naín 1 — (♂ imm.); Serranía de San Jacinto (Cansona 1 ♂; Arroyo Camaroncito 1 ♂; San Cristóbal 1 ♀; San Jacinto 1 ♀). Measurements: wing (flat) 52, 53, (♂); 52, 54.5 (♀); tail 24, 26.3 (♂); 24.5, 26.8 (♀); exposed culmen 11.3, 11.5 (♂); 11.0; 11,8 (♀).

Wetmore (1965) referred birds from the upper Sinú Valley (Socarré, Quebrada Salvajín), lower Cauca Valley (El Pescado near Valdivia) and from the Departamento Bolivar to *P. o. malleolus,* a smaller subspecies than the nominate form inhabiting the Andes (which is also distinguished by more yellowish underparts and yellowish orange, instead of reddish orange, crown tipping). The series from the Serranía de San Jacinto extends the range of *P. o. malleolus* to the hills near the Caribbean coast.

The Olivaceous Piculet inhabits open thickets and the edge of dry forest in northern Colombia. I did not encounter it in the humid forests of the Urabá region and it is also missing from the wet Pacific lowlands. It occurs, however, in southwestern Colombia *(P. o. harterti)* and in Panamá *(P. o. panamensis)* entering Colombia near Unguía, west of the Atrato delta (Wetmore 1965 a, 1968). This bird is probably extending its range following widespread forest destruction.

*Chrysoptilus punctigula striatigularis* Chapman **Spot-breasted Woodpecker**

*Specimens:* Sautatá 1 ♂, 1 —; Río Guadualito 1 ♂; Frasquillo 1 ♂ imm. The range of this woodpecker extends into central Panamá (Wetmore 1968).

*Celeus loricatus mentalis* (Cassin) **Cinnamon Woodpecker**

*Specimens:* Río Tanela 1 ♂; Unguía 1 ♂, 1 ♀, 1 —; Mutatá 1 ♂.

The black markings on the upperparts of these specimens are variable and reduced in extent. The female from Unguía and the male from Mutatá have almost no spots at all above; see also the remarks by De Schauensee (1950 b) regarding the variable black marking in birds from the upper Sinú region.

This trans-Andean species ranges into the humid Magdalena Valley and north to Nicaragua; it may represent the Amazonian *C. grammicus* (Fig. 13 A).

*Dryocopus lineatus nuperus* (Peters) **Lineated Woodpecker**

*Specimens:* Sautatá 1 —.

*Melanerpes pucherani pucherani* (Malherbe) **Black-cheeked Woodpecker**

*Specimens:* Río Guadualito 1 ♀; Río Tolo 1 ♂, 1 ♀; Quebrada Charrura 1 ♀; Río Imamadó 1 ♀ (10 mm); Río Salaquí 1 ♂.

This black and white trans-Andean woodpecker inhabits the forests around the Gulf of Urabá ranging east to the lower Cauca Valley.

*Melanerpes rubricapillus rubricapillus* (Cabanis) **Red-crowned Woodpecker**

*Specimens:* Serranía de San Jacinto (San Carlos 1 ♂; Arroyo Tigre 1 ♀; San Cristóbal 1 ♀).

Inhabits scrub and dry woodland in the Caribbean lowlands south to Tierra Alta on the Sinú River (De Schauensee 1950 b). It avoids the humid Urabá region but recurs in open and semiopen habitats of Pacific Middle America.

*Veniliornis kirkii kirkii* (Malherbe) **Red-rumped Woodpecker**

*Specimens:* Río Tanela 2 ♂; Río Guadualito 1 —; Turbo 1 ♂; Río Chigodoró 1 ♀ (0.5 mm).

*Phloeoceastes melanoleucus malherbii* (Gray) **Crimson-crested Woodpecker**

*Specimens:* Sautatá 1 ♀; Mutatá 1 ♂ imm.; Río Mulatos 1 ♀.

This large woodpecker is fairly similar to *Dryocopus lineatus*. Ecological differences which make coexistence possible refer to the time of nesting, the relative size of territories, foraging sites, and food items taken (Kilham 1972).

## Dendrocolaptidae

*Dendrocincla fuliginosa ridgwayi* Oberholser **Plain-brown Woodcreeper**

*Specimens:* Río Tanela 1 ♂, 1 —; Mutatá 1 ♂; Serranía de San Jacinto (San Cristóbal 1 ♂).

A wide ranging species of the neotropical forests which commonly follows army ants. Willis (1972 b) published a detailed biological study of this woodcreeper based on observations made on Barro Colorado Island, Panamá Canal Zone.

*Sittasomus griseicapillus enochrus* Wetmore **Olivaceous Woodcreeper**

*Specimens:* Serranía de San Jacinto (San Carlos 1 ♂; San Cristóbal 1 ♂; Lázaro 1 ♀).

This inconspicuous woodcreeper inhabits dry tropical forest and gallery forest in northern Colombia. The subspecies *S. g. enochrus* recently described by Wetmore (1970) occurs from the upper Sinú region (Quimarí) to the Caribbean coast. The species is missing from the more humid forests of the Urabá and Chocó regions but recurs in western Ecuador *(s. g. aequatorialis)* and in Panamá, where Wetmore (1972) found *S. g. veraguensis*

from the Darién region (Cana, Cerro Mali) westward. Skutch (1967) published notes on the life history of the Olivaceous Woodcreeper.

*Glyphorhynchus spirurus subrufescens* Todd **Wedge-billed Woodcreeper**

*Specimens:* Río Imamadó 1 ♂ (8×5.5 mm), 1 ♂ imm.; Pavarandocito 1 ♂ (10×5 mm); Río Salaquí 3 ♂; Río Uva 1 ♀ (1 mm); Mutatá 1 ♂, 5 ♀.

In assigning these specimens to *G. s. subrufescens* I follow Wetmore (1970) who reviewed the subspecies of Central America and northern Colombia.

*Xiphocolaptes promeropirhynchus rostratus* Todd **Strong-billed Woodcreeper**

*Specimens:* None.

Several specimens of this species have been collected in the upper Sinú Valley (De Schauensee 1950 b). One adult bird was obtained near Chigorodó in the Urabá region by a party of the Universidad de Los Andes (Bogotá), where it is deposited.

*Dendrocolaptes certhia columbianus* Todd **Barred Woodcreper**

*Specimen:* Río Napipí 1 ♂ (13×10 mm).

*Xiphorhynchus picus* (Gmelin) **Straight-billed Woodcreeper**

*Specimens: X. p. dugandi* (Wetmore & Phelps): Serranía de San Jacinto (Arroyo Tigre ♂), Tenche 1 ♂. *X. p. extimus* (Griscom): Riosucio 1 ♂.

The underparts of the bird from the lower Atrato Valley (Riosucio) are more intensively colored than in specimens from the Caribbean lowlands of northern Colombia *(X. p. dugandi).* For the same reason De Schauensee (1959) also referred the population of the upper Sinú region (Tierra Alta, Murucucú) to the Panamanian subspecies *X. p. extimus.* This woodcreeper is restricted to less humid forests of northwestern Colombia and Panamá.

*Xiphorhynchus guttatus nanus* (Lawrence) **Buff-throated Woodcreeper**

*Specimens:* Río Cope 1 ♂ (12 × 8 mm); Acandi 1 ♂; Unguía 1 ♂; Tilupo 1 ♂; 1 —; Río Mulatos 1 —; Río Tulapa 1 —; Serranía de San Jacinto (San Carlos 1 ♂, 1 ♀; Arroyo Camaroncito 1 ♀; Lázaro 1 ♂; Arroyo Tigre 1 ♀; Arroyo Playón 1 ♀; Arroyo Cacao 1 ♀; San Cristóbal 1 ♀).

This is the species of woodcreeper most frequently seen in northwestern Colombia. It is unknown, however, in the very humid Pacific lowlands.

*Xiphorhynchus lachrymosus lachrymosus* (Lawrence) **Black-striped Woodcreeper**

*Specimen:* Río Tanela 1 ♂.

A widespread species in northwestern Colombia, of which, however, only one specimen was collected.

*Xiphorhynchus erythropygius aequatorialis* (Berlepsch & Taczanowski)

**Spotted Woodcreeper**

*Specimens:* Mutatá 2 ♂, 1 ♀.

This woodcreeper is known from many localities in the Pacific lowlands of Colombia and Ecuador, but it is very rare in the less humid Urabá region, where I have not encountered it. The only record from the lower Atrato Valley is a bird from the Río Truandó that was referred to the Panamanian subspecies X. *e. insolitus* (Capman 1917).

*Lepidocolaptes souleyetii lineaticeps (Lafresnaye)*

**Streak-headed Woodcreeper**

*Specimens:* Acandí 1 ♀, 1 —; Serranía de San Jacinto (Arroyo Camaroncito 1 ♂; Cansona 1 ♂; Lázaro 1 ♀; Arroyo Playón 1 ♂, 1 —).

Our specimens from the Serranía de San Jacinto are clearly referable to *lineaticeps* because of the deep rufous back and wing coverts and the pronounced dusky tips of the primaries. Birds from the hills farther north near the coast (Pendales, Dep. Atlántico) and from the base of the Sierra Nevada de Santa Marta (Caracolicito, Dep. Magdalena) are paler and represent the subspecies *L. s. littoralis.*

The Streak-headed Woodcreeper ranges in the lower Atrato Valley south only to the Río Salaquí. It is lacking from the Chocó region but recurs in southwestern Colombia (De Schauensee 1964, Olivares 1958) and in northwestern Ecuador (Chapman 1926; *L. s. esmeraldae).* This population may have originated from immigrants that ranged along the Pacific coast during a previous dry climatic period.

*Campylorhynchus trochilirostris venezuelensis* (Chapman)

**Red-billed Scythebill**

*Specimens:* Serranía de San Jacinto (Lázaro 1 ♂; another bird observed along Arroyo Camaroncito).

De Schauensee (1950 b) reported this species from the upper Sinú region (Quimarí), where I did not encounter it.

## Furnariidae

*Furnarius leucopus endoecus* Cory **Pale-legged Hornero**

*Specimen:* Serranía de San Jacinto (San Carlos 1 ♀).

It is interesting to note that the population of the Serranía de San Jacinto apparently is typical of the southern, more deeply colored race raher than the pale northern form *longirostris.*

*Synallaxis albescens littoralis* Todd **Pale-breasted Spinetail**

*Specimens:* Sautatá 2 ♂; San Jacinto 1 ♂; Yatí 1 ♂.

*Synallaxis brachyura chapmani* Bangs & Penard **Slaty Spinetail**

*Specimens:* Pavarandocito 1 ♀ ( 1mm); Mutatá 1 ♀.

*Certhiaxis cinnamomea fusciírons* (Madarasz) **Yellow-throated Spinetail**

*Specimens:* Tenche 1 ♂, 1 ♀.

*Hyloctistes subulatus* (Spix) **Striped Woodhaunter**

*Specimens: H. s. cordobae* De Schauensee: Mutatá 1 ♂, 1 ♀. These birds are intermediate in size between *cordobae* and *assimilis. H. s. assimilis* (Berlepsch & Taczanowski): Río Uva 1 ♂ (2 × 1 mm).

*Philydor erythrocercus erythronotus* Sclater & Salvin

**Rufous-rumped Foliage-Gleaner**

*Specimen:* Frasquillo 1 — (imm.).

*Automolus ochrolaemus pallidigularis* Lawrence

**Buff-throated Foliage-Gleaner**

*Specimen:* Río Truandó 1 ♂ (17 × 7 mm).

*Xenops minutus* (Sparmann) **Plain Xenops**

*Specimens: X. m littoralis* Sclater: Río Tanela 1 —. *X. m. neglectus* Todd: Serranía de San Jacinto (Cansona 1 ♂, Arroyo Camaroncito 1 ♂; San Cristóbal 1 ♂).

The color of the wing and tail of the birds from the Serranía de San Jacinto is cinnamon rather than rufous. The birds are therefore more similar to the population inhabiting the Santa Marta region.

*Sclerurus guatemalensis salvini* Salvadori & Festa

**Scaly-throated Leafscraper**

*Specimens:* Río Napipí 1 ♂ (2 × 1 mm).

This species avoids the wet central Chocó region but recurs in western Ecuador without subspecific variation. The populations from the upper Sinú Valley east to the middle Magdalena Valley are paler in coloration and have been described by Wetmore (1951) as *S. g. ennosiphyllus.*

## Formicariidae

*Cymbilaimus lineatus fasciatus* (Ridgway) **Fasciated Antshrike**

*Specimen:* Río Truandó 1 ♂ (3 × 2 mm).

A bird of thickets along forest borders and forest streams. Skutch (1972) prepared a life history study of this antshrike.

*Taraba major obscurus* Zimmer **Great Antshrike**

*Specimens:* Río Tanela 1 ♂; Río Tolo 1 ♀; Río Cope 1 ♀ (1.5 mm).

Inhabits overgrown forest borders and thickets in partially cleared areas. Schäfer (1969) and Skutch (1969) published biological data of this species.

*Sakesphorus canadensis pulchellus* (Cabanis & Heine)
**Black-crested Antshrike**

*Specimen:* La Balsa, 30 km southwest of Montería 1 ♀, Yatí 1 ♂, 1 ♀.

This crested antshrike inhabits thickets in fairly open areas of northern Colombia. Records from the Urabá region (Haffer 1959) and from the lower Atrato Valley (Río Truandó; De Schauensee 1948—1952) are invalid.

*Thamnophilus doliatus nigricristatus* Lawrence **Barred Antshrike**

*Specimens:* Río Chigorodó 1 ♀ (0.5 mm); Quebrada Charrura 1 ♂; Serranía de San Jacinto (Cansona 1 ♀; Arroyo Camaroncito 1 ♂; Palmira 1 ♀; west of San Jacinto 1 ♂).

Inhabits fairly open seasonal forests of northern South America and has occupied cleared land that provides sufficient cover. The record from the Río Chigorodó extends the known range westward to the lower Atrato region. Because of continued deforestation in this region, the bird may soon become common around the Gulf of Urabá. Schäfer (1969) and Skutch (1969) gave biological accounts of this antshrike.

*Thamnophilus nigriceps nigriceps* Sclater **Black Antshrike**

*Specimens:* Río Tanela 1 ♂, 1 ♀; Unguía 1 ♀; Sautatá 2 ♂, 1 ♀; upper Río Sinú, mouth Río Naín 1 ♂ (3 × 2 mm); 2 ♀ (1 and 1.5 mm); Serranía de San Jacinto (Arroyo Camaronicito 1 ♀; San Cristóbal 1 ♀).

This northern Colombian forest antshrike possibly originated in the Nechí refuge and extended its range westward into eastern Panamá and northward to the Serranía de San Jacinto and the Santa Marta region. It is not rare on either side of the Gulf of Urabá in lower levels of the forest and has been found in the Atrato Valley south to Sautatá and Iguamiandó but is missing from the wet central Chocó region. *Thamnophilus bridgesi* is the Central American representative and both may be closely related to the poorly known *Th. praecox* of the upper Amazonian forest (Zimmer 1937)).

*Thamnophilus punctatus* (Shaw) **Slaty Antshrike**

*Specimens: T. p. subcinereus* Todd: Río Tanela 3 ♂, 1 ♀, Frasquillo 1 ♂. *T. p. atrinucha* Salvin & Godman: Mutatá 2 ♂, 4 ♀, Río Chigorodó 1 ♂ (5 × 3 mm), 2 ♀ (2 and 10 mm), Río Ímamadó 2 ♀ (0.5 and 0.5 mm), Pavarandocito 1 ♂ (5 × 3 mm), 2 ♀ (2 and 2 mm), Juradó 1 ♀ (10 mm), Río Salaquí 2 ♂, 2 ♀, Río Truandó 1 ♂ (6 × 3 mm), 2 ♀ (0.5 and 1.5 mm), Río Uva 1 ♀ (2 mm).

A common antshrike in lower levels of the forest. The majority of the females collected are rather intensively colored on the underparts and

agree with a series of *atrinucha* from Guapi on the Pacific coast to the south. A few specimens are lighter, medium buff, on breast and belly. This confirms the remarks by previous authors (Chapman 1917, Hellmayr 1924) on the pronounced variability of this species. De Schauensee (1948—1952) mentions paler females from Murindó and Sautatá, referring them to *subcinereus*. I found three males from the Río Tanela on the western side of the Gulf of Urabá to be slightly paler gray than all males taken south of the Gulf of Urabá. This indicates the populations of the upper Sinú and Urabá regions should be labelled *T. p. subcinereus*. I refer the specimens from the Serranía de Abibe (Chigorodó, Imamadó, Pavarandocito) as well as from the Río Salaquí southward in the Pacific lowlands to the Chocó form *atrinucha*.

*Clytoctantes alixi* Elliot **Recurve-billed Bushbird**

*Specimens:* None.

A secretive bird of dense tangled second-growth and forest borders. It is mainly restricted to northern Colombia where Carriker (1955) collected it at several localities in the Departments of Bolivar, Antioquia, Córdoba and Caldas. It is also known from the humid middle Magdalena Valley (near Ocaña and El Tambor) and from extreme northwestern Venezuela (Perijá range; De Schauensee 1966).

*Xenornis setifrons* Chapman **Speckle-breasted Antshrike**

*Specimens:* None.

This rare secretive antshrike inhabits forest undergrowth along the lower slopes of the Baudó Mountains north to Cerro Tacarcuna and Armila in the San Blas region (Fig. 22 A; Wetmore 1972: 150). The restricted range of this taxonomically isolated bird is similar to that of *Crypturellus kerriae* (Fig. 20 A); neither of these species has been found in the Urabá region.

*Thamnistes anabatinus intermedius* Chapman **Russet Antshrike**

*Specimen:* Río Imamadó 1 ♂ (1.5 × 1 mm).

*Dysithamnus puncticeps intensus* Griscom **Spot-crowned Antvireo**

*Specimens:* Mutatá 6 ♂, 2 ♀.

Quite common in the understory of the very humid forest near Mutatá. The bird ranges from there along the northern Andean foot hills to the lower Cauca Valley but is missing in the less humid forests around the Gulf of Urabá.

*Myrmotherula surinamensis pacifica* Hellmayr **Streaked Antwren**

*Specimens:* Río Sinú, mouth of Río Naín 1 ♂ (3 × 2 mm), 1 ♀ (1.5 mm); Río Chigorodó 1 ♂ (4 × 3 mm); Mutatá 1 ♂, 1♀.

*Myrmotherula fulviventris* Lawrence **Checker-throated Antwren**

*Specimens: M. f. fulviventris* Lawrence: Río Truandó 1 ♂ (1.5 × 1 mm); Mutatá 2 ♀. *M. f. salmoni* (Chubb): Frasquillo 1 ♂ (2.5 × 1.5 mm).

The more intensively colored underparts of the birds from the lower Atrato Valley serve to distinguish them from the example of *M. f. salmoni* collected near Frasquillo in the upper Sinú Valley, which possesses a more whitish throat and chest.

This antwren is found in lower levels of the forest. It is a typical Chocó element, which extended its range northward into Honduras and eastward to the humid Magdalena Valley and remains widely separated from its Amazonian representative *M. leucophthalma* (recently observed for the first time in southeastern Colombia; De Schauensee 1964: 10).

*Myrmotherula axillaris albigula* Lawrence **White-flanked Antwren**

*Specimens:* Río Tanela 1 ♂; Río Imamadó 1 ♂ (7 × 3 mm); Pavarandocito 1 ♂; Mutatá 1 ♂, 2 ♀; Río Salaquí 1 ♂, 1 ♀; Río Truandó 1 ♀ (1 mm); Río Uva 1 ♂ (5 × 3 mm).

This rather common forest antwren has a continuous range around the northern tip of the Andes and is probably a recent immigrant from the Amazon basin into the trans-Andean region north to Honduras. See Skutch (1969) for a life history study of this bird.

*Microrhopias quixensis consobrina* (Sclater) **Dot-winged Antwren**

*Specimen:* Río Imamadó 1 ♂ (2 × 1 mm).

This forest bird advanced eastward into the humid Magdalena Valley and northward into Central America. There is a wide gap between the cis- and trans-Andean populations, as this species is missing from northeastern Colombia and Venezuela.

*Formicivora grisea hondae* (Chapman) **White-fringed Antwren**

*Specimens:* Serranía de San Jacinto (Cansona 1 ♂; San Isidro 1 ♂, 1 ♀; San Carlos 1 ♂).

The White-fringed Antwren inhabits thickets and bushy pastures in open northern Colombia.

*Cercomacra tyrannina rufiventris* (Lawrence) **Dusky Antbird**

*Specimens:* Acandí 1 ♂, 1 ♀; Río Truandó 2 ♂ (4 × 1.5, 3.5 × 2.5 mm), 1 ♀ (2 mm); Río Uva 2 ♂ (3×2 mm, 4×2 mm), 1 ♀ (1 mm).

This species ranges continuously around the northern tip of the Andes; it is lacking only in the Santa Marta region. See Skutch (1969) for a life history study of this bird.

*Cercomacra nigricans* Sclater **Jet Antbird**

*Specimens: C. n. nigricans:* Río Sinú, mouth of Río Naín 1 ♂ (3.5 × 2 mm); Tenche 1 ♂; Serranía de San Jacinto (San Carlos 1 ♂; San Cristóbal 1 ♂; Arroyo Cacao 1 ♂. *C. n. atrata* Todd: Sautatá 3 ♂, 1 ♀.

The specimens from Sautatá are referred to *atrata* because of the dark coloration of the female, which has no white markings on the underparts.

The Jet Antbird inhabits seasonal forest of northern Colombia and is missing from the Chocó lowlands.

*Gymnocichla nudiceps* (Cassin) **Bare-crowned Antbird**

*Specimens: G. n. nudiceps* (Cassin): Frasquillo 2 ♂ (8 × 6, 9.5 × 5mm); Apartadó, 30 km southeast of Turbo 1 ♂ (8 × 3 mm). *G. n. sanctamartae* Ridgway: Serranía de San Jacinto (San Cristóbal 1 ♂).

This species has advanced into northern Colombia from Middle America, where it is widely distributed. It does not range into the Chocó region but remains restricted to the Urabá region and humid portions of the northern Colombian lowlands inhabiting thickets and second growth along rivers or near clearings. The populations near the Caribbean coast have dull black posterior underparts *(G. n. sanctamartae).* Although not recently reported from the Santa Marta region, the bird probably does occur there, because Marinkelle (1970) found it far to the east along the fairly humid northern flank of the Macuira Mountains, outer Guajira Peninsula.

*Myrmeciza longipes panamensis* Ridgway **White-bellied Antbird**

*Specimens:* Serranía de San Jacinto (Arroyo Camaroncito 1 ♀; 10 km west of San Jacinto 1 ♀).

This ground-dwelling antbird inhabits shady thickets in fairly open areas of northern South America. Wetmore (1972: 200) cites additional records from the Serranía de San Jacinto (Colosó), the Magdalena Valley (Santa Rosa, La Gloria, Ayacucho), and northeastern Colombia. The species is missing from the humid forest of the Urabá and Chocó regions.

*Myrmeciza exsul* Sclater **Chestnut-backed Antbird**

*Specimens: M. e. cassini* (Ridgway): Río Tanela 1 ♂; Río Guadualito 1 ♂; Río Tulapa 1 ♀; Río Chigorodó 1 ♂ (4 × 2 mm); Río Imamadó 1 ♂ (4 × 1.5 mm), 3 ♀ (0.5, 0.5, 1.5 mm); Pavarandocito 1 ♀ (1 mm); Mutatá 3 ♂, 2 ♀; Río Salaquí 2 ♀ (11 mm!); Río Truandó 1 ♀ (3 mm); Río Napipí 3 ♂ (2 × 1, 3 × 2, 4 × 2 mm), 1 ♀ (1.5 mm); Río Murri 2 ♂ (2 × 1, 5 × 2 mm); Quebrada Charrura 1 ♂. *M. e. maculifer* (Hellmayr): Río Uva 2 ♂ (3 × 1 mm).

The gray of the head and underparts in the series of *M. e. cassini* is lightest in the males taken near the Gulf of Urabá and darkens to blackish-gray southward in the Atrato Valley. The birds from the Río Napipí are somewhat variable and intermediate but are closer to the northern form *cassini.* The subspecies *niglarus* recently described by Wetmore (1962) from eastern Panamá includes the populations on the western coast of the

Gulf of Urabá near Acandí. One of the males from the Río Uva *(M. e. maculifer)* is closer in coloration to the slightly paler birds from the Río Murrí and the Río Napipí; the second male, however, is dark blackish-gray underneath. The occurrence of *M. exsul* east of the Andes, suggested as a possibility by De Schauensee (1964, 1966), appears highly unlikely.

The Chestnut-backed Antbird is common in the forests of northwestern Colombia, where it forages in the dim light near the ground. Its characteristic song is often heard and consists of a short series of two or three full, mellow whistles *"fee, few!"* or *„Fee feh few!"* Skutch (1969) and Willis et al. (1972) published detailed biological studies of this antbird.

*Myrmeciza laemosticta nigricauda* Salvin & Godman **Dull-mantled Antbird**

*Specimens:* Río Imamadó 1 ♂ (3 × 1.5 mm).

A female taken by Carriker (1959) at the Río Nuquí it the only previous record of this species in the northern Chocó region. Dr. E. O. Willis (pers. comm.) found it in humid canyons of the upper Río Verde Valley and De Schauensee (1950 b) reported it from Quimari in the upper Sinú region. The presumed occurrence of this bird east of the Andes (De Schauensee 1964, 1966) seems most unlikely.

*Gymnopithys bicolor* (Lawrence) **Bicolored Antbird**

*Specimens: G. b. bicolor* (Lawrence): Río Tanela 1 ♀; Mutatá 1 ♂. *G. b. daguae* Hellmayr: Río Truandó 2 ♂ (9 × 3, 8 × 3.5 mm); Río Murri 1 ♂ (6 × 3 mm).

The specimens from the Truandó and Murrí Rivers are referred to the southern form *daguae* on the basis of the intensively colored dark brown upperparts, the slightly blackish sides of the breast, and the large bill (20 mm). The female of the nominate form from the Río Tanela has the forehead gray as in the above specimens but is decidedly lighter brown throughout and has a smaller bill (18 mm). The northern *bicolor* intergrades with *daguae* in the Juradó and Salaquí region (De Schauensee 1948—1952) as well as east of the Atrato River in the Mutatá region (Haffer 1967 c).

Detailed studies of the behavior and nesting biology of this ant-following species have been prepared by Willis (1967) and Skutch (1969).

The trans-Andean *Gymnopithys bicolor* represents the Amazonian species *G. leucaspis* and *G. rufigula. G. leucaspis* is similar to its trans-Andean ally but has the sides of the neck and breast black. *G. rufigula* is rufescent, with paler underparts. It probably hybridizes locally with the white-bellied *G. leucaspis* in the border region of Colombia and Venezuela, where an intermediate population has been described by Phelps & Phelps, Jr. (1947) as *G. r. "pallidigula"* (P of Fig. 39). Further south, the Río Negro separates these two species. The Amazon River delimits the range of the *Gymnopithys rufigula* superspecies except near the base of the Andes in northeastern Peru (Fig. 39). *G. leucaspis* has crossed the Río Marañón


Fig. 39: Distribution of the *Gymnopithys* antbirds. The *G. rufigula* superspecies is comprised of *G. rufigula, G. leucaspis* and *G. bicolor. G. salvani* and *G. lunulata* together form a second superspecies.

*Explanation:* Hatched horizontally and crosses — *G. rufigula.* Encircled cross and P — *G. r. "pallidigula" (*probably a hybrid population beween *G. rufigula* and *G. leucaspis).* Area dashed vertically and open circles — *G. leucaspis.* Area hatched vertically — *G. bicolor.* Stippled area and solid stars — *G. lunulata.* Shaded area and open squares — *G. salvini.* Andes Mountains above 2000 m elevation are in black.

southward in this area and has reached the valley of the lower Huallaga River.

South of the Amazon, *Gymnopithys salvini,* a gray bird with a barred tail, probably takes the place of *G. leucaspis. G. lunulata* occupies the Ucayali Valley of eastern Peru and ranges north along the eastern foothills of the Ecuadorian Andes at least to Putuimi (Fig. 39), where it is dominated by the sympatric *G. leucaspis* (Willis 1968). The absence of *G. leucaspis* and *G. rufigula* south of the Amazon may be due to a combination of ecologic competition with related species and the barrier effect of the Amazon River.

A similar situation exists in the allied antbird *Pithys albifrons,* a bird with long white plumes on the forehead, a gray back and chestnut underparts and tail. This species inhabits forest undergrowth north of the Amazon from the Andes east to the Atlantic coast (Fig. 40). It crossed the Río Marañón southward and advanced along the base of the Peruvian Andes to the headwater region of the Ucayali River. Ecologic competition with other antfollowing formicariids may prevent further range expansion eastward from Peru in the forests south of the Amazon (a record of *Pithys albifrons* from the south side of the Amazon, Río Arapiuns, needs confirmation; see Haffer 1974 b: 108). Like numerous other Amazonian birds this species did not reach the trans-Andean lowlands in western Colombia and Middle America.


Fig. 40: Distribution of the White-plumed Antbird, *Pithys albifrons.*

*Explanation:* No individual records are shown in southern Venezuela and in the Guianas where this species is common. It crossed the upper Amazon southward and reached the upper Ucayali Valley, but did not enter the trans-Andean lowlands. Andes Mountains above 2000 m elevation are in black.

*Hylophylax naevioides naevioides* (Lafresnaye) **Spotted Antbird**

*Specimens:* Río Chigorodó 1 ♂ (2 × 1 mm); Río Imamadó 1 ♂ (3.5 × 2.5 mm), 1 ♀ (1.5 mm); Pavarandocito 1 ♂ (4 × 2.5 mm); Mutatá 1 ♂; Río Jurado 1 ♂ (3 × 1 mm), 1 ♀ (4 mm); Río Salaqui 3 ♂ (1.5 × 1, 2 × 1.5 mm); Río Napipí 1 ♀ (1 mm); Río Uva 1♀ (2 mm).

This common forest bird is a typical Chocó element that advanced eastward into the middle Madgalena Valley and northward into Middle America (Nicaragua). Its cis-Andean representative in the Amazonian forest is the closely similar *Hylophylax naevia* (Fig. 12 F).

Wetmore (1972) found no consistent differences between *H. n. naevioides* and *H. n. subsimilis* and synonymized these subspecies. Willis (1972) published a detailed study on the behavior and the nesting ecology of the Spotted Antbird, which will be of general significance for future investigations of the biology of tropical forest birds.

*Phaenostictus mcleannani mcleannani* (Lawrence) **Ocellated Antbird**

*Specimens:* Frasquillo 1 ♀ (0.5 mm); Río Truandó 1 ♂ (6.5 × 2.5 mm).

Wetmore (1972: 237) synonymized *P. m. chocoanus* with the nominate form. A detailed biological study of the Ocellated Antbird was published recently by Willis (1973). This species forms a monotypic genus and probably is an old trans-Andean isolate that has extended its range northward to Nicaragua and eastward to the upper Sinú—lower Cauca region; it apparently did not reach the Magdalena Valley. The nearest allies in Amazonia are among the species of *Phlegopsis*.

*Formicarius analis* (D'Orbigny & Lafresnaye) **Black-faced Antthrush**

*Specimens: F. a. saturatus* Ridgway: Frasquillo 2 ♂ (testes enlarged, 7 and 15 mm long). *F. a. panamensis* Ridgway: Río Chigorodó 1 ♂ (11 × 3.5 mm); Río Truandó 1 ♂ (12 × 6 mm); also heard at the Río Napipí.

The specimens from the lower Atrato Valley *(F. a. panamensis)* are more richly colored above than the birds from the upper Sinú region, which represent *F. a. saturatus*.

This antthrush inhabits the entire Amazon region and has a continuous range around the northern tip of the Andes. It meets the trans-Andean representative *F. nigricapillus* in the northern Chocó region and in Middle America (Fig. 41). In the latter area, *F. nigricapillus* is restricted to the Caribbean slope of Costa Rica and western Panamá, where it inhabits the upper tropical and lower subtropical belt. *F. analis* is a common resident of the lowland forests but ranges up to 4500 feet in southwestern Costa Rica where *F. nigricapillus* is absent (Slud 1964). *F. analis* and *F. nigricapillus* may meet in the lowlands of northwestern Colombia. I did not encounter either species at the Río Uva or near Mutatá.

The Black-faced Antthrush walks over the forest floor with bobbing head and erect short tail like a little rail. The song is often heard and is easily imitated *"tüt tütüt tü tü tüt"*. A fairly loud note is followed by a melancholy series of four or five whistled notes decreasing in loudness. The song of the northern Venezuelan population is longer, consisting of

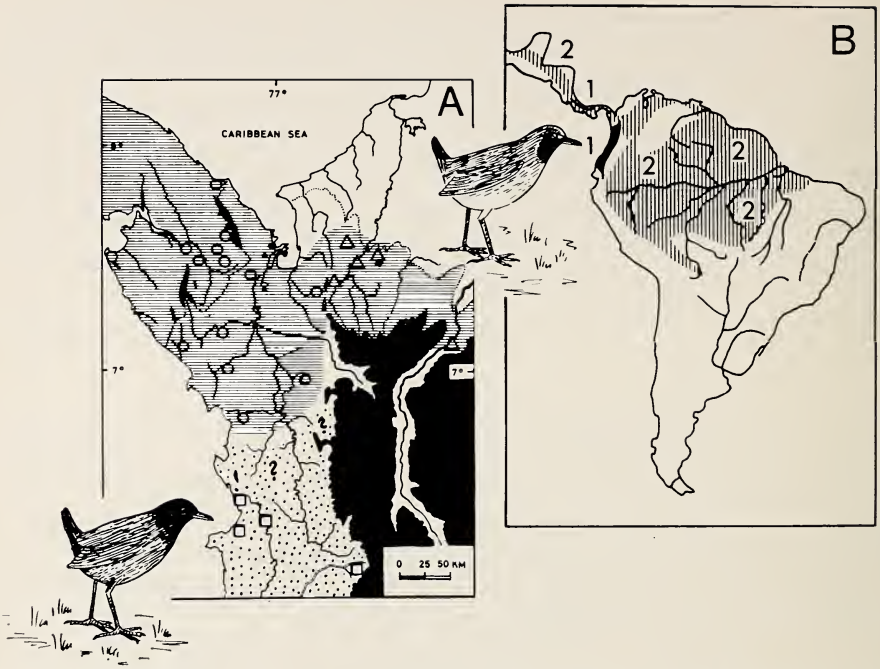


Fig. 41: Distribution of the terrestrial antthrushes, *Formicarius analis* superspecies.

*Explanation:* **A** Distribution of *F. analis* and *F. nigricapillus* in northwestern Colombia and eastern Panamá. Shaded area — *F. analis;* open circles — *F. a. panamensis;* open triangles — *F. a. saturatus.* Stippled area and open squares — *F. nigricapillus.* For identification of individual records see Haffer (1967 c). Note more extensive black coloration on the head, mantle, and breast in *F. nigricapillus.* **B** Generalized distribution of *F. nigricapillus* (1, solid area) and *F. analis* (2, area hatched vertically).

20 to 50 whistled notes and resembles that of *Chamaeza ruficauda* (Schäfer 1969). After the breeding season, the latter author encountered a sleeping assemblage in a *Miconia* bush which consisted of 10 birds each of *F. analis* and *Chamaeza campanisoma.* See Skutch (1969) for a detailed biological account of *F. analis.*

*Pittasoma michleri* Cassin **Black-faced Antpitta**

*Pittasoma rufopileatum* Hartert **Rufous-crowned Antpitta**

*Specimens:* None.

These two large antpittas form a superspecies and have no close relatives in Amazonia. The antpittas inhabit dense humid forest from Caribbean Costa Rica to western Ecuador (Fig. 42). *P. michleri* probably originated

in the Caribbean Costa Rica refuge and later advanced into Panamá and the Urabá region south to the Río Truandó. *P. rufopileatum* is a typical Chocó element ranging from northwestern Ecuador in the Pacific forests north to the Baudó Mountains and to Mutatá. Dunning (1970 and pers. comm.) captured and photographed a bird of this species at this latter locality. Both species may meet in the area of the Río Napipí. The study of the interrelationship of these markedly different species would be of particular interest. The underparts of the subspecies inhabiting the Atrato Valley *(P. rufopileatum rosenbergi)* is almost plain ochraceous but barred black and white in the Ecuadorian population *P. r. rufopileatum* (similar to *P. michleri).*

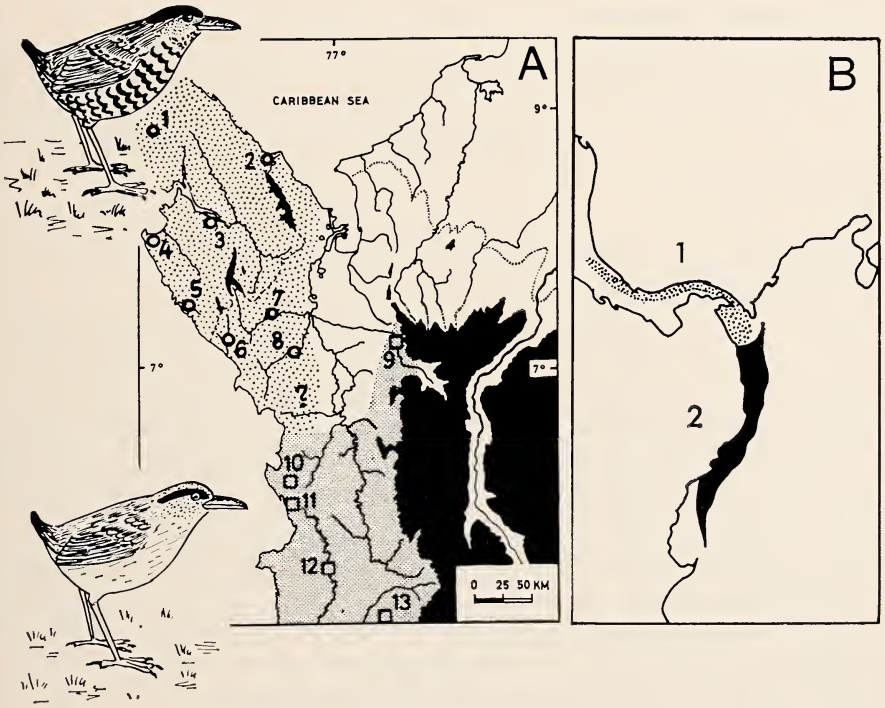


Fig. 42: Distribution of the terrestrial antpittas, *Pittasoma michleri* superspecies.

*Explanation:* **A** Distribution of *P. michleri* and *P. rufopileatum* in northwestern Colombia and eastern Panamá. Stippled area and open circles — *P. m. michleri:* 1 Cerro Chucantí, 2 Puerto Obaldía, Permé, and Armila, 3 lower Río Tuira, 4 Cerro Sapo, 5 Río Jaqué, 6 Río Juradó, 7 Río Salaquí, 8 Río Truandó (type locality). Shaded area and open squares — *P. rufopileatum rosenbergi:* 9 Mutatá, 10 Baudó Mountains (1065 m), 11 Río Jurubidá, 12 Río Baudó, 13 Nóvita. Black and white barring is present in the Ecuadorian form of *P. rufopileatum.* **B** Generalized distribution of *P. michleri* (1, stippled area) and *P. rufopileatum* (2, solid area).

*Hylopezus perspicillatus* Lawrence **Streak-chested Antpitta**

*Specimens: H. p. perspicillatus* Lawrence: Río Truandó 1 ♀ (1.5 mm). *H. p. pallidior* (Todd): Quebrada Charrura 1 ♂. *H. p. periophthalmicus* Salvadori & Festa: Río Murrí 1 ♂; Mutatá 1 ♀.

The bird from the Río Truandó *(perspicillatus)* has a white throat as *pallidior* of the upper Sinú region. However, the breast is streaked black and white and the upperparts are more deeply colored. The specimens from the Atrato Valley (Río Murrí, Mutatá) agree in the coloration of the breast with birds from the Chocó region farther south. The breast is streaked black and fulvous, not pure white as in the specimen from the Río Truandó.

Lowery et al. (1969) recommended to separate the species *perspicillata, fulviventris* and several others from the genus *Grallaria* and to unite them under Ridgway's designation *Hylopezus*.

I found *H. perspicillatus* in the interior of the forest where the floor was rather open. The voice differs appreciably from that of *H. fulviventris:* The call is a "series of clear, melancholy whistles, at first rising a little in pitch, then falling off in three descending couplets" (Eisenmann 1952, Slud 1964, Skutch 1969).

*Hylopezus fulviventris barbacoae* (Chapman) **Fulvous-bellied Antpitta**

*Specimen:* Río Tolo 1 ♂.

The characteristic song of this antpitta consists of a series of 8 to 10 clear notes rising in pitch and somewhat accelerating and increasing in loudness toward the end. I met this terrestrial species in dense tangled *Heliconia* thickets bordering a watercourse and merging backward with high forest. A male was taken at the Río Tolo west of the Gulf of Urabá; other birds were heard along small creeks in the forested Río Imamadó Valley and along overgrown forest borders near Mutatá and Alto Bonito (Haffer 1967 c). Wetmore (1972) reported this antpitta from the upper Sinú Valley (Quebrada Salvajín). It is probably a fairly common bird in the Chocó region but few records exist because of its secretive nature. Although a bird may be heard singing on the ground at one or two meters distance, it remains unobserved in the tangled vegetation which it favors. *H. fulviventris* is an antpitta that is particularly difficult to collect.

## Cotingidae

*Cotinga nattererii* (Boissonneau) **Blue Cotinga**

*Specimens:* None.

The Blue Cotinga is a typical Chocó element that extended its range into central Panamá and around the northern tip of the Andes into the middle Magdalena Valley, and it has been recorded in the forested

Maracaibo basin of northwestern Venezuela. It is rather rare in the Urabá region, where it is restricted to the more humid areas. I observed only one pair perched on a low guarumo *(Cecropia)* tree on a small clearing in the heavily forested Río Naín Valley, upper Sinú region, opposite from Tucurá (30 August 1958).

The genera *Attila, Laniocera, Rhytipterna* and several others previously listed here, have been transferred to the Tyrannidae (De Schauensee 1970, Snow 1973).

*Lipaugus unirufus unirufus* Sclater **Rufous Piha**

*Specimens:* Río Tanela 1 ♂, 1 ♀; Quebrada Charrura 1 ♀.

This trans-Andean forest bird is known in Colombia from the Pacific coast east into the humid middle Magdalena Valley. Marinkelle (1970) reported it from the humid northern flank of the otherwise very arid Serranía de Macuira, outer Guajira Peninsula (G in Fig. 13 D), far removed from the nearest known localities in central Colombia.

*Pachyramphus cinnamomeus* Lawrence **Cinnamon Becard**

*Specimens: P. c. cinnamomeus* Lawrence: Río Currulao 1 —; Río Guadualito 2 —; Sautatá 1 —; Río Chigorodó 1 ♂ (12 × 6 mm), 2 ♀ (0.5 mm); Mutatá 1 ♂; Riosucio 1 ♂, 1 ♀; Río Napipí 1 ♂ (7 × 5 mm); Río Uva 1 ♂ (10 × 5 mm); Quebrada Charrura 1 ♀. *P. c. magdalenae* Chapman: Serranía de San Jacinto (San Juán Nepomuceno 1 ♀).

The trans-Andean Cinnamon Becard advanced eastward into northwestern Venezuela occupying the forests in the Maracaibo basin and along the eastern base of the Cordillera Oriental of Colombia south at least to Villavicencio (Buenavista; Chapman 1917); see Fig. 13 E. It is probably in contact with its cis-Andean representative *P. castaneus,* which inhabits the coastal mountains of Venezuela and the Amazon basin. Both species are similar and very probably exclude each other geographically as a result of ecologic competition (see also Snow 1973: 19—20).

Marinkelle (1970) collected a specimen of *P. cinnamomeus* in the humid northern flank of the Serranía de Macuira, outer Guajira Peninsula, in northeastern Colombia. This bird is an example of the nominate subspecies as are the specimens from the Santa Marta region, the middle Magdalena Valley, and the Maracaibo basin. The pale form, *P. c. magdalenae,* is restricted to the hills of the Serranía de San Jacinto near the Caribbean coast (where I collected a pale bird) and the lower Magdalena region (Algodonal where the type was obtained). Wetmore (1972: 278) synonymized *P. c. magdalenae* and *P. c. cinnamomeus* but it is not clear whether he had material for comparison from the dry Caribbean lowlands of northern Colombia.

*Pachyramphus rufus* (Boddaert) **Cinereous Becard**

*Specimen:* Serranía de San Jacinto (San Juán Nepomuceno 1 ♂).

This is a bird of wooded savanna country which avoids the forested Urabá and Chocó regions, where I never encountered it. *P. rufus* is widely separated from its Pacific representative *P. spodiurus* of western Ecuador.

*Pachyramphus homochrous* (Sclater) **One-colored Becard**

*Specimens: P. h. homochrous* (Sclater): Río Uva 1 ♂ (14 × 6 mm). *P. h. quimarinus* (De Schauensee): Río Tanela 1 ♀, Río Guadualito 1 ♀, Río Mulatos 1 ♀.

This trans-Andean forest becard advanced eastward into the Maracaibo basin of northwestern Venezuela and westward to central Panamá (Fig. 13 F). It appears to be missing from the Pacific lowlands of southwestern Colombia, as no record is known from this region. The Middle American representative *P. aglaiae* is considered to be conspecific with *P. homochrous* by Webster (1963) and Snow (1973). A wide gap separates *P. homochrous* from its cis-Andean representative *P. minor* (Fig. 13 F). These species resemble each other in size and plumage color.

*Tityra semifasciata columbiana* Ridgway **Masked Tityra**

*Specimen:* Serranía de San Jacinto (Lázaro 1 ♀).

The tityras are not common in the Urabá region, where we did not collect them. Marinkelle (1970) reported this bird from the humid northern flank of the Serranía de Macuira on the outer Guajira Peninsula.

*Querula purpurata* (Müller) **Purple-throated Fruitcrow**

*Specimens:* Unguía 1 ♂, 2 ♀; Domingodó, lower Atrato River 1 ♂; Río Guadualito 1 —. *Taxonomy:* Monotypic. The trans-Andean populations are widely separated from the Amazonian main range of this species.

Groups of three to five birds are often seen in the forests around the Gulf of Urabá. Snow (1971) gave a biological account of this species based on observations made in Guyana.

## Pipridae

*Pipra erythrocephala erythrocephala* (L.) **Golden-headed Manakin**

*Specimens:* Río Tanela 3 ♂, 2 ♀; Frasquillo 1 ♀; Río Chigorodó 1 ♀ (2 mm); Río Imamadó 1 ♂ (7 × 3.5 mm); Pavarandocito 4 ♂ (5 × 3, 5 × 3, 6 × 3.5, 7 × 4 mm); Mutatá 12 ♂, 1 ♀; Río Napipi 1 ♀ (1.5 mm); Río Murrí 1 ♂ (4.5 × 3 mm).

See next species for comments. Snow (1962 b) prepared a detailed biological account of this species.

*Pipra mentalis minor* Hartert **Red-capped Manakin**

*Specimens:* Mutatá 2 ♂, 1 ♀; Río Uva 4 ♂ (5 × 3 mm in three males, 6 × 3 mm), 1 ♂ imm. (4 × 2 mm).

The Red-capped and the Golden-headed Manakin replace each other geographically in the lower Atrato Valley (Fig. 43), where *P. mentalis* occurs north to the Río Uva and Mutatá. *P. erythrocephala* inhabits the Urabá region and the lower Atrato Valley south to the Napipí and Murrí Rivers (Haffer 1967 b). Interactions of these parapatric manakins along the contact zone are unknown. Occasional hybrids occur where these species meet in eastern Panamá (Dr. E. Eisenmann, pers. comm.). The Amazonian *P. erythrocephala* ranges around the northern tip of the Andes and occupied a peculiar gap in the range of the trans-Andean *P. mentalis*. Both species form a zoogeographic species (= superspecies) together with the red-capped *P. rubrocapilla* of southern Amazonia and southeastern Brazil as well as *P. chloromeros* of eastern Peru and Bolivia (Fig. 43 B).

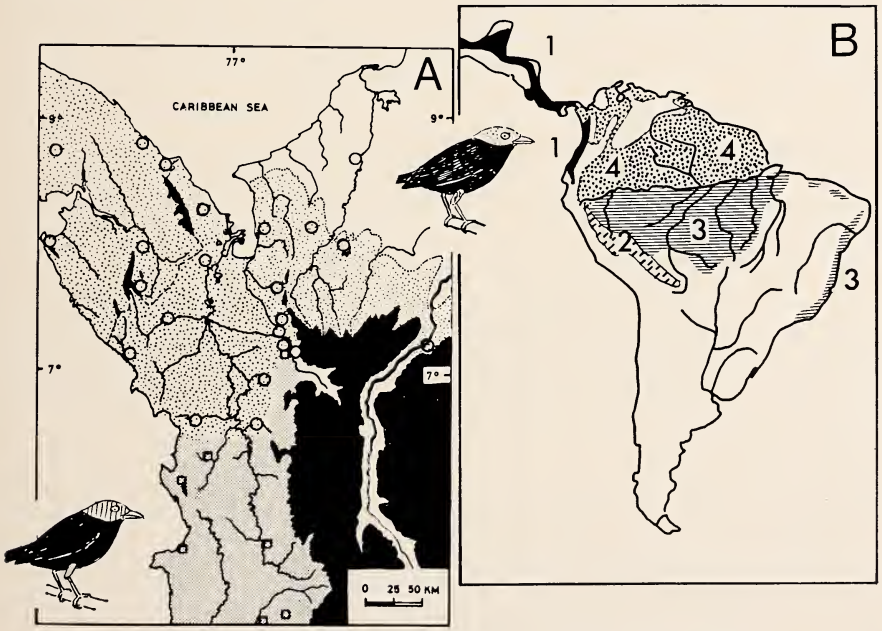


Fig. 43: Distribution of the *Pipra erythrocephala* superspecies.

*Explanation:* **A** Distribution of *P. erythrocephala* and *P. mentalis* in northwestern Colombia and easternmost Panamá. Modified from Haffer (1967 b). Stippled area and open circles — *P. e. erythrocephala*. Shaded area and open squares — *P. mentalis minor*. Plumage color in males of both species is mainly black with a yellow cap in *erythrocephala* and a red cap in *mentalis*. **B** Generalized distribution of *P. mentalis* (1, solid areas); *P. chloromeros* (2, dashed area); *P. rubrocapilla* (3, area hatched horizontally); *P. erythrocephala* (4, stippled area). Another species of this group, *P. cornuta*, inhabits montane forests of the table mountains in southern Venezuela.

*Pipra coronata minuscula* Todd **Blue-crowned Manakin**

*Specimens:* Río Tanela 2 ♂; Río Imamadó 1 ♂, 2 ♀; Mutatá 4 ♂, 11 ♀; Río Napipí 2 ♀ (1 mm); Río Murrí 1 ♀ (2 mm); Río Uva 9 ♂ (2 × 1, 5 × 3, mm in six males, 4 × 2, 6 × 3 mm), 3 ♀ (1, 2, and 10 mm).

The trans-Andean populations *(P. c. velutina* and *minuscula)* are widely separated in northeastern Colombia and northern Venezuela from the Amazonian forms.

*Chiroxiphia lanceolata* (Wagler) **Lance-tailed Manakin**

*Specimen:* Serranía de San Jacinto (San Jacinto 1 ♂).

This manakin inhabits dry forests and thickets in northern Colombia (Serranía de San Jacinto; also observed at Coveñas near the mouth of the Río Sinú). It ranges around the Santa Marta Mountains and is found throughout northern Venezuela. The species is missing in the humid forests of northwestern Colombia but recurs in the dry Pacific lowlands of Panamá and extreme southwestern Costa Rica (Slud 1964). It is replaced in Pacific northern Middle America by *C. linearis* and in southeastern Venezuela, Trinidad and Amazonia by *C. pareola.*

*Manacus manacus abditivus* Bangs **White-bearded Manakin**

*Specimens:* Serranía de San Jacinto (Cansona 1 ♂; Arroyo Camaroncito 1 ♂ imm.; Lázaro 1 ♂). *Taxonomy:* This Amazonian manakin is composed of several clinal subspecies and geographical isolates (southeastern Brazil and western Ecuador). It forms a superspecies with trans-Andean *M. vitellinus, M. aurantiacus* and *M. candei.*

The White-bearded Manakin is fairly common in densely overgrown valleys of the Serranía de San Jacinto. We found it also in the hills at Coveñas near the mouth of the Río Sinú; this is the westernmost record of the species along the Caribbean coast. Marinkelle (1970) reported this species from the Guajira Peninsula. See Snow (1962 a) for a detailed biological study.

*Manacus vitellinus* (Gould) **Golden-collared Manakin**

*Specimens: M. v. vitellinus* (Gould): Río Tanela 2 ♂; Saulatá 1 ♀; Río Cope 1 ♂ (4 × 3 mm), 1 ♂ imm. These birds agree best with the color stage of nominate *vitellinus* reported by Wetmore (1959) from Necoclí north of the Río Cope and Turbo and from Acandí. *M. v. milleri* Chapman: Quebrada Charrura 2 ♂. *M. v. viridiventris* Griscom: Río Chigorodó 1 ♂ (7 × 4 mm), 1 ♂ imm. (4 × 2.5 mm) 1 ♀; Río Imamadó 1 ♂ (6 × 4 mm), 1 ♂ imm. (4.5 × 2.5 mm); Mutatá 2 ♂, 1 ♀, 1 —; Río Truandó 2 ♂ (6 × 2.5, 6 × 3.5 mm), 1 ♂ imm. (4.5 × 2.5 mm), 1 ♀ (1.5 mm); Río Napipí 5 ♂ (5 × 2, 5 × 3, 6 ×3, 6.5 × 3.5, 6.5 × 3 mm), 1 ♂ imm. (5 × 2 mm), 2 ♀ (1 and 2 mm); Río Uva 2 ♂ (5 × 3, 6 × 3 mm), 2 ♀ (1 and 9 mm).

The young male from the Río Truandó was taken while dancing among a group of adult males. This confirms what has been said by various authors before that green-plumaged dancing birds are probably in most if not all cases immature males rather than females.

The populations of the yellow-breasted *M. vitellinus* can be arranged in a color cline in northwestern Colombia. Intensively pigmented populations *(viridiventris)* inhabit the humid Chocó lowlands north to the Río Truandó and Río Chigorodó and grade into the intermediate color stage of the nominate form *vitellinus* around the Gulf of Urabá (Turbo, Necoclí, Sautata, Acandi). To the east, the yellow and green colors of the males are much paler in the populations inhabiting the Río San Jorge and lower Cauca regions *(M. v. milleri);* see Haffer & Borrero 1965, Wetmore 1959. The birds from the upper Sinú River are somewhat intermediate but still closer to *M. v. vitellinus* (Wetmore 1959).

*Manacus vitellinus* probably was differentiated in the Chocó Refuge and later met *M. manacus* and the Middle American *Manacus candei* in the lower Cauca region and in extreme eastern Costa Rica, respectively. Hybridization apparently takes place in both these areas which may be designated zones of overlap and hybridization (Short 1969). These forms are best treated as semispecies and given species status taxonomically; see Haffer (1967 a, 1974) for further dicussion and distribution maps.

*Chloropipo holochroa* litae Hellmayr **Green Manakin**

*Specimens:* Río Uva 1 ♀ (2 mm); Mutatá 1 ♀

Wetmore (1972: 325) included *C. h. suffusa* in the synonymy of *C. h. litae.*

*Sapayoa aenigma* Hartert **Broad-billed Manakin**

*Specimens:* Mutatá 1 ♀; Río Murrí 1 ♂ (8 × 4 mm); Río Cuía, western tributary of lower Río Bojayá 1 ♀; Río Uva 1 ♂ (7 × 4 mm).

This is a very distinct western Colombian isolate (monotypic genus) whose nearest Amazonian relative remains unknown. I met the Broad-billed Manakin in intermediate levels of the forest interior.

*Schiffornis turdinus* (Wied) **Thrush-like Manakin**

*Specimens: S. t. panamensis* Hellmayr: Río Salaquí 1♂, 1 ♀. *S. t. stenorhynchus* (Sclater & Salvin): Quebrada Charrura 1 ♂.

The bird from the Quebrada Charrura is paler in plumage color than a series from the middle Magdalena Valley.

## Tyrannidae

*Sayornis nigricans* (Swainson) **Black Phoebe**

*Specimens:* None.

I observed the Black Phoebe along steep rocky river banks in the forested upper Sinú Valley (Río Naín, Río Verde) and near Mutatá along the Río Sucio, where the banks form cliffs over 15 meters high (see Plate 7, Fig. 1).

*Colonia colonus leuconota* (Lafresnaye) **Long-tailed Tyrant**

*Specimens:* Río Currulao 1 ♂, 1 ♀; Río Mulatos 1 ♂; Río Imamadó 1 ♂ (2.5 × 2 mm); Mutatá 1 ♂, 1 ♀; Río Cope 1 ♂ imm.; also observed along the Río Tanela, Tulapa, Truandó, and Napipí; Quebrada Charrura 1 —; Serranía de San Jacinto (Arroyo Camaroncito 1 —; Arroyo Tigre 1 ♂; Lázaro 1 ♂; San Cristóbal 1 ♀).

The records from the Serranía de San Jacinto show that this species ranges almost to the Caribbean coast in northern Colombia. However, it is not found in the Departamento Atlántico or in the Santa Marta region.

The Long-tailed Tyrant flycatches from dead trees on recent clearings in forested areas and is fairly widespread. Skutch (1960, 1972) gave data on behavior and breeding biology.

*Fluvicola pica pica* (Boddaert) **Pied Water-Tyrant**

*Specimen:* Riosucio 1 ♂.

Haffer (1959) reported sight records of this water-tyrant, which is common in the marshes of the lower Sinú Valley and recurs in the lower Atrato Valley and in marshes along the Pacific coastal lowlands of eastern Panamá (Wetmore 1972); see Plate 6, Fig. 1.

*Arundinicola leucocephala* (L.) **White-headed Marsh-Tyrant**

*Specimens:* Tenche 1 ♀.

Observed in the marshes of the lower Cauca and Sinú Rivers as well as along the lower Río Atrato (Riosucio). Like *Chauna chavaria* and *Agelaius icterocephalus* this marsh-tyrant also reaches the western limit of its range in the extensive marshes of the lower Atrato Valley.

*Machetornis rixosus flavigularis* Todd **Cattle Tyrant**

*Specimens:* Tenche 2 ♀ (March 29 and 31).

I observed this flycatcher on open lawns at Coveñas, near the mouth of the Río Sinú, in July 1964. Recently fledged immature birds were also present at that time. Dugand (1947) stated that he found the Cattle Tyrant in Departamento Atlántico only during the months of December to April and assumed the bird leaves the area during the rest of the year.

*Muscivora tyrannus sanctaemartae* Zimmer **Fork-tailed Flycatcher**

*Specimen:* Serranía de San Jacinto (San Cristóbal 1 ♂).

*Tyrannus tyrannus* (L.) **Eastern Kingbird**

*Specimens:* Río Tolo 1 ♂ (10 March 1959); Serranía de San Jacinto (San Isidro 1 ♂, 1 ♀, September 19 and 20, 1960).

Plate 6

Fig. 1: Pied Water-Tyrant, *Fluvicola pica,* inhabits open river banks and marshes of the swampy Sinú and lower Atrato Valleys and recurs on the Pacific side of eastern Panamá. Foto J. I. Borrero.

Fig. 2: Yellow-hooded Blackbird, *Agelaius icterocephalus,* is a bird of open marshes and grass swamps ranging from the lower Atrato Valley and the Sinú River in the Tropical Zone to the lakes of the Savanna de Bogotá at 2600 m elevation. Foto J. I. Borrero.

Plate 7

Fig. 1: Black Phoebe, *Sayornis nigricans*, was occasionally observed near cliffs along forest rivers in northwestern Colombia. Foto: J. I. Borrero.

Fig. 2: Nest cavity of the Pied Puffbird, *Notharchus tectus subtectus*, in a termitary 5 m above the ground. Forest clearing in the upper Sinú Valley near Frasquillo, 10 June 1963. Foto: J. Haffer.

*Tyrannus melancholicus chloronotus* Berlepsch **Tropical Kingbird**

*Specimens:* Río Mulatos 1 ♂; Turbo 1 ♀; Sautatá 1 ♂; Unguía 1 ♂; Río Tolo 1 ♂; Tierra Alta 1 ♂; Tenche 1 ♀; Yatí 1 ♂, 1 —.

A common bird throughout the area.

*Megarhynchus pitangua pitangua* (L.) **Boat-billed Flycatcher**

*Specimens:* Serranía de San Jacinto (San Carlos 1 ♀).

*Myiodynastes maculatus difficilis* Zimmer **Streaked Flycatcher**

*Specimens:* Río Mulatos 2 ♀; Río Guadualito 3 ♂, 1 ♀; Sautatá 1 ♀; Río Tolo 1 ♂; Acandí 1 ♂; Quebrada Charrura 1 ♀; Serranía de San Jacinto (San Carlos 1 ♂; Arroyo Tigre 1 ♀).

*Myiozetetes cayanensis hellmayri* Hartert & Goodson **Rusty-margined Flycatcher**

*Specimens:* Río Mulatos 1 ♀; Río Guadualito 1 ♂, 1 —; Sautatá 2 ♂, 1 ♀; Mutatá 2 ♀; Titumate 1 ♀; Río Tanela 1 ♂.

*Myiozetetes similis columbianus* Cabanis & Heine **Social Flycatcher**

*Specimens:* Serranía de San Jacinto (San Isidro 1 ♂; Lázaro 1 ♂; Arroyo Tigre 1 ♂).

*Myiozetetes granadensis occidentalis* Zimmer **Gray-capped Flycatcher**

*Specimens:* Río Tanela 1 ♂, 1 ♀.

*Pitangus sulphuratus* (L.) **Great Kiskadee**

*Specimens: P. s. rufipennis* (Lafresnaye): Serranía de San Jacinto (Arroyo Playón 1 ♀). *P. s. caucensis* Chapman: Yatí 1 ♀.

Very common in the open northern Colombian plains, particularly in and around village gardens, but missing from forested areas; not observed in cleared areas around the Gulf of Urabá.

*Pitangus lictor panamensis* Bangs & Penard **Lesser Kiskadee**

*Specimens:* Río Guadualito 1 ♂, 1 ♀; also observed along the lower Río Truandó.

This flycatcher is found around the Gulf of Urabá but does not enter the more humid lowlands in the Chocó region.

*Attila spadiceus sclateri* Lawrence **Bright-rumped Attila**

*Specimens:* Acandí 1 ♀; Río Tulapa 1 ♀.

The characteristic call of this attila was heard at many localities around the Gulf of Urabá, where the bird is rather common, but less so in the more humid Chocó forests. The loud call is described by Chapman (in Eisenmann 1952) as a measured emphatic "*beat-it, beat-it, beat-it, no-ó-w*" and Slud (1964) transcribed it equally well with "*weétit weétit weétit weétit weeee*".

Snow (1973) accepted the transfer of the genera *Attila, Laniocera,* and *Rhytipterna* (but not *Lipaugus!)* to the Tyrannidae, near *Myiarchus.*

*Laniocera rufescens griseigula* De Schauensee **Speckled Mourner**

*Specimens:* Quebrada Charrura 1 ♀.

*Rhytipterna holerythra holerythra* (Sclater & Salvin) **Rufous Mourner**

*Specimens:* Río Tanela 1 ♀; Río Cutí (south of Río Tanela) 1 ♂; Río Salaqui 1 ♀.

Very similarly colored relatives of this species in northwestern Colombia are *Laniocera rufescens* and *Lipaugus unirufus*. All are rufous-brown, with minor differences that are hard to see in the dim light of the forest. However, the calls help to distinguish these birds in the field (Slud 1964).

The above mentioned species are strictly trans-Andean and represent the Amazonian forms *Laniocera hypopyrrha, Rhytipterna simplex* and *Lipaugus vociferans,* respectively (Fig. 13 B, C, D). The latter species also resemble each other strikingly by their unform gray plumage. It is interesting to note that, upon reaching the trans-Andean lowlands, the plumage color was changed from gray to rufous-brown in all three rather distantly related birds.

*Myiarchus crinitus* (L.) **Great-crested Flycatcher**

*Specimens:* Río Mulatos 1 ♂ (January 11); Río Guadualito 1 ♀ (February 12); Río Tanela 1 ♂ (March 7).

*Myiarchus panamensis panamensis* Lawrence **Panamanian Flycatcher**

*Specimens:* Río Tanela 1 ♂, Mutatá 1 ♀, Serranía de San Jacinto (Arroyo Camaroncito 1 ♂). This species was previously considered conspecific with *M. ferox* but W. Lanyon (in Morony et al. 1975: 168) separated *M. panamensis* specifically.

*Myiarchus venezuelensis venezuelensis* Lawrence **Venezuelan Flycatcher**

*Specimens:* Serranía de San Jacinto (Cansona 1 —). W. Lanyon (in Morony et al. 1975: 168) separated this form specifically from *M. ferox* and *M. panamensis* with which it was combined previously.

Our specimen from the Serranía de San Jacinto has the outer web of the outermost rectrix whitish-brown in contrast to the dark inner web. The remaining rectrices and the primaries are narrowly edged with cinnamon-rufous. Therefore, this individual as well as three specimens from Los Pendales, Dep. Atlántico, in the Bogotá collection are referable to *M. v. venezuelensis* (see also Haffer et al. 1965: 43). This species may be sympatric with *M. panamensis* in the Serranía de San Jacinto unless the specimen of one of these closely similar flycatchers in our collection was a migrant.

*Myiarchus tuberculifer* (Lafresnaye and d'Orbigny) **Dusky-capped Flycatcher**

*Specimens: M. t. pallidus* Zimmer & Phelps: Serranía de San Jacinto (Cansona 1 ♂, Arroyo Camaroncito 1 ♂, Lázaro 2 ♂). *M. t. brunneiceps* (Lawrence): Río Guadualito 1 ♂; Frasquillo 1 ♀; Río Salaquí 1 ♂; Río Tanela 1 ♂, 1 ♀.

The bird from the upper Sinú River (Frasquillo) is paler than specimens from the Río Tanela and the Río Guadualito near the Gulf of Urabá; it is somewhat similar to *M. t. pallidus* of northern Colombia. The male from the Río Salaquí has the crown and tail darker than in Urabá birds, the former being almost blackish brown; the back is less green thus showing an approach towards the western Colombian form *nigriceps*.

*Contopus virens virens* (L.) **Wood Pewee**

*Specimens:* Río Cope 1 ♀ (April 19).

*Empidonax virescens* (Vieillot) **Acadian Flycatcher**

*Specimens:* Sautatá 1 — (February 17, 1959).

*Empidonax traillii traillii* (Audubon) **Traill's Flycatcher**

*Specimens:* Sautatá 1 ♂ (March 21, 1959); Yatí 1 ♂ (December 4).

*Mitrephanes phaeocercus berlepschi* Hartert **Tufted Flycatcher**

*Specimens:* Mutatá 1 ♂.

The Tufted Flycatcher is widespread from Mexico south to western Ecuador. It represents *M. olivaceus* of the eastern slope of the Andes in Peru and Bolivia, which sometimes is treated as conspecific (De Schauensee 1966). *M. phaeocercus* inhabits humid subtropical forests between 4 000 and 8 000 feet in Middle America (Webster 1968). On the other hand, in western Colombia and western Ecuador, this species inhabits the tropical lowlands *(M. p. berlepschi),* where excessively humid forests may offer similar ecological conditions as the montane forests occupied in other parts of the range. In contrast to the statements by De Schauensee (1966: 355) and Haffer (1967 c: 143) the range of *M. p. berlepschi* is continuous along the Pacific lowlands of western Colombia (Webster 1968): Mungaridó, "Malugita" (probably Malaguita on the lower Río San Juán) in the central Chocó, and "La Guayancana" (i. e. La Guayacana) in southwestern Colombia, Dep. Nariño.

*Terenotriccus erythrurus fulvigularis* (Salvin & Godman) **Ruddy-tailed Flycatcher**

*Specimens:* Río Tanela 1 ♂; Sautatá 1—; Pavarandocito 1 ♂ (6 × 4 mm); Río Salaquí 1 ♂; Río Uva 1 ♂ (5 × 3 mm).

The trans-Andean populations of this widespread small forest flycatcher are separated by a wide gap from the Amazonian populations.

*Aphanotriccus audax* (Nelson) **Black-billed Flycatcher**

*Specimens:* None.

A rare northern Colombian flycatcher that extended its range into eastern Panamá (Fig. 20 D). Previously known in Colombia only from Quimarí (De Schauensee 1950 b), Carriker collected it at Socarré on the upper Río Sinú, near Santa Rosa, Colosó, and Casacará (Wetmore 1972: 487). I did not meet it in the Urabá region, although it probably does occur there.

Authors variously combined this species generically with *A. capitalis* of Nicaragua — Costa Rica or have placed it in the monotypic genus *Praedo.*

*Myiobius barbatus aureatus* Bangs **Sulphur-rumped Flycatcher**

*Specimens:* Río Imamadó 2 ♂ (7 × 3.5, 9 × 4 mm), 1 ♀ (0.5 mm); Mutatá 1 ♂, 1 ♀; Río Napipí 1 ♂ (6 × 3 mm).

This flycatcher occurs in humid forests. The trans-Andean populations are sometimes separated from the Amazonian population under the designation *M. sulphureipygius.*

*Myiobius atricaudus atricaudus* Lawrence **Black-tailed Flycatcher**

*Specimens:* Serranía de San Jacinto (Arroyo Camaroncito 1 ♂).

Similar in behavior and coloration to the preceding species. It flicks its wings like *M. barbatus* during foraging thus displaying the yellow rump. The Black-tailed Flycatcher inhabits dry to moist tropical forests in the Caribbean lowlands and is not found in the Chocó region, where *M. barbatus* occurs (the birds listed by Olivares, 1958, as *M. "atricaudus"* from Guapi actually belong to *M. barbatus aureatus).* Specimens of *M. atricaudus* taken in the dry upper Dagua Valley (De Schauensee 1948—1952) indicate that the species probably crossed over the low divide from the Cauca Valley like other forms (such as *Myiopagis viridicata, Todirostrum sylvia, Pipra erythrocephala).*

*Onychorhynchus mexicanus fraterculus* Bangs **Royal Flycatcher**

*Specimens:* Quebrada Charrura 1 ♀; Serranía de San Jacinto (San Christóbal 1 ♂, 1 ♀).

This beautiful flycatcher avoids the more humid forests in the Chocó and Urabá regions, where I did not find it.

*Platyrinchus coronatus superciliaris* Lawrence **Golden-crowned Spadebill**

*Specimens:* Río Chigorodó 1 ♂ (8 × 4 mm); Río Imamado 1 ♀ (1 mm); Mutatá 1 ♂, 1♀; Río Salaquí 1♀; Río Uva 1 ♂ (4 × 2 mm).

The bird from the Río Uva is decidedly darker on the back and breast than the other specimens from the lower Atrato region. This was already pointed out by De Schauensee (1948—1952: 838) for birds from the Río Baudó. Possibly the population inhabiting the Chocó region deserves taxonomic recognition as a more intensively colored clinal subspecies.

*Cnipodectes subbrunneus panamensis* Zimmer **Brownish Flycatcher**

*Specimens:* Pavarandocito 1 ♂ (8 × 5 mm), 1 ♂ imm.

*Tolmomyias sulphurescens* (Spix) **Yellow-olive Flycatcher**

*Specimens: T. s. exortivus* Bangs: Serraní de San Jacinto (Cansona 1 ♂, Arroyo Playón 1 ♂). *T. s. asemus* (Bangs): Río Napipí 1 ♀ (1 mm), Río Uva 1 ♀ (1 mm).

Another female bird from the Río Tanela has a light grayish breast and a whitish gray throat; the crown is gray washed with olivaceous. This bird might be referred to *T. s. flavoolivaceus.*

*Tolmomyias flaviventris* subsp. **Yellow-breasted Flycatcher**

*Specimens:* Frasquillo 1 ♀ imm.

Birds from the humid upper Sinú Valley are very close in coloration to the cis-Andean form *T. f. collingwoodi* (De Schauensee 1948—1952: 841 and 1950 b). Adult specimens are needed to establish the identity of the population inhabiting the Sinú region.

*Rhynchocyclus olivaceus bardus* (Bangs & Barbour) **Olivaceous Flycatcher**

*Specimens:* Río Tanela 1 ♀, Sitio Nuevo, upper Río San Jorge 1 ♂ (testes 9 mm long), Río Chigorodó 1 ♀ (0.5 mm), Pavarandocito 1 ♂ (7.5 × 4 mm), Río Salaquí 1 ♂, 1 ♀ (2 mm), Río Napipí 1 ♂ (7 × 4 mm). The bird from the Río Tanela was erroneously reported by Haffer (1959) as *R. brevirostris*.

See next species for comments.

*Rhynchocyclus brevirostris pacificus* (Chapman) **Eye-ringed Flycatcher**

*Specimens:* Mutatá 2 ♂, 1 ♀; Río Uva 2 ♂ (10 × 5, 10 × 6 mm), 1 ♀ (2 mm).

*R. olivaceus* and *R. brevirostris* replace each other geographically in the lowlands of northwestern Colombia but both occur in eastern Panamá where they inhabit different altitudinal zones (Fig. 44). *R. brevirostis* is found on the higher mountain ranges while *R. olivaceus* occupies the forested lowlands. Haffer (1967 b) discussed the interrelationship of these species in northwestern Colombia and suggested that the population of *R. olivaceus mirus* (De Schauensee 1950 a) from Murindó in the lower Atrato Valley might indicate local hybridization of the two species. After examining the original series of *R. o. mirus* in Philadelphia (Academy of Natural Sciences), I now believe that the Murindó population is hardly distinguishable from *R. o. bardus* of other portions of the lower Atrato Valley by a somewhat more intensive coloration of the back. However, hybridization does not seem to occur. Wetmore (1972: 517) gave further details of the parapatric distribution of these closely similar forest flycatchers. He also confirmed my suspicion (Haffer 1967 b: 355) that the old record of *R. "brevirostris"* from the Río Truandó (Cassin 1860) actually refers to *R. olivaceus*.

*Rhynchocyclus olivaceus* is a widespread Amazonian flycatcher which ranges around the northern tip of the Andes and partly occupied a peculiar gap in the range of its trans-Andean representative *R. brevirostris* (Fig. 44 B).

*Todirostrum chrysochrotaphum nigriceps* Sclater **Painted Tody-Flycatcher**

*Specimens:* Sautatá 1 ♂; Quebrada Charrura 1 ♂; Serranía de San Jacinto (Arroyo Camaroncito 1 ♂).

*Todirostrum cinereum cinereum* (L.) **Common Tody-Flycatcher**

*Specimens:* Sautatá 1 —; Río Tolo 1 ♂; Mutatá 1 ♂; Tenche 1 ♀; Yatí 1 ♂, 1 ♀.

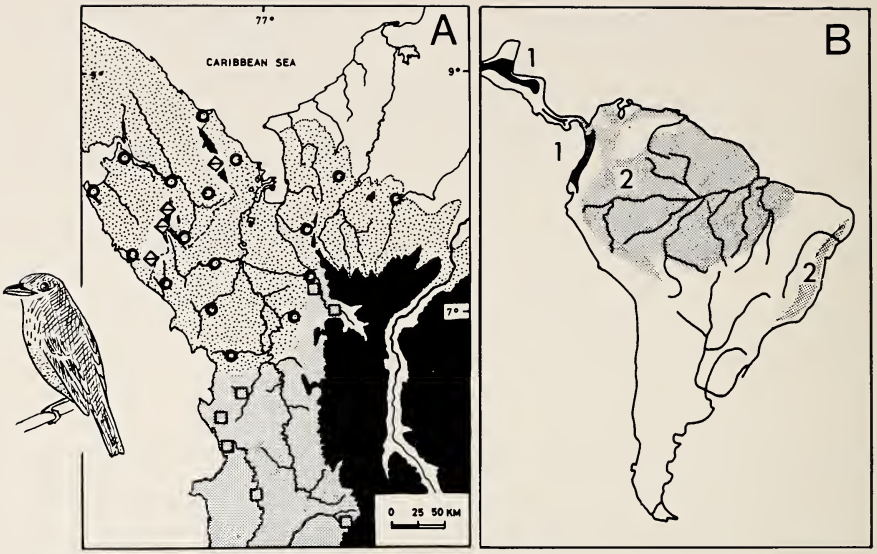


Fig. 44: Distribution of the Flat-billed Flycatchers, *Rhynchocyclus olivaceus* superspecies.

*Explanation:* **A** Distribution of *R. olivaceus and R. brevirostris* in northwestern Colombia and easternmost Panamá. Stippled area and open circles — *R. olivaceus bardus,* incl. *R. o. mirus.* Shaded area and open squares — *R. brevirostris pacificus.* Open squares on edge — *R. brevirostris hellmayri.* These olivaceous flycatchers are very similar in coloration, the trans-Andean *R. brevirostris* being darker green above and deeper yellow below than the Amazonian *R. olivaceus.* Note the occurrence of *R. brevirostris* on mountains in eastern Panamá above the lowland forest habitat occupied by *R. olivaceus.* Modified from Haffer (1967 b). **B** Generalized distribution of *R. brevirostris* (1, solid area) and *R. olivaceus* (2, shaded area).

*Todirostrum sylvia superciliare* Lawrence **Slate-headed Tody-Flycatcher**

*Specimens:* Serranía de San Jacinto (Arroyo Camaroncito 1 ♀; San Carlos 1 ♂; Arroyo Tigre 1 ♂ Palmira 1 —).

*Atalotriccus pilaris pilaris* (Cabanis) **Pale-eyed Pygmy-Tyrant**

*Specimens:* Serranía de San Jacinto (Cansona 1 ♂, 1 ♀; San Isidro 1 ♂).

This characteristic little flycatcher of northern South America occurs in thickets and dry forest near the Caribbean coast of Colombia.

*Myiornis ecaudatus atricapillus* (Lawrence) **Short-tailed Pygmy-Tyrant**

*Specimens:* Frasquillo 1 ♀ imm.

This record extends the known range of this tiny bird from the Pacific coast eastward to the upper Sinú region. The trans-Andean populations of

this species are separated from the Amazonian main range by a wide gap in northeastern Colombia and northwestern Venezuela.

*Capsiempis flaveola leucophrys* Berlepsch **Yellow Tyrannulet**

*Specimens:* Serranía de San Jacinto (San Carlos 1 ♂).

A bird of thickets in dry open portions of northern Colombia.

*Elaenia flavogaster flavogaster* (Thunberg) **Yellow-bellied Elaenia**

*Specimens:* Frasquillo 1 ♂; Tenche 1 ♀; Yatí 1 ♂.

*Camptostoma obsoletum pusillum* (Cabanis & Heine) **Southern Beardless Tyrannulet**

*Specimens:* Yatí 1 —.

*Tyranniscus chrysops chrysops* (Sclater) **Golden-faced Tyrannulet**

*Specimens:* Frasquillo 1 ♀.

Collected in the rugged hills east of the Sinú River at an elevation of about 200 meters. De Schauensee (1966, 1970) considers this tyrannulet as conspecific with the Peruvian *T. viridiflavus.*

*Tyrannulus elatus panamensis* Thayer & Bangs **Yellow-crowned Tyrannulet**

*Specimens:* Río Cope 1 ♂ (3.5 × 2.5 mm); La Balsa, 30 km southwest of Montería 1 ♂; Serranía de San Jacinto (Cansona 1 ♀; San Isidro 1 ♂; San Carlos 1 ♂).

*Leptopogon amaurocephalus diversus* Todd **Sepia-capped Flycatcher**

*Specimens:* Serranía de San Jacinto (Cansona 1 —; Arroyo Camaroncito 1—; San Carlos 1 ♂, 1 ♀).

De Schauensee (1950 b) reported specimens of this flycatcher from the upper Sinú region, which he referred to the Middle American form *L. a. faustus.*

*Mionectes olivaceus hederaceus* Bangs **Olive-striped Flycatcher**

*Specimens:* Mutatá 3 ♂.

*Pipromorpha oleaginae parca* (Bangs) **Ochre-bellied Flycatcher**

*Specimens:* Frasquillo 2 ♂ imm.; Chigorodó 1 ♂ imm.; Río Truandó 1 ♀; Río Napipí 1 ♂ (5×2 mm); Quebrada Charrura 1 ♂; Serranía de San Jacinto (Arroyo Camaroncito 1 ♂).

A fairly common and widespread species in the forests of northern Colombia.

## Hirundinidae

We observed *Tachycineta albiventris* along the upper Río Sinú, near Turbo, and along the lower Atrato River. *Stelgidopteryx ruficollis* is very

common throughout the more humid areas (Río Mulatos 1 ♂, Río Guadualito 1 ♂, 1 ♀, Serranía de San Jacinto 2 ♂, 2 ♀) and flocks of migrating *Hirundo rustica* were seen near Turbo (April) and along the lower Atrato (February). The trans-Andean swallow *Neochelidon tibialis minimus* was collected at Mutatá (1 —, imm.).

## Corvidae

*Cyanocorax affinis affinis* Pelzeln **Black-chested Jay**

*Specimens:* Río Guadualito 1 ♂, 1 ♀; Río Tolo 1 ♀; Serranía de San Jacinto (San Carlos 1 —).

This conspicuous jay is quite common on both sides of the Gulf of Urabá, where I collected specimens with pale yellow underparts, thus phenotypically intermediate between *C. a. affinis* and *zeledoni* of Panamá. I observed this bird also at clearings along the Río Napipí. Its range extends south to the Río San Juán. Birds from northern Colombia, including the Serranía de San Jacinto and the outer Guajira Peninsula (G of Fig. 45), are somewhat smaller and may be separated under the designation *C. a. sclateri* (Borrero et al. 1958, Marinkelle 1970).

The Black-chested Jay inhabits seasonal forests of northwestern Venezuela, northern Colombia and Panamá entering wet forests in the northern Chocó region and dry forests and wooded plantations near the Caribbean coast of Colombia. It forms noisy flocks of 5 to 8 birds. A typical loud call in its varied repertoire may be transcribed as *"pyou"*.

*Cyanocorax affinis* is a member of a group of allied allopatric and parapatric jays occupying a large portion of the South American lowlands (Fig. 45). The localized and widely separated Tufted Jay *(Cyanocorax dickeyi)* inhabits pine and oak forest above 4 000 feet elevation in the Sierra Madre Oriental of southwestern Mexico (Blake 1953). A common ancestor of the South American species *C. mystacalis, C. affinis* and *C. cayanus* may have reached northern Middle America when, during a somewhat drier Pleistocene climatic phase, vegetational conditions permitted the northward range expansion. It may have largely disappeared in northern Middle America possibly due to competition with newly arriving related jays (Hardy 1969 b: 364, Amadon 1944). A relict population may have been isolated and was differentiated as *C. dickeyi*.

The White-tailed Jay *(C. mystacalis)* of the dry Pacific lowlands of western Ecuador and northwestern Peru inhabits mesquite woodland, cactus steppe, deciduous forest and village gardens (Chapman 1926, Hardy 1969 a). It is isolated from *C. affinis* by the wet Chocó forest to the north and from *C. violaceus* by the Andes Mountains.


Fig. 45: Distribution of some South American jays, *Cyanocorax cayanus* species group.

*Explanation:* Restricted range in Mexico — *C. dickeyi.* Hatched vertically — *C. affinis.* Dotted circles — *C. mystacalis.* Area hatched horizontally and open triangles — *C. cayanus.* Area shaded dark and solid stars — *C. heilprini* (hei.). Stippled area and open squares — *C. violaceus* (vio; 1 *C. v. violaceus;* 2 *C. v. pallidus).* Area dashed vertically and solid circles — *C. cyanopogon.* Area shaded light and semisolid circles — *C. chrysops* (1 *C. c. chrysops,* only selected locality records shown; 2 *C. c. tucumanus;* 3 *C. c. subsp.;* 4 *C. c. insperatus;* 5 *C. c. diesingii).* For further detail and grouping of species into superspecies see text.

Brazilian Plush-crested Jay *(C. chrysops)* and White-naped Jay *(C. cyanopogon)* are similar in plumage color and form a superspecies. They differ mainly in the development of the crest (short and

plush in *chrysops* and flat-elongated in *cyanopogon)* as well as in the color of the hind neck, back, and underparts (light blue, purple-blue and yellowish, respectively, in *chrysops;* white, brown and white, respectively, in *cyanopogon).* Both species travel in bands through woodland and gallery forest along savanna rivers. They inhabit mainly the tropical lowlands south of the Amazonian forest in eastern Bolivia, Paraguay, northern Argentina and Brazil. The *chrysops* population of Tucuman, Argentinia, has been described as *C. c. tucumanus.* The birds from eastern Bolivia may also have to be separated subspecifically from the nominate form (material in Carnegie Museum; K. C. Parkes, pers. comm.). *C. chrysops* occurs in the lower Rio Madeira — Tapajóz region of southern Amazonia, where the forest is broken by more or less isolated patches of woodland savanna (cerrado) and has been reported from the following localities: Borba and Río Arapiuns *(C. c. diesingii);* Serranía de Cachimbo (Pinto et al. 1957); Río Currurú (specimens in Zool. Mus. Louisiana State Univ., Baton Rouge) and upper Río Tapajóz (Museu, Rio de Janeiro, Dr. H. Sick, pers. comm.): *C. c. insperatus.*

*Cyanocorax chrysops* and *C. cyanopogon* probably are in contact and exclude each other in southcentral Brazil [1]). However, details of their interactions along the contact zone are unknown. In the collections of the Zoological Museum, Louisiana State University, Baton Rouge, I examined a male of *C. cyanopogon* from Jacaré, upper Rio Xingú, which, in the more humid climate of the Xingú Valley, has a light bluish neck bluish mantle, and very pale yellow underparts thus somewhat resembling *C. chrysops.* Birds collected in Alagoas (I in Fig. 45) are quite variable in coloration and have been described as *C. "chrysops interpositus"* (see discussion by De Schauensee 1966: 400). However, Hardy (1969 b: 365) interpreted these specimens as "molting, worn, subadult examples of *C. cyanopogon"* (which is the species found in other parts of northeastern Brazil).

The Cayenne Jay *(Cyanocorax cayanus)* of the Guianas and northeastern Amazonia has a purplish brown mantle like *cyanopogon* and a short crest. *C. cayanus* inhabits wooded areas and broken forest reaching the lower Amazon near Manaus. It is also known from the Rio Parú (P of Fig. 45, Dr. H. Sick, pers. comm.) and Oiapoque (O of Fig. 45, Dr. F. Novaes, pers. comm.) but has not been collected around the savannas near the mouth of the Amazon. *C. cayanus* meets the Amazonian Violaceous Jay *(C. violaceus)* in southern Venezuela (lower Río Caura) and near the Kanuku Mountains of Guyana. In the latter area *C. cayanus* has been collected along the Río Takutu (spec. AMNH) and Serra Carauma (Pinto 1944). *C. violaceus* is also known from the "Kanuku Mountains" and Nappi Creek (Snyder 1966). These two species are probably still very

[1]) De Schauensee (1966: 400) included "western Paraná (rio Paracai; Porto Camargo)" in the range of *C. cyanopogon.* These records actually refer to *C. c. chrysops* (see Pinto & Camargo 1955).

similar ecologically and, despite conspicuous differences in plumage color, exclude each other geographically. *C. violaceus* inhabits large areas of upper Amazonia including the Purús Valley (Hyutanahan, spec. Carnegie Mus.; Redempção, Gyldenstolpe 1951) but has not been recorded in the Solimões or upper Río Madeira region. It may meet *C. chrysops* near the base of the Andes in eastern Bolivia.

Another localized species related to the jays discussed above is the Azure-naped Jay *(C. heilprini)* whose plumage coloration and development of stiff frontal crest is somewhat intermediate between that of largely violet blue *C. violaceus* and white and brown *C. cayanus*. In *C. heilprini* the nape is milky bluish white, the upper and underparts light violet blue shading to white on the abdomen and undertail coverts. This species is known only from southwestern Venezuela and abjacent parts of Colombia and Brazil. Published records and the extensive material in the American Museum of Natural History, New York, which I examined indicate that *C. heilprini* and *C. violaceus* have both been found at a number of localities in the upper Orinoco, Casiquiare and Guainía region, where they are in contact. However, it remains unknown whether they are also sympatric throughout the range of *heilprini* as outlined in Fig. 45. Borrero (1960) mentioned that the vocal repertoire of *C. heilprini* is very similar to that of *C. violaceus* without, however, giving any details. Hardy (1969 b: 366) believed that *C. heilprini* and *C. violaceus* were derived from *C. cayanus*, "*C. violaceus* farthest diverged and last to evolve".

The jays of the *C. cayanus* species group (Fig. 45) are closely related to one another and probably are still incompatible ecologically. For this reason they remain parapatric when in contact. All species might be considered to form only one widespread superspecies, although this broad interpretation would conceal various dissimilarities within this species group. Amadon (1944) grouped *C. violaceus* with *C. caeruleus* and *C. cyanomelas* (his „*Coronideus*" group) and combined the other jays illustrated in Fig. 45 as the „restricted *Cyanocorax* section", *C. heilprini* occupying an intermediate position between these two groups. Hardy (1969 b) combined *C. cayanus, heilprini* and *violaceus* in his Species Group II and the remaining species in his Species Group I. Short (1975) combined *C. chrysops* and *C. cyanopogon* in a superspecies but did not consider the more northern species. Pending further field studies, particularly along the various zones of contact, I would consider three superspecies in the *C. cayanus* species group as follow:

1. *Cyanocorax cayanus* superspecies: *C. cayanus, C. affinis, C. mystacalis, C. dickeyi*. Stiff frontal crest moderately to strongly developed; extensive blue to bluish white markings around the eye. Northern South America and Middle America.
2. *Cyanocorax violaceus* superspecies: *C. violaceus* and *C. heilprini*. Plumage extensively violet blue; markings around eye reduced; *C. heil-*

*prini* is somewhat intermediate between *C. cayanus* and *C. violaceus*. Forests of upper Amazonia.

3. *Cyanocorax chrysops* superspecies: *C. chrysops* and *C. cyanopogon*. Crest plush or elongated. Markings around eye conspicuous. Gallery forest and forest edge in southern and eastern South America.

## Troglodytidae

*Campylorhynchus griseus albicilius* (Bonaparte) **Bicolored Wren**

*Specimens:* Serranía de San Jacinto (Arroyo Tigre 1 ♀); Tenche 1 ♂; La Balsa (30 km southwest of Montería) 1 ♀; Río San Juán, Dep. Antioquia 1 ♀.

A common bird in the open plains of northern Colombia, where it often inhabits bushes and gardens around house sites. The species is missing in most of Middle America but a widely isolated subspecies occurs in the Pacific lowlands of Mexico *(C. g. chiapensis)*.

*Camplorhynchus albobrunneus harterti* Berlepsch **White-headed Wren**

*Specimens:* Río Tanela 1 ♂, 1 ♀; Río Napipí 1 ♀ (1 mm); Mutatá 1 ♀.

I found this forest wren nesting in a low tree next to an Indian hut with a small abandoned clearing around it in the otherwise densely forested upper Napipí Valley. Along the upper Río Tanela, west of the Gulf of Urabá, it was taken in high thickets along this forest river with no clearings or house sites nearby. Griscom's (1935: 278) inclusion of this species in the list of birds characteristic of savanna or scrub forest contradicts my experience in northwestern Colombia. To include this wren in the „Cactus Wrens" seems to be also improper. *C. albobrunneus* inhabits the humid Chocó region north to Mutatá and to the Saisa trail, where Dr. E. O. Willis (pers. comm.) observed it (Fig. 46). It has extended its range into central Panamá. In the Darién region, Dr. Wetmore (pers. comm.) reported *C. a. harterti* from Puerto Obaldía, Comarca de San Blas, and *C. a. albobrunneus* from El Real, Cana, Jaqué, and from the western base of Cerro Tacarcuna.

*C. albobrunneus* is not known to occur sympatrically with its congener *C. zonatus* which prefers less humid Moist to Dry Tropical Forests in the Caribbean lowlands of northwestern and northern Colombia, in northwestern Ecuador and in Caribbean Middle America (Fig. 46).

*Campylorhynchus zonatus imparilis* Borrero & Hernandez **Band-backed Wren**

*Specimens:* Río Mulatos 1 ♂; Serranía de San Jacinto (Arroyo Camaroncito 1 ♀; Arroyo Tigre 1 ♀; San Cristóbal 1 ♀).

This subspecies is characterized by pale cinnamon buff lower belly and flanks. The bird is fairly common in moist and dry forests; I collected it along the Río Mulatos and observed it also along the Río San Juán (Dep. Antioquia) and Río Tulapa as well as probably at the Río Zungo (Fig. 46).

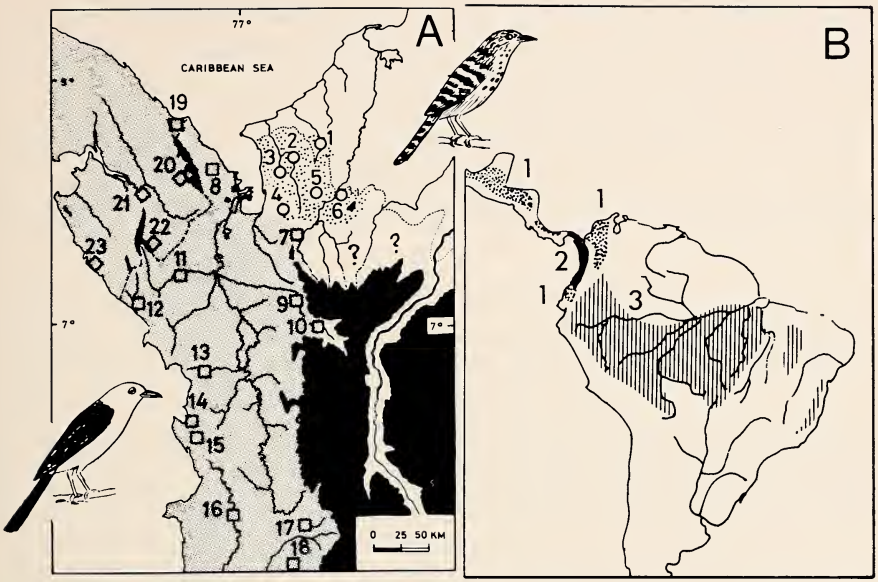


Fig. 46: Distribution of forest wrens, *Campylorhynchus zonatus, C. albobrunneus,* and *C. turdinus.*

*Explanation:* **A** Distribution of *C. zonatus* and *C. albobrunneus* in northwestern Colombia and easternmost Panamá. Stippled area and open circles — *C. zonatus imparilis.* 1 Río San Juán, Dep. Antioquia; 2 Río Mulatos; 3 Río Tulapa; 4 Río Zungo (observ.); 5 Quimarí; 6 Tierra Alta. Shaded area and open squares — *C. albobrunneus harterti.* 7 Saisa trail (E. O. Willis, observ.); 8 Río Tanela; 9 Mutatá; 10 Dabeiba; 11 Río Salaquí; 12 Río Jurado; 13 Río Napipí; 14 Bahía Solano; 15 Baudó Mountains; 16 Río Baudó; 17 Bagadó and La Vieja; 18 El Tigre and Río Tamaná; 19 Puerto Obaldía. Open squares on edge — *C. a. albobrunneus.* 20 western base of Cerro Tacarcuna; 21 El Real; 22 Cana; 23 Jaqué. Records in Darién after A. Wetmore (pers. comm.). *C. albobrunneus* is mainly white with dark brown upperparts. *C. zonatus* is barred black and white above and white with blackish spots below. Despite conspicuous color differences these species may hybridize along the contact zone in southwestern Colombia (see text). **B** Generalized distribution of *C. zonatus* (1, stippled areas); *C. albobrunneus* (2, solid area); and *C. turdinus* (3, area hatched vertically).

De Schauensee (1959) reported this form from Tierra Alta and Quimarí in the upper Sinú region. *C. zonatus* is missing in the wet forests of the Pacific lowlands and eastern Panamá (occupied by *C. albobrunneus)* but recurs in the dry forests of Middle America and northwestern Ecuador. *C. albobrunneus* and *C. zonatus* may be in contact in the forests to the southeast of Turbo and in southwestern Colombia near the Ecuadorian border. In this latter area a phenotypically very unstable population exists *(C. albobrunneus aenigmaticus* De Schauensee; 1948, 1966) which might represent a hybrid population between parapatric *C. albobrunneus* and *C. zonatus.* Based on the examination of the type series of *C. a. "aenigmati-*

*cus*", it seems to me that the strange unstable characters of this "subspecies" might be produced by introgression of *zonatus* genes rather than *turdinus* genes (as suggested by De Schauensee).

*Thryothorus fasciatoventris* (Lafresnaye) **Black-bellied Wren**

*Specimens: T. f. fasciatoventris* (Lafresnaye): Frasquillo 1 ♂ (9 mm long); Serranía de San Jacinto (Cansona 1 ♂; Arroyo Camaroncito 1 ♀). *T. f. albigularis* (Sclater): Acandí 1 ♀; Sautatá 1 ♀, 1 —.

*Thryothorus nigricapillus schottii* (Baird) **Bay Wren**

*Specimens:* Acandí 1 ♂; Río Chigorodó 1 ♂ (6×3 mm); Mutatá 1 ♂; Río Salaquí 1 ♂ (4×2.5 mm); Río Truandó 2 ♂ (4×2, 5×3 mm), 1 ♀ (1 mm); Río Uva (5×3 mm).

The Chocó form *schottii* extended its range eastward into the lower Cauca region and barely reached the forests of the humid middle Magdalena Valley (Wetmore 1959). The Panamanian forms *castaneus* and *renditus* represent two stages in the broad hybrid zone between *T. n. schottii* and *T. n. costaricensis*.

*Thryothorus thoracicus* Salvin **Stripe-throated Wren**

*Specimens: T. t. leucopogon* (Salvin & Festa): Río Chigorodó 1 ♂ (4.5×2.5 mm); Mutatá 3 ♂, 1 ♀; Río Murrí 1 ♂ (1.5×1 mm). *T. t. grisescens* Griscom: Río Tanela 1 ♂.

The specimens from the eastern side of the lower Atrato River *(leucopogon)* are darker and more brownish above than the bird from the Río Tanela. See Skutch (1972) for an account of the biology of this species.

*Thryothorus leucotis* Lafresnaye **Buff-breasted Wren**

*Specimens: T. l. galbraithii* Lawrence: Río Tanela 1 ♀; Unguía 1 —; Sautatá 1 ♀, 1 —; Río Guadualito 1 ♂. *T. l. leucotis* Lafresnaye: Serranía de San Jacinto (Arroyo Camaroncito 1 ♂, 1 ♀; Arroyo Tigre 1 ♂, 1 ♀).

Skutch (1968) published notes on the biology of this wren which inhabits thickets in fairly humid areas.

*Troglodytes aedon* Vieillot **House Wren**

*Specimens: T. a. striaticollis:* Mutatá 1 ♀. *T. a. striatulus* (Lafresnaye): Frasquillo 1 ♀. *T. a. inquietus* Baird: Sautatá 1 —, Turbo 1 ♂.

*Henicorhina leucosticta darienensis* Hellmayr **White-breasted Wood-Wren**

*Specimens:* Mutatá 3 ♂, 1 ♀, 2 — (imm.).

This wren was common in the forest near Mutatá but I never found it around the Gulf of Urabá. The cap is pure black in this series of dark-backed and rather small birds.

*Henicorhina leucophrys* subsp. **Gray-breasted Wood-Wren**

*Specimens:* Río Uva 1 ♀ (imm.).

This immature female cannot be determined subspecifically. It probably represents an undescribed form inhabiting the Baudó Mountains of western Colombia (De Schauensee 1946 a, 1948—1952).

*Microcerculus marginatus taeniatus* Salvin **Nightingale Wren**

*Specimens:* Río Uva 1 ♂ (3×2 mm), 1 —.

*Cyphorhinus phaeocephalus* Sclater **Song Wren**

*Specimens: C. p. lawrencii* (Lawrence): Río Tanela 1 —. *C. p. chocoanus* De Schauensee: Río Chigorodó 1 ♀ imm.; Río Napipí 1 ♂ (5×3 mm); Río Murrí 1 — imm.

The specimens from the northern Chocó region are not as dark as typical *chocoanus* from the central Chocó, particularly the bird from the Río Chigorodó. However, there is no trace of a grayish color indicated on the belly as is found in *lawrencii* inhabiting the area west of the Gulf of Urabá (Sautatá, Río Tanela).

## Mimidae

*Donacobius atricapillus brachypterus* Madarasz
**Black-capped Mockingthrush**

*Specimens:* Sautatá 2 —; Riosucio 1 ♂; Turbo 1 ♀.

Quite common in the marshes and nearby thickets around the Gulf of Urabá (Turbo, Sautatá) and in the lower Atrato Valley (Murindó, Riosucio).

## Sylviidae

*Microbates cinereiventris cinereiventris* (Sclater) **Half-collared Gnatwren**

*Specimens:* Río Napipí 1 ♀ (1.5 mm); Mutatá 2 ♂, 1 ♀.

## Icteridae

*Molothrus bonariensis cabanisii* Cassin **Shiny Cowbird**

*Specimens:* Sautatá 1 ♂.

A widespread and rather common bird in northwestern Colombia.

*Scaphidura oryzivora oryzivora* (Gmelin) **Giant Cowbird**

*Specimens:* Río Mulatos 1 ♂; Turbo 1 ♂.

*Zarhynchus wagleri ridgwayi* Van Rossem **Chestnut-headed Oropendola**

*Specimens:* Unguía 1 ♂; Turbo 1 ♂; Río Guadualito 1 ♂.

A common species around the Gulf of Urabá.

*Psarocolius decumanus* Pallas **Crested Oropendola**

*Specimens: P. d. melanterus* (Todd): Sautatá 1 ♀; Turbo 1♀; Río Guadualito 1 ♀; Río Mulatos 1 ♂. *P. d. decumanus* Pallas: Serranía de San Jacinto (San Cristóbal 1 ♂).

This oropendola is fairly common in northwestern Colombia.

*Psarocolius guatimozinus* (Bonaparte) **Black Oropendola**

*Specimens:* None.

I observed single individuals of this rare species east of the Gulf of Urabá (Río Naín, upper Río Apartadó, Río Currulao). In the Darién region this species has been reported from a few scattered localities (Fig. 47). Wetmore (pers. comm.) encountered it only at Pucro during his extended fieldwork in eastern Panamá.

I never met the Chestnut-mantled Oropendola *(Psarocolius cassini)* the type of which came from the Río Truandó. It is possible that the two species hybridize in the lower Atrato Valley, as De Schauensee (1966) reported an intermediate specimen from the Río Salaquí. The trans-Andean species *P. montezuma, cassini,* and *guatimozinus* represent the Amazonian *P. bifasciatus,* as discussed in more detail by Haffer (1974 b). See Skutch (1954) for an account of the biology of the Middle American *P. montezuma.*

*Cacius cela vitellinus* (Lawrence) **Yellow-rumped Cacique**

*Specimens:* None.

This cacique was common along the western side of the Gulf of Urabá (Sautatá, Rios Cutí, Arquía, and Tigre). It ranges in the Atrato Valley south to the Ríos Salaquí, Truandó, and Napipí where I have seen nest trees. A few birds were observed flying along the Río Bojayá. The species is missing in the central Chocó region but recurs in western Ecuador *(C. c. flavocrissus).* The affinities of this Ecuadorian population — whether with *vitellinus* of the Urabá region or with the nominate subspecies of the Amazonian lowlands — are uncertain (Chapman 1926).

*Cacicus uropygialis pacificus* Chapman **Scarlet-rumped Cacique**

*Specimens:* Río Imamadó 1 ♂ (12×7 mm).

*Cacicus holosericeus holosericeus* (Lichtenstein) **Yellow-billed Cacique**

*Specimens:* Upper Río Sinú, mouth of Río Naín 1 ♀ (2 mm); Serranía de San Jacinto (San Cristóbal 1 ♀; west of San Jacinto 1 ♀).

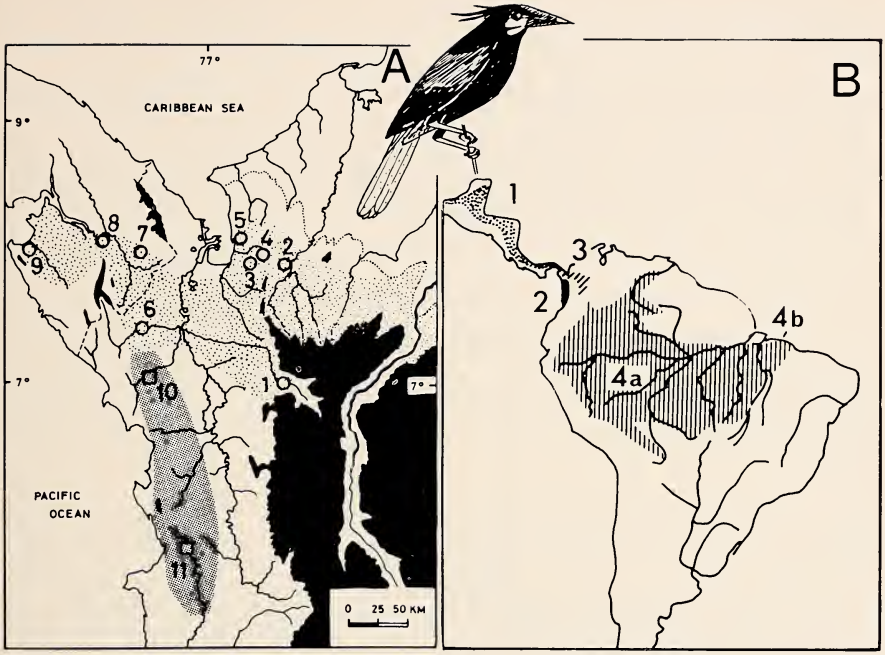


Fig. 47: Distribution of the large oropendolas, *Psarocolius bifasciatus* superspecies.

*Explanation:* **A** Distribution of *P. guatimozinus* and *P. cassini* in northwestern Colombia and easternmost Panamá. Stippled area and open circles — *P. guatimozinus.* 1 Alto Bonito; 2 Río Naín; 3 Vijagual; 4 upper Río Currulao; 5 Turbo; 6 Río Salaquí (hybrid specimen); 7 Tapalisa and Pucro; 8 El Real; 9 Río Sambú. Shaded area and open squares — *P. cassini.* 10 Río Truandó. 11 Río Baudó. The two species are similar in coloration, *P. cassini* having chestnut flanks and *P. guatimozinus* being more extensively black. **B** Generalized distribution of *P. montezuma* (1, stippled area); *P. cassini* (2, solid area); *P. guatimozinus* (3, dashed area); *P. bifasciatus* (4, area hatched vertically; 4 a *P. b. yuracares;* 4 b *P. b. bifasciatus).*

*Cassidix mexicanus peruvianus* Swainson **Great-tailed Grackle**

*Specimens:* None.

Observed along the coast near Turbo and Cartagena.

*Agelaius icterocephalus icterocephalus* (L.) **Yellow-hooded Blackbird**

*Specimens:* Sautatá 2♂, 1♀; Yatí 1♂; also observed near Turbo.

The Yellow-hooded Blackbird was known west only to the Sinú Valley but it also inhabits the marshes of the lower Atrato Valley, where it is not very common (Plate 6, Fig. 2).

*Icterus mesomelas carrikeri* Todd **Yellow-tailed Oriole**

*Specimens:* Acandí 1♀; Sautatá 2♂; Serranía de San Jacinto (Arroyo Tigre 1♀; Arroyo Playón 1♂).

*Icterus auricapillus* Cassin **Orange-crowned Oriole**

*Specimens:* Turbo 1 ♀; Serranía de San Jacinto (Cansona 1 ♀).

*Icterus nigrogularis nigrogularis* (Hahn) **Yellow Oriole**

*Specimens:* Tenche 1 —; Yatí 1 ♀.

*Icterus chrysater hondae* Chapman **Yellow-backed Oriole**

*Specimens:* Río Tanela 1 ♀, 1 —; Titumate 1 —.

*Leistes militaris* (L.) **Red-breasted Blackbird**

*Specimens:* Frasquillo 1 — imm.; Turbo 2 ♂; Mutatá 2 ♂ imm.

This open-country species entered the large clearings of the upper Sinú region from the north. It has also advanced into the Turbo area and south to Mutatá, probably following the deforested terrain along the Caribbean coast. However, it has not yet reached the western shore of the Gulf of Urabá.

## Parulidae

*Basileuterus fulvicauda semicervinus* Sclater **Buff-rumped Warbler**

*Specimens:* None.

This warbler is common along forest rivers, where it flits through drift wood and on the open sandy beaches under shady vegetation. Its buff colored uppertail coverts form a conspicuous mark.

*Basileuterus delattrii mesochrysus* Sclater **Chestnut-capped Warbler**

*Specimens:* Serranía de San Jacinto (Cansona 1 ♂, 1 —).

I found this warbler to be rather common in the coffee forest of the Serranía de San Jacinto at about 600 m elevation during the month of September 1960. The bird flits actively through the low coffee bushes near the ground. It avoids the humid Urabá forests, where I have never encountered it, and recurs on the dry Pacific slope of Middle America.

Monroe (1968) treated *B. delattrii* as conspecific with *B. rufifrons* of northern Middle Ameria. However, a zone of intergradation of these forms hat not been proven to exist (Eisenmann 1970).

I collected the following species of migratory warblers in northwestern Colombia: *Protonotaria citrea, Dendroica castanea, Seiurus noveboracensis, Oporornis philadelphia, Setophaga, ruticilla* (for dates of collection see Haffer 1959, Haffer et al. 1965).

## "Coerebidae" [1]

*Coereba flaveola caucae* Chapman **Bananaquit**

*Specimens:* Acandí 1 ♂, Río Uva 1 ♂ (4×2 mm), Serranía de San Jacinto (Arroyo Camaroncito 1 ♀).

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[1]) Regarding the composite nature of this family see De Schauensee (1966: 454).

*Cyanerpes caeruleus chocoanus* Hellmayr **Purple Honeycreeper**

*Specimens:* Río Uva 1 ♂ (6×4 mm); Mutatá 5 ♂, 3 ♀.

This widespread Amazonian species inhabits northern and western Colombia and meets its Middle American representative *C. lucidus* near the Panamanian border (Fig. 48). The fact that both species have been taken along the Río Juradó (De Schauensee 1946 b, 1948—1952) does not prove sympatric breeding. Wetmore et al. (1972) reported *C. caeruleus chocoanus* from the upper Río Jaqué, near the Pacific coast of Darién, and also from Cerro Quía, on the Colombian border southeast of Cana. The interrelationship of these closely related honeycreepers needs to be studied in detail in the field.

*Chlorophanes spiza arguta* Bangs & Barbour **Green Honeycreeper**

*Specimens:* Mutatá 2♂, 1 ♀.

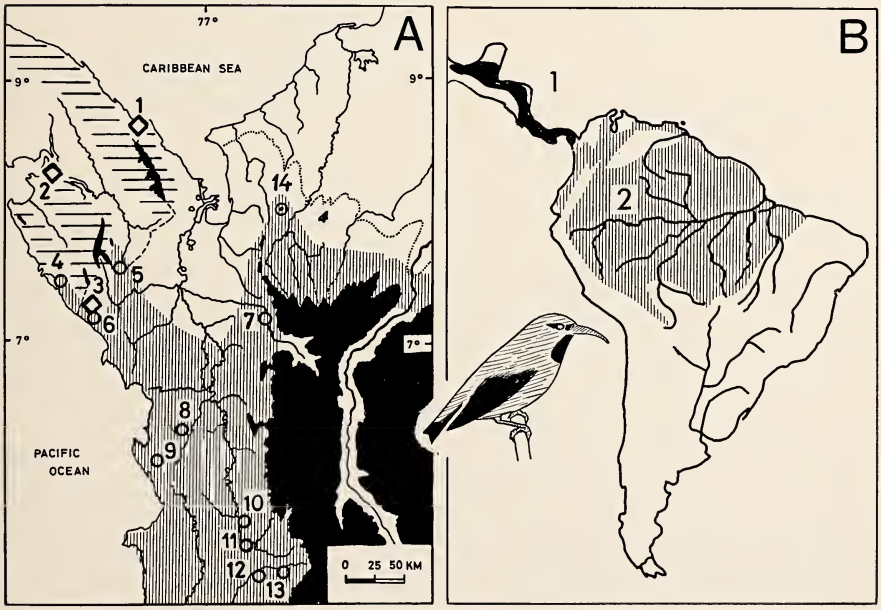


Fig. 48: Distribution of the *Cyanerpes caeruleus* superspecies.

*Explanation:* **A** Distribution of *C. caeruleus* and *C. lucidus* in northwestern Colombia and easternmost Panamá. Hatched area and open squares — *C. lucidus isthmicus:* 1 Armila; 2 Chepigana; 3 Río Juradó. Dark shading — *C. caeruleus.* Open circles — *C. c. chocoanus:* 4 upper Río Jaqué; 5 Cerro Quía; 6 Río Juradó; 7 Mutatá; 8 Río Uva; 9 Baudó Mountains; 10 Quibdó; 11 Tambo; 12 Tadó; 13 Santa Cecilia. Dotted circle — *C. c. microrhynchus:* 14 Quimarí. **B** Generalized distribution of *C. lucidus* (1, solid area) and *C. caeruleus* (2, area hatched vertically). Both species are very similar and distinguished in the field only with difficulty.

*Dacnis cayana* (L.) **Blue Dacnis**

*Specimens: D. c. napaea* Bangs: Río Cope 1 ♂ (6×5 mm), 1 ♂ imm., 1 ♀ (1 mm); Río Guadualito 1 ♂, 1 ♀. *D. c. ultramarina* Lawrence: Titumate 1 ♂. *D. c. baudoana* De Schauensee: Mutatá 1 ♂, 1 ♂ imm., 1 ♀.

The characters of these subspecies are quite conspicuous in these specimens from different portions of the northwestern Colombian lowlands around the Gulf of Urabá.

*Dacnis viguieri* Salvin & Godman **Viridian Dacnis**

*Specimens:* Río Tulapa 1 ♂.

The Viridian Dacnis is very restricted in distribution and known only from the upper Sinú region (Quimarí, Río Tulapa) to eastern Panamá (Darién) occurring on both sides of the Gulf of Urabá. Its distribution is similar to that of *Brachygalba salmoni* and *Aphanotriccus audax;* these species may have originated in the Nechí refuge.

*Dacnis venusta fuliginosa Bangs* **Scarlet-thighed Dacnis**

*Specimens:* Mutatá 4 ♂.

I found this dacnis only near Mutatá in wandering mixed bird parties during August 1966 after the breeding season. It appears to avoid the less humid forests of the Urabá region.

*Euphonia xanthogaster chocoensis* Hellmayr **Orange-bellied Euphonia**

*Specimens:* Río Uva 1 ♂ (8×5 mm), 1 ♀ (1 mm); Mutatá 3 ♂, 1 ♀.

This euphonia ranges in lower montane levels (500 to 1 700 m) along the mountains of central Colombia and southern Venezuela but is also found in portions of the Amazonian and southwestern Brazilian lowland forests (Fig. 49). It is widely distributed in the Pacific lowlands of Colombia north to the Mutatá region and, west of the Atrato River, to Cerro Pirre and El Real in easternmost Panamá (Wetmore, pers. comm.).

*Euphonia xanthogaster* is replaced along the Serranía del Darién and in western Panamá — Caribbean Costa Rica by the Tawny-capped Euphonia *(E. anneae);* males differ by a more extensive tawny-rufous (instead of yellow) crown patch and by white undertail coverts. Females of *anneae* have more tawny on the forecrown and less buffy in the abdominal region but generally are very similar to female *E. xanthogaster.* Both differ from other female euphonias by their gray nuchal collar.

*Euphonia anneae* inhabits humid forests in lower montane levels of Costa Rica and Panamá, where it clearly represents *E. xanthogaster.* This suggestion is further substantiated by the occurrence of peripheral subspecies of *E. xanthogaster* which also show a rufous crown patch. Populations inhabiting the coastal mountains of northern Venezuela as well as around Lake Maracaibo have a rufous crown patch *(E. x. exsul).* The ochraceous or orange-yellow crown patch of *E. x. brevirostris*

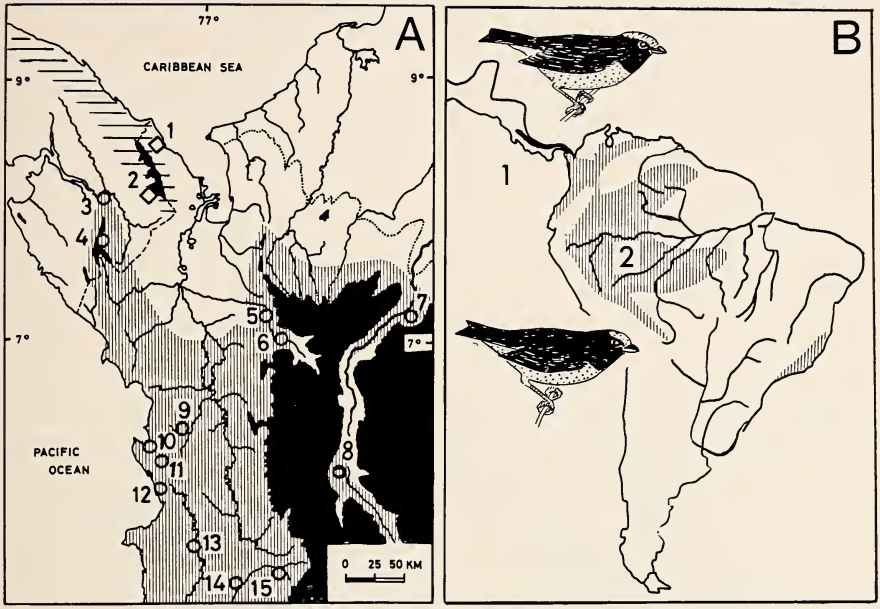


Fig. 49: Distribution of the *Euphonia xanthogaster* superspecies.

*Explanation:* **A** Distribution of *Euphonia xanthogaster* and *E. anneae* in northwestern Colombia and easternmost Panamá. Hatched area and open squares — *E. anneae rufivertex:* 1 Acandí; 2 base of Cerro Tacarcuna. Shaded area and open circles — *E. xanthogaster chocoensis:* 3 El Real; 4 Cerro Pirre; 5 Mutatá; 6 Alto Bonito; 7 La Frijolera; 8 Concordia; 9 Río Uva; 10 Bahía Solano; 11 Alto del Buey; 12 Jurubidá; 13 Río Baudó; 14 Istmina; 15 Santa Cecilia. **B** Generalized distribution of *E. anneae* (1, solid area) and *E. xanthogaster* (2, area hatched vertically).

of the eastern Andean slope of Colombia, Ecuador and Peru becomes deep ochraceous-orange in *E. x. brunneifrons* of southeastern Peru and changes clinally to rufous in *E. x. ruficeps* of eastern Bolivia.

*Euphonia fulvicrissa omissa* Hartert **Fulvous-vented Euphonia**

*Specimens:* Río Guadualito 1 ♀; Río Cope 1 ♂ (5×3.5 mm); Río Chigorodó 1 ♀ (1 mm); Río Imamadó 1 ♂ (7.5×5.5 mm); Bellavista, Río Atrato at mouth of Río Bojayá 1 ♂; Mutatá 2 ♂.

*Euphonia minuta humilis* (Cabanis) **White-vented Euphonia**

*Specimens:* Río Guadualito 1 ♂; Mutatá 1 ♂.

*Euphonia laniirostris crassirostris* Sclater **Thick-billed Euphonia**

*Specimens:* Río Mulatos 1 ♂; Frasquillo 1 ♂ (5.5×4 mm); Río Cope 2 ♀ (1 and 1.5 mm), 1 ♂ imm. (2×1 mm); Mutatá 1 ♂; Serranía de San Jacinto (Arroyo Playón 1 ♀; San Juán Nepomuceno 1 ♂).

The Thick-billed Euphonia inhabits borders of seasonal forests, second growth and gardens in fairly humid areas of northern Colombia and Panamá to Pacific Costa Rica. It avoids the wet lowlands of the Chocó region but recurs in western Ecuador *(E. l. hypoxantha)*. The upper Amazonian population *(E. l. melanura)* has a black tail; in the nominate form of eastern Bolivia and the upper Madeira Valley the inner web of the outer rectrix has a large white spot.

*Euphonia laniirostris* is replaced in eastern South America by the Violaceous Euphonia *(E. violacea)*, both allospecies forming a superspecies (Fig. 50). *E. violacea* differs from *E. laniirostris* by more extensive


Fig. 50: Distribution of the *Euphonia violacea* superspecies.

*Explanation:* Area hatched horizontally and crosses — *E. violacea;* no individual records are shown for the Guianas and for southeastern Brazil where this bird is widespread. Stippled area — *E. laniirostris;* open circles — *E. l. melanura;* half-filled circles — *E. l. laniirostris* and *E. l. zopholega.* No individual records are shown for the trans-Andean forms *E. l. crassirostris* of northern Venezuela to Costa Rica and *E. l. hypoxantha* of western Ecuador and northwestern Peru. Andes Mountains above 2000 m elevation are in black.

white marks on the two outer pairs of rectrices, by a deeper yellow forecrown reaching only the eye instead of covering the whole crown, and a shorter tail. The nest of both species it a round (domed) structure with a side entrance (Todd & Carriker 1922: 497; ffrench 1973: 405). Vocal mimicry is known among euphonias only in *E. violacea* (ffrench 1973, Snow 1974) and *E. laniirostris* (Dr. E. Eisenmann, pers. comm.).

*Euphonia violacea* is a common bird in the Guianas, in southern and eastern Venezuela and on Trinidad and meets *E. laniirostris* in Dep. Sucre, Venezuela and in the upper Orinoco Valley (see records in Phelps & Phelps, Jr. 1963). Both species occur along the lower Amazon between the mouths of the Madeira and Tapajóz Rivers, where published records indicate an overlap of their ranges. Upper Amazonian *E. laniirostris melanura* has been collected on the north bank of the Amazon at Manaus, Itacoatiara, Óbidos and Ilha Jamundá (Faro), Borba on the lower Rio Madeira, and several places along the lower Rio Tapajóz (Griscom et al. 1941, Zimmer 1943, Pinto 1944, Gyldenstolpe 1945, 1951). Detailed field studies and collecting in the area of presumed overlap of the ranges of these euphonias are needed to clarify their interrelationship. A male from Faro in the collection of the Amer. Mus. Nat. Hist., New York, has the reduced yellow forehead of *violacea* and a nearly uniform black tail like *l. melanura,* possibly indicating occasional hybridization between these species. The variable size of the white marks of the restrices of a series of *E. laniirostris* from Borba and Auará Igarapé on the right bank of the lower Rio Madeira may indicate intermediacy between *T. l. melanura* and *T. l. laniirostris* (Zimmer 1943) rather than hybridization between *E. laniirostris* and *E. violacea.* The latter species is also known from Borba.

Very few records of these euphonias are known from central Brazil, where Dr. H. Sick (pers. comm.) collected *E. violacea* along the upper Río Xingú and *E. laniirostris* at the Rio das Mortes.

*Tangara florida auriceps* Chapman **Emerald Tanager**

*Specimens:* None.

A bright emerald green bird with a golden yellow crown and conspicuous black lores and ear coverts. This attractive tanager is restricted to the wet forests covering the Pacific foothills of the Colombian Andes, where it has been reported from only a few scattered localities (Barbacoas, Río Anchicayá, and Nóvita). Although it may range along the Western Andes north to the Mutatá region approaching the Gulf of Urabá, it is so far unknown beyond the headwaters of the Río San Juán. Dr. E. Eisenmann (pers. comm.) informed me that a population 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. The nominate subspecies inhabits the foothills and wet mountain slopes on the Caribbean side of Costa Rica and western Panamá (Slud 1964).

*Tangara florida* represents the Amazonian *T. schrankii* in the trans-Andean region. Hellmayr (1936: 95) suggested that both may even be conspecific. Another close relative in this group is *Tangara johannae* which Haffer (1967 a: 45) interpreted as an earlier invasion of proto-*schrankii* stock that today is sympatric with the later arrival *T. florida* in part of its range.

F. C. Lehmann (1957) collected two specimens of *T. florida auriceps* along the Río Anchicayá (Pacific slope of Western Andes), near the road from Cali to Buenaventura. He compared these birds with *Tangara arthus* and *T. schrankii* (but not with *T. florida)* and described his specimens from the Río Anchicayá under the proposed new name *Tangara "schrankii anchicayae"* subsp. nova (Lehmann 1957; see also De Schauensee 1964: 358, 1966: 469). I suspected that this name might be a synonym of *T. florida auriceps* after comparing, in 1964, the immature male of *T. "schrankii anchicayae"* in the Cali museum with specimens of *T. f. auriceps.* The holotype of *T. "schrankii anchicayae",* an adult female, had been deposited by F. C. Lehmann with the Museum of Vertebrate Zoology, Berkeley, California several years earlier. Upon my request, Dr. Alden H. Miller (Berkeley; deceased) kindly compared the type of *T. "schrankii anchicayae"* with specimens of *T. florida auriceps* and stated (in litt., 1965): "Frankly, I can see no difference". Dr. Miller also wrote to F. C. Lehmann in August 1965 stating that *"schrankii anchicayae"* is identical with *florida auriceps.* Lehmann (pers. comm.) had intended to publish a note synonymizing these two forms (see also Haffer 1967 a, p. 46, footnote). This, however, has not yet been done; Dr. Lehmann died in 1974. I would like to thank Dr. E. O. Willis and Mr. C. O'Brien (Amer. Mus. Nat. Hist., New York) who corresponded with Dr. Miller in this matter and forwarded comparative material to Berkeley.

*Tangara johannae* (Dalmas) **Blue-whiskered Tanager**

*Specimens:* Mutatá 2♂, 1♀.

This is a typical Chocó element occupying the forests of western Ecuador and Pacific Colombia (Fig. 22 F). It had been known north only to the Baudó Mountains. Like other species it has advanced along the humid base of the Western Andes north to the Mutatá area but is not found in the Río Napipí and Río Uva regions on the opposite side of the Atrato Valley. I have never encountered this species in the Urabá region. It was seen at Mutatá along forest borders and on fruiting trees on small clearings in the forest.

*Tangara nigrocincta fanny* (Lafresnaye) **Masked Tanager**

*Specimens:* Frasquillo 1 ♂ (4×2 mm); Río Chigorodó 1 ♂ (7×5 mm); Bellavista, Río Atrato at mouth of Río Bojayá 1 ♂; Río Uva 1 ♂ (7×5 mm).

The trans-Andean forms of this common and wide ranging species are separated from the Amazonian populations by a large gap in northeastern

Colombia and Venezuela. They have been treated as separate species, *T. nigrocincta* and *T. larvata,* by several authors.

*Tangara inornata inornata* Gould **Plain-colored Tanager**

*Specimens:* Río Cope 1 ♂ (8×5 mm); Bellavista, Río Atrato at mouth of Río Bojayá 1 ♀.

These specimens were compared with *inornata* from the Magdalena Valley and *languens* from Juradó in extreme northwestern Colombia. The dark gray color of the plumage and the strongly blue forehead place my specimens closer in coloration to *inornata* than to the pale Panamanian form. This is particularly true for the male from the Cope River close to Turbo, although Hellmayr (1936: 141) reported *languens* from Turbo.

*Tangara inornata* ranges from northern Colombia with rapidly decreasing abundance through Panamá into Costa Rica (Wetmore 1963, Slud 1964). The species may have originated in the Nechí refuge.

*Tangara lavinia lavinia* (Cassin) **Rufous-winged Tanager**

*Specimens:* Río Truandó 1 ♂ (7×5.5 mm), 1 ♀ (3 mm); Mutatá 3 ♂, 2 ♀.

A characteristic trans-Andean species which ranges throughout the Pacific lowlands of western Colombia into eastern Panamá. It has rarely been recorded in central Panamá (Eisenmann 1952). On the Caribbean slope of western Panamá and Costa Rica it is restricted to "a very narrow zone following the upper tropical and lower subtropical belts" (Slud 1964). This distribution pattern is similar to that of *Formicarius nigricapillus.*

The similarly colored *Tangara gyrola* occupies a range complementary to that of *T. lavinia.* It mainly inhabits the subtropical zone of Central and South American mountains, although it is found occasionally in the lowlands of central Panamá (Eisenmann 1952). In sufficiently humid areas, *T. gyrola* ranges downward into the coastal lowlands if its presumed competitor, *T. lavinia,* is not present. This is the case in southwestern Costa Rica (Slud 1964) and in northwestern Ecuador (Chapman 1926, de Schauensee 1948—1952). *T. gyrola* occupies the lowland forests of northwestern Ecuador and extreme southwestern Colombia but ranges up into the foothills of the Western Andes, where the range of *T. lavinia* begins. Along the northwestern mountain range of Costa Rica, "*gyrola* is lacking and *lavinia* is at its greatest abundance" (Slud 1964).

*Thraupis episcopus cana* (Swainson) **Blue-gray Tanager**

*Specimens:* Río Tanela 1 ♀; Río Mulatos 1 —; Yatí 1 ♂.

*Thraupis palmarum atripennis* Todd **Palm Tanager**

*Specimens:* Juradó 1 ♂ (9×7 mm); Río Tanela 1 ♂; Río Guadualito 1 ♀; Serraniá de San Jacinto (Arroyo Camaroncito 1 ♀).

*Rhamphocelus dimidiatus dimidiatus* Lafresnaye **Crimson-backed Tanager**

*Specimens:* Sautatá, Tilupo 2♂; Frasquillo 1♀ (1.5 mm); Río Cope 1♂ (9×7 mm); Quebrada Charrura 1♂ imm.

The common trans-Andean species *R. dimidiatus* as well as *R. bresilius* of eastern Brazil and *R. melanogaster* of eastern Peru represent peripheral isolates of the wide ranging Amazonian *Ramphocelus carbo.* Possibly they have not reached full species status. Both *bresilius* and *melanogaster* hybridize freely with *R. carbo,* where they meet along narrow zones of secondary contact (Novaes 1959). *R. dimidiatus* and *R. carbo* are separated by the Eastern Cordillera of Colombia and the Mérida Andes of northwestern Venezuela (they are not in contact as shown on Novaes' map, fig. 1; 1959) and might hybridize if they were in contact.

*Ramphocelus icteronotus* Bonaparte **Yellow-rumped Tanager**

*Specimens:* Río Guadualito 1♂; Frasquilllo 1♂ (9×7 mm); Río Imamadó 1♂ (12×10 mm); Río Truandó 1 — imm.; Sautatá 1♂; Unguía 1♂; Titumate 1♂; Río Tolo 1♀; Mutatá 1♂.

The common trans-Andean form *icteronotus,* with a large yellow rump patch, hybridizes freely with *flammigerus* of the Cauca Valley (Sibley 1958). *Icteronotus* ranges along the Pacific lowlands into western Panamá and has been recorded west to Cricamola at the Chiriquí Lagoon. The exceedingly similar red-rumped species *R. passerinii* inhabits all of Middle America east to the same village of Cricamola (Peters 1931). Both species probably exclude each other geographically as a result of ecologic competition. Hybrids are not known to occur. A detailed study of these forms at the zone of contact is needed.

*Piranga rubra rubra* (L.) **Summer Tanager**

*Specimens:* Turbo 1♀ (February 4); Sautatá 1♀ (March 19); Unguía 1♀ (March 18); Río Tanela 2♂ (March 3 and 7); Río Imamadó 1♂ (April 11); Río Napipí 1♂ (March 2); Serranía de San Jacinto (Arroyo Playón 1♂, March 31; Lázaro 1♂, 1♀, February 12 and 14; Arroyo Tigre 2♀, February 17 and 22).

*Piranga olivacea olivacea* (Gmelin) **Scarlet Tanager**

*Specimens:* Río Juradó 1♂ (March 26).

*Chlorothraupis olivacea* (Cassin) **Lemon-browed Tanager**

*Specimens:* Frasquillo 1♂ (10×8 mm); Mutatá 1♂, 2♀; Río Murrí 1♂ (12×6 mm); Río Uva 1♂ (10×5 mm).

The bird from Frasquillo on the upper Sinú River is decidedly paler throughout than the more intensively colored specimens from the northern Chocó region. The olive green of the back is lighter and is washed much more with yellow on the underside. The yellow of the throat is also paler. Therefore, the population of the upper Sinú and lower Cauca regions may deserve formal taxonomic designation as a clinal subspecies.

This is a fairly common bird in the underbrush of the forests and along forests streams (Plate 5, Fig. 2).

*Habia fuscicauda erythrolaema* (Sclater) **Red-throated Ant-Tanager**

*Specimens:* Serranía de San Jacinto (Cansona 1 ♂ imm.; San Carlos 2 ♂; Arroyo Playón 1 ♂; San Cristóbal 2 ♀).

This ant-tanager is not rare in forested or densely overgrown parts of the Serranía de Jacinto. Carriker (1955) collected a single male at Colosó in the southern portion of the same range and reported a series from Turbaco in the hills to the north near the Caribbean coast (collected in 1916), suggesting this village as the type locality. Parkes (1969) compared the type specimen with Carriker's series. Rejecting Carriker's designation of Turbaco as the type locality, Parkes (l. c.) proposed Puerto Zapote (Cispatá) near the mouth of the Río Sinú as type locality, since a bird from this locality "is an almost perfect match" for the type. The series from the Serranía de San Jacinto is also very similar. Prior to the extensive deforestation in northern Colombia, *H. fuscicauda* may well have occurred in the dry forests along the Caribbean coast from the Serranía de San Jacinto to the mouth of the Río Sinú. I would assume that the forests around the Gulf of Urabá in an area of higher rainfall are too humid and dense for this species and that the distributional gap between the Colombian population *(H. f. erythrolaema)* and the Panamanian population *(H. f. willisi* Parkes 1969) is real rather than apparent. I have never encountered this species in the Urabá region. Willis (1972) published a field study of this bird.

I did not find *Habia rubica* in northwestern Colombia.

*Habia gutturalis* (Sclater) **Sooty Ant-Tanager**

*Specimens:* None

This species inhabits the forests at the northern base of the Western and Central Andes (where it possibly originated in the Nechí Refuge) and advanced southward into the humid middle Magdalena Valley (Fig. 20 F). In the upper Sinú region it has been observed near the mouth of the Río Verde (Willis 1972) and at the Río Naín (Haffer 1959). It does not reach the Gulf of Urabá. Willis (1972) has given a detailed biological account of this ant-tanager.

*Tachyphonus luctuosus panamensis* Todd **White-shouldered Tanager**

*Specimens:* Río Tanela 1 ♂; Río Imamadó (7.5×6 mm).

*Tachyphonus delattrii delattrii* Lafresnaye **Tawny-crested Tanager**

*Specimens:* Río Uva 1 ♂ (7×4 mm); Mutatá 6 ♂, 3 ♀.

This species is fairly common in the understory of the humid Chocó forests but is missing from the Urabá region.

*Heterospingus xanthopygius berliozi* Wetmore **Scarlet-browed Tanager**

*Specimens:* Mutatá 1 ♂, 1 ♂ imm.

These specimens confirm the color differences of the Chocó population compared to material from the upper Sinú region (Wetmore 1965, Haffer 1967 c). Birds from the Pacific lowlands are more intensively colored than the population along the northern base of the Western Andes (Quimarí) and in the humid middle Magdalena Valley. Specimens from the Río Juradó (Wetmore 1965) and presumably also those from the Río Truandó (Cassin 1860) are intermediate. The Scarlet-browed Tanager ranges north into eastern Panamá (Río Jaqué; El Real, 1 ♀ no. 135231 in Amer. Mus. Nat. Hist., New York), where the comparatively pale population has been referred to the nominate form by Wetmore (1965). The bird is not known from the somewhat less humid forests around the Gulf of Urabá (Fig. 51).

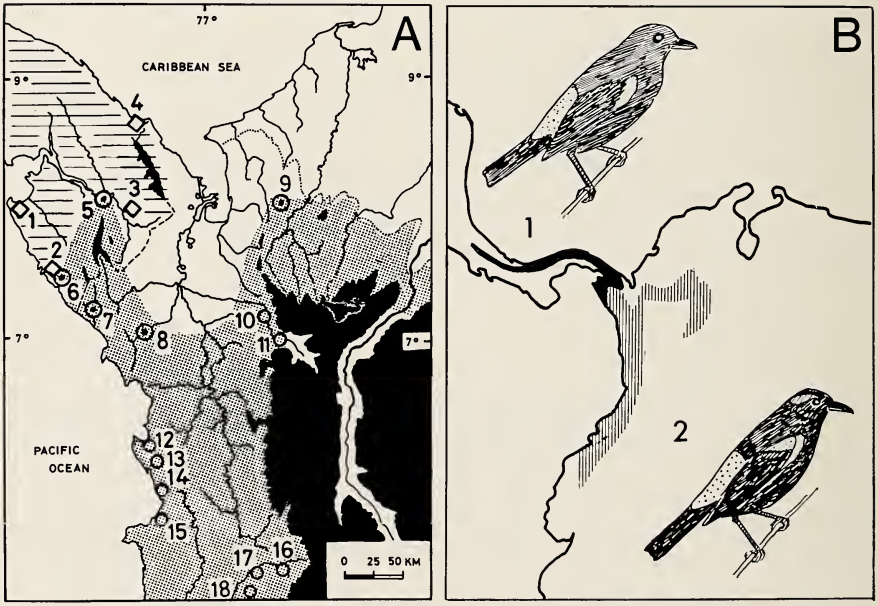


Fig. 51: Distribution of the *Heterospingus xanthopygius* superspecies.

*Explanation:* **A** Distribution *H. xanthopygius* and *H. rubrifrons* in northwestern Colombia and easternmost Panamá. Area hatched horizontally and open squares — *H. rubrifrons:* 1 Cerro Sapo; 2 Río Jaqué; 3 Pucro; 4 Obaldía. Shaded area — *H. xanthopygius:* dotted circles — *H. x. xanthopygius:* 5 El Real; 6 Río Jaqué; 7 Río Juradó; 8 Río Truandó; 9 Quimari. Open circles — *H. x. berliozi:* 10 Mutatá; 11 Alto Bonito; 12 Bahía Solano; 13 Baudó Mountains; 14 Jurubidá; 15 Nuquí; 16 Santa Cecilia; 17 Tadó; 18 Condoto. **B** Generalized distribution of *H. rubrifrons* (1, solid area) and *H. xanthopygius* (2, area hatched vertically).

The well differentiated representative of Middle America is *Heterospingus rubrifrons* which meets *H. xanthopygius* along the Río Jaqué, where Wetmore (1965 and pers. comm.) has collected both species. They are probably also in contact near El Real, where W. B. Richardson collected a female bird in 1915 that resembles others of *H. xanthopygius* in its large size and medium gray underparts (spec. in Amer. Mus. Nat. Hist., New York). It would be interesting to find out the interrelationship of these two forms which are variously treated as subspecies of *H. xanthopygius* (Hellmayr 1936) or as two distinct parapatric species (De Schauensee 1966).

*Eucometis penicillata cristata* (Du Bus) **Gray-headed Tanager**

*Specimens:* Río Tanela 1 ♂.

*Mitrospingus cassinii cassinii* (Lawrence) **Dusky-faced Tanager**

*Specimens:* Río Imamadó 1 ♂ (10×4 mm), 1 ♀ (1.5 mm); Río Truandó 2 ♂ (9×6, 9.5×6.5 mm), 1 —; Río Cuía, near Río Tanela 1 ♂; Mutatá 1 ♀.

A rather common trans-Andean species that inhabits thickets along forest borders and forest streams. Its closest relative is the restricted cis-Andean *M. oleagineus*.

*Erythrothlypis salmoni* (Sclater) **Scarlet-and-white Tanager**

*Specimens:* Mutatá 1 ♂, 1 ♂ imm., 1 ♀.

The Scarlet-and-white Tanager is a bird of the Pacific forests (Fig. 22 I). It ranges probably along the northern base of the Western Andes and may eventually be found to inhabit the region of its supposed type locality at Remedios located at the northern end of the Central Cordillera. There is not yet sufficient reason to change the type locality of *E. salmoni*, as proposed by Carriker (1955), until more collecting has been done along the northern slope of the Western and Central Cordillera of Colombia. Possibly a similar distribution pattern exists in this tanager as in other typical Chocó species such as *Trogon comptus, Dysithamnus puncticeps, Heterospingus xanthopygius*. These species range around the northern tip of the Western Andes inhabiting the humid base and foothill zone of the mountains without spreading north into the less humid lowlands.

## Fringillidae

*Saltator maximus iungens* Griscom **Buff-throated Saltator**

*Specimens:* Frasquillo 1 ♂ (10×7 mm), 1 ♀ (1 mm); Río Chigodoró 1 ♀ (2 mm); Río Napipí 1 ♂ (12×10 mm); Serranía de San Jacinto (Arroyo Playón 1 ♂, 1 ♀; Arroyo Tigre 1 ♂).

A bird of second growth thickets, forest borders and bushy pastures which is widespread in northwestern Colombia. For a detailed study of its nesting biology see Skutch (1954).

*Saltator coerulescens* Vieillot **Grayish Saltator**

*Specimens: S. c. plumbeus* Bonaparte: Serranía de San Jacinto (San Carlos 1 ♂). *S. c. subsp.:* Riosucio 1 ♂ (deposited at Acad. Nat. Sciences, Philadelphia).

The bird from the lower Atrato Valley (Riosucio) is much darker throughout than *S. c. plumbeus* of northern Colombia and has a shorter tail (96.1 mm). It "looks very much like the Costa Rican form *brevicaudus,* but is not as uniformly slate gray on the breast and shows more of a fulvous tinge below" (E. Eisenmann, pers. com.). A male and a female of this species taken by Mrs. Kerr along the lower(?) Río Atrato in 1909 and 1910, respectively, and preserved at the American Museum of Natural History, New York, "are darker than her Sinu bird, but look like another example from La Playa, near Barranquilla" (E. Eisenmann). More material from the lower Atrato Valley is needed to reach a conclusion regarding the taxonomic status this population.

The species is apparently quite rare in the Atrato Valley; only the three specimens mentioned above are known. I met the bird at Riosucio when a flock of about ten passed over a trail in partially cleared country behind the village, where I also found *Galbula r. ruficauda, Piaya minuta,* and *Bucco noanamae.*

The Atrato population of *S. coerulescens* is separated from the paler *S. c. plumbeus* of northern Colombia by the intervening forest region east of the Gulf of Urabá and from the Costa Rican populations by the entire length of Panamá and eastern Costa Rica. Possibly it represents a relict population formerly connected with the populations to the east and west and cut off rather recently by the return of a more humid climate and a corresponding growth of forests in the intervening areas. Due to the recent deforestation, *S. coerulescens* is presently advancing into the upper Sinú region where it has been observed by E. O. Willis (pers. comm.) near Tucurá and along the Río Verde.

*Saltator albicollis striatipectus* Lafresnaye **Streaked Saltator**

*Specimens:* Serranía de San Jacinto (San Carlos 1 ♂; Cansona 2 ♂).

These birds were taken in the coffee forest around Cansona at an elevation of 600 m. See Parkes (1959) for a discussion of the taxonomy of this species in northern Colombia.

*Pitylus grossus saturatus* Todd **Slate-colored Grossbeak**

*Specimens:* Río Tanela 1 ♂; Río Truandó 1 ♀ (8 mm); Río Uva 1 ♂ (10×5 mm); Mutatá 2 ♀.

*Pheucticus ludovicianus* (l.) **Rose-breasted Grossbeak**

*Specimens:* Juradó 1 ♂ (March 22); Serranía de San Jacinto (Cansona 1 — February 4; Arroyo Cacao 1 — February 5).

*Cyanocompsa cyanoides cyanoides* (Lafresnaye) **Blue-black Grossbeak**

*Specimens:* Río Tanela 1 ♂; Río Tulapa 1 ♀; Frasquillo 1 ♂ (4×3 mm); Río Chigorodó 1 ♂ (7×5 mm); Pavarandocito 1 ♀ (2 mm); Río Juradó 1 ♂ (7×4 mm).

The Blue-black Grosbeak inhabits lower levels of the forest interior and is seldom seen on clearings. Skutch (1954) prepared an account on the biology of this species.

*Passerina cyanea* (L.) **Indigo Bunting**

*Specimens:* Río Uva 1 ♂ (March 12), deposited at Acad. Nat. Sciences, Philadelphia.

This northern species usually winters south only to Panamá. Two previous records from Colombia are from Sautatá and El Dificil (Dep. Magdalena, Carriker 1954).

*Spiza americana* (Gmelin) **Dickcissel**

*Specimens:* Río Cope 1 ♂ (April 19).

*Volatinia jacarina* (L.) **Blue-black Grassquit**

*Specimens:* None.

A common bird in the grasslands of northern Colombia, where I have frequently observed the short display hop of the male during singing. Alderton (1963) studied the breeding behavior of this grassquit in Panamá

*Sporophila intermedia bogotensis* Gilliard **Gray Seedeater**

*Specimens:* Frasquillo 1 ♀ (8 and 6 mm!).

This little finch was breeding in the partially cleared hills of the upper Sinú region. De Schauensee (1948—1952) referred specimens from nearby Quimarí to *S. i. bogotensis.*

*Sporophila americana chocoana* De Schauensee **Variable Seedeater**

*Specimens:* Juradó 1 ♂ (5×4 mm); Río Guadualito 1 —; Mutatá 1 ♂.

*Sporophila minuta minuta* (L.) **Ruddy-breasted Seedeater**

*Specimens:* Acandí 1 ♀; Sautatá 1 ♂; Río Cope 1 ♂ (2.5×1.5 mm); Mutatá 1 ♂; Montería 1 ♀; Serranía de San Jacinto (San Carlos 1 ♂); Yatí 1 ♂ imm.

*Oryzoborus crassirostris occidentalis* Sclater **Large-billed Seed-Finch**

*Specimens:* Sautatá 1 ♂.

Flocks af this seed-finch were frequently seen near Sautatá. Carriker (1955) reported this species from Sautatá and Quibdó.

*Oryzoborus funereus* Sclater **Thick-billed Seed-Finch**

*Specimens:* Tierra Alta 1 ♀; also observed along the Río Naín.

*Arremon conirostris striaticeps* (Lafresnaye) **Black-striped Sparrow**

*Specimens:* Sautatá 1 ♂; Serranía de San Jacinto (Arroyo Camaroncito 1 ♂).

This northern Colombian species inhabits fairly open scrubby habitats. It is found in the lower Atrato Valley south only to Sautatá and is missing from the Chocó region but recurs in southwestern Colombia and northwestern Ecuador (Chapman 1926). Skutch (1954) and Moynihan (1963) published detailed observations of this sparrow in Central America.

*Arremon schlegeli schlegeli* Bonaparte **Golden-winged Sparrow**

*Specimens:* Serranía de San Jacinto (Cansona 2 —; San Jacinto 1 ♂).

A characteristic bird of dense thickets in the Serranía de San Jacinto but missing in forested areas.

*Arremon aurantiirostris occidentalis* Hellmayr **Orange-billed Sparrow**

*Specimens:* Río Imamadó 1 ♂ (7×5 mm), 1 ♀ (1.5 mm); Río Napipí 3 ♂ (7×4, 9×8, 9.5×7 mm), 1 ♂ imm. (2×1 mm); Río Uva 2 ♂ (5×3, 1.5×1 mm), 1 ♂ imm. (2×1 mm).

This form intergrades with the Panamanian subspecies *strictocollaris* near Sautatá and Juradó (De Schauensee 1948—1952). The population of the upper Sinú region is designated as *A. a. erythrorhynchus.*

## 12. Summary

The Urabá region of northwestern Colombia connects the isthmus of Panamá with the mainland of South America. The area is still covered extensively with dense tropical forest which, however, is rapidly being destroyed by increasing numbers of settlers entering from interior Antioquia and the lower Sinú region. Large marshes and swamps exist at the head of the Gulf of Urabá and in the broad valley of the lower Río Atrato.

The bird fauna of the Urabá region is similar to that of the adjoining lowlands of Darién (eastern Panamá) to the west and of the upper Sinú region to the east. Most species range continuously from one into the other region. However, a number of differences exist between the Urabá fauna and that of the Chocó region to the south. These differences arose due to the different climatic and ecologic conditions of the Pacific lowlands which are an area of excessive humidity.

An ornithogeographic analysis of the trans-Andean lowland forest region indicates the existence of five distribution centers *(core areas)* which probably acted as centers of faunal differentiation and dispersal: Caribbean Guatemala center; Caribbean and Pacific Costa Rica centers; Chocó center; and Nechí center. Two major regions of faunal fusion and overlap *(suture zones)* occur between the above dispersal centers and comprise Honduras—Nicaragua and Panamá-northwestern Colombia. These suture zones include clusters of zones of secondary contact of forest birds at various stages of speciation and should be studied in detail in the field. The secondary contact zones are of particular importance for an historical interpretation of faunal differentiation. Northwestern Colombia and Panamá probably were a transit area for the faunas of the more open and drier

vegetation during dry climatic periods of the past and are an important meeting place of different forest faunas today.

The main portion of this publication is an annotated list of a collection of birds made in northwestern Colombia between 1959 and 1966. The discussions contain detailed information on hybridizing subspecies and non-hybridizing allied species that meet in the Urabá region as well as on the neotropical range of several superspecies or species groups such as the *Trogon viridis* superspecies, the antbirds of the genus *Gymnopithys,* the *Cyanocorax cayanus* species group, and the *Euphonia violacea* superspecies. *Tangara "schrankii anchicayae"* is a synonym of *T. florida auriceps.*

## 13. Zusammenfassung

Avifauna von Nordwest-Columbien, Südamerika

Die Tiefländer um den Golf von Urabá in Nordwest-Columbien verbinden die Landenge von Panamá mit dem südamerikanischen Kontinent. Noch heute ist das Urabá-Gebiet weitgehend mit dichten tropischen Wäldern bedeckt, die jedoch durch die rasch anwachsende Bevölkerung in zunehmendem Maße gelichtet werden. Ausgedehnte Sümpfe erstrecken sich südlich des Golfes von Urabá im breiten Tal des unteren Río Atrato.

Die Avifauna des Urabá-Gebietes ähnelt der Fauna der Tiefländer von Ost-Panamá einerseits und der des oberen Sinú-Gebietes andererseits. Unterschiede zwischen der Urabá-Fauna und der Fauna der Chocó-Wälder des pazifischen Tieflandes von West-Columbien sind wahrscheinlich durch abweichende klimatische und ökologische Bedingungen verursacht.

Im zoogeographischen Teil der Arbeit wird die Vogelfauna der Wälder Nordwest-Columbiens analysiert als Teil der gesamten trans-andinen Regenwaldfauna, die Nordwest-Ecuador, West-Columbien und Mittelamerika bis nach Südwest-Mexiko besetzt. Fünf Verbreitungszentren *(core areas)* in diesem Gebiet werden als Differenzierungs- und Ausbreitungszentren interpretiert: das Karibische Guatemala-Zentrum; das Karibische und das Pazifische Costa-Rica-Zentrum; das Chocó-Zentrum und das Nechí-Zentrum. In zwei zoogeographisch wichtigen Kontaktgebieten *(suture zones)* zwischen den obigen Ausbreitungszentren verschmolzen und überlappten die verschiedenen Faunen bei der Ausdehnung der trans-andinen Wälder. Diese beiden Gebiete sekundärer Faunenmischung umfassen Honduras—Nicaragua einerseits und Panamá—Nordwest-Columbien andererseits. Kontaktzonen von Waldvögeln auf verschiedenen Stadien des Artbildungsprozesses sind hier gehäuft zu finden und sollten im Detail untersucht werden. Nordwest-Columbien und Panamá bildeten wahrscheinlich ein zusammenhängendes Durchgangsgebiet für die Faunen offener und trockener Vegetation während arider Klimaphasen des Pleistozän und sind heute ein wichtiges Kontaktgebiet verschiedener trans-andiner Waldfaunen und der amazonischen Waldfauna.

Im systematischen Hauptteil wird eine Balgsammlung besprochen, die der Verfasser in Nordwest-Columbien während der Jahre 1959—1966 angelegt hat. Es werden besonders solche Formen diskutiert, die in diesem Gebiet in sekundärem Kontakt stehen und entweder in ausgedehntem Maße hybridisieren („Subspezies") oder — ohne sich zu vermischen — einander in den kontinuierlichen Wäldern geographisch ausschließen, weil sie vermutlich ökologisch konkurrieren (Arten). Die Verbreitung mehrerer neotropischer Superspezies und Artengruppen wird besprochen und illustriert, z. B. die der *Trogon-viridis*-Superspezies, der Ameisenvögel der

Gattung *Gymnopithys*, der *Cyanocorax-cayanus*-Artengruppe und der *Euphonia-violacea*-Superspezies. *Tangara „schrankii anchicayae"* ist ein Synonym von *T. florida auriceps*.

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