THE ORIGIN OF THE BIRD FAUNA OF THE SOUTH VENEZUELAN HIGHLANDS

ERNST MAYR AND WILLIAM H PHELPS, JR.

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Dedicated to the memory
of
DR. WILLIAM H. PHELPS, SR.
1875–1965

Explorer, naturalist, ornithologist,
whose energy, enthusiasm, and generosity
over a period of thirty years made the
bird fauna of Venezuela the best known
in South America

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INTRODUCTION

THE AREA

THE SCHOMBURGKS, on their second expedition in 1842, discovered the presence of an endemic subtropical avifauna on Mt. Roraima, where Venezuela, Guyana, and Brazil meet. Its richness was revealed by the later work of Henry Whitely and subsequent explorers, but it was not realized until recently that this same fauna has a wide representation on other tablelands of southern Venezuela. Owing chiefly to the interest of the late Frank M. Chapman of the American Museum of Natural History, a broad program of exploration was initiated, beginning with expeditions to Roraima (1927) and Duida (1928) under the leadership of the late George H. H. Tate, and followed by a systematic exploration of previously unknown cerros by William H. Phelps, Sr., and his associates, beginning in 1937 at Auyán-tepui.

Chapman, with his keen biogeographical interests, realized at once the challenging problem of a subtropical fauna on isolated peaks and tablelands. The vast area containing these tablelands is surrounded on all sides by an unbroken expanse of tropical lowlands, separating the area by hundreds of miles from other mountain areas. How old is this fauna? How long ago and from where did it reach the mountains?

The mountains have much in common with one another, geologically and faunistically, yet there are pronounced differences. In the east, Roraima and neighboring mountains rise from much higher bases, their strata are almost level, and there is high ground between them and other similar mountainous areas in Guyana and Venezuela. In the west, the mountains rise over 6000 feet from a peneplain which is only slightly (325 feet) above sea level; their strata may be intensely folded. Between these "cornerstones" are many additional mesas, cerros, or tepuis, some closer to one another, others more isolated. A distance of 700 kilometers separates Roraima in the east and the western foot of Mt. Paraque in the west, and the greatest diameter from the north (El Negro) to the south (Cerro de la Neblina) is more than 600 kilometers. Neither of these two latter mountains is a tabletop mountain. Portions of these mountains have had collective names, such as "Guiana Highlands," the "Gran Sabana Region," and the "Sierra Pacaraima." In the geographical literature, however, no single name is available for use when one wants to refer to "the sandstone tabletop mountains in the Venezuelan Territorio Amazonas and Estado Bolívar and in the adjacent border regions of Brazil and Guyana." To avoid such cumbersome circumlocution every time the area is referred to, we have given it the artificial name "Pantepui," which is defined by the above-quoted statement. Included in Pantepui are the mountains listed below under the heading Description of the Tepuis. Faunistically to be included are the mountains on the Brazilian border, such as the Cerro de la Neblina, the Sierra Imeri, and other ranges that may differ geologically from the typical tepuis. Along the northern periphery, there are mountains that differ geologically, such as the granite mountains El Negro and Cerro Calentura. (See map 1.)

HISTORY OF ORNITHOLOGICAL EXPLORATION

Mount Roraima was the first of the tepuis to be ornithologically explored. Although discovered by Robert Schomburgk in 1838, it was not until his second expedition in 1842, when he was accompanied by his brother Richard as naturalist, that birds were collected there. According to Cabanis (1848), eight Pantepui species were secured. These included the endemic species *Campylopterus hyperythrus*, *Troglodytes rufulus*, *Myioborus castaneicapillus*, *Atlapetes personatus*, and *Diglossa major*. It was not until 41 years later that Henry Whitely revealed the richness of the indigenous avifauna of Mt. Roraima (Salvin and Godman, 1882–1884). Frederick V. McConnell and John J. Quelch visited the area in 1894 and 1898, in the latter year securing the first specimens from the summit of the mountain.

TABLE 1

DEGREE OF ORNITHOLOGICAL EXPLORATION IN THE PANTEPUI AREA

	Summit	Slopes
Mountains of Guyana	Good	Good
Roraima	Very good	Very good
Cuquenâm	—	Fair
Uei-tepui	Very good	Very good
Sororopân-tepui	Fair	Fair
Ptari-tepui	—	Very good
Auyân-tepui	Very good	Very good
Uaipân-tepui	Very good	Fair
Aprada-tepui	—	Fair
Chimantá-tepui	Poor	Fair
Acopân-tepui	—	Very poor
Upuigma-tepui	—	Very poor
Paurai-tepui	Very good	Very good
Guaiquinima	Fair	Fair
Cerro El Negro	Very good	Very good
Cerro Tabaro	Fair	Fair
Cerro Calentura	Poor	Poor
Cerro Yaví	Good	Fair
Cerro Guanay	Fair	Fair
Cerro Camani	Very poor	Very poor
Cerro Paraque (Cerro Sipapo)	Fair	Fair
Cerro Yapacana	Very good	Very good
Serranía Parú	Fair	Fair
Cerro Sarisariñama (Cerro Jáua)	Very poor	Very poor
Cerro Huachamacare	Good	Fair
Cerro Duida	Very good	Very good
Cerro de la Neblina	Good	Good

An entirely new period in the history of explorations of the area started in 1927 when Frank M. Chapman of the American Museum of Natural History organized an expedition to Roraima under the leadership of G. H. H. Tate, which brought back a magnificent collection (841 specimens). In the next year, fully 90 years after the discovery of Roraima, the first full exploration of a second tepui was undertaken. Tate led an expedition to Duida, a mountain already known to Alexander von Humboldt and other explorers in the eighteenth and nineteenth centuries who had passed up and down the Orinoco. An abortive attempt to explore Duida had been made in 1912 (Chapman, 1914) when several lowland species were discovered. On his successful expedition Tate was accompanied by the Olalla brothers (Chapman, 1931). Nine years later Auyán-tepui was explored by an expedition jointly organized by Frank M. Chapman, and William H. Phelps, Sr., of Caracas (Gilliard, 1941). This was the beginning of the period of intensive exploration of the Pantepui area by William H. Phelps, Sr., and William H. Phelps, Jr., which reached its peak in the years 1944 to 1954. Appendix: Analytical List of the Birds of Pantepui, table 1, and the Description of the Tepuis, given below, summarize the geographical and ornithological results of this exploration.

For the varying degree of ornithological exploration, see table 1.

It is evident that much can still be learned from further exploration. Cerro Jáua is still entirely unexplored. In some cases, such as Ptari-tepui, the summit area is unknown. In other cases only small collections exist, for example, Chimantá-tepui, which is an enormous tepui and presumably has a rich fauna.

ACKNOWLEDGMENTS

Work on this publication was started in 1951, but the steady addition to our knowledge induced us, again and again, to postpone completion. We are deeply indebted to many friends for their helpful cooperation and assistance. The late Dr. John T. Zimmer advised us on many aspects of avian relationship (see the Appendix). Helpful comments were received from Mr. Rodolphe M. de Schauensee (Academy of Natural Sciences of Philadelphia). Dr. Charles B. Hitchcock (American Geographical Society, New York) was immensely helpful with geographical information and the preparation of the map of the Pantepui region (map 1). Dr. Bassett Maguire (the New York Botanical Garden) and Dr. Julian S. Steyermark (Instituto Botánico, Caracas) helped with the literature, particularly the botanical bibliography, which we have added to the usual regular one. Señor Ramón Aveledo H. (Colección Ornitológica Phelps, Caracas) assisted in gathering much of the information in our lists. Señor Emilio Yamín of Caracas kindly allowed us the use of excellent photographs (pl. 15, figs. 1 and 2; pl. 17, fig. 2; pl. 18, figs. 1 and 2; pl. 19, fig. 2) as did Mrs. Kathleen D. Phelps, Caracas (pl. 17, fig. 1; pl. 20, fig. 2; pl. 21, figs. 1 and 2), and the Ministerio de Fomento, Caracas (pl. 14, figs. 1 and 2). We wish chiefly to pay tribute to the memory of Dr. William H. Phelps, Sr., who took the keenest interest in this work right up to his death and contributed much of the detailed information that is presented in the various tables and lists.

DESCRIPTION OF THE TEPUIS

The tepuis are the result of erosion of a vast pink sandstone tableland, the Roraima Formation, which covered more than a million square kilometers of the Guayana Shield (see p. 285).

Most tepuis are great isolated table mountains or mesas, about 2000 meters high, with perpendicular escarpments or vertical cliffs of pink sandstone rising abruptly above lowland savannas or forests. Their summits often appear to be flat, but many are actually strongly dissected and strewn with isolated blocks, some more than 100 meters high, and with a large variety of other rock forms, all of which make walking among them extremely difficult (pl. 18, fig. 2; pl. 19). Some summits are relatively easy to explore, whereas on others thick vegetation forms an additional impediment.

Some large tepuis, such as Auyán-tepui, Chimantá-tepui, and the unexplored Cerro Jáua, have streams on their summits which seldom go dry (pl. 18, fig. 2; pl. 20, fig. 1).

The debris of the talus consists of sandstone blocks, some very large, which have cracked off the perpendicular, and often overhanging, cliffs. Nearly everywhere these slopes are covered by a luxuriant forest, which is kept moist by clouds that form daily along the cliffs (pl. 15, fig. 1; pl. 17, figs. 1, 2; pl. 18, fig. 1). In the Pantepui area the annual rainfall averages approximately 2500 to 3500 mm., and the number of days it rains varies between 170 and 270.

There is less rain from September to March, but the seasonal difference is less marked in the southern part of the area.

During the last 50 years there have been several pronounced dry seasons when fires destroyed part of the vegetation of the tepuis (pl. 15, fig. 2; pl. 16, fig. 1; pl. 17, fig. 2). In the 1920's the slopes of Roraima, Sororopán-tepui, Auyán-tepui, and others were seriously burned as far up as the cliffs, and in 1947 the vegetation of the lower slopes of Cerro Yaví was also consumed by fire, endangering the members of the Phelps Collection expedition whose camp was in the path of the flames. Seldom do these fires start from natural causes; they are started by the Indians who, now that they can make fire easily with matches, frequently set fire to savannas to signal their presence to other Indians or sometimes merely for amusement.

The individual tepuis or other mountains mentioned in the ornithological literature are described below.

Mountains of Guyana

This locality, mentioned frequently in the last century after the explorations of Schomburgk in 1842, refers most often to Mt. Twek-quay (Salvin, 1886 [1885–1886]) and the Merumé Mountains, of typical tepui appearance, with perpendicular sandstone cliffs, and from which approximately 54 different Pantepui species are known. Additional collecting should not significantly increase this number, because these mountains, as well as others in Guyana, lack the necessary height to support many more species. There are no other mountains in Guyana as high as Roraima.

Roraima

This typical tepui, with perpendicular sandstone cliffs all around, rises to 2610 meters from a savanna area 1200 meters in elevation. The flat summit, with typical scrub vegetation, has an area of about 45 square kilometers, and the talus also has an area of 45 square kilometers (pl. 14, figs. 1, 2).

This is the most renowned of the tepuis, being the locale of A. Conan Doyle's novel "The Lost World" and the home of Rima, the heroine of W. H. Hudson's novel "Green Mansions."

It also has been ornithologically explored most thoroughly. Since Schomburgk first visited the region more than 100 years ago, many additional collections have been made there, all in Venezuelan territory (Phelps, 1938b). Seventy-six Pantepui species are represented among the 1200 specimens from Roraima in the Phelps Collection, 831 in the American Museum of Natural History and about 1000 in the British Museum (Natural History). The boundary post on the summit, near the center of the northern half, marks the point where the frontiers of Guyana, Brazil, and Venezuela meet. Only a small portion of the summit on the north, and its corresponding talus slope, are in Guyana. The talus is forested, although some of it was burned about 40 years ago.

Cuquenám

This sister tepui to Roraima, with perpendicular sandstone cliffs all around, is 2680 meters high and flat-topped like its neighbor, from which it is separated by a valley formed by the talus slopes of both mountains (pl. 14, fig. 2). Its inaccessible summit is 9 square kilometers in area, and its talus 18 square kilometers.

Henry Whitely, on one of the two occasions when he explored the Roraima area during the years 1879–1884, collected specimens of *Lepidocolaptes albolineatus*, *Lochmias nematura*, *Grallaricula nana*, and *Tangara xanthogastra* on the slopes of Cuquenám at an altitude of about 1800 meters, probably in the valley that separates the two mountains (Salvin, 1885 [1885–1886]).

Between February 22 and March 10, 1950, Manuel Castro of the Phelps Collection obtained from the talus slopes 217 specimens representing 29 species. A more complete collection would probably show an avifauna identical with that of Roraima, and, if *Zonotrichia capensis* is found on the summit, it is likely also to belong to the same population that inhabits the summit of Roraima.

Uei-tepui

The summit of Uei-tepui has an area of approximately 6 square kilometers, and a talus of 10 square kilometers.

This tepui, 2670 meters in altitude, straddles the Venezuelan-Brazilian border some 25 kilometers to the southeast of Roraima and rises from the same savanna. Only patches of the forest remain, because most of the slopes have been burned. Uei-tepui does not have the silhouette with conspicuous perpendicular cliffs that characterizes most of the other tepuis, although the sandstone is level-bedded like that of its close neighbor, Roraima.

Only one ornithological collection has been made. The Phelps Collection sent an expedition in June, 1948, which brought back from the summit and slopes 420 specimens representing 52 different species of the Pantepui avifauna. This collection may be considered an adequate sample. Of the birds taken on the Brazilian side of the frontier, near the boundary, 49 species and subspecies were new to that country.

Sororopán-tepui

This tepui rises to 2500 meters from a savana and forest area that is approximately 1200 meters in altitude (pl. 16, fig. 1). It is contiguous to Ptari-tepui, the connection between them being at approximately the same altitude, 1800 meters, as that between Roraima and Cuquenám. The summit has an area of 7 square kilometers and, with the inclusion of the talus, one of 14 square kilometers.

Fire destroyed much of the vegetation of the southern slopes about 40 years ago. Ptari-tepui was saved from this disaster because the fire came from the savannas on the east and south, consuming the forest cover to the summit of Sororopán-tepui, where it died out, thus leaving intact the entire talus vegetation of Ptari-tepui.

The Phelps Collection sent an expedition in August, 1950, which brought back from the summit and slopes 127 specimens representing 40 different species of Pantepui birds. Most of the species from Ptari-tepui not yet collected on Sororopán-tepui undoubtedly will be found there also, when a more complete collection is made. If these two mountains are considered as one single tepui, with two summits, then it can be said that an adequate sample has been obtained.

Ptari-tepui

This is one of the highest tepuis, 2620 meters, with a small flat summit area of only 5 square kilometers and, together with the talus, one of 14 square kilometers. The summit is inaccessible; its vertical, and in places overhanging, cliffs are continuous on its four almost equal sides (pl. 16, fig. 2).

Its vegetation is intact because the fire which consumed much of the forest cover of Sororopán-tepui did not reach it. Collections were made mostly near the camp established for the purpose, on the south side near the base of the wall, and also on the saddle between this tepui and Sororopán-tepui. Three expeditions were made by the Phelps Collection in 1944, and 844 specimens were collected, representing 71 species. This sample is adequate and indicates the presence of a varied avifauna.

The summit area should be visited by helicopter.

Auyán-tepui

This is one of the largest tepuis, with a summit area of 700 square kilometers and a talus area of 200 square kilometers. Its maximum altitude of 2500 meters is at the southern end; the Phelps Auyán-tepui Expedition of the American Museum of Natural History reached the summit in 1938 (pl. 17, figs. 1, 2; pl. 18, fig. 1).

This is a typical tepui with a flat-topped appearance and perpendicular sandstone cliffs all around. The summit, dissected by deep crevices, has swamps, streams, and forested valleys, as well as low vegetation on other parts that have sufficient humus (pl. 18, fig. 2; pl. 19, figs. 1, 2). Near the northern part of the mountain is Angel Falls, with a free fall of 809 meters, the highest in the world.

In a total collection of 1217 specimens taken from an elevation of 1100 meters to the summit, 448 specimens representing 59 species of Pantepui birds were collected on the talus slopes and on the summit. This sample can be considered adequate.

Uaipán-tepui

This small tepui, with a summit area of 4 square kilometers and a talus of 9 square kilometers, has an altitude of 1950 meters. It is about 15 kilometers south of Auyán-tepui.

The cliffs do not go all the way around this tepui. Several steep slopes facilitate access to the summit area, which is completely covered by low vegetation and the usual *Bonnettia* trees. Most of the talus is forested and has not been burned.

Of the 331 specimens from the talus and summit, representing 47 Pantepui species, 55 were collected by Félix Cardona in November, 1946; the remainder, by an expedition of the Phelps Collection in January–February, 1948. This sample can be considered adequate.

Aprada-tepui

No collections have been made on the summit of this tepui, which is 2400 meters in height and almost entirely surrounded by perpendicular cliffs. The summit is approximately 7 square kilometers in area; the talus covers about 54 square kilometers.

Two collections were made in the extensive, densely forested northwestern slopes as far up as the base of the cliffs. Félix Cardona in November, 1946, obtained 29 specimens, and an expedition of the Phelps

Collection in February–March, 1948, obtained 422, making a total of 451 specimens representing 51 species. This collection is an adequate sample from the talus up to the cliffs.

CHIMANTÁ-TEPUI AND ACOPÁN-TEPUI

The summit of this, one of the largest tepuis, is surrounded by perpendicular sandstone cliffs and appears flat. Its area is 730 square kilometers and that of its talus about 740.

The Indians living in the lowland savannas around Chimantá-tepui have given names to many different cliff areas as seen from their villages. The Chimantá cliffs on the western side are 2000 meters high, and the Acopán cliffs on the eastern side have an elevation of 1800 meters. Both names refer to what is basically a single widely extended tepui.

From the eastern part, on the talus below the cliffs, Félix Cardona took a total of 139 specimens for the Phelps Collection in October, 1947, of which 88 are Pantepui birds representing 30 species. From the western part a Phelps Collection expedition in June and July of 1946 brought 919 specimens, of which 450 were Pantepui birds taken on the talus and on the summit, and representing 52 different species, thereby raising to 59 the number of known Pantepui birds from this mountain.

This extensive tepui, with intact, unburned talus slopes, varied summit vegetation, and upland streams should be ornithologically explored more thoroughly.

UPUIGMA-TEPUI

This tepui, 2200 meters in elevation, is south of Acopán and rises from a savanna region, which itself is at an elevation of 1000 meters. The cliff area, which surmounts the talus slopes, has the shape of a thick isolated wall (pl. 15, figs. 1, 2). The actual summit probably has an area of not more than 3 square kilometers; the area of the talus is probably about 7 square kilometers.

Periodic burning by the Indians has left only sparse vegetation on most of the slopes, which has in turn undoubtedly reduced the number of species of birds to be found there at the present time.

Félix Cardona in October, 1947, collected 13 specimens of Pantepui birds representing five species. As a sample this total is inadequate. The summit appears to be inaccessible to man.

PAURAI-TEPUI

Of this tepui, the summit area, which is not flat-topped, covers some 12 square kilometers; its talus area, 18 square kilometers. This tepui rises to 1250 meters from forest-covered hills approximately 800 meters in elevation.

Only one ornithological collection has been made. The Phelps Collection sent an expedition in October–November of 1945, which brought back 124 specimens representing 20 different Pantepui species from the slopes between 860 and 1250 meters in altitude.

More thorough collecting in Paurai-tepui would undoubtedly add more Pantepui species to the locality, but such additional species are likely to be the same as those of the Mountains of Guyana (see above), which are similar to Paurai-tepui in height and in ecological conditions.

GUAIQUINIMA

The summit of Guaiquinima is not so flat as the summits of the more typical tepuis to the east, in the Gran Sabana region. Its highest point has an altitude of about 1800 meters. This is one of the largest mountains, having a summit area of 330 square kilometers and a talus area of 110 square kilometers. On the western side it rises steeply from the forested lowlands of the Paragua River, its sandstone cliffs surrounding a considerable part of the summit.

Shortly before a Phelps Collection expedition went to Guaiquinima in January and February of 1945, Félix Cardona had made a small collection of its subtropical birds which indicated the great interest of that avifauna. Altogether, more than 500 specimens of Pantepui birds have been taken on the subtropical slopes and the summit, representing 38 different species, which may be considered an adequate sample.

CERRO EL NEGRO

This is not at all a sandstone tepui with perpendicular cliffs; rather it is a small granite mountain, 1200 meters high, with a summit area of 3 or 4 square kilometers. It is situated in the lowland forested area of the upper reaches of the Cuchivero River in the northwest part of the state of Bolívar.

The only specimens known from the mountain were collected in November and December of 1947 by Manuel Castro for the Phelps Collection. Of these, 66 belong to 17 Pantepui species. This number we consider is an adequate sample.

Cerro Tabaro

This is not a sandstone tepui; it is the name of one of the ridges along the higher parts of a densely forested mountainous area, situated to the east of Cerro El Negro, near the headwaters of the Río Nichare.

The elevations noted on the 147 specimens that were collected during nine days in February of 1957 by Ramón Urbano for the Phelps Collection vary between 920 and 1070 meters. Of the total collected, 102 specimens belong to 29 Pantepui species. We do not consider these an adequate sample.

Cerro Calentura

The conical silhouette of this granitic mountain separates it immediately from the "tepuis." The slopes are forested to its summit area which is probably not more than 1 square kilometer or 2 square kilometers in extent and approximately 1800 meters at the highest part. The upper slopes may have an area of not more than 8 or 10 square kilometers.

In February, 1962, Félix Cardona obtained for the Phelps Collection 24 specimens, representing 16 species of Pantepui birds. A more complete collection would be of interest, although Cardona reported that birds were very scarce because of the lack of water on the upper slopes.

Cerro Yaví

This sandstone tepui is situated in the northern part of the Territorio Amazonas near the headwaters of the Río Parucito, an affluent of the Río Ventuari. It has a summit area of 14 square kilometers and 18 square kilometers of talus slopes. Its small size is offset by the dramatic silhouette. Characteristic features of this tepui are its square form and the varied vegetation of its summit, with vertical cliffs, and its altitude of 2285 meters, rising steeply on the eastern side from the Parucito savannas below, only 200 meters above sea level.

In February, 1947, a Phelps expedition made the only collection on the thickly forested and humid eastern talus and the summit. Of the 614 specimens obtained, 344 were of the Pantepui avifauna, representing 41 different species, which may be considered an adequate sampling.

Cerro Guanay

This sandstone mountain has an altitude of approximately 2000 meters, with a summit area of 125 square kilometers and a talus area of 85 square kilometers. It is situated in the northern part of the Territorio Amazonas, to the west of Cerro Yaví. It is less forested and drier than its neighbors to the south and east such as Cerro Camani and Yaví; consequently fewer species inhabit its summit and slopes.

A Phelps Collection expedition, in January and February of 1951, obtained 148 specimens representing 17 species, from the summit and southern talus slopes. It is possible that collections made on the other sides of the mountain where it is more forested would increase the number of known species. However, the fact that the expedition obtained only 17 different Pantepui species in about 30 man days of collecting indicates that this poverty is due not to inadequate sampling, but rather to the ecological conditions.

Cerro Camani

This sandstone mountain, situated near Cerro Yaví, has a rounded silhouette. Its summit has an area of only about 3 square kilometers; its steep slopes, one of about 8 square kilometers. It is entirely covered with vegetation on its sides and summit. A Phelps Collection expedition in February, 1951, spent four days on the very humid upper slopes and on the summit, making a very small collection. This sample of 53 specimens, representing 17 species, is not adequate, and a more complete collection should double the number of known species.

Cerro Paraque (Cerro Sipapo)

This sandstone mountain is 1800 meters

high and is situated near Puerto Ayacucho, the capital of the Territorio Amazonas. It has a summit area of 95 square kilometers and a talus of 55 square kilometers. Its summit and slopes, with many vertical cliffs characteristic of the tepuis, are covered with luxuriant vegetation (pl. 20, fig. 1). It is the westernmost of all the tepuis, being only about 500 kilometers from the Andes of Colombia.

The only ornithological collection was made in February, 1946. Among the 643 specimens taken for the Phelps Collection from the mountain and its environs, 347 from the summit and slopes represent 38 different Pantepui species; these may be considered an adequate sampling.

Cerro Yapacana

With an altitude of only 1200 meters, this mountain is not a typical tepui. It rises directly from the densely forested shores of the Orinoco River, about 130 kilometers west of Cerro Duida. Its summit area is approximately 3 square kilometers, and its slopes near the summit are about 5 square kilometers. In April, 1947, an adequate collection of 94 specimens was made, of which 55 represented 10 species of the Pantepui list.

Serranía Parú

The Serranía Parú, or Asisa, in the northern part of the Territorio Amazonas, 1600 meters in altitude, is situated about 130 kilometers south of Cerro Yaví and 150 kilometers west of Cerro Jáua. This mountain range has sandstone cliffs, but, like most of the tepuis of the western part of the Pantepui area, the summit is not typically flat and easily delimited, nor are the talus slopes so uniform as those of the eastern part (pl. 20, fig. 2). Serranía Parú has a "summit" area of some 400 square kilometers and a talus area of 300 square kilometers.

A Phelps Collection expedition in February, 1949, reached the summit area from the western side where the mountain rises steeply from the lowland savannas in the headwaters of the Parú and Asisa rivers. The collection, made on the western slopes and on the summit area, consisted of 323 Pantepui specimens, representing 40 different species. This sample may be considered adequate, but such an extensive mountain range should be explored more thoroughly.

Cerro Sarisariñama (Cerro Jáua)

Sarisariñama is the Indian name for one of the prominent features on the southern end of Cerro Jáua, an extensive sandstone table mountain which occupies the area between the upper reaches of the Erebato River and the upper Caura River. This tepui has a summit area of 350 square kilometers and a talus area of 120 square kilometers. The highest point of Jáua is about 2200 meters.

The only specimens from this mountain were collected by Félix Cardona in 1942 when he ascended the southern part at Sarisariñama and took 25 specimens representing nine species of Pantepui birds. This is one of the few important tepuis that remains to be explored.

Cerro Huachamacare

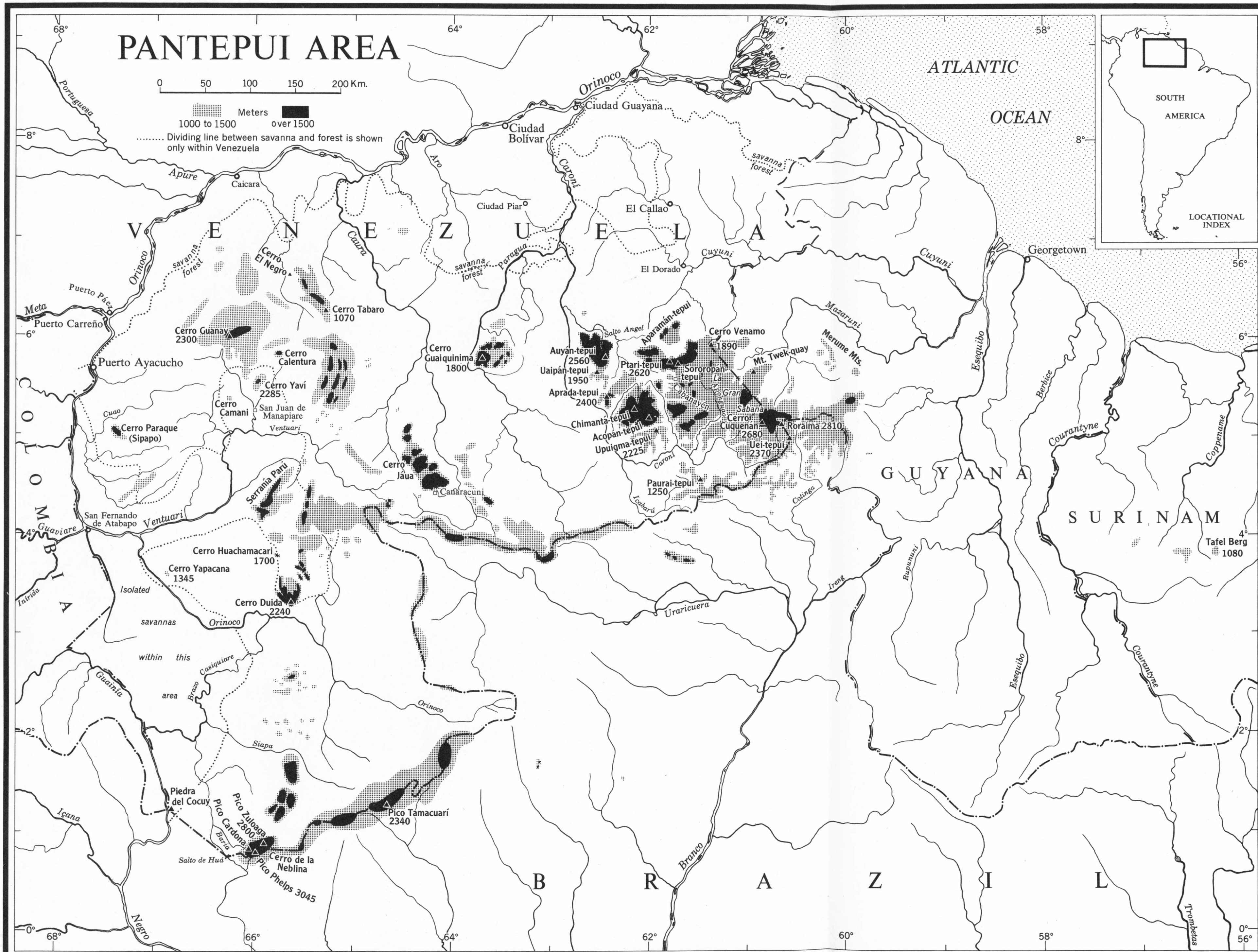
This typical tabletop tepui, situated 56 kilometers to the north of Cerro Duida, has an altitude of 1700 meters. Its summit and talus areas are approximately the same as those of Roraima. It rises from lowlands which, except for occasional savannas, are densely forested.

Dr. Bassett Maguire, Head Curator of the New York Botanical Garden, kindly permitted R. Urbano, taxidermist of the Phelps Collection, to join him and his colleagues during their botanical explorations of Cerros Duida and Huachamacare in November and December of 1950. One hundred fifty-nine specimens of birds were collected on the summit and slopes of Huachamacare, representing 18 different species. Such a total may be considered a fairly adequate sample.

Cerro Duida

The summit area of this steep-sided sandstone tepui is approximately 400 square kilometers, with a talus area of about 130 square kilometers.

This is one of the best-studied mountains of Pantepui because of the thorough exploration made by the Tyler Duida Expedition of the American Museum of Natural History in 1928–1929. This expedition was headed by G. H. H. Tate of the Department of Mammalogy, who was accompanied by Charles



PREPARED BY THE AMERICAN GEOGRAPHICAL SOCIETY 1967

MAP 1. Area of Pantepui.

B. Hitchcock of the American Geographical Society (recently retired as its Director), as topographer and geologist. Frank M. Chapman wrote of the expedition: "The conquest of Mt. Duida and the making of large zoological and botanical collections, and topographic studies, called for an exhibition of resourcefulness which should give this expedition a high place in the annals of natural history exploration" (Chapman, 1931, p. 16).

This expedition collected 1165 ornithological specimens from above approximately 1000 meters, of which about 800 are Pantepui birds representing 52 different species.

In November, 1950, 197 specimens of Pantepui birds were collected in Mt. Duida for the Phelps Collection representing 38 species, none of which was new to the known Duida avifauna, a fact that confirms the adequacy of the American Museum collection.

Cerro de la Neblina

The summit of this mountain has an area of about 600 square kilometers; the talus, an area of 150 square kilometers.

This great isolated tepui, situated at the extreme southwestern end of Pantepui, is the highest mountain in Venezuela outside the Western Andes. Since the Venezuelan-Brazilian boundary line following the height of land dividing the Orinoco-Casiquiare watershed from that of the Amazon passes 600 meters north of the highest peak (Pico Phelps, approximately 3045 meters), the Cerro de la Neblina is also the highest mountain in Brazil.

Cerro de la Neblina rises from a vast inundated forest area to the north and west and from forested lowlands on the south and east (pl. 21, fig. 1). To the north, and to the east along the boundary, are a series of sandstone tepuis, similar to Neblina but lower.

The vegetation of Neblina is still intact. From a distance, views of this mountain combine characteristic tepui cliffs, steep slopes, and valleys which correspond on the summit to level areas, very rugged peaks, and a valley of such proportions that Bassett Maguire and John J. Wurdack (1959) considered it "one of the world's greatest canyons, rivaling any of the grand canyons of the United States in total relief" (pl. 21, fig. 2).

Only one ornithological collection has been made. A Phelps Collection expedition, in February, 1954, joined a New York Botanical Garden expedition headed by Bassett Maguire (Maguire, 1955), which had opened a trail to the summit, where it had established a camp. Collections were made on the summit and slopes, and 350 specimens were taken, representing 38 different species of the Pantepui avifauna.

Although such a sample is a fairly adequate one, more thorough investigations should be made.

THE BIRD FAUNA OF PANTEPUI

More than 25 tepuis have been studied more or less intensely, and as a result the bird fauna of these mountains can be considered as reasonably well known. To be sure, some of the mountains or ranges, such as Acopán-tepui, Cerro Jáua, as well as the Sierra Imeri, are still either totally unexplored or at least insufficiently collected. No doubt a number of new subspecies are still to be discovered on the already explored or as yet unexplored mountains, possibly even a new species or two. Yet it can be stated with assurance that these future additions to the fauna of Pantepui will not modify our picture of this fauna to any major extent. There is no reason for postponing a zoogeographical analysis.

Two aspects characterize this bird fauna: the considerable number of endemic elements and the striking difference of this (subtropical) fauna from that of the surrounding tropical lowlands. Even though the bird fauna of Pantepui is far less distinct than the flora, it is sufficiently striking to have induced numerous speculations concerning its place of origin. Before these speculations can be tested, it is necessary to establish the relevant facts.

We have tabulated in the Appendix all those species that are either absent from the lowlands or have formed endemics on one or more of the tepuis. These total 96 species. We have not included tropical species with a wide altitudinal range and which (although occurring both in the adjacent lowlands and at higher altitudes on Pantepui) have failed to form endemics at the higher altitudes (see below). The 96 species counted are "zoogeographical species." If different species form a superspecies, such as *Myioborus brunniceps*, the superspecies is counted as a single species.

The choice of the species to be classified as subtropical is inevitably somewhat arbitrary. *Veniliornis kirkii*, for instance, is restricted on Pantepui to an altitude between 1500 and 1720 meters, yet occurs on the north coast at tropical altitudes (sea level to 500 meters). *Phaethornis bourcieri*, *Elaenia ruficeps*, and *Tangara gyrola* are elsewhere widespread in the tropics, but occur (subspecifically identical) at subtropical altitudes on Pantepui. They were included here because on Pantepui they are part of the subtropical avifauna and are more or less widely separated from the nearest tropical portion of the range. These species also demonstrate very convincingly the altitudinal flexibility of many avian species.

A certain degree of arbitrariness has been unavoidable throughout the analysis. No absolute decision as to altitudinal classification has been possible in the case of species that occur at both tropical and subtropical altitudes. In some cases different Pantepui populations are sufficiently dissimilar (e.g., endemic versus non-endemic) to require classification in different categories. The numbers in the lists and the percentages should not be considered final and absolute; they are merely judicious approximations. We believe, however, that whatever changes may eventually be made will not affect our basic conclusions.

SIZE OF PANTEPUI

The area in which the tepuis and mountains of Pantepui (see map 1) are found extends from the upper Orinoco in the west to the Río Esequibo in the east, a distance of almost 1000 kilometers. The north-south extension in the west (from Cerro El Negro to Cerro de la Neblina) is about 650 kilometers, whereas in the east the width of the highlands is less than 200 kilometers. In the absence of detailed maps of parts of the area (particularly the southern part), it is difficult to estimate the size of the area above 1000 meters in elevation, but it may well exceed 80,000 square kilometers.

Within this large area only a fraction of the terrain is suitable for a subtropical avifauna. This fact is well demonstrated by the measurements of the summit and talus areas (kindly made by Mr. W. Briesemeister on the basis of the most recent maps) which are given above in the descriptions of the various tepuis. The 18 mountains that were measured occupy only 5000 square kilometers, yet consist of the greater portion of the Venezuelan share of Pantepui. The total area (including Guyana and Brazil) above 1500 meters presumably does not exceed 10,000 square kilometers.

ECOLOGY, CLIMATE, AND GEOLOGY

An interpretation of the faunal history will be aided by a presentation of the essential facts on the ecology and geology of the region.

Ecological Conditions

The peculiar ecological conditions on the table mountains of Pantepui have been described by Tate (1930a, 1938a, 1939a), Tate and Hitchcock (1930), Chapman (1931, 1939b), Gilliard (1941), Hitchcock (1947), Maguire (1955), and others. They are caused by a combination of high humidity and the thinness in many places of the humus layer. The high humidity is their outstanding characteristic. On the tepuis cloud banks hide portions of the higher altitudes most of the time. The eastern tepuis either rise directly from (Ptari-tepui) or are in contact with largely forested highlands which stretch from Venezuela (Sierra de Lema) to the Guianas. The western tepuis rise from lowland forest (in some places intermixed with savanna), quite unsuited for a mountain avifauna. In the extreme south, the Cerro de la Neblina rises from a vast forest which is flooded on the northern and western sides. The tepuis are thus, ecologically speaking, islands of cool, humid, mountain forest in a sea of tropical lowlands. Some areas on the peaks have so little humus that forest is in part replaced by a distinct scrub vegetation, analogous in some respects to the temperate vegetation of the Andes and attracting a few species (such as *Catamenia*, *Campylopterus*, and *Troglodytes*) of that Andean zone.

Many of the tepuis tower over the surrounding terrain like medieval fortresses. The student of distributions is inclined to assume that the characteristic Pantepui elements are confined to the tops of the tepuis. Actually not a single one of the 30 endemic Pantepui species is restricted to the summit plateaus. They are all found also on the talus slopes. Among the endemic subspecies, however, are four that so far have been found only on the summits:

Piculus rubiginosus viridissimus
Taraba major duidae
Zonotrichia capensis macconnelli
Emberizoides herbicola duidae

The following tabulation of material in the Phelps Collection will convey the relative frequency of 17 more or less characteristic "summit" species on the summits and on the slopes (total number collected versus number collected on a summit):

	Total	Summit
Otus choliba duida	9	8
Caprimulgus longirostris roraimae	20	3
Campylopterus hyperythrus	154	26
Campylopterus duidae	186	124
Colibri coruscans	83	35
Heliodoxa xanthogonys	164	12
Thamnophilus insignis	103	13
Mecocerculus leucophrys	127	44
Elaenia dayi	44	13
Elaenia pallatangae olivina	182	10
Troglodytes rufulus	197	79
Diglossa duidae	177	135
Diglossa major	357	78
Myioborus cardonai	39	6
Myioborus albifacies	43	15
Myioborus brunniceps	207	34
Catamenia homochroa	62	28

A far richer representation of the characteristic tepui fauna is found on the talus slopes directly below the sandstone cliffs. The forests on the talus slopes grow in a climatically very different belt from the lowlands, with respect both to temperature and, particularly, to humidity. Most of the birds with which this analysis deals were collected in this subtropical belt on the talus slopes. Of several of the tepuis, e.g., Ptari-tepui, Aprada-tepui, and Cuquenám, only the fauna of the slopes has so far been explored.

Chapman classified the fauna of Pantepui as "subtropical." Actually, it is a composite fauna, which also includes ecological specialists (such as inhabitants of cliffs, grasslands, scrub) which find the proper habitat only here. It contains tropical and "upper tropical" species, which require a truly humid tropical forest, and for which the lowland forest of much of southern Venezuela and the Guianas is apparently too dry. Finally, it includes species that can be considered genuine subtropical elements. The slopes of the Andes appear to be, on the whole, more humid than the general area of Pantepui (except for Neblina). Since up to a point there is an increase in humidity with altitude, it is not surprising that the altitudinal zone at which subtropical elements occur on Pantepui is generally higher than it is at the eastern slope of the Andes. There are, however, some conspicuous exceptions, such as *Cistothorus* or *Catamenia homochroa*, which are species of the temperate-zone paramo in the Andes, yet occur on numerous mountains of Pantepui well below 10,000 feet. On the still more humid and more isolated Paria Peninsula, in extreme northeastern Venezuela, the subtropical belt is even lower than in the Andes.

The Geology of Pantepui

The interpretation of the history of the fauna of Pantepui depends a good deal on the interpretation of the geology of the region and, particularly, on its chronology. The two most important questions are: How old are the strata of which the table mountains are composed? When did the erosion take place which dissected the former plateau and left the mounts standing on an underlying peneplain?

The Guiana-South Venezuela region consists of a pre-Cambrian shield, on which stand the sandstone pillars of the tepuis and other mountain areas. The latter are nonmarine deposits consisting of a mixture of sandstones, coarser conglomerates, and finer shales. Since these strata lack fossils, the dating must be done by indirect evidence, and the estimates of different authors have varied from Proterozoic to Eocene. On the basis of the dating of similar rocks at the foot of the Andes and in Brazil, a Cretaceous age seems most probable (Gansser, 1954). The subsequent Tertiary erosion must have been very violent, to account for the steepness of the cliffs. There have been attempts to date the tepuis on the basis of an estimated age of the isolated endemics. It is evident that such a method has no validity; indeed a dating based on plants or on birds would produce widely different dates. The dating of geological events should in all cases be based strictly on geological, chemical, or paleontological evidence and not on biogeography.

THE PATTERN OF AVIAN DISTRIBUTION ON PANTEPUI

ABOUT TWO-THIRDS OF THE characteristic faunal elements of Pantepui are widely distributed in the area, others are restricted to the eastern or western tepuis, and still others are restricted to a single tepui. This pattern of distribution provides valuable clues concerning the history of this fauna and its mode of colonization.

An analysis must be tentative for two reasons. One is that, as mentioned, some of the individual mounts of which Pantepui is composed are as yet entirely unexplored, geographically or faunistically. The other is that additional discoveries may still be made on previously investigated tepuis. Nevertheless, it is evident that enough is known to permit a revealing analysis. This analysis is here based primarily on the distribution of species. Differentiation (into subspecies and semispecies) within Pantepui is treated in a later section. The unit of zoogeographical comparison is the superspecies (a superspecies that is represented on different tepuis by several semispecies is, therefore, listed as a single species).

ZOOGEOGRAPHIC SUBDIVISIONS

There are two fairly well-defined zoogeographic subdivisions of Pantepui, an eastern one and a western one, separated by the Río Caroní. The western group in turn consists of lower outliers (El Negro, Calentura, and Guaiquinima) and several groups of high peaks (Cerro Yaví and Cerro Paraque, Serranía Parú and Cerro Duida, and Cerro de la Neblina). The faunistic characteristics of these subdivisions are described below.

EASTERN GROUP: GRAN SABANA REGION

Absent from the region east of the Río Caroní, or at least not yet recorded, are the following five species:

Otus choliba
Taraba major (*duidae*)
Philydor hylobius (Neblina only)
Diglossa duidae
Pipraeidea melanonota (*venezuelensis*)

RORAIMA AND ADJACENT HIGHLANDS OF GUYANA, ALSO PTARI-TEPUI AND SOROROPÁN-TEPUI

This group of highlands is characterized by having a high percentage of all Pantepui species and by sharing most of them with the Auyán-tepui group. In addition to the five species listed above, two other species that occur in the Auyán-tepui area have not yet been recorded from the Roraima district (see below). Thus all but seven of the potential 96 Pantepui superspecies occur in the Roraima region.

AUYÁN-TEPUI, CHIMANTÁ-TEPUI

This area has only a few peculiar species and subspecies, such as *Acrochordopus zeledoni* (*leucogonys*) and *Spodiornis rusticus* (*arcanus*). Otherwise it shares with Roraima a typical eastern Pantepui fauna.

The following species are limited to this eastern group of tepuis:

Crypturellus ptaritepui[1]
Pyrrhura egregia
Caprimulgus whitelyi[1]
Chaetura cinereiventris[2]
Veniliornis kirkii monticola[1]
Percnostola leucostigma[2]
Grallaricula nana
Pipreola whitelyi
Lipaugus streptophorus
Todirostrum russatum
Acrochordopus zeledoni[3]
Cistothorus platensis[1]
Platycichla flavipes[2]
Cichlopsis leucogenys
Diglossa major
Mitrospingus oleagineus
Spinus magellanicus[4]
Spodiornis rusticus

WESTERN GROUP

LOW OUTLIERS

Cerro El Negro, Cerro Tabaro, and Cerro Calentura are very isolated in the north and

[1] Roraima group only.
[2] See Low Outliers of the Western Group, below.
[3] Auyán-tepui group only.
[4] See under Appendix: Analytical List of the Birds of Pantepui, below.

have variable proportions of the Pantepui fauna. Nearly all the species that occur are widespread in east and west Pantepui. Where there is a subspecific difference, El Negro, Tabaro, and Calentura birds agree more often with those of the western group.

Cerro Guaiquinima is not high enough for the summit elements (*Diglossa*, *Troglodytes*, and others). Being situated not far from Auyán-tepui on the other side of the Río Caroní, it has a few rather wide-ranging elements that have spilled over from the eastern group of tepuis. These include *Chaetura cinereiventris*, *Percnostola leucostigma*, and *Platycichla flavipes*. The endemics, however, clearly associate this tepui with the tepuis of the western group, as is indicated by *Campylopterus duidae*, and the *duidae* subspecies group of *Atlapetes personatus*.

Higher Mountains

The northwestern group of tepuis (Cerro Guanay and Cerro Paraque) is, in regard to subspecies, clearly close to Duida, but, as does the preceding group, it has a few Roraima species that are not found on Duida:

With Duida group
- *Campylopterus duidae*
- *Diglossa duidae*
- Many subspecies groups

With Roraima
- *Caprimulgus longirostris* (also Neblina)
- *Synallaxis moesta*
- *Grallaria guatimalensis* (also Sierra Imeri)

Only one species, *Pipraeidea melanonota* (*venezuelensis*), is limited to this area within Pantepui (Yaví and Taracuniña).

When the size of Cerro Duida, Serranía Parú, and other tepuis in this group is considered, one is amazed at how few specific elements they contain: *Otus choliba* (*duidae* is known from Duida and Neblina only), *Taraba major duidae* (Duida only), and *Emberizoides herbicola duidae* (altitudinal derivative of widespread species only formed here). *Campylopterus duidae* and *Diglossa duidae* are widespread in western Pantepui (including Neblina).

The composition of the bird fauna of Neblina is very similar to that of Duida. *Philydor hylobius* is, however, endemic, and several species (e.g., *Troglodytes rufulus*, *Atlapetes personatus*, *Zonotrichia capensis*, *Myioborus brunniceps*, and others) have well-defined endemic subspecies.

Almost equally characteristic of the composition of the fauna of the western tepuis is that many species characteristic of the eastern and northern tepuis are absent from the western group. These are mentioned in the lists above.

The data presented in these lists bring out several significant facts. Omitting the low, somewhat intermediate, and somewhat impoverished northern outposts, we can divide Pantepui into an eastern group and a western group. In the total of 96 species or superspecies, 18 are restricted to the eastern group and about five to the western group. Thus only about a quarter of the characteristic Pantepui avifauna is restricted to either the western or the eastern peaks.

The irregularity of distribution is, however, greater than these numbers indicate. Many of the species are found on only a few of the tepuis on which they might be expected to occur. For instance, in the western group, 14 tepuis have been explored ornithologically, 10 of them reasonably well. Of the 70 species found on these 10 tepuis, nine species are known on only three, 13 species on only two, and seven species on only one. Further exploration will undoubtedly change these figures, but it is certain that the bird fauna of Pantepui is not at all evenly distributed. Since savanna birds such as *Spinus magellanicus* and *Emberizoides* are absent from areas covered by forest or scrub, it seems that ecological reasons are the answer to some of the distributional phenomena. However, in large part the irregularity in the pattern of distribution can be due to nothing other than the hazards of colonization.

Regardless of what specific theory of colonization one accepts, it is evident that much of the fauna of Pantepui is derived from the Andes. One would, therefore, expect the western group, which is only 500 kilometers distant from the Andes, to be much richer in subtropical Andean elements than the eastern group, which is 600 kilometers farther away. It comes somewhat as a surprise that precisely the opposite is true. The Gran Sabana region has 18 species that are not found in the western sector.

There are several possible explanations

for this paradox. The first is that the richness of a fauna depends to a considerable degree on the ecological diversity of the available habitat. Undoubtedly, the numerous tepuis and adjacent highlands in the Gran Sabana offer far greater ecological opportunities than Duida and the other rather isolated western tepuis. Second, the eastern tepuis are more closely bunched together, whereas the distances between the western tepuis are much greater. Finally, many of the eastern tepuis are, in a way, tied together by the elevated Gran Sabana region which is or was undoubtedly a reservoir for highland elements, but the western tepuis constitute, for the most part, isolated towers in a vast area of lowlands. The eastern mountains were thus much more suitable for the development and maintenance of a highland fauna.

SUBSPECIATION AND SPECIATION IN THE PANTEPUI BIRD FAUNA AND THE DEVELOPMENT OF ENDEMICITY

We now know that populations of different species and on islands of different size may differ rather widely in the rate at which they diverge morphologically under the influence of the same degree of isolation. Nevertheless, all other things being equal, degree of differentiation of an isolated population reflects length of isolation. By a study of the degree of endemicity that has developed among the 96 upland species of Pantepui, it should be possible to determine whether the colonization took place at a single period of time or whether, on the contrary, it was a continuous process.

The most instructive way to present the data is to arrange the species according to the degree of evolutionary divergence that they have undergone since their colonization of Pantepui (for details, see Appendix: Analytical List of the Birds of Pantepui, below).

Endemic Genera

Two genera (with one species each) are considered endemics, *Nannopsittaca* and *Roraimia*, but neither seems a good genus. Although *Roraimia adusta* is not a subspecies of *Synallaxis cinnamomea*, as Hellmayr thought, it seems evident that the genus is not valid. *Waldronia* is not separable from *Polytmus*.

Endemic Species Without Known Relatives (Four)

Pipreola whitelyi
Chloropipo uniformis
Ceratopipra cornuta
Phylloscartes chapmani

Endemic Species, More or Less Closely Related to an Allopatric Species[1] (11)

Campylopterus hyperythrus
Lophornis pavonina
Heliodoxa xanthogonys
Philydor hylobius (Mt. Neblina only)
Automolus roraimae
Thamnophilus insignis
Myrmothera simplex
Lipaugus streptophorus
Phylloscartes nigrifrons
Elaenia dayi
Hylophilus sclateri

Endemic Species with a Close Relative (Eight)

Crypturellus ptaritepui
Caprimulgus whitelyi
Polytmus milleri
Herpsilochmus roraimae
Todirostrum russatum
Microcerculus ustulatus
Mitrospingus oleagineus
Atlapetes personatus

Endemic Species, Members of a More Widespread Superspecies (Four)

Troglodytes rufulus
Diglossa major
Diglossa duidae
Myioborus brunniceps-cardonai

Non-Endemic Species with Endemic Subspecies (55)

Columba fasciata
Pyrrhura egregia
Otus choliba
Otus guatemalae
Glaucidium brasilianum
Caprimulgus longirostris
Chaetura cinereiventris
Doryfera johannae
Phaethornis augusti
Colibri coruscans
Amazilia viridigaster
Trogon personatus
Aulacorhynchus derbianus
Piculus rubiginosus
Veniliornis kirkii
Xiphocolaptes promeropirhynchus
Synallaxis moesta
Cranioleuca curtata
Lochmias nematura
Taraba major
Dysithamnus mentalis
Myrmotherula behni
Percnostola leucostigma
Chamaeza campanisona
Grallaricula nana

[1] For details, see Appendix: Analytical List of the Birds of Pantepui, below.

Grallaria guatimalensis
Acrochordopus zeledoni
Pachyrhamphus castaneus
Pipra serena
Knipolegus poecilurus
Contopus fumigatus
Platyrhynchus mystaceus
Idioptilon margaritaceiventer
Mecocerculus leucophrys
Elaenia pallatangae
Pipromorpha macconnelli
Oxyruncus cristatus
Thryothorus coraya
Turdus ignobilis
Turdus olivater
Platycichla flavipes
Myadestes (= Cichlopsis) leucogenys
Parula pitiayumi
Basileuterus bivittatus
Macroagelaius subalaris
Chlorophonia cyanea
Tangara chrysophrys
Tangara xanthogastra
Tangara cyanoptera
Piranga flava
Catamenia homochroa
Spinus magellanicus
Spodiornis rusticus
Zonotrichia capensis
Emberizoides herbicola

Non-Endemic Species Without Endemic Subspecies (12)

Aeronautes montivagus
Doryfera johannae
Phaethornis augusti
Myiophobus roraimae
Hirundinea ferruginea
Elaenia ruficeps
Atticora (Notiochelidon) cyanoleuca
Cistothorus platensis
Platycichla leucops
Myioborus miniatus
Pipraeidea melanonota
Tangara gyrola

A summary of these data on the degree of endemicity on Pantepui follows:

Endemic species		
In "endemic" genera	2	
Without evident relatives	4	
Clearly but more or less distantly related to an allopatric species	11	
With a close relative	8	
Belonging to a non-endemic superspecies	4	
Total		29
Non-endemic species		
With endemic subspecies	55	
Without endemic subspecies	12	
Total		67
Total number of species		96

From the data given above, it is evident that there is a completely even gradation from endemic genera to species that have not even begun to develop endemic subspecies. Fewer than one-third (29 species) of the characteristic upper zonal element of Pantepue (96 species) are endemic species. These facts are conclusive evidence for the continuity and long duration of the colonization of Pantepui.

The unequal age of the faunal elements of Pantepui is further documented by the different degree of subspecific differentiation within Pantepui. There is no case of "archipelago-speciation" on Pantepui that can be compared with that of the Galapagos finches (Geospizinae), that of the Hawaiian honeycreepers (Drepanididae), or that of the Vangidae of Madagascar. Nonetheless two of the Pantepui elements are sufficiently old to have evolved to the level of superspecies: *Campylopterus hyperythrus-duidae*, and *Myioborus brunniceps-cardonai*. In the case of *Diglossa major* and *D. duidae*, double invasion may be involved rather than superspecies formation. In two other species, *Troglodytes rufulus* (five subspecies) and *Atlapetes personatus* (six subspecies), active geographic variation has not yet reached species level. In 42 species (or superspecies) more than one subspecies is found on Pantepui. In some cases all are endemic, and in other cases some subspecies are widespread, others endemic. Usually there are only two subspecies, one in the eastern (Roraima and elsewhere) and one in the western group. These subspecies range in degree of difference from very slight to very pronounced. Four or more subspecies are found on Pantepui in the two listed superspecies, as well as in the species *Chamaeza campanisona*, *Troglodytes rufulus*, *Microcerculus ustulatus*, *Turdus olivater*, *Diglossa major*, and *Atlapetes personatus*.

As one would expect, it is on the whole the older element that tends to a greater differentiation. The highest number of endemic subspecies (six) occurs in an endemic species:

Atlapetes personatus. Among the species with four endemic subspecies each, only two are not endemic: *Chamaeza campanisona* and *Turdus olivater*. The average number of Pantepui subspecies for the 29 endemic species-superspecies is 2.24. The average for the other 67 species is 1.57.

It must be emphasized, however, that the long occupancy of the Pantepui region is no guarantee for subspeciation or speciation. No fewer than nine of the 29 endemic elements are monotypic, including such old species as *Nannopsittaca panychlora* (not strictly endemic), *Polytmus milleri*, *Heliodoxa xanthogonys*, *Ceratopipra cornuta* (also tropical), and others.

The evidence of this section can be summarized in the statement that the degree of differentiation of the Pantepui fauna from the source fauna as well as the differentiation within the fauna indicate strongly an unequal age for the Pantepui elements. Every level is represented, from ancient to very recent arrivals. The fact that there is an evenly graded series, ranging from generic difference to subspecific identity, proves that the colonization of Pantepui has been a continuous process. The tepuis represent, ecologically speaking, islands suitable for colonization, which have been available for many millions of years.

THE ORIGIN OF THE SUBTROPICAL FAUNA OF PANTEPUI

THE EVOLUTIONARY HISTORY, the ecological tolerance, and the genetic system of every species is unique in some respects. When assigning a given species to categories, such as "endemic with a distant allopatric relative" or "derived from a tropical zone relative," a student inevitably makes subjective evaluations. Another student may prefer a different interpretation in some of the cases. The totals as well as the percentages of the various categories in the ensuing analysis should therefore be considered only as approximations. Nevertheless we are confident that the resulting minor readjustment of the figures will in no case necessitate a modification of our essential conclusions.

Five separate, although not necessarily mutually exclusive, theories have been proposed to account for the origin of the Pantepui bird fauna. The data presented on the preceding pages give us the necessary evidence to test these theories.

PLATEAU THEORY

This theory maintains that the Pantepui fauna is the remnant of a fauna formerly widespread on a plateau now dissected by erosion into separate tepuis.

This thesis has never been advanced to explain the origin of the entire Pantepui fauna. However, both Chapman and Tate have considered it in connection with the Pantepui endemics. Chapman (1931, p. 56), for instance, held that the fauna of all these mountains is very similar because "this fauna once occupied a much wider area of which these mountains formed a part." He cited in this connection the fact that these mountains were the last "remnants of a once continuous table land which became dissected by erosion and is now represented by isolated fragments." Tate (1938a, pp. 472–473) was more specific: "The development of the highly differentiated and endemic species may be held to have taken place in situ—by successive stages of adaptation to the environmental changes induced by the slowly rising plateau. Since the dissection of the area and its reduction to numerous faunal islands little marked change has taken place in the now geographically separated species. The presence of a species on one mountain top and its absence from another suggest only that some inimical condition has arisen on the latter to cause the species to die out." However, neither Chapman nor Tate seems to have placed reliance on this hypothesis to explain all the known facts of distribution, nor did they consider it the most probable hypothesis.

There are two alternate possibilities concerning this postulated former tableland. The first is that it was so large that it was connected with the Andes in the west and with the coastal cordilleras of Venezuela in the north. A number of objections to such a hypothesis can be raised. Chapman stated specifically that no geological facts would support the existence of such connections. In consequence, he seems to have supported the idea of a tableland more limited in extent, namely, the area now occupied by the remaining table mountains. This second hypothesis agrees with the geological evidence (Gansser, 1954).

The plateau theory is contradicted by many facts. Most important are: the plateau is geologically vastly more ancient than its bird fauna, and its dissection must have taken place long before most of the elements of the fauna could have been evolved. The irregular distribution within Pantepui, the different degrees of differentiation from the nearest relatives, and the various degrees of differentiation within Pantepui all contradict the assumption that the present fauna of Pantepui is the remnant of an old, formerly uniform plateau fauna.

It may be suggested that this theory should be restricted to the genera and species that are endemic on Pantepui, but even such a restriction is not feasible. The summary of the degree of endemicity given above (p. 290) shows that the endemics are of very unequal age. Furthermore, they were derived from very different sources. Some are derivatives of lowland groups; others are Andean subtropical forms that became isolated on Pantepui (see below). These facts contradict the assumption that the origin of any of the Pantepui forms antedates the dissection of the former plateau into isolated mountain tops.

COOL CLIMATE THEORY

This theory maintains that the subtropical fauna of Pantepui was able to reach these mountains when the lowlands had a subtropical climate during the cool periods of the Pleistocene.

Both Chapman and Tate considered this explanation of the colonization of Pantepui the most likely one. Chapman (1931, p. 58) stated that about half of the fauna "is composed chiefly of forms showing more or less close resemblance to birds of the Andean Subtropical and, in smaller part, Temperate Zones. The existence of these representative forms in such widely separated regions may be explained by the disappearance of the . . . connecting forms in the intervening area. The cause of their disappearance is attributed chiefly to the influence of climatic changes." Again, Tate (1938a, p. 472) was more specific. Instead of a bridge connection between the Andes and Pantepui, "the theory of generally lowered earth temperature (including the last glacial epoch) seems more acceptable. A fall of nine degrees mean annual temperature would be equivalent, measured by present day standards, to a general elevation of 3000 feet. Relatively low ridges would readily bring members of the subtropical faunas within close range of one another."

That the lowlands have been more passable for colonists during periods of lowered temperatures is not in doubt. However, there are a number of grave objections against accepting the Chapman-Tate theory in its sweeping simplicity. Climatological and botanical evidence is opposed to the acceptance of a lowering of the temperature in the equatorial lowlands by more than 3° C., even at the height of the Pleistocene glaciation. Some authors deny that there has been a lowering of even that much. If the temperature in the tropics had dropped by 9° C., making them suitable for subtropical elements, it would have caused the extermination of the tropical fauna. The fact of the continued existence of a tropical fauna indicates that there was no such drastic climatic change in the past.

If the Pantepui fauna had arrived during a specific past period of cooler climate, this fauna should be uniformly different from the fauna from which it had been derived and we should find a more or less uniform fauna throughout Pantepui. The facts presented above indicate, however, that the faunal elements of Pantepui arrived there as a continuous stream, ranging from species that are so distinct that they are now placed in endemic "genera" (which must have arrived there many millions of years ago) to undifferentiated populations on single cerros which, for all we know, might have arrived there only during the last 100 years, or more recently.

It is not claimed that this stream of colonization was entirely even. It probably subsided to a trickle during geological periods that were warmer and drier than average, and was particularly vigorous during cool and humid periods such as existed during the various Pleistocene glaciations. Nevertheless, it was essentially a continuous stream, as is discussed below in more detail.

A former faunal continuity between Pantepui and the Andes is contradicted by all known facts of distribution. If such a connection had once existed, one would expect a much greater similarity of faunas, particularly if such a direct connection had existed during the recent Pleistocene glaciations.

HABITAT SHIFT THEORY

This theory postulates the derivation of the avifauna of Pantepui from tropical lowland elements owing to a shift in habitat preference of that fauna.

The available evidence strongly supports this theory for a part of the Pantepui fauna. It is becoming increasingly evident that species do not necessarily have typologically rigid ecological requirements. There is no such rule as "once tropical, always tropical." It is impossible to classify all species into simple pigeonholes, "tropical," "subtropical," "temperate," as was done by some of the pioneers of biogeographical research. Each population of a species has a preference for certain optimal conditions, which include many factors besides temperature. Chapman pointed out (1931) that the poverty of the upper altitudes on Roraima and Duida in truly subtropical elements (and perhaps some climatic-vegetational factors) permits numerous tropical species to occur at higher levels than is normal for tropical species. He (1931, p. 30) listed 66 species of tropical birds taken on the slopes of Mt. Roraima at or above 4000 feet in altitude and 14 tropical species taken at or above 3250 feet on Mt. Duida.

Three species, which elsewhere are largely or entirely tropical, have upper tropical-subtropical populations on Pantepui (*Phaethornis bourcieri*, *Elaenia ruficeps*, and *Tangara gyrola*), but they are not found at the immediate foot of Pantepui. The Pantepui mountains seem to form ecological oases for these species by offering them a more suitable habitat than the adjacent lowlands.

In addition to the above-mentioned species, the following 18 species, which are widespread in the tropical lowlands, most of them actually at the foot of Pantepui, have formed endemic subspecies on Pantepui itself:

Otus choliba
Otus guatemalae
Glaucidium brasilianum
Veniliornis kirkii
Xiphocolaptes promeropirhynchus
Glyphorhynchus spirurus
Taraba major
Dysithamnus mentalis
Percnostola leucostigma
Pachyramphus castaneus
Pipra serena
Platyrhynchus mystaceus
Pipromorpha macconnelli
Thryothorus coraya
Turdus ignobilis
Parula pitiayumi
Tangara xanthogastra
Spinus magellanicus
Emberizoides herbicola

Several cases in the above list may be discussed. *Percnostola leucostigma* at Sierra de Lema: *P. l. leucostigma* occurs at 700 meters (elsewhere from 280 meters to 1000 meters); *P. l. obscura*, at 1000 meters (elsewhere from 700 meters to 1500 meters). The two subspecies are strikingly different. *Emberizoides herbicola* at Mt. Duida: *E. h. sphenurus* occurs at tropical and lower subtropical altitudes (elsewhere occasionally up to 1600 meters); *E. h. duidae*, at higher subtropical levels (1323 meters to 2010 meters). In several species, there are a lower subspecies and a higher subtropical subspecies, for instance: *Piculus rubiginosus guianae* occurs at upper tropical and subtropical altitudes (500 meters to 1900 meters), and *P. r. viridissimus* occurs on the summit of Auyántepui (1800 meters to 2200 meters); and *Zonotrichia capensis roraimae* is found on the talus slopes of Mt. Roraima at the bases of the cliffs, whereas *Z. c. macconnelli* occurs on the summit (2500 meters).

The distinction between tropical and subtropical elements becomes even more blurred when we notice that the reverse is also found, namely, the occasional occurrence of typically subtropical or upper tropical species at tropical lowland localities:

Pyrrhura egregia
Doryfera johannae
Amazilia viridigaster
Piculus rubiginosus
Synallaxis moesta
Dysithamnus mentalis
Chamaeza campanisona
Grallaria guatimalensis
Ceratopipra cornuta
Knipolegus poecilurus
Platycichla flavipes
Cichlopsis leucogenys
Zonotrichia capensis

Amazilia viridigaster, for instance, a typically subtropical species, is known only from the subtropical zone on the slopes of the eastern Andes and from five tepuis, but it has also been found at two stations in the tropical zone, namely, as the Roraima subspecies *cupreicauda* at El Dorado (60 meters) and the Duida form *duidae* at Salto Para (180 meters). *Synallaxis moesta*, a strictly subtropical species in the Pantepui region, has been found on the Mana River in French Guiana and in the tropical zone of several departments in Peru. It is easy to see how stepping-stones in the tropics could be utilized by such species to move from one subtropical area to a widely separated one.

The same lack of definition is found at the border between subtropical and temperate-zone elements. There are, for instance, five species in the subtropical zone of Pantepui which are considered temperate-zone or páramo elements in the Andes: *Caprimulgus longirostris*, *Cistothorus platensis*, *Mecocerculus leucophrys*, the *Diglossa major* group, and *Catamenia homochroa*. Chapman (1931, p. 33) pointed out that all these species are wide-ranging, aggressive species and that all have also succeeded in colonizing isolated Santa Marta Mountain in northeastern Colombia.

It is evident from this information that the allegiance of a species to a given climatic or ecologic zone is not nearly so rigid as is sometimes implied in the literature. Species have not only the ability to pick suitable niches within rather widely varying climatic limits, but often clearcut geographic variation occurs. Quite a few subtropical Andean species occur, for instance, in tropical habitats in Central America or on Trinidad or Tobago. The occurrence of *Zonotrichia capensis* in tropical Brazil, on Curaçao, and in the mountains of Hispaniola above 3500 feet is another illustration of this phenomenon.

It does not require much imagination to visualize a situation in which a tropical species becomes extinct in the lowlands, while the isolated populations on Pantepui survive. These then, in time, may become a new species. Perhaps there is not even a need for a complete continuity of populations during the early stages of this process. Some tropical species have considerable dispersal facility and are able to jump from one particularly favorable location to another one that is more or less isolated. The exceptionally humid environment of the tepuis and their slopes form humid tropical islands in an area most of which (at least at present) is drier than the normal humid tropics. Even today a number of upper tropical species are found on Pantepui, the nearest localities of some of which are quite distant because the lowlands near Pantepui seem to be unsuitable for them: *Amazilia viridigaster*, *Lochmias nematura*, and *Idioptilon margaritaceiventer*. Other cases are included in the summary on page 302. Such unsuitability of the lowlands also favors isolation and, ultimately, speciation. With the fluctuation of the climatic and ecological conditions and with all species having considerable dispersal facilities, no sharp line can be drawn between the tropical and upper tropical species. In either case a long-continued isolation may lead to the development of a Pantepui endemic, ultimately derived from a tropical species. It is easy to reconstruct the history of those subtropical subspecies on Pantepui that belong to otherwise essentially tropical species.

Conclusive proof for tropical derivation is more difficult to supply in the case of full species endemic on Pantepui. In some of them the derivation from a closely related tropical species is highly probable (table 2). Others are such old endemics that the proof is far less conclusive (table 3). All that one can definitely say for this second group of species is that the habitat of the most nearly related species or of the whole genus to which they belong is more tropical than subtropical or temperate.

TABLE 2

ENDEMIC PANTEPUI SPECIES AND THE CLOSELY RELATED SPECIES IN THE TROPICS FROM WHICH THEY SEEM TO HAVE BEEN DERIVED

Endemic Species	Related Species in Tropics
Caprimulgus whitelyi	*C. nigrescens*
Polytmus milleri	*P. guainumbi*
Herpsilochmus roraimae	*H. dorsimaculatus*
Myrmothera simplex	*M. campanisona*
Microcerculus ustulatus	*M. philomela*
Mitrospingus oleaginus	*M. cassini*

TABLE 3

OLD PANTEPUI ENDEMICS AND THE TROPICAL SPECIES TO WHICH THEY ARE DISTANTLY RELATED

Old Endemics	Relatives
Crypturellus ptaritepui	*C. obsoletus*
Automolus roraimae	*A. ruficollis* or *A. ochrolaemus*
Thamnophilus insignis	*T. amazonicus*
Lipaugus streptophorus	*L. cineraceus*
Hylophilus sclateri	*H. pectoralis*

It is clear from the evidence presented on the above pages that at least part of the fauna of Pantepui owes its origin to a shift in ecological tolerance or preference among species that elsewhere are essentially tropical. Indeed on Pantepui we have the complete gradation from species that have not yet developed endemic subspecies through tropical species with endemic subspecies (see list on p. 295), and endemic species with close allopatric relatives in the lowlands (table 2) to old endemics (table 3) that belong to an essentially tropical group but for which a tropical derivation is, at best, probable but is not proved.

The endemic Pantepui fauna that is of tropical origin very graphically illustrates two phenomena. First, a new fauna can originate in an empty habitat or life zone by an ecological shift of elements originally belonging to a different set of habitats (or life zones). Many specialized faunas are formed by such a process of ecological "segregation" (Mayr, 1965a). Second, the isolation offered by the altitudinal barrier, incomplete as it is, permits speciation in all of its stages.

Finally, we must answer the question as to the percentage of Pantepui elements that are to be attributed to this process of "altitudinal segregation." The species listed on page 295 and in tables 2 and 3, together with some others mentioned in the text, add up to at least 30, possibly 33. Some of the old endemics may also be of this origin. Three species (*Pyrrhura egregia*, *Automolus roraimae*, and *Phylloscartes nigrifrons*), listed as old endemics, probably started as tropical derivatives. Tropical derivatives, then, total about 32 per cent to 38 per cent of the Pantepui elements, or 39 per cent if the ecological specialists (five species) and old endemics (nine species) be excluded.

SPECIALIZED HABITAT THEORY

This theory maintains that some of the Pantepui element is not at all subtropical but is found on Pantepui only because the very specialized requirements of this element cannot be met in the flat terrain of the surrounding lowlands.

This explanation is clearly correct for a number of cliff dwellers and other ecological specialists. The following five species fall in this category:

Chaetura cinereiventris (swift)
Chaetura (*Cypseloides*) *rutila* (swift)
Aeronautes montivagus (swift)
Hirundinea ferruginea (tyrant)
Atticora cyanoleuca (swallow)

These species have a wide altitudinal tolerance provided they find suitable cliffs, canyons, or precipices. They comprise 5 per cent of the Pantepui avifauna.

DISTANCE DISPERSAL THEORY

This theory is that the subtropical fauna of Pantepui is derived from that of other subtropical regions by "island hopping."

The theory that Andean birds might have crossed the unsuitable lowland area by flight "would not be entertained by any student of the distribution of birds," Chapman (1931) stated categorically, undoubtedly echoing a then-widespread belief. Chapman went beyond, however, merely denying the possibility. He cited various facts that to him contradicted the possibility of such flights. For instance, he remarked that, if the bird life of Pantepui had been derived from the Andes by flight, one would expect the mountaintops nearest the Andes, namely, those of the Paraque-Duida group, to have the richest fauna. Actually, as mentioned above, the opposite is true. We answer this argument by pointing out that the generally much more favorable ecological conditions of the Gran Sabana region are principally responsible for this seeming discrepancy.

Chapman's second point concerns the essential faunistic similarity of all the mountains of Pantepui. This also, he believed, should militate against any theory of chance colonization. We also answer this point, above (pp. 287–288), under pattern of distribution. To begin with, there is actually enough heterogeneity in the faunas, particularly among the more recent elements, to suggest chance colonization. What is more important is the fact that colonization is not strictly passive; some species are more apt to undertake colonization flights than others. It is these venturesome species which, once they have reached one of the tepuis, also seem to be able to reach others. Among the 30 endemic species, no fewer than 23 (77%) are found both in the eastern and the western group, and most of them are evenly distributed. Just as in the Pacific the same species of birds again and again succeed in getting from island to island, so it is among South American highland birds. Some species are active, indeed aggressive colonizers; others are not.

Different families of birds have different dispersal facilities. If we classify the "hoppers" into the zoogeographic categories adopted by Mayr (1964) and compare the relative frequency of these categories with that among the inhabitants of the Amazonian rain forest, we have the results that are shown in table 4 (four of 47 species omitted as belonging to a family of uncertain zoogeographic assignment). As one would expect, the two zoogeographically aggressive groups comprise 66.5 per cent of the "hoppers" and only 42 per cent of the Amazonian fauna.

TABLE 4

RELATIVE FREQUENCIES (IN PER CENT) OF "HOPPERS" AND FAMILIES OF THE AMAZONIAN RAIN FOREST

	"Hoppers"	Amazonians
Primary South American families	23.5	47.5
Expanding and secondary South American families	43.9	33.0
Pan-American families	10.5	10.5
North American and Old World elements	23.5	9.0

Chapman wrote frequently that a jump of 1000 miles was necessary for colonization of Pantepui from the Andes. This figure was calculated apparently at the time when the Pantepui fauna was known only from Mt. Roraima. Paraque, the westernmost mountain of the Pantepui group, is, however, only 300 miles (500 kilometers) from the slope of the Andes, which reduces quite drastically the length of the jump. Much recent zoogeographic research indicates that far longer jumps are well within the capacity of colonizing birds.

In 1931, when Chapman wrote his comprehensive account of the zoogeography of Roraima and Duida, it was quite generally assumed among biogeographers that existing discontinuities in ranges must be explained on the basis of previous land connections—not that a different viewpoint had not been often expressed, beginning with Darwin, yet it had not found much acceptance. During recent years, however, it has been acknowledged, particularly owing to the influence of Simpson (1940, 1943, 1950, 1952), Darlington (1938, 1957), and Stresemann (1939) that the dispersal facilities of animals are far greater than previously has been admitted. Dispersal is not an "all-or-none" phenomenon, but rather one with a low probability. If the probability that an individual of a given species crosses a certain barrier is one in 10 million and the species produces 1 million individuals annually, even this high improbability becomes a virtual certainty approximately once every 10 years.

The actual occurrence of highly improbable cases of dispersal is a matter of record. The classical case in the ornithological literature is that of the Australian White-Eye (*Zosterops lateralis*), a flock of which (apparently belonging to the Tasmanian subspecies) arrived in New Zealand about 1856, having crossed an expanse of the South Pacific Ocean at least 1500 kilometers wide. As remarkable as was the original invasion is the subsequent history of this colonization. The species not only was so successful on New Zealand that it is now the most common passerine bird on the island, but it also colonized actively most of the surrounding islands (Chatham, Snares, Aukland, Campbell, Macquarie, Kermadecs, and Norfolk) (Williams, 1953).

The most remarkable aspect of this case of colonization of an island is that there was no possibility of utilization of an intervening stepping-stone. The particular importance of insular zoogeography is that it permits the unambiguous demonstration of the dispersal power of animals. In the eastern Pacific (east of the Andesite line) all islands and archipelagos are nothing but the tops of volcanoes that have arisen from the largely undisturbed ocean bottom. In view of this unequivocal geology, it is evident that all animal and plant dispersal must have been transoceanic. The distances involved in some of these colonizations are truly miraculous. The Rotuma Honeyeater (*Myzomela cardinalis chermesina*) came to the island of Rotuma from Micronesia, a distance of about 3000 kilometers. About 12 of the 14 colonizations of Hawaii by land birds were made from the American mainland, a distance of at least 3500 kilometers. These figures, which are only a few of many that could be cited, give an indication of the potential order of magnitude of such colonization flights. Even if one makes the assumption that these species might have used as stepping-stones other islands that have since disappeared below the ocean, it is still necessary to postulate distances of flight that are far greater than the tance between the Andes and Pantepui.

The objection might be raised that these Pacific birds are lowland birds, to which a flight across the ocean might be comparable to a flight across low-lying land, but that no mountain bird would fly across such unsuitable terrain. The facts, again unambiguous because collected in an island region, conclusively contradict this notion. All the mountain birds of the Solomons and Bismarcks, most of them occurring on islands that have never been in contact with one another, must have reached their habitats by island hopping. We cite only four species among dozens of possible examples (all four species are normally not found below 3000 feet):

Micropsitta pusio: Moluccas, New Guinea, New Ireland, Bougainville, Kulambangra, Guadalcanal.

Phylloscopus trivirgatus: From Malaya and the Philippines on mountains east as far as Malaita, Guadalcanal, and San Cristobal.

Petroica multicolor: In Australia in lowlands, Norfolk Island, New Hebrides, Fiji, Samoa, and mountains in the Solomons (San Cristobal, Guadalcanal, Kulambangra, and Bougainville).

Turdus poliocephalus: High mountains from Sumatra and the Philippines to Samoa.

All mountain species on Timor are recent immigrants, having crossed water and ecologically unsuitable terrain (Mayr, 1944). It is abundantly evident that individuals of colonizing species undertake vast dispersal flights across ecologically unsuitable terrain, including the open ocean.

Dispersal Facility

What makes one species a more successful colonist than another species is still obscure (Mayr, 1965b; Voipio, 1952). Close relatives (the *Zosterops rendovae* group) of that champion colonist *Zosterops lateralis*, are confined to the New Georgia archipelago (200 kilometers in diameter) in the central Solomons, and strikingly different subspecies or semispecies are confined to islands that are separated from one another by gaps not wider than 2 to 6 kilometers. Physically, it would be very easy for these birds to undertake the five- or 10-minute flight required to span these gaps. It is thus not a physical, but rather a psychological or ecological, cause that determines dispersal. If we study island faunas, we find that a very limited number of species is involved in most of the successful colonization flights, a fact that is equally true for the birds of isolated mountaintops. Chapman (1931), for instance, commented on the fact that, of the four species of the temperate zone of the Andes that succeeded in colonizing Pantepui, "all have a wide range, extending from Venezuela to Peru or Argentina and . . . all are found on Santa Marta," but, he continued (*ibid.*, p. 33), "the reason is not obvious." To us it seems to be due to an intrinsic ability of these species to cross unsuitable areas.

The analysis of the bases of this ability is still at its beginning. Mayr (1941, 1944, 1965b, and other papers) called attention to the fact that certain types of birds are better colonizers than others. For instance, woodpeckers, with their essentially solitary habits, are, on the whole, poor long-distance dispersers; social birds of treetops disperse much more easily. Furthermore, birds of the forest edge and of second growth seem to be less easily discouraged by ecological barriers. A study of the Pantepui fauna supports only in part the correctness of these generalizations. To be sure, only two subtropical woodpeckers (*Piculus*, *Veniliornis*) managed to reach the area, but, among the birds of the forest undergrowth, a higher number contribute to the Pantepui fauna than one would expect.

Periods of Colonization

That different species differ in their ability to cross ecological barriers is related in detail above. There is also evidence that a species varies in its colonizing ability during various periods of its existence. It would seem easiest to explain the colonization of Pantepui as due to the occurrence of a limited number of waves during periods of changed climate when the intervening barrier (tropical lowlands) was less impassable. There is much to suggest that such a possibility is not the only one. An analysis of cases of range expansion among European birds indicates that there are essentially two types of colonizers. One includes those birds that take advantage of changing conditions, in other words, those in which changes in range are obviously correlated with changed conditions in their preferred habitat. The invasion of Finland, northern Scandinavia, and Iceland by southern species during the warm period of the 1930's is a typical instance. The other type of colonization is that in which the bird itself seems to change and is suddenly able to spread into areas that were previously inaccessible to it. The recent spread through all Europe of the Collared Ring Dove (*Streptopelia decaocto*) is a typical example. Such cases of explosive colonization by previously stationary species may well be caused by a change in their genetic constitution, as has been suggested by Mayr (1926) for the Serin Finch (*Serinus serinus*). Abundant evidence suggests that in many species there is an alternation, so far as range expansion is concerned, between stagnant and aggressive periods. The geographic variation of some of the species on Pantepui likewise suggests an alternation between aggressive periods of colonization, when the species was able to reach many isolated tepuis and other localities, and subsequent periods of stagnation when gene flow subsided and speciation took place. Such an alternation is indicated by all the polytypic species and superspecies, most dramatically by the superspecies to which *Myioborus brunniceps* belongs.

As we show above, 500-kilometer jumps are of regular occurrence among island birds, and the inhabitants of Pantepui are simply inhabitants of subtropical islands in a sea of tropical lowlands. Actually, the colonists of Pantepui have a much easier time than the colonists of oceanic islands; they can rest between the starting point and the final goal. We point out above (pp. 295–296) that many of the subtropical forms are not nearly so rigidly limited to the subtropical zone as has often been stated in the literature. Many of them are, indeed, known from an occasional tropical station, and such occurrence would greatly help to explain the colonization flights. Among the upper tropical-subtropical species, no fewer than 13 have been also recorded from lower tropical localities either near Pantepui or in some more distant areas of the range (see p. 295).

SOURCE OF THE AVIFAUNA OF PANTEPUI

THE AVIFAUNA OF PANTEPUI, both recent and old, consists mainly of two elements: derivates from the tropical fauna and subtropical "hoppers." Even among the endemics there seem to be about as many with tropical as with subtropical ancestry.

The composition of the Pantepui avifauna is, then, as follows:

Long-distance colonists ("hopper")	48
Tropical derivatives	34
Old "endemics" (or tropical derivatives)	9
Ecological specialists	5
	96

If the last two categories in the above list be excluded, 61 per cent of the birds are long-distance colonists, and 39 per cent are tropical derivatives.

The reason for the development of the Pantepui fauna is mainly ecological. These mountains offer especially favorable habitats to at least three classes of birds: (1) species with specialized habitat niches such as cliffs, (2) tropical species that can enter previously not fully occupied habitats in the upper tropical and lower subtropical zone, and (3) species of the remainder of the subtropical zone that are capable of reaching the equivalent zone on Pantepui by "island hopping."

The colonization of Pantepui is a continuous process. It has presumably accelerated during periods in which the intervening lowlands were less hostile to upland birds, but it has presumably never stopped altogether, even during less favorable periods.

Analogy with the colonization of island regions suggests that much of the colonization of Pantepui is due to long-distance flights.

SOURCE OF LONG-DISTANCE COLONISTS

There are three potential sources of subtropical immigrants: (a) the Andes, (b) the northern Venezuelan coast ranges, and (c) the highlands of Brazil south of the Amazon.

The decision as to which of the three was the point of origin is easy in only a few cases.

RELATIONSHIP OF PANTEPUI LONG-DISTANCE IMMIGRANTS (48 SPECIES)

1. Non-endemic Pantepui subspecies identical with Andean form; absent from north coast:

Myioborus miniatus verticalis
Myiophobus roraimae roraimae

2. Endemic subspecies nearest to Andean form; species absent from the northern Venezuelan coast ranges and the highlands of Brazil south of the Amazon:

Doryfera johannae
Amazilia viridigaster
Trogon personatus
Aulacorhynchus derbianus
Synallaxis moesta
Cranioleuca curtata demissa
Myrmotherula behni
Elaenia pallatangae
Myioborus brunniceps
Macroagelaius subalaris
Catamenia homochroa

3. Endemic Pantepui subspecies nearer to Andean than to north coast subspecies:

Acrochordopus zeledoni
Piranga flava

4. Endemic species, closely or distantly related to Andean species:

Lophornis pavonina
Heliodoxa xanthogonys
Troglodytes rufulus
Diglossa duidae
Diglossa major

5. Pantepui subspecies identical with or closer to subspecies of the north coast range than to those of the Andes:

Platycichla flavipes venezuelensis (identical)
Tangara chrysophrys chrysophrys (identical)
Otus guatemalae roraimae
Piculus rubiginosus
Grallaricula nana kukenamensis
Contopus fumigatus
Mecocerculus leucophrys
Turdus olivater

TABLE 5

PROBABLE SOURCES OF 48 PANTEPUI LONG-DISTANCE IMMIGRANTS

Category	Andean Source	Coast Range Source	More Distant Source
1	2	—	—
2	11	—	—
3	2	—	—
4	5	—	—
5	—	10	—
6	—	1	—
7–9	4	8	—
10	—	—	5

Tangara cyanoptera whitelyi (species absent from Andes)
Chlorophonia cyanea

6. *Grallaria guatimalensis* occurs both at the Andes of Mérida and on the island of Trinidad and may be assumed to have colonized from the north, even though the species has not been found in the coast range.

7. Non-endemic Pantepui forms identical with both the Andean subspecies and north coast subspecies:

Platycichla leucops
Pipraeidea melanotota venezuelensis
Cistothorus platensis alticola

8. Endemic subspecies on Pantepui; nearest relative subspecifically identical on Andes and coast range:

Columba fasciata
Caprimulgus longirostris
Phaetornis augusti
Colibri coruscans
Lochmias nematura
Chamaeza campanisona
Knipolegus poecilurus
Spodiornis rusticus

9. Endemic species, nearest relative on both Andes and coast range:

Elaenia dayi

10. Nearest relative neither in Colombian-Venezuelan Andes nor in coast ranges:

Todirostrum russatum (endemic, related to South Brazilian-Argentine *T. plumbeiceps*)
Oxyruncus cristatus (Central America, Amazonia, south Brazil)
Cichlopsis leucogenys (Peru, southern Brazil)
Basileuterus bivittatus (from Argentina through Bolivia to southeastern Peru)
Atlapetes personatus (endemic, related to *A. fulviceps* of Bolivia and northwestern Argentina)

Summarizing these data, we can say that the source area is fairly evident for categories 1 to 6, but ambiguous for categories 7 to 10. Because the coast ranges are presumably better stepping-stones across the Orinoco lowlands than the Andes, we can assume that the majority of the species in categories 7 to 9 came from the coast ranges.

Having made these assumptions, we can partition categories 7 to 9, and allocate the 48 species as shown in table 5.

Of the 48 long-distance dispersers, therefore, about 40 per cent are presumed to have come from the north coast range; 50 per cent, from the Andes; and 10 per cent, from more distant areas. These are rough estimates, which (except in the case of *Grallaria guatimalensis*) do not allow for extinctions and other uncertainties.

THE COLONIZING ELEMENT OF THE SOURCE FAUNA

Only a portion of any fauna has good dispersal facility. To find out what determines the difference between failure or success would require a far better knowledge of the habits and the ecology of these birds than we possess. However, we can give a few figures. Of the 176 species that Chapman (1917) recorded as typical species of the subtropical zone of the eastern Andes of Colombia, only 19 (about 11%) are also represented on Pantepui. De Schauensee (1948) listed a much higher number of birds as members of the subtropical zone of the eastern Andes, but this does not result in a significant change of the stated percentage (11%).

The fact that only so small a proportion of the Andean subtropical avifauna was able to make the crossing adds to the evidence opposed to the theory of climatic change. If the climate of the separating tropical lowlands had been subtropical at one time, one would expect that more than 11 per cent of the subtropical Andean fauna could have colonized Pantepui. The subtropical fauna of passerine birds of the coastal cordillera of northern Venezuela consists of 93 species. Of these 21 species (22.5%) have been able to cross over to Pantepui.

We admit that the above account is not the whole story. The subtropical areas in the Pantepui region form rather small islands, which no doubt reduces their carrying capacity for subtropical elements. Pantepui has, however, 71 passerine subtropical species, as compared to 93 for the coast range. The easternmost portion of the coast range in Sucre, Monagas, and Anzoátegui is completely isolated from the coast ranges to the west (Miranda to Yaracuy), yet it still has some 44 subtropical passerines, and additionally 83 species that reach from the tropical into the subtropical zone. The area available to the subtropical fauna is much smaller than in Pantepui, but the tropical gaps in the series of cordilleras from the Venezuelan Andes to the Paria Peninsula are much smaller than the gaps that isolate the mountaintops of Pantepui one from another.

Sixteen of the 96 Pantepui species are also found on the Sierra Macarena (up to 1675 meters) in eastern Colombia. Eight of these are altitudinal derivatives, and eight are long-distance colonists.

THE OLD ENDEMICS OF PANTEPUI

A LIST OF THE 29 endemic species of Pantepui is presented above (p. 290). At least six species are so distinct as to have no close relatives, whereas 12 other species have more or less remote relatives. These old endemics are interesting for a number of reasons.

First, most endemics are remarkably widespread in Pantepui, not giving the impression of being surviving relicts. Of the 29 endemic species, 21 are widespread on Pantepui. Of the six old endemics, only three have a limited distribution: *Philydor hylobius* (restricted to Cerro de la Neblina), and *Pipreola whitelyi* and *Lipaugus streptophorus* (both widespread, but only in eastern Pantepui). Thus, on the whole, the endemics give the impression of being highly successful species in the area of their occurrence. This is confirmed by their subspeciation. Seventeen of the 29 endemic species are represented by more than one subspecies, some having as many as five or six (*Atlapetes personatus*). The mean number of subspecies per endemic species is 2.2. Of the 67 non-endemic species, only 24 are represented by more than one subspecies and none by more than four. The mean number of Pantepui subspecies per non-endemic species is only 1.5.

The second point is that the list includes several species, usually called Pantepui endemics, which, although appearing to be indigenous in the area, are not entirely confined to it. This includes *Nannopsittaca panychlora* (also found in the Paria Peninsula), *Ceratopipra cornuta* (also at Obidos and elsewhere) and *Pyrrhura egregia* (at various stations in the country around Pantepui). These, and species such as *Myrmotherula behni* and the superspecies *Myioborus brunniceps*, might well have reached species level in the Pantepui area and spread out subsequently, using Pantepui as a base (see below).

It is evident that the old endemics of Pantepui pose many questions which can perhaps never be answered satisfactorily. It is quite conceivable that Pantepui has been a minor center of differentiation which has contributed elements to other parts of South America, yet many elements on Pantepui give the impression of being relicts of formerly more widely distributed types.

EXTINCTION AND REPLACEMENT

The subtropical avifauna of Pantepui consists of about 96 species. The avifauna of a single mountain (Roraima) may include as many as 80 of these species. If we analyze this fauna, we see that it consists of very old elements (endemic genera and species), not so old elements (endemic subspecies), and recent elements (non-endemic subspecies). Even though evolutionary rates in different species are different, it can hardly be questioned that these elements arrived on Pantepui at different times.

Therefore, if we assume that the faunal capacity of Pantepui has been essentially the same during most of the later Tertiary, we cannot avoid the conclusion that there must have been much extinction to make room for (or caused by) the more recent arrivals. If we assume (for the sake of the argument) that the 29 endemic species are a remnant of the early Pleistocene (or Pliocene) fauna of Pantepui, we are entitled to ask what happened to the 60-odd additional bird species of that fauna that must have existed at one time to round out the fauna of that earlier period (also comprised of some 90-odd species).

All that we know about distribution and speciation in birds indicates that there has been a rich and diversified fauna since the early Tertiary, and there is no obvious reason why the fauna should have been significantly poorer in the mid-Tertiary than it is today. The tepuis, exposed to continuous erosion throughout the Tertiary, may well have been a good deal more extensive in the Oligocene, Miocene, and Pliocene, than they are today and thus would have offered even more living space during those periods than is presently available. The assumption that the subtropical bird fauna of Pantepui was at least of the same order of magnitude in the

Miocene, Pliocene, and early Pleistocene as it is at the present time appears not unreasonable.

What then happened to the 60-odd missing species? (For the problem as such, the precise number is immaterial. The total Pliocene Pantepui bird fauna may have been as low as 50 or as high as 110 species.) Two possibilities suggest themselves, and presumably both have occurred. One, obviously, is extinction. As in islands, so also in the isolated Pantepui region there must have been steady extinction (Mayr, 1956c). Presumably this is not a uniform process, and there may have been periods of accelerated extinction and some with none. If there was a comparatively arid spell during the Pliocene or during one of the Pleistocene periods, it may well have caused much extinction. At the present time little extinction seems to be going on, if we can judge from the rather wide distribution of most of the endemic species. However, *Atlapetes personatus* seems to be absent from Uei-tepui.

We cannot entirely ignore a second possibility, namely, that a few indigenous Pantepui elements have broken out of their isolation and have thereby lost their status as endemics. The fact that such essentially Pantepui elements as *Pyrrhura egregia*, *Nannopsittaca panychlora*, and *Ceratopipra cornuta* also occur outside Pantepui suggests such a possibility (although these may also be relict species). It is quite possible also that several of the 66 non-endemic Pantepui species originated on Pantepui. For instance, in the superspecies *Myioborus brunniceps* the Andes (Bolivia-Argentina) may have been colonized from Pantepui rather than the reverse, in view of the two endemic species on Pantepui. *Myrmotherula behni* has such a limited toehold in eastern Colombia (Macarena Mountains) that one could imagine it to be a rather recent arrival from Pantepui. If such a species should expand rapidly after reaching the Andes, its Pantepui range would soon seem to be a mere annex to the extensive Andean range, and the original direction of immigration would become completely obscured.

We shall never know the relative size of these groups, but it is certain that there is a continuing shift in the "insular" fauna of Pantepui and that the steady arrival of new species is inevitably compensated for by an equally steady withdrawal or extinction.

RELICT ELEMENTS

Botanists have found many relicts in the flora of Pantepui. There are several definitions for "relict," but a relict is generally considered a remnant of a formerly more widespread and more dominant fauna or flora. Are there any relicts in the Pantepui bird fauna, and, if so, how strong is the relict element?

Obviously, only endemic species can be considered, which leaves only 29 of the total number of 96 species. We have, however, cut this number in half again, because seven species are allopatric to widespread Andean elements, and eight species are altitudinal derivatives of tropical species (for list, see above, p. 290). Among the remaining 14 species are four that are allopatric to species occurring in distant places such as Guatemala, Peru, or Argentina and may therefore rightly be considered relicts, because their occurrence on Pantepui almost certainly indicates a former more widespread occurrence. Such a statement should be even more true for the remaining 10 species, which have no known relatives. But how truly "relict" are these relicts?

It is evident at once that they are relicts only at the species level. There is no "lost world" of birds on Pantepui. The relict fauna does not include a single *good* genus (*Nannopsittaca* and *Roraimia* are both of doubtful validity), much less any primitive genera or families that would be characteristic elements of former geological periods. In fact the "old endemics" belong to the very families (parrots, ovenbirds, antbirds, manakins, and tyrant flycatchers) that appear to be among the currently most actively speciating elements in the bird fauna of South America.

One must conclude, therefore, that the endemic bird fauna of Pantepui does not contain any element that could truly be designated a "relict element," a remnant of formerly dominant types, now elsewhere extinct, such as one finds in such areas as New Zealand or Australia.

If a thorough analysis of the flora of Pantepui should show that there is indeed a difference between the situation in plants and that in birds, one might ask for causes. The fact that the "turnover" of the avifauna is apparently very rapid is one cause. This cause in turn is perhaps due to the fact that a local bird fauna is not an integrated whole, as a local plant association is, to a considerable extent. Species among birds are largely self-sustaining units, each operating independently on the general substrate presented by the local environment. A new arrival is therefore not faced by the problem of having to crash into a largely balanced association (as is the problem of a newly arrived plant), but is merely placed in competition with one or the other of the indigenous species. Too little is yet known about the dynamics of such competition to go beyond this rough outline of possible differences between plants and animals. It is certain, however, that an analysis of the endemic plants of Pantepui, in comparison to the bird endemics, will be of much interest.

SUMMARY

1. THE ISOLATED TABLETOP MOUNTAINS in southern Venezuela (including Roraima and Duida), the adjacent border of Brazil, and Guyana are the home of an interesting highland avifauna rich in endemics. We have designated the area as Pantepui.

2. The history of the ornithological exploration of these mountains, beginning in 1842 with the work of the Schomburgks, is presented. Birds have been collected on a total of 26 cerros and tepuis. Of the approximately 10,750 specimens taken, 8340 are in the Phelps Collection in Caracas.

3. Ninety-six species can be considered typical subtropical elements. Twenty-nine of these are endemic species or superspecies.

4. The subtropical elements are found on the summits and in the cool humid forests of the talus slopes.

5. About two-thirds of the characteristic elements are widely distributed in the Pantepui area. Five species have not yet been found east of the Río Caroní; 18 species are found only to the east of it.

6. Many (viz., 42) species are represented on Pantepui by several subspecies, six in the case of *Atlapetes personatus*, five or four in several other species. Nine of the 29 endemic species are monotypic. Two species have evolved into superspecies.

7. The 96 Pantepui elements represent every stage of endemicity, from endemic genera (two or three weakly characterized ones) and species (29), to non-endemic species with endemic subspecies (55), and non-endemic species without endemic subspecies (12).

8. The 96 Pantepui species can be assigned to four kinds of faunal elements: (a) specialized cliff dwellers (five species), (b) altitudinal derivatives of elements that are tropical in other areas (34), (c) long-distance colonists which reached Pantepui by "hopping" across the unsuitable lowlands (48), and (d) old endemics which may have originated as either (b) or (c) (nine).

9. Many species exhibit strong geographic variation in habitat preference. Basically subtropical species may have tropical populations and vice versa. Such plasticity unquestionably facilitates the crossing of ecological barriers, such as lowlands present for mountain birds.

10. Among the 48 species of long-distance colonists 24 species presumably came from the Andes; 19 species, from the coastal cordilleras of northern Venezuela; and five species, from more distant areas.

11. The small number of old endemics indicates a rapid replacement in the bird fauna of these mountains, which must have existed for some 30 million years.

12. Although a few of the Pantepui endemics can be called relicts, they are not remnants of a formerly more widespread fauna, which is now extinct elsewhere. Most endemics belong to the most actively speciating genera and families of South American birds.

APPENDIX: ANALYTICAL LIST OF THE BIRDS OF PANTEPUI

IN THE FOLLOWING LIST of the 96 species of birds on Pantepui, the abbreviations after the name indicate the following:

AD, altitudinal derivative
E, endemic species
H, long-distance colonist ("hopper")
S, ecological specialist (cliff dweller)

Crypturellus ptaritepui, E, AD

Monotypic endemic species. Perhaps distantly related to tropical and subtropical *C. obsoletus*, which is found in northern Venezuela and the Amazon Valley. No definite statement is possible until the notoriously difficult genus *Crypturellus* has been revised.

Columba fasciata, H

The band-tailed pigeon is a widespread subtropical and temperate-zone element from the Rocky Mountains south to Tucumân (Argentina). No doubt it reached Pantepui by "hopping" from the Andes or the coastal cordilleras. Endemic Pantepui subspecies: *roraimae*.

Pyrrhura egregia, AD

Largely confined to the Pantepui area but also found at tropical altitudes in Guyana. Nearest relative perhaps *P. melanura*. Endemic (*obscura*) and non-endemic subspecies.

"Nannopsittaca" panychlora, E

An old element and a very distinct species. Similar to, but not with certainty congeneric with various species of *Forpus*, *Touit*, and *Brotogeris*, but without any obvious peculiarities that would justify maintenance of a monotypic genus. Not strictly an endemic, because the species is also found in Sucre in northeastern Venezuela.

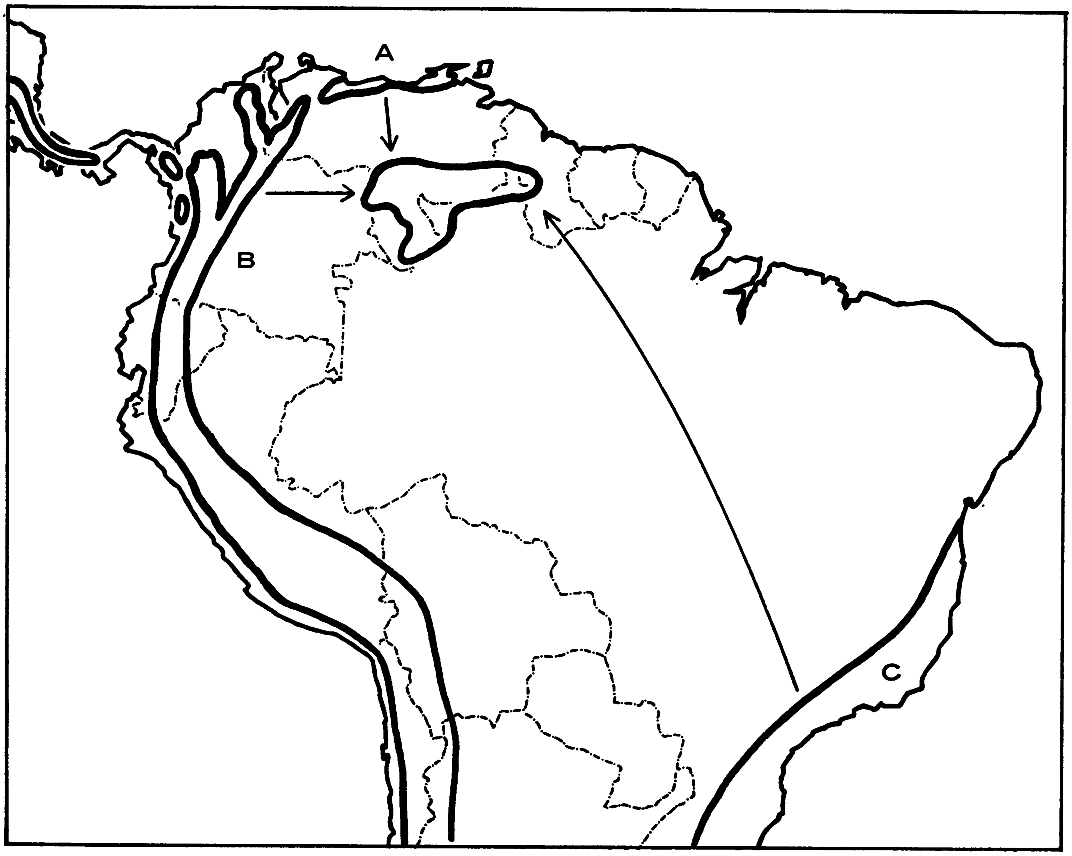


FIG. 1. Sources of colonization of subtropical Pantepui elements. A. Coast ranges of northern Venezuela. B. Eastern Andes. C. Brazilian highlands.

Otus choliba, AD

An essentially tropical species which is very widespread, extending from Costa Rica to Argentina. Altitudinal derivative in western Pantepui: *duidae.*

Otus guatemalae, H

A species with considerable altitudinal range, with the nearest stations in the Paria Peninsula (lowlands to 800 meters) and western Venezuela (Perijá region, lowlands to 2000 meters) and eastern Colombia and Ecuador (upper tropical). Endemic subspecies: *roraimae.*

Glaucidium brasilianum, AD

A widespread tropical owl with altitudinal derivatives (*olivaceum, duidae*) in the Pantepui region.

Caprimulgus longirostris, H

A largely temperate zone species of the Andes, but also in the temperate zone of Argentina and in the arid littoral of Peru. Endemic Pantepui subspecies: *roraimae.*

Caprimulgus whitelyi, E, AD

An endemic species, perhaps ultimately derived from the widespread tropical species *C. nigrescens.* (For the evidence in favor of the specific distinctness of *C. whitelyi,* see Phelps and Phelps, 1948, pp. 190–192.) Known only from Roraima and Ptari-tepui.

Chaetura cinereiventris, S

A widespread tropical-subtropical species, the distribution of which may be determined more by special ecological conditions than by altitude. Subspecies *guianensis* endemic in Venezuelan and Guyanan highlands.

Cypseloides rutilus, S

Widespread tropical species, occurring where conditions are suitable.

Aeronautes montivagus, S

Ranging in the mountains from Bolivia to northern Venezuela. The type of *tatei,* described from Duida, agrees with a series of birds from the north coast ranges of Venezuela (Aragua, Miranda, Perijá Mountains). Not yet critically compared with nominate *montivagus* to confirm validity of *tatei.*

Doryfera johannae, H

Upper tropical-subtropical zone of the eastern Andes to Macarena. Endemic subspecies on Pantepui: *guianensis.* Absent from intervening area. See text figure 2.

Phaethornis bourcieri, AD

Tropical and upper tropical from upper Amazon basin to the Guianas; the non-endemic subspecies *whitelyi* occurs on many tepuis (up to 1600 meters) but also in southeastern Colombia, upper Rio Negro, Guyana, Surinam, and French Guiana.

Phaethornis augusti, H

Subtropical zone, from the eastern Andes of Colombia to coast ranges of northern Venezuela (to Paria Peninsula); an endemic subspecies on Pantepui: *incanescens.*

Superspecies **Campylopterus hyperythrus**

Campylopterus duidae, E

Peters (1945, p. 20) considered the two forms conspecific. The Guaiquinima subspecies is closer to *duidae.* The nearest relative of this Pantepui endemic is *C. rufus* (Guatemala), as was correctly remarked by Zimmer and Phelps (1946, p. 6), but the relationship is not very close.

Colibri coruscans, H

Widespread in the subtropical and arid temperate zones of the Andes. Two endemic subspecies (*germanus, rostratus*) on Pantepui.

Lophornis pavonina, E, H

An endemic species with three subspecies on Pantepui. Distantly related to *L. chalybea,* a subtropical species of the eastern slope of the Andes.

Polytmus milleri, E, AD

A monotypic endemic species, originally described as an endemic genus (*Waldronia*). A fairly closely related altitudinal derivative of the tropical species *P. guainumbi* (Venezuela, Guianas, and parts of eastern and central Brazil).

Amazilia viridigaster, H

Upper tropical on the eastern slope of the Andes in Colombia and Venezuela (Táchira); two endemic subspecies on Pantepui: *cupreicauda* and *duidae.*

Heliodoxa xanthogonys, E, H

A monotypic endemic species, more closely related to *H. jacula* (subtropical of eastern Andes) than to the two other species of this genus.

Trogon personatus, H

Widespread in the subtropical and temperate zones of the Andes (see Zimmer, 1948). Three endemic subspecies on Pantepui. See text figure 3.

Aulacorhynchus derbianus, H

Subtropical zone of eastern Andes. Three

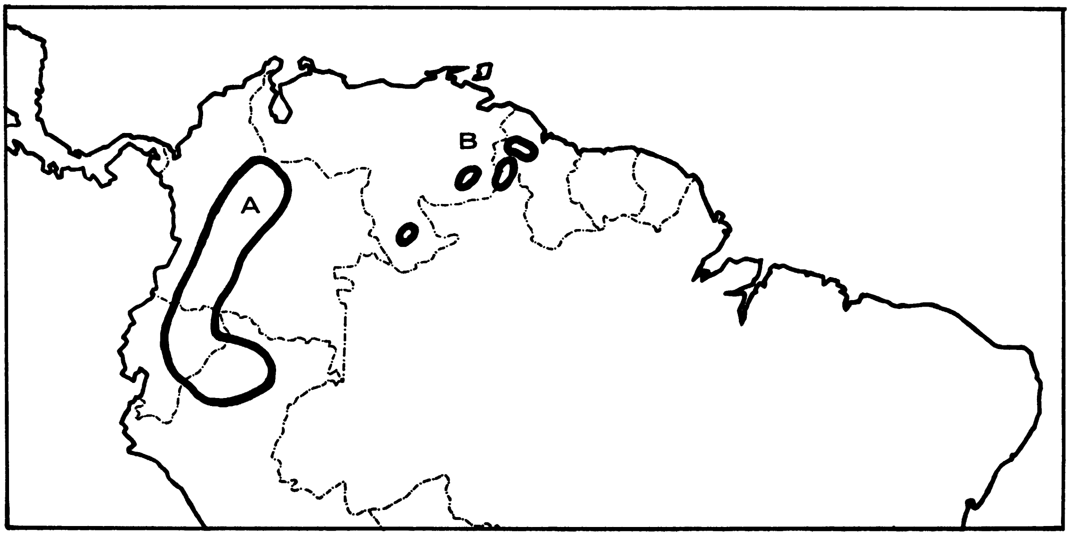


FIG. 2. Distribution of *Doryfera johannae*. A. *Doryfera johannae johannae*. B. *Doryfera johannae guianensis*.

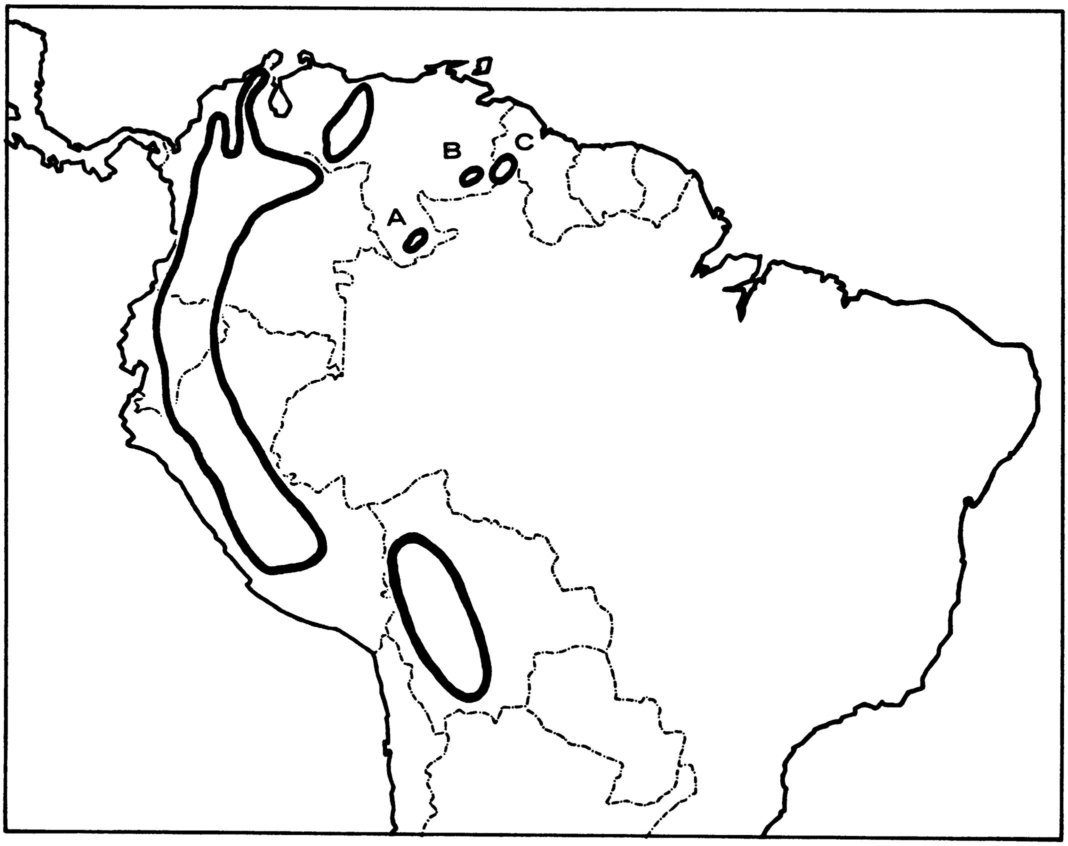


FIG. 3. Distribution of *Trogon personatus*. The three subspecies of Pantepui are: A, *duidae;* B, *ptaritepui;* C, *roraimae*.

endemic subspecies in the area of Pantepui and adjacent Guyana. See text figure 4.

Piculus rubiginosus, H

Widespread in the subtropical zone of Central America, the Andes, and Venezuelan coast ranges; occasionally in the arid tropical zone. Several essentially endemic subspecies in Pantepui (*guianae*, *paraquensis*), including an upper altitudinal derivative (*viridissimus*). *Piculus rubiginosus guianae* is also found in the tropical zone of Guyana. Occurrence of a race in the Orinoco delta suggests another possible route of immigration.

Veniliornis kirkii, AD

Tropical from Costa Rica to western Ecuador. Northern Venezuela and Trinidad are the points in the range of this species nearest to the endemic subtropical Roraima subspecies (*monticola*, 1500 meters to 1800 meters).

Xiphocolaptes promeropirhynchus, AD

An ecologically heterogeneous species. Largely restricted to the subtropical and temperate zone in the coastal ranges, and the Andes, but occurs on the south bank of the Amazon in the tropical zone (*berlepschi* and *paraensis*), and likewise on the north bank between the upper Amazon and the Orinoco (*orenocensis*). Of the two Pantepui endemics one (*tenebrosus*) occurs at the upper tropical level (700 meters to 1200 meters); the other (*neblinae*) is definitely subtropical (1800 meters).

Synallaxis moesta, H

Upper tropical and subtropical zones of the Andes and a few scattered localities in Venezuela and the Guianas. Three endemic subspecies in Pantepui (*macconnelli*, *griseipectus*, *yavii*). The late Dr. Zimmer kindly informed us that the supposed overlap between "*cabanisi*" and *moesta* is due to a misidentified specimen. *Synallaxis cabanisi* is conspecific with *S. moesta*.

Cranioleuca curtata, H

Subtropical zone of the Andes. A very distinct endemic subspecies on Pantepui: *demissa*.

"Roraimia" adusta, E

Endemic species and generally listed as endemic genus, but generic splitting seems to have been carried too far in the *Margarornis-Premnoplex*

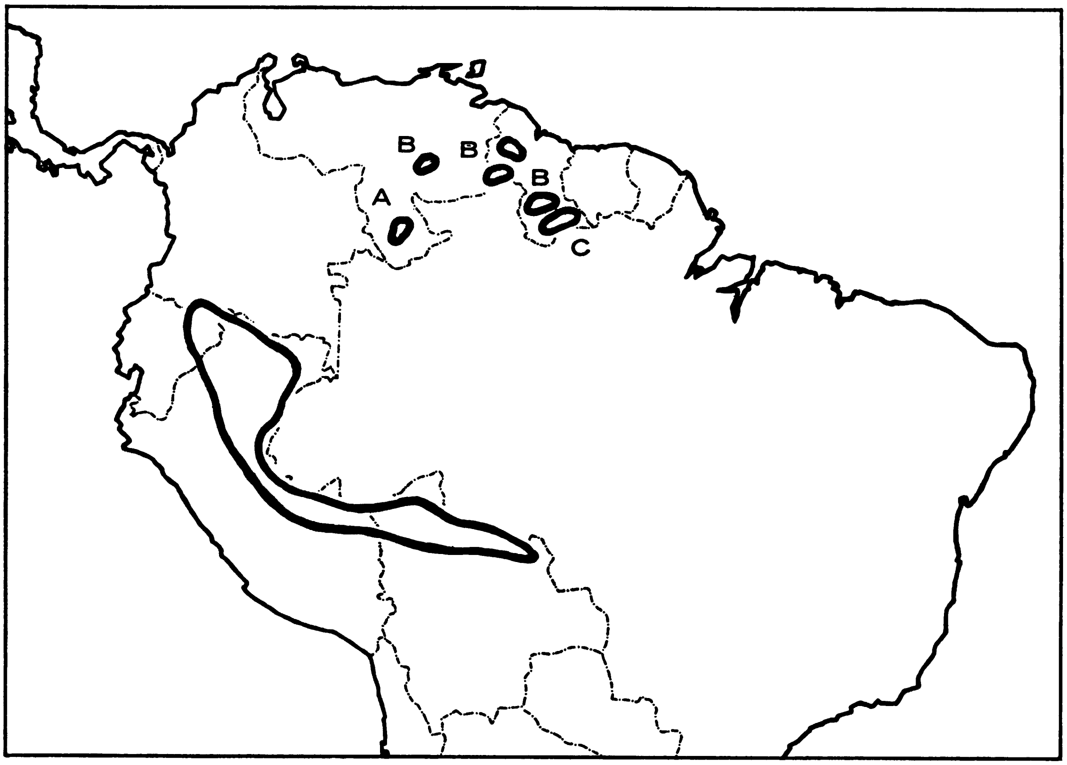


FIG. 4. Distribution of *Aulacorhynchus derbianus*. The three subspecies of Pantepui and adjacent Guyana are: A, *duidae;* B, *whitelianus;* C, *osgoodi.*

complex to which *Roraimia* belongs. *Roraimia*, *Premnornis*, and *Premnoplex* certainly appear to be congeneric. Distantly related to *Premnoplex brunnescens* (subtropical zone of northern Venezuela and of the Andes). Three endemic subspecies: *adusta*, *duidae*, *obscurodorsalis*.

Philydor hylobius, E

Known only from the Cerro de la Neblina. Most nearly related to *P. atricapillus* from eastern Brazil (Bahia and Minas Gerais), Paraguay, and northern Argentina (Wetmore and Phelps, 1956, pp. 2–4).

Automolus roraimae,[1] E

Distantly related to *A. ruficollis* (arid subtropical species of Andes) and *A. ochrolaemus* (widespread in tropical zone). Three endemic subspecies: *roraimae*, *duidae*, *paraquensis*.

Lochmias nematura, H

Upper tropical and subtropical zones in suitable habitat from Panama to Argentina. Andes and coastal ranges of Venezuela eastward only to Caracas region. Two endemic subspecies: *castanonota*, *chimantae*.

Taraba major, AD

A widespread, essentially tropical species. An altitudinal derivative endemic on Pantepui: *duidae*.

Thamnophilus insignis, E, AD

Endemic species with two subspecies. No obvious close relatives, but perhaps distantly related to *T. amazonicus* (tropical Amazonia).

Dysithamnus mentalis, AD

Widespread tropical-subtropical species from Mexico to Argentina. Altitudinally derived Pantepui endemics (*spodionotus*, *ptaritepui*); nearest lowland stations (Sierra de Imataca, Río Cuyuni).

Myrmotherula behni, H

Upper tropical species, eastern Colombia. Three endemic subspecies at Pantepui (*inornata*, *yavii*, *camanii*) and adjacent northern Brazil (Serra Parima; Novaes, 1965).

Herpsilochmus roraimae, E, AD

Monotypic endemic species. Altitudinal derivative of tropical *H. dorsimaculatus*, from which it differs by having the tail about 20 per cent larger, more gray in the plumage, and the tail not solid black but with about seven light bars.

[1] *Philydor albigularis* Salvin and Godman, 1884, is preoccupied by *Philydor albogularis* Spix, 1824 (=*Automolus leucophthalmus* Wied, 1821).

Percnostola leucostigma, AD

A widespread tropical and upper tropical species with two altitudinally derived endemic Pantepui subspecies (*saturata*, *obscura*).

Chamaeza campanisona, H

Upper tropical and subtropical species of south Brazil, the Andes, and mountains of northwestern Venezuela (eastward to Miranda). Four endemic subspecies on Pantepui. See text figure 5.

Grallaricula nana, H

Subtropical Andes and coast ranges of northern Venezuela. Endemic subspecies on eastern Pantepui (*kukenamensis*), more closely related to Paria than to Andean subspecies.

Myrmothera simplex, E, AD

Endemic species with three subspecies. Distantly related to the only other congeneric species, *M. campanisona*, of tropical upper Amazonia.

Grallaria guatimalensis, H

Widespread upper tropical and subtropical species with irregular distribution. The Andes of Mérida and Trinidad are the stations nearest to Pantepui where an endemic subspecies occurs (*roraimae*, also Serra da Curupira, northern Brazil).

Pipreola whitelyi, E

Endemic species, with two subspecies. Very different from the other congeneric species.

Acrochordopus zeledoni, H

Subtropical species, eastern Andes, Costa Rica, and coast ranges of northern Venezuela. An endemic subspecies (*bunites*) is found on Chimantá-tepui. The coast range also has an endemic subspecies (*viridiceps*).

Lipaugus streptophorus, E, AD

Monotypic endemic species. Only very distantly related to tropical *L. cineraceus* which lacks the bright pink pattern. *Lipaugus cineraceus* is one of the most conspicuous birds of the forest, with a loud, explosive whistle, whereas *L. streptophorus* has a quiet, subdued song.

Pachyrhamphus castaneus, AD

A widespread upper tropical species. One widespread subspecies (*saturatus*) occurs at lower altitudes in the eastern part of Pantepui; an endemic altitudinal derivative is restricted to Parú (*parui*).

Pipra serena, AD

An essentially tropical species (Guianas, northeast Amazonia), with an altitudinally derived

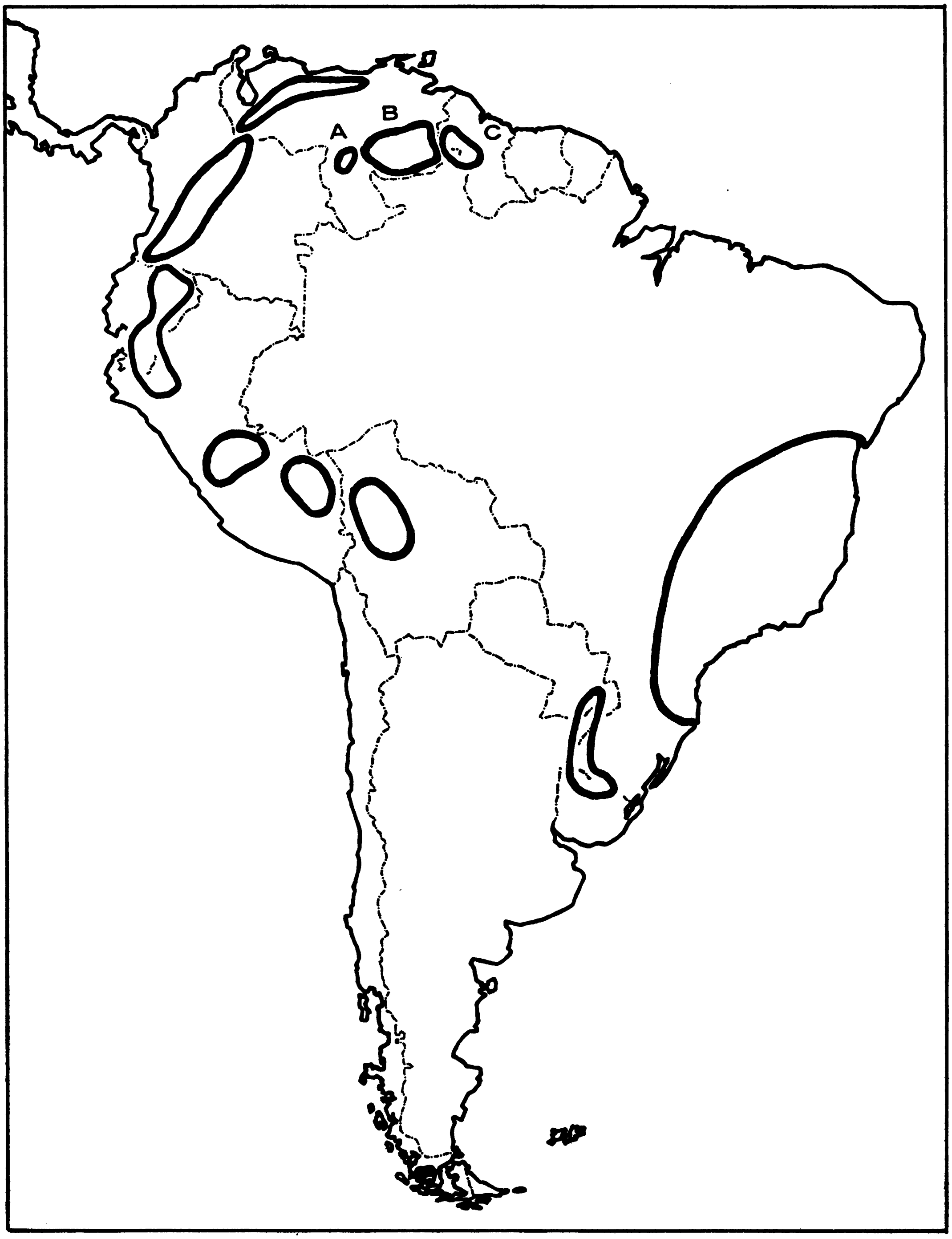


FIG. 5. Distribution of *Chamaeza campanisona*. The three endemic subspecies of Pantepui are: A, *yavii;* B, *obscura;* C, *fulvescens.*

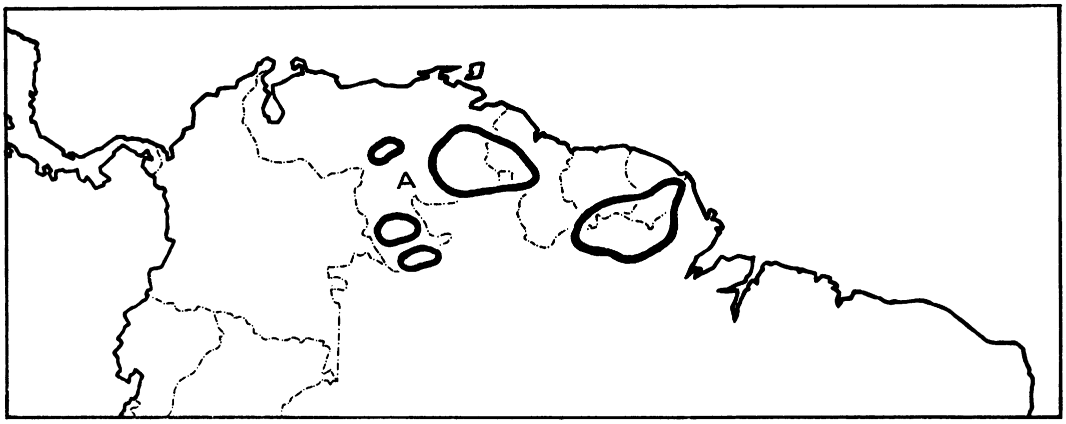


FIG. 6. Distribution of *Pipra serena*. A. Altitudinal endemic on Pantepui: *suavissima*.

endemic on Pantepui (*suavissima*). See text figure 6.

Chloropipo uniformis, E

Endemic species with two races. No close relative.

Ceratopipra cornuta, E

Monotypic species, essentially endemic in Pantepui, but not entirely restricted to it (occurs also at Obidos and elsewhere). An old "relict" endemic, without obvious relatives.

Knipolegus poecilurus, H

Subtropical zone, from Peru to coast ranges of northern Venezuela (eastward only to Caracas region). Also tropical zone of northern Brazil (Rio Igana). Two endemics on Pantepui: *salvini*, *paraquensis*.

Contopus fumigatus, H

Subtropical zone, from northwestern Argentina to the coast ranges of northern Venezuela (eastward only to Caracas region). One endemic race: *duidae*.

Myiophobus roraimae, H

Long considered a Pantepui endemic, but now recognized as an Andean species. The subspecies *roraimae* has been reported from Caño Cubiyú and Caño Negro, Territorio Vaupés, southeastern Colombia (Olivares, 1964, p. 174); the subspecies *rufipennis* Carriker from La Oroya, Sândiaz, Departamento Puno, Peru. More distantly related to *M. fasciatus* (tropical) and *M. rufescens* (arid tropical).

Hirundinea ferruginea, S

Widespread on the upper tropical and subtropical zones where suitable habitat (cliffs) is available. Also found on precipices in the Guianas and northern Brazil (Rio Negro).

Platyrhynchus mystaceus, AD

A widespread mostly tropical species. Three altitudinally derived endemic subspecies: *ptaritepui*, *duidae*, *ventralis*.

Todirostrum russatum, E, H

Monotypic endemic species. Fairly closely related to *T. plumbeiceps* of south Brazil and Argentina.

Idioptilon margaritaceiventer, AD

Widespread tropical, partly tropical savanna. Two endemic subspecies: *auyantepui*, *duidae*. Nearest occurrence northern Venezuela (Zulia to Sucre) and Maranhão, Brazil. *Euscarthmornis* is a synonym.

Phylloscartes chapmani, E

Endemic species with two subspecies. No near relative.

Phylloscartes nigrifrons, E

Monotypic endemic species. Distantly related to *P. ventralis* (Guianas and southern Brazil to Peru).

Mecocerculus leucophrys, H

Widespread, temperate and subtropical zones, including coast ranges of northern Venezuela (east to Sucre). Two endemic subspecies: *roraimae*, *parui*.

Elaenia ruficeps, AD

Monotypic species widespread in tropics of Guianas and northwestern Brazil. On Pantepui altitudinal populations without morphological change.

Elaenia dayi, E, H

Endemic species with three subspecies. Perhaps more nearly related to *E. obscura* (southern Brazil to Peru) than to *E. frantzii* (subtropics of Colombia, north Venezuelan coast ranges, and Central America).

Elaenia pallatangae, H

Subtropical and temperate zones of Andes. Endemic subspecies on Pantepui: *olivina.*

Pipromorpha macconnelli, AD

Tropical and upper tropical Guianas and lower Amazonia. An altitudinally derived endemic subspecies on Pantepui: *roraimae.*

Oxyruncus cristatus, H

Widely scattered, essentially subtropical. Two endemic subspecies on Pantepui (*hypoglaucus, phelpsi*). See Chapman (1939a) for a discussion of the distributional history of this species.

Atticora (Notiochelidon) cyanoleuca, S

An extremely widespread species, Patagonia to Costa Rica, temperate and subtropical zones. Occurrence on Pantepui apparently due to ecological factors (cliff nesting). The same subspecies occurring on Trinidad and from Costa Rica to Argentina and south Brazil.

Cistothorus platensis, H

A widespread temperate and subtropical species. Pantepui birds not subspecifically different from those of the coast range (east to Monagas) and eastern Andean subspecies (*alticola*).

Thryothorus coraya, AD

Tropical and upper tropical (occasionally subtropical) species, widespread in Guianas and Amazonia; subtropical altitudinal derivative (*obscurus*) endemic on Pantepui; others (*ridgwayi, caurensis*) are upper tropical.

Superspecies **Troglodytes solstitialis**

Troglodytes rufulus, E, H

The widespread, subtropical-temperate zone, Andean species *T. solstitialis* is represented on Pantepui by an allopatric species, *T. rufulus* (five subspecies). See text figure 7.

Microcerculus ustulatus, E, AD

Endemic with four subspecies. Very closely related to and evidently derived from tropical-subtropical *M. marginatus,* Central America to Andes of Ecuador and Venezuela and northern coast ranges.

Turdus ignobilis, AD

A tropical species, widespread in Amazonia, northern Venezuela, and the Guianas. An altitudinally derived endemic subspecies: *murinus.*

Turdus olivater, H

A subtropical species, occurring in the Colombian and Venezuelan Andes and in the coast ranges of northern Venezuela. Three endemic Pantepui subspecies. See text figure 8.

Platycichla flavipes, H

A widespread subtropical species, south Brazil to Venezuelan coast ranges and Trinidad. One endemic subspecies (*polionota;* 1200 meters to 1800 meters) and one (*venezuelensis*) also occurring on the north coast ranges.

Platycichla leucops, H

Subtropical zone of the Andes and north coast range. Monotypic species. See text figure 9.

Myadestes (=Cichlopsis) leucogenys, H

Scattered distribution in the upper tropical zone. Endemic Pantepui subspecies: *gularis.* Nearest occurrence of species is in southern Brazil and Peru. See text figure 10.

Hylophilus sclateri, E, AD

Monotypic endemic species. Only distantly related to *H. pectoralis* (tropical Guianas and Brazil).

Diglossa duidae, E, H

Endemic species with two subspecies. Although allopatric with *D. major* (see next species), this species may be the product of an independent invasion from the Andes. It is impossible to determine which Andean species is nearest to *duidae* until the genus *Diglossa* has been properly monographed. *Diglossa carbonaria* (temperate zone of the Andes) is probably the closest relative.

Diglossa major, E, H

Endemic species with four subspecies. A very isolated species, probably not particularly close to *D. duidae.*

Parula pitiayumi, AD

A widespread tropical and subtropical species, virtually conspecific with *P. americana,* the Parula Warbler. Endemic subspecies (*roraimae*) is an altitudinal derivative.

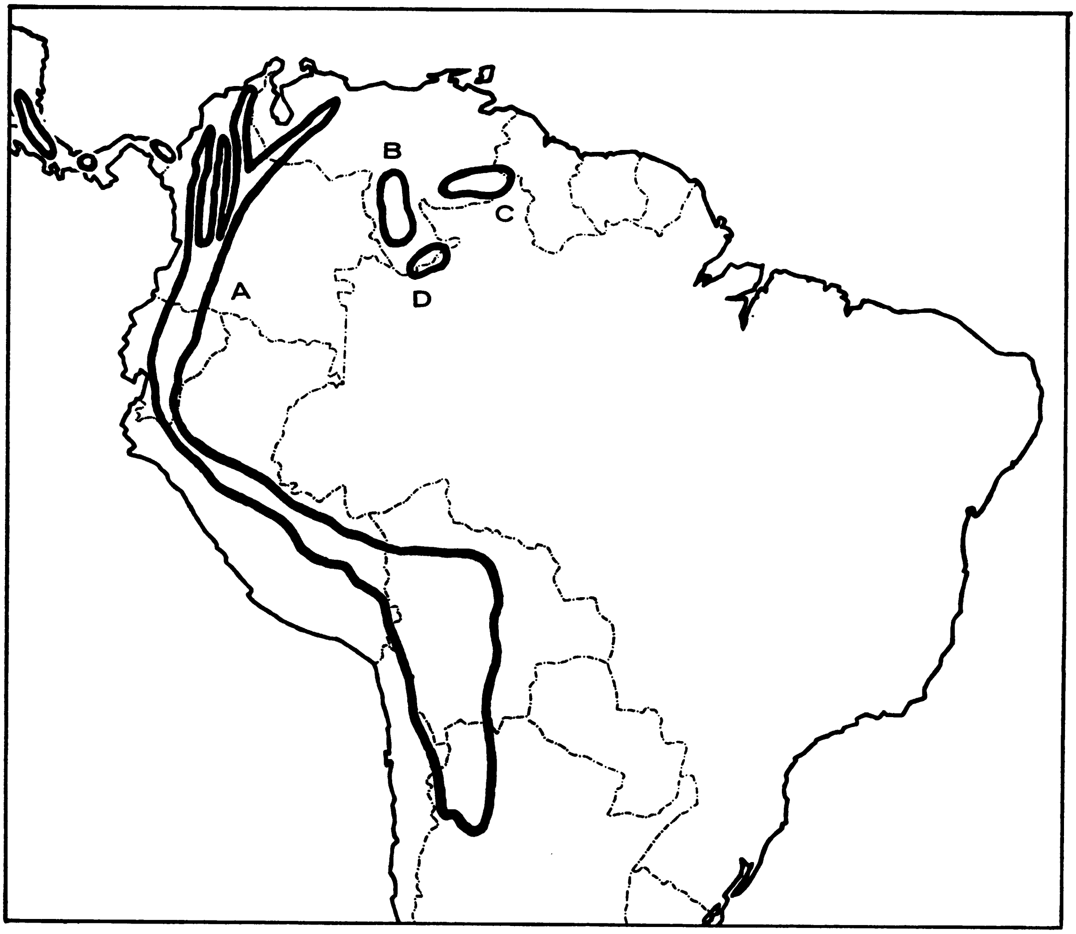


FIG. 7. A. Distribution of *Troglodytes solstitialis*. Distribution of the derived *T. rufulus* with its subspecies: B, *duidae* and *yavii;* C, *rufulus* and *fulvigularis;* D, *wetmorei*. For individual subspecies, see Phelps and Phelps (1963, pp. 269–270).

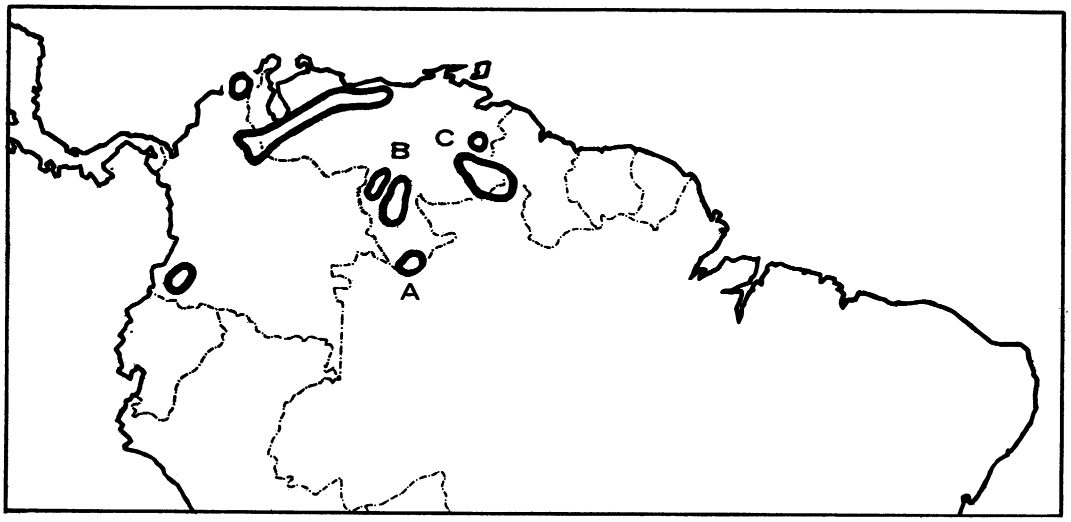


FIG. 8. Distribution of *Turdus olivater*. The three endemic subspecies on Pantepui are: A, *kemptoni;* B, *duidae;* C, *roraimae.*

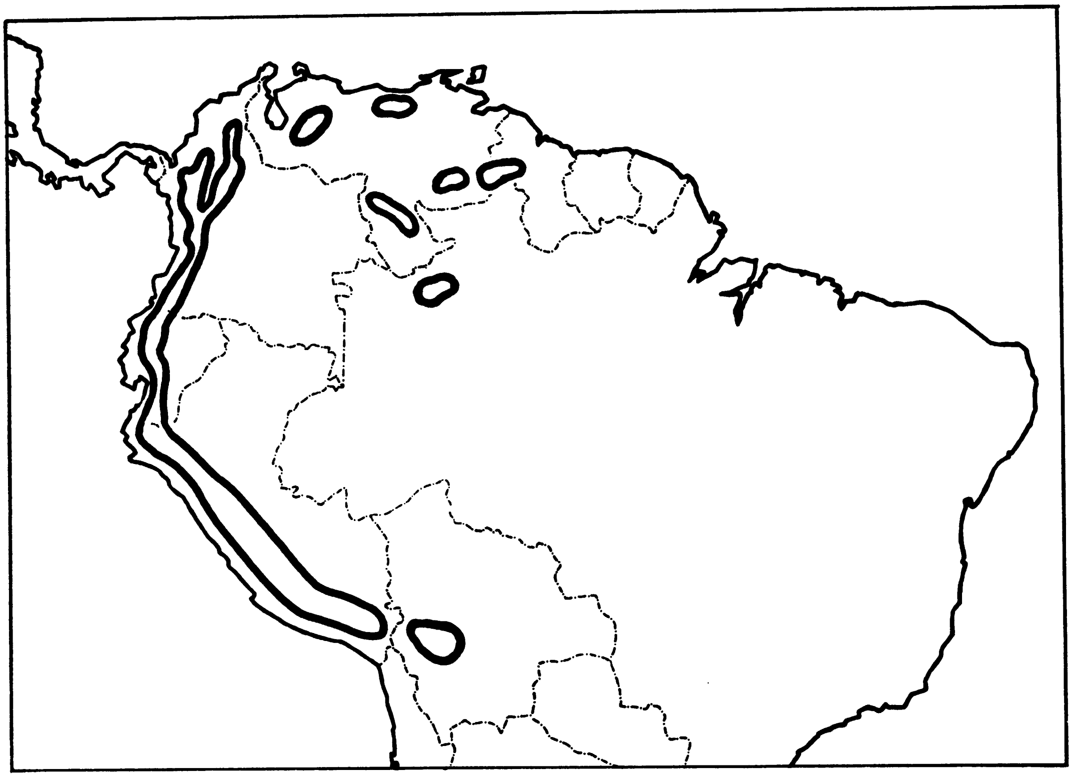


FIG. 9. Distribution of *Platycichla leucops*, a monotypic species.

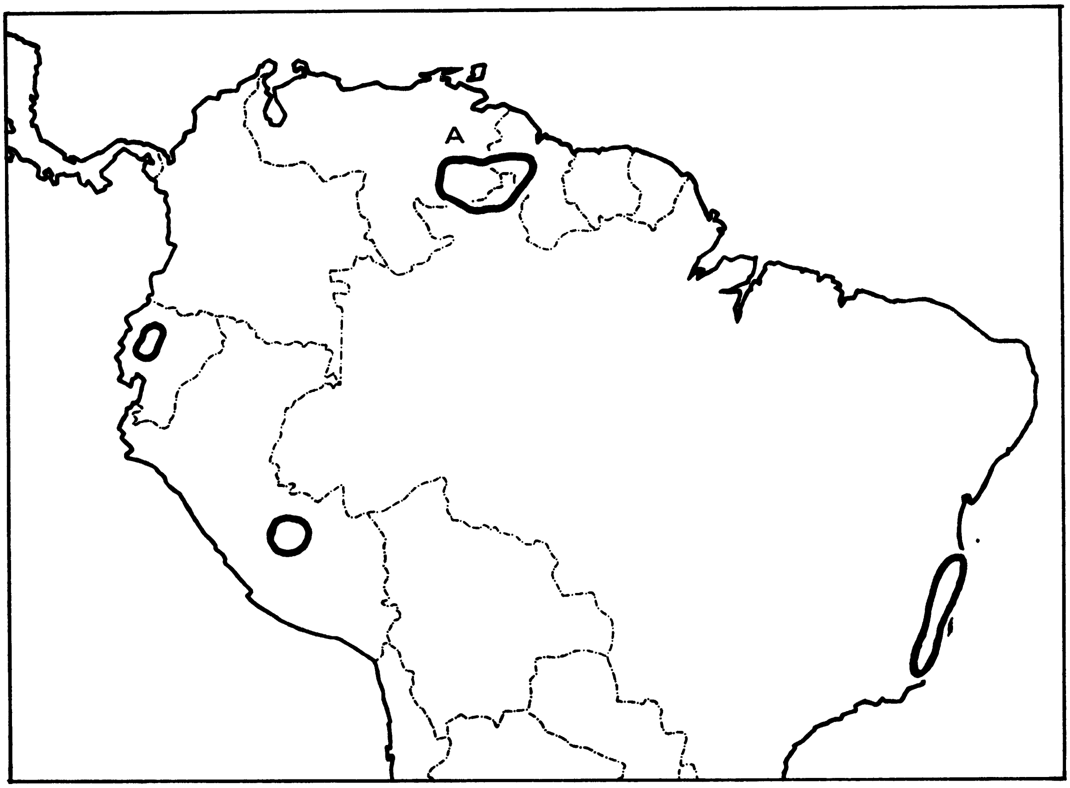


FIG. 10. Distribution of *Myadestes* (*Cichlopsis*) *leucogenys*. A. Endemic Pantepui subspecies: *gularis*.

Myioborus miniatus, H

Widespread subtropical species. The Pantepui population (*verticalis*) is subspecifically identical with birds from parts of the Andes, whereas endemic races occur on the north coast ranges and Venezuelan Andes.

Superspecies Myioborus brunniceps,

Myioborus cardonae, E, H

Myioborus albifacies, E, H

Two endemic allopatric species in Pantepui (*cardonai*, *albifacies*), the subtropical Andean (Bolivia, Argentina) *M. brunniceps* (with three endemic subspecies in Pantepui), and *M. pariae* (Paria Peninsula) form this superspecies. Degree of relationship with the allied *M. melanocephalus-albifrons* complex remains to be determined.

Basileuterus bivittatus, H

The endemic subspecies (*roraimae*) on Pantepui is widely separated from the range of the remainder of the species: upper tropical zone, from Argentina through Bolivia to southeastern Peru.

Macroagelaius subalaris, H

Temperate zone of Colombian Andes. A very

FIG. 11. Distribution of *Pipraeidea melanonota*. A. The occurrence of the Andean subspecies, *venezuelensis*, in Pantepui.

distinct endemic subspecies (*imthurni*) on Pantepui (de Schauensee, 1951, p. 993).

Chlorophonia cyanea, H

Widespread in the subtropical zone of the Andes from Bolivia to Venezuela, in subtropical southern Brazil, Paraguay, and Argentina, and in the coast ranges of Venezuela. One widespread Pantepui endemic (*roraimae*).

Pipraeidea melanonota, H

Subtropical zone of Andes and coastal ranges of Venezuela. The widespread Andean *venezuelensis* (Venezuela to Argentina), subspecifically identical, occurs on Yaví and Taracuniña. See text figure 11.

Tangara chrysophrys, H

Subtropical and upper tropical zones, from Costa Rica to the Andes of Colombia and the Venezuelan coast ranges. Of the two Pantepui subspecies, one (*guttata*) is endemic; the other (*chrysophrys*) is also found on the northern Venezuelan coast ranges. See text figure 12.

Tangara xanthogastra, AD

Widespread in tropical western Amazonia from Colombia and Venezuela to northern Bolivia. An endemic altitudinal derivative (*phelpsi*) in Pantepui.

Tangara gyrola, AD

Widespread in the tropical zone of Guianas and Amazonia. Non-endemic altitudinally derived populations on Pantepui.

Tangara cyanoptera, H

Subtropical northern Venezuela (coast ranges and Andes) and Santa Marta region. Endemic subspecies on Pantepui: *whitelyi*.

Piranga flava, H

Widespread tropical and subtropical species ranging from Arizona to Argentina. The endemic Pantepui subspecies (*haemalea*) is more similar to the subspecies from the subtropical zone of the western Andes of Colombia (*desidiosa*) than to that of the coast range (*faceta*) or to the adjacent tropical subspecies (*macconnelli*) of the Guianas and northern Brazil.

Mitrospingus oleaginus, E, AD

Endemic species with two subspecies. Related to tropical *M. cassini* (western Ecuador to Panama and Costa Rica).

Catamenia homochroa, H

Temperate-zone Andean species (Venezuela and Colombia to Bolivia). Endemic Pantepui subspecies: *duncani*.

Spinus magellanicus, AD

Pantepui subspecies (*longirostris*) an altitudinal representative of a widespread savanna species.

Spodiornis rusticus, H

Species widespread in subtropical Andes and Central America. A single Pantepui record (endemic subspecies *arcanus*). See text figure 13.

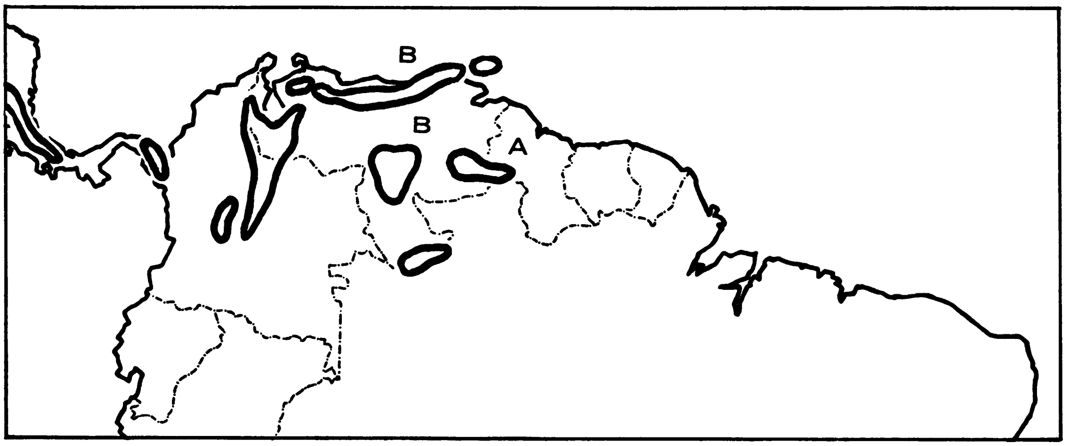


FIG. 12. Distribution of *Tangara chrysophrys*. Two subspecies are represented in Pantepui: A, the endemic *guttata;* B, *chrysophrys*, also found on the northern coast ranges of Venezuela.

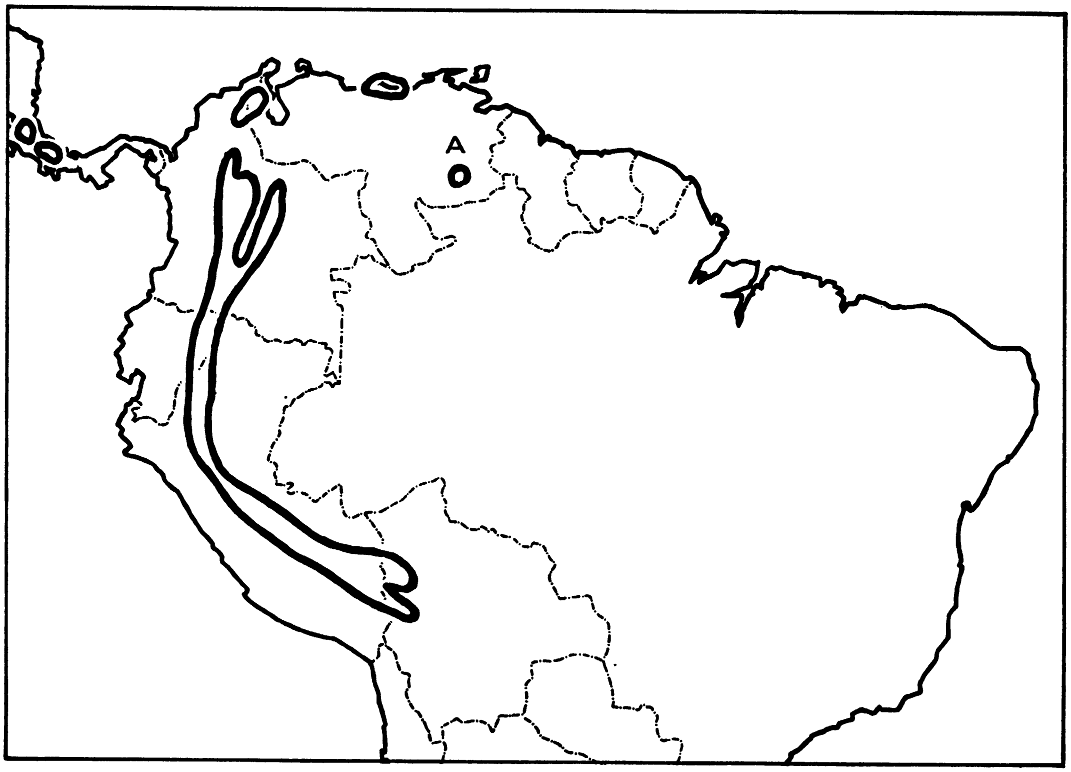


FIG. 13. Distribution of *Spodiornis rusticus*. A. Endemic Pantepui subspecies: *arcanus*.

Atlapetes personatus, E, H

Endemic species, with six Pantepui subspecies. Closely related to *A. fulviceps* of Bolivia and northwestern Argentina.

Zonotrichia capensis, AD

Widespread species (see Chapman, 1940). One Pantepui subspecies (*roraimae*) widespread in upper tropical and subtropical localities of the Pantepui area (extending into Guyana and northern Brazil); two others (*macconnelli* and *inaccessibilis*) are altitudinal derivatives.

Emberizoides herbicola, AD

Pantepui subspecies (*duidae*) an altitudinal derivative of a widespread, tropical-subtropical, grassland species.

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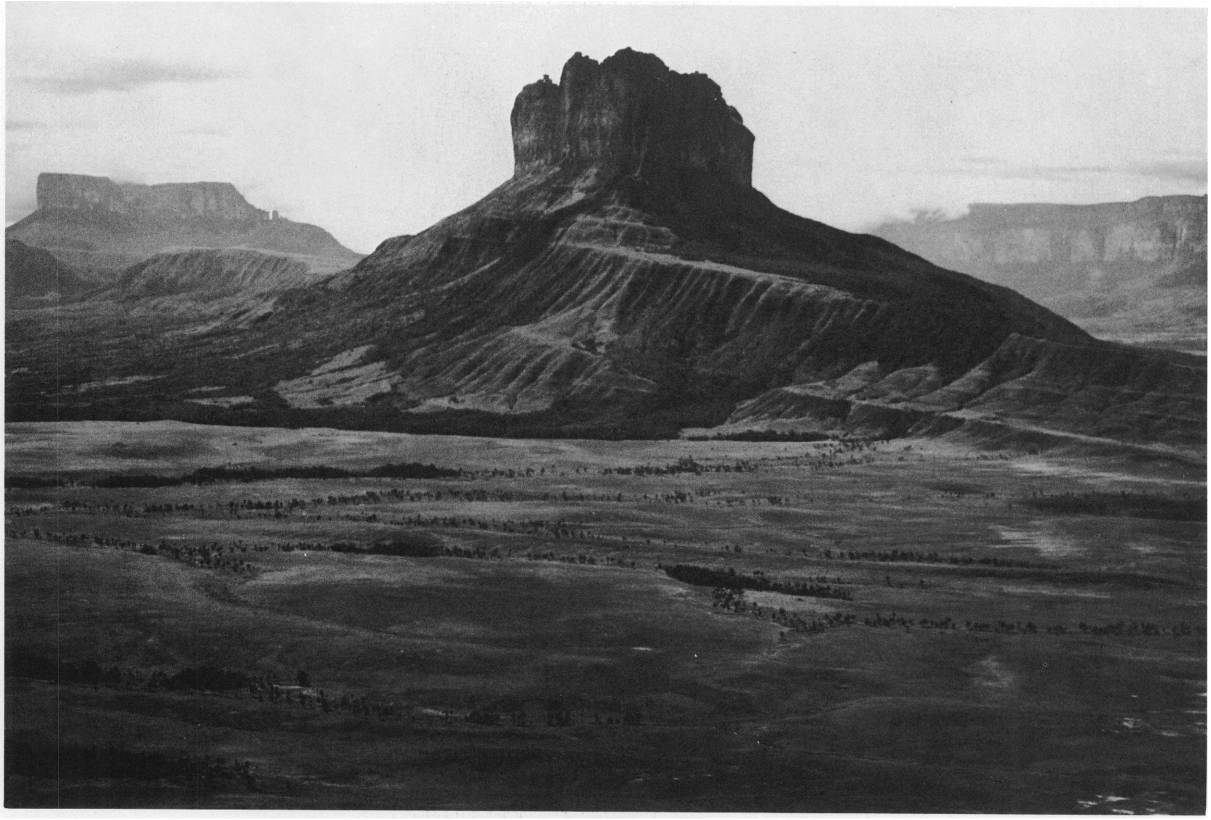
1

2

1. Roraima. View approximately to the east, from the savannas on the Venezuelan side
2. Roraima. View, approximately toward the north, of the cliffs on the southwestern side. Cerro Cuquenám is on the left. The path of access to the summit of Roraima is along the base of the upper cliffs on the extreme right, continuing under the waterfall shown on the right, and up the steep slope to the left of the waterfall

1

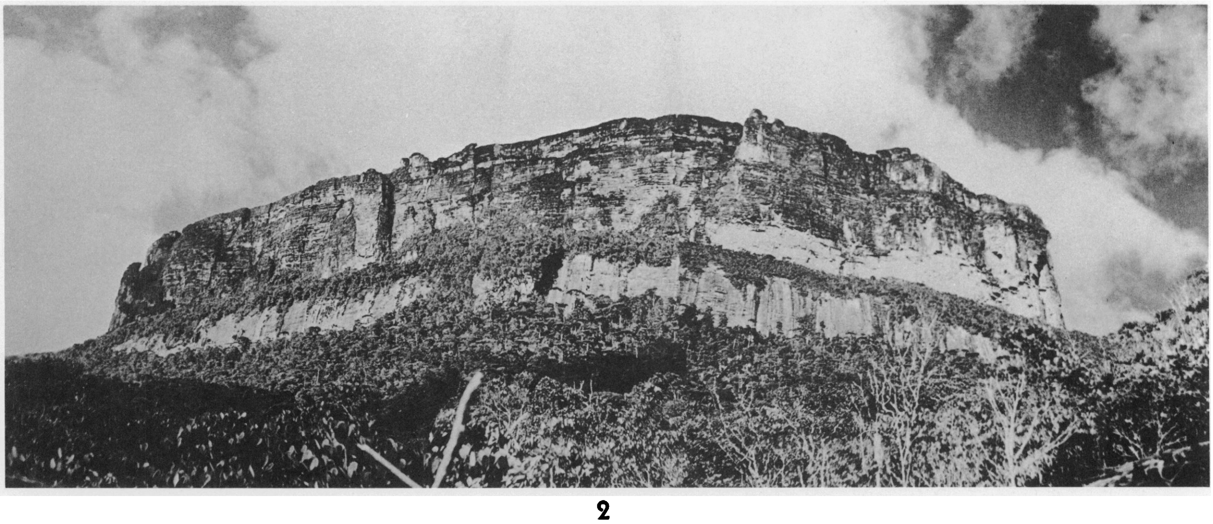


2

1. Cerro Upuigma-tepui on the left and cliffs of Acopán-tepui on the right. Characteristic tepui landscape. The sandstone cliffs, the heavily wooded talus slopes, and the peneplains from which the tepuis rise are well developed. Peneplains either are savannas (particularly in the northeast) or are more or less heavily wooded

2. Cerro Upuigma-tepui. Cerros Angasima-tepui on the left and Acopán-tepui on the right. Cliffs, talus slopes, and plateaus

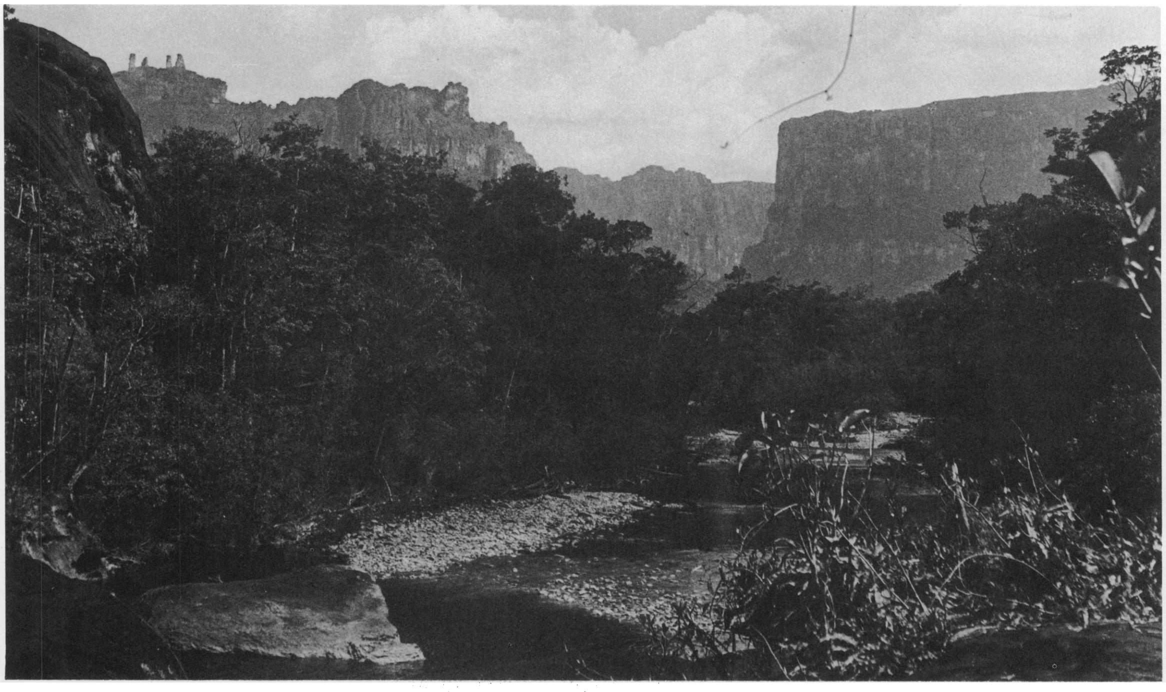
1



2

1. Sororopán-tepui. Burned forest has not yet recovered after 40 years. Heavy bracken covers the ground between charred treetrunks. From a photograph taken in 1966

2. Cerro Ptari-tepui. View from the south. A tepui with a perpendicular solid rock wall that has not yet been scaled

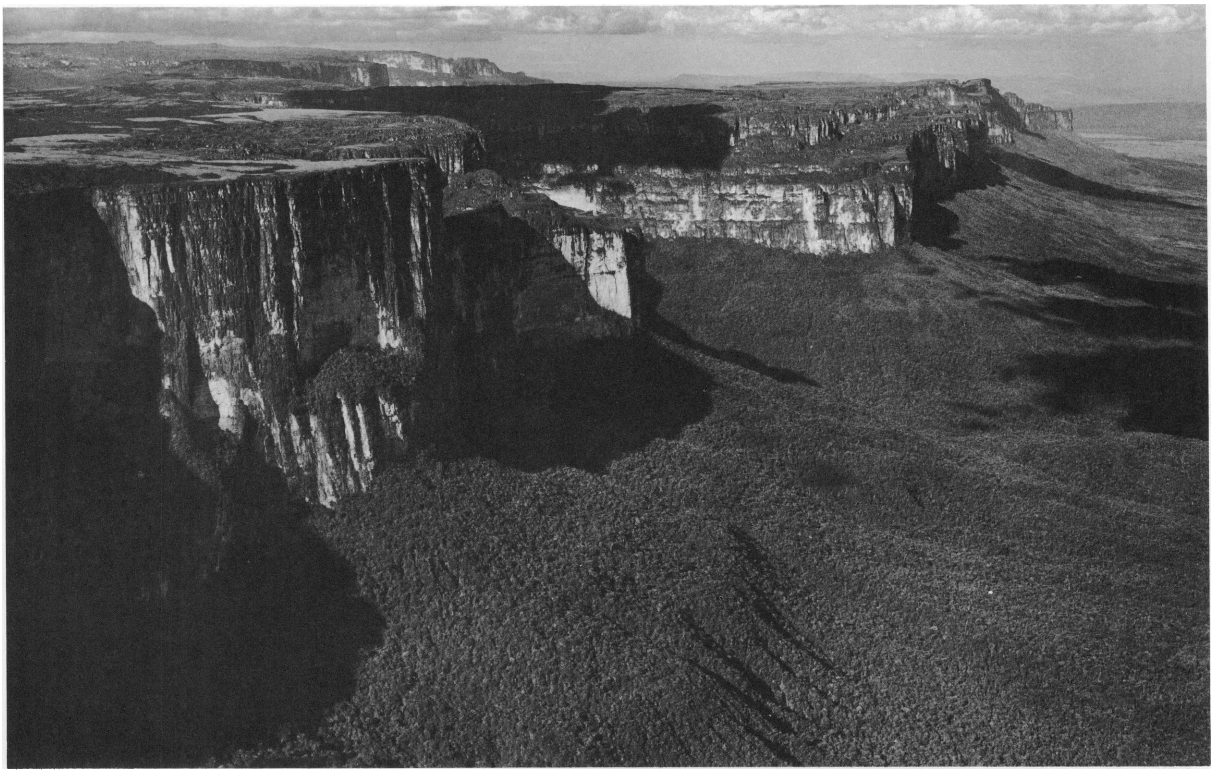


1

2

1. Cliffs of Cerro Auyán-tepui from the Churún River, near the base of Angel Falls. Rich, well-watered forests are found on the talus slopes of most tepuis

2. Cerro Auyán-tepui, south face. The talus slopes consist of a series of steps. Gallery forests are well developed along rivers and in ravines



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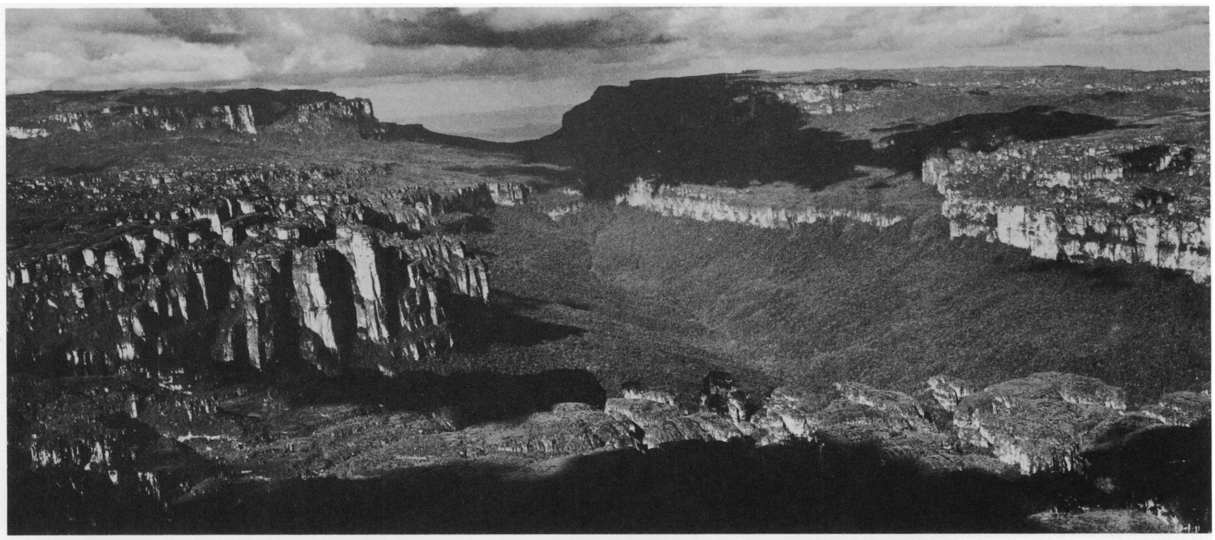
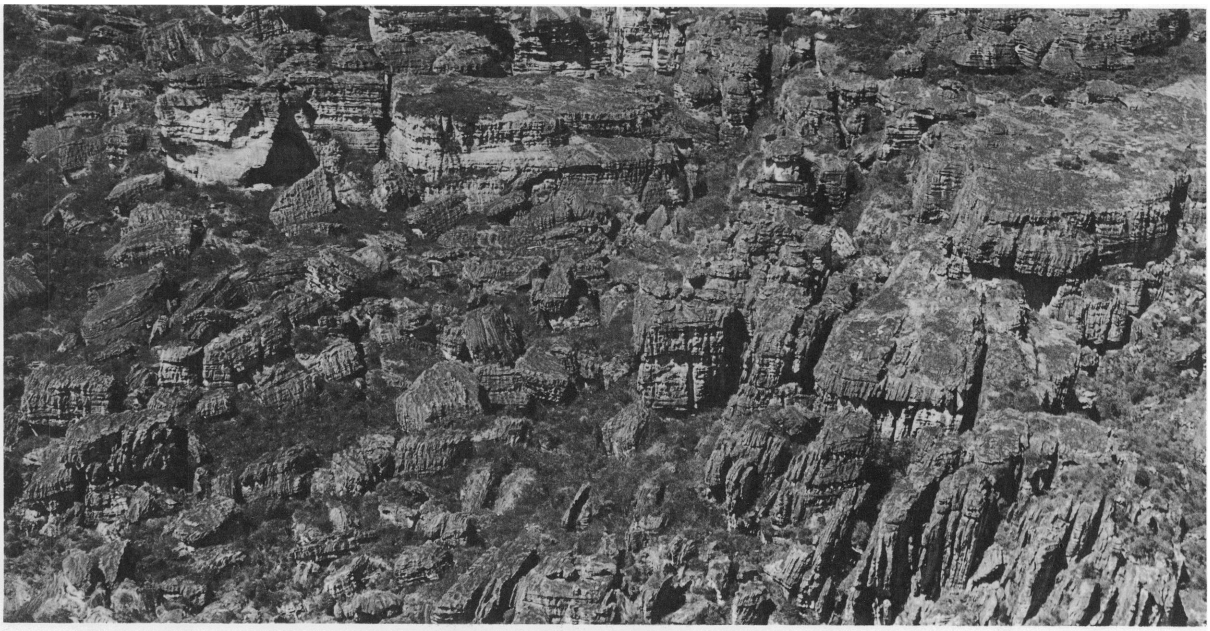


2

1. Cerro Auyán-tepui, showing the summit plateau, the broken rock wall, and the magnificent forest of the talus slopes
2. Cerro Auyán-tepui, summit. Part of the summit plateau is occupied by larger valleys and by individual mesas



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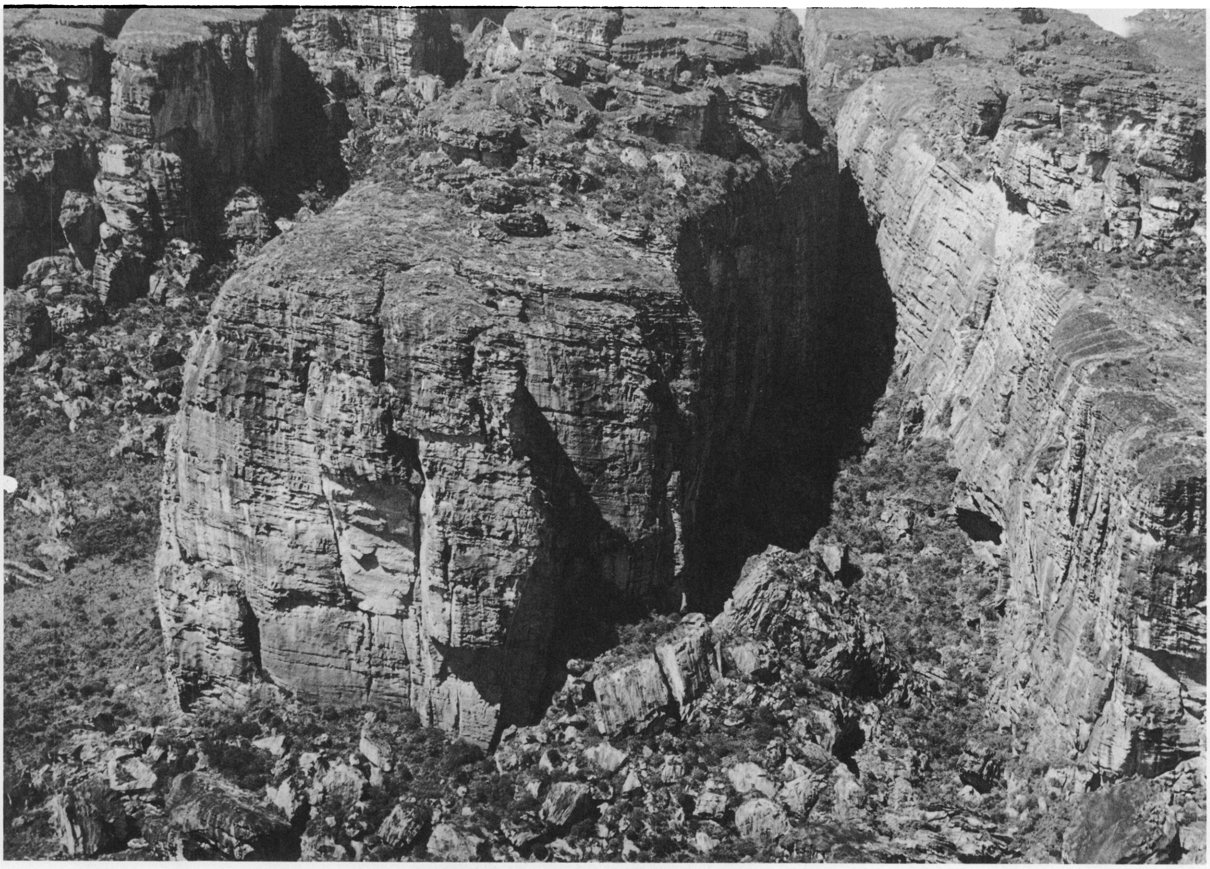
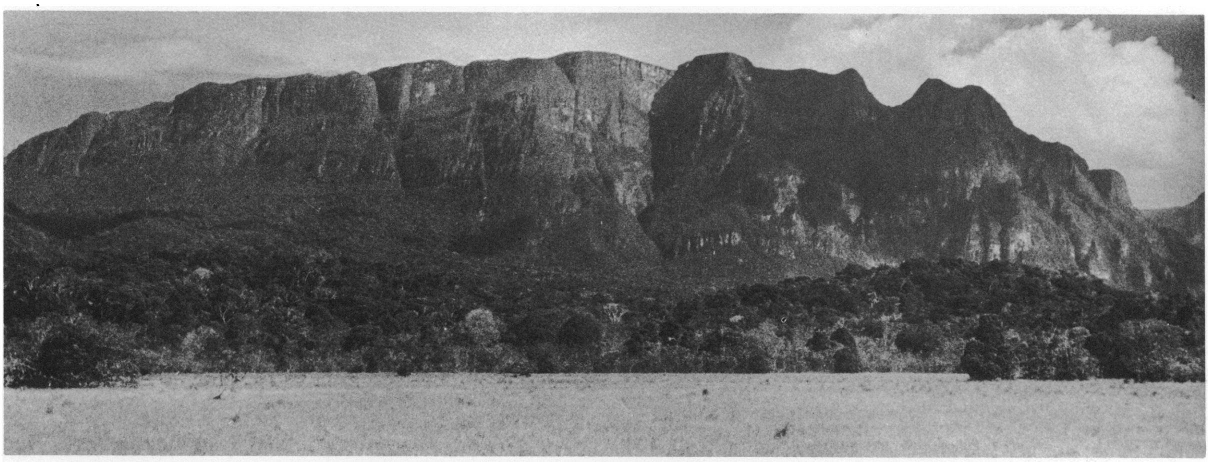


2

1, 2. Cerro Auyán-tepui, summit. These scenes illustrate the ruggedness of the summit plateau, dissected by deep clefts and canyons, much of it covered by broken rock

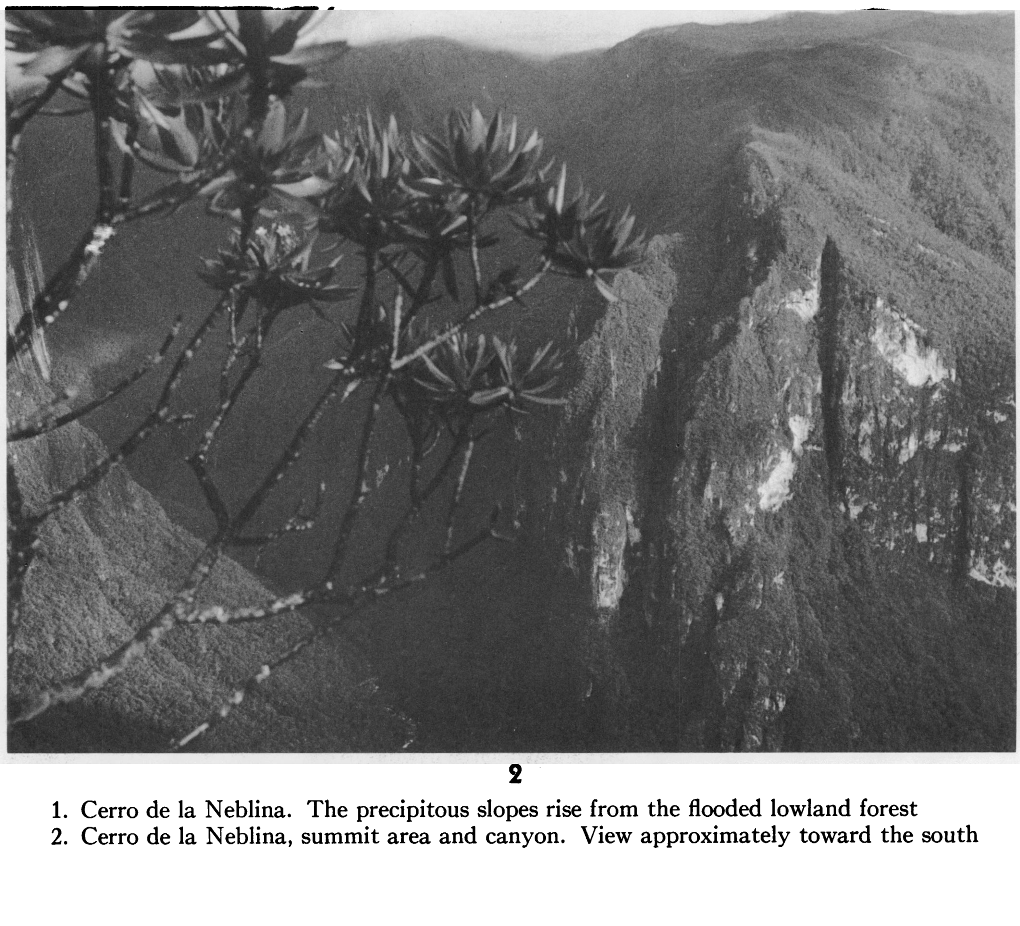
1



2

1. Summit area of Cerro Paraque, or Sipapo. An unexpectedly diversified landscape on the summit of Paraque
2. Cerro Parú

1



2

1. Cerro de la Neblina. The precipitous slopes rise from the flooded lowland forest
2. Cerro de la Neblina, summit area and canyon. View approximately toward the south