TAXONOMY AND GEOGRAPHICAL DISTRIBUTION OF THE FURNARIIDAE (AVES, PASSERIFORMES)

CHARLES VAURIE

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PREFACE

There are about 214 species of ovenbirds or horneros, as the Furnariidae are usually called, which makes it the fourth largest American family of birds, after the Tyrannidae (about 365 species), the Trochilidae (about 319), and the Formicariidae (about 222). Very few monographic studies of this family have been attempted by ornithologists, who were perhaps awed by the number of species and their relative morphological and color uniformity.

To be sure, we have Hellmayr's (1925) classic treatment, Peters's (1951) list of taxa and summary of distribution, and Meyer de Schauensee's (1966) compilation, three works that constitute the basic references to which one turns again and again for details of classification, nomenclature, and geographical distribution. More recently still, Vaurie (1971a) published a preliminary summary of his classification of the family (somewhat modified in this text), and Feduccia (1973) attempted an analysis of the radiation of ovenbirds (Furnariidae) and woodhewers (Dendrocolaptidae). We can also turn to general accounts of the Furnariidae in the New Dictionary of Birds (Thomson, 1964), and the popular texts by Austin and Singer (1961) and Gilliard (1958). Unfortunately, only a small number of ornithologists have intensively studied the Furnariidae in the field, and even fewer of them have published any results of their observations.

Because the published information on Furnariidae is widely scattered in many journals, monographs, and books, and also because so much about ovenbirds is still unpublished (although I know of many notes, and even some manuscripts, lying dormant in file cabinets), the need for a comprehensive survey of all species of Furnariidae has been sorely felt for a long time. Such a survey should ideally include an overhaul of the existing classification, a thorough description of geographical distribution, summaries of habitat preferences, nesting behavior and external morphology, and a critical assessment of geographical variation.

In short, such a work should offer the serious student both the factual information necessary to see at a glance what we know about the Furnariidae, and an inspirational basis from which to draw questions and problems for further work. Vaurie's authoritative monograph goes a long way toward fulfilling these ambitious goals: it is clearly a landmark in Neotropical ornithology and crowns a remarkably productive career in systematic ornithology.

Charles Vaurie fully realized that the Furnariidae represent an extraordinary continental adaptive radiation. He marveled at the convergence between furnariids and birds in unrelated groups or families not represented in South America, such as larks, wheatears, and nuthatches, and was astonished that this phenomenon had not attracted more attention. (I believe Vaurie would have been pleased, therefore, had he known that in 1969 and 1970 I gave lectures on this very topic to students taking a course in evolutionary biology at the University of Massachusetts.) But, to my knowledge, no one has pursued this problem further in the Furnariidae, although Keast (1972) attempted to find the ecological counterparts of the Tyrannidae in the Old World.

Inspired by the challenge of the Furnariidae, Vaurie set out to work on this difficult group in the late sixties. Convinced from the start that the great variation in nest structure could be used as a taxonomic character of great value, he endeavored to gather what was known about the nests of furnariids. Since published descriptions of nests are rather few, he corresponded with many ornithologists to obtain unpublished data. His classification of the ovenbirds into genera and subfamilies was based in large part on his assessment of variation in nest structure.

As in his previous systematic work, Vaurie painstakingly and meticulously studied the external morphology of as many specimens of each species as possible, including many types. Working part of the year at the Muséum d'Histoire Naturelle in Paris and

part in New York at the American Museum of Natural History, Vaurie published, alone or with others, nine preliminary notes and short papers between 1971 and 1975. But he devoted most of his time to writing the monograph itself, drafting distribution maps, and supervising the painting of color plates. Thus, contrary to his custom in his previous systematic studies, Vaurie did not embark on the publication of a long series of papers preparatory to the final work. Fortunately for ornithology, Vaurie had virtually completed the manuscript at the time of his sudden death in 1975. With its wealth of detail and yet with its constant attempt at an overview, this monograph is characteristic of Vaurie's well-known care and fine craftsmanship.

As an introduction had not been completed by Vaurie, I have undertaken to write one on the basis of manuscript notes he left. As much as possible, Vaurie's own words have been respected, but I have somewhat modified the sequence of his notes to provide greater continuity, and have inserted a few comments in the form of footnotes.

In spite of the effort at completeness, shown for instance by Vaurie's extensive correspondence (see Acknowledgments) about unpublished information on Furnariidae, especially nesting, the text of this monograph contained rather few references to published or unpublished sources, and did not include mention of papers with important information, in particular on geographical variation (and subspecies, since they express such variation), geographical distribution, ecology, and behavior. In order to insert all this material in the text at proper places would have meant, not only much work, but also substantial additions or even modifications of the original manuscript, which was otherwise in very good shape. Rather than to provide this documentation and to alter the text accordingly, I decided, after much thought and consultation with my colleagues in the Ornithology Department at the American Museum of Natural History, and in agreement with them, that the text of the monograph itself, in other words the discussions of the 34 genera and 214 species recognized by Vaurie, beginning with *Geositta* and ending with *Pygarrhichas,* should be left as unaltered as possible, so that the reader may be able to read this work as Vaurie wrote it, and as he intended it to be. Thus only minor changes have been brought to the text. These corrections, which were kept to a minimum, are all of an editorial nature, and were made so that Vaurie's meaning be made more clear. After all, Vaurie himself did not have a chance to "polish" his manuscript before he died, and I expect that he would have made these editorial changes. However, because Vaurie's manuscript did not benefit from the usual critical comments of referees or of persons asked to read a text before it is submitted for publication, I thought that it might be useful to insert some remarks about systematic, distributional, ecological, or behavioral matters insofar as they might provide additional information of interest to readers and users of this monograph. All these comments are made as footnotes, and are initialed to clearly distinguish them from Vaurie's own writing.

Three appendices were prepared because they were thought to complete the monograph usefully. The first is the list of species of Furnariidae, compiled by Patricia Vaurie. The second is a list of synonymized genera, and the third a list of species for which no description of nest appears to exist.

The closing date of information for the manuscript as it was left before editing appears to be about 1973.

FRANÇOIS VUILLEUMIER

ABSTRACT

This monograph brings together for the first time a great deal of previously scattered information about the taxonomy, geographical distribution, general behavior, habitat preferences, nesting behavior, and morphological variation of the 34 genera and 214 species of the Neotropical family Furnariidae. Three subfamilies are retained: the Furnariinae (with five genera and 35 species), the Synallaxinae (with 17 genera and 116 species), and the Philydorinae (with 12 genera and 63 species). For each genus a key to species and detailed descriptions of every species are provided together with their geographical ranges. Data on measurements are summarized in 24 tables, and information on distribution is summarized in 55 maps. A series of 10 color plates illustrates 107 birds representing 33 of the 34 genera.

RESUMEN

Esta monografía ofrece la primera síntesis de mucho de lo que se conoce sobre taxonomía, distribución geográfica, comportamiento general, biótopos, nidificación y variabilidad geográfica de los 34 géneros y 214 especies de la familia neotropical Furnariidae. Tres subfamilias son admitidas: Furnariinae (con cinco géneros y 35 especies), Synallaxinae (con 17 géneros y 116 especies), y Philydorinae (con 12 géneros y 63 especies). Una llave analítica es presentada para todas las especies de cada género, y para cada especie se da una descripción detallada de la morfología y otra de la distribución geográfica. Las medidas de cada especie son resumidas en 24 tablas, y las distribuciones en 55 mapas. Diez láminas en color illustran 107 aves en 33 de los 34 géneros.

INTRODUCTION

The avifauna of South America is the richest of any continent, not so much perhaps in the variety of its families as in the unusually great number of species, and, in some cases, in the diversity of evolutionary radiation. This is true of the ovenbirds. For example, in four genera the birds are thrushlike (*Sclerurus*),[1] pseudo-corvids (*Pseudoseisura*), an exaggerated wren with the most fantastic tail of any passerine bird (*Sylviorthorhynchus*), or are strikingly similar to the long-billed marsh wrens of North America (*Phleocryptes*). In fact, the ovenbirds behave like and often resemble morphologically to an amazing degree almost any passerine bird one can think of, provided it belongs to a group lacking or poorly represented in South America. This is my theory, and it is astonishing that so little attention has been paid to this previously—probably because it is too simple to be true.[2] These "little brown jobs" are very unusual indeed, "probably more diverse than any other avian family" as the British Ornithologists' Union's "New Dictionary of Birds" states.[3]

But the most remarkable things about ovenbirds are their nests and the great attention they lavish on them. The four genera mentioned above provide good examples of completely different nests, but this is only a sample which does not exhaust the variation by any means.[4] The nest seems to be another "secondary sexual character," compensating for the modesty of its architect—another theory!

Other than in Sclater and Hudson's "Argentine Ornithology" of 1888, which dealt only with Argentina and was neither complete nor always accurate, no work has been done on the family as a whole other than listing its species.[5] Similarly, many "subspecies" have been described without any attempt at synthesis. Ornithologists were aware of this unsatisfactory condition but shrank from undertaking the study of a family consisting of about 214 species,[6] most of them very obscure, plain, and rather small. It was known that variation in their behavior and nests was great, probably unparalleled in the bird world, but this paradoxically

dampened enthusiasm rather than stimulated it. It was a case of too much work for too long.

Format of the Text

Each genus is introduced with a mention of its relationship(s) to other genera, and of the number of species included in it. The species are named when not too numerous. Next stated is the range. I worked out the altitudinal ranges when the birds are montane because I think this is important although it had been neglected. General appearance and behavior are discussed with stress on ecology, adaptive behavior, and nests.

Most genera are homogeneous or relatively so. Hence what is true of the one species for which most information exists is, or tends to be, true of the other species as well. However, variation may exist, and it is carefully noted as it may prove to be of taxonomic importance eventually. Morphological variation of the species in the genus is then summarized, and is followed by a section on phylogeny, under which I dispose of nearly all taxonomy. In the next section I synthesize the geographical variation which has been treated so very poorly previously. The recognition of subspecies is a matter of opinion; it is subjective. I prefer to recognize only subspecies which seem very distinct to me, or the recognition of which serves a useful function in my opinion, but I do not follow a standard and my judgment varies as seems appropriate.

Keys and descriptions identify the species. For each species, the range and number of specimens examined are also given. These details, especially the notes on immature plumages, which have been almost completely neglected, should be most useful to professional ornithologists. Capitalized color names are from Ridgway (1912).

There are 10 color figures representing 107 species (50% of 214), about four-fifths of which have not been illustrated before.[7] Thirty-three of 34 genera are illustrated. Geographic ranges are summarized in 55 maps, and measurements of most species are given in 24 tables.

The following abbreviations are used in the section Specimens Examined:

AMNH, American Museum of Natural History, New York
ANSP, Academy of Natural Sciences, Philadelphia
BM, British Museum (Natural History), Tring
CM, Carnegie Museum, Pittsburgh
FMNH, Field Museum of Natural History, Chicago
MNHN, Muséum National d'Histoire Naturelle, Paris
NMW, Natural History Museum, Vienna
NRS, Naturhistoriska Riksmuseet, Stockholm
USNM, National Museum of Natural History, Washington, D.C.
UZM, Universitetets Zoologiske Museum, Copenhagen
ZIW, Institute of Zoology, Polish Academy of Sciences, Warsaw
ZSM, Zoologische Sammlung des Bayerischen Staates, Munich

Diagnosis of Furnariidae[8]

—Small to medium-sized birds of the American tropics that are either terrestrial, arboreal, or scansorial, with a unique and extreme degree of ecological radiation; about 214 species and 34 genera.
—All species in which the skull has been examined are schizorhinal; apparently a unique character in the Passeriformes with the possible exception of the little-known New Zealand wrens (Acanthisittidae).
—No horns on the *processi vocales* of the syrinx, except in the genus *Geositta*.
—Anterior toes free, or not united to the full length of the basal phalanges, or, when united to a varying degree, only the middle and outer toes are united, the inner toe remaining free.
—Tail typically soft, or somewhat stiffened, but shafts not modified to form rigid spines as in the Dendrocolaptidae, except in the monotypic genus *Pygarrhichas*.
—Habitat extremely varied, from desert or barren regions to rocky coast, cliffs, swamps, savannas and forest, and great altitudinal range from sea-level to the puna of the high Andes.

—Closed nest of three basic types:

(1) a hole or gallery dug in the ground by the bird or adopted from a rodent burrow, or holes under stones or in walls; the oven built of mud above ground by *Furnarius* is a modification of this type, in my opinion;

(2) aboveground, built of sticks, twigs, various grasses, or moss;

(3) a cavity in a tree, either natural or dug by the bird.

FURNARIIDAE VERSUS DENDROCOLAPTIDAE[9]

I certainly believe the two are related, but when we consider how difficult it is to find enough characters to separate passerine families, the evidence for separating the ovenbirds and woodhewers is really overwhelming:

—Dendrocolaptidae average bigger, are only scansorial and are much more homogeneous morphologically, behaviorally, and ecologically.

—Skull is holorhinal in Dendrocolaptidae.

—Syrinx is different in number of cartilage rings and attachment of muscles; in Dendrocolaptidae syrinx has prominent horns dorsally and ventrally on the processes.

—In Dendrocolaptidae all anterior toes are united, and legs are usually shorter and feet stronger.

—In Dendrocolaptidae the tail ends in rigid spines.

—Dendrocolaptidae inhabit only forests or well-wooded regions, and, so far as known, nest only in holes or cavities in trees.

—Dendrocolaptidae differ in pterylosis from Furnariidae.

ACKNOWLEDGMENTS

The following list of persons was prepared on the basis of correspondence and other material left by Vaurie. It may not be complete, and Vuilleumier, who compiled it, apologizes to those who might inadvertently have been left out. These persons provided Vaurie with information on specimens under their care, gave him unpublished data on nests of Furnariidae, or on the geographical distribution of some species, or exchanged opinions about taxonomic and distributional matters.

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FIG. 1. a. *Geositta saxicolina*. b. *G. maritima*. c. *G. tenuirostris*. d. *Upucerthia andaecola*. e. *U. validirostris*. f. *Cinclodes comechingonus*. g. *C. nigrofumosus*. h. *C. antarcticus*. i. *C. palliatus*.

FIG. 2. a. *Furnarius rufus*. b. *F. cristatus*. c. *Sylviorthorhynchus desmursii*. d. *Leptasthenura platensis*. e. *Aphrastura spinicauda*. f. *Leptasthenura andicola*. g. *L. setaria*. h. *L. fuliginiceps*.

FIG. 3. a. *Schizoeaca fuliginosa palpebralis*. b. *Schizoeaca moreirae*. c. *Synallaxis* (*Schoeniophylax*) *phryganophila*. d. *Synallaxis* (*Synallaxis*) *courseni*. e. *S. subpudica*. f. *S. tithys*. g. *S. elegantior*. h. *S. macconnelli*. i. *S. cherriei*. j. *S. castanea*. k. *S. hellmayri*. l. *S. zimmeri*.

FIG. 4. a. *Synallaxis* (*Synallaxis*) *scutata*. b. *S. c. candei* (front), *S. c. atrigularis* (back). c. *S. stictothorax*. d. *S. cinnamomea*. e. *S. fuscorufa*. f. *S. gularis*. g. *Certhiaxis cinnamomea*. h. *C. sulphurifera*. i. *C. pallida*. j. *C. gutturata*. k. *C. mülleri*. l. *C. furcata*.

FIG. 5. a. *Thripophaga baeri*. b. *T. heterura*. c. *T. berlepschi*. d. *T. punensis*. e. *T. urubambensis*. f. *T. anthoides*. g. *T. steinbachi*. h. *T. flammulata*. i. *T. macroura*. j. *T. cherriei*. k. *T. hypochondriaca*. l. *T. hudsoni*.

FIG. 6. a. *Spartonoica maluroides*. b. *Limnornis curvirostris*. c. *Phleocryptes melanops*. d. *Coryphistera alaudina*. e. *Eremobius phoenicurus*. f. *Anumbius annumbi*. g. *Phacellodomus striaticollis*. h. *P. dorsalis*. i. *P. fusciceps*. j. *P. erythrophthalmus*. k. *P. dendrocolaptoides*.

FIG. 7. a. *Siptornis striaticollis*. b. *Xenerpestes minlosi*. c. *Metopothrix aurantiacus*. d. *Margarornis rubiginosus*. e. *M. stellatus*. f. *M. brunnescens distinctus*. g. *M. squamiger*. h. *Lochmias n. nematura*. i. *Xenops contaminatus*. j. *X. milleri*. k. *X. tenuirostris*. l. *Pygarrhichas albogularis*. m. *Xenops minutus*. n. *X. rutilans*. o. *Megaxenops parnaguae*.

FIG. 8. a. *Berlepschia rikeri*. b. *Pseudocolaptes boissonneautii*. c. *Pseudoseisura gutturalis*. d. *P. cristata*. e. *P. lophotes*.

FIG. 9. a. *Philydor strigilatus*. b. *P. leucophrus*. c. *P. amaurotis*. d. *P. guttulatus*. e. *P. subulatus*. f. *P. rufosuperciliaris*. g. *P. dimidiatus*. h. *P. erythropterus*. i. *P. rufus*. j. *P. ucayalae*. k. *P. striatus*. 1. *P. fuscus*.

FIG. 10. a. *Thripadectes rufobrunneus*. b. *T. scrutator*. c. *T. holostictus*. d. *T. flammulatus*. e. *Automolus dorsalis*. f. *A. ruficollis*. g. *A. erythrocephalus*. h. *A. rectirostris*. i. *Sclerurus guatemalensis*. j. *S. mexicanus*. k. *S. scansor*.

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The distribution maps were prepared by Vaurie (seven of them, left unfinished, were completed by the staff of the Graphic Arts Department of the American Museum of Natural History). The color plates were painted by Mr. Francis Berille and Mr. John C. Yrizarry.

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SUBFAMILY FURNARIINAE

GENUS *GEOSITTA*

This genus is composed of 12 species distributed from sea level to the páramos in western and southern South America, from the northern end of the Central Andes of Colombia south to Tierra del Fuego (map 1). The majority are Andean and reach a great height; *Geositta excelsior* has been collected at 5200 m. and may be found higher; other species are found at 4500 m. or more. Only three species are coastal, *G. antarctica* along the Straits of Magellan, *G. maritima* and *G. peruviana*[10] in Chile and Peru. Among the Andean and coastal species one can also include the widely ranging *G. cunicularia* which inhabits virtually the whole of western and southern South America, from 4600 m. or more in central Peru and 4800 m. in Bolivia, and the coast and inland districts of Rio Grande do Sul, Brazil south to Tierra del Fuego; *G. poeciloptera,* farther north, is restricted to southern Brazil.

All the species are strictly terrestrial and inhabit only open arid country, or predominantly so, from the páramos and puna down to the coast, in flat or rolling sandy or stony areas, bare or with sparse dwarf vegetation; also hills, dunes, cliffs, rocky slopes, or out-

crops. They never perch above the ground as far as known, and apparently, are all very active on the ground, walking or running about a great deal, preferring to run rapidly away, rather than fly, when disturbed.

These birds are small, or of moderate size, with a short tail, and the wing and upperpart of the tail are rufous (or also fulvous white in the case of the tail), in the large majority of the species. These bright or pale areas are concealed, however, when the wing and tail are folded, and the rest of the plumage is exceedingly plain and dull, "cryptically" adapted for life on the open ground. The coloration of the body plumage is more or less plastic in some species, suggesting adaptation to the general color of the substratum.

The nest of nine of the 12 species is known and is always in a cavity "underground," at the end of a burrow in the earth, a hole under stones, or at the rear of crevices among rocks. *Geositta cunicularia* digs its own burrows, and this is assumed or has been implied to be the case for other species. However, *G. cunicularia* also adopts the burrows of rodents when available, and *G. punensis* probably does so as a rule, because this bird is said to be closely associated with rodents, such as the gopher-like *Ctenomys*; all the nests of *G. punensis* discovered so far were in rodent burrows. The nest of *G. isabellina* is placed under or among rocks. The location varies in *G. rufipennis* as the nest is placed in a burrow under the ground, at the rear of deep narrow crevices in piles of rocks, and has been found also among the stones of walls. The nest of *G. tenuirostris* seems to be unknown, but the long and slender decurved bill of this species suggests that this bird probably does not dig burrows. The other two species for which no information on the nest seems to exist are *G. crassirostris* and *G. excelsior*.

The habit of nesting in a subterranean passage, or cavity, is appropriately expressed by the vernacular name "miner" for *Geositta*, but "caminera" or "caminante," which are very widely used in Spanish, are equally appropriate for these ground birds which are said to be such active walkers.

Some species of *Geositta* have been compared in their ecology and some aspects of behavior to pipits (*Anthus*), or some larks, such as *Galerida cristata*. However, it seems to me that some species of *Geositta* are more similar in many morphological and behavioral respects to some wheatears (*Oenanthe*) and are their counterpart in the New World. Ecology, general size and structure, cryptic coloration, and, especially, characteristic tail pattern with its very conspicuous pale base, are exceedingly similar; locomotion, nesting in holes in the ground, and constant wagging of the tail (reported in *G. cunicularia*), are also very similar.[11] Affinities between *Geositta*, *Upucerthia*, and *Cinclodes* are discussed in the respective sections on these other two genera.

Morphological Variation

The morphological variation within *Geositta* is well marked, with the exception of the coloration of the body plumage, and consists of differences in size, shape of the bill, size of the feet, and pattern of the wing and tail.

The species are small or of moderate size and have a short tail. The lengths of the wing, tail, and bill, shown by the means in round numbers (mm.), vary from 78 to 120 for the wing, with an average of 99; from 39 to 79, with an average of 55, for the tail; and from 17 to 33, with an average of 22, for the bill. The ratio between the lengths of the tail and wing varies from 0.49 to 0.69 with an average of 0.56.

The interspecific differences in the length of the bill are relatively small, but the variation in shape is great, the bill varying from straight and rather weak, to strongly decurved, and from very coarse and thick, to slender and attenuated.

The length of the tarsus was not measured; the feet vary from relatively weak to very strong.

The general color pattern of the wing and tail remains the same in nine of the 12 species, but changes abruptly in the other three (see below). In the nine species with a "normal" pattern, the wing and tail are bright rufous or ferruginous, or fulvous white

in the case of the tail. The rufous or pale areas vary in extent but are concealed when the wing and tail are folded by the tips of the feathers, outer web of the primaries, and normally by the central pair of rectrices, which are brown. In the tail, the bright or pale area is normally restricted to the base or upper half of the tail, with the apex dark brown, but the brown area is reduced only to apical or subapical spots in some species.

In the three species lacking this pattern, the wing is rufous in *Geositta excelsior,* but not the base of the tail which is dark brown; in *G. saxicolina,* the rufous pattern exists in the tail, but not the wing; and, in *G. maritima,* it is lacking in both the wing and tail in the adult plumage, but a very poorly marked and much restricted dull ferruginous area exists in the wing in the immature plumage.[12]

The coloration of the body plumage is plain and dull in all the species and they all possess a conspicuous buffy superciliary streak. The upperparts vary from more or less earthy brown to sandy or buffy brown, mouse gray, or sandy buff, and are uniform as a rule, but with more or less darker centers to the feathers in a few species. The underparts contrast from the upperparts by being paler; the throat is whitish, and the plumage below the throat is buffy to a varying degree, or dull, grayish, or dingy white, uniform, or more or less distinctly streaked or mottled with brown on the breast. The brown pigment spreads to the flanks to a greater or lesser extent; in one species (*Geositta maritima*) the flanks and lower abdomen are pale pinkish cinnamon.

The tail is slightly stiffened in all the species and its tip varies somewhat in shape, from squarish to slightly forked or graduated.

Phylogeny

The phylogeny of *Geositta* is not clear, but it seems best to start the sequence of species with the small *G. poeciloptera* of Brazil, which is the most isolated geographically and had been placed in a separate monotypic genus (*Geobates*) before I proposed a new classification in 1971.

Geositta poeciloptera is probably not distantly related to *G. cunicularia* and the behavior of the two species is approximately similar according to Sick (1965). The color pattern of their outer primaries differs, as the rufous area of the inner web of the first and second primaries and sometimes also that of the third is banded or irregularly spotted with dark brown in *G. poeciloptera,* but not in *G. cunicularia.* However, this difference, which varies individually a great deal in *G. poeciloptera,* does not seem to be more than a species character as the rufous area and the details of its pattern vary specifically in the other species of *Geositta* with a rufous wing.

The other characters which allegedly distinguish *Geobates* from *Geositta* are the former's short tail and short straight bill. However, the bill of *Geositta poeciloptera* is identical in shape with that of several other species, and is not shorter than the bills of the two small species (*G. maritima* and *G. peruviana*), which are comparable to *G. poeciloptera* in general size (table 1). The tail of *G. poeciloptera* is quite short, but the ratio between its length and that of the wing is identical to this ratio in other *Geositta,* or does not differ appreciably. This ratio is 0.51 in both *G. poeciloptera* and *G. antarctica,* increases to 0.53 only in both *G. saxicolina* and *G. cunicularia,* and decreases very slightly to 0.49 in *G. isabellina* in which the tail is proportionally shorter than in any other species.[13] In short, I can find no ground for upholding *Geobates,* and, as stated above, I believe that *G. poeciloptera* is probably related to the very widely distributed *G. cunicularia,* the type of *Geositta.*

Geositta peruviana and *G. maritima,* both small coastal species with a short straight bill, are always assumed to be closely related. This assumption may be correct, but, nevertheless, their morphological resemblance is superficial. *Geositta maritima* is strongly aberrant in coloration as it differs from *G. peruviana* and all other species by lacking the characteristic pattern of both the wing and tail in the adult plumage (see above).[14]

I have ended the sequence with *G. crassirostris, G. excelsior,* and *G. tenuirostris*

TABLE 1
Measurements (in Millimeters) of *Geositta*

	Wing			Tail			Bill		
Species	N	Mean	Range	N	Mean	Range	N	Mean	Range
poeciloptera									
Both sexes	16	77.45	76–81	12	39.31	35–42	12	17.75	17–19
cunicularia									
Males	60	95.35	87–104	52	50.50	46–55	50	21.88	19–24
Females	38	92.19	85–102	34	48.88	43–55	35	21.47	20–23.50
Both sexes	108	94.12	85–104	88	49.84	43–55	—	—	—
maritima									
Males	16	84.37	80–88	16	49.00	46–53	16	17.25	16–18
Females	8	82.75	80–86	8	48.00	45–52	8	17.12	16.50–17.50
Both sexes	28	84.28	80–88	27	48.66	45–53	—	—	—
peruviana									
Males	25	79.90	76–83	23	50.17	47–54	25	18.30	17–19.50
Females	20	78.90	76–81	20	49.35	46–52	20	18.25	17.50–19.50
Both sexes	49	79.37	76–83	47	49.85	46–54	—	—	—
punensis									
Males	15	92.46	89–95	12	52.83	50–57	11	19.03	18–20
Females	10	91.40	89–94	7	50.71	48–54	6	18.33	17–20.50
Both sexes	28	92.32	89–96	21	52.19	48–57	—	—	—
saxicolina									
Males	17	105.47	99–109	17	55.70	53–61	17	18.50	18–20
Females	10	104.25	100–107	10	55.90	52–59	10	18.42	17.20–20.50
Both sexes	27	105.01	99–109	27	55.77	52–61	—	—	—
isabellina									
Both sexes	17	120.23	115–125	17	59.29	53–66	17	23.86	21.50–25.50
antarctica									
Males	10	109.60	103–114	10	56.40	50–61	10	18.60	17–20
Females	9	107.54	103–112	7	56.57	53–59	11	18.90	18–20
Both sexes	23	108.56	103–114	20	56.20	50–61	—	—	—
rufipennis									
Males	17	105.88	101–110	17	58.29	53–64	16	20.34	19–22
Females	18	105.16	100–112	17	57.64	51–63	17	20.26	18.50–22
Both sexes	54	105.11	98–112	42	57.76	51–64	—	—	—
crassirostris									
Males	7	94.50	92–96	7	55.57	53–57	5	31.10	30–32
Females	5	92.00	89–97	5	53.40	53–55	5	30.10	29–31
Both sexes	14	93.03	89–98	14	54.42	53–57	—	—	—
excelsior									
Males	27	116.18	109–124	27	80.03	74–86	27	29.83	28–32
Females	28	113.64	109–123	26	78.96	71–86	25	29.18	25–32
Both sexes	55	114.16	109–124	53	79.51	71–86	—	—	—
tenuirostris									
Males	45	113.36	106–119	45	59.91	55–65	43	33.40	30–36
Females	25	110.54	105–114	25	58.88	55–63	23	33.30	29–37
Both sexes	78	112.34	105–119	77	59.57	54–65	—	—	—

because their bills are more specialized than in the other species; the bill of *G. tenuirostris* is well decurved, slender, and attenuated; the bill of *G. crassirostris* and *G. excelsior* is very coarse, thick, and somewhat decurved. The bills are also very distinctly longer in these three species than in the other species.

The inclusion of *excelsior* in *Geositta* may be questioned because *excelsior* had been allocated to either *Cinclodes* (by Peters, 1951 and Meyer de Schauensee, 1966) or *Upucerthia* (by Hellmayr, 1925) before my revision (1971a). It seems clear, however, that *excelsior* does not belong in *Upucerthia,* but to decide between *Cinclodes* and *Geositta* is more difficult. The tail pattern of *excelsior,* and its tail/wing ratio (0.69), are more similar to *Cinclodes* than to *Geositta,* but, everything considered, *excelsior* is morphologically more similar to *G. crassirostris* than to any species of *Cinclodes.* The wing pattern of *excelsior* is more similar to that of *Geositta,* generally speaking, and *excelsior* and *G. crassirostris* show similarity in the size and shape of their bills, size of their very powerful feet, and mottled coloration of their underparts. These similarities suggest that *excelsior* is best included in *Geositta,* with *G. crassirostris* as its nearest probable relative. However, a comparison of behavior may reopen this question; no adequate information exists so far for these two species.[15]

Geographical Variation

The coloration varies geographically in five species: *Geositta cunicularia, G. peruviana, G. rufipennis, G. crassirostris,* and *G. excelsior.* Differences in size or in the shape of the bill have been noted in two species but they are slight and not constant.

The differences in coloration are known to be correlated with the color of the ground in *Geositta peruviana* and in some populations of *G. cunicularia,* but a greater or lesser degree of adaptation of this kind probably accounts for all the geographical variation in *Geositta.* This type of variation, it seems to me, should not be recognized in the nomenclature.

The variation in coloration is more notable in *Geositta peruviana* and *G. cunicularia* than in the other three species, and most clearcut in *G. peruviana.* In *G. peruviana,* the population from the northern part of the range is very pale and "sandy"-colored south to about the Department of Lima, Peru, but in Lima it is replaced by distinctly darker, browner birds which, in the Department of Ica, south of Lima, are in turn replaced by pale birds indistinguishable from those of the north. Ica constitutes the southern end of the range of the species. It seems to me that this geographical trend is more accurately described in the simple terms that I use than by splitting *G. peruviana* nomenclaturally (three "subspecies" are recognized in current lists).

The geographical variation of *Geositta cunicularia* is more confusing and less clearcut than that of *G. peruviana,* although eight "subspecies" are accepted. However, the variation is only one of degree between a dark and pale extreme that is less sharply differentiated than in *G. peruviana.* These two forms of *G. cunicularia,* which are both found in Chile, have been named *fissirostris* for the dark form, and *deserticolor* for the pale one. The latter ranges from Atacama, north along the desert coast and equally arid central valley to southern Peru; the dark *fissirostris* replaces the pale *deserticolor* from Atacama south to Llanquihue. The population found north of *deserticolor* in the coastal hills of southern Peru is dark again, about similar to *fissirostris,* though not quite so saturated. The pattern of variation is therefore about similar to that of *G. peruviana* (though less sharply distinct), but reversed, as the geographically intervening form is pale in *G. cunicularia,* rather than dark in *G. peruviana.*[16]

The nominate form in *Geositta cunicularia* is intermediate between the dark and pale extremes of Chile, and this is true to a varying and very vague degree of all the other forms named and currently accepted as "subspecies." The nominate form occupies the most extensive range of all, from Rio Grande do Sul, Brazil, and southern Paraguay, southward through Uruguay and the

pampas of Argentina to Tierra del Fuego and Aysén in Chile. I see no need for any nomenclatural recognition of the variation.

In *Geositta rufipennis,* the population of northwestern Argentina is pale below, but is more cinnamon, less buffy, in Mendoza, and perhaps also in the region south of Mendoza from which I have seen no specimens. However, in Bolivia and in Chile the birds are vaguely intermediate, not constant. No separation in nomenclature seems necessary. In *G. crassirostris,* which has a very restricted range, subspecies names distinguish only local populations.

The recognition of two subspecies in *G. excelsior* is desirable as it calls attention to the fact that the range of this species is highly disjunct (map 1) with two populations that are apparently well isolated and quite distinct in the coloration of their underparts. These two subspecies are nominate *excelsior,* distributed from the Central Andes of Colombia south to the Andes of Ecuador, and *aricomae* in southeastern Peru. The latter is known from only one specimen collected at the Aricoma Pass in the Department of Puno, a distance of roughly 1500 km. from the southern border of Ecuador, and is the only specimen of *G. excelsior* taken so far in Peru.

The specimen from the Aricoma Pass is similar to the birds of Colombia and Ecuador in every respect, other than the coloration of its underparts which are conspicuously darker and, especially, much more uniform. In the bird from the Aricoma Pass, the whole of the underparts is well suffused with brown below the whitish throat, whereas the brown pigment is more or less restricted to the flanks in the birds of Colombia and Ecuador.

The birds of Colombia are somewhat darker brown, less fulvous, than those of Ecuador, and more grayish on the abdomen, but the difference is slight and one of degree only, whereas the specimen from the Aricoma Pass is far more distinct. The populations of Colombia and those of Ecuador have been separated subspecifically, but I believe this separation is not warranted because the geographical variation of this species is certainly better expressed by the recognition of only *aricomae* in Peru and nominate *excelsior* in Colombia and Ecuador. The range is continuous from Colombia to Ecuador,[17] but *aricomae* is far isolated, though probably not to the very great degree indicated by present evidence.

KEY TO THE SPECIES OF *GEOSITTA*

1. Rufous area of the inner web of the first, second, and, sometimes, third outer primaries interrupted by a band of dark brown, or with the band reduced to irregular spots of varying size on the second and third primaries ..... *poeciloptera*
   First, second, and third outer primaries not banded or spotted 2
2. Bill long, length of culmen exceeding anteroposterior measurement of the crown ... 3
   Bill shorter, culmen not exceeding the crown 5
3. Bill very long, slender, attenuated, and well decurved ..... *tenuirostris*
   Bill distinctly shorter, very coarse, thick, and stout 4
4. All rectrices (with exception of central pair) rufous, and with very conspicuous apical or subapical spots of dark brown ..... *crassirostris*
   Rectrices dark brown, the three outer pairs rufous apically to a varying degree, but not spotted ..... *excelsior*
5. Upper breast more or less distinctly or faintly streaked, or mottled 6
   Upper breast not streaked or mottled 8
6. Under wing coverts and scapulars white or whitish; upper breast very faintly streaked; small, wing length averaging below 80 mm. (in part) ..... *peruviana*
   Under wing coverts and scapulars very distinctly cinnamon; upper breast distinctly streaked or mottled; large, wing length averaging over 90 or 100 mm. 7
7. Wing tip pointed (fourth and fifth outer primaries very conspicuously shorter than the first, second, and third); tertials shorter (extending to about the level of the inner primaries); breast more mottled than streaked ..... *antarctica*
   Wing tip rounded (first to fifth outer primaries subequal); tertials very long (extending to nearly the tip of the wing or exceeding it slightly); breast more streaked than mottled ..... *cunicularia*
8. Base of the tail, or upper half, or more, buffy,

creamy white, cinnamon, or rufous, contrasting completely from the dark brown tips of the feathers, or apical portion ... 9
Upper and lower part of the tail dark brown, with the pale area restricted only to the outer web of the outer rectrix .... *maritima*
9. Small, wing length averaging about 80 mm. (in part) ..... *peruviana*
Large, wing length averaging about 92 mm. or between about 105 and 120 mm. ... 10
10. Wing wholly brown, without rufous .... *saxicolina*
Wing strongly rufous 11
11. Brown apical area of the tail occupying about the distal third of the tail 12
Brown apical area of the tail very restricted, to only relatively small subapical spots ... . *rufipennis*
12. Very distinctly bigger, wing length averaging about 120 mm., and bill about 24 mm.; under wing coverts and scapulars strongly cinnamon ..... *isabellina*
Very distinctly smaller, wing length averaging about 92 mm., and bill about 19 mm.; under wing coverts and scapulars creamy white ..... *punensis*

List of the Species

Geositta poeciloptera

Description: Dark fawn brown above; buffy below, with the feathers at the sides of the lower throat and on the upper breast more or less distinctly bordered with brown, the dark pigment forming poorly defined streaks on the breast. Axillaries chestnut, tipped with white. Wing bright rufous, with the rufous area of the inner web of the first outer primary interrupted by a band of dark brown, this dark band extending also to the second, and sometimes the third primaries, or replaced on these feathers by irregular brown spots of varying size. Tail strongly rufous, more or less extensively tipped with brown. Bill straight and short.

Immature Plumage: Similar to that of the adult, but pattern of the tip of the tail less sharp, and brown edges of the feathers of the breast less distinct and more reduced. Feathers of the back and rump pale at the tips, narrowly margined with rufous, not uniformly brown as in the adult.

Range: Brazil, in the cerrado and campos of southern Mato Grosso, Goiás, and Minas Gerais, to São Paulo.

Specimens Examined: 17, including the two cotypes in AMNH.

Geositta cunicularia

Description: Dull earthy to grayish brown above; crown feathers darker at the center, and feathers of the back uniform, or with more or less distinct narrow pale edges. Creamy buff to whitish below, with the feathers of the upper breast more or less bordered with brown, the dark pigment forming rather poorly defined streaks as a rule, to a varying extent. Rufous area of the wing very extensive. Tail fulvous white, with an extensive brown apical area, and with the outer pair of rectrices white on the outer web and at the tip. Bill straight and relatively short.

Immature Plumage: Similar to that of the adult, but tail pattern and streaks on the breast less defined, and feathers of the crown uniform as a rule, not dark at the center. In some individuals, faint and poorly defined fulvous spots are present on the crown and mantle.

Range: Peru, from the plateau of Junín, and from Arequipa on the coast, south through the Andes and the whole of Chile (including Isla de la Mocha), to Tierra del Fuego, east to the coast of Argentina and north to Córdoba, Santa Fe, and Entre Rios, Argentina; Uruguay; and Rio Grande do Sul, Brazil; reported also from Paraguay (specimen examined by me from Villarrica in the southeast). Altitudinal range, from sea level on the coast, to about 4800 m. in Bolivia, 4600 m. in Peru and Chile, and at least 3800 m. in Argentina (specimen examined), but probably higher.

Specimens Examined: 317.

Geositta maritima

Figure 1

Description: Mouse gray above; pale grayish white below, tinged with pinkish cinnamon on the flanks, lower abdomen, "thighs," and under tail coverts. Wing gray brown, not rufous as a rule, but with a faint

and narrow ferruginous trace along the edge of the inner web of the inner primaries. Tail not rufous, wholly dark brown with the exception of the outer web of the outer rectrix which is white or whitish. Bill straight and relatively short.

IMMATURE PLUMAGE: Wing not wholly gray brown, but with a much restricted and very poorly defined ferruginous area on the inner primaries and on the secondaries; edges of most rectrices pale, more or less ferruginous at the tip. Body plumage more buffy, less gray above than that of the adult, with the edges of the upper wing coverts and inner secondaries paler and more buffy; crown feathers uniform, lacking dark centers which are present in the adult, though not well developed.

RANGE: Coast of Peru and Chile, from La Libertad (Trujillo) in Peru, south to at least the region of Huasco, Atacama, in Chile; ranging inland to a restricted extent in southern Peru and northern Chile.

SPECIMENS EXAMINED: 28, including the type in MNHN.

Geositta peruviana[18]

DESCRIPTION: A small species, similar to *Geositta maritima* in size, but with a well-developed rufous area in the wing, and paler, very pale sandy brown above, or paler gray than *G. maritima,* more whitish below, not tinged with pinkish cinnamon. Tail fulvous white or pale rufous at the base, but pale area restricted, not conspicuous, and with all the rectrices edged with fulvous white to the tip. Bill straight and relatively short.

IMMATURE PLUMAGE: Similar to that of the adult and difficult to distinguish from it, but crown feathers uniform, lacking the narrow dark shaft streaks of the adult; tail pattern less distinct, and with the buffy edges of the uper wing coverts and inner secondaries more conspicuous.

RANGE: Narrowly restricted to the coast of Peru, from the Department of Piura, south to and including the Department of Ica.

SPECIMENS EXAMINED: 96, including type of "*paytae*" in MNHN, and of "*rostrata*" in ZIW.

Geositta punensis

DESCRIPTION: Pale "warm" sandy brown above; whitish and uniform below. Wing strongly rufous; greater part of the tail rufous cinnamon, with a relatively restricted brown apical region, and with the outer web of the outer rectrix creamy white. Bill straight and short. This species is about similar to *Geositta cunicularia* in size, but differs from *G. cunicularia* by being uniformly whitish on the breast, not streaked or spotted with brown; *G. punensis* is also paler above than *G. cunicularia,* generally speaking.

RANGE: Puna and altiplano, in sandy or arid areas with scanty or dwarf vegetation, from western Bolivia in Oruro, south through Jujuy, and western Salta, to at least Lago Blanco (examined) in Catamarca, northwestern Argentina; west to neighboring Chile from Tarapaca south to Atacama. Southwestern Peru has been mentioned also in the range—which is possible, but records from Peru are unknown to me. Normal altitudinal range from about 3200 to 4600 m., but has been recorded lower, at about 3050 m., and higher, near 5000 m.

SPECIMENS EXAMINED: 32.

Geositta saxicolina

Figure 1

DESCRIPTION: Pale earthy brown above; uniformly buffy on the underparts below the whitish throat. Wing uniformly brown, without rufous pigment; upper half or more of the tail buffy white; the outer web of the outer rectrix and its tip are white, and the outer web, but not the tip, of the next pair are whitish. Bill straight and short.

IMMATURE PLUMAGE: Similar to that of the adult, but much more buffy throughout.

RANGE: Altiplano of central Peru in the Departments of Lima, Pasco, Junín, and Huancavelica, between about 3700 and 4900 m.

SPECIMENS EXAMINED: 32.

Geositta isabellina

DESCRIPTION: Pale cinnamon sandy brown above; dingy cinnamon buff below. Wing

strongly rufous, and upper half of the tail or more fulvous white, with the outer web of the outer rectrix white or whitish. Bill relatively long and thick, slightly decurved, rather than straight. This species resembles *Geositta saxicolina* superficially, but its wing is rufous, rather than uniformly brown, and *G. isabellina* is larger, with a stronger bill.

IMMATURE PLUMAGE: Two birds, which appear to be immature, differ from adults by having a spotted crown, but more comparative material is needed.

RANGE: Andes of central Chile from Atacama south to Talca, above 2000 m., also very probably Andes of Argentina from Jujuy south to Mendoza, up to at least 3050 m. in Mendoza. It has been suggested that birds collected in Argentina are probably migrants from Chile, but they occur in Argentina during the breeding season and considerably farther north than in Chile.

SPECIMENS EXAMINED: 19, including cotype in MNHN.

Geositta antarctica

DESCRIPTION: Pale gray brown above; well banded with brown across the breast, the brown area being uniform at the sides of the breast and spreading somewhat down onto the flanks, but center of the breast band mottled as the brown pigment is restricted to the edges of the feathers; rest of underparts buffy below the dark breast band. An extensive "rufous" area is present in the wing, but it is very dull, tawny, rather than bright rufous or ferruginous. Base of the tail pale and cinnamon, but pale area not well defined, the tail being predominantly dark brown, with the exception of the outer webs of the three outer rectrices which are creamy white to a varying degree. Bill small, straight and short.

IMMATURE PLUMAGE: Similar to that of the adult but pattern of the underparts less distinct, the dark breast band is not well defined and the plumage is darker buff, more or less smudged with pale grayish brown on the abdomen as well as on the breast. Pale edges of the entire plumage, including wing and tail, more conspicuous, forming faint spots on the crown lacking in the adult.

RANGE: Breeding range seems to be restricted only to the Straits of Magellan and its islands, but may include other non-forested parts of Tierra del Fuego, and perhaps the region near the mouth of the Rio Gallegos in southern Santa Cruz, Argentina. Migratory and wanderer, migrating east of the Andes where it has been recorded as far north as Mendoza. Records for Chile, other than the region of the Straits, are dubious.

SPECIMENS EXAMINED: 23.

Geositta rufipennis

DESCRIPTION: Pale drab brownish or cinnamon gray above; whitish below with a faint grayish or cinnamon cast. Wing and tail strongly rufous, the rufous area of the tail being very extensive as the brown tips of the rectrices are much restricted generally speaking. Bill very straight, small, and short.

IMMATURE PLUMAGE: Similar to that of the adult but more buffy throughout, with a faint brownish tinge on the breast, and with the pale edges of the body plumage, wing, and tail better developed.

RANGE: Andes and coastal Chile, from southern La Paz in Bolivia, south to Chubut in Argentina, west to the coast of Atacama in Chile, south to Aysén. Santa Cruz in Argentina and Magallanes in Chile have also been included in the range, but the record for Magallanes is based on two old specimens of *G. cunicularia* in the Berlin Museum that were misidentified, and no record of any kind seems to exist for Santa Cruz. The altitudinal range reaches about 4400 m. in Bolivia, and at least 4000 m. in Tucumán in Argentina.

SPECIMENS EXAMINED: 54.

Geositta crassirostris

DESCRIPTION: Umber brown above, with narrow pale brown or fuscous edgings to the feathers; dingy grayish white below, with a poorly defined mottled band of brown across the breast, the brown extending more or less to the flanks, the center of the abdomen being paler. Wing and tail rufous, with the brown apical area of the tail relatively restricted. Feet very stout; bill very coarse,

stout, thick and long, and somewhat decurved.

RANGE: Central Peru where it is known only from the Departments of Lima and Ayacucho, ranging altitudinally from the low hills of the coast to about 2500 m. on the western slope of the Andes, but not known from the coast of Ayacucho.

SPECIMENS EXAMINED: 14, including the type of *crassirostris* in BM, and of "*fortis*" from Ayacucho in ZIW.

Geositta excelsior

DESCRIPTION: Dark brown above; dingy below, with a poorly defined mottled band of brown across the breast, the brown invading the flanks to a varying degree, the center of the abdomen being paler, dingy white or buffy. Rufous area of the wing restricted, and tail dark brown, not pale or rufous at the base, but with the outer webs and tips of the three outer pairs of rectrices rufous, the rufous area decreasing in size from the first to the third pair. Feet and bill very stout and coarse, similar to the feet and bill of *Geositta crassirostris*, to which *G. excelsior* shows also some similarity in the coloration of the underparts.

The description given above applies to nominate *excelsior* from Colombia and Ecuador; the birds of southeastern Peru (*aricomae*) are similar to nominate *excelsior* in every respect, other than the coloration of the underparts below the whitish throat, which is darker brown in *aricomae*, and, especially, much more uniform, well suffused with brown throughout, whereas the center of the abdomen is pale in nominate *excelsior* with brown restricted largely to the flanks.

IMMATURE PLUMAGE: Similar to that of the adult, but underparts more mottled with brown and breast band less distinct.

RANGE: Greatly disjunct with two subspecies: nominate *excelsior* inhabits the upper zone of the Andes and páramos, between about 3200 and 5200 m., from the northern end of the Central Andes of Colombia south to the Andes of Ecuador; *aricomae* is known so far from only a single specimen collected at 4572 m. at the Aricoma Pass, Puno, southeastern Peru.

SPECIMENS EXAMINED: 125, including type of *excelsior* in BM, of *aricomae* in ANSP, and of "*columbiana*" in AMNH.

Geositta tenuirostris

Figure 1

DESCRIPTION: Pale sandy brown above, with narrow pale edgings to the feathers of the crown and back: buffy below, with ill-defined pale brown streaks on the breast, and upper flanks brownish. Wing and tail very strongly rufous, with small brown subapical spots on the rectrices, much reduced, and lacking on the first pair, and, sometimes, on the second pair also. Bill very long and slender, well decurved.

IMMATURE PLUMAGE: Similar to that of the adult, but pale edges of the feathers of the crown and back much better developed, and streaks on breast less distinct.

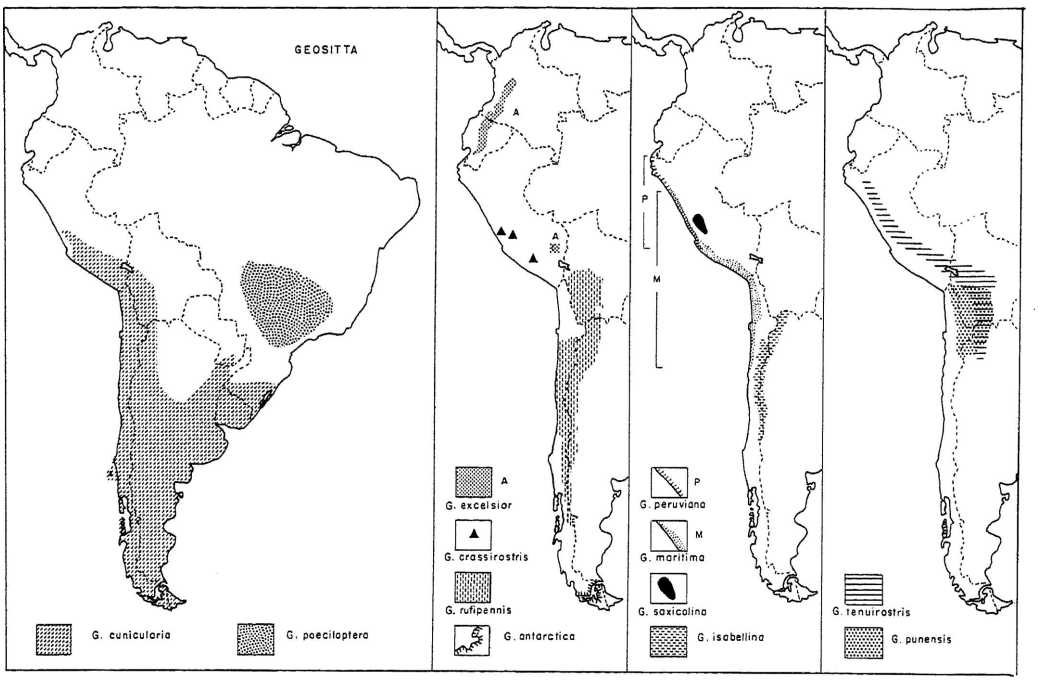
RANGE: Andes, between about 2500 and 4600 m., from Cajamarca in northern Peru, south, through Bolivia, to Tucumán and Catamarca in northwestern Argentina.

SPECIMENS EXAMINED: 125, including type of *tenuirostris* in MNHN, and of "*juninensis*" in BM.

GENUS *UPUCERTHIA*

Upucerthia is composed of seven species and is very closely related to *Geositta*. Strong similarities exist in distribution, ecology, morphology, and behavior, including the location of the nest which is "under ground," at the end of a burrow under the earth or at the rear of crevices among rocks.

The similarities in the ecology, coloration, and behavior of the two genera are well summarized by Hudson (in Sclater and Hudson, 1888) in his comparison of *U. dumetaria* and *G. cunicularia*. These two species are the best known in their genera and the most widely distributed, breeding from the coast in Chile and Argentina to high elevations in the Andes, *dumetaria* to nearly 4000 m., and *cunicularia* to nearly 5000 m. The two species are also the types of their respective genera.[19]

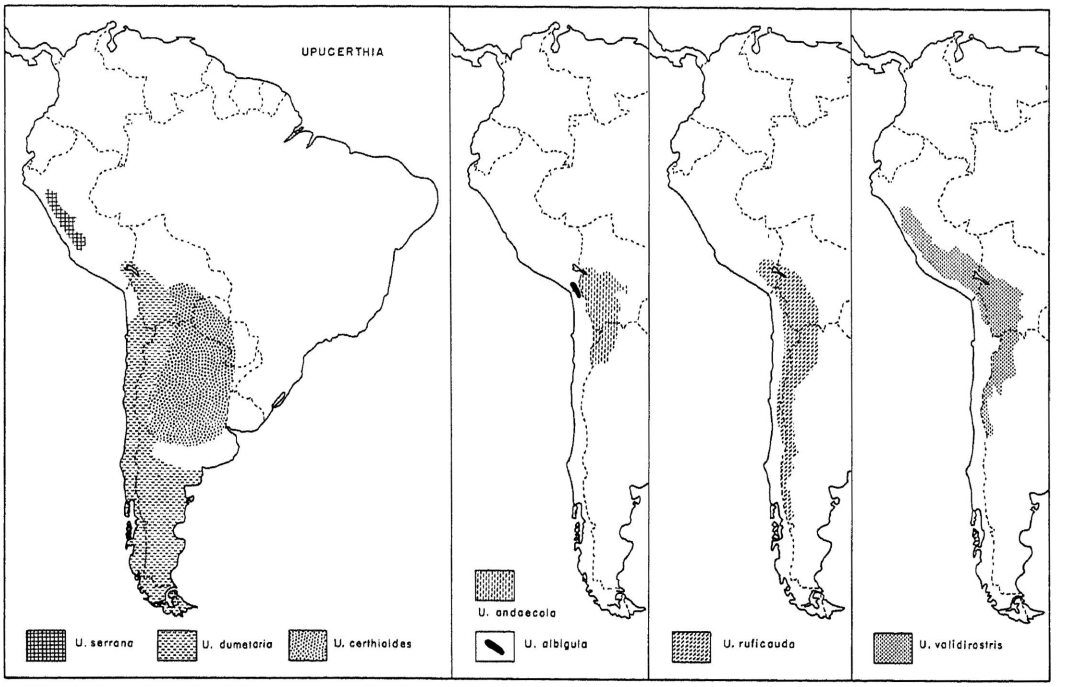


MAP 1. Geographical distribution of *Geositta*.

Hudson described *Upucerthia dumetaria* by saying "Their legs are short, but on the ground their movements are very rapid, and, like the Miner (*Geositta*) already described, they fly reluctantly, preferring to run rapidly from a person walking or riding, and at such times they look curiously like a very small Curlew with an extravagantly long beak. They are active, lively birds, and live in pairs, sometimes uniting in small, loose flocks; they are partial to places where scattered bushes grow on a dry sterile soil, and have a swift low flight; when flying they frequently utter a shrill, trilling, or rapidly reiterated note, in sound resembling laughter. In manners, flight, language, and colouring this bird closely resembles the smaller short-beaked *Geositta cunicularia,* and like that species it also breeds in holes in banks; but I am not able to say whether it excavates the breeding-hole or takes possession of one already made. Durnford found it breeding in a hole four feet deep in the bank of a dry lagoon."

Differences in structure and posture exist, however, between *Upucerthia* and *Geositta* and are discussed below in the general account of *Upucerthia* and comparison to *Geositta*.

The distribution of the two genera is very similar (maps 1 and 2). To be sure, *Upucerthia* is not represented in Brazil and lacks species restricted to the coast, but the similarity in distribution is nevertheless great, especially when we consider that *Upucerthia* consists of only seven species, as against 12 for *Geositta*. The ranges of *U. dumetaria* and *G. cunicularia* are comparable, as stated above; *U. certhioides* is about the counterpart of *G. poeciloptera* in lowlands; and the other five species of *Upucerthia* are Andean and reach roughly the same altitude as the Andean species of *Geositta,* though somewhat less high. The highest altitudes (in m.) for the Andean species of both genera are about: *U. ruficauda,* 4500; *U. andaecola,* 4000; *U. albigula,* 3700; *U. serrana,* 4270; *U. validirostris,* 5000; *G. punensis,* 5000; *G.*



MAP 2. Geographical distribution of *Upucerthia*.

saxicolina, 4900; *G. isabellina*, 3100; *G. rufipennis*, 4400; *G. excelsior*, 5200: *G. tenuirostris*, 4600.

The ecology of the two genera is comparable; both genera inhabit arid open country with sparse low vegetation and rocky areas, but some differences do exist as *Upucerthia* frequents also regions with better plant growth, and four of its seven species are reported to be associated with water (at least to some extent), unlike any *Geositta*. These four are *U. andaecola*, *U. albigula*, *U. dumetaria*, and *U. validirostris*, which have been reported as frequenting streams, river flats, marshes, or wet meadows.

The general behavior of *Upucerthia* and *Geositta* seems very much alike, as far as I can judge by the literature, with the notable exception of the posture of the tail, which seems related to its length.

No clearcut morphological differences exist between the two genera except for the length of the tail which is much longer in *Upucerthia*. The length of the tail varies, in round numbers (mm.), from 39 to 79 mm. in *Geositta* (table 1), with an average of 55, as against 69 to 81, with an average of 75 in *Upucerthia* (table 2), but by eliminating *G. excelsior* with a tail length of 79, the range shrinks to 39–59 in *Geositta*, with an average of 53, and no overlap in actual measurements exists. *Geositta excelsior* is aberrant and its generic affinities have been questioned (see p. 14).

The difference in tail length is clear, but is appreciated far more by comparing the ratios between the lengths of the tail and wing than by mere measurements. The ratios vary from 0.49 to 0.69 (average 0.56) in *Geositta*, with *excelsior* included, or from 0.49 to 0.63 (average 0.55) without *excelsior*, as against 0.76 to 0.98 (average 0.87) in *Upucerthia*. The relative difference between 0.56 or (0.55) and 0.87 is certainly great and the long tail of *Upucerthia* gives its species a more graceful appearance (whereas *Geositta* is very stocky), and a different posture when they come to rest.

In this posture, the bird raises its tail very sharply over its back when it alights or comes to a sudden stop when running on the ground, a functional posture that has not been observed in the much shorter-tailed *Geositta*. This posture has been mentioned explicitly for *Upucerthia validirostris, U. ruficauda,* and *U. andaecola,* and Hellmayr (1932) added that Lane wrote [1897] that the tail of *validirostris* "is carried erect when running." This behavior is implied for *U. albigula* by Johnson (1967), and also for *U. dumetaria,* although his drawing of *U. dumetaria* shows a bird with a somewhat raised tail, much less than in a drawing of *U. serrana* supplied by Koepcke (1964). Wetmore (1926) has observed *U. dumetaria* singing from the "top of a bush or post, with its tail slightly raised," but, apparently Wetmore did not observe this posture when this species alights or comes to a stop when running, and neither did Hudson (see above). A colleague, who has recently returned from prolonged fieldwork in Argentina, has also told me that he did not observe this posture in *U. dumetaria.* It seems, therefore, that *U. dumetaria* does not normally erect its tail, or does so less often and sharply than in the other species, a difference which can be accounted for, perhaps, by the fact that its tail is proportionally shorter than in the other species, with a tail/wing ratio of 0.76. I have found no information for *U. certhioides,* although Wetmore says it is "wrenlike [in] appearance and action." This probably implies that *U. certhioides* erects its tail which is proportionally longer than in the other species, with a tail/wing ratio of 0.98.

The length of the tail has been used for separating the two genera, but the length and shape of the bill have received more emphasis. The bill of *Upucerthia* is longer on average than that of *Geositta,* and is more or less decurved, not short and straight as in some species of *Geositta.* However, the bill varies a great deal specifically in *Geositta* and the differences between the two genera are not constant. For instance, the bill of *Geositta tenuirostris* is long and decurved like that of *Upucerthia* species. Moreover, the morphology of the bill is not a reliable index of generic relationship in the Furnariidae, generally speaking.

The general coloration of the two genera is plain and dull, adapted for life on the open ground. The similarity in color pattern is strong, but the base of the tail is dark and uniform in *Upucerthia,* lacking the pale or bright rufous area which exists in 10 of the 12 species of *Geositta,* and the rufous area in the wing is also less developed in *Upucerthia* as a rule.

The nesting habits of the two genera seem to be identical, but Johnson remarked that the burrows of *Upucerthia* tend to be larger than those of *Geositta.* The nest of *U. certhioides* is placed in a deep fissure or cavity among rocks, as in the case of some species of *Geositta.* Its nest has been described by Castellanos (1932), and by one of my correspondents, but Venturi (Hartert and Venturi, 1909) stated that the nest of *U. certhioides* is in a very deep cavity in the trunk of trees, which is probably an error, because his statement conflicts with all the evidence on record on the ecology and nesting habits of *Upucerthia.* The nests of *U. andaecola* and *U. serrana* are still undescribed,[20] but there is no reason to assume that their location differs from that of the other five species.

The account given above shows that *Upucerthia* and *Geositta* share many similarities and appear to be closely related. The question may then be asked whether or not their generic separation is warranted. I believe that it is, and I consider that the character which distinguishes them morphologically is the clearcut difference in the length of the tail. The longer tail of *Upucerthia* results in a more graceful appearance than in the very stocky *Geositta* with its short tail, and also in different postures, which, however, do not seem to be assumed regularly in *U. dumetaria.*

It has been mentioned also that *Upucerthia* differs from *Geositta* by being less strictly terrestrial, but the very few observations of perching birds, which exist only for *U. dumetaria* and *U. serrana,* should not be accorded any undue importance, as *Upucerthia* is certainly essentially terrestrial.

The English name "Earthcreeper" given

to the birds of this genus is not appropriate because they run very actively on the ground, but do not creep. I suggest they be called "Earthrunners" instead. The English name "Earthcreeper" is an adaptation of the scientific *Upucerthia* which was injudicious from the start as these birds are not related to the creepers (*Certhia*) with the bill of the hoopoes (*Upupa*), despite the belief of Geoffroy Saint-Hilaire who named *Upucerthia*. Cabanis (1859) did not approve of *Upucerthia*, and substituted *Coprotretis* (i.e., "dungborer") for it. The Spanish names "Bandurrilla," or "Bandurrita," signify a small ibis ("Bandurria"), or small curlew, a comparison which Hudson considers is appropriate (see above).

Generally speaking, the counterparts of *Upucerthia* in North America are the thrashers (*Toxostoma*), which belong to the family Mimidae.

Morphological Variation

The birds of this genus are more gracefully proportioned than those of *Geositta*, as stated above, and vary much less morphologically. Some of their characters were mentioned in the comparison with *Geositta*, but are repeated below to present a coherent account of the variation.

Upucerthia has a much longer tail than that of *Geositta*, and its bill averages longer and its wing shorter. All the measurements vary within a relatively restricted range, less than in *Geositta*. The means of the lengths of the tail, wing, and bill vary in round numbers (mm.), from 70 to 81, average 75, in the case of the tail; 72 to 103, average 87, for the wing; and 26 to 37, average 32, for the bill (table 2). The ratio of the length of the tail to that of the wing varies from 0.76 to 0.98, average 0.87

The variation in the length of the bill is not much inferior to that in *Geositta*, but its shape remains essentially the same, though more or less decurved. This contrasts strongly with *Geositta* in which the variation in shape is exceptionally great.

The feet and shape of the tail are also less variable than in *Geositta*. The feet are moderately strong, not weak, or very stout as in some species of *Geositta*. The tip of the tail is more or less moderately graduated and the tail is slightly stiffened in all the species. The degree of stiffness is roughly the same in both genera, but the shape of the tip is more variable in *Geositta*.

The general coloration of *Upucerthia* is very similar to that of *Geositta*, plain and dull, not conspicuous, but less variable than in *Geositta*, as is consistently true of all other characters. The upperparts are more or less earthy and brownish, and are uniform with the exception of *U. serrana* which is slightly streaked on the forecrown and upper mantle. All of the species of *Upucerthia* have a conspicuous buffy superciliary streak, as in *Geositta*, and are also contrastingly pale on the underparts, uniform below the whitish throat in *U. certhioides*, but with dark edges or borders that are more or less distinct in the other six species.

The wings and tail are rufous to a varying degree in six species, but are brownish in *U. dumetaria*. All the species have a rufous area in the wing, and in all of them the base of the tail is dark and uniform. This contrasts with *Geositta* in which three of its 12 species lack the characteristic tail and/or wing pattern. The tail of *Upucerthia* is uniform, with the exception of *U. andaecola* and *U. dumetaria*; in *U. andaecola* the rufous tail is very extensively invaded with black or blackish brown on the inner webs of the second to the fifth rectrices, and, in *U. dumetaria*, the tips of the three outer rectrices are rufous to a varying degree, not brown.

Phylogeny

The species of *Upucerthia* can be arranged in three pairs that seem to be more or less closely related: *U. ruficauda* and *U. andaecola* in one, *U. serrana* and *U. dumetaria* in another, and *U. albigula* and *U. validirostris* in the third. The nearest relative of the seventh species (*U. certhioides*) is not clear, but, as *U. certhioides* occupies a position somewhat apart, it seems best placed at the head of the sequence. In *U. certhioides*, the underparts are uniform below

TABLE 2
Measurements (in Millimeters) of *Upucerthia*

Species	Wing			Tail			Bill		
	N	Mean	Range	N	Mean	Range	N	Mean	Range
certhioides									
Males	24	72.37	69–78	22	70.40	64–75	23	25.67	23–28
Females	23	70.50	67–77	23	68.91	64–73	21	25.70	23–30
Both sexes	53	71.66	67–78	49	69.75	64–76	48	25.65	23–30
ruficauda									
Males	18	84.88	80–90	17	72.35	65–80	19	29.32	27.50–32
Females	8	81.75	78–89	8	70.37	62–78	8	30.00	27–33
Both sexes	30	83.56	78–90	28	71.57	62–80	30	29.90	27–33
andaecola									
Males	20	82.95	80–86	20	75.20	69–81	19	29.63	25–32
Females	24	79.79	76–83	23	74.65	67–79	23	29.19	27–34
Both sexes	48	81.06	76–86	47	74.51	67–81	46	29.29	24–34
serrana									
Males	23	88.00	81–92	23	80.82	76–90	22	29.86	26–33
Females	16	85.50	80–90	16	80.81	74–86	16	29.46	27–33
Both sexes	39	86.97	80–92	39	80.82	74–90	38	29.69	26–33
dumetaria									
Males	33	104.21	97–113	32	78.37	69–86	31	36.83	31–43
Females	24	101.70	97–109	23	79.08	71–85	21	37.57	32–41
Both sexes	67	103.17	95–113	65	78.49	69–86	61	37.09	31–43
albigula									
Male	1	—	100	1	—	80	1	—	37
Female	1	—	93	1	—	77	1	—	36
Both sexes	3	94.66	91–100	3	78.00	77–80	2	36.50	36, 37
validirostris									
Males	42	89.58	82–100	42	70.85	58–89	41	35.12	31.50–42
Females	36	87.61	81–97	35	70.16	62–82	35	35.10	29–41
Both sexes	81	88.64	81–100	78	70.62	58–89	77	35.09	29–42

the whitish throat, whereas they are streaked, or the feathers of the breast have dark borders, in the other six species.

In *Upucerthia ruficauda* and *U. andaecola,* the underparts are more or less distinctly streaked with rufous brown below the breast, as the pigment is restricted to the edges of the feathers, but in the other four species the feathers of the lower throat and breast are bordered with brown to a varying degree with creates a scaly, rather than streaked pattern.

Upucerthia ruficauda and *U. andaecola* seem to be quite closely related and are virtually identical with the very conspicuous exception of the pattern of the tail. In *U. ruficauda,* the inner webs of the second to the fifth rectrices are extensively invaded with black or blackish brown, or the inner webs are wholly blackish, whereas the tail of *U. andaecola* is uniformly bright rufous, or with only a faint and small brownish spot at the tip of one or two rectrices in a rare specimen. This alternate difference in pattern is so striking that it probably serves for species recognition as the two birds are sympatric.

Upucerthia albigula and *U. validirostris* seem also to be very closely related. Johnson

(1967) said that they are so similar that "either in appearance or habits" in the field he "could detect no difference between the two species," and that he was "forced" to collect specimens for identification. His observation was made in a small river valley near Putre in the Andes of Arica, northern Chile, where he found the two species breeding and occurring together. In fact the two birds were confused until fairly recently, before Hellmayr (1932) demonstrated that they are not conspecific. In *U. albigula,* the dark borders of the feathers are very narrow but quite distinct, whereas they are faint in *U. validirostris,* becoming obsolete or vanishing in some of its populations.

In *Upucerthia serrana* and *U. dumetaria,* the dark borders are broad and conspicuous. They are less regular in *U. serrana,* which differs also from *U. dumetaria* by having a different pattern at the apex of the tail, and, in the adult plumage, on the forecrown and upper mantle. In *U. serrana,* the forecrown and upper mantle are narrowly striated with buff, and the tail is uniform, not patterned, whereas *U. dumetaria* is uniform on the forecrown and upper mantle in the adult plumage, and the tip of the tail is not uniform, but spotted with rufous on the three outer rectrices. These differences can be interpreted as a lack of close relationship, but fairly close relationship is suggested, nevertheless, by the fact that the immature plumage of *U. dumetaria* is similar to that of the adult plumage of *U. serrana,* with streaks on the forecrown and mantle, lacking in the adult plumage of *U. dumetaria.*

The immature plumage of *Upucerthia andaecola* (a member of the first pair of species discussed) is also interesting and revealing, because it is scaly below, not streaked as in the adult plumage. The pattern of *U. andaecola* in this plumage is quite similar to the pattern of the underparts in the immature plumage of *U. dumetaria,* and also shows some degree of similarity to the pattern in the adult plumage of *U. albigula* and *U. validirostris.* In short, all six species are more or less closely related.

The classification that I proposed earlier (1971a) is now modified by transferring *Upucerthia albigula* to its correct position as a close relative of *U. validirostris,* and by eliminating *U. jelskii,* which I have since concluded is conspecific with *U. validirostris,* thus reducing the number of species in *Upucerthia* from eight to seven.

Wetmore and Peters (1949) have revived *Ochetorhynchus* Meyen, 1834 (type *ruficauda*) for the species with the least decurved bill: *certhioides* and *ruficauda,* and also *harterti,* which I believe is conspecific with *certhioides* (see below), but which Wetmore and Peters considered a separate species. However, *Ochetorhynchus* cannot reasonably be maintained as a separate genus. To recognize *Ochetorhynchus* separates *ruficauda* and *andaecola* generically, whereas these two species are not only most certainly congeneric, but very closely related as stated above. Furthermore, the difference in the shape of their bill is not constant and very trivial at best; in most specimens of the two species that I have compared, the bill was actually identical in all respects of length, curvature, or thickness.

I have mentioned above that the shape of the bill was essentially the same in all the species, although it varies in the degree of curvature. The progression from a slightly to a well decurved bill is gradual, *Upucerthia certhioides* and *U. validirostris* representing the two extremes in the variation. *Ochetorhynchus* Meyen, 1834, is a synonym of *Upucerthia* Geoffroy Saint-Hilaire, 1832.

Geographical Variation

Some species of *Upucerthia* vary geographically and subspecies have been named and recognized in five species: *U. certhioides, U. ruficauda, U. serrana, U. dumetaria,* and *U. validirostris.* However, the specimens of *U. serrana* and *U. ruficauda* which I have examined (and which include the types of the forms separated), fail to confirm the existence of geographical variation.

In *Upucerthia certhioides, U. dumetaria,* and *U. validirostris,* it seems sufficient to me to recognize only two subspecies in each. The second subspecies are *harterti* in *U. certhioides, saturatior* in *U. dumetaria,* and

jelskii in *validirostris,* which have all been considered to be separate species at one time or another.

In *Upucerthia certhioides* the range of *harterti* is restricted to Bolivia where it represents nominate *certhioides* of Paraguay and Argentina geographically. The two taxa were considered to be separate species before my revision (1971a), but they do not differ by any character which seems to be of species importance in *Upucerthia,* and all the differences which distinguish them are relative and a matter of degree.

The birds of Bolivia (*harterti*) are paler below than those of Paraguay and Argentina, with the white area of the throat less restricted, but the character which has received more attention is the color of the forehead. The center of the forehead is brown in *harterti,* whereas it is rufous to a varying extent in the populations of Paraguay and Argentina. However, the feathers at the base of the bill are rufous in *harterti* also, though duller as a rule, and form a band which extends posteriorly until it vanishes into the superciliary streak above the eye; this band is about 2 mm. broad, or somewhat more, at its broadest. The rufous feathers extend posteriorly to the same degree in the birds of Paraguay and Argentina, but, in contrast to *harterti,* they also extend over the center of the forehead. This character varies individually in both forms and does not seem to be of specific importance.

The populations of Paraguay and Argentina are not uniform. They differ in the saturation of their plumage. The birds of Paraguay and of the general region of the Paraná in Argentina are the most richly colored; birds from Mendoza and La Rioja are paler, with a distinct grayish cast lacking in the birds of Paraguay and of the Paraná; and, in the remainder of the range, the birds are more or less intermediate. Differences in measurements have been mentioned, but the overlap is virtually complete in the birds I have measured from any part of the range, including Bolivia. The general coloration of *harterti* accords well with the variation in Paraguay and Argentina; birds from Bolivia are a little brighter rufous on the rump, upper and under tail coverts, and top of the tail, but, otherwise, are virtually identical above to the intermediate populations of Argentina. In short, it seems quite sufficient to admit only two subspecies, *harterti* in Bolivia, nominate *certhioides* in the remainder of the range.

Little agreement exists about the subspecies of *Upucerthia dumetaria.* The reason for this lack of accord is apparently the very low degree of variation, on the one hand, and the existence, on the other, of a form (*saturatior*) which is so distinct that it has been considered to be a separate species. *U. d. saturatior* of central Chile, and of Neuquén and Chubut in Argentina, is conspicuously darker above than the other populations of *U. dumetaria,* olive brown, rather than grayish brown, darker, less buffy below, and has a shorter bill which is usually stouter, the bill being proportionally thicker when shorter. In 10 males of each form measured by me, the bill measures 31–37 mm. (mean 34.0) in *saturatior,* as against 35–43 mm. (mean 38.5) in the other populations of *U. dumetaria.*

Esteban (1951) has discussed the status of *saturatior*; he says that he believes *saturatior* to be a distinct species because it is sympatric with *U. dumetaria* in Chile during the breeding season. However, no evidence of overlap seems to exist during the breeding season and Johnson (1967) considers that *saturatior* is conspecific with *dumetaria.* I may add that no character exists between *saturatior* and *dumetaria* which seems to be of species importance, as in the similar case of *harterti* and *certhioides* discussed above.

Additional material studied since my first revision (1971a) shows that I was wrong in following Meyer de Schauensee (1966) in separating *jelskii* specifically from *Upucerthia validirostris.* The variation is very clearly clinal and involves both size and coloration. Birds belonging to nominate *validirostris,* which occupies the southern end of the range of the species, are dull rufous brown above, strongly buffy below with a cinnamon tinge, and have a very extensive rufous area in the wing; but, from south to north, the populations have progressively smaller birds, which are browner above, pal-

er on the underparts (but see below), and in which the size of the rufous area in their wing decreases until the rufous area virtually disappears at the northern extremity of the range of the species in Ancash, Peru. However, the variation is not clinal in all characters because the birds of Ancash (which have been named *saturata*) are darker below than *jelskii* from central Peru; and, in the populations (*pallida*) which intervene geographically between nominate *validirostris* and *jelskii*, the tail is slightly more rufous as a rule than in nominate *validirostris* to the south, becoming brown in *jelskii* to the north. But, with these exceptions, the variation is clinal in all important respects. The form *saturata* is known so far from only two females and one male.

Clinal variation is difficult to express in the nomenclature, but, in the case of this species it is evident, nevertheless, that it is best expressed by recognizing only nominate *validirostris* and *jelskii*. This separation corresponds to the one proposed by Meyer de Schauensee, but with the exception, of course, that I do not consider that *jelskii* is a separate species.

The measurements (in mm.) of adult females, for which the series is more representative, are as follows, nominate *validirostris* being represented by six specimens, *pallida* by 18, *jelskii* by nine, and *saturata* by the only two in existence.

	Wing		Tail		Bill	
Taxon	Range	Mean	Range	Mean	Range	Mean
validirostris	91–97	(92.75)	76–82	(78.84)	34–41	(38.83)
pallida	83–91	(87.10)	65–78	(69.59)	31–39	(34.58)
jelskii	84–87	(85.25)	62–69	(65.00)	29–36	(33.78)
saturata	81, 82	(81.50)	62, 62.5	(62.25)	32, 35	(33.50)

KEY TO THE SPECIES OF *UPUCERTHIA*

1. Breast feathers uniform ..... *certhioides*
   Breast feathers not uniform, with dark borders or edges 2
2. Dark borders of breast feathers broad and conspicuous 3
   Dark borders of breast feathers faint or very narrow, or dark borders replaced by streaks 4
3. Tail uniform and strongly rufous; forecrown and upper mantle narrowly striated ..... *serrana*
   Tail not uniform and almost wholly dark brown, the rufous area being narrowly restricted to the outer web, or extreme tips of the three outer rectrices; forecrown and upper mantle uniform, not striated ..... *dumetaria*
4. Underparts streaked below the upper breast 5
   Underparts not streaked 6
5. Tail uniformly rufous, or virtually so ..... *andaecola*
   Tail not uniformly rufous, the inner webs of the second to the fifth rectrices being very extensively invaded with black or blackish brown, or wholly black or blackish brown ..... *ruficauda*
6. Coloration not uniform above and below, the crown being distinctly darker than the back, and the whitish upper throat contrasting conspicuously with the lower throat and breast which are dark buff; superciliary streak broad and well developed behind the eye[21] ..... *albigula*
   Coloration of the crown and back uniform, and no contrast or virtually none between the coloration of the whole throat and breast; superciliary streak poorly developed behind the eye, relatively speaking .. *validirostris*

LIST OF THE SPECIES

Upucerthia certhioides

DESCRIPTION: Earthy brown above, but rufous on the feathers which extend from the nostril posteriorly and narrowly to the eye (in *harterti*), the rufous area spreading across the forehead in nominate *certhioides* and related populations, but not in *harterti* where the center of the forehead is brown. Underparts uniform below the whitish throat, without dark edges or borders to the feathers as in all the other species of the genus; the coloration varying from grayish brown (nominate *certhioides* and related populations) to grayish buff (*harterti*); with the whitish area of the throat extending to the breast (*harterti*), less restricted to the throat than in nominate *certhioides* and re-

lated populations; flanks and lower abdomen more or less suffused with rufous brown. Rufous area of the wing restricted, not very distinct. Bill relatively short, slightly decurved at the tip.

IMMATURE PLUMAGE: Similar to the adult, but more rufous throughout, especially below. In nominate *certhioides* and related populations, the rufous area on the forehead is scarcely evident, or less distinct than in the adult.

RANGE: Eastern Bolivia (between about 1400 and 2865 m.) in the Departments of Cochabamba, Santa Cruz, and Chuquisaca, south through the Chaco in Paraguay, and Argentina to Mendoza, San Luis, and northern Buenos Aires, east to Entre Rios and Corrientes; recorded up to 1330 m. in Salta, and reaching at least 1000 m. in Mendoza.

The two subspecies recognized by me are *harterti,* which is restricted to Bolivia, and nominate *certhioides* in the remainder of the range.

SPECIMENS EXAMINED: 64.

Upucerthia ruficauda

DESCRIPTION: Pale earthy brown above with a rufous cast. Pale buff below, becoming tinged with pale rufous brown on the flanks and lower abdomen, and with the feathers edged with pale rufous brown below the whitish throat and upper breast, thus producing more or less distinct streaks. Rufous area of the wing very restricted; tail strongly rufous, but with the inner webs of the second to the fifth rectrices very extensively invaded with black or blackish brown, or inner webs wholly blackish. Bill relatively short, slightly decurved at the tip.

IMMATURE PLUMAGE: Generally similar to that of the adult but very strongly tinged with rufous throughout. The pattern is less distinct below, and the feathers of the crown and mantle have very faint pale tips, whereas they are uniform in the adult.

RANGE: Andes, between about 2800 and 4500 m., from Arequipa in southern Peru, south through western Bolivia (Departments of La Paz, Oruro, and Potosí), to Santiago in Chile, and Chubut in Argentina.

SPECIMENS EXAMINED: 36, including the type of "*montana*" in MNHN.

Upucerthia andaecola

Figure 1

DESCRIPTION: Virtually identical with *Upucerthia ruficauda* in appearance, but with the very conspicuous exception that the tail is uniformly rufous, or with only a faint and small brownish spot at the tip of one or two of the rectrices in a rare specimen. The streaks on the underparts tend also to be darker and better defined than in *U. ruficauda.* Rufous patch in the wing and bill similar to that of *U. ruficauda.*

IMMATURE PLUMAGE: Quite distinct from that of the adult; the feathers of virtually the whole of the underparts are narrowly but distinctly bordered with dusky brown below the pale throat, producing a scaly appearance similar to that of the immature plumage of *Upucerthia dumetaria,* and to that of the breast in the adult plumage of *U. albigula* and *U. validirostris,* whereas the dark pigment is restricted to the edges of the feathers in the adult plumage of *U. andaecola,* producing streaks. The upper parts are similar in the immature plumage of *U. andaecola* and *U. ruficauda,* strongly tinged with rufous, not uniform, as the feathers are paler at the tip or borders.

RANGE: Andes, between about 2500 and 4500 m., but down to about 2100 m. in Argentina, from Bolivia south to northern Catamarca in Argentina, probably also Andes of Antofagasta in Chile. In Bolivia, this species has been collected in the Departments of La Paz, Cochabamba, Chuquisaca, and Potosí, not in Oruro, so far, but probably occurs also in Oruro as it has been collected about 5 km. east of Oruro in Potosí.

SPECIMENS EXAMINED: 51, including the two cotypes in MNHN, and that of "*bridgesi*" in BM.

Upucerthia serrana

DESCRIPTION: Raw umber brown above, with the forecrown and upper mantle narrowly striated with buff; dingy buff below,

with the feathers of the throat and breast bordered with dark brown. Rufous area of the wing relatively extensive, and tail strongly and uniformly rufous. Bill relatively short, slightly decurved at the tip.

IMMATURE PLUMAGE: Similar to that of the adult, but pattern of the underparts less distinct.

RANGE: Andes of Peru, between about 2740 and 4270 m., from Cajamarca south to Huancavelica.

SPECIMENS EXAMINED: 39, including the type of "*huancavelicae*" in BM.

Upucerthia dumetaria

DESCRIPTION: Grayish brown above (or dark olive brown in *saturatior*); dingy buff below, with the feathers of the breast conspicuously bordered with dark brown (more regularly and distinctly so than in *Upucerthia serrana*), and with the center of the throat whitish, without dark borders to the feathers, the dark borders being restricted to the feathers at the sides and base of the throat. Rufous area of the wing relatively extensive; tail brown, but not uniform at the apex, as the three outer rectrices are more or less extensively tipped with rufous, the rufous area being larger on the outer pair and spreading partly upward along the outer web, the rufous area being much smaller on the second pair, and very small or virtually absent at the tip of the third. Bill well decurved and long, but shorter in *saturatior*.

IMMATURE PLUMAGE: Differs distinctly from that of the adult by being similar above to the adult plumage of *Upucerthia serrana*, with narrow buffy streaks on the forecrown and upper mantle. The dark borders of the feathers of the underparts are narrower and less regular than in the adult, and exist over virtually the whole of the underparts (with the exception of the center of the lower abdomen), below the pale throat, but the borders become fainter and less regular below the breast. In the adult plumage, the dark borders are lacking below the breast.

In a nestling of *saturatior*, all the feathers of the underparts (with the exception of the center of the lower abdomen), but including those of the throat, are very conspicuously bordered, or heavily spotted, with dark brown at the tip.

RANGE: Southern Peru (Puno), and western Bolivia (Departments of Cochabamba, Oruro, Potosí, and very probably La Paz), south to Chile (from the Rio Loa on the border of Tarapaca and Antofagasta, south to Tierra del Fuego), and western and southern Argentina. In Argentina, it breeds in the Andes from Jujuy to Neuquén, and, in southern Argentina, in the region south of about the Rio Colorado, from the Andes east to the coast, south to Santa Cruz, and probably Tierra del Fuego. The altitudinal range is from sea level in Chile and Argentina, up to about 3100 m. in Chile and Argentina, and about 3900, or somewhat more, in Bolivia and Peru.

Partly migratory, moves to lower elevations in winter, east to Santiago del Estero and Córdoba (it is said to breed in western Córdoba, but all the specimens seen by me were collected during the heart of the winter and probably were migrants); also north to Buenos Aires and Entre Ríos. It breeds in southern Buenos Aires north of the Rio Colorado (perhaps regularly), and occasionally in northern Buenos Aires.

The two subspecies recognized by me are *saturatior* and nominate *dumetaria*. The breeding range of *saturatior* is imperfectly known, but seems to consist of Chubut and Neuquén in Argentina, and of Bío-Bío south to Valdivia in Chile, but *saturatior* occurs in winter north to Aconcagua in Chile and San Juan in Argentina. The populations from the remainder of the range of the species are nominate *dumetaria*.

SPECIMENS EXAMINED: 147, including the type of *dumetaria* in MNHN, of *saturatior* in BM, of "*darwini*" in BM, of "*tamucoensis*" in BM, of "*fitzgeraldi*" in BM, and of "*hallinani*" in AMNH.

Upucerthia albigula

DESCRIPTION: Dull pale brown above, but darker (warm sepia) on the crown; dark buff on the underparts below the whitish throat which is very conspicuous, with the feathers

of the lower throat and upper breast very narrowly but distinctly bordered with dusky brown, producing a scaly appearance. Rufous area of the wing very extensive, and tail strongly rufous. Bill long and well decurved.

RANGE: Andes of Tacna in extreme southern Peru, and of Arica in extreme northern Chile, between about 3050 and 3700 m.

SPECIMENS EXAMINED: 3, including the type in FMNH.

This species is very rare in collections and the existence of only a few specimens is known to me. They consist of the three above, two of which are in the Field Museum of Natural History, and the other in the American Museum of Natural History. These three specimens were seen by Hellmayr (1932) who mentions another specimen in the Senckenberg Museum, Frankfurt. Johnson (1967) says he collected "additional specimens" in 1943, but does not state how many.[22a]

Upucerthia validirostris
Figure 1

DESCRIPTION: Varies geographically (see discussion of geographical variation) from dull rufous brown above to dark sepia brown; from dark buff, with a cinnamon tinge, below, to pale buff, and grayish ochraceous buff; the tail from dull rufous to sepia brown; and the rufous area of the wing, greatly, from very extensive and bright rufous, to very restricted and dull, and virtually absent. Bill long, well decurved.

Some populations of *Upucerthia validirostris* are similar to *U. albigula* in appearance, but their coloration is more uniform, with no contrast between the color of the crown and back, and with virtually no contrast between the color of the throat, breast, and abdomen. The dark borders of the feathers of the lower throat and breast are not evident in some populations, and, when indicated, are always fainter than in *U. albigula*.

IMMATURE PLUMAGE: Generally similar to that of the adult, but the breast is more mottled, the dark borders of the feathers are usually better indicated than in the adult, but less regular, more or less interrupted at the center. The pattern of the upperparts differs also from that of the adult by not being uniform, as the feathers are paler subapically, with very faint dark borders.

RANGE: Andes, from Ancash in Peru, south to the Andes of Arica and Tarapacá in Chile, and, through western Bolivia, to Mendoza in Argentina; between about 3250 and 5000 m., and possibly higher, in Peru and Bolivia, but down to about 3050 m. in Chile, and about 2700 m. in Argentina.

The two subspecies recognized by me are nominate *validirostris* in Argentina north to Jujuy, and *jelskii* in the remainder of the range. Zotta (1938) has identified a single specimen, collected at some unspecified date in April, at San Antonio de los Cobres, northwestern Salta, as *pallida,* a form I do not separate nomenclaturally from *jelskii*; see discussion of geographical variation.

SPECIMENS EXAMINED: 120, including the type of "*dabbenei*" in AMNH.

GENUS *CINCLODES*

The genus *Cinclodes,* composed of 10 species,[22b] is closely related to *Geositta* and *Upucerthia* yet quite distinct from both.

The general distribution of the three genera is similar, and morphological, ecological, and behavioral resemblances exist, especially the nest which is "under ground," a location identical or essentially similar in all the three genera. The three genera are also terrestrial or essentially so, but *Cinclodes* is normally much more closely associated with water than *Geositta* or *Upucerthia,* and assumes postures which have been compared to those of the dippers (*Cinclus*) and wagtails (*Motacilla*).[23] *Cinclodes* is also more generalized in every aspect, despite some contradictions, such as the "marine" behavior of *C. taczanowskii.* One aspect of the behavior of *Cinclodes* which is mentioned often is that the birds are unusually confiding and inquisitive as a rule, a behavior not reported in *Geositta* and *Upucerthia.*

Ecology and behavior vary very widely in *Cinclodes,* but a good general impression is given by an account of *C. fuscus* in central Peru by Jelski (in Taczanowskii, 1884); *C.*

fuscus is the best known, most "typical," and the most widely distributed species of the genus. In this account (translated by me from the French with slight condensation), Jelski said "[*Cinclodes fuscus*] is one of the most common birds of the pasture-land (*puna*), frequenting equally the edge of the forest and the *puna* proper. It follows the streams which descend through the sierra, but never enters into the forest. Although found chiefly near water, it is met everywhere, even on arid hills and within corrals, near houses, and in the center of villages. It is the most common bird at Junin, as well as the most confiding, and, on top of the local dam, can be approached within two or three steps, only to fly for a few feet or merely sidestepping away. It roosts at night [when not breeding] within the holes in the dam, or in hedges, under the roof of the houses, under the bridges, and so on. It is elegant in its posture, and in bearing and actions recalls our wagtail [*Motacilla alba*]. It raises slightly the feathers of the crown; erects its wings often, and fluttering them, emits the sound, sirrrrr . . . ; but sometimes it erects its wings several times in a row without vocalizing. It raises its tail slightly when it alights, and does not fly high above the ground, except to reach a perch on the top of a roof. It catches insects on the ground by running or hopping, and breeds in April and May, nesting within the same holes where it roosts."

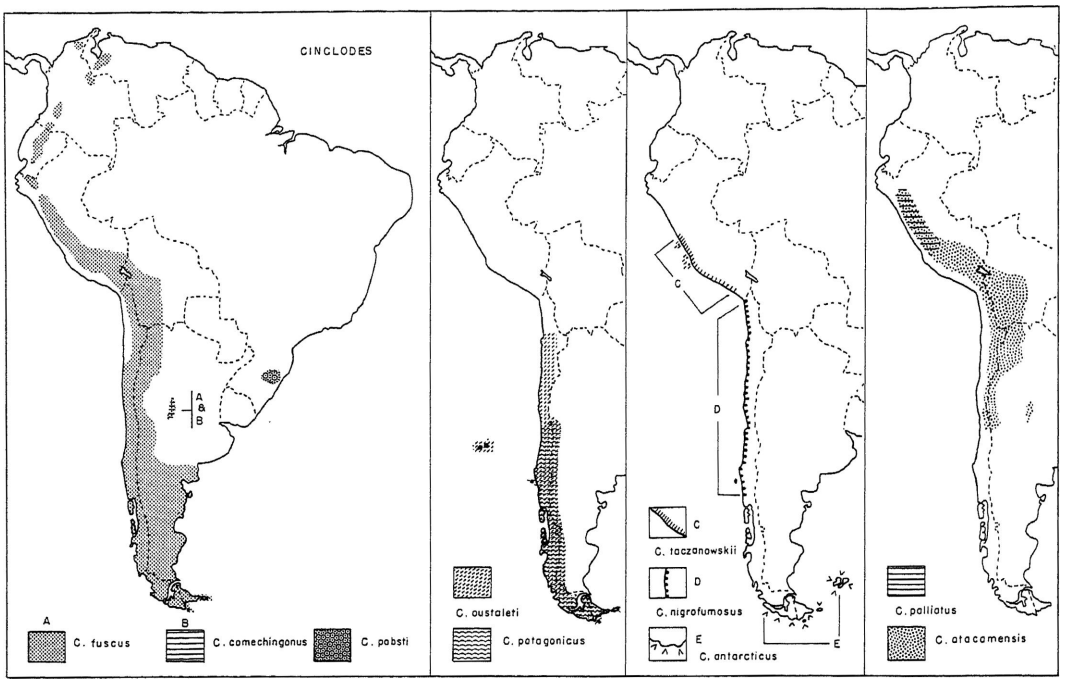
The vocalization mentioned by Jelski is expressed as "*P-i-r-r-r-r*" by Crawshay (1907) in English, and this shrill or trilling call seems to be characteristic of all the species for which vocalizations are reported, as well as postures or other actions similar to those of *Cinclodes fuscus*.

Jelski, Reynolds (1935), and other authors agree in stressing the confiding behavior of *Cinclodes fuscus*, but it is mentioned for other species as well, and seems to reach a peak in the population of *C. antarcticus* from the Malvinas, or Falkland Islands, as Cawkell and Hamilton (1961) report that *C. antarcticus* in these islands approaches observers and even perches on them, flies out to the rail of approaching boats, and boldly enters houses to share the meals of the inhabitants. *Cinclodes fuscus, C. patagonicus, C. nigrofumosus,* and *C. atacamensis* also enter dwellings or other edifices, and *C. comechingonus* and *C. oustaleti* are also said to be very confiding. Virtually no information on behavior exists for the rare *C. palliatus,* or for the recently discovered *C. pabsti,* other than that this bird has not been found associated with water so far. In the case of *C. taczanowskii,* attention has been concentrated on its "marine" behavior (see below), but *C. taczanowskii* does not seem to be at all timorous.[24]

The behavior of *Cinclodes* varies ecologically, but apparently not in *C. taczanowskii,* which is restricted to a very narrow and specialized niche on the rocky coasts of Peru. This bird does not seem to ever leave the edge of the water and forages on or around rocks, boulders, rocky promontories, or on the sandy beach of small coves between the promontories—within the zone where waves break, retreating or advancing with the waves. It feeds on small crustaceans, molluscs, and other small marine animals, and nests within the crevices of the rocks situated at the edge of the water. Short and Morony (1969), and Paynter (1971), who have observed *C. taczanowskii,* compare the behavior of this bird to that of a Purple Sandpiper (*Calidris maritima*) in the case of Short and Morony, or a Surfbird (*Aphriza virgata*) in the case of Paynter.

Cinclodes taczanowskii is related to two other coastal species (*C. nigrofumosus* and *C. antarcticus*) which also live on rocky coasts and behave in the same manner as *C. taczanowskii,* although they are less restricted ecologically.[25] *C. nigrofumosus* usually nests in the crevices of rocks or slopes near the sea, but also digs a burrow in the earth which can be located inland, rather far from the beach, up to about a distance of half a kilometer, according to Valenzuela (1964), who says also that *C. nigrofumosus* nests as well in holes under the roofs of, or within the walls of edifices near the beach; the food consists of insects as well as marine animals.

The habitat and behavior of *Cinclodes antarcticus* differ also, and more markedly than in *C. nigrofumosus. C. antarcticus* seems to



MAP 3. Geographical distribution of *Cinclodes*.

behave in the same manner as *C. taczanowskii* on the rocky coasts of the Cape Horn Archipelago, judging by the report of Reynolds (1935), but not in the Malvinas where it is not restricted to the coast, penetrating inland on islands where tussock grass grows, and where its behavior and choice of nesting sites is very eclectic, entering homes to share the meals of the inhabitants, as stated above, being especially fond of butter or scraps of meat, according to Cawkell and Hamilton (1961).

The "marine" behavior of *Cinclodes taczanowskii* has received considerable attention, but is not unduly significant in my opinion when one considers that this "marine" behavior breaks down in its relatives. Moreover, it is shared more or less by *C. fuscus, C. oustaleti,* and *C. patagonicus,* which are not closely related to the three coastal species, but the breeding range of which comes down to the coast.

The intimate association of *Cinclodes taczanowskii* with salt water has led Short and Morony (1969) to suggest that physiological-anatomical adaptations to this habitat exist perhaps in this species. They collected two specimens 95 km. south of Lima, but they have not been dissected to date. Two specimens were also secured independently for Paynter, about 85 km. south of Lima, but upon dissection the nasal gland turned out to be small which suggests that it is not a salt-excreting organ. But, "in contrast to the diminutive nasal gland," Paynter (1971) found that the Harderian gland "is of a substantial size, covering about one-third of the orbital wall." He says that this is characteristic of many marine birds, the viscous secretion of this gland probably protecting the eye from irritation by salt water, but it seems premature to draw a conclusion because this gland is apparently not especially well developed in some sea birds and has not been examined in the other species of *Cinclodes* frequenting the coast.

No obvious morphological adaptations seem to exist in *Cinclodes,* and, other than for close association with water, this genus seems quite unspecialized to me. This may

explain its unusually wide distribution from Cape Horn to northern South America in a great variety of habitats, and its expansion to islands that are relatively far from the mainland. In the case of the Malvinas the jump is of roughly 400 km., and is of about 750 km. to the Juan Fernández Archipelago, including Masafuera Island. *Geositta* and *Upucerthia* are restricted chiefly to open arid regions, but not *Cinclodes* which is decidedly catholic, inhabiting virtually all types of open country provided water exists; even the presence of water is not always essential, for *C. fuscus* and *C. oustaleti* frequent also arid slopes, and, as stated above, *C. pabsti* may not be associated with water at all.

Cinclodes seems to have originated in southern South America, as did also *Geositta* and *Upucerthia*, and the general distribution of the three genera is similar (maps 1–3). Three of the 10 species (*C. taczanowskii, C. nigrofumosus,* and *C. antarcticus*) are coastal, as in the case of *Geositta,* and their distribution is roughly similar. One very widely distributed species is characteristic in each of the three genera, *C. fuscus* being the geographical counterpart of *Geositta cunicularia* and *Upucerthia dumetaria.* But *C. fuscus* has expanded farther north than these two species and its ancestor was evidently plastic, as contemporary *C. fuscus, C. comechingonus,* and *C. pabsti* all seem to be derived from the same ancestral form. Two species (*oustaleti* and *patagonicus*) recall in their distribution *Geositta rufipennis,* ascending from the coast of Chile into the cordilleras. *Geositta* and *Upucerthia* have several species each that are strictly Andean; their geographical counterparts are *C. palliatus* and *C. atacamensis* in *Cinclodes,* although *C. atacamensis* exists also in the isolated Sierra de Córdoba in Argentina, probably a case of secondary expansion.

The altitudinal ranges of the three genera are identical or virtually so; in *Cinclodes palliatus, C. atacamensis,* and the Andean populations of *fuscus* they reach 5000 m., or slightly higher, the same altitude reached by some species of *Geositta* and *Upucerthia.*

Cinclodes comechingonus is migratory, *C. fuscus* and *C. oustaleti* are partly so, and *C. atacamensis* moves altitudinally but these movements are not well documented. In *C. fuscus,* only the populations from southern Argentina and southern Chile are migratory and the winter quarters are in northern Argentina, Uruguay, and Rio Grande do Sul in Brazil, the birds arriving in April or late March to leave in September and October. In *Upucerthia,* only *U. dumetaria* (*q.v.*) is known to winter north of its breeding range, but is much less migratory than *C. fuscus,* and migratory movements are unknown in *Geositta.*[26]

Cinclodes resembles *Geositta* and *Upucerthia* morphologically, but generally speaking, its species are bigger, less stocky than those of *Geositta,* less slender and graceful than those of *Upucerthia.* The difference in general appearance is best shown by the length of the tail which is 72 percent of the length of the wing in *Cinclodes,* as against 56 in *Geositta,* and 87 in *Upucerthia.* The bill of *Cinclodes* is similar to that of some species in the other two genera, but is straighter and shorter than that of *Upucerthia* on the whole, not very long, slender, and decurved as in most species of *Upucerthia* and one species of *Geositta* (*tenuirostris*).

The general coloration in *Cinclodes* is dull as in the other two genera but it is usually darker and browner above and does not seem to be more or less closely adapted to the color of the substratum as in the other two genera. *Cinclodes* is very closely associated with water as a rule and five of its species are dark brown above, identical with or very similar to *Cinclus,* which, ecologically speaking and in some aspects of behavior resembles *Cinclodes.*

All three genera have a conspicuous rufous area in the wing, but the pattern of this area is normally more interrupted in *Cinclodes* and, in some instances, is white rather than rufous. Similarities exist also in the color pattern of the tail but the base of the tail is uniformly dark in all *Cinclodes* (a character shared by *Upucerthia*), whereas the base of the tail is rufous, brighter, or conspicuously paler than the tip in nearly all species of *Geositta.*

The general behavior of *Cinclodes* has been discussed above, but the location of the nest was mentioned incidentally in three species only. Information is available for nine of the 10 species and indicates that the location of the nest is identical or essentially similar in all three genera, although the choice of site is more eclectic in *Cinclodes*. In *Cinclodes*, the nest is also "under ground," at the end of a burrow under the earth, or in crevices among or under rocks. The burrow is either excavated by the bird, or the existing burrow of a rodent or of some other bird such as a kingfisher, or other suitable hole, is adopted when situated in a bluff, bank, or the face of a cutting in the earth overlooking water. *Cinclodes fuscus, C. pabsti, C. patagonicus,* and *C. nigrofumosus* have been reported to excavate their own burrows, and other species probably do so also.

However, any suitable site that is available seems to be used by *Cinclodes,* although some species are probably more partial to one location than another. For instance, *C. nigrofumosus* usually nests within crevices among rocks, boulders, or cliffs along or near the shore, at least in some localities, but also digs a burrow at a fair distance from the beach, and, in some localities, selects the walls of houses or other edifices, or holes under their roofs. *Cinclodes taczanowskii* does not seem to nest elsewhere than within crevices of the rocks and boulders at the edge of the sea. In species that are not narrowly restricted ecologically, the location of the nest varies greatly. For instance, *C. fuscus* nests not only in burrows, but also in holes in dams, in hedges, under the roofs of houses, or within the under structure of bridges, according to Jelski; but its nest is placed also within cavities in rocky outcrops, under rock ledges along streams, within the walls of corrals or other man-made structures, and even within the interior of occupied dwellings. *Cinclodes oustaleti, C. patagonicus, C. antarcticus,* and *C. atacamensis* are also very eclectic in the choice of nesting sites, which may include hollow tree trunks in *C. patagonicus* on Tierra del Fuego, or such very artificial cover as an abandoned inverted bucket in *C. antarcticus*. The only species for which no information exists is the rare *C. palliatus,* but as *C. palliatus* seems to be closely related to *C. atacamensis,* it can be inferred that it probably nests also within a burrow or some sort of cavity.

Morphological Variation

Cinclodes varies morphologically, but only to a moderate degree when reservations are made for a few aberrant characters mentioned below.

Cinclodes palliatus is considerably bigger than the other species, has exceptionally big feet, and its tail is abnormally long, but, with these exceptions, the morphological variation in structural characters is quite limited. It is apparent chiefly in the size of the bill which varies in length from 19 to 30 mm., with an average of 25, being relatively weak in some species, such as *C. fuscus,* but coarse in others, such as *C. nigrofumosus*. The bill is straight, "normal" in shape, but the tip of the maxilla is slightly decurved in the species with the coarsest bill, though not the mandible.

The mean measurements of the wing (*C. palliatus* excluded), and of the tail (*C. palliatus* and *C. pabsti* excluded), vary within a relatively narrow range (in mm.), from 91 to 118, average 106, in the case of the wing; from 64 to 82, average 74, in the case of the tail. This range of variation is comparable to that prevailing in *Upucerthia* which is much more uniform than *Geositta*. With *palliatus* added, the wing measurements (mm.) are 91–133 (mean 109), and the tail measurements 64–98 (78) with *palliatus* and *pabsti* added. Measurements of *Cinclodes* species are given in table 3.

The ratio of tail length to wing length varies in *Cinclodes* (all species) from 0.66 to 0.86, average 0.72. This ratio is intermediate between the ratios of *Geositta* (0.56) and *Upucerthia* (0.87). The tail is slightly stiffened in all species, to about the same degree as in *Geositta* and *Upucerthia,* and its tip is more or less moderately graduated as in *Upucerthia*.

TABLE 3
Measurements (in Millimeters) of *Cinclodes*

Species	Wing			Tail			Bill		
	N	Mean	Range	N	Mean	Range	N	Mean	Range
fuscus									
Males	100	100.47	94–109	100	68.32	60–75	100	21.03	19–23
Females	100	96.78	90–105	100	67.13	60–76	100	20.98	19–24
Both sexes	206	98.60	90–109	207	67.60	60–76	206	20.99	19–24
comechingonus									
Males	2	93.50	93, 94	2	68.00	66, 70	2	18.60	18.2, 19
Female	1	—	87	1	—	65	1	—	19
Both sexes	3	91.33	87–94	3	67.00	65–70	3	18.73	18.2–19
pabsti									
Both sexes	2	109.50	108, 111	2	94.00	91, 97	2	26.50	26, 27
oustaleti									
Males	21	93.61	89–100	21	64.23	60–69	20	22.04	19.50–24
Females	14	93.32	88–97	13	63.69	58–68	12	21.79	21–22.50
Both sexes	50	93.11	88–100	49	64.06	58–69	46	21.81	19.50–25
patagonicus									
Males	53	104.49	100–111	37	75.45	70–81	33	26.39	24–29
Females	27	102.55	96–110	21	75.57	70–82	21	26.19	24–30
Both sexes	84	103.76	96–111	62	75.30	69–81	57	26.22	24–30
taczanowskii									
Males	11	115.81	111–122	10	81.10	75–85	11	27.59	25–30
Females	18	114.94	111–118	17	81.29	75–85	18	27.27	24–29
Both sexes	35	115.00	110–122	32	81.18	75–85	35	27.45	24–30
nigrofumosus									
Both sexes	23	118.04	111–126	22	82.40	74–90	23	29.02	28–31
antarcticus									
Both sexes	29	112.72	105–125	29	74.82	68–87	28	24.50	21.50–26.50
atacamensis									
Males	31	114.12	108.50–124	29	80.75	73–87	31	28.51	25–30
Females	31	112.22	106–117	27	79.70	70–85	33	27.93	25–30
Both sexes	64	113.28	108.50–124	58	80.25	70–87	66	28.21	25–30
palliatus									
Both sexes	10	133.10	128–140	10	98.30	92–104	10	29.90	28–31

The feet are normally well developed in all the species with the exception of *Cinclodes palliatus*. They are neither exceptionally weak nor strong and their strength is proportionate to the size of the bird, except in *C. palliatus* which has exceptionally big feet, curiously thick and massive.

The variation is coloration is more evident than the variation in structural characters, but the plumages of *C. palliatus* and *C. antarcticus* are aberrant.

All the species are very plain, and (with the exception of *Cinclodes palliatus*) are uniform above. They are all brown, varying from grayish brown, with a tinge of olive, to fuscous, reddish brown, chestnut, and dark chocolate brown, rather similar to the coloration of *Cinclus*. In *C. palliatus*, the

crown is pale soft gray, contrasting strongly with the color of the back which is chestnut as in *C. atacamensis* but slightly brighter.

The underparts contrast with the upperparts by being "pale," but the difference is extremely slight in *Cinclodes antarcticus* because this species has an extremely somber plumage, sooty chocolate brown or dark fuscous both above and below to virtually the same degree and is uniform with the exception of a very vaguely paler, poorly defined area on the throat. In the other species, the color of the underparts varies from pure snowy white in *C. palliatus,* to buffy, ochraceous, grayish, or brown, with or without white or whitish shaft streaks below the throat that are more or less sharply defined.

The throat is whitish, or paler than the breast, in all the species with the exception of *Cinclodes palliatus,* in which the whole of the underparts are uniformly pure white from the chin to the under tail coverts, as well as the face below the pale rusty brown ear coverts. A buffy superciliary streak exists in eight of the 10 species and is conspicuous as a rule, but this streak is absent altogether in *C. palliatus* and *C. antarcticus.*

All the species have a pale area in the wing which is more or less irregular, but consists chiefly of a bar across the secondaries and primaries near the base; the bar varies in width but is normally broad. The tips of the three outer pairs of rectrices are pale to a varying degree, contrasting well or not with the remainder of the tail which is dark brown or blackish and uniform; the pale tips vary in color from white to grayish white, buff, or rufous. The wing bar is pure white in *C. palliatus* and *C. atacamensis,* rufous and normally bright in the other species; it varies geographically in *C. fuscus* from brightly rufous to dull white. In *C. antarcticus,* however, the pale area in the wing and the spots at the tips of the rectrices have almost completely vanished in some populations, and completely so in others.

Phylogeny

The 10 species of *Cinclodes* can be arranged into four groups: *C. fuscus, C. comechingonus,* and *C. pabsti* in one; *C. oustaleti* and *C. patagonicus* in another; *C. taczanowskii, C. nigrofumosus,* and *C. antarcticus* in a third group; and *C. atacamensis* and *C. palliatus* in the fourth.

The species of the first group (*Cinclodes fuscus, C. comechingonus,* and *C. pabsti*) are closely related; *C. fuscus* and *C. comechingonus* are generally similar, but *C. pabsti* is better differentiated and "can be considered an ice age relict" according to Sick (1969). At present, the breeding range of *C. fuscus* does not seem to extend north of the Rio Colorado in Argentina east of the Andes (although it breeds also in the mountains of western Córdoba), but, when the climate was colder, the breeding range very probably extended much farther north, including the plateau of northeastern Rio Grande do Sul and neighboring Santa Catarina, Brazil, to which *C. pabsti* is restricted (map 3). *C. fuscus* occurs commonly on this plateau but only as a winter visitor.

Cinclodes pabsti is paler below than *C. comechingonus* and *C. fuscus,* has a more conspicuous superciliary streak, and very considerably larger and brighter spots at the tips of the outer pairs of rectrices. *C. pabsti* is also larger with a much longer tail, and its innermost secondaries (or "tertials") are also longer and the wing is more rounded than in *C. comechingonus* and the populations of *C. fuscus* from Argentina which are migratory and winter in southeastern Brazil, *C. comechingonus* being migratory also.

The difference in the shape of the wing is most probably an instance of secondary adaptation because *C. pabsti* seems to be strictly sedentary and no essential difference in shape exists between *C. pabsti* and the non-migratory populations of *C. fuscus.* Sick has discussed at length the significance of the long innermost secondaries suggesting that they are also an adaptation to the much denser vegetation of the region to which *C. pabsti* is restricted and which seems to consist chiefly of tall grasses with sharp edges, whereas *C. fuscus* breeds in more open regions with sparser vegetation; the long innermost secondaries protect, in principle, the tips of the inner primaries from abrasion.

The significance of the long tail is not clear, but, perhaps, represents also a secondary adaptation to a more gliding type of flight than in *C. fuscus*.

Sick's description of *Cinclodes pabsti* was published in 1969, but this population had been identified as a new species by me also, and independently, before that date. My conclusion was based on my examination of two specimens in the collection of the American Museum of Natural History collected by E. Kaempfer at Vaccaria, Rio Grande do Sul, in December 1928. These two specimens had been identified provisionally as the little known *C. comechingonus,* but when I decided they were a new species, not *C. comechingonus,* the description of *C. pabsti* had been in press for some time, unknown to me. The description of *C. pabsti* (illustrated by comparative photographs) was based by Sick on these two specimens and one other he collected in 1966. It seems somewhat strange that the existence of *C. pabsti* (named in 1969, but first collected in 1928), and of *C. comechingonus* (named in 1944, but first collected in 1936) had escaped detection before these dates, but this can largely be explained by the fact that the ranges of these two species are very restricted (map 3).

Cinclodes comechingonus was described by Zotta and Gavio in 1944 (1945) based on eight specimens collected in the isolated mountains of western Córdoba, Argentina, to which its breeding range seems to be very narrowly restricted. One specimen was taken by Daguerre in October 1936 at Pampa de Achala, and the other seven by Zotta and Gavio in the Sierra de Comechingones in February 1943 and January 1945 in the general region east of La Paz, the two localities being about 60 km. apart. These mountains rise steeply from the plains to about 2900 m., and, according to Zotta and Gavio, *C. comechingonus* is restricted to the zone above treeline, which starts at about 2000 m., and where it frequents small grassy or brushy areas. This zone is very narrow, as it seems to be only about 5 km. broad or less in the region east of La Paz.

Cinclodes comechingonus and *C. fuscus* coexist in these mountains but Zotta and Gavio say that *C. comechingonus* is more abundant. *Cinclodes comechingonus* is characterized by having a very extensive and strongly rufous area in the wing, and a pale lower bill, which is "strongly yellow" in life, according to Zotta and Gavio. In skins, most of the mandible is yellow, becoming dusky brown only at about the center of the cutting edge and toward the center of the gonys. The pale area in the wing varies from orange-russet to pale but very bright reddish chestnut, and is brighter rufous and more extensive than in any other species. In the forms of *C. fuscus* with which *C. comechingonus* coexists on the breeding, as well as on the wintering grounds, the pale area in the wing is very much smaller and is dull white or creamy white externally, grading into buff and very pale cinnamon internally, and the mandible is usually very dark, although a small vaguely defined yellowish spot exists at the very base in some individuals.

The differences noted above become much less conspicuous, however, when *Cinclodes comechingonus* is compared to the populations from the northern end of the range of *C. fuscus,* from Ecuador to Colombia and Venezuela. In the birds from the north, the pale area in the wing is also strongly rufous and extensive, but more restricted and less bright than in *C. comechingonus,* and the base of the mandible is yellowish or yellow in most specimens, but not so extensively as in *C. comechingonus,* although in Venezuela the mandible is almost as pale as in *C. comechingonus* in all specimens. I may add also that the pale area in the wing becomes rufous again in the populations of *C. fuscus* from the southern end of the range, although it does not increase in size and is distinctly paler than in the birds from the northern end of the range.

In other words, two characters are displaced: coloration of the wing and bill.[27] This divergence probably serves for species recognition as it is very apparent in the field according to Dr. C. Olrog who wrote to me that he "could distinguish the two species easily at a distance of 50 meters," and noted also differences in behavior in a mixed flock

of winter visitors of the two species he observed in June 1971 in northern Santiago del Estero, some of which he collected. This letter was to announce that Olrog had discovered then that *C. comechingonus* was migratory, although it had been believed to be sedentary by Zotta and Gavio, and seems to confirm the conclusion that I had reached about the significance of the divergence in characters.

Cinclodes comechingonus differs also from *C. fuscus* in other less conspicuous characters. It is a smaller bird (table 3) with a shorter and very distinctly weaker bill, and its tail is proportionally longer, with a ratio of 0.74 between its length and that of the wing, as against 0.69 in *C. fuscus*. The apical spots on its outer rectrices are also considerably larger and more strongly rufous, a difference which is especially evident in the case of the forms of *C. fuscus* with which it coexists; *C. comechingonus* differs also from these forms by being more grayish above, and darker, more brownish, on the flanks.

Cinclodes fuscus, C. pabsti, and *C. comechingonus* all seem to have been derived from the same ancestor, a form which most probably was more widely distributed when the climate was colder, but which receded later, and of which *C. pabsti* seems to be a relict.

The theory that *Cinclodes pabsti* represents a relict was advanced by Sick, and I believe a similar theory can be invoked to account for *C. comechingonus* and its very restricted breeding range—but as *C. fuscus* breeds sympatrically with *C. comechingonus* in the mountains of western Córdoba[28]—this region seems to have been invaded on two occasions and it is reasonable to assume that *C. comechingonus* was the first to arrive. This is suggested by the rufous wing of *C. comechingonus* and also the fact that it is reported to be more successful than *C. fuscus* in this region. The rufous-winged *C. comechingonus* had apparently become reproductively isolated when a white-winged form of *C. fuscus* invaded the region later and selection has probably reinforced the most evident characters which distinguish the two taxa (very large and very rufous area in the wing, conspicuously yellow bill, and also larger and more rufous apical spots on the rectrices). A rufous wing seems to be a much more conservative character than a white one as it is shared by nearly all the species in the three related genera (*Geositta, Upucerthia,* and *Cinclodes*), to which also the related and rufous-winged *Chilia* can be added, whereas a white wing appears only in two species of *Cinclodes* and some populations of *C. fuscus*.

The two species of the second group (*Cinclodes oustaleti* and *C. patagonicus*) seem to be not distantly related, and their distribution (map 3) is very similar although *oustaleti* ranges farther north and has spread to Juan Fernández Archipelago, well off Chile. These two species are best listed between the *C. fuscus* group and the group consisting of the three coastal species, but the actual relationships of the four groups of species are uncertain and any linear sequence is more or less unsatisfactory.

The three species which follow (*Cinclodes taczanowskii, C. nigrofumosus,* and *C. antarcticus*) are related to each other and restricted ecologically to the coast. The somber plumage of *C. antarcticus* is aberrant but is probably an adaptation to the very inclement and stormy region to which *C. antarcticus* is restricted.[29]

These three species are or seem to be allopatric. The gap between the ranges of *Cinclodes antarcticus* and *C. nigrofumosus* is certainly great, but the correct extent of the gap between *C. nigrofumosus* and *C. taczanowskii* is uncertain and it is possible that the ranges of these two species actually meet. The records available to date suggest that a gap of about 230 km. exists between Arica in northern Chile (*C. nigrofumosus*) and Islay-Mollendo in southern Peru (*C. taczanowskii*), but the coastal region which intervenes is poorly known and has not been investigated ornithologically because this coast is virtually inaccessible. The gap, if any, may be very much less than 230 km., for a modern map, which shows something of the relief and nature of the coast, suggests that suitable breeding habitat may exist in

some coastal hills or cliffs about 170 km. south of Mollendo; only about 60 km. of coast with low relief remain between this point and Arica. The fact that the range of *C. nigrofumosus* has been said in the literature to extend north to "southwestern Peru" adds also to the uncertainty.

Some modern authors consider that *Cinclodes taczanowskii* and *C. nigrofumosus* are conspecific, an opinion which is probably influenced by the fact that they appear to be allopatric. But *C. taczanowskii* and *C. nigrofumosus* seem to me to be too sharply differentiated morphologically to be conspecific, and, as stated above, differ also significantly in behavior. My opinion that they are distinct species is supported also by a total lack of morphological intergradation. If they were conspecific one would expect to find some degree of intergradation as their ranges approach, if they do not actually meet. The sharp morphological differences between *C. taczanowskii* and *C. nigrofumosus* are quite evident in their descriptions given below. Here, it may be sufficient to say that their coloration and its pattern differ in virtually all respects, including the near elimination of a superciliary streak in *C. taczanowskii,* whereas this streak is quite conspicuous in *C. nigrofumosus.*

The two species of the last group (*Cinclodes atacamensis* and *C. palliatus*) are closely related. Their relationship is quite evident, yet they diverge so strikingly in some morphological characters that they do not seem to be congeneric at first glance, and Cabanis proposed a monotypic genus (*Cillurus*) for *palliatus.* The back is chestnut in both species, and the pale area in the wing is pure snowy white, rather than characteristically rufous for *Cinclodes,* but *palliatus* is considerably larger and more heavily built than *C. atacamensis,* with much larger feet, and differs strikingly from *C. atacamensis* and all other *Cinclodes* by being uniformly pure snowy white on the underparts and most of the face.

In life, *Cinclodes palliatus* is said to resemble a jay more than a *Cinclodes,* and is a "distinctly rare bird" according to Morrison (1939); not many specimens exist.[30]

Geographical Variation

Cinclodes fuscus and *C. antarcticus* are the only two species in which the geographical variation is well marked.

Slight population differences exist also in *Cinclodes oustaleti* and *C. patagonicus,* and perhaps also in *C. atacamensis* but seem dubious in the case of *C. atacamensis.*[31] In *C. patagonicus,* the only difference I can note is that birds from the northern part of its range tend to be slightly less streaked on the breast. In the case of *C. oustaleti,* I find only that specimens from the Juan Fernández Archipelago are normally somewhat paler, more rufous on the flanks, than birds from the mainland, but the difference is not constant; the material I have seen from the islands consists of 12 specimens and includes the type and original series of the form named from Juan Fernández. This poor degree of differentiation suggests that the expansion of *C. oustaleti* to the islands is probably fairly recent.

Geographical variation is quite distinct in *Cinclodes antarcticus,* as the birds from the islands off Tierra del Fuego (which have been named *maculirostris*) are darker, more blackish, than those of the Malvinas, and altogether lack the pale bar in the wing which persists faintly in the Malvinas; their bill is also somewhat heavier, more yellowish at the base of the mandible, and occasionally on the commissure.

The geographical variation of *Cinclodes fuscus* is well marked and predominantly clinal, affecting the size and coloration of the pale area in the wing and of the apical spots of the rectrices, general coloration, and yellowish spot at the base of the mandible. This variation has been mentioned partly above in the comparative discussion of *C. comechingonus* and *C. fuscus.*

The populations from the northern part of the range of *Cinclodes fuscus* (from Piura, northern Peru, north through Ecuador to Colombia and Venezuela) are not uniform, differing chiefly to a greater or lesser degree in the saturation of their plumage but, taken as a group, are rufous brown above, more or less ochraceous, and suffused with russet brown below, and all have a conspicuously

large and bright rufous area in the wing. The yellowish spot at the base of the mandible is present in most individuals and fairly well developed in those of Venezuela.

The populations become progressively paler and duller, generally speaking, as they range farther south. The upperparts become more grayish, less rufous; the underparts more grayish or whitish, less ochraceous; the apical spots decrease in size and become less rufous, and also the pale area in the wing which decreases markedly in size and becomes whitish, rather than rufous. The yellowish spot at the mandible also decreases and exists in fewer individuals.

The underparts are palest in northern Argentina, and the pale area is now relatively small and is dull white where exposed, grading internally into pale buff faintly tinged with cinnamon. The yellowish spot at the base of the mandible is lacking in most individuals, and, when present, is very small, most inconspicuous.

At the southern end of the range, from about Atacama in Chile, and Mendoza in Argentina, southward, the pale area in the wing does not increase in size but becomes rufous again, although very much paler than at the northern end of the range of the species. These southern populations are also most grayish above, fuscous rather than rufous, with a faint olive tinge in unworn plumage. Their wing is also more pointed, because they are migratory, but a trend toward a pointed wing starts already in northern Argentina.

KEY TO THE SPECIES OF *CINCLODES*

1. Underparts pure snowy white ..... *palliatus*
   Underparts not white 2
2. Underparts uniformly sooty brown below a paler but brownish throat ..... *antarcticus*
   Underparts not uniformly sooty brown 3
3. Wing bars on secondaries and primaries, and apical spots on the outer pairs of rectrices, pure snowy white ..... *atacamensis*
   Wing bars and apical spots not pure white 4
4. Axillaries white ..... *oustaleti*
   Axillaries not white 5
5. Axillaries chocolate brown ... *nigrofumosus*
   Axillaries not chocolate brown 6
6. Superciliary streak obsolete, very faint, barely suggested ..... *taczanowskii*
   Superciliary streak very conspicuous, or very evident 7
7. Underparts dark grayish brown below the whitish throat, and conspicuously streaked with buffy white ..... *patagonicus*
   Underparts pale, not dark grayish brown, and not streaked 8
8. Tail very long, measuring 91 mm. or more ... . *pabsti*
   Tail much shorter, averaging about 67 mm., and not exceeding 76 9
9. Pale area of the wing very extensive, very bright and strongly rufous; mandible very pale at the base, also at the sides, and on the under surface to about the center of the gonys. Restricted to Argentina..... ..... *comechingonus*
   Pale area of the wing very distinctly smaller or less extensive, varying from rufous to cinnamon, buff, or dull white; mandible very dark, or with a poorly defined and usually quite restricted yellowish area at the base, not reaching to the gonys, or extending to the sides. Not restricted to Argentina .... *fuscus*

LIST OF THE SPECIES

Cinclodes fuscus

DESCRIPTION: This species varies markedly geographically (see geographical variation above) from rufous brown above, to fuscous with a grayish tinge and faint olive cast; from ochraceous below, more or less suffused with russet brown, to dingy ashy buffy white, and grayish brown. In all the populations, the feathers of the upper breast, and also those of the white throat, are more or less darkly and distinctly edged with dull brown, producing a scaly but variable appearance. The wing is broadly barred near the base, and this bar and other pale areas of the wing form an area varying in size from very extensive to relatively small, and in coloration from very strongly rufous to dull white. The apical regions, or more, of the three outer pairs of rectrices, vary from bright rufous, or ferruginous, to dull cin-

namomeous or grayish white. The bill is slender, relatively short and weak, and is dark above and below, with or without an ill-defined yellowish area restricted to the base of the mandible, and normally quite small.

IMMATURE PLUMAGE: Similar to that of the adult, except that the upper mantle is spotted, the center of the feathers being pale and rufous, contrasting with the dark and brown edges of the feathers, whereas the mantle is uniform in the adult. The pattern of the entire plumage is also more confused, less well defined, than in the adult.

RANGE: Andes of western Venezuela from the border of southern Lara to Mérida; Colombia in the Santa Marta Massif, Eastern Andes (Boyacá), Central Andes (Cauca), and Andes of Nariño south through Andes of Ecuador; Peru, in the Andes of Piura, and Andes from Cajamarca south through Peru, western Bolivia, Chile, and Argentina, to Tierra del Fuego, Isla de los Estados, and islands south of Tierra del Fuego including the Cape Horn Archipelago; also west to the coast in Chile from Atacamá south, east to the coast in Argentina south of about the Rio Colorado, and also mountains of western Córdoba.

The altitudinal range varies during the breeding season from the coast in Chile and Argentina, up to about 4500 m. in Argentina (over 2000 in Córdoba), 3700 but probably more in Chile, and, approximately, 3400–4700 in Bolivia, 3000–4500 in Peru, 3600–4600 in Ecuador, 3000–4000 in Andes of Colombia, 3600–4800 in the Santa Marta Massif, and 3800–5000 in Venezuela.

The populations from southern Chile and southern Argentina are migratory; migrants winter north to eastern Tucumán, northern Santiago del Estero, Santa Fe, Entre Rios (Argentina), Uruguay, and Rio Grande do Sul (Brazil), arriving in Uruguay in early April and occasionally end of March, to leave in September and October. Seasonal altitudinal movements have been reported also in Chile and Argentina, but are not well documented.

Paraguay is mentioned occasionally in the range, a record which is probably based on Azara (1805) who said that he saw four birds in Paraguay which is quite possible, but since no other record exists for Paraguay to the best of my knowledge I reject this record as doubtful.

SPECIMENS EXAMINED: 568, including the types of "*albidiventris*" in BM, "*oreobates*" in BM, "*tucumanus*" in AMNH, and "*vulgaris*" in MNHN.

Cinclodes comechingonus

Figure 1

DESCRIPTION: Grayish brown above, with conspicuous pale cinnamomeus superciliary streak. Dingy buff below the whitish throat, the feathers of which are more or less distinctly edged at the tip with very pale grayish brown; grading into pale brown on the flanks. Wing bar very broad, forming with the other pale areas of the wing a very extensive rufous zone which is orange-russet or pale bright reddish chestnut, and is brighter rufous and more extensive than in any other species. Apical spots of the rectrices very extensive and bright russet. Bill slender, short and weak, dark on the maxilla, but pale yellow on the mandible over its greatest area, from the base to about the center of the gonys. The mandible is strongly yellow in life.

This species is similar to *Cinclodes fuscus* in general appearance, but the pale area in its wings is brighter rufous and more extensive, its lower bill is paler. *Cinclodes comechingonus* coexists with *C. fuscus* in Córdoba and is also associated with it on its winter grounds, and probably also during the migration, but only with forms of *C. fuscus* which have a very dark bill, and pale areas in the wing which are more restricted in size than in *C. comechingonus,* and are dull white, buffy, or cinnamomeous, not strongly rufous.

RANGE: Restricted to Argentina, breeding in the mountains of western Córdoba above 2000 m., and migrating north to eastern Tucumán and northern Santiago del Estero.

The breeding range known so far seems to consist only of the Sierras of Achala and Co-

mechingones, but Dr. C. C. Olrog (personal communication) believes *C. comechingonus* probably breeds in other regions in the mountains of western Córdoba, and perhaps also in neighboring San Luis in the Sierra de San Luis.

SPECIMENS EXAMINED: 3.

Cinclodes pabsti

DESCRIPTION: Pale grayish olive brown above, with the crown slightly darker and browner than the back, and with an unusually conspicuous buffy white superciliary streak which is very long, reaching well onto the nape. Throat white, with slight traces of brown at the edges of the feathers, chiefly at the sides of the throat. Remainder of the underparts pale dull yellowish buff (Naples yellow), including the under tail coverts, and nearly uniform, but slightly paler and more whitish on the center of the abdomen, and with a very pale brownish wash on the upper breast and flanks, with faint darker edges to the feathers of the upper breast. Middle and greater upper wing coverts, and innermost secondaries, conspicuously tipped or edged by bright ochraceous buff, with an ochraceous cinnamon bar at the base in the secondaries and primaries. Apical spots of the three outer pairs of rectrices varying from Naples yellow to bright ochraceous buff and very extensive, invading the distal half or more of the outermost pair, with also a very small spot of the same color at the tips of the fourth rectrices. Bill slender, but relatively long and strong.

RANGE: Southeastern Brazil, where it is restricted to the plateau of northeastern Rio Grande do Sul and neighboring Santa Catarina.

SPECIMENS EXAMINED: 2.

Cinclodes oustaleti

DESCRIPTION: Dark fuscous gray-brown above. Throat white, well barred with dark gray or grayish brown. Breast and flanks very dark, varying from dark mouse gray and fuscous to rufous brown; uniform on the lower flanks, but with dull white centers to the feathers of the upper breast which narrow into vaguely defined thin shaft streaks farther down on the breast and upper sides of the body; and with the center of the lower breast and abdomen dingy buffy white, very much paler than the flanks. Under tail coverts brown, more or less distinctly tipped with buffy white. Bend of the wing, under wing coverts, and axillaries white, the axillaries pure white as a rule, but the coverts mixed with gray. Rufous wing bar, and other rufous areas of the wing, as well as the ferruginous apical spots of the rectrices, relatively restricted in size. Bill very slender, thin and compressed laterally distally, but relatively long.

RANGE: Chile, from Antofagasta, and Argentina, from Mendoza, south to Tierra del Fuego, and islands south of Tierra del Fuego (London, Desolación, Beagle Channel, and Cape Horn Archipelago), also Juan Fernández Archipelago. Altitudinal range, from the coast up to about 3700 m. in Chile, and "above 3400" m. in Argentina. Partly migratory and said also to move altitudinally, but movements scarcely known.

SPECIMENS EXAMINED: 55, including the type of *oustaleti* in BM, and of "*baeckstroemii*" in NRS.

Cinclodes patagonicus

DESCRIPTION: Dark bistre brown above. Grayish brown below, with distinct whitish shaft streaks below the whitish throat which is barred with grayish brown, but not very distinctly so. Under tail coverts brown with distinct buffy white tips. Axillaries brown. Rufous wing bar, and ferruginous apical spots of the rectrices rather poorly developed. Bill long, slender, and compressed laterally distally.

This species shows a general resemblance to *Cinclodes oustaleti* to which it is closely related, but *C. patagonicus* is a distinctly bigger bird; more brownish, and uniform in coloration below the throat, with the exception of the shaft streaks that are better developed, and its axillaries are brown, rather than white.

IMMATURE PLUMAGE: Similar to the adult,

but not uniform in coloration on the upper back, the feathers of which are narrowly edged with buffy white. The pattern of the underparts is also more confused, the shaft streaks being broader and less sharply defined than in the adult.

RANGE: Chile, from Aconcagua, and Argentina, from Mendoza, south to Tierra del Fuego, and islands south of and east of Tierra del Fuego (London, Londonderry, Navarino, Cape Horn Archipelago, and Isla de los Estados); also Isla de la Mocha, north of Valdivia. Altitudinal range from the coast up to about 3400 m. in Chile.

The range of *Cinclodes patagonicus* is roughly similar to that of *C. oustaleti,* but more restricted, as it does not include the Juan Fernández Archipelago, and does not extend so far north in Chile, or quite so high in the Andes. But *C. patagonicus* is apparently a more common bird than *C. oustaleti* at the southern extremity of the range.

SPECIMENS EXAMINED: 103, including the type of "*molitor*" in BM.

Cinclodes taczanowskii

DESCRIPTION: Bistre brown above, darker on the head, paler and fawn on the rump and upper tail coverts, with the superciliary streak extremely reduced, only faintly and barely suggested. Russet and fawn below, with the pale area of the throat indistinct, buffy and very cloudy, much mixed with pale brown; and breast more or less indistinctly streaked with few buffy streaks. Under wing coverts cinnamon and axillaries pale fawn. Rufous wing bar and pale area of the wing extensive, and ferruginous apical spots of the rectrices well developed and conspicuous. All the rows of the upper wing coverts with well-defined conspicuous pale or bright ferruginous broad tips, forming several bands across the wing. Bill moderately strong but relatively short.

IMMATURE PLUMAGE: Similar to that of the adult, but with the feathers of the crown and back with faint and very narrow whitish shaft streaks, and with very faint pale edges to the feathers of the back, not uniform on the upper parts as in the adult.

RANGE: Very narrowly restricted to the edge of the water in rocky sites or promontories of the coast of Peru from the Department of Lima, south to the region of Islay-Mollendo in Arequipa; also small coastal islands such as San Lorenzo, Viejas, and Chincha Islands.

SPECIMENS EXAMINED: 35, including the type of *taczanowskii* in ZIW, and of "*sparsim-striatus*" in BM.

Cinclodes nigrofumosus

Figure 1

DESCRIPTION: Dark chocolate brown above, with a conspicuous whitish superciliary streak. Bistre brown below the white throat which is nearly uniform, and distinctly and sharply, but narrowly, streaked with white, down to and including the under tail coverts. Under wing coverts and axillaries dark brown. Rufous wing bar and pale areas of the wing, and also the ferruginous apical spots of the rectrices, rather poorly developed. Middle and greater upper wing coverts with very dull, poorly defined, dark ferruginous tips that are not conspicuous. Bill long and coarse.

RANGE: Restricted to the coast of Chile from Arica south to Valdivia, also Isla de los Pájaros, off Coquimbo, and Isla de la Mocha; perhaps also southwestern Peru which has been mentioned in the range, but no record from Peru is known to me, although it is possible that this bird occurs in Tacna, north of Arica.

SPECIMENS EXAMINED: 23, including the type of *nigrofumosus* in MNHN.

Cinclodes antarcticus

Figure 1

DESCRIPTION: Entire plumage very somber, chocolate or dark sooty and fuscous brown above and below, but somewhat paler below, and nearly uniform. The throat is paler, but not a conspicuous pale area, as it is dark dull yellowish brown, with dark gray or dark brown edges to the feathers. No superciliary streak or apical spots exist, and the wing bar is greatly reduced, dark dull brown

and barely suggested, or altogether lacking. Bill relatively short, stronger in some populations than others with a yellowish area at the base of the mandible. See discussion of geographical variation.

RANGE: Malvinas, islands east of and south of Tierra del Fuego (Isla de los Estados, islands of the Beagle Channel, Navarino, and Cape Horn Archipelago), Dawson Island in the Straits of Magellan, Brecknock Peninsula of western Tierra del Fuego, and probably also along south coast of Tierra del Fuego.

SPECIMENS EXAMINED: 30, including the type of *antarcticus* in MNHN, and the type of "*fuliginosus*" in MNHN.

Cinclodes atacamensis

DESCRIPTION: Chestnut above, becoming brighter and more reddish on rump, and with a conspicuous white superciliary streak. Throat whitish, with some feathers faintly grayish or pale brown at tip, and pale grayish brown below the throat, becoming dark on flanks which vary from hazel to reddish brown; a few very slight whitish shaft streaks are present on upper breast. Bend of wing, and wing bar on the secondaries and primaries, pure snowy white, with relatively small white spots at the tips of the outer rectrices. Bill long and strong.

IMMATURE PLUMAGE: Similar to that of the adult, but feathers of the lower mantle, rump, and upper tail coverts, with very narrow, pale buffy tips; also, the pattern is less regular, more smudged, at the junction of the lower throat and upper breast.

RANGE: Andes, normally between about 3000 and 5200 m., from Cajamarca in Peru, south through western Bolivia, to Santiago Province in Chile, and to Mendoza in Argentina; also mountains of western Córdoba. This species has been collected at 2650 m. in Bolivia on December 26, about 2440 m. in Jujuy, northwestern Argentina on February 8, and at 2300 m. on March 10 in Tucumán, Argentina; it probably moves altitudinally with the season to some extent.[32]

SPECIMENS EXAMINED: 91.

Cinclodes palliatus

Figure 1

DESCRIPTION: Crown pale soft gray, grading into reddish chestnut on the nape, the coloration of the upperparts being reddish chestnut and uniform from the nape down to the upper tail coverts, about similar to the coloration of *Cinclodes atacamensis,* but a little brighter rufous. Pure snowy white over the whole of the underparts, from the point of the chin down to the tail coverts, and also on the face below the pale rusty ear coverts. No superciliary streak exists, but a blackish band extends posteriorly from the lores through the eye to a short distance behind it. Pale area of the wing snowy white as in *C. atacamensis,* but somewhat more extensive, and with relatively small white apical spots on the rectrices, similar in size or smaller than in *C. atacamensis.* Bill long and very strong. The legs and feet are also exceptionally big and thick, truly huge, about twice as large as in *C. atacamensis,* in which the legs and feet are also quite strong.

IMMATURE PLUMAGE: Probably similar to that of *C. atacamensis* on the back, with narrow pale edges to the feathers of the mantle, rump, and upper tail coverts. This is suggested by a specimen that I have seen, in which these pale edges exist, although this bird seems completely adult in every other respect as far as I can determine.

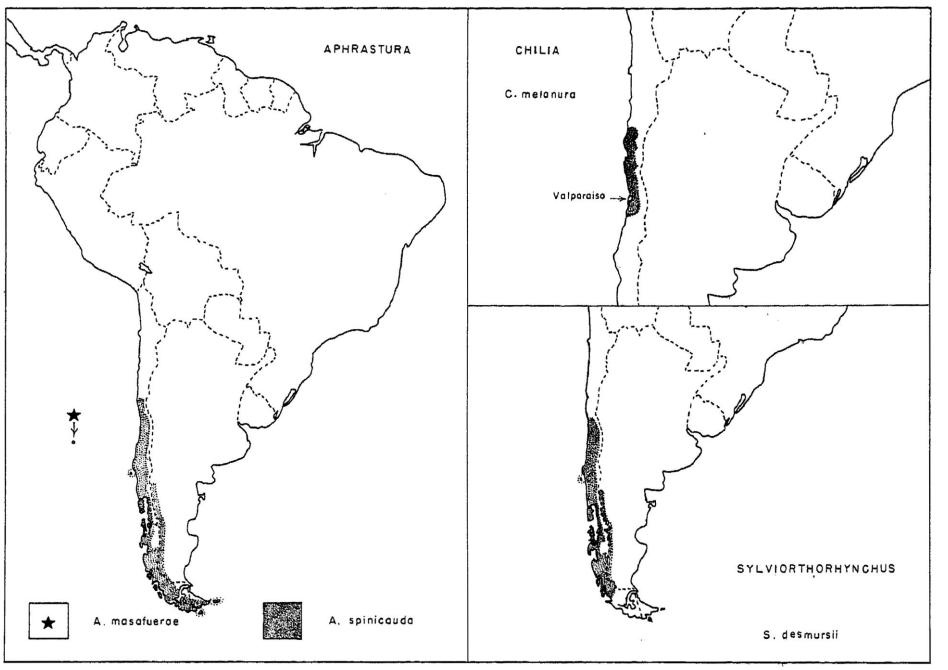
RANGE: Andes of northern and central Peru, between about 4400 and 5000 m. from Cajamarca south to Huancavelica.

SPECIMENS EXAMINED: 10, including the type of "*simonsi*" in BM. This species was found to be "distinctly rare" by Morrison (1939), and the 10 specimens that I have seen seem to represent nearly all those in existence.

GENUS *CHILIA*

This monotypic genus of central Chile forms part of the generic group consisting also of *Geositta, Upucerthia,* and *Cinclodes* and is closely related to the latter.

Chilia melanura differs from the species of *Cinclodes* by having a straighter bill and a



MAP 4. Geographical distribution of *Aphrastura, Chilia,* and *Sylviorthorhynchus.*

proportionally longer tail with a different color pattern. The mean ratio between the lengths of the tail and wing is 0.93 in *Chilia melanura,* as against 0.66–0.86 (0.72) in *Cinclodes,* or 0.66–0.74 (0.70) if we exclude *Cinclodes pabsti* which has an abnormally long tail. The tail of *Cinclodes* is dark brown and uniform with the exception of more or less extensive and conspicuous pale spots at the apices of the three outer pairs of rectrices, but in *Chilia melanura* the basal third or fourth of the tail is very strongly rufous and reddish and contrasts with the distal part of the tail which is dark brown, without pale apical spots, but rufous on the outer web of the outer pair of rectrices.

Chilia melanura is more specialized ecologically than most species of *Cinclodes,* frequenting only dry hills and slopes with scanty vegetation, especially where most arid and stony, and shows a marked preference for broken cliffs and crags; it is said to be elusive, avoiding close approach by scuttling immediately under bushes or dodging behind rocks. *Cinclodes,* on the other hand, is very eclectic ecologically and confiding, generally speaking, and its only customary requirement is the presence of water in the vicinity, to which it is normally very closely associated.

Some of the characters of *Chilia melanura* mentioned above, such as the straighter bill and longer tail, are not necessarily of generic importance. They can be interpreted as species characters, which is why I accepted this taxon as a monotypic genus only reluctantly in my classification of the Furnariidae (1971a). However, everything considered, it seems best not to merge *Chilia* with *Cinclodes.*[33]

The location of the nest is "under ground" and similar in all the four related genera. *Chilia melanura* seems to prefer to place it within a deep crevice or cleft in rocks or face of a crag, but Johnson (1967) said *C. melanura* will place it in a hollow cactus, or digs a burrow in the earth, when a suitable site is not available in rocky outcrops.

Chilia melanura

DESCRIPTION: Earthy brown above on the head and back, but very strongly rufous and reddish, rusty red, on the rump and upper tail coverts, as also (see above) at the base of the tail and outer web of the outer pair of rectrices. A poorly defined whitish superciliary streak is present, separating the paler top of the head from dark brown lores and ear coverts. Dull white below on the throat and upper breast, and also on the ear coverts, the white area grading into grayish brown on the breast, the feathers of which are more or less whitish along the shaft, creating a few poorly defined streaks. The brown of the abdomen grades into strongly rufous flanks, and the under tail coverts are also strongly rufous. The wing is also rufous at the basal half of the secondaries and inner primaries, and this rufous area is very extensive and bright.

MEASUREMENTS (in millimeters): 19 adults, wing, 78–87 (mean 82.15); tail, 69–82 (mean 76.11); bill, 25–30 (mean 27.28).

IMMATURE PLUMAGE: In one specimen, which is probably not adult, the feathers of the breast, abdomen, and border of the upper mantle are paler and buffy subapically, and on the breast and abdomen have dark edges, which results in a faintly barred appearance. The facial pattern is less distinct also.

RANGE: Central Chile, from Atacama south to Valparaiso and Santiago provinces, and (*fide* Johnson) Colchagua (map 4); in the coastal ranges, hills, and slopes of the cordilleras up to at least 3000 m.

A paler population has been named from a very arid region in southern Atacamá.

SPECIMENS EXAMINED: 20, including the type of *melanura* in BM.

GENUS *FURNARIUS*

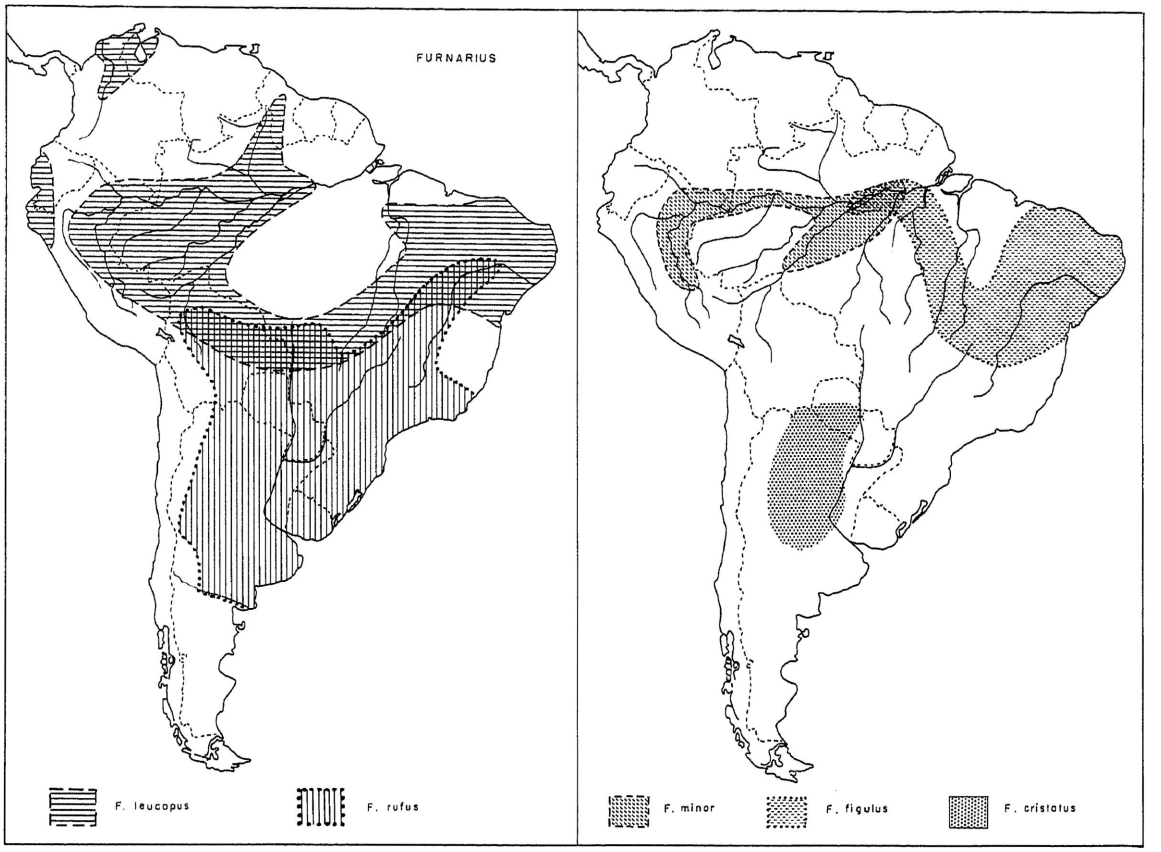
Furnarius is composed of five species (*minor, figulus, leucopus, rufus, cristatus*) and has no close relatives.

Furnarius is very widely distributed (map 5) from northern Colombia and the region of Lake Maracaibo, Venezuela, south to the valley of the Rio Negro in Argentina, chiefly in low lying open regions east of the Andes. However, *F. minor, F. figulus,* and *F. leucopus* are also very well established in the humid Amazonian forests, but apparently live only along the river valleys and their floodplains, and probably not within the denser forest. *Furnarius minor* is restricted to the Amazon and some of its tributaries, but the major part of the range of *F. figulus* consists of the open arid scrub forest of northeastern Brazil where *F. leucopus* is also very widely distributed. *Furnarius leucopus* inhabits also roughly the same arid environmental zone in western Ecuador and neighboring northern Peru, across the Andes, and, again disjunctly, northern Colombia and northwestern Venezuela, but it is established also in the humid forested region south of Lake Maracaibo and of the lower and middle Motagua Valley, but perhaps chiefly along rivers and in clearings as in the case of the Amazon Basin.

Furnarius rufus follows the arid valley of the Rio San Francisco to northern Bahia, Brazil, but is chiefly a bird of the savannas and open wide grassy plains with a few trees required for shelter. With the expansion of grazing and the planting of protective screens or groves of trees about the ranches and estâncias, *F. rufus* has now spread almost everywhere, and, as it is universally regarded with much friendly respect, it has become generally very confiding, almost semi-domesticated. It has also spread to towns and even to the heart of the largest cities, such as Buenos Aires and São Paulo, where it is common in parks and large gardens.

Furnarius cristatus is much less common and ubiquitous than *F. rufus* and is mainly restricted to dry savannas dotted with acacias, dry and stony arroyos or other ravines, or the sand banks of rivers; it is a typical bird of the Chaco.

Furnarius is not montane, but *F. rufus,* nevertheless, ascends into the piedmont of the eastern Andes to about 3500 m. in Bolivia, *F. leucopus* to about 2700 m. in the same region, and *F. cristatus* to about 1000 m. in the mountains of Córdoba. The trans-Andean population of *F. leucopus* of western Ecuador and neighboring Peru has probably



MAP 5. Geographical distribution of *Furnarius*.

reached this region either by way of the valley of the Marañon, or before the rise of the Andes.[34]

A whole literature exists on *F. rufus*, which is by far the best known member of its family. It resembles a large thrush, such as the American Robin (*Turdus migratorius*) in general morphology and some aspects of behavior. It spends most of its time on the ground, walking about with a hesitant stride, nodding slightly, or with the "head thrown back and bosom prominent . . . lifting its foot high at each step, and holding it suspended for a moment in the air before setting it firmly down," according to Hudson (Sclater and Hudson, 1888), but according to Friedmann (1927), it also "hops and runs . . . and in flight resembles a large *Hylocichla*." As in the case of the robin, *F. rufus* is also very partial to feeding on earthworms.

Furnarius rufus is very vociferous and so loud that Wetmore (1926) said its "notes may be audible at half a mile"; some of these notes are similar to the distress call of the robin, according to Friedmann (1927), but apparently much louder. The calls are normally given when the bird is alarmed, but at other times, Hudson says mated pairs engage frequently in loud "concert," the pair bond being maintained throughout the year. The calls seem to be given in rapid sequence. Niethammer (1956) said they reminded him of those of a Lesser Spotted Woodpecker (*Dendrocopos minor*), at least at the start.

The observations of Jelski and Sztolcman (in Taczanowski, 1884) on the general behavior and vocalizations of *Furnarius leucopus* in northern Peru are similar to what has been reported for *F. rufus*. Sztolcman said also that *F. leucopus* is very loud, and

that "*Sa voix est composée d'une série de sons très élevés au commencement et s'abaissant en gamme chromatique, ces derniers répétés plus lentement et plus prolongés. On peut les exprimer par les syllabes suivantes: Pi-pi-pi-pi-pi-pi-pi-piou-piou-piou.*"

Very little or nothing is known about the behavior of the other three species other than on the nest. But Friedmann (1927) said that *Furnarius cristatus* "in general . . . acts and sounds much like [*F. rufus*], but seems less terrestrial in its feeding habits." *Furnarius cristatus* is not only distinctly more arboreal than *F. rufus* but is also much less confiding, according to Masramon (1971); it is apparently more alert, singing, and moving about in trees as well as on the ground, with its crest fully erected.

The one aspect of behavior which has, of course, received most attention is the structure and location of the remarkable nest, which is similar in structure in all the five species, although proportionally smaller in the small *Furnarius cristatus,* and very probably also in *F. minor* and *F. figulus.*

The nest is built of clay, or "mud," above the ground, well mixed with vegetable fibers or hair for strengthening, and is rounded and domed, shaped outwardly like an old-fashioned baker's oven, but with a deeper and narrower entrance at the base. Hence, the name "ovenbird," or "hornero," which, in English, is used for all the birds of the family. The scientific name *Furnarius* has the same meaning and was adopted from the pre-Linnean French authors who called *F. rufus* the "Fournillier," a translation of the Spanish "Hornero," and the family becomes Furnariidae.

A great deal of information has been published on the nest of *Furnarius rufus* in almost every issue of the Argentine ornithological journal "*El Hornero,*" most of it illustrated with photographs. Its size and shape vary somewhat, but, generally speaking the nest is rounded above the flat base, and arched near the top like a dome, and measures roughly some 20 cm. or more in height by about 30 cm. in width, and its walls are anywhere between about 25 to 35 mm. thick. Hudson (1920) wrote that it "is sometimes very massive, weighing eight or nine pounds [or about three and a half to four kilograms], and so strong that . . . it often remains unharmed for two or three years" short of an accident. Clay, rather than "mud," is the preferred building material but toward the end of construction, cow dung may be used also.

When the structure has assumed a globular form, the wall at one side of the entrance is folded inward to divide the oven into two chambers, the partition reaching from the floor to the roof with the exception of an opening at the top that leads into the inner or incubation chamber which is lined with soft grass to receive the eggs. A new oven is built every year and the abandoned one may be used by other birds, notably swallows (*Progne tapera*), or occasionally by wasps. Friedmann (1927) found an oven which was the home of a small colony of tree frogs (*Hyla nasica*).

A controversy rages as to the site of the entrance to the oven and its orientation. Some observers maintain it is always at the left, facing the wind, but no rigid pattern prevails, although in some regions it is normally at the left. For instance, Friedmann wrote "In the great majority of nests found in the provinces of Buenos Aires and Entre Rios the entrance was on the left side, while in Tucuman, Santiago del Estero, and Cordoba, about as many nests had the entrances on the right side as on the left. Of approximately 600 nests observed, some 450 had the opening at the left."

The nest is built in the open in the most conspicuous situations imaginable without any attempt at concealment whatever. The most favored site, at least in the pampas, is at the top of a fence post but any site can be used and some locations which seem to be very extravagant are reported in the columns of "*El Hornero,*" such as within rotating or other movable structure of windmills, or inside odd receptacles, such as a chamber pot. One clever bird used a clay jar with a wide mouth and, approving of the solidity and composition of its walls, merely narrowed

down the entrance with clay to a suitable size.

The other locations that are used commonly, besides fence posts, are the top or cross bars of public utility poles, cornices or other projecting features of houses or other structures, and limbs or forks in trees, and, not very rarely, the nest may be built directly on the flat ground, even though posts or trees may be nearby. Occasionally three to four ovens may be lined in a row on the ground, touching one another, or "towers" of three to six supporting nests may be built on the cornice of a building. These "multiple nests" have been interpreted as evidence of colonial nesting, but most probably represent only attachment to a favorite location, as *Furnarius rufus* is said to be decidedly territorial and to build anew every year.

The only location of the nest which seems to be reported so far for *Furnarius leucopus* and *F. cristatus* is on the limbs of trees or in their forks, usually not far above the ground, or in bushes, and it is probable that this was also the site used originally by *F. rufus*. Nothing is known for *F. minor*, other than that it also builds a clay oven, presumably on the limb of a tree.

Furnarius figulus builds its oven on the limbs of trees also, but Snethlage (1935) reported that she did not find any nest on the lower Iriri River (an affluent of the lower Rio Xingu in Brazil) although *F. figulus* was common in this region. Instead, she was brought some unfledged young by her Indian assistants who said they had taken them from a hole in a tree trunk, and, as Snethlage found no clay along the Iriri, she suggests that *F. figulus* has perhaps taken to nesting in holes or cavities in trees in this region. This radical modification in nesting habits requires confirmation, as Snethlage said, and it is also possible that she may have misidentified the birds because she mentioned that they had barely grown any feathers.

Morphological Variation

The morphological variation of *Furnarius* is not great but nevertheless quite evident in size, development of the crest, and coloration of the crown and back.

Two of the species (*Furnarius minor* and *F. cristatus*) are rather small but sturdy, and *F. rufus* attains a fair size and bulk. The generally robust appearance of these birds is created by a combination of a well-developed but rather short tail, long and strong legs and feet, and a rather long but well-proportioned bill with a slightly decurved culmen.

The means of the lengths of the wing, tail, and bill vary, in round numbers (in mm.), from 76 to 101, average 87, in the case of the wing; 47 to 70, average 57, for the tail; and 19 to 27, average 23, for the bill. The ratio of the length of the tail to that of the wing varies from 0.59 to 0.74, average 0.66.

The feathers of the tail are well integrated, but not stiffened, and its tip is slightly rounded. The feathers of the center and posterior part of the crown show a tendency to be slightly elongated in all the species and have developed to form a rather short but distinct crest in *Furnarius cristatus* which measures about 20 mm. or somewhat more when erected.

The variation in the coloration and its pattern is very limited. The back is strongly rufous, clear and bright, in *F. minor*, *F. figulus*, and *F. leucopus*, but the rufous coloration becomes much duller in *F. rufus* and in some of its populations gives place to pale grayish earthy brown, and to cinnamon-brown in *F. cristatus*. The tail is strongly rufous in all the species and uniform with the exception of *F. figulus* in which some of the rectrices are irregularly tipped with black to a small degree. The crown and back are uniform in *F. rufus* and *F. cristatus*, or the crown is very slightly darker than the back in *F. rufus*, whereas *F. minor*, *F. figulus*, and *F. leucopus* are "capped" with dark brown or gray, but in one of the two subspecies of *F. figulus* the dark brown cap is much less conspicuous and replaced by pale chestnut. In these three "capped" species, the superciliary streak is whitish and unusually conspicuous, but the superciliary is dull and dark, dull cinnamon rather than whitish, and is vaguely defined, nearly obsolete, in *F. rufus* and *F. cristatus*, which lack the dark cap.

The underparts contrast strongly from the

upperparts by being "whitish." The throat is white in all the species, and below the white throat a faintly defined ochraceous or grayish band extends across the upper breast, the remainder of the underparts being more or less "whitish," tinged to a varying degree with buff, pale ocher, pale gray, or cinnamon gray. All the species have a pale, rufous or ferruginous, area in the wing which varies specifically and is best developed in *Furnarius figulus* where it extends to the outer primary and forms two bars divided by a band of dark brown.

Phylogeny

All five species are closely related to each other to the point that any linear sequence is unsatisfactory. Nevertheless, it seems best to group the three species with dark caps together, starting with *Furnarius minor* which is the plainest of all the five species and quite small. *F. figulus* is intermediate in size between *F. minor* and *F. leucopus,* and in some respects more specialized than either (strong geographical variation, and different wing and tail patterns), but as I believe it would be an error to separate *F. leucopus* and *F. rufus* by listing *F. figulus* between them, the sequence of the species with a cap becomes *F. minor, F. figulus,* and *F. leucopus.*

Furnarius leucopus and *F. rufus* are quite clearly closely related, although the coloration of their upperparts differ, and, as is evident (map 5), the ranges of the two birds are largely complementary, *F. leucopus* in the north, and *F. rufus* in the south, of South America.

Furnarius cristatus is small and seems more specialized than the other four species (crest, longer tail, and probably more arboreal habits), but I am confident, nevertheless, that its closest relative is *F. rufus.*

Geographical Variation

Three species (*Furnarius figulus, F. leucopus,* and *F. rufus*) vary geographically.

The geographical variation of *F. figulus* is sharp, and, as two quite different groups of populations compose this species in regions which differ very strongly ecologically, it seems advisable to recognize two subspecies: *pileatus* in the humid part of the range, and nominate *figulus* in the regions that are distinctly arid.

The populations (*pileatus*) from the humid regions of the range (lower Amazon, Rio Xingu, and Rio Araguaya), differ from nominate *figulus* of arid northeastern Brazil and of the valley of the Rio São Francisco in Minas Gerais, in having a very strikingly darker "cap," which is dusky chocolate brown, rather than pale chestnut. The two subspecies differ also in a number of other characters. For instance, the black spots at the tip of the tail are more abundant and distinctly larger in *pileatus,* the ear coverts are much darker, the superciliary streak is whiter and more conspicuous, the coloration of the back is considerably richer than in nominate *figulus,* and individuals tend to be smaller, although the average measurement of the wing length is only 2 mm. shorter.

The geographical variation of *Furnarius leucopus* is surprisingly slight when one considers that its range is very extensive and partly disjunct. All the geographical variation is merely one of degree and individual variation is well marked and becomes striking in some populations of the upper Amazon Basin.

The populations that inhabit the more arid parts of the range (in northern Colombia and northwestern Venezuela; western Ecuador and neighboring Peru; and northeastern Brazil) are pale and tawny rufous to virtually the same degree, but the crown is gray and palest in the birds of Colombia and Venezuela, darker gray with a faint admixture of brown in those of Ecuador and Peru, and darkest, most brownish, in those of Brazil. The underparts are washed with ochraceous buff, below the white throat, to about the same extent in the populations of Colombia, Venezuela, and Brazil, but are more whitish, pale buff as a rule, in the birds of Colombia and Peru.

The populations inhabiting the more humid parts of the range (south of Lake Mar-

acaibo and middle Motagua Valley, and the Amazon Basin, including the lower Rio Negro, and the upper Rio Branco in Brazil and neighboring Guyana) are darker above, more richly colored, more amber rufous or amber-brown, less tawny, than the populations mentioned above from the more arid parts of the range. The coloration of their crown shows about the same range of variation as in the pale populations although it is darker; the crown is more grayish in Colombia and Venezuela, darkest and most brownish or sepia in the birds from Guyana, Rio Branco, and Rio Negro, but the difference between these birds and those from other parts of the Amazon Basin is very slight, and the latter are distinguished chiefly by having a paler, less blackish culmen, and by being darker, more blackish, at the base of the under tail coverts, the dark area being more extensive.

The rufous area in the wing varies individually to a great extent in all the populations whether pale or dark. This character cannot be measured accurately but the geographical trend is exemplified by the presence or absence and the relative size of a rufous spot near the base of the inner web of the outer primary. A fairly large spot is present in all the specimens that I have examined from western Ecuador and neighboring northwestern Peru; also in all the specimens seen from northeastern Brazil, but is smaller as a rule than in the birds from Ecuador and Peru; whereas the spot was lacking altogether in the large majority of specimens from northern Colombia and northwestern Venezuela, and is quite small when present. The proportion of birds with a spot is about one to six, and, in this population, the birds with a spot are quite distinctly darker and more richly colored below than specimens without a spot. This spot exists also in the dark populations to about the same extent in all, but is always small, and the proportion of spotted birds drops down to only about one in 10.

The length of the bill varies geographically, but much overlap exists when measurements are compared from the range of the species taken as a whole. The measurements (in mm.) of some representative populations are as follows: Western Ecuador and northwestern Peru, 40 males, 26–32 (mean 29.4); northern Colombia, 14 males, 26–28.5 (mean 27.2); northeastern Brazil, 11 males, 25.5–27.5 (mean 26.4); Rio Madeira, Brazil, 13 males, 23.5–27.5 (mean 25.5); Santa Cruz, Bolivia, 7 males, 24–26 (mean 25.3); Guyana and Rio Branco, 12 adults, 23–26 (mean 24.2).

I have mentioned that *Furnarius leucopus* varies individually to a marked extent which reaches a striking degree in the populations of the upper Amazon Basin. Along the Amazon from the region of Tonantins and São Paulo de Olivença, west to the lower Napo River, lower Huallaga, and about the middle Ucayali, specimens that are exceptionally dark (chestnut on the back and tail, brownish ochraceous below) have been collected in most instances with birds of normally paler coloration (amber above and ochraceous below). The dark and pale forms are connected by intermediates, as stated by Hellmayr (1925), but Zimmer (1935) concluded that the dark form represents a distinct species which he calls *F. torridus*, the type of *F. torridus* Sclater and Salvin, from the lower Ucayali being a dark individual. I have reinvestigated this question in detail elsewhere (Vaurie, 1973) and agree with Hellmayr that the dark birds are only individual variants.[35]

The geographical variation of *Furnarius rufus* is clinal throughout and affects the general coloration. Three main trends can be discerned. The populations of Argentina (with the exception of the northwest and northern Chaco) are the most grayish and brownish above, the most "earthy," and the palest and most grayish below. Birds of this coloration range north through Uruguay to southeastern Brazil, but grade farther north in Brazil into populations that are distinctly more rufous above, darker below, more ochraceous, less grayish. The darkest and most rufous specimens that I have seen were taken at the northern extremity of the range in southern Piauhí and neighboring northern Bahia, whereas birds from São Paulo were more or less intermediate. The populations of Bolivia resemble the more rufous populations of Brazil, but are paler below, more

cinnamomeous, less ochraceous, and somewhat brighter rufous above.

Many intermediate populations exist; for instance in the northern part of the Argentinian Chaco and Paraguay, northwestern Argentina (Tucumán, Jujuy, Salta, and northwestern Santiago del Estero), Beni in Bolivia, interior of Brazil in the western Mato Grosso and western Minas Gerais, and also in São Paulo as mentioned above.

KEY TO THE SPECIES OF *FURNARIUS*

1. With a crest ..... *cristatus*
   Without a crest 2
2. Outer primary with two rufous spots on the inner web, one spot near the base, the other near the tip, separated by a dark area .... *figulus*
   Outer primary with only a single rufous spot near the base of the inner web, or uniform, not spotted 3
3. Crown and back uniform, or with only a slight difference between the color of the crown and back ..... *rufus*
   Crown and back not uniform, with a very sharp contrast between the color of the crown and back 4
4. Small, with relatively small feet; wing length averaging about 77 mm., and bill length about 21.50 mm. ..... *minor*
   Large, with very big and strong feet; wing length averaging about 93 mm., and bill length about 27.0 mm. ..... *leucopus*

LIST OF THE SPECIES

Furnarius minor

DESCRIPTION: A small species (see table 4), rufous hazel above but rather dull, with a dark grayish brown crown, and a very conspicuous dull white superciliary streak. Throat white, upper breast and flanks more or less darkly washed with ochraceous cinnamon or pale clayish brown, whitish on the center of the abdomen. Rufous area of the wing rather restricted, with a small rufous spot near the base of the inner web of the outer primary. Tail uniformly rufous.

IMMATURE PLUMAGE: Similar to that of the adult, but with very faint and narrow grayish edges on the white feathers of the throat; and faintly and indistinctly mottled on the breast and back.

RANGE: Amazonian Basin, from the region of Obidos and the mouth of the Rio Tapajós, westward along the Amazon to Peru, to the lower Napo River, valley of the lower Huallaga, and valley of the Ucayali; this species follows also the valley of the Rio Madeira up to at least Porto Velho, but is apparently unknown from the valleys of the Rio Purús and Rio Juruá.

SPECIMENS EXAMINED: 81.

Furnarius figulus

DESCRIPTION: This species varies geographically (see discussion) and is bright pale reddish above, with a darker, more chestnut crown (in nominate *figulus*), or with a very much darker crown (which is chocolate-brown in *pileatus*); with a very conspicuous superciliary streak which is whitish (*pileatus*) or faintly tinged with cinnamon (nominate *figulus*). Throat white, with the breast and flanks washed with pale grayish cinnamon, and whitish on the center of the abdomen. Rufous area of the wing very extensive with two rufous spots of good size on the inner web of the outer primary, one basally and brighter, the other subapically and duller, the two rufous spots separated by a broad band of dark blackish brown. Tail strongly rufous, with most of the rectrices tipped irregularly with black on the inner web; the individual variation is great and in some individuals the black spots are small, reduced in number, or lacking altogether, especially in nominate *figulus*.

IMMATURE PLUMAGE: Similar to the adult, the crown is darker, tinged with dusky brown in nominate *figulus*, and is less dark than in the adult in *pileatus*, not so sharply defined, and also the black spots at the tips of the rectrices are fewer and smaller in *pileatus*, less pure black. In both subspecies, the white feathers of the throat have narrow faint dark grayish edges.

RANGE: Eastern Brazil, with two subspecies: *pileatus* distributed along the middle and lower Amazon, from the mouth of the Rio Madeira and region of Itacoatiara, east

TABLE 4
Measurements (in Millimeters) of *Furnarius*

Species	Wing			Tail			Bill		
	N	Mean	Range	N	Mean	Range	N	Mean	Range
minor									
Males	40	78.03	73–82	35	47.45	42–52	33	21.81	20–23
Females	29	75.84	72–80	25	46.72	44–48	25	21.48	20–23
Both sexes	87	77.27	72–82	70	47.21	42–52	67	21.62	20–23
figulus									
Males	39	88.38	85–95	39	56.70	50–61	35	23.51	22–25
Females	26	87.00	82–92	26	56.57	52–63	24	23.03	21.50–25
Both sexes	77	88.04	82–96	78	57.17	50–63	72	23.25	21–25
leucopus									
Males	108	94.87	84–105	109	56.09	46–64	109	27.40	23–32
Females	69	92.73	83–103	71	55.19	47–63	68	27.07	22.50–30
Both sexes	203	93.64	83–105	206	55.36	46–64	202	26.97	22.50–32
rufus									
Males	100	102.97	94–110	100	71.67	62–77	100	25.66	22.50–28
Females	100	98.51	91–107	100	69.06	57–78	100	25.35	22.50–28
Both sexes	212	100.73	90–110	211	70.33	57–78	205	25.49	22.50–28
cristatus									
Males	9	77.44	75–81	9	57.11	56–58	9	19.50	18–20.50
Females	13	76.15	73–78	13	55.69	53–58	13	19.20	17–20
Both sexes	22	76.19	73–81	22	56.40	53–58	22	19.35	17–20.50

to the Rio Xingú, south along the valley of the Xingú to the lower Iriri River, and on the middle Araguaya south to Leopoldina (now Aruaña); and nominate *figulus* in northeastern and eastern Brazil from eastern Maranhão, northern Piauhí, and Ceará, south through Bahia and Minas Gerais to Pirapora.

SPECIMENS EXAMINED: 97, including the type of "*superciliaris*" in MNHN.

Furnarius leucopus

DESCRIPTION: A large species, bright rufous above, varying from tawny rufous to rufous amber on the back and tail, and the crown from gray to brown or sepia, with a very conspicuous whitish superciliary streak. Throat white, with the remainder of the underparts varying from ocher, ochraceous orange or ochraceous buff, to pale buff, and more whitish on the abdomen. Rufous area of the wing relatively restricted, with or without a rufous spot, which is normally small, near the base of the inner web of the outer primary. Tail uniformly rufous. Legs and feet long and strong, and paler than in the other species. This species varies geographically and individually (see discussion), and very dark individuals (that are chestnut on the back and tail, and brownish ochraceous below) occur in the upper Amazon Basin, together with individuals of normal (paler) coloration.

IMMATURE PLUMAGE: In a few, but not in all young seen, the small whitish feathers at the sides of the upper throat have dusky narrow grayish brown borders, but, other than this, the plumage seems to be indistinguishable from that of the adult—although a young can always be identified by structural differences, such as a very short bill, blunter primaries, and somewhat narrower rectrices with more acute tips.

RANGE: Disjunct, with three main groups

of populations. One in northwestern Venezuela and northern Colombia, consisting of western Falcón, border of western Lará, and Zulia, including the region south and southwest of Lake Maracaibo; and in Colombia, from Rio Hacha, and coast and lowlands around the base of the Santa Marta Massif, south to southern Bolívar along the Magdalena Valley. The second group in western Ecuador and neighboring northwestern Peru, from Manabí in Ecuador, south to the region of Pacasmayo, in La Libertad, Peru.

The third group is distributed along a great arc from western Guyana (and a record exists also from the Demerara River without mention of a locality) to Brazil, Amazonian Peru, and Bolivia. In Brazil, this species ranges from the headwaters of the Rio Branco south to the Amazon, from the region of Parintins, west of Obidos, westward (including the valleys of the Madeira, Purús, and Juruá) to Amazonian Peru, south to northern and eastern Bolivia, and eastward from Bolivia through the central Mato Grosso and Goiás, north to eastern Brazil, north to Maranhão, Piauhí, and Ceará, and south to about central Bahia: and west from Maranhão to the region of the lower Tocantins. A great hiatus seems to exist in most of central Brazil (map 5) between the Rio Madeira and eastern Brazil.

SPECIMENS EXAMINED: 384, including the type of "*torridus*" in BM, of "*hauxwelli*" in BM, and of "*agnatus*" in BM.

Furnarius rufus
Figure 2

DESCRIPTION: A large species, with the upperparts uniform, or nearly so, without any or with only a slight difference between the color of the crown and back (lacking the dark cap of *Furnarius minor, F. figulus,* and *F. leucopus*), and varying geographically (see discussion) from grayish brown, or "earthy," to dull reddish brown; superciliary streak quite inconspicuous, cinnamomeous, dull and very poorly defined. The underparts, below the white throat, vary from grayish white with a faint cinnamon tinge, to cinnamon, and tawny ochraceous. Rufous area of the wing relatively quite restricted, with a rufous spot near the base of the inner web of the outer primary, which varies individually in size but is usually small. Tail uniformly rufous.

IMMATURE PLUMAGE: Virtually indistinguishable from that of the adult, but, as a rule, the white feathers of the throat have faint and narrow dark borders.

RANGE: Bolivia, from La Paz and Beni, south through eastern Bolivia and Paraguay, to Argentina and Uruguay, south in Argentina to Mendoza and the valley of the Rio Negro, and north and east from Uruguay, Argentina, Paraguay, and Bolivia, to Brazil, north to central Mato Grosso, southern Goiás, southern Espirito Santo, and, in the basin of the Rio São Francisco, to northern Bahia, and region of Parnagua in southern Piauhí.

SPECIMENS EXAMINED: 622, including the type of "*paraguayae*" in AMNH, of "*ruficaudus*" in AMNH.

Furnarius cristatus
Figure 2

DESCRIPTION: A small species, with the upperparts uniform in coloration, cinnamon brown, but with the feathers of the crown elongated and forming a crest, about 20 to 25 mm. long; superciliary streak dull and faint, virtually absent. Underparts washed with pale cinnamomeous gray, or slightly ochraceous, below the white throat, and more whitish on the abdomen. Rufous area of the wing quite restricted, but with a small rufous spot near the base on the inner web of the outer primary. Tail dull rufous and uniform.

IMMATURE PLUMAGE: Similar to the adult, but more ochraceous below and faintly mottled on the breast, and with the crest less well developed.

RANGE: Chaco, from central Paraguay, south to San Luis and Córdoba in Argentina, also northern Entre Ríos.

SPECIMENS EXAMINED: 22.

SUBFAMILY SYNALLAXINAE

GENUS *SYLVIORTHORHYNCHUS*

Sylviorthorhynchus is monotypic and the most remarkable member of the family from a morphological point of view. It has no close relative although it seems to me to belong in the same group of genera which consists of *Synallaxis* and relatives.

Sylviorthorhynchus desmursii is restricted to central and southern Chile and a narrow zone of forest along the foothills of the Andes in Argentina from Neuquén to Santa Cruz (map 4). In Chile, it breeds along the coast and in the low coastal mountains and inland valleys, and, in Argentina, ascends to over 1000 m. on the lower slopes of the cordillera, according to Radboone (1935). It is normally a bird of the very dense underbrush of humid temperate forest, especially where favored by secondary growth, and frequents as a rule virtually impenetrable thickets of bamboo, quillaja, or other thick vegetation, preferably along or in the near vicinity of streams and lakes.

Sylviorthorhynchus desmursii is a little, furtive bird with a very weak flight which Johnson (1967) said "might easily be mistaken for a mouse were it not for its habit of calling repeatedly as it searches for insects. The call-note is weak, high-pitched and staccato, but changes to a much louder, sonorous scolding somewhat similar to the notes of the Chucao [a Tapaculo, *Scelorchilus rubecula*][36] if the bird is approached too closely." But Johnson says this bird is much less secretive during the breeding season; it then become oblivious to observers, according to Olrog (1948).

The closed nest is globular or oval in shape, with a small circular entrance at one side, and is composed of dry grasses and small dry twigs; leaves, moss, and shreds of sheep's wool are also used. It is placed near or not far above the ground. Johnson (1967) reported finding one "placed just off the ground among the new shoots and long grass growing out of and around a fallen log and [looking] like a round ball of dry grass with a tiny hole in one side." Radboone (1935) said he found a nest 1 m. above the ground in a thickly overgrown ravine, and Valenzuela (1960) found one 1.60 m. above the ground in a shrub. The bird that Johnson flushed from the nest "slipped away . . . [with its] incredible tail, which had been curled up inside, undulating in the air."

The tail of *Sylviorthorhynchus desmursii* is quite extraordinary as it is composed virtually of only four feathers which are greatly stiffened and wirelike for they are almost completely denuded of barbs. A third pair exists but it is very rudimentary and vanishing, and *S. desmursii* represents the climax in the process of reduction of the tail feathers in the Synallaxinae from 12 to practically only four in *S. desmursii*.

The central pair of rectrices is extremely long (see below) and averages about three times the length of the wing, but in some individuals is nearly four times longer. The next pair (or middle tail feathers) is roughly half the length of the central pair, and the third pair (or outer tail feathers) is exceedingly short and barely projects beyond the tail coverts. The central and middle pairs are excessively narrow, reduced near the base to virtually only the shaft, but the barbs become more evident toward the tip which attains a width of about 5–6 mm. at best, the barbs being decomposed and apparently devoid of barbules. The barbs do not expand distally, however, on the middle pair which becomes greatly attenuated at the tip. The shaft of these two pairs of rectrices is very strongly keratinized as stated above, and is wirelike, justifying the vernacular name of Des Murs' Wire-Tail for this species. In the outer pair, the shaft and barbs are so very reduced and so slightly stiffened, that this feather is best described as hairlike, and sometimes is not easy to distinguish from the coverts.

Only two other genera in the Passeriformes have a tail reduced to six feathers, to the best of my knowledge. These are *Pnoe-*

pyga (Timaliinae) of the Himalayas, China, and Oriental Region, and *Stipiturus* (Sylviinae) of Australia and Tasmania. But no other similarity exists between the tails of *Pnoepyga* and *Sylviorthorhynchus,* as the tail of *Pnoepyga* is extremely short (averaging only about 15 to 20 mm. long) and its feathers are roughly "normal" in structure, with a broad and relatively well-integrated web. The tail of *Pnoepyga* is completely buried in the coverts and is probably not functional in either flight or courtship.

The rectrices are quite long in *Stipiturus,* but very much shorter than in *Sylviorthorhynchus* (only two-thirds of their length or less) and are regularly graduated with well-developed barbs, although the barbs are much reduced in number and seem to lack barbules, resulting in a "skeletonized" appearance. These feathers have been compared to "delicate plumes" and are normally carried cocked high at a sharp angle over the back when the bird is not flying, a posture which has not been observed in *Sylviorthorhynchus,* and which probably plays a part in courtship or other behavior in *Stipiturus.* In the genus *Dromaeocercus* (also Sylviinae) of Madagascar, which is composed of two species, the tail is also very skeletonized and stiffened, but is shorter, more "spiny" than in *Stipiturus,* and is composed of a "normal" complement of 10 rectrices, not six.

Sylviorthorhynchus of Chile and Argentina is the counterpart of *Stipiturus* of Australia in many respects as suggested by the accounts of *Stipiturus* given by Serventy and Whittell (1951), and McGill (1970).[37] Convergence is strong, notably in the structure and location of the nest, which is also closed in *Stipiturus,* rounded or oval in shape with a small circular entrance at one side, and built close to the ground of dry grasses to which some species add also fibers of shredded bark bound with spider's web.

Sylviorthorhynchus desmursii
Figure 2

DESCRIPTION: Upperparts rufous brown and uniform, except for the forecrown which is pale chestnut, brighter and more reddish than the top and posterior part of the crown and back; with a buffy superciliary streak, best indicated behind the eye. Underparts strongly ochraceous, but more whitish on the center of the abdomen. Wing dark brown, without a rufous area on the inner webs of the feathers, but with the edge of the outer web ferruginous. Bill long, thin, and attenuated. Tail composed of only six rectrices that are virtually denuded of barbs, and the central and middle pairs of which are extremely long and greatly stiffened—these feathers being wirelike—the outer pair very short and vestigial (see description and discussion above).

MEASUREMENTS (in mm.; range, and average in parentheses): Adults, wing, 39 birds, 48.5–56 (52.58); outer tail feathers (O.T.F.), 34 birds, 16–32 (21.88); middle tail feathers (M.T.F.), 32 birds, 64–87 (77.40); central tail feathers (C.T.F.), 33 birds, 120–175 (152.72); bill, 37 birds, 17–20 (18.39).

Males, wing, 22 birds, 50–56 (52.81); O.T.F., 20 birds, 16–29 (21.25); M.T.F., 17 birds, 70–87 (77.82); C.T.F., 19 birds, 132–174 (155.36); bill, 20 birds, 17.5–20 (18.61). Females, wing, 13 birds, 49–55 (52.19); O.T.F., 11 birds, 20–32 (22.90); M.T.F., 12 birds, 64–86 (76.08); C.T.F., 11 birds, 120–167 (146.18); bill, 13 birds, 17.5–20 (18.30).

IMMATURE PLUMAGE: Similar to that of the adult, but mottled above and below, not uniform, with dull orange above, and with brown below. Tail feathers much shorter and better barbed.[38]

RANGE: Central and southern Chile, and Argentina along the foot or lower slopes of the Andean cordillera from Neuquén south to Santa Cruz. In Chile, north to Aconcagua, and south to Messier and Smyth Channels in Magallanes, also Isla de la Mocha, Chiloé, and other islands. The populations of southern Chile are sedentary, whereas those of central Chile are said to be partly migratory, moving north with the rains.

SPECIMENS EXAMINED: 44, including the type *Sylviorthorhynchus desmursii* in MNHN.[39]

GENUS *APHRASTURA*

Aphrastura is composed of only two species, *A. spinicauda* which is distributed from central Chile and southwestern Argentina to Tierra del Fuego, and *A. masafuerae* which is restricted only to Masafuera Island in the Juan Fernández Archipelago (map 4).

Aphrastura is related to *Leptasthenura* but the two genera differ distinctly in morphology, ecology, and behavior. The tail of *Aphrastura* is much shorter than that of *Leptasthenura,* stiffer, and the apical portion of its rectrices is quite different. In *Aphrastura,* about the distal third of the inner web of the rectrices is very abruptly and deeply excised, to the shaft or virtually so, the tips of the feathers being thornlike, whereas the apical portion of this web is more or less emarginated in *Leptasthenura,* but not abruptly and deeply excised (fig. 2). The tail is longer than the wing in both genera, but is roughly a third longer in *Leptasthenura,* proportionally speaking, as the ratio between the lengths of the tail and wing varies from 1.30 to 1.78 with an average of 1.53 in *Leptasthenura,* as against 1.04 and 1.12 in *Aphrastura.*

The ecology varies geographically, and little or no information exists for some species of *Leptasthenura. Aphrastura spinicauda* is essentially a bird of the deep forest and low lying regions,[40] and *A. masafuerae* is known to occur only in dense and humid tree fern forest, whereas all the species of *Leptasthenura* are essentially birds of open, commonly arid country, chiefly frequenting scrub and shrubby vegetation, and are markedly montane with some exceptions, six of its nine species breeding at 4000 m. or more, two of them over 5000 m.

The species in both genera all seem to be quite active, even restless birds, as far as known, but act differently, as *A. spinicauda* is generally compared to a titmouse or chickadee (*Parus*), whereas *Leptasthenura aegithaloides* (and other congeners) very much resemble the long-tailed tits (*Aegithalos*) in behavior and many other respects.[41]

No information is available for *A. masafuerae,* other than that it seems confined to the dense, misty tree fern forest of the higher parts of Masafuera Island. *Aphrastura spinicauda* is quite common, on the other hand, and well known. It is an extremely active bird, constantly investigating the foliage and bark of the branches or of the trunk of trees, but paradoxically, without normally using its well stiffened, "thorny" tail for support—a posture quite different from that assumed by *Leptasthenura aegithaloides* which uses its long tail for support as well as balance.

Peterson and Humphrey (in Humphrey et al., 1970) who have observed *A. spinicauda* on Tierra del Fuego, described its behavior as follows: "These birds were very reminiscent of chickadees, although they were considerably more active on the vertical surfaces of the bark of trees. They would run up and down, the tail lifted away from the bark, not down on the bark, as one would think from the spines that are on it, and they would bob the tail very actively . . . . The tail was also cocked at an angle so the bird suggested both a wren [*Troglodytes*] and a chickadee. However . . . it is neither wrenlike nor chickadee-like in its liking for vertical surfaces of trees . . . . It can be seen sometimes, hanging chickadee-like, upside-down from a small twig, yet at the same time, it has this extraordinary behavior of running up and down the bark with the tail cocked and bobbing its body up and down on the legs."

This characteristic posture—with the tail stiffly carried at an angle over the back, and used neither for support nor any apparent degree of balance—is well illustrated by the plate of *A. spinicauda* supplied by Johnson; another plate given by Johnson depicts the comparative, but quite different posture of the tail in *L. aegithaloides.*

Aphrastura spinicauda feeds also on the ground and inhabits small islands off Tierra del Fuego where there are only a few low trees or none. On the islands of the Cape Horn Archipelago it "spends much of its time in the undergrowth [where] it scratches amongst the fallen leaves in the company of

TABLE 5
Measurements (in Millimeters) of *Aphrastura*

Species	Wing			Tail			Bill		
	N	Mean	Range	N	Mean	Range	N	Mean	Range
A. spinicauda									
Males	28	63.32	60–67	21	72.90	67–78	28	14.48	13–15.50
Females	26	60.28	56–63	24	70.95	59–81	26	14.00	13–15
Both sexes	57	61.78	56–67	48	72.22	59–81	57	14.24	13–15.50
A. masafuerae									
Both sexes	12	69.00	64–72	11	72.09	66–80	11	17.86	17–19.50

Zonotrichia and *Phrygilus,*" according to Reynolds (1935) and skulks "in the bushes of *Berberis* and *Ribes* . . . when the berries are ripening." On the smallest islands, *Berberis* bushes are used as a substitute for trees, according to Olrog (1950), or "huge groves of tussock-grass," according to Reynolds.

All observers agree that *Aphrastura spinicauda* is inquisitive and easily alarmed, resenting intrusion very readily and vociferously. Crawshay (1907) said that on Tierra del Fuego "Go where one will, it comes to one, following one persistently within reach of one's person, chirping incessantly, and attracting others of its kind—until one is accompanied by two or three pairs, exclusive of allies in Wrens and Thrushes." These chirps are evidently very loud and shrill because Crawshay says they are "ear-piercing," and this alarm is described by Reynolds (1935) as "a shrill scold of excitement, the notes pouring out in breathless continuity and matching admirably the energetic nature of this restless little sprite."[42] Johnson witnessed a mobbing attack on an owl by a dozen individuals which were scolding so loudly that "the noise they made was deafening."

The location of the nest of *Aphrastura spinicauda* varies, but it is usually constructed high above the ground in a tree, within a natural crevice in the trunk, under bark loosened from the trunk; or, in other cases, in a tear or split of suitable size in a broken limb, or an old woodpecker hole. The nests reported in these situations varied from about 6 to 13 m. above the ground, but *A. spinicauda* nests also much lower in cracks in old rotten or burnt-out stumps, or crevices in living trees, about 1 to 3 m. above the ground. Johnson (1967) reported that he also found one nest that was very well concealed in the under structure of a bridge, and Valenzuela (1960) found one within a crevice eroded by the rain in the vertical surface of an isolated tall bluff of earth. But "whatever the site selected, its walls are loosely lined with twigs and soft grasses, with an abundant supply of feathers for the actual nest," according to Johnson (1967), although Valenzuela reported finding only much fur and some horse hair in the nest he found in the wall of the bluff. The hole or cavity is also used regularly for shelter and sleeping on Tierra del Fuego according to Reynolds (1934).

The nest of *Aphrastura masafuerae* is not known, but is probably constructed in a crevice or some irregularity of the trunks of tree ferns.

Morphological Variation

The two species are very distinct although their general color pattern is similar. *Aphrastura masafuerae* is a much duller bird than *A. spinicauda,* with a less distinct pattern (see descriptions below), and is considerably bigger and coarser. Its bill and especially its feet are much stronger. This is not well shown by measurements, as the length of the tarsus averages about 25 mm. in *A. masafuerae,* as against about 19 mm. in *A. spin-*

icauda, and the bill of *A. masafuerae* is only about 3.5 mm. longer, but, nevertheless, the feet of *A. masafuerae* give the impression of being almost twice as big and strong, and it is very evident that its bill is much stronger.[43]

Geographical Variation

Aphrastura spinicauda varies geographically and two populations have been named, one from Chiloé Island which is clearly differentiated, and the other from Mocha Island which shows only a tendency to be darker, more buffy below than birds from the remainder of the range other than Chiloé. On Chiloé Island, the birds differ by being strongly ochraceous below over virtually the whole of the underparts, whereas the throat and breast are whitish in the other populations. The population of Chiloé has been named *fulva*. It is possible that birds from the islands farther south (Guaitecas and Chonos Archipelago) are also similar to those of Chiloé, as one specimen taken on Melchor Island in the Chonos has been identified as *fulva* by Trimble (1943). Specimens from Mocha Island vary much individually and some are identical with birds from central Chile.[44]

KEY TO THE SPECIES OF *APHRASTURA*

Crown and face sooty black, divided sharply by a broad and very conspicuous dull orange superciliary streak ..... *spinicauda*

Crown and face earthy brown, scarcely divided by an unusually dull, buffy brown superciliary streak, not at all conspicuous and well defined ..... *masafuerae*

List of the Species

Aphrastura spinicauda
Figure 2

Description: Sooty black on the crown, hind neck, and face, with a broad, most conspicuous dull orange superciliary streak dividing the black of the face from the black of the crown, the streak being very long, prolonged to the back of the nape, or farther, to the shoulders, where it merges into the brown of the back. Remainder of the upperparts fulvous brown, with dusky dark edges to the feathers of the mantle, becoming strongly rufous and uniform on the rump and upper tail coverts. Underparts whitish (or very faintly tinged with gray) on the throat, breast, and center of the abdomen (or strongly ochraceous on Chiloé Island, see geographical variation) becoming buffy brown, or fulvous, on the flanks and under tail coverts.

Wing variegated, with a bright rufous area at the base of the remiges, and with duller rufous markings on the outer web of some secondaries and primaries. Lesser and middle upper wing coverts bright rufous with blackish or dark dusky brown edges; greater upper wing coverts dark brown with small pure white tips; the inner webs of the innermost secondaries, and also their tips, dull white to a varying extent. Tail strongly rufous on the central rectrices, and, to a varying extent, also strongly rufous at the apical portion of the other rectrices, the basal portion of which is blackish. The apical portion of the inner web of all the rectrices (see general discussion) is very abruptly and deeply excised to the shaft, or virtually so, creating a "spiny" or "thorny" appearance. Tail well stiffened; bill moderately long, relatively straight and attenuated.

Immature Plumage: Similar to that of the adult, but pattern less distinct, and with more conspicuous, heavier, darker borders to the feathers of the mantle; the "spines" of the tail are also much less well developed.

Range: Central Chile, from Coquimbo southward, including Isla de la Mocha, Chiloé, and many other islands, to Tierra del Fuego and islands south of Tierra del Fuego, including the Cape Horn Archipelago; also southwestern Argentina, along the forested lower slopes and foothills of the Andes, from Neuquén to Tierra del Fuego and Isla de los Estados. In Chile, the range ascends to over 1600 m., and to about 2000 in Argentina.

No subspecies are recognized by me, but the population of Chiloé is clearly differentiated (see geographical variation).

SPECIMENS EXAMINED: 130, including the type of "*bullocki*" in AMNH.

Aphrastura masafuerae

DESCRIPTION: Dull earthy brown on the back, with a darker, more dusky crown with small narrow rufous streaks on the anterior portion, and with the rump paler, more rufous than brown. Superciliary streak very dull, buffy brown, and not at all well defined. Underparts dark and very dull, buffy brown, and virtually uniform, but paler, dingy buffy white on the throat. Wing and tail pattern similar to that of *Aphrastura spinicauda*, but much duller and much less well defined, and lacking the white tips on the greater upper wing coverts. Structure of the tail similar to that of *A. spinicauda*, but "spines" better developed, and with the bill, and also the feet, much bigger and stronger.

IMMATURE PLUMAGE: Indistinguishable from that of the adult in the only specimen seen, but "spines" of the tail less developed.

RANGE: Confined to the forested higher parts of Masafuera Island, Juan Fernández Archipelago.

SPECIMENS EXAMINED: 13.

This species is probably very rare, perhaps vanishing or extinct. Johnson (1967) said that only three individuals were seen in 1928 in the habitat to which it was apparently restricted, and none in 1955, despite a search of several days.

GENUS *LEPTASTHENURA*

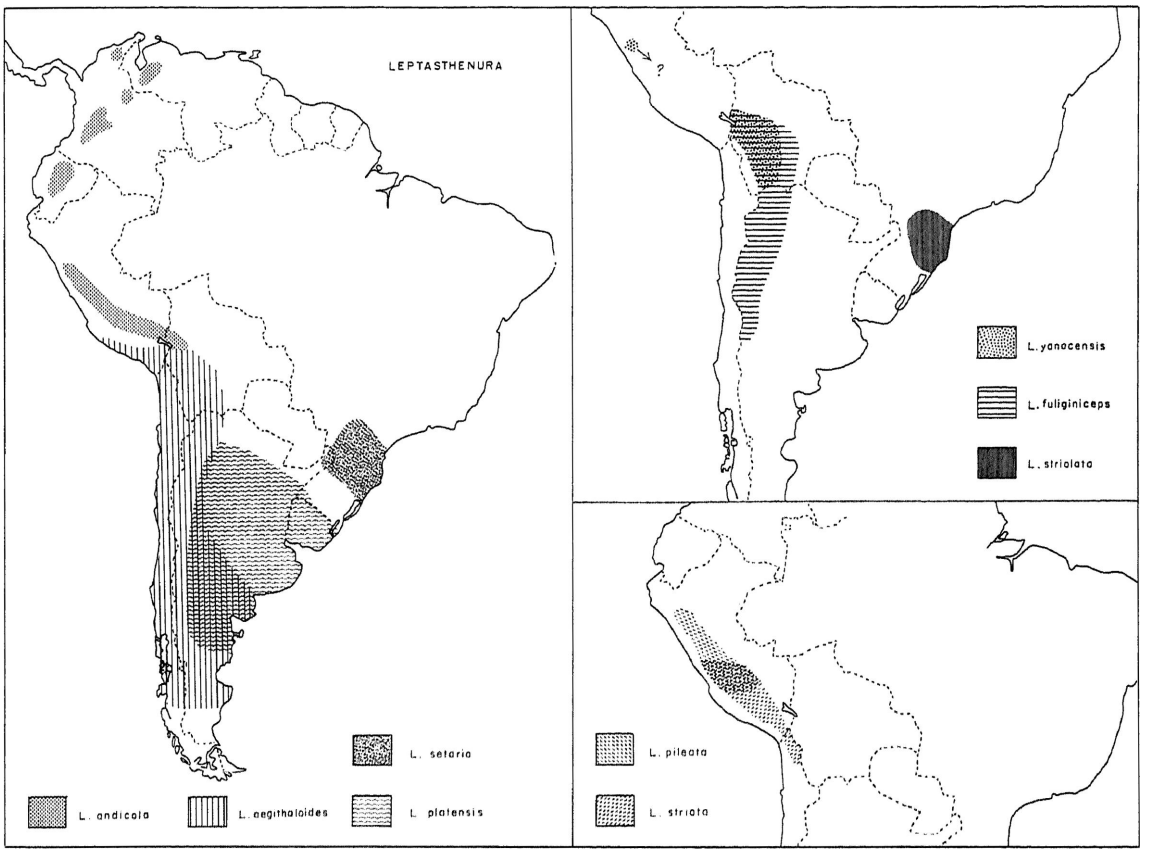
Leptasthenura is composed of nine species and seems to be closely related to *Aphrastura*.

The two genera were already compared in the general discussion of *Aphrastura*. The most conspicuous difference in morphological characters is in the structure of the tail which is less stiffened, much longer, and not abruptly and deeply excised at the distal portion of the inner web of the rectrices in *Leptasthenura*. The rectrices are more or less well emarginated in *Leptasthenura*, and, in most species, the central rectrices taper to a very acute point (fig. 2), but they are not abruptly excised as in *Aphrastura*. As the central rectrices are much longer than the adjoining pair, the pronounced emargination of these long feathers creates a tail very deeply and decidedly "forked" in appearance.[45] The inner webs of the other rectrices taper also, but very much less than in the case of the central pair, and the acute shape of the tips diminishes on the outer pairs of rectrices which become progressively more rounded than acute at the tip; specific variation is discussed below.

But other morphological differences exist also between the two genera: the feathers of the posterior part of the crown show a tendency to be more or less elongated in all the species of *Leptasthenura* and form a short but true crest in *L. platensis*; the bill is shorter than in *Aphrastura* and very weak as a rule; and the coloration differs also, as most *Leptasthenura* are well streaked, but not *Aphrastura*.

The ecology of the two genera is quite different. The two species of *Aphrastura* are essentially birds of the deep forest, and *A. spinicauda* ascends only to 2000 m. or much less[46] (*A. masafuerae* is confined to a small island), whereas all species of *Leptasthenura* for which information exists are very predominantly birds of open regions, commonly arid, where they frequent chiefly scrub, bushes, thin open woodland, steppe, semidesert, or regions well above the limit of arborescent vegetation in the páramos and on the puna of the altiplano.

The range of *Leptasthenura aegithaloides* overlaps partly that of *Aphrastura spinicauda* from the seacoast or lowlands upward, but whereas *A. spinicauda* does not seem to ascend over 2000 m., as stated above, *L. aegithaloides* reaches the great height of roughly 4600 m.[47] *Leptasthenura platensis* ascends from the pampas to about 3000 m. or slightly more, and five other species (*L. fuliginiceps, L. yanacensis, L. pileata, L. striata* and *L. andicola*) are Andean, all reach 4000 m. or even more, roughly 5200 m. in the case of *L. yanacensis* and *L. andicola*. However, two species (*L. setaria* and *L. striolata*), for which no information



MAP 6. Geographical distribution of *Leptasthenura*.

exists, or virtually none, seem to be restricted chiefly to the forest of *Araucaria angustifolia* of southeastern Brazil, below about 900 m. The distribution of *Leptasthenura* species is shown on map 6.

The general behavior of *Leptasthenura* (when known) is probably best characterized by saying that it resembles closely that of the long-tailed tits (*Aegithalos*) in many respects—of which they seem to be the counterparts in South America—whereas *Aphrastura spinicauda* is generally compared to a titmouse or chickadee (*Parus*).

Leptasthenura aegithaloides is the most widely distributed and best known species. It is described by Hudson (in Sclater and Hudson, 1888) as follows: "This is a restless little bird, seen singly or in parties of three or four. In manner and appearance it resembles the Long-tailed Titmouse [*Aegithalos*], as it diligently searches for small insects in the trees and bushes, frequently hanging head downwards to explore the under surface of a leaf or twig, and while thus engaged continually uttering a little sharp querulous note. They are not migratory, but in winter seem to wander about from place to place a great deal; and in Patagonia, in the cold season, I have frequently seen them uniting in flocks of thirty or forty individuals, and associating with numbers of Spine-tails of other species, chiefly with *Synallaxis sordida* [=*Thripophaga pyrrholeuca*], and all together advancing through the thicket, carefully exploring every bush in their way."

This gregarious habit is mentioned by oth-

er authors, and Johnson (1967) said the long tail is used for both support and balance, a characteristic posture illustrated by him in a plate showing two individuals of *L. aegithaloides* investigating the partly decayed trunk of a tall cactus. The flight is described as irregular and rather labored, "tilting," probably because of the drag of the long tail, and which apparently is similar to the flight of *Aegithalos*.

The location of the nest varies a great deal, but it seems to be always placed within a hole, or inside a secure shelter, and the abandoned nests of larger furnariids are regularly used, such as the clay oven of *Furnarius,* or the large domed stick nest of *Thripophaga pyrrholeuca,* which, Hudson said, is "almost always select[ed]" in regions where *Furnarius* is absent. Johnson has found the nest in holes in trees, often in cacti, stone walls, under the roof of houses, clefts among rocks, and once in a "salty" concretion, or "blister," that had accumulated on the "vertical wall of a high cliff overlooking the sea." In the field notes of J. R. Pemberton, which were kindly made available to me by the Western Foundation of Vertebrate Zoology, Pemberton mentioned he also found the nest in the short burrow of some rodent in the side of a bank, or in the ground under a bush.

The hole, or an abandoned nest which has been adopted, is loosely walled with twigs, soft grasses or other plant fibers, and then seems to be invariably lined profusely with feathers. The unusually lavish use of feathers for the inner lining is very characteristic of *Leptasthenura,* and Johnson (1967) said that when the "favourite . . . domed nests of other birds . . . are chosen, the usual stick or root-fibre framework is dispensed with and the actual nest-cavity so profusely lined with soft feathers that some of these are almost invariably visible around the entrance hole and give advice to all and sundry that the nest no longer harbours its original owner but has been occupied and remodelled by the 'Tijeral,'" the vernacular name of *L. aegithaloides* in Chile.

The nest of only four other species is known (*L. platensis, L. andicola, L. fuliginiceps,* and *L. yanacensis*), but whatever its location or construction, it is always profusely or well lined with feathers as in *L. aegithaloides*.

The general behavior of *L. platensis* is similar to that of *L. aegithaloides*. It chiefly frequents thickets and shrubs, but also forages in trees of dense foliage, or, according to Masramon (1971), takes refuge into them when disturbed. *Leptasthenura platensis* also nests in holes in trees, but seems even more partial than *L. aegithaloides* to the abandoned nests of other furnariids, including some really huge ones. Masramon stated that *L. platensis* uses the ovens of *Furnarius rufus* and *F. cristatus,* the very large stick nests of *Anumbius* and *Coryphistera,* and the smaller ones of unspecified species of *Synallaxis*.

Very little information exists on *L. andicola,* other than it is a secretive species which frequents low matted vegetation, usually along small streams on the puna and páramos.[48] These regions are above treeline, and, with rare exceptions, devoid of arborescent plants. The only nest on which information is published was discovered by Dorst (1957, and personal commun.) on February 26, 1955, at Checayani, Puno, on the altiplano of southern Peru, at an altitude of 4100 m., in a stand of *Puya Raimondii,* a gigantic Bromeliaceae which grows to about 10 m. high. The nest, which contained one young, was situated 1.20 m. above the ground, in an almost inaccessible location very well concealed between the trunk of the *Puya* and a cluster of hanging dead leaves. It was very loosely constructed of vegetable fragments, rounded and about 16 cm. in diameter, with an opening at the side, and profusely lined with feathers mixed with wool.[49]

The only two other species for which published information on the nest is known are *Leptasthenura fuliginiceps* and *L. yanacensis*. In the case of *L. fuliginiceps,* Hoy (1968), who seems to be the only one who has described its nest, found it in deep crevices in rocks, with a remarkably narrow entrance measuring 2 cm. or less in width, or within a crack in the wall of an abandoned

rancho, also with a very narrow entrance of about 2 cm. The nesting cavity was widened beyond the entrance and was lined with soft vegetable fibers, richly provided with feathers and plant down.

The only nest of *Leptasthenura yanacensis* was discovered by Vuilleumier (1969), built of dried grass stems about 2.5 m. above the ground in the fork of a tall *Polylepis* tree. It was "roundish," about 25 cm. in diameter, with an opening at the side, and lined with threads, wool, plant down, and feathers.

I have found no information on other aspects of the behavior of these two species, but their ecological requirements (dense scrub in *L. fuliginiceps*, open brushland with bushes and small trees in *L. yanacensis*) seem essentially similar[50] and there is no reason to believe that their general behavior differs importantly from that of *L. aegithaloides*.

Little or no information exists for the other four species (*Leptasthenura pileata, L. striata, L. setaria,* and *L. striolata*) and their nests remain undescribed. Koepcke (1954, 1958) said that *L. pileata* frequents open woodland and shrubs on the western slopes of the Andes above Lima, and in another paper (1965), said that the related *L. striata* frequents more open ground, steppe with sparse bushes, in the same region. In the note published in 1958, Koepcke said that the behavior of *L. pileata* is similar to that of *Aegithalos,* and her accounts imply that the general behavior of these two species is similar (although their vocalizations are different, see below) and quite comparable to that of *L. aegithaloides*.[51]

I have found no information whatever for *Leptasthenura setaria* and *L. striolata*.

Morphological Variation

This genus is relatively homogeneous, but there is variation in the coloration and pattern of the plumage, and in the shape of the tail feathers and their number. The tail has 12 rectrices, with the exception of *Leptasthenura yanacensis* in which they are reduced to 10.

The plumage is brown or grayish above and is either uniform or streaked. *Leptasthenura fuliginiceps* and *L. yanacensis* are brown and not streaked anywhere; *L. platensis* and *L. aegithaloides* are grayish or grayish brown, uniform on the back, but not on the crown which is streaked; *L. setaria* is reddish brown on the back and uniform with a black crown streaked with buff. In the four remaining species (*L. striolata, L. pileata, L. striata,* and *L. andicola*) the back, as well as the crown, are streaked.

The underparts are paler than the crown and back, varying from buffy or ochraceous to gray or dusky sooty gray, with a paler throat. The throat is buffy or whitish, and is uniform or more or less spotted or streaked with dusky brown or blackish markings. A pale superciliary streak, which may be well defined or not, exists in all the species.

The tail is strongly rufous, or blackish, and is uniform or not. In species in which it is not uniform, the outer webs of some of the rectrices, and the tips or distal portion of the inner webs, are paler than the remainder of the feather which is dark dusky brown or blackish, the pale webs or tips contrasting with the dark area by being rufous, tawny, silvery, or grayish white. A rufous area is present in the wing of all the species where it is restricted to a very variable extent to the base of the remiges and some of their outer webs.

The structural variation is relatively slight. The feathers of the posterior part of the crown tend to be more or less elongated in all the species, but form a true but short crest only in *Leptasthenura platensis*. All the species are small, with a long and sharply graduated tail, a small bill, and weak feet. The variation in size is quite slight. The means (in mm.) of the lengths of the wing, tail, and bill vary in round numbers only from 56 to 71, with an average of 62, in the case of the wing; 90 to 103, average 94 for the tail; and 11 to 15, average 12 for the bill. The extent to which the length of the tail exceeds that of the wing is shown by a ratio varying from 1.30 to 1.78, average 1.52.

The shape of the tip of the tail, which was

described above when comparing *Leptasthenura* to *Aphrastura*, varies somewhat specifically. The shape is most "typical" in *L. platensis*, *L. aegithaloides*, and *L. striolata*, in which the inner web of the central rectrices is sharply emarginated and tapers to an acute tip. The other rectrices of these three species also end in acute tips to a varying degree, but they are much less deeply emarginated, and for a short distance only, than in the case of the central pair. In *L. striata*, *L. pileata*, and *L. andicola*, the tips of the rectrices are less acute as a rule than in *L. platensis*, *L. aegithaloides*, and *L. striolata*, and the emargination of the inner web of the central rectrices is normally less extensive. It usually starts closer to the apex, with the result that the "fork" is less deep.

The tail of *Leptasthenura* is not truly forked, but in well prepared skins, the deep emargination of the central rectrices forms a very distinct notch when the normal arrangement of these feathers is not disturbed. The depth of this "fork" cannot be measured accurately because the emargination starts imperceptibly, but in specimens in which the feathers are fresh or little worn, and not disturbed by handling, the depth of the "fork" averages about 25 mm. in *L. striata*, *L. pileata*, and *L. andicola*, as against about 33 mm. in *L. platensis* and *L. aegithaloides*, but although the tips are also very sharply acute in *L. striolata* (to the same degree as in *L. platensis* and *L. aegithaloides*), the "fork" of *L. striolata* is distinctly more shallow, averaging about 27 mm. in depth.

The ends of the rectrices taper in *Leptasthenura fuliginiceps* and *L. yanacensis*, but the tips are relatively blunt, not sharply acute, and, as the inner web of the central rectrices is also rather poorly emarginated in these two species, their "fork" is shallow, averaging only about 18 mm. deep. In *L. setaria*, on the other hand, the "fork" is deeper than in all the other species, about 40 mm. deep on average. The inner web of the central rectrices of *L. setaria* is emarginated over a long distance, but the end of the feather is merely narrowed to a width of about 4 mm. The apex is not acute, but distinctly rounded when not worn (fig. 2). This modification of the central rectrices (combined with its longer bill) has led to the totally unwarranted generic separation of *L. setaria* (see below).

Phylogeny

All the species are more or less closely related, but some form groups and two pairs of closely related species stand out sharply.

One of the species pairs consists of *Leptasthenura fuliginiceps* and *L. yanacensis*, the ranges of which are complementary (*L. fuliginiceps* in the south, and *L. yanacensis* in the north) but overlap broadly in Bolivia (map 6).[52] The little that is known about the ecology of these two species does not suggest any essential differences and their morphological resemblance is striking. These two birds are excessively plain, pale earthy brown above, not streaked anywhere, and have a strongly rufous tail, uniform in coloration, and ending in a shallow "fork"; the tips of the rectrices are also relatively blunt, not sharply acute, as stated above. These two species seem to be so incontrovertibly related, and to such a close degree, that I cannot understand the reservation of Carriker (1933) who says he is "not at all sure" *yanacensis* is a *Leptasthenura*.

The very plain, unstreaked plumage of these two species can be interpreted as "primitive," and, taken together with the poor development of the characters of the tail, suggests that the systematic sequence is best started with *L. fuliginiceps* and *L. yanacensis*.

The other pair of species which are closely related consists of *Leptasthenura pileata* and *L. striata*, the ranges of which are also complementary (*L. pileata* in the north, and *L. striata* in the south) but overlap in Peru. These two species are exceedingly similar when allopatric, their crowns being conspicuously streaked with rufous (reddish cinnamon or hazel in *L. striata*, bright reddish chestnut in *L. pileata*) on a blackish ground. In the zone of overlap, however, the rufous

streaks coalesce completely or virtually so in *L. pileata*. The crown becomes uniformly rufous in most specimens, or very nearly so in others, and this fact seems to represent a clear case of character displacement. Species recognition is emphasized also by sharp differences in vocalizations noted by Koepcke (1965).[53]

The great morphological similarity between the two species when allopatric caused taxonomic confusion until Hellmayr (1932), and also Carriker (1933), demonstrated that the population of northern Peru with a streaked crown is conspecific with *L. pileata*, but not *L. striata*, as had been believed before them.

Leptasthenura andicola seems also to belong clearly in the same group, but is more distantly related to *L. pileata* and *L. striata*.

The systematic position of the other four species (*Leptasthenura platensis, L. aegithaloides, L. striolata,* and *L. setaria*) is more dubious. However, the fact that *L. platensis* and *L. aegithaloides* are both grayish above, and streaked on the crown, but not on the back, suggests that they are best grouped together and listed after *L. fuliginiceps* and *L. yanacensis* in a linear arrangement. They thus constitute a transition between *L. fuliginiceps* and *L. yanacensis* with their "primitive" plumage, and the species (*L. striolata, L. pileata, L. striata,* and *L. andicola*) with a more "specialized" plumage, streaked on both the crown and back.

The two species of southeastern Brazil (*Leptasthenura striolata* and *L. setaria*) complicate the systematic sequence. They are sympatric and quite different. *Leptasthenura striolata* is heavily streaked on both the crown and back, and its central rectrices terminate in sharply acute tips similar to those of *L. platensis* and *L. aegithaloides*. *Leptasthenura setaria* is streaked only on the crown and its central rectrices are more modified in shape than in any other species. The two species probably represent distinct evolutionary lines and their nearest relatives are unknown. Judging by both the rectrices and the pattern of the plumage, *L. striolata* is best listed between *L. platensis* and *L. aegithaloides* on the one hand and *L. pileata, L. striata,* and *L. andicola* on the other.

It seems best to place *Leptasthenura setaria* last in the sequence—not only because its nearest relative is unknown to me, but also because the apex of its tail is more modified than in the other species. This modification, which was described above, led Hellmayr (1925) to separate *setaria* generically from *Leptasthenura* under the name *Dendrophylax*, a new name proposed by him to replace *Bathmidura* Reichenbach, 1853, which Hellmayr had concluded erroneously was preoccupied by *Bathmidurus* Cabanis, 1847. This generic separation is unwarranted and has never been accepted.

I may add that Hellmayr supported his generic separation by stating also that the bill of *setaria* is "much longer and slenderer, with strongly curved culmen" than in any other *Leptasthenura*. But this statement is not correct. The differences in shape are extremely slight at best and not at all constant, and, unknown to Hellmayr, *L. yanacensis*, which was discovered later (in 1932), has a bill which is virtually as long as that of *L. setaria*, averaging only less than 1 mm. shorter.

Geographical Variation

Five species which vary geographically or are said to vary are *Leptasthenura fuliginiceps, L. aegithaloides, L. pileata, L. striata,* and *L. andicola*. However, the large series of comparative material that I have examined in the case of *L. fuliginiceps* failed to confirm any appreciable difference between the populations of Argentina and those of Bolivia, although the birds of Argentina are said to be much paler.

The material of *Leptasthenura striata* in existence is not abundant, but I have seen skins of all the forms named, including types. This material suggests to me that the geographical variation is trivial. The two forms (*albigularis* and *superciliaris*) which have been separated from, respectively, Huancavelica and Lima in Peru are based only on very insufficient or inadequate material.

The geographical variation of *Leptasthenura aegithaloides, L. pileata,* and *L. andicola* is evident, but it seems advisable to me to acknowledge it nomenclaturally only in *L. pileata* where I advocate the recognition of merely two subspecies (*cajabambae* with a streaked crown, and nominate *pileata* with uniformly rufous crown). This variation seems to represent an interesting instance of character displacement and, as such, quite worthy of recognition.

The geographical variation of *Leptasthenura aegithaloides* is apparently correlated chiefly with rainfall and relative humidity. The populations of more humid central Chile are darker than the others, more brownish above, darker gray below, whereas the populations of more arid northern Chile, southern Peru, Bolivia, pampas of Argentina and Patagonia are paler above and below, and the rufous streaks on their crown are brighter and more conspicuous. The least saturated and most grayish populations are those of northern Chile and southern Peru, whereas the birds of Bolivia and of the Andes of northern Chile are more buffy above and below less grayish and less whitish below than the birds of very arid northern Chile and southern Peru. The birds of Argentina are so vaguely differentiated that it is difficult to characterize them.

The range of *Leptasthenura andicola* is more or less disjunct and virtually all the populations differ irregularly to some extent in their measurements, or both in size and some details of coloration, such as degrees in the pigment saturation of the plumage, streaking, or relative extent of the rufous area in the wing. The measurements of the males of some populations are given in table 6.

The geographical variation of *L. pileata* is most interesting and has been briefly mentioned above. The populations with a streaked crown (*cajabambae*) range as far south as Junín and are replaced by nominate *pileata* in the region east of Lima. The crown of nominate *pileata* is uniformly rufous and populations of this type occur apparently as far south as Torontoy in the valley of the Urubamba, and the valley of the upper Rio Pisco in Huancavelica.

The birds of the Urubamba and Rio Pisco valleys are not well known as only three specimens exist so far, one from Torontoy, and two from the Rio Pisco. The latter, which I have not seen, were described as a new subspecies by Koepcke (1965) which she named *latistriata,* and which she says differs from nominate *pileata* by being better streaked on the back, and also somewhat more distinctly so on the breast.

The specimen from Torontoy was described as a full species by Chapman (1921) and named *Leptasthenura xenothorax.* I have examined this bird, which is in the collection of the National Museum of Natural History, and agree fully with Zimmer (quoted by Meyer de Schauensee, 1966, footnote) that *xenothorax* is conspecific with *Leptasthenura pileata.* This specimen differs from nominate *pileata* by being much more heavily spotted with black on the throat, and its breast and abdomen are more uniform, with only a slight suggestion of the pale streaking of nominate *pileata*; the ground coloration of the back is also slightly darker, more blackish, less brownish. The other characters mentioned by Chapman (and Hellmayr, 1925, who had also examined *xenothorax*) fall very well, however, within the range of individual variation of topotypical nominate *pileata,* of which insufficient comparative material was available to Chapman and Hellmayr.

More material from the Urubamba and Rio Pisco valleys is needed, but birds from these regions appear to be distinct, although their crown is apparently uniformly rufous also, as in nominate *pileata,* not streaked as in *cajabambae.* However, I believe that a better concept of the interesting geographical variation of *L. pileata* is obtained by recognizing only two subspecies: *cajabambae* and nominate *pileata.*

KEY TO THE SPECIES OF *LEPTASTHENURA*

1. Tail composed of 10 rectrices ... *yanacensis*
   Tail composed of 12 rectrices 2

TABLE 6
Measurements (in Millimeters) of *Leptasthenura*

Species	Wing			Tail			Bill		
	N	Mean	Range	N	Mean	Range	N	Mean	Range
fuliginiceps									
Males	25	63.74	56–68	24	91.62	83–98	25	11.62	11–12.50
Females	24	60.91	57–65	21	88.57	84–95	24	11.83	11–13
Both sexes	52	62.31	56–68	47	90.34	83–98	52	11.70	11–13
yanacensis									
Males	4	62.75	62–63	3	102.33	102–103	4	14.05	13.20–15
Females	5	63.00	61–65	3	95.33	94–96	5	14.74	14.20–15
Both sexes	10	62.90	61–65	8	98.87	94–103	10	14.34	13.20–15
platensis									
Males	37	60.75	57–64	32	91.28	85–102	37	11.10	10–12
Females	33	59.28	56–62	30	90.23	83–98	32	10.72	10–12
Both sexes	75	60.14	56–64	65	91.00	83–102	74	10.93	10–12
aegithaloides									
Males	44	62.38	54–70	42	89.73	72–104	42	11.06	10–12
Females	28	60.83	53–67	26	87.88	72–98	28	10.94	10–12
Both sexes	74	61.86	53–70	69	89.72	72–104	73	11.01	10–12
striolata									
Males	6	57.33	54–60	5	90.80	87–95	6	11.08	10.50–11.50
Females	3	54.66	54–55	1	—	87	3	11.16	11.00–11.50
Both sexes	9	56.44	54–60	6	90.16	87–95	9	11.11	10.50–11.50
pileata									
Males	15	63.85	60–68	13	100.69	94–105	14	12.45	11–13
Females	7	61.57	58–65	6	101.33	95–103	7	12.17	11–13
Both sexes	24	63.00	58–68	21	100.71	94–105	23	12.32	11–13
striata									
Males	11	64.09	58–69	9	91.22	80–98	11	12.35	11.50–13.20
Females	6	62.00	58–67	5	92.80	90–97	6	12.00	11.50–12.50
Both sexes	18	63.33	58–69	14	91.78	80–98	18	12.17	11.50–13.20
andicola									
Males[a]	38	71.42	62–77	21	92.09	84–102	24	12.34	11–13
Females	32	70.37	63–77	20	91.15	85–100	28	12.25	11–13
Both sexes	73	70.68	62–77	44	91.72	84–102	55	12.28	11–13
setaria									
Males	16	58.37	56–62	15	102.66	93–110	17	15.11	14.50–16
Females	15	57.33	56–59	13	103.92	93–113	15	14.89	14–16
Both sexes	37	57.67	56–62	34	102.73	93–113	38	15.02	14–16

[a] Geographical variation of *L. andicola* as shown by the lengths of the wing and tail in males: Peru, Ecuador, and Colombia, wing, 27 specimens, 69–77 (73.38); tail, 12 specimens, 89–102 (93.66). Santa Marta, wing, 4 specimens, 65–68 (66.25); tail, 4 specimens, 84–95 (89.75). Andes of Mérida, wing, 5 specimens, 62–66 (64.30); tail, 3 specimens, 87–89 (87.67). The bill averages 12.56 in Peru, Ecuador, and Colombia; 12.00 in Santa Marta and the Andes of Mérida.

2. Mantle uniform 3
   Mantle streaked 6
3. Crown uniform ..... *fuliginiceps*
   Crown streaked 4
4. Mantle and rump bright chestnut ... *setaria*
   Mantle and rump gray or grayish brown ... 5
5. Distal or apical portion of the four outer pairs of rectrices rufous; feathers of the hind crown conspicuously elongated, forming a crest ..... *platensis*
   Distal or apical portion of the four outer pairs of rectrices varying from buffy to grayish white or silvery gray; feathers of the hind crown not conspicuously elongated ..... *aegithaloides*
6. Tail strongly rufous on the distal or apical portion of the five outer pairs of rectrices ..... *striolata*
   Tail blackish, fuscous or dark sooty gray brown on the distal or apical portion of the four outer pairs of rectrices, with grayish areas, or whitish edges on some feathers, but not rufous anywhere 7
7. Underparts very heavily and coarsely streaked with white; superciliary streak very conspicuous ..... *andicola*
   Underparts uniform below the upper breast, or with ill-defined, faint, dull white streaks or spots, but not heavily streaked; superciliary streak not conspicuous 8
8. Rufous area of the wing at the base of the remiges very restricted, concealed, or virtually so, by the greater upper wing coverts ..... *pileata*
   Rufous area of the wing less restricted, extending conspicuously beyond the greater upper wing coverts ..... *striata*

In one of the two subspecies of *Leptasthenura pileata* (nominate *pileata*) the crown is uniformly rufous, or virtually so, but all the populations of *L. pileata* are conspicuously streaked on the mantle and cannot be confused with *L. fuliginiceps* in which the back is always uniform, not streaked. In bracket 8 of the key, the uniformly rufous crown of nominate *L. p. pileata* distinguishes this taxon from *L. striata,* but in *L. pileata cajabambae* the crown is streaked, and identification rests on the extent of the rufous area in the wing, although the throat of *L. pileata cajabambae* is also much more distinctly spotted with black than in *L. striata* in which the spotting is poorly defined and much more reduced.

List of the Species

Leptasthenura fuliginiceps

Figure 2

Description: Pale earthy brown above, with a distinctly darker, chestnut-brown crown, contrasting with the color of the back. Pale buffy brown below, with an ill-defined whitish area on the throat, and with the lower abdomen, lower flanks, and under tail coverts more or less darkly ochraceous. Rufous area in the wing reddish chestnut and well developed, especially on the outer webs of the remiges. Tail uniformly reddish chestnut, or with poorly developed, vague, small fuscous tips to the central rectrices. Tail composed of 12 rectrices, with the "fork" (see morphological variation) shallow, and with the tips of the rectrices relatively blunt, not sharply acute.

Immature Plumage: Similar to that of the adult, but faintly mottled on the breast, not uniform, the apices of the feathers being indistinctly margined with grayish brown. Brown crown less distinctly defined than in the adult.

Range: Highlands and Andes of western Bolivia, southward, in the Andean zone of Argentina, to Mendoza. The normal breeding range seems to vary from about 3200 to 4200 m. in Bolivia, and from about 2500 to over 4000 m. in Argentina, but during the winter, some individuals move down to about 1600 m. in Bolivia, and 1200 m. in Argentina, or occasionally much lower to the plains in Argentina.

Specimens Examined: 78, including the type of *fuliginiceps* in MNHN, of "*paranensis*" in BM, and of "*boliviana*" in AMNH.

Leptasthenura yanacensis

Description: Resembles *Leptasthenura fuliginiceps* closely, but darker, more brownish, less dull above, and without a contrast between the color of the crown and back, which are concolorous, with the exception of a small area on the forehead, which is bright reddish chestnut. The underparts are also more richly colored than in *L. fuliginiceps,* dull pale orange, or more strongly ochraceous, rather than buffy brown on the

breast and upper abdomen as in *L. fuliginiceps*. The coloration of the wing and tail, and also the shape of the tip of the tail and of the rectrices, are similar in the two species, but the tail is composed of only 10 rectrices in *L. yanacensis*, as against 12 in *L. fuliginiceps*.

IMMATURE PLUMAGE: Similar to that of the adult, but differs from it by being darker on the back, and by lacking the rufous, bright chestnut area on the forehead.

RANGE: Northern Peru, where it is known so far only from Yánac in Ancash where it was collected at 4572 m.; and Andes of western Bolivia between about 3200 and 5200 m.

SPECIMENS EXAMINED: 11.

Leptasthenura platensis

DESCRIPTION: Mouse gray above and uniform on the back, with a darker, browner, crown, well streaked with dull rufous cinnamon, the feathers of which are elongated posteriorly to form a short crest. Underparts pale grayish brown, with a very extensive whitish area on the throat, which invades the upper breast, and is spotted irregularly with dark, fuscous markings. Rufous area of the wing relatively small and inconspicuous, and restricted chiefly to the base of the remiges. Four outer pairs of the rectrices dull rufous, but dark brown at the base, the rufous area decreasing in size progressively from the first to the fourth feather where it is restricted chiefly to the tip. The "fork" of the tail is deep, and the tips of the rectrices are very sharply acute.

IMMATURE PLUMAGE: Similar to the adult, but dark markings on the throat, and streaks on the crown, much less developed and virtually lacking; the back is not uniform as in the adult, but indistinctly spotted with buff. The immature bird has no crest, and its tail is much shorter, not "forked," and the rectrices are not elongated, terminating in blunt, rounded tips.

RANGE: Chaco of Argentina, extreme southwestern Rio Grande do Sul in Brazil, and Uruguay, south to Chubut. The northern end of the range is not accurately known, but extends to at least Tucumán, Santiago del Estero, and Corrientes in Argentina.

SPECIMENS EXAMINED: 89, including the type of "*punctigula*" in AMNH.

Leptasthenura aegithaloides

DESCRIPTION: Upperparts varying from pale sandy gray to mouse gray or brownish gray, and underparts from pale, "whitish" buffy gray, to darker gray or buff, with an extensive whitish area on the throat, indistinctly spotted with dark fuscous markings. Crown darker than the back, fuscous black, and well streaked, the color of the streaks varying from dull and ferruginous to bright rufous; upper border of mantle more or less extensively and distinctly streaked with dull white. The rufous area in the wing is extensive, and the distal portion of the inner web of the four outer pairs of rectrices is buffy or grayish white, the pale area decreasing in size progressively from the first to the fourth feather; the outer webs of these rectrices is white or whitish, and the base of the rectrices is dark brown. The structure and shape of the tail are similar in this species and *Leptasthenura platensis* (*q.v.*).

IMMATURE PLUMAGE: Similar to that of the adult, but dark markings on the throat, and streaks on the crown, very indistinct, much less developed and virtually lacking. The back is also indistinctly spotted with buff, not uniform below the upper border of the mantle as in the adult. The crest and the characters of the tail are not developed, the tail is much shorter than in the adult, not "forked," and the rectrices have blunt rounded tips; also they are not emarginated.

RANGE: Southern Peru, Bolivia, Chile, and Argentina. In Peru, the range extends north, along the coast to the region of Lomas in northern Arequipa, and on the plateau to Lake Titicaca, and then southward through Chile to Aysén, and the Andes of Bolivia, to Santa Cruz in Argentina, and east to La Rioja, San Luis, La Pampa, and southern Buenos Aires. The altitudinal range rises from the coast to 4000 m. or more in Peru, to about 4600 m. in Chile, and about 4000 m. in Argentina, varying between about 3400 m. and 4500 m. in Bolivia.

SPECIMENS EXAMINED: 124, including the

types of "*fuscescens*" and "*berlepschi*" in AMNH.

Leptasthenura striolata

DESCRIPTION: Upperparts dark russet-brown, somewhat darker, more fuscous, on the crown, and very heavily streaked, with bright russet on the crown, and with hazel on the back. Underparts strongly buffy, below a paler, more "whitish," throat, the lower throat and upper breast being indistinctly spotted with brown. Rufous area of the wing restricted, but tail very strongly rufous on the five outer pairs of rectrices, the rufous area decreasing progressively in size from the first to the fifth rectrix. The central pair is wholly brown, deeply emarginated at the apex, which produces a deep "fork," and the tips of the rectrices are very sharply acute.

IMMATURE PLUMAGE: Similar to the adult, but streaked pattern much less distinct; tail much shorter, with adult characters ("fork," emargination, and acute tips) not developed.

RANGE: Restricted to southeastern Brazil, from eastern and central Paraná, south to northeastern Rio Grande do Sul.

SPECIMENS EXAMINED: 10.

Leptasthenura pileata

DESCRIPTION: Blackish to dark chestnut brown above, with a paler, more umber, rump, and very heavily streaked. The streaks on the crown are very strongly rufous and bright, reddish hazel or reddish chestnut, in *cajabambae,* but coalesce completely or virtually so in *pileata,* the crown becoming uniformly rufous, or with more or less evident traces of the dark fuscous edges of the feathers in some individuals. The feathers on the back and rump are blackish or dark brown laterally with very bold, broad, whitish or buffy centers. The underparts are dingy gray below the upper breast, with very faint, ill-defined, dull white streaks or spots, better indicated in some individuals than others, or are uniform or virtually so. The throat is whitish (the pale area extending to the upper breast) and is more or less boldly and distinctly spotted with black, or dull black, the blackish markings dwindling on the upper breast, or restricted to the throat.

The rufous area in the wing is very restricted, concealed, or nearly so by the greater upper wing coverts. The distal or apical portion of the four outer pairs of rectrices is silvery or buffy gray, the pale area decreasing in size progressively from the first to the fourth rectrix. The tail is rather deeply "forked," but (see morphological variation) the emargination of the central rectrices is moderate, and the apices not very sharply acute as a rule.

IMMATURE PLUMAGE: Not examined, but judging by the immature plumage of the closely related *L. striata* (*q.v.*), the streaked and spotted pattern of the adult is not well developed.

RANGE: Northern and central Peru, from Cajamarca south at least to the valley of the upper Rio Pisco in Huancavelica, and region of Torontoy above Machu Picchu in the valley of the Urubamba, Cuzco. The recorded altitudinal range varies between about 2000 and 4300 m.

I recognize two subspecies as stated in the discussion of the geographical variation: *cajabambae* (with a streaked crown) ranging from Cajamarca south to Junín; and nominate *pileata* (with a uniformly rufous crown) replacing *cajabambae* from Lima southward.

SPECIMENS EXAMINED: 24, including the types of *pileata* and *cajabambae* in BM, and of "*xenothorax*" in USNM.

Leptasthenura striata

DESCRIPTION: Resembles *Leptasthenura pileata* (*q.v.*) very closely, but the rufous area in the wing is better developed, extending conspicuously beyond the greater upper wing coverts; the streaks on the upperparts are also somewhat less boldly indicated, duller rufous on the crown, and the dark spotting on the throat and upper breast is considerably more reduced, the spots being fewer and paler, poorly defined as a rule. The crown of *L. striata* is always streaked, not uniformly rufous as in nominate *L. p. pileata.*

IMMATURE PLUMAGE: Generally similar to that of the adult, but the streaked pattern of the upperparts is much less distinct, much less developed, especially on the crown where the streaks are virtually lacking and most indistinct. No dark spots are present on the throat and upper breast, but the feathers of the lower breast and abdomen are faintly barred, these feathers being narrowly margined with brown. The rufous area in the wing is also much more extensive and brighter than in the adult, the tail is much shorter, and the adult characters not developed.

RANGE: Central Peru, from the region east of Lima, south to the Andes of Arica and Tarapacá in northern Chile. The altitudinal range seems to vary between about 2000 and 3800 m. in Peru, and between about 2500 to over 4000 m. in Chile, but in May, this species has been collected down to 1219 m. in Chile.

SPECIMENS EXAMINED: 21, including the types of "*superciliaris*" and "*albigularis*" in BM.

Leptasthenura andicola
Figure 2

DESCRIPTION: Fuscous black or blackish brown above, heavily and coarsely streaked with dull white on the back and rump, and well streaked with ferruginous cinnamon, hazel, or russet on the crown, with a very conspicuous white superciliary streak. Grayish brown below with heavy, coarse white streaks which become broader and more convergent on the upper breast, the lower throat being chiefly white, and the center of the upper throat and chin wholly white. The coarse white streaking above and below results in a flammulated appearance. The rufous area in the wing is dull to very dull, more or less restricted, becoming inconspicuous in some populations. The tail is very dark, chiefly dark brown, or "blackish," but dull white to a varying degree on the outer web of the four outer pairs of rectrices, vaguely grayish on the distal or apical portion of the inner web of these rectrices.

IMMATURE PLUMAGE: Similar to that of the adult, but without streaks on the crown, or with the streaks only faintly and vaguely indicated. The streaked, flammulated pattern of the remainder of the plumage is also much less regular and much less developed, and the abdomen is more ochraceous than in the adult, with narrow dark margins to the feathers producing an irregular barred, rather than streaked, pattern as in the adult.

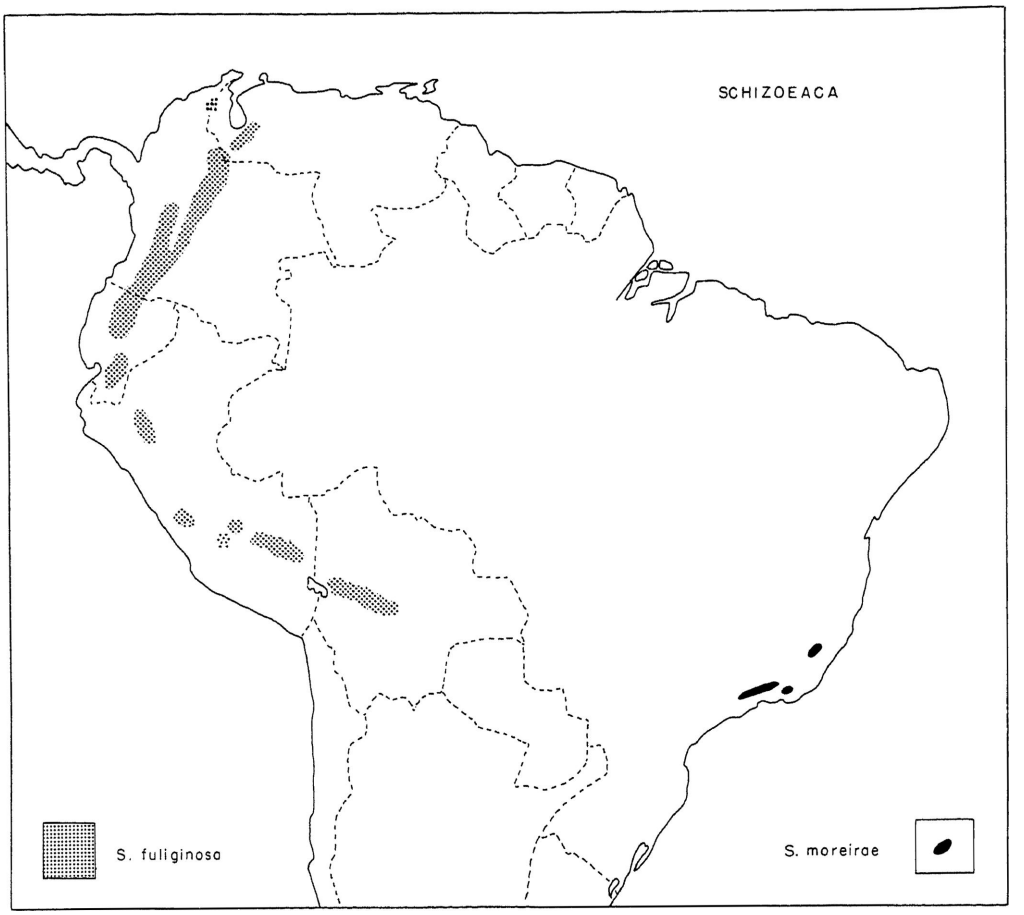
RANGE: Interrupted, and apparently restricted to the páramos of the Santa Marta Massif, Andes of Trujillo and Mérida in Venezuela, Eastern and Central Andes of Colombia, Andes of Ecuador, and the puna of Peru from Ancash south to the region above La Paz in Bolivia. The altitudinal range recorded varies between about 2600 and 4600 m. in the Santa Marta Massif, about 3000 to 4500 m. in Venezuela,[54] about 3400 to 4000 m. in the Andes of Colombia, about 3500 to 5200 m. in Ecuador, and about 4100 to 4700 m. in Peru; in Bolivia, the species was collected at roughly 4600 m., northeast of the city of La Paz.

SPECIMENS EXAMINED: 103, including the type of *andicola* in BM.

Leptasthenura setaria
Figure 2

DESCRIPTION: Bright chestnut on the back, which is uniform, and black on the crown which is streaked with very sharply defined whitish shaft streaks. Underparts dingy ochraceous buff below the whitish throat and upper breast, becoming more or less suffused with pale umber or pale grayish brown on the flanks, the whitish throat and upper breast being freckled or irregularly spotted with blackish brown. Rufous area of the wing very restricted, but inner remiges broadly edged with bright chestnut on the outer web. Tail very strongly rufous, but dark brown, or fuscous, to a varying degree on the inner webs and basal portion of the three inner pairs of rectrices. Tail very deeply "forked," with the central rectrices emarginated over a long distance, but the end of the feather is merely narrowed gradually to a great degree and the apex is rounded, not acute.

IMMATURE PLUMAGE: Similar to the adult,



MAP 7. Geographical distribution of *Schizoeaca*.

but pattern less distinct and with virtually no streaks on the crown which is more brownish, less black than in the adult.

RANGE: Southeastern Brazil, from northern, central, and eastern Paraná, south to northern and eastern Rio Grande do Sul, and also to Misiones in Argentina.

SPECIMENS EXAMINED: 50, including the type of *setaria* in MNHN.

GENUS *SCHIZOEACA*

This genus is composed of only two species[55] and seems related to both *Leptasthenura* and *Synallaxis*, occupying a position roughly intermediate between them. The two species are montane birds with interrupted distributions (map 7) and are *S. fuliginosa* in the Andes from western Venezulea to Bolivia, and *S. moreirae* which is restricted to the few high mountains of southeastern Brazil.

Schizoeaca fuliginosa is not well known and its populations were divided into six "species" before my revision (1971a), but, in the years 1967–1970, Weske and Terborgh discovered two new populations in Peru in the mountain ranges east and west of the Apurimac Valley in the Departments of Cuzco and Ayacucho, which we have described jointly (Vaurie et al., 1972) and named *vilcabambae* and *ayacuchensis*. It is evident that *vilcabambae* differs from the six older

forms to about the same degree as these differ from one another, and that *ayacuchensis* appears to be a link between *vilcabambae* and one of the older forms (*palpebralis*). The nine forms now known, linked from north to south, with the dates when they were described, are: *perijana,* 1977; *coryi,* 1888; *fuliginosa,* 1843; *griseomurina,* 1882; *palpebralis,* 1873; *vilcabambae,* 1972; *ayacuchensis,* 1972; *helleri,* 1923; and *harterti,* 1901.

As most of these forms are known from few specimens and three are new, a synthesis of the entire group, which I consider to be conspecific, is given below. My opinion that they are conspecific is based on their morphology, distribution, and ecology. All the forms (with the exception of *ayacuchensis*) differ morphologically only by various combinations of the same characters developed to a greater or lesser degree. All nine replace one another geographically, their ranges being more or less widely interrupted by ecologically unsuitable gaps. Ecological information is very deficient, but, as far as known, the ecological requirements of the populations probably do not differ essentially as they inhabit wet areas on the páramos, or an intermediate zone above timber line or above true montane forest, at altitudes which vary roughly from 3000 m. or somewhat less, to about 4000 m. The recognition of subspecies in *S. fuliginosa* is a matter of opinion and convenience.

Geographical Variation

The population of the Andes of Venezuela (*coryi*) is rufous "earthy" brown above and on the tail, has no eye-ring, and has a rufous, hazel patch on the chin and upper throat, the base of the feathers being dusky or blackish on the throat. This population has also a dark hazel or russet superciliary streak which broadens out greatly behind the eye, but is not sharply defined. The range of *coryi* extends from Trujillo to Táchira, but south of the deep river valleys of southern Táchira which interrupt the range of the species, *coryi* is replaced by nominate *fuliginosa* on the páramos on the border of Colombia.

The population from the Sierra de Perijá (*perijana*) is olive brown above (no chestnut or rufescent tinge), has a rufous chin patch, has the throat and breast brownish gray, the abdomen grayish white, and conspicuous gray superciliary streaks.[56]

Nominate *fuliginosa* is distinctly more rufous brown above and on the tail than *coryi,* less earthy, has a narrow white eye-ring, and is white or whitish, not rufous, on the chin and upper throat. Its superciliary streak is gray and rather poorly defined. The range of nominate *fuliginosa* is much more extensive than that of the other forms, extending from the border of southern Táchira (see above) south to central Ecuador, with an isolated population in Amazonas in northern Peru. Two attempts have been made to separate "subspecies" within this range, but the forms named were based on individual variants or slight inconstant differences; see also Carriker (1933) who found that the birds of Peru are not distinct.

Nominate *fuliginosa* is replaced by *griseomurina* in southern Ecuador from Azuay to Loja, *griseomurina* differing from nominate *fuliginosa* only by being olive brown above and on the tail, rather than rufous brown. The diagnosis of *griseomurina* given by Hellmayr (1925) is misleading as it was based only on one specimen which, I find, is somewhat abnormal.

The population found in Amazonas, northern Peru, is indistinguishable from nominate *fuliginosa,* as stated above, but, in central Peru, nominate *fuliginosa* is replaced by three quite distinct populations, *palpebralis, vilcabambae,* and *ayacuchensis* with ranges which appear to be very restricted. The form *palpebralis* is known only from central Junín where it has been collected at Maraynioc and near Comas, about 60 m. southeast of Maraynioc. The form *palpebralis* resembles nominate *fuliginosa* by being rufous brown above and on the tail, and by having a white eye-ring, but the eye-ring is more conspicuous in *palpebralis,* measuring about 2 mm. in width, as against only 1 mm. or less in nominate *fuliginosa.* But, on the other hand, the patch on the chin and throat of *palpebralis* is hazel (as in *coryi*), not white as in

TABLE 7
Character Variation of *Schizoeaca fuliginosa*

Subspecies	General size	General coloration of upperparts	Eye-ring	Superciliary streak	Chin and upper throat	Underparts
perijana[a]	large	olive brown	[b]	gray	rufous	variable
coryi	small	rufous brown	0	rufous	rufous	uniform
nom. *fuliginosa*	large	rufous brown	+	gray	white	variable
griseomurina	large	olive brown	+	gray	white	uniform
palpebralis	large	rufous brown	+	rufous	rufous	squamated
vilcabambae	large	olive brown	0	grayish	rufous	squamated
ayacuchensis	large	olive brown	[c]	[c]	rufous	squamated
helleri	medium	rufous brown	+	gray	rufous	uniform
harterti	small	olivaceous	+	buffy	white/black	uniform

[a]Data added by F.V., based on his examination of the type specimen at AMNH and on Phelps (1977a).
[b]In *perijana* a few white spots exist on the lower "lid."
[c]In *ayacuchensis* a few tiny white spots exist on the lids of some specimens, but none in the others; no superciliary streak exists, or only an extremely faint grayish trace of it in some individuals.

nominate *fuliginosa* and *griseomurina*; and the superciliary streak of *palpebralis* is hazel also (as in *coryi*), but much more reduced and has virtually vanished in some individuals, whereas it is exceedingly broad posteriorly in *coryi*.

The coloration of the underparts varies individually in *palpebralis*, but it is less uniform than in the four forms considered so far. In *palpebralis*, the edges of the feathers of the breast and upper abdomen are dull white and contrast with the gray centers, thus producing a somewhat "squamated" appearance better defined in some individuals than others. This squamation exists also in *ayacuchensis* and *vilcabambae* (see below), and in a small minority of the specimens of nominate *fuliginosa* that I have seen, but less distinct than in *palpebralis*.

The population (*vilcabambae*) discovered by Weske and Terborgh, at about 73° 30′ W. long. by about 12° 36′ S. lat., east of the Apurimac Valley at the northern end of the Cordillera of Vilcabamba, Cuzco, is distinguished from all the other populations of the species by a combination of characters which is confusing and difficult to describe briefly, but which is summarized above in table 7. The most salient characters of *vilcabambae* are that its plumage is well squamated on the breast and abdomen, more distinctly so than in any other populations, from which it differs also by being more ochraceous buff on the lower throat, less grayish below the gular patch; the lack of an eye-ring (resembling *coryi* in this respect); and the color of its upperparts which are olive brown (resembling *griseomurina* in this respect), not rufous brown as in *coryi*, nominate *fuliginosa*, and *palpebralis*.

The other population (*ayacuchensis*) was discovered by Weske and Terborgh in 1968 northeast of Tambo, Ayacucho, where, together with J. P. O'Neill, they collected additional specimens in 1970. This locality is not very far removed from the locality where Weske and Terborgh discovered *vilcabambae*, but is situated west of the Apurimac Valley, not east of it where *vilcabambae* was discovered. The throat of *ayacuchensis* is darker rufous, more richly colored than in any other populations, and the gular patch is far more conspicuous, but, with this exception, *ayacuchensis* is more similar to *vilcabambae* than to any other subspecies. However, the squamation on the breast and abdomen of *ayacuchensis* is less well defined than in *vilcabambae*, and a few tiny white feathers exist around the eyelid in some individuals. The degree of squamation

TABLE 8
Measurements (in Millimeters) of Adult Males in *Schizoeaca fuliginosa*

Subspecies	Wing			Tail			Bill		
	N	Mean	Range	N	Mean	Range	N	Mean	Range
perijana[a]	4	61	60–62	4	115	113–120	4	13.2	12.8–13.5[b]
coryi	14	57.86	55–61	9	87.36	84–95	14	16.28	15–17
nom. *fuliginosa*	15	63.77	59–70	13	103.69	93–116	14	16.51	15–18
griseomurina	4	61.25	59–64	4	103.50	97–112	4	16.37	16–17
palpebralis	4	62.63	61–63.5	3	112.33	105–117	4	17.37	17–18
vilcabambae	6	65.33	64–67	6	102.00	95–106	6	17.25	16.5–18
ayacuchensis	5	62.60	60–66	5	109.00	100–115	5	18.30	17.5–18.5
helleri	1	—	59	1	—	105	1	—	17.0
harterti	10	54.60	52–57	9	92.66	84–99	10	16.40	16–17

[a]Data added by F.V., based on measurements of 4 adult males (in Phelps, 1977a).

[b]Bill measured was "exposed culmen" (Phelps, 1977a, p. 49), which may explain the large difference in bill length between *perijana* and other subspecies (F.V.).

is similar in *ayacuchensis* and *palpebralis*, and the existence of some white feathers (which are totally lacking in *vilcabambae*), suggest some approach between *ayacuchensis* and *palpebralis*, although *ayacuchensis* is not truly intermediate between *palpebralis* and *vilcabambae* and all three subspecies are probably well isolated geographically from one another.

The populations (*helleri*) which replace *vilcabambae* and *ayacuchensis* farther south in Peru, from the southern end of the Cordillera of Vilcabamba south to the cordilleras of Vilcanota and Carabaya are distinguished by being rufous brown above and on the tail, pale hazel on the chin, and by having an indistinct white eye-ring, and a gray superciliary streak. The eye-ring of *helleri* is very dull and faint, reduced to an even greater degree than in nominate *fuliginosa* where it is quite narrow and not very conspicuous as a rule. In *helleri*, the rufous gular patch is restricted almost completely to the chin and the feathers below it are chiefly blackish.

The southernmost populations of the species are placed in *harterti*, which replaces *helleri* in Bolivia in the cordilleras of La Paz and Cochabamba. The chin of *harterti* is white and the center of its upper throat is chiefly black or blackish, although a rufous area exists at the sides of the upper throat and spreads onto the sides of the neck. The form *harterti* has a quite distinct eye-ring, though less conspicuous than in *palpebralis*, and also a very distinct superciliary streak which is buffy, becoming more rufous posteriorly, but not white as stated by Hellmayr. The upperparts of *harterti* are olivaceous, not rufous, but more brownish, less olive brown, than in *griseomurina*, *vilcabambae*, and *ayacuchensis*, and its underparts are uniform, not squamated.

All the populations are comparable in size, with the exception of *coryi* and *harterti* which have a quite appreciably shorter tail, a somewhat shorter wing, and in which the bill is also short, but similar in size to that of other subspecies. The measurements of adult males, of which I have seen a larger and more representative series, are given in table 8.

The confusing combination of characters is shown in tabular form (table 7) in an attempt to describe it as clearly as possible. However, not all the character differences can be expressed in this manner when their variation is a question of degree; for instance, the relative saturation and hue of the plumage from rufous to olive, the degree of squamation, variation in the size of the eye-ring, variability in the distinctness and hue of the superciliary streak, and variation in

saturation and size of the patch on the chin and upper throat.

Very little information exists on the habitat and behavior of *Schizoeaca fuliginosa* other than that for *S. f. harterti,* the nest of which was found and described by Vuilleumier (1969). *Schizoeaca fuliginosa* is known, however, to frequent páramos with isolated shrubs and small thickets, or an intermediate zone above true montane forest. The habitat is apparently very wet, at least in Bolivia, and it has been collected also in the thickets of very humid "Elfin Forest" in the cordillera of Vilcabamba in Cuzco and in the cordilleras of Ayacucho in Peru. The habitat of *harterti* is described by Vuilleumier (1969) as "a mixture of wooded thickets and patches of grassland on steep slopes. The area is extremely wet. Trees and shrubs are covered with mosses and lichens, and the ground is like a soggy sponge."

The nest found by Vuilleumier was "lying on top of a clump of grass next to a thin shrub . . . [and] was an oval structure measuring 20 × 15 cm. It had a side entrance (but no lateral tunnel). It was made mostly of *Sphagnum* moss and to a lesser extent of twigs . . . . The inside cavity was lined entirely with soaking wet moss, upon which rested the two young."

Vuilleumier has also sent me the notes he made when observing *Schizoeaca fuliginosa coryi* in the Andes of Mérida. He wrote "Seen in the shrubs at the edge of *Polylepis* woodland (mixture of Composite shrubs and *Espeletia*), and within the *Polylepis* woodland. The bird moves about in the bushes calling frequently: *vihi* or *tih*. The call notes sound a little like the calls heard from *Oreophylax* [i.e., *Schizoeaca moreirae,* see below]."[57]

Schizoeaca moreirae is restricted to the few high mountains of southeastern Brazil, occurring in the Itatiaia Range and probably elsewhere in the Serra da Mantiqueira on the boundary of the states of São Paulo, Minas Gerais, and Rio de Janeiro, in the Serra dos Orgãos north of Rio de Janeiro, and in the Serra do Caparão on the boundary of Minas Gerais and Espirito Santo. These mountains rise to slightly over 2000 m. in the Itatiaia, about 2300 m. in the Serra dos Orgãos, and to nearly 2900 m. in the Serra do Caparão, where *S. moreirae* frequents the zone above timber line in grassy areas interspersed with bushes and thickets. This species has been observed by Holt (1928), Sick (1970) who discovered and described its nest, and by Vuilleumier who sent me his field notes. *Schizoeaca moreirae* does not vary geographically.

Phylogeny

The systematic position of *Schizoeaca moreirae* was considered doubtful until I concluded (1971a) that it is congeneric and related to *S. fuliginosa*. Before that, the species *moreirae* had been segregated in a monotypic genus for which Hellmayr (1925) had proposed the name *Oreophylax*.

The relationship of *Oreophylax moreirae* to *Schizoeaca fuliginosa* is very strongly suggested by the fact that *S. moreirae* appears to be clearly of Andean origin (a belief stressed also by Sick), resembles *S. fuliginosa* morphologically, ecologically, and in some aspects of behavior, including the location and structure of the nest which seems to me to be very similar, if not identical, to the nest of *S. f. harteri* described above by Vuilleumier. This similarity is emphasized by Sick who says it is striking ("*auffalend nahe kommt*") although he was not directly acquainted with the nest of *S. f. harterti,* but which he knew from Vuilleumier's account (1969) and discussions with him.

The vocalizations of *Schizoeaca moreirae* apparently differ from those of *S. fuliginosa*. Sick was not acquainted with any form of the latter, but wrote that the vocalizations of *S. moreirae* resemble those of some *Asthenes* [=*Thripophaga*], *Leptasthenura,* and *Cranioleuca* [=*Certhiaxis*]; and Vuilleumier has written to me that "The songs of *Asthenes* and *Oreophylax* [i.e., *S. moreirae*] appeared (to me) much alike, whereas the call notes of *Oreophylax* appeared, again to me, more like those of *Schizoeaca coryi.*" However, these observations are ambiguous because the ex-

istence of strong differences in vocalizations does not necessarily contradict generic relationship, as demonstrated by Vaurie and Schwartz (1972) in a spectrographic analysis of the vocalizations of related species of *Synallaxis*. The vocalizations of *Schizoeaca fuliginosa* and *S. moreirae* have not been analyzed in similar fashion as they do not seem to have been recorded so far.[58]

The location and structure of the nest can also be quite different within the same genus (as will be discussed later in *Certhiaxis*), but the nest is nevertheless one of the most conservative taxonomic characters for the family as a whole. The fact that the nest is so extremely similar in both *Schizoeaca moreirae* and *S. fuliginosa* is certainly suggestive of close relationship and much similarity exists also in morphological characters.

Morphological Variation

Both *Schizoeaca fuliginosa* and *S. moreirae* are small species of virtually the same size (table 9) with a very long, well stiffened, and strongly graduated tail composed of 10 rectrices, the webs of which are loosely integrated. The proportions are also virtually identical, as the extent to which the length of the tail exceeds that of the wing (or the ratio) is 1.67 in *S. fuliginosa* and 1.70 in *S. moreirae*. However, the webs of the rectrices are broader in *S. moreirae*, better integrated, and the terminal portion of the tail is less stiffened, and the rectrices much less attenuated, whereas the webs are usually more or less decomposed in *S. fuliginosa*. But these differences are hardly of generic importance and are far exceeded in other related genera, such as *Synallaxis*. All the other morphological differences between the two species are very slight and in *S. moreirae* we find again a hazel gular patch with blackish bases to its feathers, a whitish chin, and a narrow white eye-ring. The eye-ring of *S. moreirae* is found only in a minority of adult specimens, but it does not exist in all the forms of *S. fuliginosa*, nor in all the individuals of its forms which have one. The eye-ring of *S. moreirae* is dull and faint when present, but developed to exactly the same degree as in *S. f. helleri* in which it is less conspicuous than in the other forms of *S. fuliginosa* with an eye-ring. The immature plumages of *S. fuliginosa* and of *S. moreirae* are very similar.[59]

KEY TO THE SPECIES OF *SCHIZOEACA*

Rectrices broader (attaining a width of about 9 mm.), and relatively well integrated as a rule; restricted to the high mountains of southeastern Brazil ..... *moreirae*

Rectrices narrower (attaining a width of about 6 mm.), and more or less decomposed as a rule; restricted to the Andes from western Venezuela to Bolivia ..... *fuliginosa*

List of the Species

Schizoeaca fuliginosa

Figure 3

Description: The upperparts and tail vary from rufous brown to olive brown, with the crown uniform, or paler, more rufous on the forehead. A superciliary streak exists in all the populations but is not sharply defined and varies from gray to dark rufous or hazel, is very faint in some populations, but in *Schizoeaca coryi* of Venezuela, where the streak is russet, broadens out behind the eye to merge into the russet sides of the face and neck. A white or dull white eye-ring exists in most populations (see table 7), varying in width from about 2 mm. to 1 or less. The chin and upper throat are white or whitish, or vary from strongly rufous to hazel, the base of the feathers at the lower border of the rufous area being dusky or blackish to a varying extent, the blackish area replacing the rufous pigment to a great degree in some populations, or completely so in *S. f. harterti* of Bolivia. The underparts below the upper throat are buffy or dingy gray, becoming brownish on the flanks, the breast and upper abdomen being uniform, or more or less distinctly squamated in individuals or populations where the edges of the feathers are dull white and contrast with the darker, grayish center of the feathers. The long tail is strongly graduated and well stiffened, with the

TABLE 9
Measurements (in Millimeters) of *Schizoeaca*

Species	Wing			Tail			Bill		
	N	Mean	Range	N	Mean	Range	N	Mean	Range
fuliginosa									
Males	60	60.58	52–70	52	99.69	84–117	59	16.72	15–18.50
Females	34	59.63	53–65	28	98.64	81–113	32	16.69	15–18
Both sexes	101	60.40	52–70	84	99.50	81–117	98	16.68	15–18.50
moreirae									
Males	20	62.80	61–65	20	107.05	102–115	19	18.28	17–19
Females	7	60.78	58–62	7	103.00	95–113	6	17.33	17–18
Both sexes	29	62.43	58–65	28	106.14	95–115	27	18.10	17–19

webs of the rectrices narrow and not well integrated, more or less decomposed as a rule to a degree which becomes greatly pronounced in some individuals; but when fresh, or relatively so, the inner rectrices are strongly attenuated over a long distance and taper to an acute tip.

IMMATURE PLUMAGE: Similar to that of the adult, but more or less distinctly and narrowly barred on the breast and upper abdomen, the tips of the feathers contrasting by being dark brown, and facial and throat pattern less distinct.

RANGE: Andes, from western Venezuela to Bolivia, between about 3000 and 4000 m., with very few exceptions, but has been collected also at roughly 2500 in Bolivia and 4300 in Peru. The range is interrupted (map 7) and extends from Perijá, and Trujillo to Táchira in Venezuela, and south through the Eastern and Central Andes of Colombia to Nariño and Ecuador; in Peru, populations are known from Amazonas, Junín, northern Ayacucho, Cuzco, and Puno, and, in Bolivia, the range appears to be restricted to the cordilleras of La Paz and Cochabamba.

SPECIMENS EXAMINED: 123, including the types of *griseomurina* in BM, and of *helleri, vilcabambae,* and *ayacuchensis* in AMNH.

Schizoeaca moreirae
Figure 3

DESCRIPTION: Dull olive brown above and on the tail, with the crown and back uniform, or with the crown slightly darker, with a very faint and indistinct dark buff superciliary streak, and, in a small number of individuals, a narrow and dull, faint white or buffy eyering. Chin dull white or buffy white, with the upper throat strongly rufous or dull hazel, the base of the feathers at the lower border of the rufous area being dusky or blackish. Underparts below the throat are grayish buff, paler on the abdomen, and darker on the flanks which are brownish. Tail with broader better integrated webs than in *Schizoeaca fuliginosa,* and with the inner rectrices less attenuated.

IMMATURE PLUMAGE: Similar to that of the adult, but more or less distinctly and narrowly barred with brown on the breast.

RANGE: Mountains of southeastern Brazil, between about 2000 and 2800 m., in the Serra da Mantiqueira in which it is quite common in the Itatiáia Range, but very probably occurs elsewhere, Serra dos Orgãos north of Rio de Janeiro, and Serra do Caparão on the border of Minas Gerais and Espirito Santo.

SPECIMENS EXAMINED: 37.

GENUS *SYNALLAXIS*

Synallaxis with 37 species is the largest and the most widely distributed genus of the Furnariidae. It ranges (map 8) from southern Mexico to central Argentina, but does not occur west of the Andes south of northwestern Peru. In this region, the range of the genus extends south to the northern part of the

MAP 8. General distribution of *Synallaxis* with the distribution of the subgenus *Schoeniophylax* (*S. phryganophila*); the isolated record in western Peru is *Synallaxis zimmeri*.

Department of La Libertad, but an isolated species (*S. zimmeri*), which is barely known and has apparently a very small range, is restricted to the western slope of the Andes in central Ancash, south of La Libertad.

Synallaxis can be divided into two subgenera, the monotypic *Schoeniophylax,* and *Synallaxis* with 36 species.

SUBGENUS *SCHOENIOPHYLAX*

Synallaxis phryganophila "stands quite by itself"—at least morphologically—as Sclater (1874) remarked in his review of *Synallaxis* and, for this reason, seems more conveniently placed in a subgenus of its own. *Schoeniophylax phryganophila* differs from the 36 other species by being heavily streaked on the back, by being bright sulphur yellow on the upper half of its gular patch, and by having a longer, more strongly graduated tail, with narrower rectrices, than the other 36 species.

However, the structure of the tail is clearly not of generic importance because it varies so very much specifically in *Synallaxis* as shown below, and the only characters of *S. phryganophila* that are not met in the other species are its streaked back and the yellow pigment on its upper throat which, however, does not exist in the immature plumage. The mantle is uniform, not streaked, in the other 36 species, and no trace of yellow exists in any of their plumages.

Distribution, ecology, and general behavior, including the structure of the nest, do not offer characters that permit any degree of generic separation as no essential differences exist between *S. phryganophila* and the other species.

Synallaxis phryganophila is sympatric with several other species, such as *S. albes-*

cens and *S. frontalis* in the Chaco and no important ecological differences seem to exist between the three species although each species probably prefers slightly different types of habitat. For instance, the streaked back of *S. phryganophila* suggests that this species is better adapted to open grasslands. In some regions *S. phryganophila* appears to be more closely associated with swamps and marshes than the other two species, especially where tall saw-grass and bunch grass are interspersed with low bushes. However, *S. albescens* is also said to be abundant in bunch or saw-grass, and the main requirements of the three species are steppes, savannas, or other open areas and sites with dense growth of weeds, shrubs, thickets, and scattered trees.

The nest of *S. phryganophila* is a typical bulky *Synallaxis* nest, consisting of interwoven slender twigs and sticks, thatched over, having a very characteristic lateral tubular entrance, and lined chiefly with soft plant material. Naumburg (1930) has given a description of the nests observed by Cherrie and a photograph of one of them. The nest of *S. phryganophila* seems to be very similar to that of *S. frontalis* and also of *S. erythrothorax* from southern Mexico; also of *S. albescens,* but more massive. The photograph published by Naumburg shows a nest built horizontally in the terminal branches of a tree with thin foliage, probably not very far above the ground, although its height is not mentioned. But Cherrie noted that in the region of Puerto Piñasco in Paraguay "probably more nests are found between the leaf stems, up close to the body of the tree, of the cabbage palm, than in any other locality," after stating that "all sorts of places are chosen as nesting-sites," apparently elsewhere. Cherrie did not mention that thorny twigs were used in the construction of the nest of *S. phryganophila,* but Venturi (in Hartert and Venturi, 1909) did; as a rule, thorny twigs are especially favored by *Synallaxis* when available.

In short, the streaked back of *S. phryganophila,* and the existence of yellow pigment (a rare character in the Furnariidae) in its adult plumage, sets this species apart. But this distinction alone does not seem to me to warrant full generic separation, although it is probably best acknowledged by the recognition of a separate subgenus.

Synallaxis (Schoeniophylax) phryganophila
Figure 3

DESCRIPTION: Top and hind part of the crown bright reddish chestnut, with a broad band of brown on the forehead, very rarely uniform, as the top of the head is more or less abundantly and sharply streaked with narrow, dark brown or blackish shaft streaks extending to the nape. Back pale tawny fulvous brown, very heavily and broadly streaked with blackish streaks extending from the hind neck onto the mantle, but not to the rump which is uniform. Lores and very distinct superciliary streak whitish; auriculars brown. Upper half of the center of the throat bright sulphur yellow, but lower half pure black, the yellow and black areas separated by a band of white from the brown auriculars and sides of the lower neck, the white band broadening greatly posteriorly to form a roughly triangular white patch at the sides of the lower throat. Underparts ferruginous or cinnamon rufous on the breast below the black gular patch, becoming whitish on the center of the abdomen, and washed with ochraceous buff of the flanks.

Lesser and middle upper wing coverts bright reddish chestnut; greater coverts, primaries, and secondaries chiefly dark brown, but bordered to a varying degree with pale cinnamon along the edge of the inner webs of the secondaries and primaries; axillaries and under wing coverts fulvous white. Tail, composed of 10 rectrices, very long and strongly graduated, with relatively narrow webs becoming acute or subacute at the apex; grayish brown above with dark shaft streaks. The great length of the tail, and the strong degree of graduation, are contributed chiefly by the central pair of rectrices which are abnormally elongated, and separate to form a very deep "fork" when not disturbed. Mean tail length 117 mm. representing pro-

portionally 189 percent of the length of the wing. Bill moderately strong and straight; blackish, or pale on the distal half of the mandible.

IMMATURE PLUMAGE: Quite distinct from the adult, with the color pattern much less defined, and the tail characters undeveloped; the rectrices are broader than in the adult, rounded at the tips, and much less graduated, the central rectrices being only slightly longer than the next pair, not elongated. The crown is brown, not reddish, and its streaking is blurred, indistinct, and the streaks are also much less sharply defined on the back. The upper half of the gular patch is whitish, not yellow, and the black area of the lower half is very indistinct, much obscured by the tips of the feathers which are whitish.

RANGE: Eastern Bolivia, south of about 14° S. in the Beni, and neighboring Brazil (Mato Grosso), south through Paraguay, Uruguay (and neighboring Rio Grande do Sul in Brazil, and northern Argentina to the region of Buenos Aires, west to eastern Salta and eastern Santiago del Estero; apparently not Misiones. Also eastern Brazil in the valley of the Rio São Francisco, from Pirapora in Minas Gerais, north to Bahia.

The population of the valley of the Rio São Francisco may average paler and less heavily streaked on the back. It has been separated as a subspecies, but a specimen I have seen from Bahia falls within the range of individual variation of the other populations, and, in any event, a population difference of this kind does not warrant nomenclatural recognition in my opinion.

SPECIMENS EXAMINED: 217, including the type of "*tecellata*" in MNHN.

SUBGENUS *SYNALLAXIS*

The 36 species of the subgenus *Synallaxis* are distributed from southern Mexico to central Argentina, chiefly in lowlands, but some reach a fair elevation and about one-third are montane or ascend to high or relatively high elevations.

The species which ascend from the lowlands, and sometimes the coast, to fair elevations, are *S. moesta* and *S. cabanisi* which ascend to about 1400 m.; *S. maranonica,* from the valley of the Marañon to over 1500 m.; and *S. candei,* from the coast to roughly 1000 m. in Venezuela. Other lowland species ascend higher still; they are *S. spixi* to about 2000 m., *S. macconnelli* to about 1900 m., *S. cinnamomea* and *S. scutata* to roughly 1700 m., *S. brachyura* to about 2100 m., *S. frontalis* to about 2300 m., and *S. albescens* to 2500 m. or more.

The following five species can be called montane, as their ranges follow the Andes: *Synallaxis superciliosa* ascending from about 600 to 2900 m.; *S. azarae* from about 1250 to 3750 m.; *S. elegantior* from about 1100 to 3800 m.; *S. unirufa* from about 1000 or 1200 to 3700 m.; and *S. gularis* from about 1300 to 4000 m. The following montane species have restricted ranges: *S. subpudica,* to the Eastern Andes of Colombia where it has been collected between 2600 and nearly 3000 m.; *S. courseni,* discovered very recently, known only from a single region in the Andes of Apurimac, Peru, where it occurs between about 2450 and 3400 m.; *S. zimmeri,* known only from two small valleys on the western slopes of the Andes in central Ancash, Peru, at altitudes between 1900 and 3000 m.; *S. castanea,* restricted to the Coastal Cordillera of Venezuela between 1300 and 2200 m.; and *S. fuscorufa,* found only in the Santa Marta Massif of northern Colombia from 760 to about 2750 m.

The extent of the range of some species is badly known but is apparently very restricted in some cases, whereas it is unusually widespread in some species, and is enormous in the case of *Synallaxis albescens* which is distributed (map 10) from Costa Rica, Colombia, Venezuela, and the Guianas, south through Brazil, eastern Bolivia, and Paraguay, to central Argentina. Other species with great ranges are *S. frontalis, S. gujanensis, S. rutilans,* and *S. scutata*; the range of *S. brachyura* is also very extensive, from Honduras south to Colombia and Ecuador. The range of *S. cherriei* can be mentioned as an instance of a poorly known range; this range seems quite extensive (map

14) but this species is known from little more than a dozen specimens. *S. hypospodia* is in the same category as *S. cherriei,* although *S. hypospodia* is known from more specimens, which, however, have been taken at very widely separated localities over a very great range (map 11).

In contrast to species with extensive ranges, *Synallaxis courseni* and *S. zimmeri,* which were mentioned above, are known from only one or two localities and three specimens each. These two species must be very local as they were discovered in regions which had been far from neglected, and only in 1956 in the case of *S. zimmeri,* and 1968 in the case of *S. courseni.* Other species with very restricted ranges are *S. infuscata,* known from only six or seven specimens from eastern Pernambuco and neighboring Alagoas in Brazil; *S. kollari* from very few specimens taken on the upper Rio Branco and some of its small affluents in Brazil; *S. maranonica* from a small region in and near the valley of the Marañon in Cajamarca and Amazonas in Peru; *S. subpudica* from a small region of the Eastern Andes of Colombia; *S. fuscorufa* restricted to the Santa Marta Massif of Colombia; and *S. castanea* in the Coastal Cordillera of Venezuela from only Aragua to Miranda and the Distrito Federal. The range of *S. tithys* is also small, extending from southwestern Ecuador only to neighboring Tumbes and northern Piura in Peru.

Information is also very deficient on ecology and behavior, including the structure and location of the nest. The nest of only 15 of the 36 species is known, but a good or adequate knowledge of the nest and ecology exists for only eight species: *Synallaxis frontalis, S. albigularis, S. albescens, S. spixi, S. brachyura, S. gujanensis, S. erythrothorax,* and *S. cinnamomea.* The reports on *S. albescens, S. brachyura,* and *S. erythrothorax* published by Skutch (1969b) are the most detailed and noteworthy which exist for any species. The other seven species are *S. ruficapilla, S. superciliosa, S. azarae, S. elegantior, S. albilora, S. rutilans,* and *S. stictothorax,* but in *S. albilora* the information consists only of two photographs of the external structure of the nest that are rather old and not very instructive.

The 21 species for which the nest is not known, or has not been reported to the best of my knowledge (with one possible exception in the case of *Synallaxis candei* which is discussed below), are as follows, with a mention of all that seems to be known of their habitat, when reported: *S. infuscata* ("capoeiras"), *S. hypospodia, S. courseni* (very dense low tangles of thorns and briars in mixed open cloud forest with much moss), *S. moesta* (scrub), *S. cabanisi, S. macconnelli, S. subpudica* (forest undergrowth), *S. tithys* (dense thickets and tangles of vines and creepers), *S. cinerascens* (forest undergrowth), *S. maranonica* (large and dense thickets much invaded by vines situated near water), *S. propinqua, S. hellmayri, S. cherriei* (thick undergrowth in forest and savanna), *S. unirufa* (forest undergrowth), *S. castanea*[60] (dense brush and thickets of bamboo), *S. fuscorufa* (open areas with bushes, shrubs, and tangled thickets), *S. zimmeri* (steppe with dense thickets with low scattered trees, some of them evergreen), *S. candei* (waste land, weed grown pastures with shrubs, thorn scrub, cacti, and outer fringes of mangroves), *S. kollari, S. scutata* (forest undergrowth, "cerradão"), and *S. gularis* (forest undergrowth).

The information that *Synallaxis courseni* frequents tangles in mixed cloud forest was supplied to me by Peter Hocking, the collector who discovered this rare species (described by Blake, 1971). The statement that a number of these 21 species inhabit "forest undergrowth" was obtained from Meyer de Schauensee (1970); to these, *S. cabanisi* can possibly be added because Meyer de Schauensee states also that *S. cabanisi* inhabits "forest undergrowth," but this is not certain as the form he refers to under this name is a composite of two species, *S. cabanisi* and *S. macconnelli.*

I doubt, however, that any *Synallaxis* is a bird of true unbroken forest and believe that species which occur in the forest probably frequent only thickets along streams,

paths, cuts, clearings or other open sites, but not tracts where the forest is shady and compact.

The three species for which the most complete ecological information exists are *Synallaxis albescens, S. brachyura,* and *S. erythrothorax* which, probably, give a good measure of the normal requirements of *Synallaxis*. Dickey and van Rossem (1938) stated that *S. erythrothorax* is "strictly a resident of the undergrowth, either beneath forest or in the dense scrub bordering clearings, and seems never to be found in regions where little or no woods are left."

It is possible that *Synallaxis erythrothorax* frequents, at times, a more "wooded" habitat than *S. brachyura* does, but the detailed reports of Skutch (1969b) suggest that no essential difference exists in the ecology of the two birds as the habitat of *S. erythrothorax* is characterized by Skutch as "low, dense second-growth," and that of *S. brachyura* as "low, dense, secondary vegetation." I have also observed *S. erythrothorax* at the nest in southern Veracruz, Mexico, finding it in a garden with bushes and low trees on the shores of Lake Catemaco that was far from forest, in a region where the forest had probably been destroyed many generations ago.

The habitat of *Synallaxis brachyura* and of *S. albescens* seems characteristic of many other species and is described by Skutch as follows, the vegetation frequented by *S. brachyura* being denser as a rule than in the case of *S. albescens*. Skutch stated that *S. brachyura* "is most at home in vegetation that is low but dense. It becomes abundant in grain fields that have rested a year or two and are encumbered with bushes and vines that form a head-high tangle, through which a man can hardly force his way. As the second-growth develops a higher and denser canopy of foliage, resulting in a sparser stand of herbage on the more deeply shaded ground, the castlebuilders [*S. brachyura*] desert it in favor of newer and lower growth. They frequent neglected pasture lands where the grass and weeds are dense and high, but they are absent from clean, close-cropped pastures, whether they are shady or open to the sunlight. In more intensively cultivated districts, they are confined to bushy hedgerows and riverside thickets. They never enter the forest."

The habitat of *Synallaxis albescens* is "bushy neglected pastures, 'savannas' with coarse grass interspersed with scattered low trees and clumps of shrubs, fields covered with low weedy growth, and similar areas. [*S. albescens*] avoids the higher, denser, vine-entangled second-growth thickets which [*S. brachyura*] prefers, but the habitats of these related species overlap and I have found both together" (Skutch, 1969).

Synallaxis albescens and *S. brachyura* range south to Colombia, or farther where they inhabit regions that are much more arid than those where they are normally found in Central America. For instance, *S. albescens* is "fairly common" in shrubs and weeds on the salt flats along the lower reaches of the Rio Hacha near the base of the very arid Guajira Peninsula, according to Carriker (in Todd and Carriker, 1922), and *S. brachyura* is "common in the thorn scrub at the edge of the arid western foothills" in the floor of the Cauca Valley below Yumbo, situated below Cali, according to Miller (1960). The range of *S. albescens* overlaps that of *S. candei* in Colombia and northwestern Venezuela, and Carriker says that *S. candei* frequents also the salt flats, as well as "thorny scrub and cacti in almost equal abundance" at the base of the Guajira Peninsula. *S. albescens* is found also in other arid regions of Colombia, such as the valley of the upper Magdalena in Huila, upper Dagua Valley in Valle, and upper Patía Valley in Cauca.

However, various species of *Synallaxis* inhabit a great variety of regions and the very widely distributed *S. albescens* is a good example. Savannas, or similar grassy areas, seem to be its preferred habitat in Central America, but in Colombia it is found also on salt flats and arid open regions, as stated above, as well as in humid, heavily forested regions, such as the lower valley of the Atrato, and the eastern foothills of the Eastern Andes in Meta. In these two humid regions, the annual rainfall varies between 2000 and

4000 m. according to Haffer (1967), but *S. albescens* seems to occur only along the rivers, or, probably, in sites where the forest has been destroyed.[61]

The information available on the behavior of *Synallaxis* has been concentrated almost entirely on the bird at its nest, but in postures or other behavior, *Synallaxis* has been compared to the wrens (Troglodytidae) or the wrentit (*Chamaea*), which it resembles roughly in general appearance and size and of which it is, more or less, the ecological counterpart.[62] However, *Synallaxis* is less furtive, more deliberate in its actions, and certainly more sluggish, especially when compared to the wrens. Some observers give the impression that *Synallaxis* is much given to hiding and skulking in tangled vegetation, but, although its habitat may make *Synallaxis* difficult to observe, it does not seem to be especially diffident or wary. For instance, Carriker comments that *S. fuscorufa* "is tame and easily approached," and Skutch says that *S. erythrothorax* "often permits" close approach when it occasionally forages in the open at the edge of thickets, close enough to distinguish its eye and fine details in its plumage.[63]

The observations of Skutch and my own indicate that *S. erythrothorax* is not at all wary at its nest. Skutch wrote that he has observed this species carrying sticks to its nest "in full view hardly more than an arm's length away," and has approached the nest by cutting his way "noisily through the brush" with a machete to "within a yard of the nest" without interrupting the birds engaged in constructing. I watched a nest for five consecutive days that was built in full view, about 3 m. above the ground in a small lime tree growing in a garden only 5 m. behind the bungalow that Mrs. Vaurie and I were occupying. The birds, when carrying sticks to the nest, paid no apparent attention to my presence, readjusting those that had been previously incorporated, or entering within the nest or leaving it, even when I watched them for part of the time perched on a step ladder at eye level with the entrance platform (see below), easily within my reach.

Synallaxis species feed by foraging low in the vegetation, or directly on the ground, hopping about, usually scratching or investigating plant debris when on the ground.

A study of the vocalizations of *S. unirufa* and *S. castanea*, with observations on those of other species, has been published by Vaurie and Schwartz (1972). Analysis of the bioacoustic evidence by means of spectrograms shows that important differences exist between the phrases of each species. Observations made by playing back recorded vocalizations in two pairs of species, *S. unirufa* and *S. castanea* in one, *S. azarae* and *S. elegantior* in another, show also that each of these species distinguishes between vocalizations readily and reacts normally only to those of its own species. Opportunity was taken also to discuss briefly the vocalizations of nine other species, illustrated by spectrograms of their typical "song" phrases; these nine species are *S. ruficapilla, S. albigularis, S. albescens, S. spixi, S. gujanensis, S. rutilans, S. erythrothorax, S. cinnamomea,* and *S. candei*. This study did not include *S. brachyura,* for lack of recordings, but in southwestern Costa Rica where this species occurs with *S. albescens,* the vocalizations of the two birds are said to be "completely different" by Slud (1964; see also Wetmore, 1972, for Panamá).[64]

The structure of the nest is known for only 14 of the 36 species but is so remarkably constant when known that it is probably essentially similar in all the species. The nest is composed of interlaced twigs, sticks, or sometimes weed stems and is roughly oblong in shape, consisting of two parts, the nest proper being enclosed in a chamber which is normally thatched over to shed the rain, and onto which is built a lateral extension through which an entrance tube or tunnel leads into the chamber; the nest is usually bulky but size and location vary.

Very good and detailed descriptions of the nests of *Synallaxis albescens, S. brachyura,* and *S. erythrothorax,* and of their construction, have been given by Skutch (1969b). The account given below is based on or adapted chiefly from his publication.

The nest of *Synallaxis erythrothorax* is

very bulky, built in a bush or small tree of interwoven twigs or small sticks that are often thorny, usually between 2 and 4 m. above the ground, although some may be somewhat lower and Skutch found one about 7 m. high. When built in a tree, a nearly horizontal branch with lateral twigs, or two or more branches that are nearly parallel and close together, are selected for support. The section in which the chamber is located is roughly globular in shape and reached through a long horizontal tube or tunnel which opens, externally, not at the end of the lateral extension, but above it onto a broad platform. Skutch stated that the entrance is not flush with the platform, but is raised above it, at the top of a "miniature tower" or "squat chimney," built of "usually thorny twigs, which are not only shorter but always much finer than the sticks used elsewhere in the structure."

The bottom of the nest chamber where the eggs are laid is lined with soft downy green leaves, usually of a species of *Solanum,* which "are carried in chiefly after laying has started . . . [and fresh ones] are brought daily and placed above the withering old ones until the eggs hatch." The nest is furnished also with fragments of the cast skins of snakes and lizards, a few scraps of which "may be mixed with the leaves on which the eggs rest." The ceiling of the chamber is vaulted and its roof is well covered by a thick thatch to shed the rain, consisting of coarse material such as short thick sticks, broad pieces of bark or leaves, the dry petioles of cecropias, and stalks of weeds and herbs.

Skutch gave the measurements of "a fairly typical" nest (in inches, converted here metrically) as 74 cm. horizontally at its greatest length, 48 cm. high at the large end where the chamber is situated of which about 25 cm. was thatch, with the tunnel about 35 cm. long with a diameter of about 4 cm.; the platform was very large, measuring about 44 cm. The length and thickness of the lateral extension were not mentioned, but its thickness is not uniform in a photograph published by Skutch which probably represents another nest. In this photograph, the lateral extension seems to be somewhat longer than the diameter of the large end of the nest which appears to be roughly globular and is much constricted where it is attached to it—to about one-third of the diameter of the large end of the nest—whereas it expands to about twice that size at its free end. In other words, the nest shown is shaped somewhat like a "dumb-bell," but with ends of unequal size.

The nest that I watched at Lake Catemaco, Mexico, was similar in general size to the nest mentioned by Skutch (it was 76 cm. long at its greatest length, with a diameter of 46 cm. at the large end), but more compact than the nest he photographed. It was shaped very much like a retort, not a "dumb-bell," with a relatively short thick neck, curving upward at its free end, and which was attached very broadly to the large end of the nest which was globular. The lateral extension (or neck of the retort) was about 30 cm. long and about 25 cm. thick, but a little thicker where attached, and the platform was not especially large, probably considerably smaller than the large platform (44 cm.) mentioned by Skutch though I failed to measure it. The birds always alighted on this platform; they apparently were not concerned with my presence although I watched them at eye-level—only about an arm's length away as stated above—but despite this very close proximity I did not notice any special structure erected around the entrance hole which was not situated at the center of the platform, but to one side of it near the large end of the nest. The platform itself was slightly depressed at the center, shaped somewhat like a large but shallow saucer. I have no information on the internal structure of the nest which I did not disturb.

Lowery and Dalquest (1951) reported three nests from Veracruz as those of *Synallaxis erythrothorax* but I believe an error was made because their description does not correspond at all to the structure and size of the nest of *S. erythrothorax*. One was cup shaped, but "perhaps unfinished," and was about 10 cm. in diameter; the other two "were nearly spherical," about 13 cm. in diameter, and all three were provided "with numerous openings extending completely through the nest."

The nest of *Synallaxis brachyura* is bulky also, but smaller than that of *S. erythrothorax* and less complex as it lacks the platform built by *S. erythrothorax* on which the entrance opens, the entrance of the tunnel opening directly at the distal end of the lateral extension in the nest of *S. brachyura*. It is built also of interlaced twigs and sticks, some of them thorny, and the large end containing the chamber is also well and thickly thatched over. The eggs rest also on downy leaves of *Solanum* plucked while green, which both species continue to bring to the nest until the eggs hatch; fragments of snake skin are also brought to the nest. One difference noted by Skutch is that the leaves are bound by "a liberal amount of cobweb" in the case of *S. brachyura,* whereas cobweb is not used by *S. erythrothorax*. A "typical" nest, which was apparently shaped like "a low, round tower" at its larger end containing the chamber, measured about 36 cm. in height by about 23 cm. in diameter, and the greatest dimension for the nest as a whole was about 43 cm. "from the end of the tunnel to the back of the chamber." The nests observed by Skutch ranged from about 43 cm. to 5 m. above the ground, and were constructed in bushes or small trees with closeset branches; one was found on the flat top of a low stump. Miller (1960) states that the nest of *S. brachyura* lacks an entrance tunnel, but this is not correct; in a nest reported by Skutch, it was 33 cm. in length, or relatively quite long.

The nest of *Synallaxis albescens* is simpler and smaller than those of *S. brachyura* and of *S. erythrothorax,* but similar in general structure. Skutch states that it is constructed "chiefly of straws, fine twigs, and the like" that are carefully interlaced and built "in a tussock of coarse grass or in a shrub overgrown with tangled grass or vines" from about 60 cm. to 1.5 m. above the ground. The nest chamber is also well and thickly thatched with coarse material that sheds the rain. The measurements of one nest given by Skutch are about 30 cm. horizontally, by 18 cm. high, and 15 cm. "in greatest width"; but another nest was larger, about 30 cm. high, and 15 cm. wide "at the chamber," but also about 30 cm. "long." The bottom of the chamber is lined with fragments of downy leaves of *Solanum,* as in the other two species, and, usually, a few scraps of snake skin are present also. Skutch did not report that thorny twigs were used in its construction, but they are employed in other regions, such as Argentina, according to Serié and Smyth (1923).

The general structure of the nest is known in 11 species in addition to *Synallaxis erythrothorax, S. brachyura,* and *S. albescens,* and seems to vary little, basically, in any species. However, it is more simply constructed in some species than others and is most complex in *S. erythrothorax* with its entrance platform, the only species in which this feature exists or has been reported. The information given for some species does not go beyond a few words on the general structure and is not complete for any of these 11 species, but thorny twigs are widely mentioned and, less often, the thatching. When mentioned at all, the lining of the chamber on which the eggs are incubated consists also of soft green leaves (*S. spixi*), or other soft plant material, and snake skins have also been mentioned as incorporated in the soft layer where the eggs rest, or in the furnishing of the nest, in *S. ruficapilla* and *S. frontalis*; snail shells have been reported also in *S. ruficapilla*. The shape of the nest has also been described as retort-like and most nests are usually reported to be "bulky," or "very bulky," but with the exception of *S. albigularis* which Cherrie (1916) said has a nest measuring "40 to 50 cm. in length," and of *S. spixi,* in which the nest attains a size of 70 cm., according to Serié and Smyth, I have no information on measurements.

The height at which the nest is built above the ground varies. In the case of *Synallaxis cinnamomea,* Paul Schwartz has written to me that the nests he found in Venezuela were "almost invariably built on the ground on a sloping surface," not on level ground, of thick twigs, thatched over with dead leaves, and with a long entrance tunnel. In these nests, the tunnel "bends to enter the inside

chamber near the top . . . [rather than at the center or near the bottom as in other species, such as *S. albescens*] and when finished the [external] entrance [of the tunnel] tends to turn upward with respect to the long axis of the nest." On Trinidad, on the other hand, the nest of *S. cinnamomea* is built in a tree, about 3 m. or a little more above the ground, and is built in "low scrub" in Tobago, according to Herklots (1961).

I have mentioned above that I hesitated to accept the information available on the nest of *Synallaxis candei*. This information consists, to the best of my knowledge, of only a brief note transmitted to me from Colombia by Dr. C. J. Marinkelle and, apparently, concerns only one nest. Marinkelle wrote that the nest of *S. candei* is "made of grass and fine twigs, with side entrance, in [a] natural cavity of [a] rotten tree at ground level." However, no *Synallaxis* has ever been reported as building a nest within a tree cavity, but it is possible that this nest is an exception without precedent in the normal location of the nest in this genus.

Morphological Variation

All the species are small with a plain plumage which is usually brownish above, with or without a rufous cap, but uniform, not streaked. A superciliary streak exists in some species but is not well defined as a rule. The underparts are normally paler than the upperparts below the throat, more or less cinereous, ochraceous, buffy, or whitish and the center of the throat is black in all the species, although more sooty than pure black in some species. The black or sooty area is more or less concealed in some species by the tips of the feathers which may be whitish or rufous, but rarely completely so, and the gular patch is apparently more evident in life than in skins because the feathers of the throat are erectile and puffed out when the bird sings or is active. The upper surface of the wing, or its coverts at least, is conspicuously rufous with the exception of *Synallaxis gularis* in which it is brownish. In some species, the rufous pigment replaces brown over large areas of the plumage; *S. unirufa* and *S. castanea* are entirely rufous with the exception of the black gular patch, which, moreover, is well concealed in *S. unirufa*. All the variations in the coloration of the plumage and its pattern are subtle and best described separately, species group by species group.

The variation in the length of the wing is relatively slight as the means vary only from 52 to 71 mm., in round numbers, with an average of 60 mm., but the variation in the length of the tail is great as the means vary from 55 to 112 mm., with an average of 75 mm. The ratio between the lengths of the tail and the wing varies from 0.98 to 1.78, with an average of 1.27, the tail being longer than the wing in all but two species (*S. cherriei* and *S. gularis*), often very much more so.

The variation in the structure of the tail is also exceptionally great and can be made clear only by discussing it as a whole, not species group by species group. The most noteworthy variation is in the number of rectrices which, curiously enough, has received little attention. The rectrices vary from 12 to eight. *Synallaxis hellmayri* has 12 rectrices, seven species have eight, and all the others have 10, but in *S. cinnamomea* the number varies geographically and also, apparently, with age.

All the adults of *Synallaxis cinnamomea* that I have examined from the continent (Colombia and Venezuela) had 10 rectrices, but on Trinidad and Tobago, adults with 10 or eight rectrices seem to be about equally common, and, in one adult from Tobago, the tail had four rectrices on one side, but five on the other, making a total of nine. The number of rectrices also varies apparently in immature birds, but I have seen only a few, none from Trinidad, and none from Tobago and Colombia in which I could count the feathers because too many were missing, but in three immature birds from Venezuela, the tail had eight rectrices in two specimens (although adults from Venezuela have 10), and had 10 rectrices in the third. The adult specimens seen by me in which I was able to count the rectrices consisted of five from

Colombia and 31 from Venezuela, all of which had 10 rectrices; six from Trinidad divided equally between individuals with eight or 10 rectrices; 15 from Tobago, nine of which had eight rectrices and the other six had 10, not counting a sixteenth specimen with nine rectrices mentioned above.

The seven species which have eight rectrices (not including *Synallaxis cinnamomea*) are *S. ruficapilla, S. superciliosa, S. azarae, S. moesta, S. macconnelli, S. tithys,* and *S. castanea.* The fact that about one-fifth of the species have only eight rectrices is certainly most unorthodox for a genus which was characterized "diagnostically" by my predecessors as having 10 rectrices, especially when one considers that *S. ruficapilla* (with only eight rectrices) is the type of the genus.

The number of rectrices seems to be constant intraspecifically, with two exceptions, *Synallaxis cinnamomea* in which it varies geographically as discussed above, and *S. castanea.* Although the normal number is eight in *S. castanea,* as shown by about 130 specimens examined personally or on my behalf, two of the specimens I saw were abnormal and had four rectrices on one side, and five on the other, making a total of nine. These two birds are those which Hellmayr (1925) has mentioned as having 10 rectrices, but he was incorrect as explained by Vaurie and Schwartz (1972).

It is quite evident that the number of tail feathers is undergoing a reduction in *Synallaxis* and relatives. The number decreases from 12 to eight, and to six in *Sylviorthorhynchus,* although virtually only four in the latter genus, as the outer rectrix is reduced to a short filament, which is usually buried in the coverts and is obviously vanishing. In *Thripophaga* (includes "*Asthenes*"), *Certhiaxis* (includes "*Cranioleuca*"), and *Leptasthenura,* the number varies from 12 to 10, and, in *Synallaxis,* the development of the fifth (outer) rectrix varies also considerably in the species in which its exists. It is relatively well developed, normally integrated and stiffened, and projects conspicuously beyond the under tail coverts in such species as *Synallaxis frontalis, S. gujanensis, S. albilora, S. zimmeri,* and *S. candei,* but is shorter and generally more poorly developed in other species such as *S. albigularis* and *S. courseni,* becoming more or less vestigial in two or three species, such as *S. brachyura,* where it is normally difficult to examine it as it is well buried in the coverts as a rule, not stiffened, and becoming somewhat decomposed. Much variation thus exists from species to species.

The reduction in the number of tail feathers and other modifications in tail structure are difficult to account for.[65] It may be an adaptation to dense scrub or other tangled habitat and, probably, to nesting habits in a closed nest, reached by a long tunnel in *Synallaxis* and built with a strong predilection for thorny twigs. But this explanation is certainly open to question in the case of the many species in which the structure of the tail is quite normal, with well integrated feathers, and often quite long, especially in *S. phryganophila.*

The variation in the number of rectrices in a few species was discussed by Zimmer (1925). He stated that some species have eight and others 10, but that a new subspecies which he was describing in his paper is "definitely intermediate," giving evidence of "metamorphosis" of an upper tail covert into a fifth rectrix. However, I believe Zimmer was misled by specimens which may have been somewhat abnormal, and, apparently, by misidentifying one of his specimens.

Zimmer was describing a new subspecies of *Synallaxis azarae* (which he named *infumata*), based on six specimens. Three of these had eight rectrices (normal for *S. azarae*) but, according to Zimmer, in the other three, an upper tail covert was undergoing transformation into a fifth rectrix to a varying degree, the most "advanced stage in the metamorphosis" being represented by an "atypical" female. I have not examined Zimmer's material, but as he (1936b) has reidentified this "atypical" female as *fruticicola* (a subspecies of *S. elegantior* which has 10 rectrices) the "covert" was actually a gen-

TABLE 10
Measurements (in Millimeters) of *Synallaxis*

Species	Wing			Tail			Bill		
	N	Mean	Range	N	Mean	Range	N	Mean	Range
phryganophila									
Males	39	62.69	60–66	16	121.12	106–132	38	14.90	13.80–16
Females	35	61.20	57–64	18	113.66	94–126	34	14.99	14–16.50
Both sexes	77	61.96	57–66	36	117.25	94–132	75	14.96	13.80–16.50
ruficapilla									
Males	55	58.04	54–64	46	76.60	68–84	52	15.43	14–17.50
Females	30	56.78	53–63	25	75.04	67–82	30	15.44	14–17.50
Both sexes	91	57.60	53–64	74	76.12	67–84	86	15.45	14–17.50
superciliosa									
Males	14	56.14	54–60	12	86.83	81–92	14	14.40	13–15
Females	7	55.92	53–58	6	86.00	80–89	6	13.91	13–14.50
Both sexes	21	56.07	53–60	18	86.55	80–92	20	14.26	13–15
frontalis									
Males	101	59.51	53–65	71	78.35	68–86	98	14.11	13–15.50
Females	65	58.90	54–64	44	77.75	70–86	63	15.33	13–15
Both sexes	169	59.27	53–65	118	78.12	68–86	164	14.58	13–16
azarae									
Males	57	57.96	53–65	36	90.69	82–106	50	15.34	14–16.50
Females	39	57.91	53–63	24	88.91	83–98	40	15.28	14.50–16
Both sexes	107	57.96	53–65	67	90.05	83–106	99	15.33	14–16.50
elegantior									
Males	61	58.27	52–64	43	93.23	82–107	59	15.32	14–16.50
Females	51	57.61	51–61	32	90.15	80–107	51	15.44	14.20–17
Both sexes	123	58.02	51–64	85	92.08	80–107	123	15.39	14–17
albigularis									
Males	24	57.91	55–63.50	21	67.71	62–76	24	15.44	15–17
Females	16	56.68	54–60	15	63.80	58–73	17	15.42	15–16.80
Both sexes	41	57.47	54–63.50	36	66.08	58–76	42	15.45	15–17
albescens									
Males	145	56.31	52–60.50	103	75.82	65–85	139	14.36	12–16.50
Females	70	55.16	51–62	45	73.22	64–84	69	14.17	13–16
Both sexes	224	55.91	51–62	155	74.93	60–85	217	14.28	12–16.50
spixi									
Males	43	53.82	50–58	31	86.96	79–95	42	13.49	12.50–15
Females	34	52.82	50–56	20	87.65	80–93	30	13.41	12–15
Both sexes	83	53.40	50–58	55	87.92	79–95	78	13.45	12–15
hypospodia									
Males	15	58.76	57–62	11	72.09	69–78	13	15.70	15–16.50
Females	7	56.85	54.50–59	7	69.14	63–73	7	15.50	15–16
Both sexes	26	57.73	54–62	22	71.50	63–78	24	15.55	15–16.50
infuscata									
Males	2	64.50	64, 65	2	72.50	72, 73	2	17.00	17, 17
Both sexes	3	63.66	62–65	3	72.00	71–73	3	17.00	all 17

TABLE 10—(*Continued*)

Species	Wing			Tail			Bill		
	N	Mean	Range	N	Mean	Range	N	Mean	Range
brachyura									
Males	77	60.87	55–67	63	73.49	63–90	72	17.43	16–19
Females	31	59.45	55–64	26	72.46	63–82	30	17.31	16–18.50
Both sexes	109	60.47	55–67	90	73.33	63–90	103	17.39	16–19
courseni									
Males	3	63.00	62–64	3	111.66	109–113	3	15.16	15–15.50
moesta									
Males	25	66.10	60–69	20	70.45	63–78	25	17.78	16.50–19.50
Females	15	63.93	60–67	12	68.25	61–76	14	17.34	16.50–18
Both sexes	45	65.10	60–69	36	68.97	61–78	44	17.57	16.50–19.50
cabanisi									
Males	16	65.90	62–70	13	67.07	59–74	15	17.13	16–18
Females	10	64.50	62–70	7	63.14	58–67	7	16.71	16–17.50
Both sexes	26	65.36	62–70	20	65.70	58–74	22	17.00	16–18
macconnelli									
Males	15	62.66	60–66	12	71.08	65–74	15	16.38	16–17
Females	7	61.64	58–64	7	70.14	66–75	7	16.84	16–17.50
Both sexes	24	62.27	58–66	21	70.66	65–75	24	16.44	15–17.50
subpudica									
Males	3	66.00	64–67	3	109.66	100–115	3	15.83	15–16.50
Females	2	64.50	64, 65	2	97.00	95, 99	2	15.50	15, 16
Both sexes	16	65.62	62–69	16	106.37	95–115	16	16.08	15–17
tithys									
Males	5	59.20	58–61	4	68.00	65–71	5	15.60	15–16
Females	4	59.50	58–61	4	68.25	67–71	4	15.50	15–16
Both sexes	11	59.36	57–62	10	67.90	62–72	11	15.50	15–16
cinerascens									
Males	22	55.90	54–58	20	64.70	57–70	21	12.97	12–14
Females	17	54.50	52–58	16	63.56	57–74	16	13.01	12–14
Both sexes	46	55.30	52–58	39	63.89	57–74	44	12.98	12–14
maranonica									
Males	4	65.12	64–66	2	68.50	65, 72	3	17.56	17.20–18
Females	5	61.70	59–65	5	63.00	59–68	5	16.70	15.50–18
Both sexes	10	63.00	59–66	8	64.25	59–72	9	16.94	15.50–18
propinqua									
Males	18	62.33	60–65	9	71.22	66–78	16	19.29	18–20.50
Females	14	60.92	59–63	8	63.50	55–72	14	18.90	18–20
Both sexes	33	61.63	59–65	18	67.61	55–78	31	19.10	18–20.50
hellmayri									
Males	3	71.33	68–75	3	80.66	80–82	3	17.73	17.20–18
Females	1	—	69	1	—	72	1	—	18
Both sexes	4	70.75	68–75	4	78.50	72–82	4	17.80	17.20–18
gujanensis									
Males	60	63.04	59–67	46	70.82	63–79	57	16.51	15–17.50

TABLE 10—(*Continued*)

Species	Wing			Tail			Bill		
	N	Mean	Range	N	Mean	Range	N	Mean	Range
Females	64	60.89	53–65	44	67.90	62–78	63	16.32	15–17.50
Both sexes	134	61.91	55–67	99	69.41	62–79	129	16.41	15–17.50
albilora									
Males	6	65.75	64–67.50	5	71.80	66–79	6	16.20	15–17.20
Females	4	63.75	62–65	4	73.25	72–75	4	15.50	15–16
Both sexes	10	64.95	62–67.50	9	72.44	66–79	10	15.92	15–17.20
rutilans									
Males	95	62.03	58–67	68	66.30	55–77	93	15.51	14.50–17
Females	67	60.61	56–64	41	65.31	58–71	67	15.35	14–17
Both sexes	167	61.41	56–67	113	65.96	55–77	165	15.44	14–17
cherriei									
Males	5	60.60	59–62	5	56.40	54–59	5	15.04	14.20–16
Females	2	60.50	60, 61	2	—	both 55	2	15.50	15, 16
Both sexes	7	60.57	59–62	7	56.00	54–59	7	15.17	14.20–16
unirufa									
Males	26	61.48	58–66	21	87.91	83–100	22	16.87	15–18
Females	22	59.93	57–63.50	18	83.50	79–90	21	16.39	14–17.80
Both sexes	53	60.88	57–66	43	85.97	79–100	47	16.68	14–18
castanea									
Males	25	62.00	60–64	24	101.45	96–108	22	16.75	15–18
Females	18	59.61	58–62	18	97.66	92–105	18	16.70	16–18
Both sexes	49	61.10	58–64	48	100.06	92–108	46	16.76	15–18
fuscorufa									
Male	1	—	60	1	—	90	1	—	16
Not sexed	1	—	60	1	—	100	1	—	16
zimmeri									
Female	1	—	57	1	—	88	1	—	15
erythrothorax									
Males	36	58.94	54–63	24	66.20	60–75	33	16.51	16–17.50
Females	23	57.91	55–60	17	64.29	58–68	21	16.41	15.50–17.20
Both sexes	64	58.29	54–63	44	65.20	58–75	59	16.46	15.50–17.50
cinnamomea									
Males	27	58.70	56–63	24	65.37	61–72	26	15.84	14–18.50
Females	24	57.41	54–61	24	63.70	57–70	23	16.16	15–17.50
Both sexes	61	58.62	54–63	56	64.64	57–72	59	16.01	14–18.50
stictothorax									
Males	25	51.68	47–55	20	57.05	50–68	23	13.50	13–16
Females	24	51.68	49–55	24	57.62	51–67	24	13.73	12–16
Both sexes	62	52.50	49–55	53	57.45	50–68	56	13.62	12–16
candei									
Males	9	62.05	58–66	8	70.87	63–79	9	16.50	15.50–17
Female	1	—	59	1	—	70	1	—	16.50
Both sexes	13	61.50	58–66	12	70.66	63–79	13	16.42	15.50–17

TABLE 10—(*Continued*)

Species	Wing			Tail			Bill		
	N	Mean	Range	N	Mean	Range	N	Mean	Range
kollari									
Males	4	58.75	57–60	4	69.25	67–71	4	—	all 16
Female	1	—	57	1	—	66	1	—	16
Both sexes	6	58.50	57–60	6	68.83	66–71	6	—	all 16
scutata									
Males	18	59.47	56–63	18	65.16	59–70	18	14.57	14–15
Females	15	57.26	55–58.50	14	64.42	60–68	15	14.68	14–15.20
Both sexes	37	58.67	55–64	36	65.11	59–70	37	14.65	14–15.20
gularis									
Males	39	59.21	56–63	35	55.85	50–66	38	15.53	14–17
Females	27	58.64	56–62	22	53.36	50–58	26	15.37	14–17
Both sexes	70	59.04	56–63	61	54.77	50–66	68	15.46	14–17

uine rectrix in this case. Zimmer's description of the other two specimens suggests very strongly that he was misled by coverts that were probably somewhat abnormal and misarranged, or growing somewhat out of line, as the transformation of a covert into a flight feather is highly improbable and, in any event, could be established with assurance only by embryological study.

Zimmer stated also that in 30 specimens of *Synallaxis elegantior* he had examined during his study, one had eight rectrices and the others had 10. But I am reluctant to credit this statement without confirmation because reexamination under magnification may show that a feather had been lost, undetected by Zimmer. At any rate, I have found no evidence of a reduction from 10 to eight in the 265 specimens of *S. elegantior* that I have examined, or of an increase from eight to 10 in the 142 of *S. azarae*.

In fact, the number of rectrices seems to be remarkably constant within species, with the two exceptions noted above, and appears to be a good species character, very well confirmed by bioacoustic evidence (Vaurie and Schwartz, 1972) in the two instances where the vocalizations of related species with a different number of rectrices have been compared.

The structure of the tail varies also greatly in other respects—in addition to length, number of rectrices, and relative development of the fifth rectrix when present. Graduation, width of the rectrices, shape of their tips (acuminate or not), integration of the webs, and general degree of stiffening vary from species to species. To discuss this variation in detail is impracticable as all sorts of intermediates exist, but, generally speaking, the tail is more stiffened when shorter and its tips are more acuminate.

It is evident that the variations in the structure of the tail are not of generic importance although they have led to the proposal of three "genera," two of which remained monotypic. These are *Poecilurus* Todd, 1917; *Hellmayrea* Sztolcman, 1926; and *Gyalophylax* Peters, 1950.

Todd proposed *Poecilurus* for *candei*, and another form (*atrigularis*) now held to be conspecific with *candei*, because the tail of *candei* is less stiffened, and its rectrices are better integrated, and broader, blunter at the tip, than in most other species. Two other species (*kollari* and *scutata*) were added to *Poecilurus* by Peters (1951), but no demarcation can be drawn in *Synallaxis*; other species exist which differ only slightly from *candei*, or are intermediate in every respect between the three species named and others.

Sztolcman proposed *Hellmayrea* for *gu-*

laris on the ground that its tail is shorter than the wing and its bill "very much thinner" than in *Synallaxis*. However, the bill of *gularis* is no thinner than in some other species, the tail of *cherriei* is also shorter than the wing, and, in several species, only a slight difference exists between the lengths of the tail and wing (table 10).

The inconvenient number of rectrices, and the shape of the bill led Peters (1950) to propose *Gyalophylax* for *hellmayri*. But, as I have shown elsewhere (Vaurie, 1971b), the shape of the bill can scarcely be used for generic separation, as this type of bill occurs in several unrelated genera, is not at all constant when these genera (including *Xenops*) are polytypic, and is possessed also by some species in the Formicariidae. *Synallaxis hellmayri* differs from all the other species by having 12 rectrices and by having a bill of the "*Xenops*-type," with a straight culmen and an ascending gonys. As the diagnostic "generic" character of *Synallaxis* was held by fiat to be the possession of 10 rectrices before my revision (Vaurie, 1971a), Hellmayr (1925) and Peters (1950) decided that *hellmayri* could not be maintained in *Synallaxis*. Hellmayr placed it in *Asthenes*, of which, he says, *hellmayri* is a "typical" member. This opinion is certainly incorrect as Peters (1950) has emphasized, saying that *hellmayri* "is no doubt closely related to *Synallaxis* as evidenced by the black gular patch and chestnut humeral patch, but [from which it] is excluded by reason of its possession of 12 rectrices."[66]

PHYLOGENY

Sclater reviewed *Synallaxis* in 1874 and recognized to his "greater or less satisfaction the validity of some fifty-eight species" of which he had seen specimens. His aim was to give a synopsis of the genus, species group by species group, for which he adopted a scheme consisting of two divisions: "A," with 33 species, and "B," with 25, each subdivided in turn into seven sections.

Sclater decided later (1890) to transfer his entire section B to the genus *Siptornis*, and 10 of the 33 in section A have also been pruned since Sclater, chiefly by transfer to other genera, or to another family (Rhinocryptidae). Only 23 were left in *Synallaxis* (including *phryganophila* which I have placed in the monotypic subgenus *Schoeniophylax*), but, since 1874, this number has been increased to 37 by the description of 11 new species and the revival of three, described before 1874, but which Sclater had believed to be invalid.

The review of 1874 was a landmark in the taxonomy of *Synallaxis*. It is still of considerable interest, but is mentioned by me chiefly because I found that I also had to resort to a division into groups to present a coherent synopsis. The four groups that I have adopted are based on the adult plumage and do not include *phryganophila*—the thirty-seventh species. These four groups respect phylogeny, in so far as I have a concept of it, but this division is made without pretensions—other than for convenience—as the relationships of many species are not clear to me.

GROUP ONE: Species with a well-defined rufous crown ("cap") that are not rufous on the underparts. This group appears to be a single phylogenetic assemblage and is composed of 16 species: *Synallaxis ruficapilla, S. superciliosa, S. frontalis, S. azarae, S. elegantior, S. albigularis, S. albescens, S. spixi, S. hypospodia, S. infuscata, S. brachyura, S. courseni, S. moesta, S. cabanisi, S. macconnelli,* and *S. subpudica.*

Another form (*poliophrys* Cabanis, 1866) with a rufous cap was rejected by me as invalid (Vaurie, 1971c) as it rests only on a single misidentified specimen of *S. frontalis* Pelzeln, 1859, allegedly from "Cayenne," from where it may have been received, although this bird was most probably collected in eastern Brazil. I discovered the misidentification when the Berlin Museum lent me this specimen, which, apparently, had not been reexamined before me since Cabanis described it as *poliophrys* in 1866.

GROUP TWO: Species with a brownish or grayish crown that are not rufous on the underparts. This group is composed of seven

species: *Synallaxis tithys, S. cinerascens, S. maranonica, S. propinqua, S. hellmayri, S. gujanensis,* and *S. albilora.* The relationships of most of these seven species are not clear, but, taken as a group, they seem to occupy a position intermediate between the species of Group One and Group Three.

GROUP THREE: Species which are very strongly rufous on the underparts, and may be rufous or not on top of the head, but lack a rufous cap (with the exception of *Synallaxis fuscorufa*). This group consists of six species: *S. rutilans, S. cherriei, S. unirufa, S. castanea, S. fuscorufa,* and *S. zimmeri* which all seem to be more or less closely related.

GROUP FOUR: A variable group which cannot be characterized satisfactorily as it is more or less heterogeneous, although about half of its species are probably related. It is composed of seven species: *Synallaxis erythrothorax, S. cinnamomea, S. stictothorax, S. candei, S. kollari, S. scutata,* and *S. gularis.*

GROUP ONE

KEY TO THE SPECIES

1. Tail with eight rectrices 2
   Tail with 10 rectrices 6
2. Forehead rufous 3
   Forehead brown 4
3. Forehead and crown bright rufous; with a distinct dull orange streak above and behind the eye; abdomen ochraceous ..... *ruficapilla*
   Forehead and crown chestnut; pale streak above and behind the eye dark rufous and very indistinct, scarcely evident; abdomen ashy ..... *macconnelli*
4. Underparts below the upper breast grayish, with a more or less well-defined scalloped pattern ..... *azarae*
   Underparts below the upper breast whitish, buffy, or grayish olive, without pattern 5
5. Underparts below the upper breast whitish or buffy; forehead dull pale brown; crown dull rufous behind the brownish band on forehead; with a dull buffy, not well-defined superciliary streak ..... *superciliosa*
   Underparts below the upper breast grayish olive; forehead dark brown; crown chestnut behind the brown band on forehead; without superciliary streak ..... *moesta*
6. Forehead and crown uniformly rufous, without a brownish or grayish band on the forehead 7
   Forehead and crown not uniformly rufous, with a brownish or grayish band on the forehead 9
7. Tail olivaceous brown; strongly graduated, and one-third longer than the wing or more; tips of the longer rectrices well emarginated on the inner web ..... *spixi*
   Tail rufous; not strongly graduated, relatively short and only about as long as or slightly longer than the wing; tips of the rectrices acuminate, but not emarginated 8
8. Ashy gray below the throat; crown bright rufous ..... *infuscata*
   Pale olivaceous brown below the throat; crown chestnut ..... *cabanisi*
9. Tail rufous 15
   Tail brown, or dark sooty brown, "blackish" 10
10. Tail dark sooty brown, "blackish" 11
    Tail brown 13
11. Abdomen whitish ..... *hypospodia*
    Entire underparts slate gray below the black gular patch, uniform or virtually so (not whitish on abdomen) 12
12. Tail with a diffused, ill-defined rufous band along the shaft of the inner web of the rectrices ..... *courseni*
    Tail uniform, without rufous ... *brachyura*
13. Tail conspicuously elongated (average length 106 mm.); very strongly graduated ..... *subpudica*
    Tail much shorter (average length 66 or 75 mm.); not strongly graduated, or much less so than in *subpudica* 14
14. Tips of rectrices sharply acuminate; webs of rectrices loosely integrated; rufous patch on shoulder extensive (extending uniformly over all the coverts); tail strongly stiffened; shorter (averaging 66 mm. in length) ..... *albigularis*
    Tips of rectrices relatively blunt (not very sharply acuminate); webs of rectrices more closely integrated; rufous patch on wing less extensive (not extending uniformly beyond the middle coverts, or restricted uniformly only to the lesser coverts); tail not markedly stiffened; longer (averaging 75 mm. in length) ..... *albescens*
15. Crown and upper surface of the wing bright

rufous (more orange); tail more strongly graduated, averaging distinctly longer (92 mm.) ..... *elegantior*

Crown and upper surface of the wing duller rufous (more chestnut); tail less strongly graduated, averaging distinctly shorter (78 mm.) ..... *frontalis*

Note that for number 15 above *Synallaxis elegantior* and *S. frontalis* resemble each other, but the rufous pigment is brighter throughout the plumage (including tail) in *S. elegantior*; the tail of *S. elegantior* averages distinctly longer, and the gap between the tips of the fourth and central rectrices is normally about one-half or more of the total length of the tail in *S. elegantior*, as against, normally, only about one-third, or less, of the total length of the tail in *S. frontalis*. The distribution of the two species is also quite different (map 9), extending from northern Peru, north to Colombia and western Venezuela in the case of *S. elegantior*; from eastern Brazil (south of the Amazon) and central Brazil, south to eastern Bolivia, Paraguay, Uruguay, and central Argentina in the case of *S. frontalis*.

MORPHOLOGICAL VARIATION, PHYLOGENY, AND GEOGRAPHICAL VARIATION IN GROUP ONE

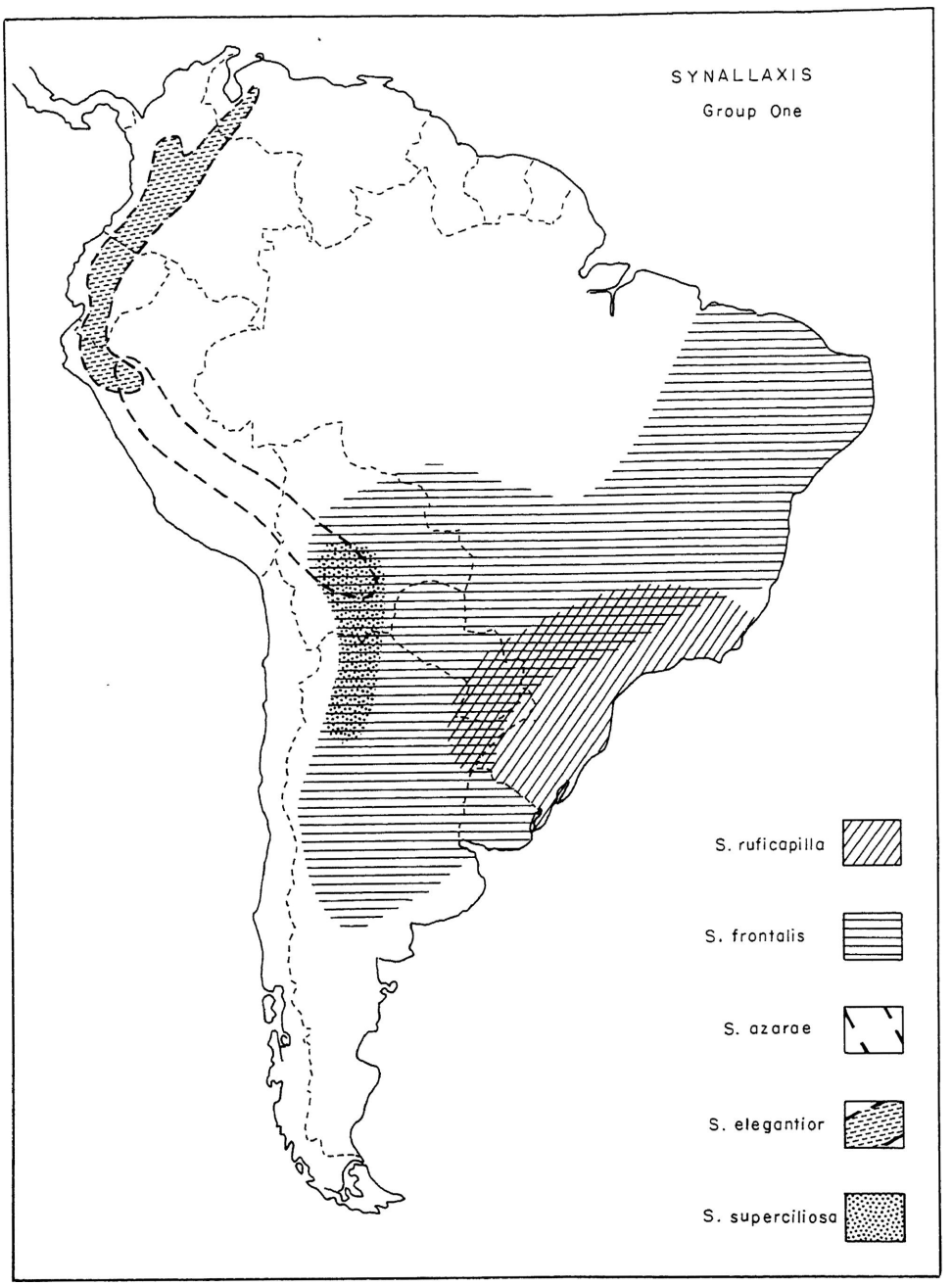
The variation in the coloration of the plumage is relatively slight and so consistent as a rule that the relationships of the species seem clear, with two or three exceptions.

Nearly all the species are brownish on the back, but two are very distinctly gray (*Synallaxis brachyura* and *S. courseni*), and the brown pigment is duller, with a faint grayish cast in some species, but is richer, more rufous in others. The crown is rufous in all the species as stated above, brighter or duller, and uniform or not, the forehead being grayish or brown in some species, forming a dark band which varies in width from rather narrow to fairly broad. The rufous area on the upper surface of the wing is conspicuous in all the species, but more restricted in extent in *S. albescens* and *S. albigularis*. A superciliary streak exists in only a few species, varying from dull orange to buffy or dull white, but is vague as a rule, poorly defined with the exception of *S. ruficapilla* in which it is dull orange, quite distinct behind the eye. The color of the tail varies from rufous to brown or dark sooty brown, virtually "blackish," and sharp variations exist in the structure of the tail as discussed above and are mentioned below in the individual description of the species.

The coloration of the underparts varies below the black gular patch and is uniform or not, being pale ashy gray, slate gray, or olivaceous brown in the species in which the coloration is uniform or virtually so. In about half of the species, the abdomen is paler than the breast, more or less dingy white, with a pale grayish or ochraceous tinge. *Synallaxis azarae* differs from all the other species by being patterned with gray below the upper breast, a somewhat scalloped pattern better defined in some populations than others, created by the fact that the subapical portion of the feather is gray, in a crescentic pattern, contrasting with the whitish tips of the feather and another whitish area above the gray subapical portion. The black gular patch is quite evident in all the species, but the white or whitish tips of the feathers are developed to a varying degree from species to species.

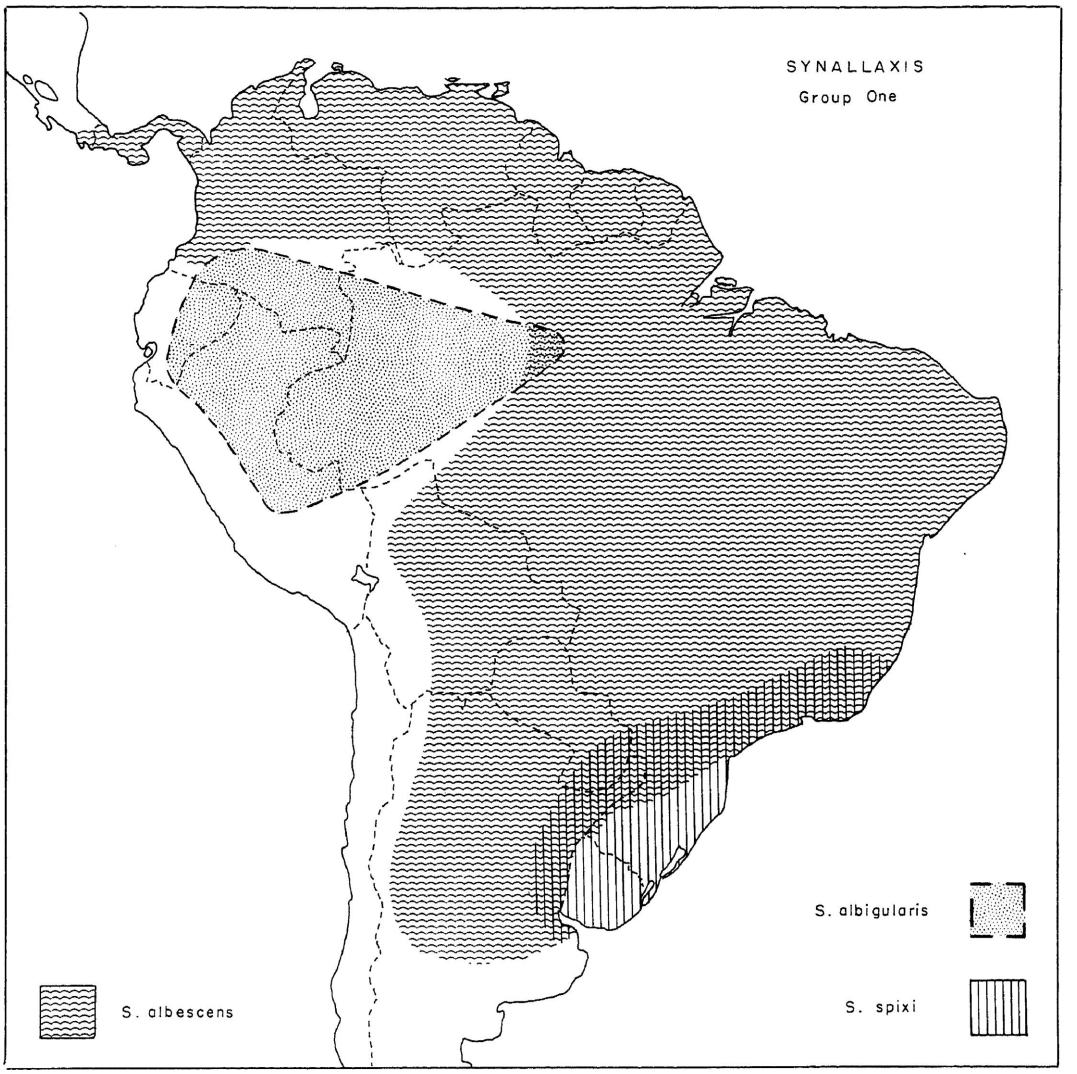
The variation in the coloration, and the distributions of the species concerned, show that the 16 species can be divided quite clearly into four groups.

In the first subgroup[67] (map 9) consisting of *Synallaxis ruficapilla, S. superciliosa, S. frontalis, S. azarae,* and *S. elegantior* the back is brighter brown than in the species of the other groups, and the tail is strongly rufous. These five species all seem to be closely related to about the same degree. It has been suggested that *S. frontalis* is conspecific with *S. azarae,* and all authors considered that *S. azarae* and *S. elegantior* were conspecific before my revision (Vaurie, 1971a). However, distribution and morphology contradict these opinions. The structure of the tail, which appears to be a very good species character, is characterized by eight rectrices in *S. azarae,* as against 10 in *S.*



MAP 9. Geographical distribtion of five species (Subgroup One) of Group One of the subgenus *Synallaxis* of the genus *Synallaxis*.

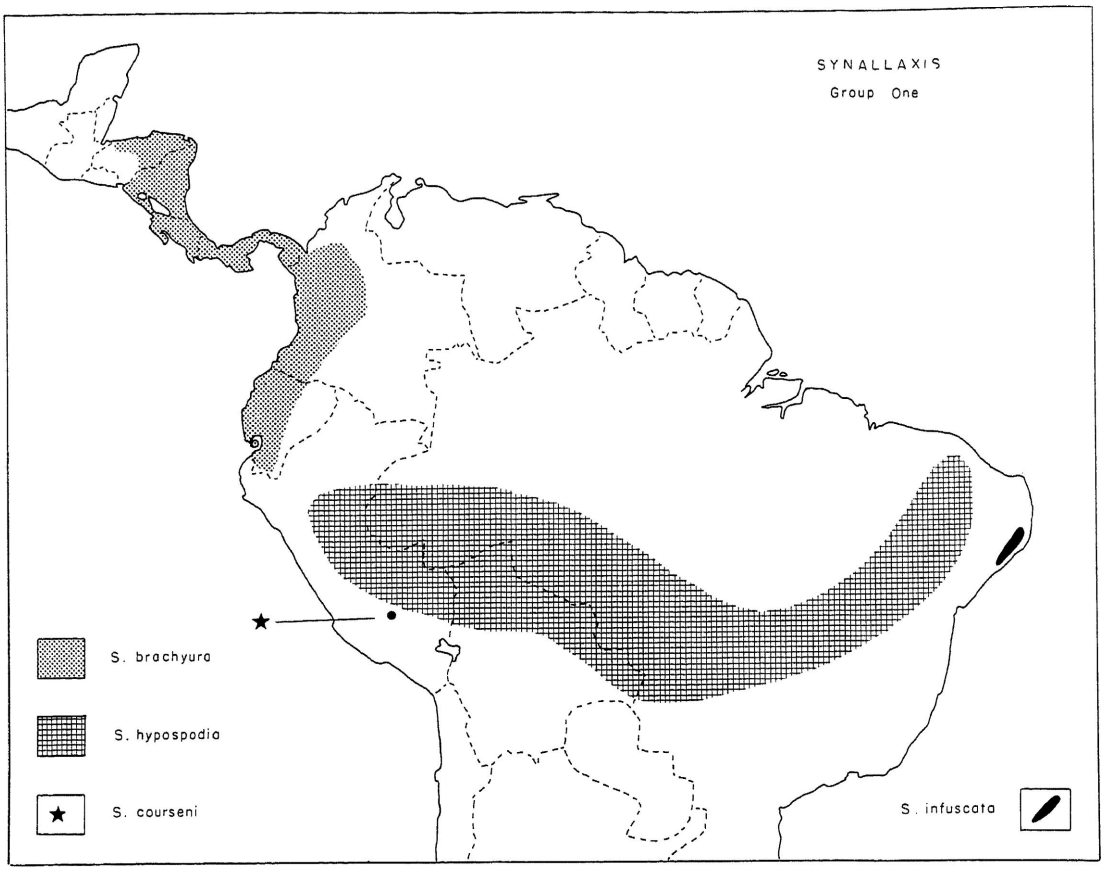
frontalis and *S. elegantior*. The three species come in contact and overlap in their zone of contact, *S. frontalis* with *S. azarae*, and *S. azarae* with *S. elegantior*. In addition, the



MAP 10. Geographical distribution of the three species of Subgroup Two of Group One of the subgenus *Synallaxis* of the genus *Synallaxis*.

study of the vocalizations, done by Vaurie and Schwartz (1972) in the case of *S. azarae* and *S. elegantior*, supports the conclusion that these two taxa are not conspecific. *S. elegantior* lacks also the scalloped pattern of the underparts of *S. azarae* which exists in no other species of the genus.

The second subgroup[68] consists of *Synallaxis albescens*, *S. albigularis*, and *S. spixi* (map 10) which appear to be closely related and differ from the five species of the first group by being duller brown, more grayish on the back, and by having a tail which is olivaceous brown, not rufous. The tail of



MAP 11. Geographical distribution of the four species of Subgroup Three of Group One of the subgenus *Synallaxis* of the genus *Synallaxis*.

these three species is also better stiffened and its rectrices are more loosely integrated, and, on the whole, their tips are more acuminate—characters that are best developed in *S. albigularis*. The latter was considered to be conspecific with *S. albescens* by Hellmayr (1925), but the ranges of the two birds come in contact and overlap in Brazil on the lower Rio Madeira, and, as Chapman (1931) was the first one to show, they differ morphologically in a number of relatively small but constant characters which exist also in immature birds. The distinction is stated in the key and is more evident in the structure of the tail which is distinctly shorter in *S. albigularis*, better stiffened, with rectrices that are more loosely integrated and end in more sharply acuminate tips.

The third subgroup[69] consists of *Synallaxis hypospodia, S. infuscata, S. brachyura,* and *S. courseni* (map 11). It is more heterogeneous than the other three groups, but its species differ from the birds in the other groups by a varying combination of characters which suggests they are, or may be, more or less closely related. The most salient differences are the color of the tail and underparts. The tail is dark sooty brown, virtually "blackish" in *S. hypospodia, S. brachyura,* and *S. courseni,* but rufous in *S. infuscata*; the underparts are very dark, slate gray, and uniform or virtually so in *S. infus-*

cata, S. brachyura, and *S. courseni,* but the abdomen is whitish in *S. hypospodia.* The back is dark gray, with a very faint tinge of brown in *S. courseni* and in some populations of *S. brachyura,* but it is dull brown, "darkish" in other populations of *S. brachyura,* and in *S. hypospodia* and *S. infuscata.*

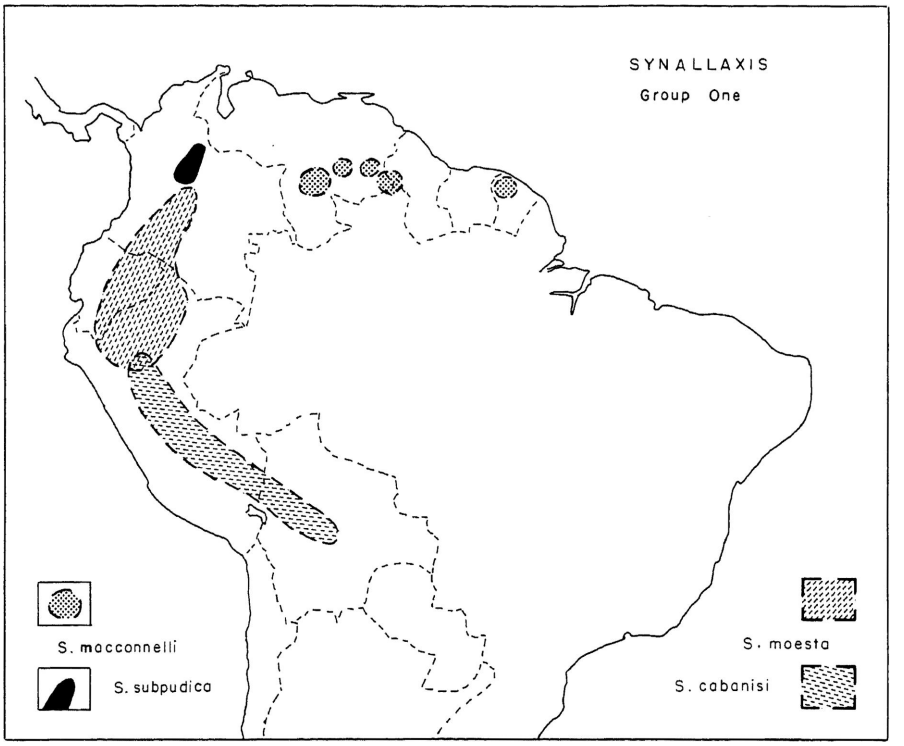
Hellmayr (1925) held that *Synallaxis hypospodia* and *S. spixi* were conspecific, stating that *S. hypospodia* "differs from [*S. spixi*] merely by somewhat stouter bill and by having the forehead brownish gray [rather than rufous]," but this opinion was contested quite correctly by Zimmer (1936b), because the two birds have really little in common and belong in different groups in my opinion and that of Zimmer. *S. hypospodia* is an altogether coarser bird than *S. spixi,* with a very distinctly shorter and much darker tail which is quite different from the tail of *S. spixi* in appearance. The tail of *S. hypospodia* is blackish, its rectrices are unusually broad (as stated by Zimmer), and are relatively blunt at the apex; whereas the tail of *S. spixi* is brown and its rectrices are narrower, especially toward their tips which are far more sharply acuminate than in *S. hypospodia.* The inner web of the long central pair is well emarginated in *S. spixi,* and, when the feathers are not badly worn or disarranged, this emargination creates a deep "fork," about 20 mm. in depth on an average, but exceeding 30 mm. in some individuals. This "fork" does not exist in *S. hypospodia.* The difference in the length of the tail of the two species is well marked, in actual measurements (table 10) or proportions, as the ratio between its length and that of the wing is 1.23 in *S. hypospodia,* as against 1.64 in *S. spixi.*

In short, *Synallaxis hypospodia* does not appear to be closely related to *S. spixi,* but rather appears to me to belong in a distinct group of species which includes also *S. infuscata, S. brachyura,* and *S. courseni.* The precise interrelationships of these four species are not clear, although *S. brachyura* and *S. courseni* certainly seem to be more closely related to one another than they are to *S. hypospodia* and *S. infuscata.*

The rufous tail of *Synallaxis infuscata* is aberrant, but the dark slaty gray and uniform coloration of its underparts suggest that *S. infuscata* is best included in this group. *S. infuscata* was described from Brazil as a subspecies of *S. ruficapilla* by Pinto (1950), but Pinto's taxonomic concept of *Synallaxis* is very confused and his statement that *S. ruficapilla,* like all the other members of *Synallaxis* ("*como os demais representantes do gênero*"), has 10 rectrices is incorrect. *S. ruficapilla*—the type of *Synallaxis*—has only eight rectrices, as emphasized above, whereas *S. infuscata* has 10, and, in this respect, as well as in other characters, little similarity exists between the two taxa *infuscata* and *ruficapilla.* They are quite distinct species, and the fact that *S. infuscata* was a new and well-differentiated species had been recognized by workers in the American Museum of Natural History roughly 20 years before Pinto described it erroneously as a subspecies of *S. ruficapilla,* but unfortunately the existence of this bird was not reported before Pinto. Additional confusion has also been caused by Pinto (1936) when he misidentified two specimens of *S. hypospodia* from Goiás, Brazil, which he described as a "new subspecies" of *S. brachyura,* naming it *jaraguana.* These two specimens were kindly lent to me by the São Paulo Museum through the intermediacy of Dr. H. Sick, and I am most grateful for their loan which made it possible to correct this error.

The fourth subgroup[70] consists of *Synallaxis moesta, S. cabanisi, S. macconnelli,* and *S. subpudica* (map 12) and is quite uniform, with the exception of *S. subpudica* the position of which is quite uncertain. The coloration of *S. moesta, S. cabanisi,* and *S. macconnelli* is virtually identical;[71] they differ from the species of the other three subgroups by being dark brown on the back with a rufous tinge (most pronounced in *S. cabanisi*), and by being olivaceous brown, with or without an admixture of gray, on the underparts which are uniform or virtually so below the black gular patch. Their tails are rufous, and the rufous pigment throughout their plumage is chiefly chestnut, darker rufous than in all other species.

Synallaxis cabanisi and *S. macconnelli*



MAP 12. Geographical distribution of the four species of Subgroup Four of Group One of the subgenus *Synallaxis* of the genus *Synallaxis*.

were considered to be conspecific before my revision (Vaurie, 1971a), but the tail is composed of 10 rectrices in *S. cabanisi,* as against eight in *S. macconnelli,* a difference which appears to be a species character in *Synallaxis* as discussed above. Zimmer (1936b) mentioned that *S. moesta* showed also "the transitional development" of upper tail coverts into rectrices that he had first mentioned in *S. azarae* (Zimmer, 1925). I have discussed this question above, expressing my complete conviction that Zimmer is incorrect. I find no evidence of this highly improbable "transition" in the 58 specimens of *S. moesta* that I have examined, which include all the specimens seen by Zimmer.

Synallaxis subpudica differs strongly from the other three species of the fourth subgroup by being "mousy" in coloration, brownish on the back and tail, dull pale gray on the underparts beneath the black gular patch, and by having a most conspicuously elongated tail, which is also more strongly graduated than in other species of all the subgroups, with tips which taper sharply but are not truly acuminate. *Synallaxis subpudica* does not seem to be closely related to any of the other 15 species of Group One, including *S. brachyura* (formerly called *pudica*) to which it had been compared. The affinities of *S. subpudica* are not clear, but from a practical point of view it seems better included in the fourth subgroup than in any other. I suspect that *S. subpudica* represents a relict without any modern close relatives, and now confined to a restricted range in the Eastern Andes of Colombia.

Nine of the 16 species of Group One vary geographically: *Synallaxis superciliosa, S. frontalis, S. azarae, S. elegantior, S. albescens, S. brachyura, S. moesta, S. cabanisi,* and *S. macconnelli.* In the case of *S. fron-*

talis, the variation takes the form of a definite cline over a very extensive region (described below); in the case of the other species, the geographical variation consists of differences between populations that are relative only or do not seem to be of major importance to me. I believe the variation does not warrant the recognition of subspecies and is made sufficiently clear by describing it briefly in four species in addition to *S. frontalis*.

Synallaxis elegantior, ranging from the Andes of Venezuela south to northern Peru (map 9) between 1100 and 3800 m., has been divided into four subspecies. The populations from the northern end of the range (nominate *elegantior*) are relatively pale and are replaced farther south by darker populations (subspecies *media*), which give way to paler populations at the southern end of the range, named *ochracea* and *fruticicola*. Nominate *elegantior* is bright brown on the back, more or less ochraceous and cinereous on the breast and flanks, and is distributed from Venezuela south through the Eastern Andes of Colombia. *Synallaxis elegantior media* is darker, duller on the back, and more grayish below than nominate *elegantior*, and occupies the Central and Western Andes of Colombia south to northern Ecuador. *Synallaxis elegantior ochracea* and *fruticicola* are not at all well differentiated from nominate *elegantior* or from one another; the best that can be said is that *ochracea* averages faintly paler than nominate *elegantior*, whereas *fruticicola* averages slightly duller and more grayish than *ochracea* and is very vaguely intermediate between nominate *elegantior* and *media*. The ranges ascribed to *ochracea* and *fruticicola* are southern Ecuador south to Lambayeque in Peru for *ochracea*, and northern Peru, in the region south and east of the range of *ochracea* for *fruticicola*.

Synallaxis moesta, distributed from eastern Colombia south to northern Peru (map 12) and occupying a lower altitudinal zone, than *S. elegantior*, ascending only to about 1400 m., is not closely related to *S. elegantior* (they are placed in two different subgroups) but the geographical variation of the two species tends to be similar although only three subspecies have been recognized in *S. moesta*. The populations from the northern end of the range (nominate *S. m. moesta*) are relatively paler and more brownish (as in the case of nominate *S. e. elegantior*) than the populations (*S. m. obscura*) which replace them farther south; *obscura* is darker, duller, more grayish than nominate *moesta*, and also gives way to paler populations (*S. m. brunneicaudalis*) at the southern end of the range of the species. However, the southern *brunneicaudalis* does not become as pale as nominate *moesta* from the north, as the coloration of *brunneicaudalis* is more similar to that of *obscura*, including the color of the tail which is chestnut in both, less bright than in nominate *moesta*.

Synallaxis macconnelli is closely related to *S. moesta* (both are in subgroup 4), but its geographical variation appears to be quite irregular, affected or not, or only very slightly so, by geographical isolation. All the populations of *S. macconnelli* are more or less isolated, as this species is apparently restricted to isolated mountains in southern Venezuela and occurs again in northern French Guiana after a relatively large gap in distribution (map 12). Nevertheless, geographical isolation has apparently been ineffective in the case of some of the populations of Venezuela, a few of which appear furthermore to be identical, or virtually so, with the population of French Guiana which has been named *S. m. obscurior*. The specimens of *obscurior* which I have seen, including four of the six specimens on which this subspecies was based, are either identical in coloration with the type of *griseipectus*, or only very faintly darker. *S. m. griseipectus* is known only from Ptari-tepui, Soropán-tepui, and nearby Cabanayén, Venezuela, and together with *obscurior* is distinctly more gray below, less brownish than nominate *macconnelli*, and also duller and somewhat darker throughout. Nominate *macconnelli* is known from Cerro Camani in northern Amazonas, Cerro El Negro in northwestern Bolivar, and Roraima and Ueitepui on the borders of Venezuela, Guyana, and Brazil. All these mountains are more dis-

tantly isolated from one another than Roraima is from Ptari-tepui and Soropán-tepui, but isolation has apparently been ineffective in creating differences in their bird populations. A fourth "subspecies" (named *yavii*) is known from only a single specimen taken on Cerro Yavi, about 80 km. north of Cerro Camani; the specimen, I find, is only very faintly paler than nominate *macconnelli*.

It is possible that differences in measurements exist between populations, as stated by Todd (1948), who said that *S. m. obscurior* is smaller than nominate *macconnelli*, but the number of specimens in existence is insufficient to determine this with assurance and it is highly probable that any difference which may exist is slight and in average only. In the 15 males I have measured, the wing length measures 60, 61, and 63 mm. in three of *S. m. obscurior*, 60–66 mm. (mean 63.2 mm.) in 11 of nominate *macconnelli*, and 60 mm. in the type of *griseipectus*. In females, the wing measures 61.5 mm. in the type of *yavii*; in females of *obscurior*, the wings measure 58 and 60 mm.; and they measure 60, 61, 63, 63, and 64 mm. in five specimens of nominate *macconnelli*.

Synallaxis albescens has an enormous range from Costa Rica south to central Argentina (map 10) and 13 subspecies were recognized by Peters (1951). I have seen 390 specimens of this species, representing all the forms recognized by Peters. This species is grayish brown on the back, has a wide band of gray across the forehead, and is whitish on the underparts below the black gular patch, tinged more or less darkly and extensively with gray or pale ochraceous brown on the breast and flanks. The saturation of its pigmentation appears to be correlated chiefly, perhaps entirely, with the humidity of the regions it inhabits. Populations from regions where annual precipitation is greater are darker, more brownish, less grayish on the back, darker, less whitish below, and the rufous areas on wing and crown are darker and richer, more extensive, whereas populations from the more arid regions are duller and paler. In the populations from the more arid regions, the back is more grayish or paler brown, the rufous pigment is more "faded," and the rufous area is usually more restricted in extent on both the wing and crown, and, on the crown, becomes invaded or varied anteriorly with gray; the underparts show also a tendency to be "purer," more whitish as a rule. Differences in measurements have been mentioned between some populations but measurements overlap when variation is considered for the species as a whole. Some of the "subspecies" recognized by Peters seem indistinguishable to me, but when geographical variation exists it is quite relative only and slight in most instances.

I have seen two specimens taken at São Paulo de Olivença, on the Rio Solimões in Brazil, which were described by Ripley (1955) as an additional "subspecies," named *pullata*. However, they were misidentified and are, I find, quite normal specimens of *S. albigularis*, not *S. albescens*. This error was corrected promptly by Bond (1956) but this was not known to me when I reached the same conclusion.

The range of *Synallaxis frontalis* is also large (map 9), extending from Maranhão, northeastern Brazil, south to central Argentina, but this species is more stable than the others which vary geographically. Slight population differences can be discerned but are much overshadowed by a cline starting in northeastern Brazil and in Bolivia and Argentina. The populations of northeastern Brazil are bright above, very rufescent on the wing, crown, and tail, and relatively pale and ochraceous on the flanks. But the populations become progressively duller and more grayish on the back, darker rufous on the crown, more brownish on the wing, duskier on the tail, and more grayish on the flanks as they range farther south, the cline culminating in Bolivia and Argentina. The populations of Bahia are more similar to those of northeastern Brazil, and those of the Mato Grosso and Paraguay to the populations of Bolivia; other, more or less vaguely intermediate, populations are found. Three subspecies names exist: *juae* based on specimens from Ceará, Brazil; nominate *frontal-*

is, the type locality of which is Bahia, Brazil; and *fuscipennis* based on specimens from Bolivia; although the distinction is quite clear at the ends of the range, the existence of an evident cline makes subspecific separation most undesirable.

List of the Species of Group One

Synallaxis ruficapilla

Description: Rufous amber brown and bright on the back, and uniform, with a bright reddish brown crown with an orange tinge, and also strongly rufous, but darker, more chestnut, on the upper surface of the wing, and with a dull orange superciliary streak well developed behind the eye, separating the rufous crown from the blackish ear coverts. Feathers of the throat black or dusky black, but with silvery gray tips and margins that conceal the black gular patch to varying degrees when the feathers are not erected or disturbed on the study skin; grayish below the black gular patch, the gray area merging posteriorly into ochraceous brown on the flanks and sides of the abdomen, the center of which is paler, more buffy.

Tail strongly rufous, bright chestnut, composed of eight rectrices which are slightly stiffened, acuminate at the tips, with the three inner pairs moderately graduated, the fourth (or outer) rectrix quite short, but projecting conspicuously beyond the under tail coverts.

Immature Plumage: Similar to that of the adult in general coloration but color pattern much less distinct. The crown is dull, dark orange-brown, not contrasting strongly with the color of the back, and the black gular patch is ill defined. The remainder of the underparts is chiefly ochraceous, or dingy, faintly mottled as the tips and margins of the feathers are somewhat darker, brownish, as a rule.

Range: Southeastern Brazil, from southern Goiás, southern Minas Gerais, and Espirito Santo, south to Rio Grande do Sul, eastern Paraguay, and to Misiones and Corrientes in Argentina; a record from Uruguay is doubtful and probably invalid.

Specimens Examined: 138, including the type of *ruficapilla* in MNHN, and of "*olivascens*" in BM.

Synallaxis superciliosa

Description: Similar to *Synallaxis ruficapilla,* but rufous of the crown darker and duller, burnt sienna, and not uniform, as the forehead is brown, this brown band being rather poorly defined, as well as the superciliary streak, and ear coverts brownish instead of blackish. Black gular patch as a rule more distinct than in *S. ruficapilla,* the base of the feathers being usually purer black and less concealed by the white tips. Remainder of the underparts distinctly paler than in *S. ruficapilla,* chiefly dingy white, smudged with pale brown, darker on flanks.

Tail strongly rufous, composed of eight rectrices, somewhat similar to the tail of *Synallaxis ruficapilla* in coloration and structure, but slightly duller, more chestnut, and with a tendency to be more stiffened, with the webs of the rectrices not quite so well integrated.

Immature Plumage: More distinct than in *Synallaxis ruficapilla,* as the crown is brown and uniform with the back, and the underparts are more distinctly mottled or barred with brown.

Range: Eastern Bolivia (Cochabamba, Santa Cruz, Chuquisaca, Tarija) south to northwestern Argentina (Jujuy, Salta, and Tucumán); altitudinal range varies from about 600 to 2900 m.

Specimens Examined: 37.

Synallaxis frontalis

Description: Back bright brown as in *Synallaxis ruficapilla,* with the crown and upper surface of the wing strongly rufous, but with a band of brown across the forehead, and without a superciliary streak, or streak reduced to a very vague grayish trace behind the eye; sides of the face brown. Black gular patch very distinct, upper breast pale mouse gray; flanks ochraceous, and

center of abdomen whitish. This description is based on specimens from the northern end of the range in northeastern Brazil, the populations becoming progressively duller, more grayish, duller rufous, and more dusky on the tail, as they range farther south (see geographical variation).

Tail strongly rufous, composed of 10 rectrices, and, relatively speaking, regularly but not very sharply graduated, not well stiffened, and with the tips rather blunt, not so sharply acuminate as in *Synallaxis ruficapilla* and *S. superciliosa*.

IMMATURE PLUMAGE: Similar to that of *Synallaxis superciliosa*, with the crown brown and uniform with the back in coloration, but not mottled or barred below, although somewhat smudged or "clouded" with brown on the breast.

RANGE: Eastern and central Brazil from Maranhão and Mato Grosso south to São Paulo, eastern Bolivia (yungas of southern La Paz, Cochabamba, Santa Cruz, Chuquisaca, and Tarija), Paraguay, and northern and central Argentina south to Mendoza, and La Pampa; also Uruguay and southwestern Rio Grande do Sul in Brazil along the Rio Uruguay, from Uruguayana north to at least Itaqui. The Beni, in Bolivia, is usually included in the range, but to the best of my information, this species has not been recorded north of the mouth of the Rio Chapare which is situated in Cochabamba near the border of El Beni.

SPECIMENS EXAMINED: 293.

Synallaxis azarae

DESCRIPTION: Similar above to the three preceding species, with a band of brown across the forehead as in *S. superciliosa* and *S. frontalis*, but band broader and darker as a rule, varying from dark brown to dark grayish olive; no genuine superciliary streak exists, but the region above the eye is dark brown as on the forehead and becomes very faintly paler, more grayish behind the eye; sides of the face gray brown. Black gular patch very distinct, with narrow whitish tips to the feathers; breast and upper flanks dark dingy, "smoky" gray, becoming brownish on the lower flanks, and center of abdomen whitish but more or less distinctly patterned with gray, as the feathers of the upper abdomen and also of the lower breast are gray subapically, in a somewhat crescentic pattern, contrasting with the region above the gray, and below it at the tips of the feathers, which are whitish. This species varies slightly geographically as the coloration of some of its populations is somewhat more saturated than that of others, with a more distinct pattern on the underparts.

Tail strongly rufous, duller and more chestnut in some populations than others, and composed of eight rectrices, which, relatively speaking, are well graduated, somewhat stiffened, not very firmly integrated, and acuminate at the tip.

IMMATURE PLUMAGE: Crown and back brown, uniform, or with faint, narrow, darker margins to the feathers; black gular patch somewhat less distinct than in the adult; and underparts smudged with pale brownish ocher below the gular patch, especially on the breast, the feathers being somewhat mottled or indistinctly barred with darker brown at the edges and tips of the feathers.

RANGE: Andes, between about 1250 and 3700 m., from northern Peru (southern Amazonas, and San Martin), south to La Paz and Cochabamba in Bolivia.[72]

SPECIMENS EXAMINED: 142, including the type of *azarae* in MNHN, and of "*griseiventris*," "*carabayae*," and "*urubambae*," all three in AMNH.

Synallaxis elegantior

Figure 3

DESCRIPTION: This species is similar to *Synallaxis frontalis* in general coloration and both have 10 rectrices. However, the tail of *S. elegantior* is distinctly longer than that of *S. frontalis* and more strongly graduated (see key and table 10), and its rectrices are also somewhat broader and usually more acuminate at the tip. The rufous crown and rufous area of the upper surface of the wing are brighter also in *S. elegantior*, reddish brown with an orange tinge, similar to the coloration of the crown in *S. ruficapilla*, but *S.*

elegantior differs from *S. ruficapilla* and the other three species described so far by being very brightly rufous on both the crown and wing, whereas the rufous area on the upper surface of the wing is darker, more chestnut in the other species. Other differences exist, notably in the structure of the tail which is composed of only eight rectrices in *S. ruficapilla, S. superciliosa,* and *S. azarae,* in the darker underparts which are ochraceous brown in *S. ruficapilla,* and dingy gray in *S. azarae,* whereas *S. elegantior* is very whitish on the abdomen.

IMMATURE PLUMAGE: Quite distinct from that of the adult, and, on the underparts, from the immature plumage of the other four species, as it is strongly ochraceous in *Synallaxis elegantior,* with a tendency to be uniform, paler in some individuals which are dark ochraceous buff, or clay color. The crown and back are brown and uniform.

RANGE: Andes, between about 1100 and 3800 m., from western Venezuela (Trujillo, Mérida, and Táchira), south through Colombia and Ecuador, to northern Peru, south to Lambayeque, southern Cajamarca, Amazonas, and San Martín.

SPECIMENS EXAMINED: 265, including the type of *elegantior* in BM, and of "*media,*" and "*ochracea,*" both in AMNH.

Synallaxis albigularis

DESCRIPTION: Dull grayish brown on the back and forehead, dark dull orange rufous on the remainder of the crown and upper surface of the wing, the brown frontal band is broad, but the rufous area of the wing relatively restricted. Black gular patch quite distinct, breast and flanks gray, becoming olivaceous brown on the lower flanks, abdomen whitish.

Tail olivaceous brown, composed of 10 rectrices that are strongly stiffened, loosely integrated, and sharply acuminate at the tips.

IMMATURE PLUMAGE: Quite different from that of the adult, brown on the crown, the color of the crown and back being uniform and paler brown than in the adult, and almost uniformly dark ochraceous buff on the underparts, but more brownish on the breast and flanks, with the gular patch less well defined than in the adult and more sooty than black.

RANGE: Amazonia, from southeastern Colombia, south through eastern Ecuador and eastern Peru to northern Cuzco, east in the upper Amazonian Basin, to the region at the mouth of the Rio Madeira.

SPECIMENS EXAMINED: 79, including the type of "*S. albescens pullata*" in Peabody Museum, originally described in the wrong species (*S. albescens*).

Synallaxis albescens

DESCRIPTION: Similar to *Synallaxis albigularis,* but differing from it constantly in the structure of the tail, which is composed also of 10 rectrices which are more firmly integrated, not so markedly stiffened, and less sharply acuminate at the tip and relatively blunt; the tail also averages distinctly longer (see key and table 10). *Synallaxis albescens* is also normally paler and more whitish below than *S. albigularis,* more ochraceous, less gray on the breast and flanks, and, as a rule, the rufous areas on its crown and upper surface of the wing are, or tend to be, more restricted.

Synallaxis albescens varies geographically (see discussion), some populations are darker than others, more brownish or grayish, and the variation affects also the saturation of the rufous pigment and the extent of the rufous areas on the crown and wing; the rufous pigment is relatively darker or more faded, the rufous areas on the crown and wing more restricted or not, invaded irregularly by grayish brown in the case of the crown.

IMMATURE PLUMAGE: Similar to that of *Synallaxis albigularis.*

RANGE: Far more extensive than that of any other species, extending from southwestern Costa Rica and Panama, south throughout virtually all of the range of the genus in South America to La Pampa in central Argentina, with the exception of the large region of the upper Amazonian Basin inhabited by *S. albigularis* (map 10). *S. albescens* is found also on Trinidad, and Margarita Island off northern Venezuela, but is

unknown, apparently, in extreme southeastern Brazil (south of northern Rio Grande do Sul), and in Uruguay.

SPECIMENS EXAMINED: 390, including the types of "*josephinae*" in BM, of "*griseonota*" in CM, and of "*australis,*" "*inaequalis,*" "*trinitatis,*" and "*insignis,*" all four in AMNH.

Synallaxis spixi

DESCRIPTION: Umber brown on the back (but varying somewhat individually from specimens which are brighter and more rufescent, to others that are duller and more grayish); with a bright and uniformly rufous crown (without a band of brown on the forehead). Black gular patch unusually distinct, with or without narrow whitish tips to the feathers; and remainder of underparts conspicuously gray, neutral gray with or without a very faint olivaceous tinge, becoming more olivaceous or ochraceous on the lower flanks, and paler, dingy white on the center of the abdomen.

Tail olivaceous brown, composed of 10 rectrices, moderately stiffened, not very firmly integrated, and sharply acuminate at the tip.

IMMATURE PLUMAGE: Differs from that of the adult by lacking the rufous crown, the crown and back being uniformly brown, darker than in the adult, and underparts chiefly ochraceous brown, not gray, with the black gular patch poorly defined.

RANGE: Southeastern Brazil, from southern Espirito Santo and neighboring Minas Gerais, south to eastern Paraguay, Uruguay, and Argentina in Misiones, Corrientes, eastern Santa Fe, and Entre Ríos, to northern Buenos Aires. In the mountains of southeastern Brazil, this species ascends to at least 2000 m.

SPECIMENS EXAMINED: 135, including the type of *spixi* in BM.

Synallaxis hypospodia

DESCRIPTION: A "coarse" species, olive brown on the back, with a chestnut crown, and a relatively narrow olive brown band across the forehead; with the rufous area on the upper surface of the wing relatively large, extending over all the coverts. Black gular patch very distinct, but usually dull, not pure black, with few or no whitish tips to the feathers at its lower half; dingy gray on the breast, pale olivaceous brown on the flanks, and whitish on the abdomen.

Tail dark sooty brown or blackish, composed of 10 rectrices that are unusually broad, with broader webs than in all the other species, not strongly stiffened, well integrated, and relatively blunt at the tip.

IMMATURE PLUMAGE: Uniformly brown on the upperparts, not rufous on the crown, and underparts strongly ochraceous or clay color, not gray, and nearly uniform with the exception of the center of the abdomen; black gular patch poorly defined.

RANGE: Apparently quite extensive from Peru to central and northeastern Brazil, but badly known. This species occurs in eastern Peru where it is recorded from the Departments of San Martin, Junín, and Cuzco; northern Bolivia (Beni); and in Brazil at widely separated localities on the upper Rio Madeira (Humaytha), Mato Grosso (region of Corumba), southern Goiás (Inhumas and Jaragua), northern Bahia, and Ceará.

SPECIMENS EXAMINED: 37, including the type of *hypospodia* in BM, and of "*jaraguana,*" lent to me by the Museum Páulista of São Paulo, erroneously described by Pinto (1936) as a "subspecies" of *S. brachyura.*

Synallaxis infuscata

DESCRIPTION: Grayish brown on the back, and bright reddish chestnut on the crown and upper surface of the wing; the crown is uniformly rufous, without a band of brown on the forehead, and the rufous area on the wing is unusually extensive, including nearly the whole of the wing with only the exception of the dusky dark brown tips of the primaries. Black gular patch quite distinct, but not conspicuous because it does not contrast strongly with the remainder of the underparts which are very dark slaty gray and uniform, with or without a faintly paler area on the center of the lower abdomen.

Tail chestnut, composed of 10 rectrices that are well stiffened and end in moderately acuminate tips, but acuminate over a short distance only.

RANGE: Northeastern Brazil, where it seems to be narrowly restricted to a small region near the coast, extending only from eastern Pernambuco south to neighboring northern Alagoas. This distinctive species is known so far from only eight or nine specimens.

SPECIMENS EXAMINED: 3.

Synallaxis brachyura

DESCRIPTION: Back dark grayish brown, crown reddish chestnut with a broad band of dark gray-brown across the forehead, and rufous area of the upper surface of the wing reddish chestnut also. Black gular patch quite distinct, but more sooty than pure black in some individuals, and remainder of underparts very dark, nearly uniform, but somewhat paler on the center of the lower abdomen, the coloration of the underparts, below the throat, varying from dark slaty gray to dark sooty gray, becoming dark olivaceous gray-brown on the lower flanks. This species varies somewhat geographically but the variation is complicated by a great deal of individual variation and is difficult to describe succinctly. Generally speaking, the coloration of some populations and individuals is more saturated than that of others, including the pigmentation of the rufous areas and gular patch, of the back, which is more "brownish," less gray, and of the underparts which are more "gray," less sooty or slaty.

Tail dark sooty olivaceous brown, nearly "blackish" in some cases, composed of 10 rectrices, well stiffened, with relatively broad webs that are not firmly integrated, and end in moderately acuminate tips.

IMMATURE PLUMAGE: Differs from that of the adult by being uniformly brown or olivaceous brown above, not rufous on the crown; olivaceous gray or umbraceous below the throat which is whitish on the chin, with the "black" area poorly defined.

RANGE: Northern and eastern Honduras, and Costa Rica, south through Colombia to southern Ecuador. The range extends to the Pacific slope and coast in Colombia and Ecuador, but not into the eastern lowlands of these two countries, and ascends to about 2100 m. in the Andes.

SPECIMENS EXAMINED: 262, including the type of "*pudica*" in BM, and of "*caucae*" and "*griseonuchus,*" both in AMNH.

Synallaxis courseni

Figure 3

DESCRIPTION: Back dark neutral gray, slightly tinged with olivaceous brown on the lower back and rump; crown dull rusty red, with a broad band of dark gray across the forehead; rufous area on the upper surface of the wing very extensive and brighter rufous than the crown. Black gular patch very distinct with very narrow whitish tips to the feathers, and remainder of the underparts uniformly dark neutral gray.

Tail exceptionally long, composed of 10 rectrices, and blackish, except for diffused, very ill-defined, narrow rufous areas along the shaft on the inner web of the rectrices; slightly stiffened only, with blunt, or only vaguely acuminate tips.

RANGE: Southern central Peru where it is known only from three specimens collected at a single locality at 2743 m. in the mountains northwest of Abancay, northern Apurimac.

SPECIMENS EXAMINED: 3, including the type of *courseni* in FMNH.

Synallaxis moesta

DESCRIPTION: Dark rufous brown on the back, reddish chestnut on the crown and upper surface of the wing, with a conspicuous dark grayish brown band across the forehead. Gular patch sooty, rather than pure black, with well developed whitish tips to the feathers, and remainder of the underparts uniformly dark olivaceous brown, with or without a very slight tinge of gray on the breast and center of the abdomen. This species varies somewhat geographically (see

discussion), some populations being relatively paler and browner, darker and more grayish, with the rufous of the tail brighter or more chestnut.

Tail chestnut (or slightly brighter rufous), composed of eight rectrices, that are strongly stiffened, and sharply acuminate at the tip.

IMMATURE PLUMAGE: Differs from that of the adult by being uniformly dark brown, or dark sooty brown above, without a rufous crown, and more grayish or umbraceous below, with the tips and margins of the feathers faintly darker, producing a vague mottled appearance.

RANGE: Foothills and lower slopes of the Andes in eastern Colombia and eastern Ecuador, south to northern Peru to the region west of and near Moyobamba in northern San Martín; ascending to about 1400 m.; occurring also in lowlands of northern Loreto, Peru.

SPECIMENS EXAMINED: 58, including the types of *moesta* in BM, and of "*obscura*" in AMNH.

Synallaxis cabanisi

DESCRIPTION: Similar to *Synallaxis moesta,* but slightly brighter and paler, and tail composed of 10 rectrices, instead of eight in *S. moesta.* The rufous tinge is more pronounced on the back of *S. cabanisi,* the underparts are very slightly paler, and the crown is uniformly rufous, without a band of brown across the forehead.

IMMATURE PLUMAGE: Similar to that of *S. moesta.*

RANGE: Peru, from the region of Moyobamba in northern San Martín, south to Puno, and La Paz and Cochabamba in Bolivia, ascending to about 1400 m. in both Peru and Bolivia.

SPECIMENS EXAMINED: 40, including the type of "*fulviventris*" in AMNH.

Synallaxis macconnelli
Figure 3

DESCRIPTION: Similar to both *Synallaxis moesta* and *S. cabanisi,* but very slightly darker on the back. The three species are virtually identical in nearly all respects, but can be differentiated constantly as follows: *Synallaxis moesta* has eight rectrices and its crown is not uniformly rufous, the forehead being conspicuously banded with dark brown; *S. cabanisi* has 10 rectrices and its crown is uniformly rufous, without a band of brown on the forehead; *S. macconnelli* has eight rectrices and its crown is uniformly rufous, as in *S. cabanisi,* not banded with brown as in *S. moesta.*

IMMATURE PLUMAGE: Not examined, but presumably similar to that of *Synallaxis moesta* and *S. cabanisi,* as all three species are certainly closely related.

RANGE: Southern Venezuela, from Amazonas and Bolívar, east to Roraima and Ueitepui on the borders of Venezuela, Guyana, and Brazil, also northern French Guiana. All populations are more or less isolated geographically, apparently restricted only to mountains in Venezuela east to Guyana and Brazil, ascending to about 1900 m. or more in the mountains, but the population of French Guiana is a lowland one. The distribution and irregular geographical variation of *Synallaxis macconnelli* have been discussed above.

SPECIMENS EXAMINED: 31, including the type of *macconnelli* in BM; and the types of "*yavii*" and "*griseipectus*" in the Phelps Collection, both of which are deposited in AMNH.

Synallaxis subpudica
Figure 3

DESCRIPTION: Coloration "mousy," dull pale brown on the back, and dull pale gray below except the throat; dull rusty red on the crown and upper surface of the wing, with a band of dull brown across the forehead. Gular patch black or sooty black, more or less concealed by the grayish white margins of the feathers which are well developed. The underparts are dull pale gray below the throat, but become ochraceous on the lower flanks, and paler, very dingy white on the center of the abdomen.

Tail very distinctive, dull brown and conspicuously elongated, composed of 10 rec-

trices that are very strongly graduated, more so than in any other species, relatively well stiffened but not markedly so, with the webs of the rectrices relatively narrow, loosely integrated. The rectrices taper sharply at the apex, but are not truly acuminate, as the tapering exists only along the inner web, which becomes progressively narrower over a long distance, not on the outer web which is very narrow.

IMMATURE PLUMAGE: Similar to that of the adult, with the exception that it is uniformly brown above, without a rufous crown.

RANGE: Quite restricted, consisting only of the Eastern Andes of Colombia from Santander south to Cundinamarca, between about 2600 and 3000 m. Records from Ecuador in the literature are most probably erroneous.

SPECIMENS EXAMINED: 21, including the type of *subpudica* in BM.

GROUP TWO

KEY TO THE SPECIES

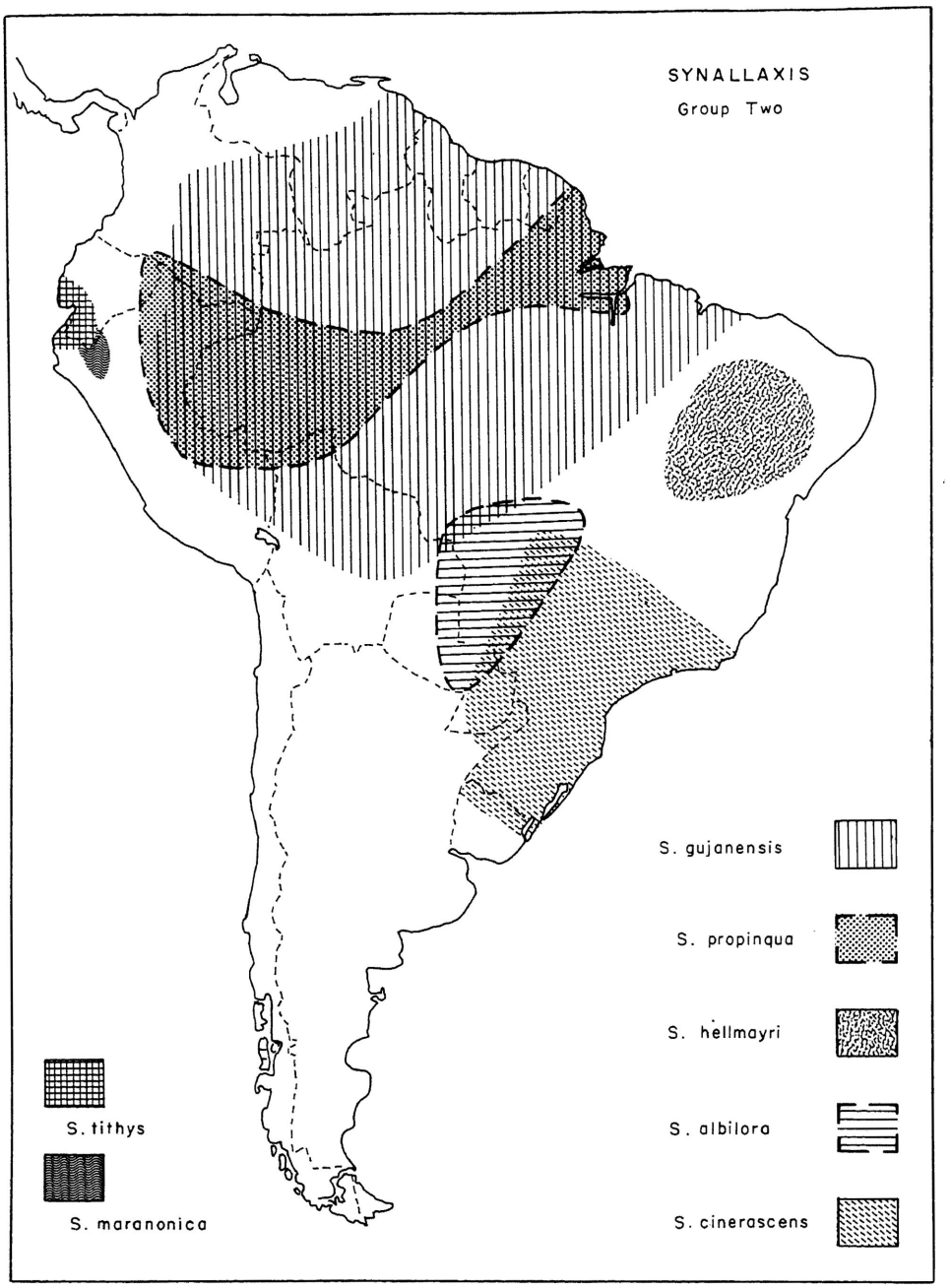
1. Tail with 12 rectrices ..... *hellmayri*
   Tail with 10 or eight rectrices 2
2. Tail with eight rectrices ..... *tithys*
   Tail with 10 rectrices 3
3. Throat white 4
   Throat gray or black 5
4. Crown dull olive brown, contrasting with the color of the back which is very strongly rufous (reddish orange-brown); underparts very bright (orange or buffy orange) below the white throat ..... *albilora*
   Crown and upper back dull olive brown, or grayish brown, uniform as a rule, or with only a very slight contrast between the color of the crown and back ..... *gujanensis*
5. Throat pale gray, with the sooty bases of the feathers concealed ..... *maranonica*
   Throat black, with the black bases of the feathers not completely concealed 6
6. Tail burnt sienna, or ferruginous, with the rectrices strongly stiffened, loosely integrated, and sharply acuminate to an unusual degree; upperparts pale gray-brown; underparts pale dull gray on the breast, whitish on the abdomen ..... *propinqua*
   Tail chestnut, with the rectrices not well stiffened, well integrated, and relatively blunt at the tip; upperparts strongly olive brown; underparts very dark, slaty or dark neutral gray, and uniform or virtually so ..... *cinerascens*

Note that for number 3 above the bases of the feathers of the throat are sooty or black in all the species, but are completely concealed in *Synallaxis albilora, S. gujanensis,* and *S. maranonica* (they are sooty rather than black in all three) by the pale tips of the feathers which are unusually well developed in these three species, creamy white or whitish in *S. albilora* and *S. gujanensis,* gray in *S. maranonica,* with or without narrow silvery white margins and shaft streaks.

MORPHOLOGICAL VARIATION, PHYLOGENY, AND GEOGRAPHICAL VARIATION IN GROUP TWO

The seven species of this group differ from the 16 in Group One by lacking a rufous cap, and from the six in Group Three by not being strongly rufous on the underparts. The upperparts are gray, olive brown, or rufous brown, and uniform with two exceptions, the olive brown crown of *Synallaxis albilora* contrasting with the color of its back which is rufous brown, and the gray crown of *S. tithys* being interrupted by a broad band of black across the forehead. The pattern of the crown of *S. tithys* (though not the coloration) is thus similar to that of the species of Group One and *S. tithys* probably represents a transitional form between the two groups.

Five of the species of Group Two are gray or grayish on the underparts below the throat, ochraceous with a tinge of gray in some populations of *Synallaxis gujanensis,* and buffy orange in *S. albilora.* In these two species the throat is white or dull white superficially as the sooty bases of the feathers are completely concealed. The general similarity in the coloration of the underparts of these two species suggests that they are closely related. They were considered conspecific by Hellmayr (1925), Zimmer (1936b), and Peters (1951), but this opinion is not correct and was questioned as early as 1890 by



MAP 13. Geographical distribution of the seven species of Group Two of the subgenus *Synallaxis* of the genus *Synallaxis*.

Sclater. Their ranges appear to overlap slightly in Brazil (map 13), and the structure of their tail is distinct; both species have 10 rectrices but the rectrices are more strongly graduated in *S. gujanensis,* more strongly stiffened, less well integrated, and quite distinctly more acuminate at the tips which are relatively blunt in *S. albilora.*

The close relationship of *Synallaxis gujanensis* and *S. albilora* is quite clear, but the relationships of the other five species are quite uncertain. The black gular patch is lacking also in *S. maranonica,* at least superficially, and the bases of the feathers of its throat are sooty, rather than pure black, as in the case of *S. gujanensis* and *S. albilora,* but no resemblance seems to me to exist between *S. maranonica* and *S. gujanensis,* contrary to the opinion of Zimmer, who believed they were conspecific. Peters followed Zimmer, but Hellmayr correctly considered that *S. maranonica* is a distinct species, "somewhat similar" to *S. cinerascens.* I agree with Hellmayr to a certain extent, but the resemblance between *S. maranonica* and *S. cinerascens* is superficial; the throat of *S. maranonica* is gray, without a visible "black" gular patch; however, this gular patch is very distinct in *S. cinerascens* and the tips of its rectrices are distinctly acuminate, though not conspicuously so, whereas in *S. maranonica* they are blunt and usually quite rounded. The distribution of the two species argues also against close relationship, *S. maranonica* being restricted to a small region in the valley of the Marañon in Cajamarca and neighboring Amazonas, Peru, whereas *S. cinerascens* is a very characteristic species of southeastern Brazil (map 13).[73]

Taczanowski (1884) implied a certain degree of relationship between *Synallaxis maranonica* and *S. tithys, S. maranonica* "replacing" *S. tithys* inland. However, close relationship between these two species is very doubtful. The nearest relatives of *S. tithys* are probably the species of Group One, although I believe *S. tithys* is best placed in Group Two. The pattern of the crown is distinct in these two species (see above); *S. tithys* has a very distinct sooty black gular patch, whereas *S. maranonica* has none (see above); and the tail of *S. tithys* is very dark brown, "blackish," with somewhat acuminate tips, whereas the tail of *S. maranonica* is chestnut with unusually blunt rectrices.

The measurements of *Synallaxis propinqua* do not differ appreciably from those of *S. maranonica, S. cinerascens,* and *S. tithys,* other than in the size of the bill which is quite long in *S. propinqua* (table 10), but it is quite evident, nevertheless, that *S. propinqua* is a "coarser" bird, and that the structure of its tail is different. The rectrices of *S. propinqua* are very strongly stiffened, much more so than in the other three species, loosely integrated, whereas the webs are well integrated in the other three birds; the tips of the rectrices are exceptionally acuminate in *S. propinqua,* widely separated in the case of the central rectrices, forming a "fork" reaching about 20 mm. in depth when not disturbed. Such a "fork" either does not exist, or is very shallow in the three other species.

The interrelationships of *Synallaxis tithys, S. cinerascens, S. maranonica,* and *S. propinqua* are not clear, but these four species are best grouped together as they are probably more or less distantly related.

The position of *Synallaxis hellmayri* (once put by Peters, 1950, in the monotypic genus *Gyalophylax*) is more uncertain. This species seems to me quite definitely to belong in Group Two, but it has 12 rectrices, as against eight in *S. tithys,* and 10 in the other species, and its bill has a straight culmen with an ascending gonys of the "*Xenops*-type." I have discussed these characters above in the general discussion of the morphological variation of the genus and I believe no undue importance should be attached to them. It is quite possible that *S. hellmayri* retains the ancestral number of rectrices (12) and is something of a relict which is vanishing, known from very few specimens, and for which I have found no field observations although its range is or was relatively extensive.[74] *S. hellmayri* seems best listed after

the four species mentioned, ahead of *S. gujanensis* and *S. albilora* which appear to be closely related.

The only one of the seven species which varies geographically is *Synallaxis gujanensis*. The populations from the northeastern part of the range are relatively more ochraceous below than the populations of Colombia which are more whitish. Color saturation increases in the Amazonian Basin, but in Peru and Bolivia the populations become grayish above and below, less ochraceous below, less brownish above. All differences are merely questions of degree and intermediates are common. *S. simoni* of Hellmayr (1907) is not a form of *S. gujanensis*, but of *S. albilora*, representing only a single individual variant paler than normal for *S. albilora*.

List of the Species of Group Two

Synallaxis tithys

Figure 3

DESCRIPTION: Slaty gray on the crown and upper back grading into olivaceous slaty gray on the lower back, with a broad band of black, or dark sooty slaty gray across the forehead; upper wing coverts and outer webs of the inner primaries orange rufous. Gular patch distinct, but more sooty than pure black with narrow silvery gray or whitish edges to the feathers; remainder of the underparts pale slaty gray, or ashy, nearly uniform, but becoming more whitish on the center of the abdomen.

Tail dark brown, more "blackish" in some individuals than others, composed of eight rectrices that are not strongly stiffened, are well integrated, and somewhat acuminate at the tip.

IMMATURE PLUMAGE: Similar to that of the adult, but more olivaceous, less gray above, and with the black frontal band indistinct; somewhat "mottled" on the breast and abdomen as the ends of the feathers are darker and more brown than gray.

RANGE: Southwestern Ecuador and northwestern Peru, from Guayas in Ecuador, south to Tumbes and northern Piura in Peru.

SPECIMENS EXAMINED: 14.

Synallaxis cinerascens

DESCRIPTION: Uniformly and strongly olive brown above; chestnut on the upper surface of the wing. Black gular patch distinct, and remainder of underparts pale slaty gray, ashy, or neutral gray, virtually uniform, with the exception of the lower flanks which are olivaceous rather than gray, and becoming faintly paler or not on the center of the abdomen.

Tail chestnut, composed of 10 rectrices, slightly stiffened, well integrated, with slightly or moderately acuminate tips.

IMMATURE PLUMAGE: Scarcely distinct from that of the adult, but a little paler and less uniform on the underparts, with very vague, faintly darker tips to the feathers, and gular patch less distinct.

RANGE: Southeastern Brazil, from southern Goiás, southern Minas Gerais, and extreme southern Espirito Santo, south to eastern Paraguay, Misiones in Argentina, and northern Uruguay.

SPECIMENS EXAMINED: 80.

Synallaxis maranonica

DESCRIPTION: Similar to *Synallaxis cinerascens* above, but somewhat duller, less olivaceous, more grayish on the head, more brownish on the back, and with a more extensive and brighter rufous area on the upper surface of the wing. Bases of the feathers of the throat sooty, but without a true gular patch, the throat being ashy gray with or without very narrow silvery white shaft streaks and narrow whitish margins to the feathers; coloration of the remainder of the underparts gray and similar to that of *S. cinerascens*.

Tail chestnut, composed of 10 rectrices, slightly stiffened, very well integrated, blunt at the tip and usually quite rounded.

IMMATURE PLUMAGE: One specimen, which is whiter on the throat, paler, more whitish, below the breast is perhaps not fully

adult and may represent the immature plumage.

RANGE: Northern Peru, in the valley of the Marañon, and side valleys, in Cajamarca and Amazonas.

SPECIMENS EXAMINED: 10.

Synallaxis propinqua

DESCRIPTION: Uniformly dull grayish brown above, with an extensive but rather dull rufous area on the upper surface of the wing. Gular patch distinct, but dull or sooty black, rather than pure black, with distinct narrow whitish tips to the feathers; remainder of the underparts ashy gray on the breast and upper flanks, becoming more olivaceous on lower flanks, and with a very extensive whitish area on the abdomen.

Tail burnt sienna or ferruginous, composed of 10 rectrices that are strongly stiffened, loosely integrated, very sharply acuminate at the tip, the tips of the central pair separating (see discussion above) to form a rather deep "fork" when the feathers are not disturbed.

IMMATURE PLUMAGE: Very distinct from that of the adult, only slightly paler above, but much paler below, pale ochraceous gray or grayish buff, rather than gray on the breast and flanks; brown on the upper surface of the wing rather than with a rufous area; throat creamy white, with the dark gular patch completely concealed.

RANGE: Eastern Ecuador, south through eastern Peru to Madre de Dios, and northern Beni in Bolivia, east, apparently south of the Amazon only, to the region at the mouth of the Rio Tocantins, but also, north of the Amazon, to the Oyapock River in French Guiana.

SPECIMENS EXAMINED: 44, including the type of "*terricolor*" in BM.

Synallaxis hellmayri
Figure 3

DESCRIPTION: Uniformly pale fuscous brown above, with a dull reddish chestnut, or hazel area on the upper surface of the wing restricted to the coverts. Black gular patch somewhat dull but unusually distinct, without any whitish tips to the feathers, except for a few directly under the chin; remainder of the underparts drab brown, darker on the breast (which is only slightly paler than the back), but becoming paler, vaguely cinnamomeous on the center of the abdomen.

Tail blackish and relatively long, composed of 12 rectrices, slightly stiffened only, very well integrated, and very blunt, rounded at the tip. Bill straight with ascending gonys (see fig. 3).

RANGE: This most distinctive species is known from only a few specimens taken in northeastern Brazil in northern Bahia, neighboring western Pernambuco, and in Piauhí.

SPECIMENS EXAMINED: 4.

Synallaxis gujanensis

DESCRIPTION: Uniformly dull olive-brown, or grayish brown on the crown and upper back (or with a very slight, faint contrast between the color of the crown and upper back); bright rufous over a very extensive area on the upper surface of the wing. Bases of the feathers of the throat pale sooty or grayish, but tips of the feathers creamy white and unusually well developed, concealing completely the dark bases; remainder of the underparts chiefly ochraceous, umbraceous, or pale ochraceous gray. This species varies somewhat geographically (see discussion).

Tail strongly rufous (duller, more chestnut in some populations), composed of 10 rectrices, moderately stiffened, not very firmly integrated, and sharply acuminate at the tip.

IMMATURE PLUMAGE: Similar to that of the adult, but with narrow, darker, more brownish margins which produce a faint pattern.

RANGE: Venezuela south of the Orinoco, delta of the Orinoco, and the Guianas, west to the region of Villavicencio at the foot of the Eastern Andes of Colombia, south through eastern Peru to northern and eastern Bolivia, and Brazil, south to central and northeastern Mato Grosso, northern Goiás, and Maranhão.

Specimens examined: 270, including the types of "*canipileus*" and "*colombianus*," both in AMNH.

Synallaxis albilora

DESCRIPTION: Crown dull olive brown, contrasting with the color of the back which is strongly rufous; upper surface of the wing almost wholly rufous with the exception of the dusky dark brown tips of the primaries. Throat creamy white superficially as in *Synallaxis gujanensis*, but remainder of the underparts very much brighter than in *S. gujanensis*, orange or buffy orange, not ochraceous, umbraceous, or grayish as in *S. gujanensis*.

Tail auburn, composed of 10 rectrices, slightly stiffened, relatively well integrated, and relatively blunt at the tip, not sharply acuminate.

IMMATURE PLUMAGE: Very much duller below than that of the adult, much more ochraceous.

RANGE: Central parts of southern Brazil, from central and eastern Mato Grosso, and southern part of central Goiás, south to the region of Asunción in Paraguay.

SPECIMENS EXAMINED: 11, including the type of "*simoni*" in AMNH.

GROUP THREE

KEY TO THE SPECIES

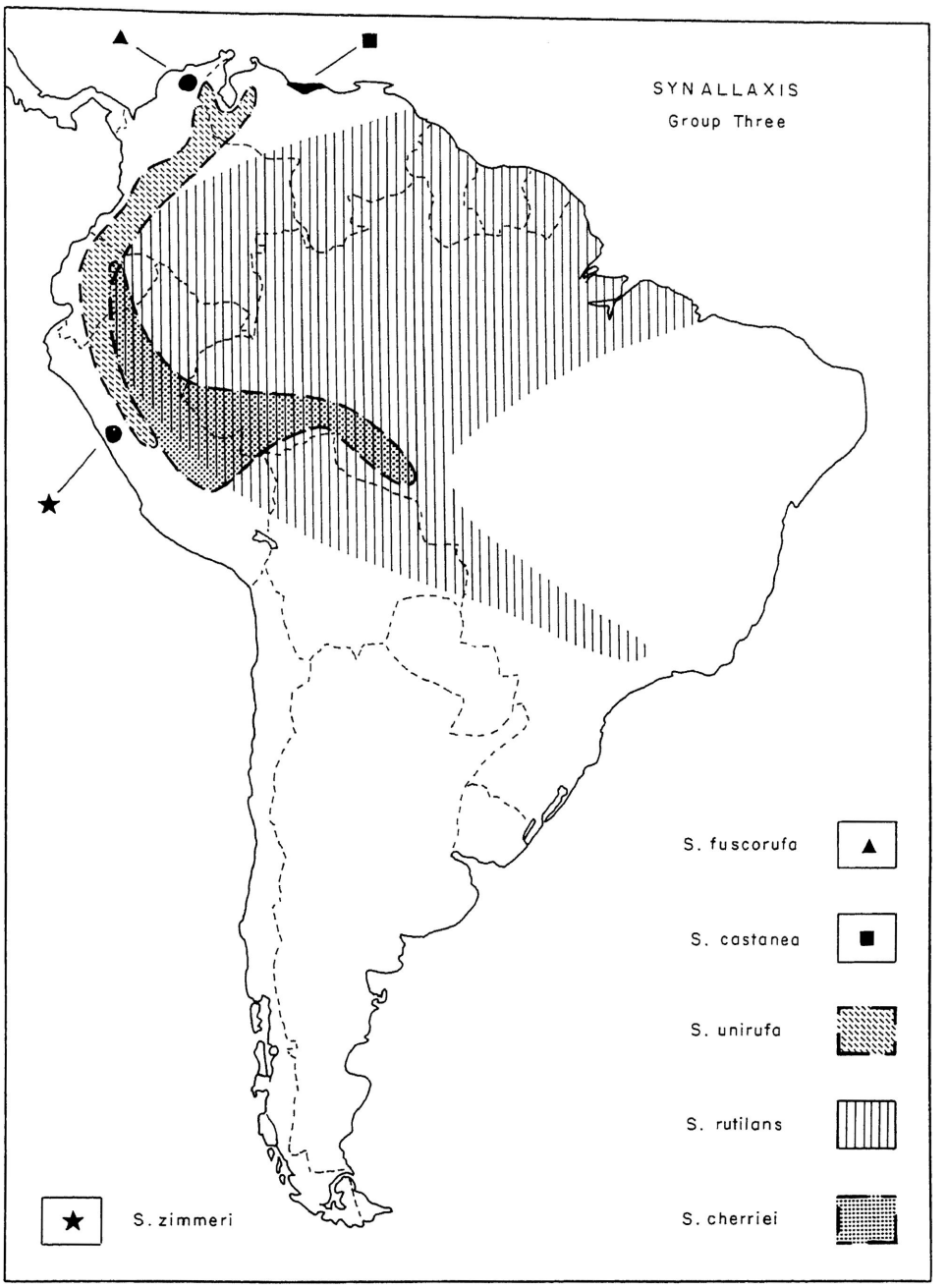
1. Tail with eight rectrices ..... *castanea*
   Tail with 10 rectrices 2
2. Crown ashy gray ..... *zimmeri*
   Crown rufous, or olive brown more or less tinged with rufous; or very dark fuliginous, not tinged with rufous 3
3. Crown uniformly rufous, contrasting strongly from the pale grayish brown back ..... *fuscorufa*
   Crown and back uniformly rufous, or virtually so; or olivaceous brown with or without a slight tinge of rufous; or very dark fuliginous on the head, brown on the back, not tinged with rufous on the head and back 4
4. Crown and back uniformly rufous; black gular patch completely concealed superficially ... *unirufa*
   Crown and back rufous with or without a slight tinge of olivaceous, and with a very conspicuous black gular patch; or crown and back very distinctly olivaceous with or without a slight tinge of rufous; or head very dark fuliginous, back brown, not tinged with rufous 5
5. Crown (and head) very dark fuliginous, back brown, not tinged with rufous on the head and back ..... *rutilans omissa*
   Crown and back rufous, with or without a slight tinge of olivaceous; or crown and back olivaceous, with or without a slight tinge of rufous 6
6. Crown and back rufous, with or without a slight tinge of olivaceous ... *rutilans amazonica*
   Crown and back olivaceous, with or without a slight tinge of rufous 7
7. Gular patch black and very conspicuous ..... *rutilans rutilans*
   Gular patch lacking (the bases of the throat feathers are black, but are completely concealed superficially by the strongly rufous tips and edges ..... *cherriei*

MORPHOLOGICAL VARIATION, PHYLOGENY, AND GEOGRAPHICAL VARIATION IN GROUP THREE

Group Three is composed of six species: *Synallaxis rutilans, S. cherriei, S. unirufa, S. castanea, S. fuscorufa,* and *S. zimmeri* which are all strongly rufous on the underparts although *S. rutilans* varies geographically and the rufous pigment has almost completely vanished in one of its subspecies (*S. r. omissa*). Geographical distribution of Group Three species is illustrated in map 14.

The morphological variation between species of Group Three is distinct, but, nevertheless, all six species appear to be more or less closely related. The variation affects chiefly the coloration of the upperparts, throat, and structure and color of the tail. The upperparts are uniformly rufous or not, gray in *Synallaxis zimmeri,* and sooty brown in *S. rutilans omissa*; the black gular patch is evident or not; and the tail varies from rufous to dark brown or blackish, with eight or 10 rectrices that are distinctly acuminate or blunt at the apex.

Some species seem to be more closely related than others and the two most closely



MAP 14. Geographical distribution of the six species of Group Three of the subgenus *Synallaxis* of the genus *Synallaxis*.

related appear to be *Synallaxis rutilans* and *S. cherriei*. The coloration of *S. cherriei* is very similar to that of some of the populations of *S. rutilans* with the conspicuous exception that the black gular patch of *S. rutilans* is completely concealed superficially in *S. cherriei* by the rufous margins of the feathers. In these two species the tail is blackish, and the rectrices are moderately acuminate in both, but the tail of *S. cherriei* is distinctly shorter than that of *S. rutilans*, shorter than the wing, whereas the tail of *S. rutilans* is longer than the wing. In *S. cherriei* the top of the crown and upper back are olivaceous brown with a tinge of rufous, and the underparts are olivaceous below the lower breast; this coloration and pattern are matched by some of the populations of *S. rutilans*.

Synallaxis unirufa and *S. castanea* are allopatric (map 14) and appear to be closely related, but probably more distantly so than in the case of *S. cherriei* and *S. rutilans*. These two taxa (*unirufa* and *castanea*) were considered to be conspecific by all modern authors before my revision (Vaurie, 1971a) and my paper with Schwartz (1972). Schwartz and I have established with assurance that they are quite distinct species, differing sharply in their vocalizations and in the structure of their tails; the tail is composed of only eight rectrices in *S. castanea*, as against 10 in *S. unirufa*, and is distinctly longer, with broader and better integrated webs in *S. castanea*, the rectrices of which are also much blunter. I may add that the black gular patch is very conspicuous in *S. castanea*, but completely concealed superficially in *S. unirufa*.[75]

The degrees of relationship in the case of *Synallaxis fuscorufa* and *S. zimmeri* cannot be determined with confidence, but the affinities of *S. fuscorufa*, which is isolated on Santa Marta, northern Colombia, are probably with *S. unirufa*. In *S. fuscorufa* the rufous crown contrasts with the color of the back which is dull brown, and its black gular patch is concealed also as in the case of *S. unirufa*.[76]

Synallaxis zimmeri is the only species of the genus isolated on the western slopes of the Andes south of extreme northern Peru and is the most distinct species of Group Three. *Synallaxis zimmeri* is mouse gray above with a rufous rump, and is rufous on the underparts below the grayish, ashy throat, the grayish margins of which do not quite conceal, however, the sooty black bases of the feathers.

Synallaxis rutilans and *S. unirufa* vary geographically, but the variation of *S. unirufa* is not worthy of taxonomic consideration in my opinion; it is very trivial, consisting only of slight variations in the shade or saturation of the rufous pigment. By contrast the geographical variation of *S. rutilans* is strongly marked.

Three trends are evident in the geographical variation of *Synallaxis rutilans*; first, the populations from the northern part of the range (Venezuela and the Guianas, south through northern Brazil east of the Rio Negro, and south to the region extending south of the Amazon from the right bank of the Tapajós east to the left bank of the Tocantins) are olivaceous brown on the top of the head and back; second, the olivaceous pigment has disappeared completely or is reduced to a faint trace in the populations distributed in Brazil in the region west of the Rio Negro and Tapajós, extending west to eastern Colombia, eastern Ecuador, eastern Peru, Bolivia, and south to central Brazil, east to São Paulo; these populations are strongly rufous, not olivaceous on the head and back; third, in northeastern Brazil, the rufous pigment has vanished from the whole of the plumage with the exception of the rufous area on the upper surface of the wing, although irregular traces of it persist on the back and breast that are better indicated in some individuals than others; these populations, which are very fuliginous throughout, are distributed from the right bank of the Tocantins, east to Pará and Maranhão.

Slight differences in coloration can be noted, usually in average only, in the populations involved in the first two trends (olivaceous versus rufous upperparts). These slightly different forms have been named but

are not of subspecific importance in my opinion; to recognize these forms nomenclaturally would serve only to obscure the pattern of geographical variation described above. I believe that only three subspecies should be admitted, representing the three trends: nominate *rutilans* Temminck, 1823, for the olivaceous populations; *amazonica* Hellmayr, 1907, for the rufous populations; and *omissa* Hartert, 1901, for the fuliginous populations. As first reviser, I select *amazonica* (Hellmayr, 1907, p. 14) as the name of the rufous populations, rather than *tertia* (Hellmayr, 1907, p. 15), which Hellmayr (1925) himself later stated is "closely similar" to *amazonica*.

Synallaxis cherriei varies somewhat individually but I cannot detect that it varies geographically after comparing specimens from Brazil (the type of *rufogularis* Cherrie), Peru, and Ecuador (the type of *napoensis* Gyldenstolpe). The name *rufogularis*, proposed for this species by Cherrie (1916), was preoccupied by *Synallaxis rufogularis* Gould, 1839, and the species was renamed *cherriei* by Gyldenstolpe (1930), who, in the same paper described *napoensis*, but Gyldenstolpe's comparative material was insufficient and consisted only of a single specimen from Ecuador.

List of the Species of Group Three

Synallaxis rutilans

Description: Strongly rufous, reddish chestnut on the forecrown, face (except for the lores which are dull black or grayish black), sides of the neck, upper surface of the wing (other than the primaries which are very dark brown, sometimes verging on blackish), breast, upper flanks, and upper abdomen, the rufous pigment being brighter and paler on the forecrown, deeper chestnut on the wing, verging on burnt sienna on the flanks and upper abdomen; top and posterior part of the crown, and back olivaceous brown, with a more or less pronounced rufous tinge which disappears on the lower back and upper tail coverts which are dark raw umber. Gular patch sooty black and very distinct; lower abdomen brownish olive or fuliginous.

Tail blackish, composed of 10 rectrices, slightly stiffened, not very firmly integrated, moderately acuminate at the tip.

Immature Plumage: Duller than that of the adult, with the rufous areas more restricted, especially on the underparts, and with the gular patch grayish, rather than black. The throat, breast, and abdomen are also "streaked" to an individually highly variable degree as the shafts of the feathers are paler, normally very narrowly and very faintly so on the throat and breast; the streaks are usually not well defined, but they broaden, as a rule, and become more conspicuous on the lower breast and abdomen.

This species varies geographically (see discussion) and the description given above is based on nominate *Synallaxis r. rutilans*; in *S. r. amazonica*, the olivaceous pigment has disappeared completely, or virtually so, from the upperparts and the back is strongly rufous, reddish chestnut, verging on reddish mahogany; in *S. r. omissa*, the rufous pigment has vanished from the whole of the plumage, with the exception of the rufous area on the upper surface of the wing, and this subspecies is dark and fuliginous throughout. In the immature plumage, the streaking does not seem to exist in *S. r. amazonica*, or is hardly discernible, but the tips of the feathers are narrowly bordered with dark brown, giving a somewhat "mottled" appearance; in *S. r. omissa*, the streaks exist, but are extremely faint and ill-defined. No geographical variation is discernible in the tail.

Range: Venezuela, south of the Orinoco, and the Guianas, west to eastern Colombia, and south through eastern Ecuador and eastern Peru to northern and eastern Bolivia, and through Brazil, to Pará and eastern Maranhão in the east, to the Mato Grosso in central Brazil, and east from the southern Mato Grosso to São Paulo. For distribution of the three subspecies I recognize, see discussion of the geographical variation.

Specimens Examined: 286, including the

types of *amazonica, omissa,* "*dissors,*" "*confinis,*" and "*caquetensis,*" all in AMNH.

Synallaxis cherriei
Figure 3

DESCRIPTION: Coloration and pattern generally similar to that of nominate *Synallaxis rutilans* (olivaceous above, rufous below), but with the conspicuous exception that the black gular patch is completely concealed superficially by the rufous tips of the feathers in *S. cherriei.* Other slight differences to be noted are that the olivaceous pigment is slightly darker in *S. cherriei*; the lower back and rump more fuliginous, less umbraceous or brownish; the rufous area on the upper surface of the wing is more restricted (to the coverts, or only to their margins in *S. cherriei*); and that the rufous pigment of the face, neck (including the throat), and breast is brighter, and is usually more restricted to the breast, not extending so far down onto the abdomen as a rule.

Coloration and structure of the tail similar to that of *Synallaxis rutilans,* but the tail of *S. cherriei* is shorter—shorter than the wing, whereas the tail of *S. rutilans* is longer than the wing (table 10).

IMMATURE PLUMAGE: Differs very distinctly from that of the adult by a general absence of the rufous pigment which is represented only by a ferruginous tint on the forehead, superciliary region, sides of the head and neck, and upper breast, and to rufous-chestnut margins on the greater upper wing coverts. The throat is whitish with narrow dusky tips to the feathers, and the feathers of the lower breast and upper abdomen are also narrowly bordered with dark brown; the coloration of the upperparts is darker, deeper olive brown than in the adult, without a rufous tinge.

RANGE: Not well known, but recorded from eastern Ecuador, south through eastern Peru to Ayacucho and northern Cuzco, east to Rondonia (Barão de Melgaço on the upper Rio Ijiparana) in western Brazil.

SPECIMENS EXAMINED: 9, including the type of *rufogularis* (the name under which this species was first described; but it proved to be preoccupied) in AMNH, and of "*napoensis*" in NRS.

Synallaxis unirufa

DESCRIPTION: Uniformly rufous, with the exception of the lores which are black or blackish, and the tips of the primaries which are dark dusky brown; the feathers of the throat are blackish at the base, but the black gular patch is either concealed superficially by the rufous tips and edges of the feathers, or only shows through faintly on the surface. The shade of the rufous pigmentation is difficult to characterize as it varies somewhat individually, geographically, and in different areas of the plumage, but is chiefly reddish auburn or dull reddish chestnut above, paler on the face and underparts, also on the forehead or not, varying from dark rufous cinnamon, to tawny, and russet.

Tail chestnut or reddish bay, composed of 10 rectrices, moderately stiffened, not firmly integrated relatively speaking, and acuminate at the tip.

IMMATURE PLUMAGE: Quite distinct from that of the adult, not rufous, but dark amber brown above, with or without a very faint olivaceous tinge on the head and upper back; paler on the underparts which are very dark ochraceous, more or less suffused with raw umber, and with a vague ferruginous tinge on the breast better indicated in some individuals than others; dark buff, or very dusky and "cloudy," on the throat, with or without pale sooty or grayish bases to the feathers.

RANGE: Andes, from western Venezuela (Trujillo, Mérida, and Táchira) and Sierra de Perijá, south through Colombia and Ecuador to Pasco in Peru. The normal altitudinal range varies between about 1700 and 3200 m., but this species has been recorded higher, to nearly 3700 m. in Ecuador, as well as lower, down to about 1200 m. and 1300 m. in Colombia and Venezuela.

SPECIMENS EXAMINED: 70, including the types of "*meridana*" and "*ochrogaster,*" both in AMNH, and of "*munoztebari*" in the Phelps Collection, on deposit in AMNH.

Synallaxis castanea
Figure 3

DESCRIPTION: Strongly rufous and virtually uniform, as in *Synallaxis unirufa,* but with the conspicuous exception that the black gular patch in *S. castanea* is boldly defined, pure black, and not concealed as in *S. unirufa*. The rufous pigmentation of *S. castanea* is also paler and brighter throughout than that of *S. unirufa,* bright English or Light Red, or more reddish cinnamon, less dull.

Tail uniformly and strongly rufous, but somewhat darker and duller, more "chestnut" than the coloration of the body plumage, conspicuously elongated, composed of eight rectrices, slightly stiffened, with broad and well-integrated webs, blunt or relatively blunt at the tip, not very distinctly acuminate as in *S. rutilans*.

IMMATURE PLUMAGE: Differs from that of the adult by being more "brownish," less rufous and duller throughout, with a gular patch which is poorly defined and very dull; faintly "mottled" on the head and underparts, as the feathers are usually narrowly darker at the edges.

RANGE: Coastal cordillera of northern Venezuela in Aragua, Distrito Federal, and Miranda, between about 1300 and 2200 m.

SPECIMENS EXAMINED: 58, personally, including the type of *castanea* in MNHN; a somewhat larger number were also examined for me, following my directions, in the Phelps Collection in Caracas, and in the collection of the Munich Museum.

Synallaxis fuscorufa
Figure 4

DESCRIPTION: Rufous, dull reddish chestnut on the head and crown, which contrast strongly with the color of the back which is dull pale grayish brown; rufous also on the face, throat (with the black gular patch completely concealed by the rufous tips and edges of the feathers), and remainder of the underparts, but brighter, more ferruginous and cinnamomeous on the face and underparts than on the top of the head, becoming umbraceous on the lower flanks, and paler rufous, more ochraceous, on the lower abdomen. Rufous area on the upper surface of the wing chestnut and extensive.

Tail reddish chestnut, composed of 10 rectrices, strongly graduated, slightly stiffened, well integrated, slightly acuminate at the tip.

RANGE: Restricted to the Santa Marta Massif of northern Colombia where it is distributed between about 760 and 2800 m.

SPECIMENS EXAMINED: 2, including the type of *fuscorufa* in BM.

Synallaxis zimmeri
Figure 3

DESCRIPTION: Gray on the upperparts with the exception of the rump and upper tail coverts which are strongly rufous, pale dull reddish chestnut; the crown is ashy gray, but the back, above the rump, is more brownish than the crown, "warmer" gray. Underparts very strongly rufous, pale English or Light Red, or strongly dark reddish cinnamon, below the throat which is pale ashy gray superficially, the gray margins and tips of the feathers concealing almost completely the black bases of the feathers, the grayish part of the feathers being very faintly whitish along the shaft, forming very vague "streaks." Rufous area on the upper surface of the wing chestnut and restricted chiefly and irregularly to the coverts.

Tail well elongated, composed of 10 rectrices, slightly stiffened only, very well integrated, and very blunt, rounded at the tip. The coloration is variegated, the central pair of rectrices is almost wholly very dark brown, almost "blackish," with the exception of a narrow chestnut elongated wedge along the outer web at and near the base of the feather; the extent of the rufous area increases progressively and externally on the other rectrices and the two outer pairs are almost wholly rufous.

RANGE: This species seems to be rare and very restricted in its distribution, known only from four specimens, taken in two small valleys, where it occurs between 1900 and 3000 m., near Colcabamba, situated west of Huarás, on the western slopes of the Andes in central Ancash, central Peru.

SPECIMEN EXAMINED: 1.

GROUP FOUR

KEY TO THE SPECIES

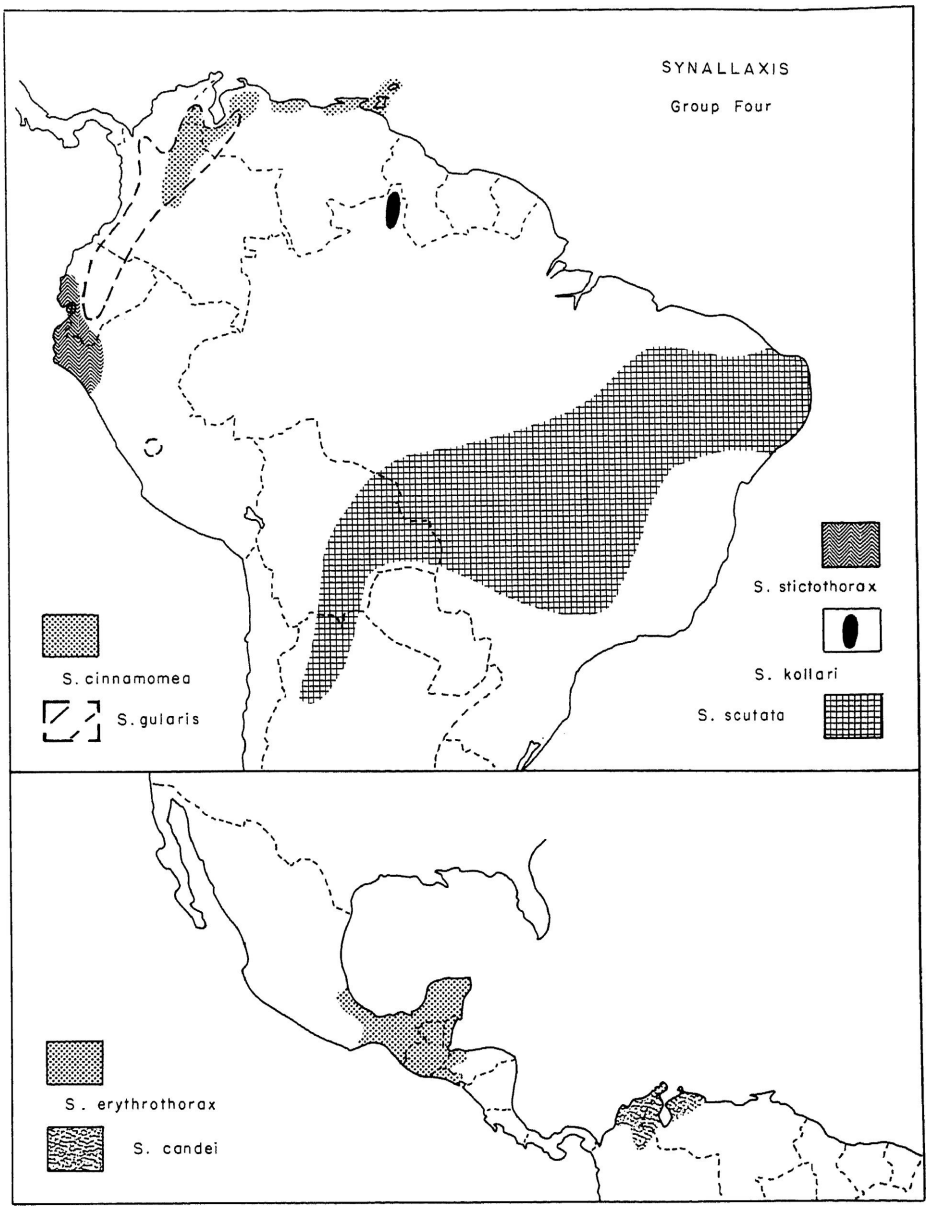
1. Upper surface of the wing dark brownish orange, without a rufous patch ..... *gularis*
   Upper surface of the wing rufous to a varying extent, but with a very distinct rufous patch 2
2. Underparts streaked (or spotted) on the breast, or on both the breast and abdomen 3
   Underparts not streaked or spotted 4
3. Streaks (or spots) restricted to the upper breast; abdomen and throat white, the sooty bases of the feathers of the throat being completely concealed by the white tips of the feathers ..... *stictothorax*
   Streaks not restricted to the upper breast (extending very heavily and conspicuously over the whole of the underparts in some populations); black gular patch not completely concealed; abdomen not white, its ground coloration varying from dark rufous brown to dark ochraceous, or dark buff ..... *cinnamomea*
4. Crown gray or olivaceous gray, contrasting very sharply with the coloration of the back which is strongly rufous and bright 5
   Crown dark grayish brown, uniform with the back, or contrasting only slightly from the paler, more brownish back 7
5. Lores, ear coverts, and throat deep black, with the black face divided most conspicuously from the black throat by a broad band of pure white ..... *candei candei*
   Lores white or grayish, ear coverts buffy, pale brown, or strong dark rufous cinnamon, not separated from the black throat by a conspicuous and broad band of pure white .. 6
6. Lores grayish; ear coverts strong dark rufous cinnamon; throat sooty black with narrow white tips to the feathers under the chin and at the upper half of the black patch; breast dark rufous cinnamon ..... *kollari*
   Lores white; ear coverts buffy or pale brown; superficially visible portion of the black gular patch restricted only to the lower half of the throat or less; breast pale buffy, pale grayish white, or pale cinnamon .. *scutata*
7. Crown and back uniformly dark grayish brown; breast and upper abdomen extensively dull reddish chestnut; center of lower abdomen gray; rectrices very well stiffened, not very firmly integrated, and sharply acuminate at the tip ..... *erythrothorax*
   Crown dark grayish brown, contrasting with the brown back, but not sharply so; rufous area on the underparts more restricted to the breast, and ferruginous rather than reddish chestnut; center of the lower breast and abdomen whitish; rectrices moderately stiffened only, very firmly integrated, with blunt, rounded, not acuminate tips ..... *candei atrigularis*

MORPHOLOGICAL VARIATION, PHYLOGENY, AND GEOGRAPHICAL VARIATION IN GROUP FOUR

Group Four is composed of seven species: *Synallaxis erythrothorax, S. cinnamomea, S. stictothorax, S. candei, S. kollari, S. scutata,* and *S. gularis*. This group is heterogeneous but its species seem best grouped together as they do not appear to be closely related either to the species in groups One, Two, or Three, or to one another, with the probable exception of *S. candei, S. kollari,* and *S. scutata*.

In these three species, placed by Peters (1950, 1951) in the genus *Poecilurus* the crown is grayish brown or olivaceous gray, contrasting sharply with the coloration of the back which is bright rufous and uniform; the rufous hue is difficult to define but is perhaps best characterized as a rich, dark shade of reddish cinnamon, with a slight vinaceous tinge in *Synallaxis candei* and some individuals of *S. scutata*. In these two species, which vary geographically, some populations (*atrigularis* in *S. candei,* and *whitii* in *S. scutata*) are plain dull olive brown on the back rather than rufous, and, in all three species, the tail is strongly rufous, with rectrices that are very well integrated, and unusually blunt and rounded at the tip in *S. candei* and *S. kollari,* though not in *S. scutata* in which the apex is distinctly acuminate. These three species appear to be related, but some differences which exist in the color pattern of their head and throat, and their widely disjunct distribution (map 15) suggest that this relationship is relatively distant.[77]

I have started the sequence of Group Four with *Synallaxis erythrothorax* and ended it with *S. gularis*. The latter is the most aber-



MAP 15. Geographical distribution of the seven species of Group Four of the subgenus *Synallaxis* of the genus *Synallaxis*.

rant species in Group Four and the entire genus because it lacks a rufous area on the upper surface of the wing and its black gular patch has virtually vanished. A rufous area on the upper surface of the wing, and a black gular patch exist in all the other members of the genus, although the gular patch may be more or less completely concealed superficially, and the bases of its feathers may be more gray or sooty than pure black. In *S.*

gularis, the melanistic pigment, which varies from dark gray to sooty black, exists only on one or two rows of feathers at the very base of the throat, forming a more or less sharply defined "necklace" above which the feathers are white, without dark bases. I have mentioned earlier that a monotypic genus (*Hellmayrea*; Sztolcman, 1926) was proposed for *S. gularis* because its bill is "thin" and its tail very short, but these characters vary interspecifically in *Synallaxis* and the only significant differences which distinguish *S. gularis* are the two mentioned above (lack of a rufous area on the wing and virtual elimination of the black gular patch). One can grant that these differences are a legitimate reason for placing *S. gularis* at the end of the species sequence, but not for generic separation.

The affinities of *Synallaxis erythrothorax* are uncertain, although *S. erythrothorax* is normally associated with *S. rutilans* (of Group Three) in systematic lists. In fact, Peters (1951) listed *S. erythrothorax* between *S. rutilans* and *S. cherriei*, which is certainly incorrect, as *S. rutilans* and *S. cherriei* are very closely related, in my opinion, to each other, but not to *S. erythrothorax*, which they resemble only superficially.

The affinities of *S. cinnamomea* and *S. stictothorax* are completely obscure to me, but, in any event, it seems obvious that these two species are not closely related although they differ from all the other species of *Synallaxis* by being streaked on the underparts. However, the streaking is more probably fortuitous than evidence of relationship because its pattern and distribution are quite unlike in the two species. *Synallaxis cinnamomea* is a very richly colored species, heavily and broadly streaked over the whole of its underparts, including the throat, in most of its populations, whereas *S. stictothorax* is quite pale throughout, and its streaking is restricted only to the upper breast, the streaks being modified into mere spots in some populations.

Peters (1951) stated that he retained *stictothorax* in *Synallaxis* "with some misgivings" because its rectrices are blunt at the tip and it is much whiter below than the other members of the genus. However, it seems quite certain that *S. stictothorax* is congeneric with the other species although its nearest relative is difficult to determine.

The difference in the coloration of the underparts noted by Peters is relative and not constant in the case of the throat, as Peters apparently failed to observe that the black gular patch exists in *Synallaxis stictothorax*, although it is concealed superficially by white as in the case of other species of *Synallaxis*. It seems unnecessary also to return here to a discussion of the structure of the tail and the shape of the tips of its rectrices. I have given abundant evidence throughout my account of *Synallaxis* to establish that the morphology of the tail varies a great deal specifically and that these variations are certainly not of generic importance.

Six of the seven species in Group Four vary geographically; the exception is *Synallaxis kollari*, which has an extremely restricted range. This geographical variation is worthy of taxonomic consideration in five species (*S. cinnamomea, S. stictothorax, S. candei, S. scutata*, and *S. gularis*), but not in *S. erythrothorax* where it is very trivial.

The only evidence of geographical variation which seems to me to exist in *Synallaxis erythrothorax* is that in the populations of the lowlands and coastal region of the Pacific in Central America, the lower flanks average very faintly paler and the gular patch is somewhat more grayish, less blackish as a rule.

The geographical variation in the coloration and streaked pattern of *Synallaxis cinnamomea* is strongly marked. The populations of Colombia (nominate *cinnamomea*) are the most richly colored; in this subspecies birds are dark rich rufous brown on the upperparts, Mahogany Red, and very strongly and darkly ferruginous below the black gular patch, heavily, but not sharply streaked as a rule on the breast and abdomen. Birds from northeastern Venezuela (*S. c. striatipectus*) are more heavily and sharply streaked than nominate *cinnamomea*; their streaks contrast far more because the ground

coloration is very considerably paler in the birds of Venezuela, more buffy or cinnamomeous, less dark and rusty than in the birds of Colombia. The white spots on the throat are larger also in the birds of Venezuela, and coalesce or tend to coalesce to form longitudinal streaks, and the upperparts are duller brown and somewhat paler than in nominate *cinnamomea*.

The two insular populations (*S. c. carri* of Trinidad, and *S. c. terrestris* of Tobago) are also quite distinct. They are very poorly and indistinctly streaked below the throat and *carri* is very dark, dark bister brown on the breast and abdomen, much darker than any other population, whereas *terrestris* is quite pale, paler than any other population. Other differences can be noted in the geographical variation of this species, for instance in the relative development of the superciliary streak, saturation of the rufous pigment of the tail and upper surface of the wing, and in the number of rectrices, which, as mentioned above, varies from 10 to eight, in about the same proportion, in the populations of Trinidad and Tobago, whereas a count of 10 seems to be constant on the continent in adults. *Synallaxis cinnamomea* is quite plastic and other populations have been named from Venezuela. However, these forms differ only in minor respects from *S. c. striatipectus* and it seems to me their recognition is not useful as it serves only to obscure the pattern of the geographical variation that I have outlined above.

Subspecies I recognize in *S. cinnamomea* are the following: nominate *cinnamomea* in Colombia, *striatipectus* in Venezuela, *carri* in Trinidad, and *terrestris* in Tobago. I am uncertain about the subspecific status of the birds of the Sierra de Perijá. I have not examined these specimens but I believe they belong to nominate *cinnamomea*. This is suggested by Phelps and Phelps (1946) who identified three specimens from this region as nominate *cinnamomea* when describing another subspecies of *cinnamomea* from western Venezuela, but, without explanation, the Sierra de Perijá was included later by Phelps and Phelps (1963) in the range of the form described in 1946, which may have been an error.

The range of *Synallaxis stictothorax* is not very extensive, including only the region from southwestern Ecuador south to northwestern Peru, but the birds of Peru (other than those from Cajamarca, see below) have a more rufous tail, less invaded by dusky areas, a more extensive rufous area on the upper surface of the wing, and are slightly more rufescent brown on the back, less grayish, than the birds of Ecuador. The differences between these populations are relative only, but are sharper in birds from the valleys of the Marañon and Rio Chinchipe in Cajamarca. The latter (which have been named *S. s. chinchipensis*) resemble the birds of Ecuador in being grayish above (although they are slightly darker and more uniform with little or no contrast between the color of the crown and back), in the extent of the rufous area on the wing, and in the color of their more dusky tail—but they differ quite distinctly from them and from those of the other regions of northwestern Peru by being grayish or pale olivaceous on the lower flanks (rather than dark buff or cinnamomeous), by having a much more poorly defined superciliary and post-ocular streak, and by being more spotted than streaked on the breast. Although the population of *stictothorax* which inhabits northwestern Peru is clearly differentiated from that of southwestern Ecuador, their ranges are continuous and the differences between the two populations are relative only, whereas I attach greater taxonomic importance to the existence of a population in the valleys of Cajamarca (*chinchipensis*) which is apparently isolated and more sharply differentiated.

In *Synallaxis stictothorax* I recognize nominate *stictothorax* ranging from southwestern Ecuador to northwestern Peru, and *chinchipensis* in the valleys of Cajamarca.

In *Synallaxis candei,* the birds of Venezuela and northern Colombia have a dark crown which is olivaceous gray and contrasts sharply with the color of the back which is reddish cinnamon, but these birds with a rufous back are replaced in the Mag-

dalena Valley, south of about 9° N., by a population (*S. c. atrigularis*) in which the back is wholly olive brown, without a trace of rufous; *atrigularis* differs also from nominate *candei* by lacking a rufous post-ocular streak, by having a less distinct white malar streak, and by being duller, more ferruginous on the breast. Thus, the geographical variation of *S. candei* is similar to that of *S. scutata* in the transformation in the color of the back from strongly rufous to olive brown, but is more abrupt in *S. candei* as its range seems to be far too restricted to permit much clinal variation, although some intermediates exist according to Hellmayr (1925). The birds of Venezuela and those of Colombia (north of the range of *S. c. atrigularis*) have been divided subspecifically, but the difference is hardly discernible in the specimens I have seen.

In *Synallaxis candei* I recognize nominate *candei* in Colombia and Venezuela, replaced by *atrigularis* in the middle Magdalena Valley south of about 9° N.

The geographical variation of *Synallaxis scutata* is strongly clinal; birds from northeastern Brazil are grayish brown on the crown and hind neck, which contrast very sharply with the reddish cinnamon color of the back, but the brownish area spreads farther onto the back as the populations range farther south, and the cline culminates in southwestern Mato Grosso, Brazil, in Bolivia, and in northwestern Argentina where the whole of the upper parts have become grayish olive brown, the rufous pigment persisting only as a slight trace on the rump. A corresponding cline exists in the coloration of the underparts which are chiefly whitish at the northern end of the range, becoming progressively more buffy and ochraceous farther south. Many populations are intermediate. The populations that are grayish olive brown on the back and darker below have been named *S. s. whitii,* which is based on specimens from Argentina, whereas the type of nominate *S. s. scutata* came from Bahia.

In *Synallaxis scutata,* I recognize two subspecies, nominate *scutata* and *whitii,* which represent the two extremes of a strongly marked cline.

The geographical variation of *Synallaxis gularis* requires further study because two forms with distinct coloration are represented by trade skins from Bogotá. In one form, the plumage is very rufous; its coloration is difficult to describe accurately, but it is more or less brownish orange, or rusty brown, on the upperparts, and paler below, dull orange rufous, or dark rusty cinnamon below the throat. Hellmayr (1925) assumed that the type of *gularis* Lafresnaye, which was apparently a trade skin from "Colombia," was a specimen of this form with rusty underparts. In the second form, the underparts are distinctly more "grayish," more umbraceous, less rufous. Three specimens of the second form seen by Chapman from the Andes of Mérida, Venezuela, were named *cinereiventris* by him, and, to the best of my knowledge, all the specimens that have been taken so far in Venezuela are similar to them. A third, but not very distinct form, has been described from the Sierra de Perijá and named *brunneidorsalis,* which is similar below to *cinereiventris,* but is more brownish, less rufous on the upperparts.

The range of nominate *Synallaxis gularis* extends from Colombia (with the exception of the Páramo de Tamá on the border of Venezuela, and probably the Sierra de Perijá), south through Ecuador to perhaps central Peru, but the subspecific status of the birds of Peru is unknown. Only a single specimen seems to have been taken in Peru to date (at Maraynioc, Junín); it was named *rufiventris* by Berlepsch and Sztolcman in 1896. Hellmayr (1925) examined it and found it to be darker than specimens from Ecuador, but he apparently was not satisfied that this form was truly distinct, as he remarked that "more material is needed to show whether this form is really distinct from the birds inhabiting Ecuador and western Colombia." This specimen was kept in the Warsaw Museum, but has disappeared since Hellmayr saw it, probably lost or destroyed during the war.

In *Synallaxis gularis* I recognize two sub-

species: nominate *gularis* with rusty underparts in Colombia, Ecuador, and probably Peru, and *cinereiventris*, with grayish underparts, in Venezuela.

List of the Species in Group Four

Synallaxis erythrothorax

DESCRIPTION: Dark, dull grayish brown above on the head and back, uniform, or virtually so, with or without the head slightly darker and more grayish than the back; without a superciliary streak, and with the sides of the face slaty or dark brown. Breast and upper flanks strongly but rather dull reddish chestnut, becoming umbraceous on the lower flanks, and grayish, very faintly mottled, on the abdomen; the rufous area is quite extensive and varies individually, invading the upper abdomen in many specimens. Black gular patch very conspicuous, deeper and purer black, duller, more sooty in some individuals, with its feathers narrowly tipped with white under the chin, and, to a lesser extent, on the upper half of the throat. Rufous area on the upper surface of the wing very extensive, brighter chestnut than the breast as a rule.

Tail chestnut or bay, composed of 10 rectrices, very well stiffened, not firmly integrated, and sharply acuminate at the tip.

IMMATURE PLUMAGE: Differs distinctly from that of the adult by being darker above, more fuliginous, less brown, and by being almost uniformly brown, not rufous, below the throat, though more grayish on the center of the abdomen; black gular patch much less distinctly defined, and grayish or sooty, less black.

RANGE: Southern Mexico, from south central Veracruz, and the region of the isthmus in Oaxaca, south to northwestern Honduras and El Salvador.

SPECIMENS EXAMINED: 155, including the type of "*pacifica*" in AMNH.

Synallaxis cinnamomea

Figure 4

DESCRIPTION: Dark rufous brown, mahogany red, on the upperparts, with or without a very faintly indicated post-ocular streak. Dark, and very strongly ferruginous red below the black gular patch, but browner on the lower flanks, and heavily, but not very sharply streaked with rufous cinnamon or buffy cinnamon; the cinnamomeous area of the individual feathers follows the shaft and adjacent sides and is more or less distinctly bordered and outlined by the outer edges of the feather which is dark brown. Black gular patch very conspicuous, but with very distinct guttate white spots which form longitudinal "streaks," but do not coalesce as a rule. Rufous area on the upper surface of the wing very extensive and dark reddish chestnut.

Tail chestnut or bay, composed of 10 rectrices, well stiffened but not markedly so, not firmly integrated, and acuminate at the tip.

IMMATURE PLUMAGE: Browner, less rufous throughout than that of the adult, with the streaks only very vaguely indicated, the plumage being more mottled than streaked; and gular patch quite indistinct, more dusky than blackish, and blurred, rather than distinctly spotted with white.

This species varies very strongly geographically (see discussion). The description given above is based on nominate *S. c. cinnamomea* from Colombia, but the populations (*S. c. striatipectus*) of Venezuela are more heavily and sharply streaked on a quite distinctly paler ground, have larger white spots on the throat which coalesce as a rule, and have a better defined post-ocular streak. In the populations of Trinidad (*S. c. carri*), and of Tobago (*S. c. terrestris*), the streaks on the breast and abdomen are greatly reduced, more or less indistinct as a rule. The breast and abdomen are unusually dark bister brown, and the white guttate spots on the throat are smaller than in any other population, although very distinct in *S. c. carri*. The entire plumage of *S. c. terrestris* is distinctly much paler than in any other population, but the white spots on the throat are quite large, as large as in *S. c. striatipectus*. In Trinidad and Tobago, the number of rectrices varies from 10 to eight in about the

same proportion, but the number seems constant on the continent, consisting of 10 rectrices, at least in the adults. No important geographical variation seems to exist in the immature plumage, but immature *S. c. striatipectus* is darker brown and more mottled than immature nominate *cinnamomea,* and immature *terrestris* is paler, less mottled.

RANGE: Colombia, in the Eastern Andes from Tolima northward (also very probably Sierra de Perijá, but not the Santa Marta Massif where the species is absent); Venezuela, in the Sierra de Perijá, Andes north to Falcón, coastal and interior ranges east to Miranda, coastal range from Sucre and adjacent northern Anzoategui and Monagas to the Paria Peninsula; Trinidad and Tobago. This species ascends to about 2000 m. in Venezuela and Colombia.

SPECIMENS EXAMINED: 70, including the types of *terrestris* in BM; of *carri* and *striatipectus* in AMNH; of "*bolivari*" in AMNH; and of "*pariae*" and "*aveledoi*" in the Phelps Collection, which are on deposit in AMNH.

Synallaxis stictothorax
Figure 4

DESCRIPTION: Pale dull grayish brown on the upperparts, with the exception of the rump and upper tail coverts which vary from dark buff to ochraceous or rufous cinnamon; with the color of the head nearly uniform with that of the back, though usually somewhat more grayish, less brownish than the back; with a few whitish or buffy feathers on the forehead, and a more or less vaguely defined whitish superciliary and post-ocular streak. Chiefly dull white or whitish on the underparts, with the exception of the flanks which are rufous cinnamon, and the breast which is crossed by a band of narrow dark brown streaks, more or less distinctly drawn and extending to the border of the upper abdomen in some individuals. The throat is white, but the bases of its feathers are grayish black, the "black gular patch" persisting, although completely concealed superficially, more than in any other species. Rufous area on the upper surface of the wing dull reddish chestnut, relatively restricted in extent, chiefly to the coverts.

Tail bright rufous (with or without irregular dusky brown areas that are absent or virtually so in the population of northwestern Peru, and vary individually in Ecuador), composed of 10 rectrices, very slightly stiffened only, well integrated, and blunt at the tip, not acuminate.

IMMATURE PLUMAGE: I have not seen a bird in immature plumage, but in one which does not seem to have attained the fully adult plumage, the streaks on the breast are very indistinct, much blurred, and the flanks are very pale, faintly buffy only.

This species varies geographically (see discussion). The description given above is based on specimens from Ecuador and northwestern Peru, but in the valleys of the Marañon and Rio Chinchipe in Cajamarca, Peru, the population (*S. s. chinchipensis*) is gray or pale olivaceous on the flanks, rather than cinnamomeous, uniform on the upperparts, and is more spotted than streaked on the breast.

RANGE: Southwestern Ecuador, from Manabí, south to northwestern Peru, to the region north of Trujillo in La Libertad, and the valley of the Marañon and some of its affluents in northern Cajamarca, south to the region of Jaén, or about 6° S. latitude.[78]

SPECIMENS EXAMINED: 67, including the type of *stictothorax* in BM, and of *chinchipensis,* and "*piurae,*" both in AMNH.

Synallaxis candei
Figure 4

DESCRIPTION: Crown olivaceous gray, with the feathers darker, blackish along the shaft or at the center, the gray crown contrasting more sharply with the back which is uniformly bright rufous with a slight vinaceous tinge, and with a conspicuous broad post-ocular streak, rufous as on the back. Lores, ear coverts, and throat deep velvety black, with the black areas on the face and throat conspicuously divided by a broad, pure white malar band, the malar bands joining under the chin. Sides of the neck, breast, and flanks strongly rufous, of the same in-

tensity as the color of the back, or slightly paler, but pure white on the center of the abdomen, and distinctly paler and duller rufous on the lower flanks. Upper surface of the wing almost wholly strongly rufous, with only the dusky dark brown tips of the primaries evident.

Tail strongly rufous, bright reddish chestnut, composed of 10 rectrices, well stiffened only at the base, quite firmly integrated, and with well rounded, not acuminate tips. The two outer pairs of rectrices, and the basal two-thirds of the three other pairs are rufous, but the apical portion of the three inner pairs is dark dusky brown.

This species varies geographically (see discussion). The population (*S. c. atrigularis*) from the lower part of the middle Magdalena Valley is not rufous on the back, but wholly olive brown, lacks the post-ocular streak, its white malar streak is cloudy, much less pure and distinct, and the rufous areas on the underparts are much duller, ferruginous on the breast, ochraceous brown on the flanks.

RANGE: Northwestern Venezuela (Falcón, Lara, and Zulia), and northern Colombia south to about 8° N. latitude in the Magdalena Valley; the distribution skirts the base of the Santa Marta Massif, but the species does not ascend into it.

SPECIMENS EXAMINED: 14.

Synallaxis kollari

DESCRIPTION: Crown gray-brown, contrasting most sharply with the back which is uniformly bright rufous, with a conspicuous post-ocular streak rufous as on the back. Lores grayish, ear coverts dark rufous cinnamon, and throat dull black with small narrow white tips to the feathers; remainder of the underparts dark rufous cinnamon on breast and upper flanks, buffy or pale cinnamomeous white on the center of the abdomen, and pale ochraceous on the lower flanks. Upper surface of the wing almost completely rufous, with only the dark dusky brown tips of the primaries evident.

Tail strongly and uniformly rufous, English Red, composed of 10 rectrices, well stiffened only at the base, firmly integrated, and with well rounded, not acuminate tips.

RANGE: Apparently quite restricted, as this species is known from relatively few specimens collected along the small affluents of the upper Rio Branco, Brazil (such as Rio Cotinga and Rio Surumu), and along the upper Rio Branco south to about 3° N. latitude.

SPECIMENS EXAMINED: 6.

Synallaxis scutata
Figure 4

DESCRIPTION: Similar to *S. kollari* with a gray-brown crown, contrasting sharply with the uniformly bright rufous back, but very distinctly paler and more whitish on the underparts, washed only with creamy buff, or pale grayish buff across the breast, with darker, more ochraceous, or cinnamomeous lower flanks; and with the upper half or more of the black gular patch concealed completely superficially by the white tips of the feathers. *Synallaxis scutata* differs also from *S. kollari* by being white on the lores, rather than grayish, dark buff or pale brown on the ear coverts, rather than dark rufous cinnamon, and by having a much paler but more conspicuous post-ocular streak which is buffy, rather than strongly rufous. Upper surface of the wing almost completely rufous as in *S. kollari* and *S. candei*.

Tail strongly and uniformly bright rufous, composed of 10 rectrices, well stiffened only at the base, firmly integrated, but with acuminate, not well rounded tips as in *Synallaxis kollari* and *S. candei*.

This species varies geographically (see discussion). Its variation is strongly clinal from northeastern Brazil south to northwestern Argentina, and the description given above is based on nominate *S. s. scutata* from the northern end of the range. As the populations range farther south, the grayish brown pigment of the crown spreads progressively farther down onto the back and, at the culminating end of the cline, replaces the rufous pigment completely with the exception of a slight trace persisting on the rump. A corresponding cline exists on the underparts

which become progressively more saturated, darker buff and much more ochraceous. The populations with a gray back and dark underparts are named *S. s. whitii*, but it is impossible to draw any demarcation between the ranges of *whitii* and nominate *scutata*.

RANGE: Northeastern Brazil, from central Maranhão, Ceará, Pernambuco, Piauhí, and northern Bahia, southwest through Goiás and the Mato Grosso (east to the western parts of Minas Gerais and São Paulo), to eastern Bolivia, and south to Catamarca in northwestern Argentina. A record from Santa Fé (Mocovi) in Argentina is very probably incorrect, and this species is apparently not recorded for Paraguay.

SPECIMENS EXAMINED: 38, including the type of *scutata* in BM.

Synallaxis gularis
Figure 4

DESCRIPTION: Uniformly dark brownish orange, or rusty brown, on the upperparts, with a conspicuous white superciliary and post-ocular streak. Paler on the underparts, uniformly dull orange rufous, or dark rusty cinnamon, below the throat which is white, with the exception of the last one or two rows of its feathers at its very base which are dark gray or sooty black, forming a more or less sharply defined "necklace." The upper surface of the wing is brown, with the outer webs of the coverts and remiges dark brownish orange, of the same color as the back, but a rufous area does not exist, and the blackish "necklace" at the base of the throat is the only vestige of the "black gular patch."

Tail chestnut or bay, unusually short, composed of 10 rectrices, that are only very slightly stiffened, quite loosely integrated, and sharply acuminate at the tip.

IMMATURE PLUMAGE: Similar to that of the adult, but duller, with the white throat and superciliary streak ill defined, and more or less mottled and spotted below on the breast and abdomen as the feathers are narrowly bordered or tipped with dark brown.

This species varies geographically (see discussion). The description given above is based on specimens from Colombia and Ecuador which probably represent nominate *S. g. gularis*. In the population of Venezuela (*S. g. cinereiventris*), the underparts are distinctly more grayish and umbraceous, less rufous and "rusty."

RANGE: Andes, between about 2500 and 4000 m.[79] from Trujillo south to Táchira in Venezuela, and south through Colombia and Ecuador, to presumably Junín in central Peru (known from Peru by only a single specimen, collected in 1891 but which is no longer in existence), also Sierra de Perijá where it has been recorded up to about 3000 m.

SPECIMENS EXAMINED: 124, including the types of *cinereiventris*, and of "*rufipectus*" in AMNH; and of "*brunneidorsalis*" in the Phelps Collection, which is on deposit in AMNH.

GENUS *CERTHIAXIS*

Certhiaxis is composed of 20 species. I listed only 19 in my revision (1971a) but added *furcata* Taczanowski, 1882, later; *furcata* had not been listed because its status seemed to be doubtful, but I have found (1971b) that it is a very distinctive species.

I merged *Cranioleuca* Reichenbach, 1853, with *Certhiaxis* Lesson, 1844, in my revision (1971a) because I was not able to find that any morphological differences of generic importance distinguished *Cranioleuca* from *Certhiaxis*. Only two species (*cinnamomea* and *mustelina*), which are superficially similar, were included in *Certhiaxis* by Hellmayr (1925) and Peters (1951) before my revision; all the others were allocated to *Cranioleuca*. Taxa *cinnamomea* and *mustelina*, to be sure, differ from some of the species allocated to *Cranioleuca* in their ecology and general behavior, including the structure and location of the nest, but it seems unreasonable to me to base a generic separation on ecology and behavior when ecology and behavior are completely inconstant in the species of "*Cranioleuca*" for which we have any information; this is shown below.

To return to a generic separation on morphological characters, *Certhiaxis* (including "*Cranioleuca*") is closely related to *Synallaxis* and all the species known to Sclater were included by him in *Synallaxis* in his first revision (1874). In his revision, Sclater (1874) grouped the species into two divisions: Division A, which includes the species which Sclater considers are "*Synallaxes normales,*" with 10 rectrices; and Division B, or "*Synallaxes abnormales*" with 12 rectrices. But, in his second revision, Sclater (1890) decided to adopt *Siptornis* Reichenbach, 1853, for the species of Division B (12 rectrices), listing *Cranioleuca* as a synonym of *Siptornis*. *Certhiaxis* was not mentioned by Sclater, not even as a synonym, in either of the two revisions, although he was quite aware of its existence as shown by his reference to "numerous genera" in 1874 which did not seem to him to possess "sufficient structural differences for recognition." I may add that Sclater was not wholly consistent in 1890, because he retained *semicinerea* Reichenbach, 1853, and *cinnamomea* Gmelin, 1788, in *Synallaxis* although they both have 12 rectrices.

The genera were revised by Hellmayr (1925), who considered that *Siptornis* is monotypic (for *striaticollis* Lafresnaye, 1843)—an opinion which seems correct—and assigned the other species to *Certhiaxis* and *Cranioleuca,* as stated above. Hellmayr's reasons are that ". . . *cinnamomea* and allies have twelve rectrices, which at once rules them out of *Synallaxis* where they have been placed by authors. The group [i.e., *Certhiaxis,* in which Hellmayr includes only *cinnamomea* and *mustelina*] appears more nearly related to *Cranioleuca,* but may be distinguished by its much more rounded wing and short tail (about equal to length of wing)." It is quite evident, however, that the number of rectrices is not of generic importance in *Synallaxis* and related genera. I have discussed this question at length under *Synallaxis*; the number of rectrices varies from eight to 12 in *Synallaxis,* and 10 to 12 in *Certhiaxis*. Hellmayr insisted that *Certhiaxis* is characterized generically by having 12 rectrices, but *mustelina* has only 10 and is the only other species which Hellmayr included in *Certhiaxis* in addition to *cinnamomea,* which does have 12 rectrices.

It is also incorrect to state that *Certhiaxis* has a "much more rounded wing and short tail than *Cranioleuca.*" These characters are not constant in the 20 species; the tail is as short, or shorter than in *cinnamomea* and *mustelina,* in the majority of the other species, as is quite evident from the measurements given in table 11. The best that can be said about the shape of the wing is that it seems to be correlated with habits. It is less rounded in distinctly arboreal species, such as *Certhiaxis erythrops,* but no differences exist, or they are quite minimal, in a number of the species allocated to "*Cranioleuca*" by Hellmayr.

The length of the tail is best appreciated in terms of its proportion to the length of the wing. In *Certhiaxis mustelina,* the tail length/wing length ratio is 0.93; and it is 1.03 in the case of *C. cinnamomea*. In 17 of the other 18 species, the ratio varies from 0.88 to 1.08, with a mean of 0.998; in other words, the length of the tail is "about equal to [the] length of [the] wing" in *Cranioleuca,* as it is in *Certhiaxis*. The single exception is *C. sulphurifera* in which the ratio is 1.31, but the tail is not truly longer in *C. sulphurifera,* as the higher ratio is due only to the pronounced elongation of the tips of the central rectrices, and the wing is very round, at least as rounded, if not more so than in *C. cinnamomea* and *C. mustelina*. This is not surprising because the general behavior of *C. sulphurifera* is similar to that of *C. cinnamomea* and *C. mustelina,* to the extent that these three species are wrenlike and inhabit marshes, and are not arboreal, although the structure and location of their nests are completely different.

Sclater (1874, 1890) considered that *Synallaxis* and the species which I include in *Certhiaxis* were very closely related. I share his opinion, but the species I assign to *Certhiaxis* seem to represent a distinct evolutionary line and the recognition of *Certhiaxis* as a genus is legitimate. The distinction be-

TABLE 11
Measurements (in Millimeters) of *Certhiaxis*

Species	Wing			Tail			Bill		
	N	Mean	Range	N	Mean	Range	N	Mean	Range
erythrops									
Males	43	67.90	63–72	41	67.48	59–78	44	15.88	14–17
Females	28	66.10	62–70	23	65.21	60–74	29	15.65	14–16.50
Both sexes	75	67.26	62–72	68	66.85	59–78	77	15.79	14–17
demissa									
Males	5	66.10	65–67	5	67.00	58–71	4	15.35	15–16
Females	14	63.39	61–67	13	64.69	60–68	14	14.98	14–16
Both sexes	20	64.10	61–67	19	65.10	58–71	19	15.03	14–16
antisiensis									
Males	21	67.76	64–73	20	69.30	64–77	19	16.35	15–18
Females	10	66.20	60–73	9	67.55	61–74	10	16.32	15–18
Both sexes	34	67.14	60–73	32	68.75	61–77	32	16.35	15–18
baroni									
Males	25	78.18	70–84	26	79.46	69–86	24	18.92	17–20.50
Females	26	76.71	72–83	25	78.96	73–87	25	18.84	17–20.50
Both sexes	52	77.32	70–84	52	79.07	69–87	49	18.88	17–20.50
pallida									
Males	7	63.42	61–67	7	67.85	63–74	7	15.17	14.50–16
Females	7	61.50	60–63	6	66.83	59–71	7	14.78	14–16
Both sexes	22	62.43	59–67	21	67.42	58–74	22	15.09	14–16
curtata									
Males	14	69.75	65–73	13	68.23	63–73	13	15.90	15–17
Females	4	66.75	65–68	1	—	62	4	16.32	15.50–17
Both sexes	22	69.31	65–73	18	67.16	63–73	21	15.97	15–17
furcata									
Female	1	—	71	1	—	70	1	—	18
obsoleta									
Males	36	59.08	56–62	35	62.31	55–70	35	14.23	13–15.50
Females	33	57.51	54–60	28	61.03	52–65	30	14.03	13–15
Both sexes	76	58.48	54–63	69	61.97	52–70	72	14.12	13–15.50
hellmayri									
Both sexes	3	67.00	66–69	3	64.00	62–67	2	16.50	16, 17
subcristata									
Males	4	65.87	63–68	4	68.25	63–73	3	15.83	15–17
Females	3	64.33	62–67	3	67.33	65–70	3	16.33	16–17
Both sexes	13	65.19	62–68	11	66.54	62–73	12	16.33	15–17
pyrrhophia									
Males	60	64.93	57–74	54	68.20	62–75	59	16.30	15–18
Females	46	62.67	55–71	44	65.84	59–72	46	16.09	14.50–18
Both sexes	120	63.91	55–74	110	67.25	59–75	118	16.22	14.50–18
marcapatae									
Female	1	—	71	1	—	71	1	—	17
Both sexes	2	72.00	71, 73	2	73.90	71, 75	2	17.00	17, 17

TABLE 11—(*Continued*)

Species	Wing			Tail			Bill		
	N	Mean	Range	N	Mean	Range	N	Mean	Range
albiceps									
Males	9	66.88	64–69	8	66.87	64–71	9	16.97	15–17.80
Females	2	64.75	64.50, 65	2	64.50	64, 65	1	—	17
Both sexes	15	66.50	64–69	14	65.71	62–71	13	16.94	15–17.80
semicinerea									
Males	3	65.33	63–68	1	—	73	3	17.16	17–17.50
Female	1	—	61	1	—	63	1	—	16
Both sexes	9	63.33	60–68	6	64.66	60–73	9	16.83	16–17.50
albicapilla									
Males	8	76.00	72–79	8	79.37	73–85	7	18.14	17–19
Females	11	74.27	72–76	11	79.27	73–85	11	17.70	17–18.20
Both sexes	25	75.08	72–79	25	79.44	73–85	24	17.84	17–19
vulpina									
Males	97	69.95	62–79	91	61.76	55–70	95	16.65	15–19.50
Females	77	67.51	62–73	66	60.51	54–67	76	16.46	14.20–19
Both sexes	183	68.87	61–79	164	61.19	54–70	180	16.55	14.20–19.50
mülleri									
Males	9	73.11	70–76	9	67.55	63–73	9	18.24	18–19
Females	13	70.15	62–78	11	65.81	60–73	13	17.84	16.20–19
Both sexes	22	71.36	62–78	20	66.60	60–73	22	17.98	16.20–19
gutturata									
Males	45	70.31	66–76	40	61.97	57–70	44	17.97	17–19.20
Females	41	67.76	64–74	38	60.15	56–65	41	17.32	16–19
Both sexes	93	69.13	64–76	84	61.17	56–70	92	17.66	17–19.20
sulphurifera									
Males	17	58.41	56–62	15	78.46	66–93	18	17.57	16.50–19
Females	9	56.00	54–58	8	72.25	65–78	9	17.48	17–18.50
Both sexes	26	57.57	54–62	23	76.30	65–93	27	17.54	16.50–19
cinnamomea									
Males	87	60.87	56–66	83	62.16	53–72	85	17.20	15–18.50
Females	61	59.66	54–63	55	62.25	53–69	61	16.98	15–19
Both sexes	164	60.35	54–66	153	62.11	53–72	161	17.09	15–19
mustelina									
Males	23	60.04	58–63	23	55.30	52–58	22	18.94	17.50–20
Females	32	58.76	56–62.50	28	54.85	50–61	27	18.55	17.20–19.20
Both sexes	60	59.22	56–63	54	55.03	50–61	53	18.71	17.20–20

tween the two genera can be summarized in a few words: *Certhiaxis* varies a great deal in its ecology, behavior, and in the structure and location of its nest, but not morphologically, whereas the reverse is true for *Synallaxis* in all respects.

The general ecology and behavior and also nests have been discussed above for the species of *Certhiaxis* for which this information exists. It is quite evident that ecology, behavior, and nests are not all constant in *Certhiaxis,* whereas the general ecology and behavior of *Synallaxis* vary little and the structure of its nest is similar in all its

species, when known. In strong contrast, *Certhiaxis* is remarkably homogeneous morphologically, whereas *Synallaxis* is highly variable.

The coloration of its plumage and its pattern vary in *Certhiaxis*, but within a much more restricted range than in *Synallaxis*. For instance, the color of the tail is strongly rufous and its pattern is uniform in 19 of the 20 species, and varies only very slightly in the twentieth species (*C. sulphurifera*), whereas the color of the tail varies from rufous or brown to olivaceous, fuscous or virtually black in *Synallaxis* and its pattern is uniform or not.

Variations in the structure of the tail are not of generic importance (as I have emphasized in discussing *Synallaxis*), but when the structure of the tail is remarkably constant, as in *Certhiaxis*, the constancy acquires significance. In *Certhiaxis*, the ratio between the lengths of the tail and wing varies from 0.88 to 1.08, with an average of 1.00 in 19 of the 20 species; this ratio varies from 0.98 to 1.78 in *Synallaxis*, with an average of 1.27, and increases to 1.89 in *S. phryganophila* (subgenus *Schoeniophylax*). In the twentieth species (*C. sulphurifera*) the ratio is 1.31, but this greater ratio is misleading as it is created merely by the greater elongation of the tips of its central rectrices. In other words, the lengths of the tail and wing are on average equal in *Certhiaxis*, whereas the tail is decidedly longer than the wing in *Synallaxis* as a rule. The number of rectrices, their shape, the modification of their tips, the stiffening of the tail, and the degree of the integration of their webs, are all highly variable in *Synallaxis*, but not in *Certhiaxis*. Only one species (*mustelina*) of *Certhiaxis* departs from the rule of 12 rectrices by having 10, but nine of the 36 species of *Synallaxis* have 12 or eight rectrices, rather than the "normal" 10. The webs of the rectrices also never become disintegrated to the same extent in *Certhiaxis* as they do in *Synallaxis*. Variation in the shape or size of the bill is also quite slight in *Certhiaxis*, but much more pronounced in *Synallaxis*.

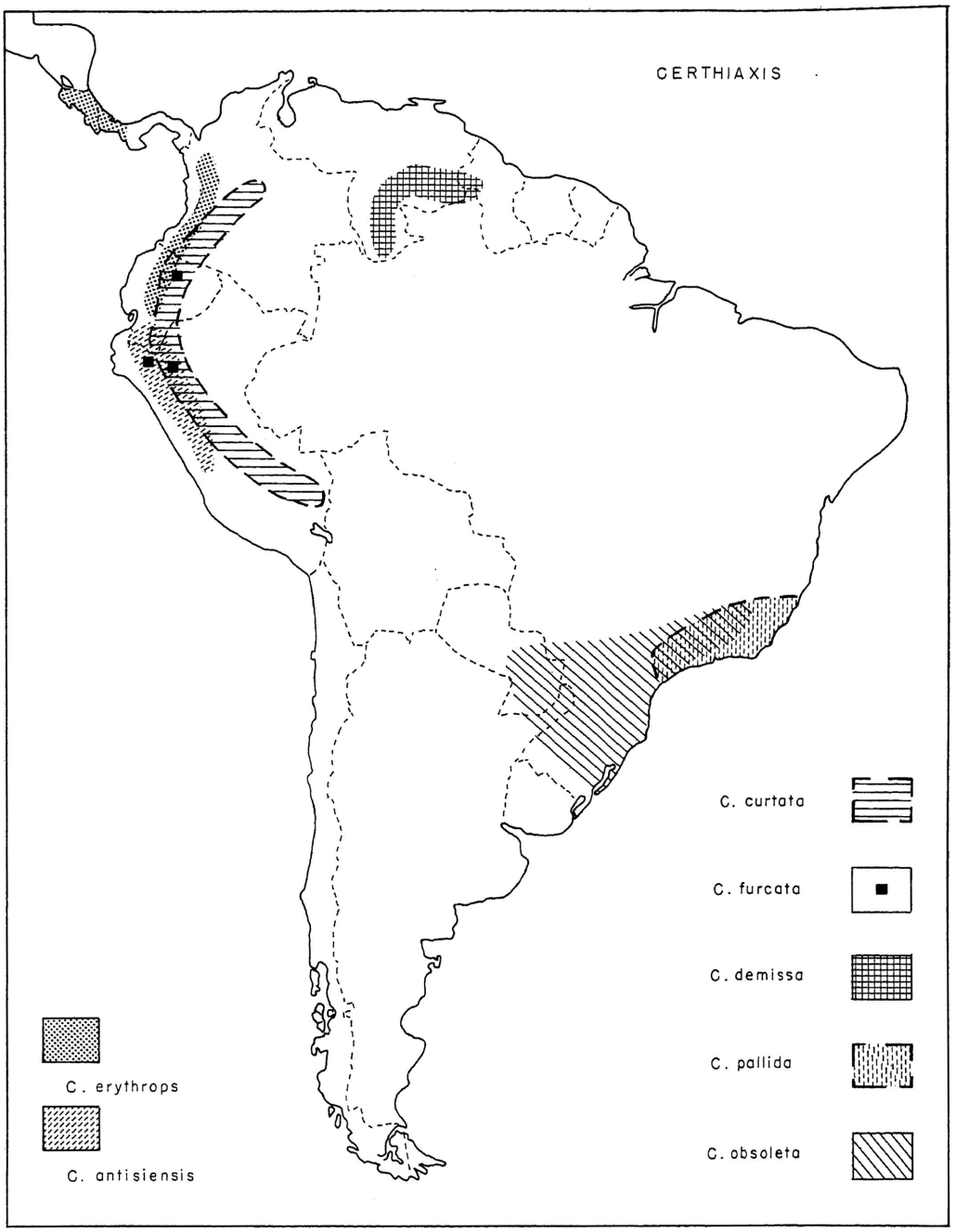
The feathers of the center and posterior part of the crown show a definite tendency to be elongated in most of the species of *Certhiaxis* and develop into a short crest in some species. This tendency exists in only very few species of *Synallaxis* and is slight, as the feathers do not develop into a crest.

I may add that *Certhiaxis* differs conspicuously from *Synallaxis* by lacking the black gular patch which is characteristic of *Synallaxis*. The bases of the feathers of the throat are dusky or sooty in some species of *Certhiaxis*, but this character does not seem to possess any significance from a behavioral point of view as the feathers of the throat do not seem to be erectile in *Certhiaxis*, in contrast to *Synallaxis*, with one exception (*C. sulphurifera*) in which the feathers are, however, bright glossy yellow, not black as in *Synallaxis*.

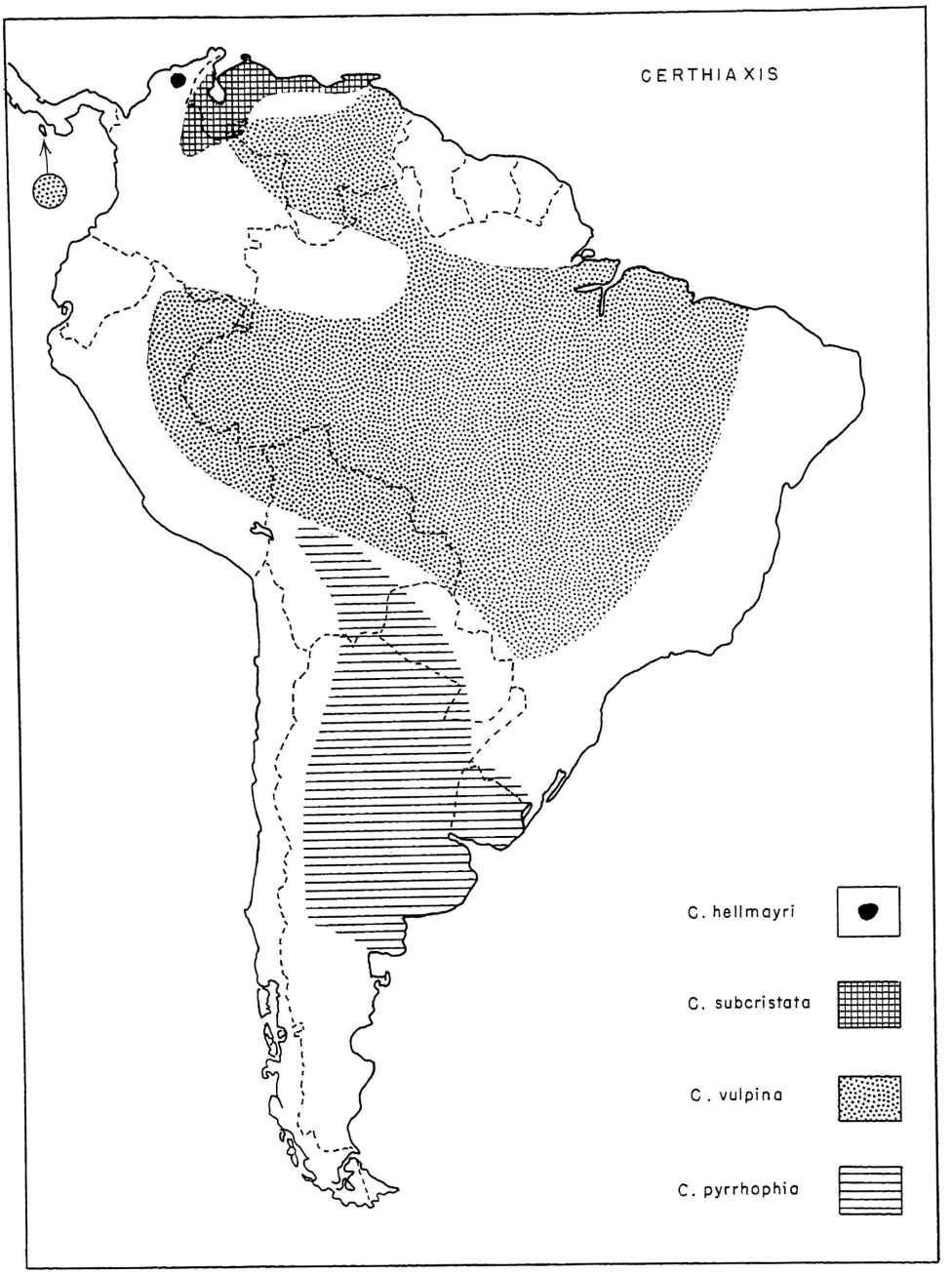
Certhiaxis is very widely distributed and its distribution is comparable to that of *Synallaxis*, extending from Central America south to central Argentina. But it is more restricted at the northern extremity of the range, *Certhiaxis* reaching only to Costa Rica, not to southern Mexico as does *Synallaxis* (maps 16–19).

Some species (such as *Certhiaxis mülleri*,[80] *C. gutturata*, *C. cinnamomea*, and *C. mustelina*) are restricted to the lowlands, and *C. sulphurifera* is primarily coastal. The two Brazilian species (*C. obsoleta* and *C. semicinerea*) reach very modest elevations between about 900 and 1000 m., but most of the other species reach moderate or relatively high elevations. *C. demissa*, *C. pallida*, *C. curtata*, *C. furcata*, and *C. subcristata* reach about 2000 m. or more; *C. hellmayri* ascends to about 2800 m. in the Santa Marta Massif of Colombia, *C. erythrops* to about 3150 m. in Panama, and *C. pyrrhophia* to about 3100 m. in Bolivia. Four species (*antisiensis*, *marcapatae*, *albiceps*, and *albicapilla*) are Andean, but do not seem to ascend much above 3300 m., with the exception of *C. antisiensis* which has a remarkably great altitudinal range, from about 1200 to 4500 m. The altitudes reached by the Andean species of *Synallaxis* are roughly similar.

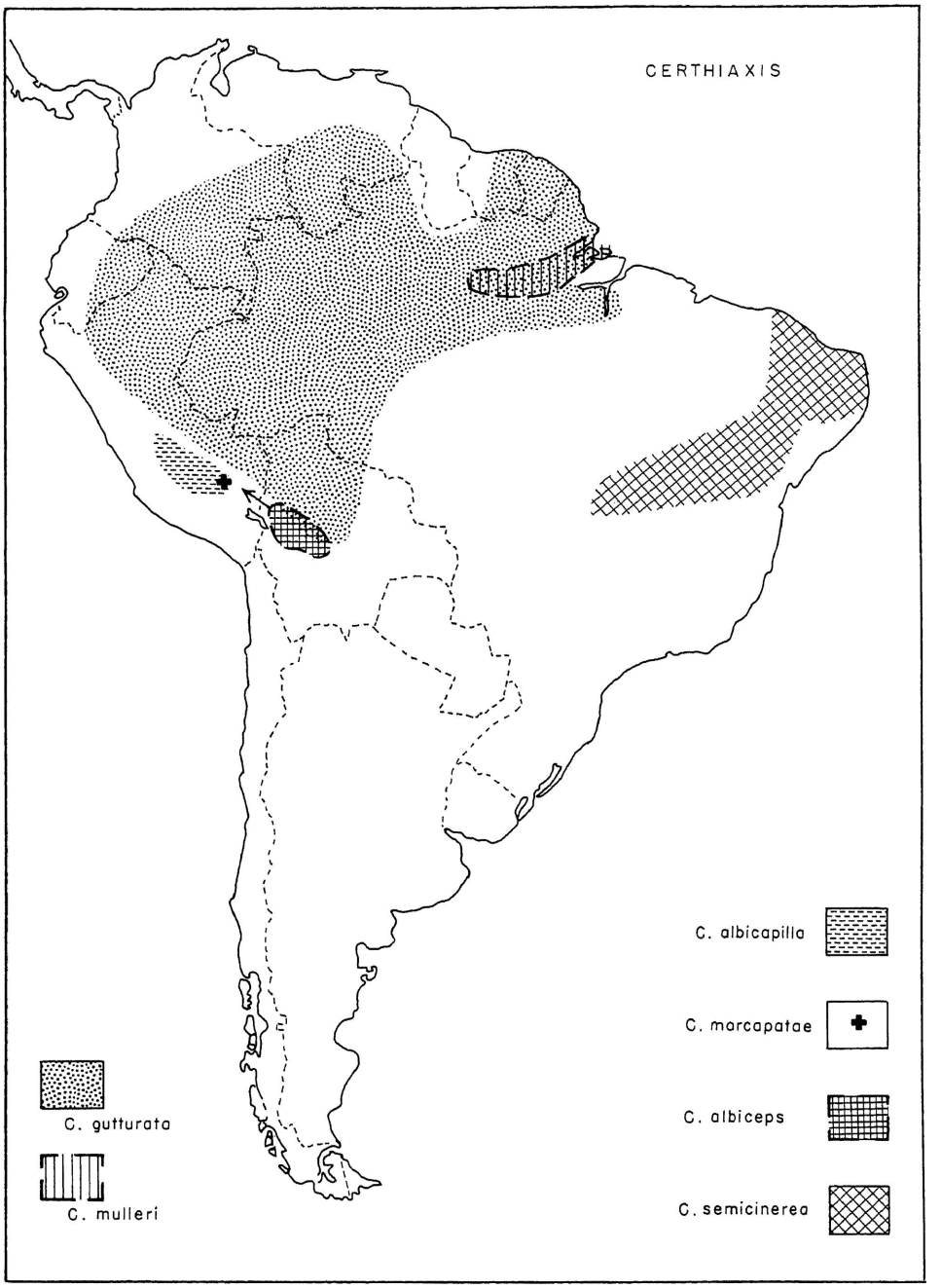
The ranges of the species are also com-



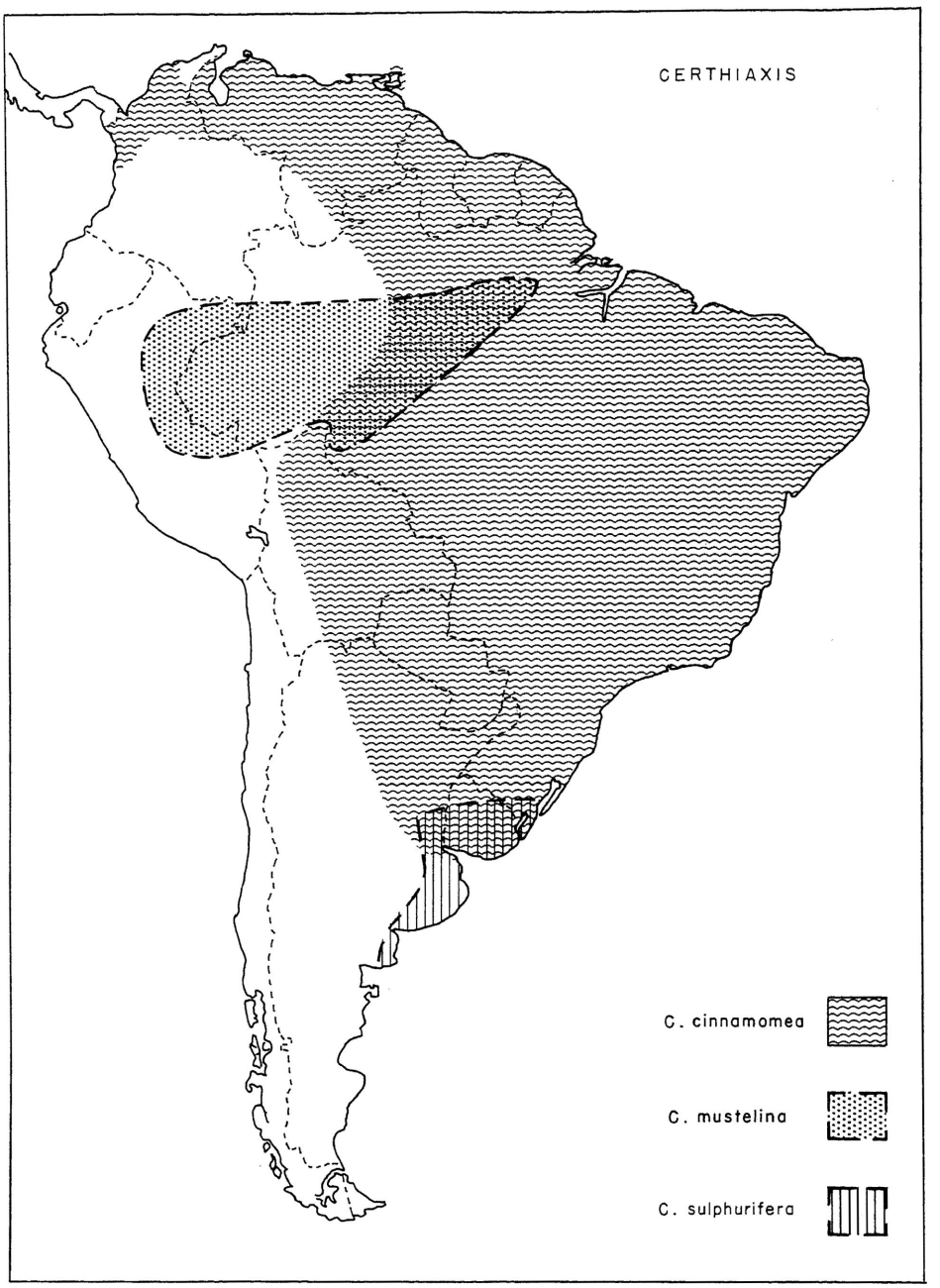
MAP 16. Geographical distribution of seven species of *Certhiaxis*, including five that seem closely related: *erythrops*, *demissa*, *antisiensis*, *pallida*, and *curtata*.



MAP 17. Geographical distribution of four species of *Certhiaxis*, including three that seem closely related: *hellmayri*, *subcristata*, and *pyrrhophia*; *C. vulpina* appears isolated.



MAP 18. Geographical distribution of six species of *Certhiaxis*, including four that seem closely related: *C. marcapatae*, *C. albiceps*, *C. semicinerea*, and *C. albicapilla*.



MAP 19. Geographical distribution of three species of *Certhiaxis*.

parable in extent in *Synallaxis* and *Certhiaxis*. Some species, such as *C. cinnamomea* and *C. vulpina* are very widespread, although not to the enormous extent displayed

by *Synallaxis albescens*; the ranges of *C. pyrrhophia* and *C. gutturata* are also quite extensive. The ranges of *C. albiceps* and *C. albicapilla* are quite restricted, relatively speaking, and *C. hellmayri* is restricted only to the Santa Marta Massif, as in the case of *Synallaxis fuscorufa*; *C. marcapatae* is known from two specimens taken at the same locality in Cuzco, Peru. The range of *C. furcata* is also very badly known and may be restricted, as the only two specimens known were taken at the same locality in southern Amazonas, northern Peru, although I have seen three other specimens which are immature and may represent this species, one taken in Cajamarca, and the other two at the same locality in eastern Ecuador.

The structure and location of the nest, other aspects of behavior, and the ecology are normally of much taxonomic importance in the Furnariidae. Behavior and ecology have been quite consistent as a rule in the polytypic genera treated so far in this monograph, but *Certhiaxis* is an exception.

The information available is very incomplete but what exists reveals a great lack of constancy. The nest of only nine of the 20 species is known, but only superficially so in some instances, and little or no information exists on the ecology, or other aspects of behavior, for more than half of the species. However, as implied above, some species are distinctly arboreal and others not at all; some inhabit very dense humid forests, others frequent open forests and the edge of clearings, groves and thickets in open regions, scrub and thick bushes, or are very closely associated with water, along streams, lakes, in marshes, mangroves, or, in the case of *Certhiaxis sulphurifera,* are restricted to dense beds of rushes and reeds. The nine species for which the nest is known are *C. erythrops, C. antisiensis, C. pallida, C. subcristata, C. pyrrhophia, C. vulpina, C. sulphurifera, C. cinnamomea,* and *C. mustelina.*

The species for which the most complete published information exists is *Certhiaxis erythrops,* much of it contributed by Skutch (1969b). This species frequents dense, humid, montane or highland forest and is very arboreal and active, foraging in moss and lichens on the limbs of trees, epiphytes, or in curled dead leaves caught in vine tangles; creeping or climbing on trunks and limbs, or clinging to twigs, in the most diverse attitudes and positions, "upside down as readily as upright." The nest, according to Skutch, is a very bulky, roughly globular or ovoid structure, about 30 cm. in diameter or more, and is pensile, hung far above the ground from the end of a slender, hanging branch of a tree. The nests reported by Skutch were about 6 to 9 m. above the ground, and constructed largely of living green moss, bound with thin, long pieces of dry herbaceous vines. The entrance is inconspicuous and near the bottom, but no information is available on the internal structure of the nest. Some of the nests may be used only as a dormitory, or shelter, not for breeding, as in the case of one nest mentioned by Skutch.

Straws and leaves may be used for construction when, presumably, the preferred moss is not available. Edwin O. Willis has told me he observed a nest built of yellow straws and leaves, hanging from the end of a pendent limb about 10 m. above the ground. He says this nest resembled very much the nest of *Passer domesticus,* when built in a tree, but was neater and more rounded. This nest was discovered by Willis in secondary growth at the edge of the forest, not in dense forest.

The information that I have found in the literature, or that has been supplied to me, for *Certhiaxis antisiensis* and *C. subcristata* is scanty, but the nests of these two species and their location are about similar to the nests of *C. erythrops.* The active, arboreal habits of *C. antisiensis* mentioned by Koepcke (1958), and its pensile nest, hung several meters above the ground, composed chiefly of moss, suggest that the behavior of *C. antisiensis* is similar to that of *C. erythrops,* although *C. antisiensis* is reported by Koepcke from thin, open mountain forest.[81]

The description of the pensile nest of *C. subcristata,* supplied to me by Paul Schwartz, suggests that it is similar to those of *C. erythrops* and *C. antisiensis* in location and general structure, but Schwartz says it is constructed of grass, not moss—however, the nest of *C. erythrops* is not always constructed with moss, as stated above.

The general ecology and arboreal behavior of *Certhiaxis pallida* seem to show much similarity to the behavior and ecology of the three species discussed above. The nest of *C. pallida* is also constructed of lichen and moss, according to von Ihering (1914), and is of about the same size, with a lateral entrance, not near the bottom of the nest as in *C. erythrops* and *C. subcristata*. The location of the entrance (at the side) may be affected by the location of the nest, which is not pensile (as in the three other species), but constructed against the trunk of a tree, among the bulbs of epiphytes and orchids, according to von Ihering. However, Mitchell (1957) stated she observed an individual "building" [a nest?] of fibers obtained from an evergreen in "a terminal cluster of a Parana Pine." This information seems to contradict the description of the nest given by von Ihering, but Mitchell was a relatively inexperienced observer who observed this bird for only three or four days, whereas von Ihering was a man of long experience, especially interested in the breeding biology of the birds of Brazil, whose observations of the nests of *C. pallida* covered two complete breeding cycles.

Von Ihering described the internal structure of the nest of *Certhiaxis pallida* (information not on record for the three other species). He says that the entrance to the nest of *C. pallida* is at one side, but "*inferior,*" and opens into a small chamber from which a very tortuous tunnel leads upward to the top of the nest, and then opens directly down into the incubating chamber which is not lined, this tunnel making one or two very sharp bends, virtually at right angles, before opening into the breeding chamber. The roof of the nest seems to be used for roosting by its owners, as suggested by a large accumulation of their droppings.

Certhiaxis pyrrhophia is widely distributed in the Chaco, or other regions that are not normally heavily forested, frequenting chiefly isolated groves or thickets. The description of its attitudes given by Wetmore (1926) shows that *C. pyrrhophia* is actively arboreal, similar to *C. erythrops* in its actions, but its breeding behavior is totally different. Wetmore gives no information on the nest, as the birds he observed were not breeding, but the nest has been described by several authors and I have also obtained direct information from three of my correspondents in Argentina.

The information is plentiful, but confusing as it is not generally appreciated that *Certhiaxis pyrrhophia* constructs two quite different types of nest, one used only for shelter or as a dormitory, the other for breeding. Much of the information that has been published is certainly incorrect, for instance the report of Hudson (in Sclater and Hudson, 1888) who said that *C. pyrrhophia* (which he and Sclater call *striaticeps*) "builds an open nest in the fork of a branch, of soft grasses and hair, thickly lined with feathers." An open nest in the fork of a branch would be extremely unusual for a furnariid. Hudson probably misidentified the makers of the nest, because all the other authors and my correspondents agree that the nest of *C. pyrrhophia* is closed and globular in shape. And, generally speaking, it is constructed of dry and thorny twigs, and is about similar in size, shape, and structure to the well-known nests of some "*Asthenes,*" though less strongly built.

The information I believe to be the most satisfactory was sent to me by Gunnar Hoy of Salta, Argentina. This information is thorough, well documented, accompanied by an excellent photograph of the shelter nest and a carefully drawn diagram of the structure of the breeding nest.

The shelter nest, according to Hoy, is globular, about 25–30 cm. in diameter, constructed of dry and thorny twigs, bound with shreds of wool and strands of vegetable fiber, on the top of a strong branch, at or near its tip, 2 to 3 m. above the ground or less. It is provided with two round entrances which

open directly underneath the nest through its floor. In the photograph that Hoy sent me, the entrances are separated by the supporting branch and are large, with a wide diameter.

The breeding nest is similar in size to the shelter nest, built of the same material externally, but has only a single entrance which also opens directly under the nest, through its floor. The entrance is at one side, and in the diagram which Hoy sent me (a cross section of the nest), it opens into the nest at the side of a platform (on the broader, opposite side of the nest from the entrance) which is provided with a depression, lined with feathers, in which the eggs are incubated. The inside of the entire nest is well lined with lichen, or other soft material, according to Hoy, who says he found two of these breeding nests ". . . alike, both with newly hatched young . . . built in the same manner, in the center of a dense bush well hidden . . . about one meter [above the ground]."

I have also received information from Samuel Narosky, consisting of a copy of an account which he had prepared for publication together with a colleague, Dario Yzurieta. This account agrees with the information given to me by Hoy in describing two types of nest, a shelter nest with two entrances underneath, and a breeding nest with a single entrance. However, important discrepancies exist between the two accounts. Narosky and Yzurieta stated that the shelter nest is only 12 cm., or less, in diameter, more or less adapted to the size of the bird, and that its entrances are no wider than a finger; they also said that the single entrance into the breeding nest is at the top of the nest ("*arriba*") and that these nests are built from 2 to 8 m. above the ground.

It is possible that the nests of *Certhiaxis pyrrhophia* vary in different regions, but the discrepancies between the two accounts seem too important to be reconciled. All I can say is that I have more faith in Hoy's account, which is especially well documented, and that a shelter nest which is only 12 cm. or less, and with such narrow entrances, does not seem convincing to me, as *C. pyrrhophia* is about 16 cm. and not an appreciably slender bird.

The breeding habits of *Certhiaxis vulpina* are most unusual as this species does not construct a nest in the ordinary sense. This species is not truly arboreal but clambers actively in dense undergrowth and tangled vegetation in river bottoms or backwaters, along lakes, ponds, or on the edge of swamps, and Cherrie (1916, 1930) has found its nests in Venezuela and in Mato Grosso, Brazil. He reported that *C. vulpina* fashions a crude nesting cavity within nondescript masses of drift grass, small sticks, or other vegetation caught in some obstruction along or above receding waters, or adapts old decrepit nests of other birds. Cherrie believes these nests are probably those of flycatchers for the greater part, and I suspect that *C. vulpina* uses also the old nests of *Synallaxis*. This is suggested by a report of Snethlage (1935) who said she found abandoned nests, and one with eggs, which she assumed had been built by *C. vulpina*. However, as Snethlage described these nests as shaped "like a retort with a long entrance tunnel at one side" (translation)—the typical nest built by *Synallaxis*—I believe they were probably old nests of a *Synallaxis*.

The nest of *Certhiaxis sulphurifera* is totally different from that of the other species. *Certhiaxis sulphurifera* is specialized ecologically, not at all arboreal, and is narrowly restricted to dense beds of reeds, or rushes, growing in the water, inland, or in riverine and coastal swamps. Its nest is more or less globular in shape, constructed of reeds that are woven, but in which clay is apparently not incorporated as in the case of the well-known nest of *Phleocryptes* which is more or less similar to that of *C. sulphurifera*; the entrance is at the side. Like *Phleocryptes*, *C. sulphurifera* resembles also the marsh wrens ecologically and behaviorally, including the structure and location of its nest.

The nest of *Certhiaxis sulphurifera* is normally attached to the stems of reeds, not far above the surface of the water, but Durnford (1878) found a nest placed on the top of a willow stump in a dense bed of reeds and scrub, about 1.5 m. high.

Certhiaxis cinnamomea is like *C. sulphurifera,* closely associated with water, as a rule, inhabiting dense thick undergrowth or tangles in marshes, swamps, edge of the mangrove, or along ditches, pools, lagoons, or other bodies of water. However, *C. cinnamomea* also frequents small groves on dry land provided that they are not too far removed from water. *C. cinnamomea* is furtive, wrenlike, not arboreal.

The nest of *Certhiaxis cinnamomea* is basically similar to that of *Synallaxis*. It is very bulky, constructed of slender sticks or twigs with a marked preference for thorny ones when available, and is entered through a long tunnel. The entrance is normally near the base, the tunnel then curving upward, vertically or essentially so, then, presumably, opening down into the breeding chamber. The nest is invariably constructed near the ground, in a low bush, or among the roots of a stump, the bushes growing near or even actually in water; it is said to be conspicuous.

The only information that I have been able to obtain for *Certhiaxis mustelina* is brief. It was sent to me by J. P. O'Neill who said he has seen the nests of *C. mustelina* in eastern Peru and that they are "a ball of thorny sticks [built] in vegetation that overhangs water," most nests varying from "about 15–18 inches [38–46 cm.] in diameter." This suggests that the nest (and probably also the general behavior) of *C. mustelina* is more or less similar to that of *C. cinnamomea,* although the latter does not construct an "overhanging" nest.

The information presented above for only nine of the 20 species shows that the interspecific variation in general ecology and behavior, including the structure and location of the nest, is very great; no information, or virtually none, exists for the other 11 species, but we certainly cannot presume that their behavior and ecology are constant when the variation is so great in species that are known. Only two logical conclusions can be drawn from this evidence: either the 20 species are not a natural assemblage, or, as seems to be the case, variations in ecology and behavior are only of specific importance, not of generic importance, in *Certhiaxis*.

If the nine species are not a natural assemblage, and more importance is accorded to ecology and behavior than to morphology, these nine species would have to be divided in no fewer than five genera, for which only two generic names exist, *Certhiaxis,* and *Acrorchilus* Ridgway, 1909, the type of which is *erythrops*. The type of *Certhiaxis* is *cinnamomea*; *Certhiaxis* could be used also for *mustelina,* in addition to *cinnamomea,* as these two species build a nest of thorny twigs similar to that of *Synallaxis* in structure, although this is not certain in the case of *mustelina* as the internal structure of its nest is not known and its location differs significantly from the location of the nest of *cinnamomea* (see above); *cinnamomea,* and probably *mustelina* also, are not arboreal. *Certhiaxis erythrops* (the type of *Acrorchilus*) is highly arboreal and builds a pensile nest constructed chiefly of moss, high above the ground; *Acrorchilus* would include *antisiensis* and *subcristata,* in addition to *erythrops,* and perhaps *pallida* also, although the nest of *pallida* is not pensile according to von Ihering. This leaves *pyrrhophia, vulpina,* and *sulphurifera* for which three "new genera" would have to be proposed—not to mention the 11 species for which no information exists.

The type of *Cranioleuca* is *albiceps* for which no information seems to exist on the structure and location of its nest, or on general behavior, other than a few words from Niethammer (1956) who said that *albiceps* is a shy bird inhabiting thick bushes; hence, quite distinct in general behavior from *Certhiaxis erythrops* and relatives.[82]

However, I do not believe that a division based on ecology and behavior is admissible because no morphological differences of generic importance exist between the 20 species. For instance, *Certhiaxis pyrrhophia* and *C. subcristata* are strikingly similar morphologically in important respects; they may not be quite so closely related as their resemblance suggests, but they certainly appear to be congeneric although their nesting behav-

ior is completely different. *Certhiaxis sulphurifera* and *C. cinnamomea* appear to be related (as suggested by the yellow coloration of their upper throat), but their ecology differs significantly and their nests are not at all comparable.

The second conclusion (morphological similarity is of greater generic importance than ecology and behavior) seems to be correct in the case of *Certhiaxis*. This conclusion contradicts the general rule for the Furnariidae in which general ecology and behavior, including the structure and location of the nest, are normally constant and of generic importance. But as only a morphological generic concept seems legitimate for *Certhiaxis*, it is evident that more than one "kind" of genus exists in the Furnariidae.[83]

Morphological Variation

Certhiaxis is morphologically very homogeneous, relatively speaking, but interspecific variation exists and is most evident in the coloration and pattern of the crown; a few species are also slightly or very distinctly patterned on the underparts, rather than uniform. The back is brownish in nearly all the species, but rufous in a few, and is uniform or not with the color of the crown.

In eight species, in which the coloration of the crown contrasts with that of the back, the crown is strongly rufous, with or without a band of brown across the forehead. These birds (*C. erythrops, C. demissa, C. antisiensis, C. pallida, C. curtata, C. furcata, C. mülleri,* and *C. gutturata*) have a rufous "cap" quite similar to that of the species of Group One in *Synallaxis*. In three other species (*C. albiceps, C. semicinerea,* and *C. albicapilla*) having a contrasting crown, the top, or the whole of the crown, varies from white or whitish to ochraceous buff or ochraceous orange, and contrasts also completely with the color of the back. In one of these species (*C. albiceps*), the pale crown is strongly emphasized by a very broad band of black laterally on the superciliary and post-ocular region. The crown is uniform, but is heavily patterned by very dark, blackish brown streaks in three other species (*C. hellmayri, C. subcristata,* and *C. pyrrhophia*). A superciliary streak exists in the majority of the species, but is not always well defined. In many species, the feathers of the crown are distinctly elongated and form or tend to form a short crest.

The underparts vary in coloration from dull white to buffy, ochraceous, olivaceous, grayish olive, ashy gray, or ochraceous orange. The range of variation is quite extensive, but the underparts are uniform or very nearly so in the great majority of the species, although the chin and throat are normally paler, distinctly or not. In two pale species, however, the underparts are more or less faintly mottled or streaked, and are sharply and profusely spotted with very dark brown in *Certhiaxis gutturata,* or sharply and heavily scalloped with very dark brown in *C. mülleri.*

Yellow pigment is quite rare in the plumage of the Furnariidae but exists on the upper throat, or on its center, in two species (*Certhiaxis sulphurifera* and *C. cinnamomea*), and the chin of *C. gutturata* is also dull pale yellow in a large majority of specimens.

The tail is uniformly and strongly rufous in all the species, with the single exception of *Certhiaxis sulphurifera* in which the tail is chiefly cinnamon brown, but more rufous on the outer pairs of rectrices. The upper surface of the wing is strongly rufous in all the species, but the intensity of the pigment and the extent of the rufous area varies from species to species.

The structure of the tail has been mentioned above when comparing *Certhiaxis* to *Synallaxis*. The tail varies little in length and is about equal to the length of the wing, is slightly stiffened only, and composed of 12 rectrices with the single exception of *C. mustelina* which has 10. The webs of the rectrices are well integrated as a rule. The apex of the rectrices is relatively quite blunt in *C. gutturata,* but is acuminate in all the other species, varying in shape, as the acumination is of two types, best shown by the central rectrices. In a few species (such as *C. eryth-*

rops, or, to some extent, *curtata*) the apex is cuneiform, but, in the other species, the terminal portion of the outer web becomes very attenuated, tapering to a fine point; this outer web is narrow, but the inner web is much broader and is more or less deeply excised in a concave fashion. This type of acumination is met only in *Certhiaxis,* for which it is most characteristic.

The length of the wing varies little also, from 58 to 75 mm. in round numbers, with an average of 66 mm., and the variation of the bill and feet is also very slight. The culmen is slightly decurved, and both the bill and feet are moderately strong.

Phylogeny

The relationships of many species are not clear. However, the five following species have a red "cap," differ only slightly morphologically from each other, and are probably closely related: *Certhiaxis erythrops, C. demissa, C. antisiensis, C. pallida,* and *C. curtata.* Little or no information exists on the behavior of *C. demissa* and *C. curtata,* but I believe their general behavior is probably more or less similar to that of the other three species. The latter species are highly arboreal, construct a nest of moss, which is pensile in the case of *C. erythrops* and *C. antisiensis,* but not in the case of *C. pallida,* according to von Ihering.

Mayr and Phelps (1967) in their paper on the origin of the bird fauna of the highlands of southern Venezuela considered that *Certhiaxis demissa* and *C. curtata* were conspecific. However, they did not offer a single word to substantiate their opinion and I believe *C. demissa* must be maintained as a separate species. To be sure, *demissa* and *curtata* are allopatric and probably closely related, but *erythrops* and *antisiensis* form part of the same complex (map 16) and are also allopatric with *demissa,* and, moreover, all four species differ morphologically from one another to about the same degree. In other words, no evidence supports the opinion of Mayr and Phelps.[84]

Three other species (*Certhiaxis furcata, C. mülleri,* and *C. gutturata*) have a red cap also, although not so sharply defined. The relationship of *C. mülleri* and *C. gutturata* to the other species seems distant, however, as suggested by the coloration of their underparts. The latter are heavily patterned or spotted in *C. mülleri* and *C. gutturata,* not uniform as in all the other species with red caps. It is possible also that *C. furcata,* in which the underparts are uniform, is not very closely related to the other species in which the underparts are uniform, because its adult plumage is "retarded," similar to the immature plumage of many other species.

The existence of a red cap in these eight species suggests, perhaps, that they are the species of *Certhiaxis* least removed from *Synallaxis,* in which the red cap is characteristic of a large group of 16 species (Group One). However, the significance of this character is ambiguous when one considers that about half of the species of *Synallaxis* do not have a red cap. I suspect that *C. mülleri* and *C. gutturata* are not very closely related to the other species of *Certhiaxis* with a red cap.

The three species with heavily streaked crowns (*Certhiaxis hellmayri, C. subcristata,* and *C. pyrrhophia*) appear to be related. The morphological resemblance between *C. subcristata* and *C. pyrrhophia* is striking, but their nesting habits are very different. It is possible that these two species are not so closely related as they appear to be morphologically. The distribution of this group of three species suggests that it may be ancient, as *C. hellmayri* is restricted to the Santa Marta Massif only, *C. subcristata* chiefly to the coastal mountains of Venezuela, and *C. pyrrhophia* chiefly to the Chaco (map 17).[85]

The closest relatives of the three species with streaked crowns appear to be *C. marcapatae, C. albiceps, C. semicinerea,* and *C. albicapilla* (map 18). These four species have a short crest and the color of the crown contrasts completely with the color of the back in the case of *C. albiceps, C. semicinerea,* and *C. albicapilla,* but not of *Certhiaxis marcapatae,* in which the crown and back are strongly rufous and uniform. *Certhiaxis*

marcapatae seems quite different at first glance but shows a certain similarity to *C. albiceps* as stated by Zimmer (1936a) who believed the two species are related. Zimmer is probably correct as a very strong similarity exists in the color of the rufous back of the two species, and, in *C. marcapatae*, a broad dusky band borders and outlines the rufous crown which seems to be the counterpart of the broad black band which outlines the pale crown in *C. albiceps*.

The relationships of the other five species (*C. obsoleta, C. vulpina, C. sulphurifera, C. cinnamomea,* and *C. mustelina*) are more doubtful. *Certhiaxis cinnamomea* and *C. mustelina* are quite similar superficially and build the same type of nest (at least externally, but not in the same location). Although *C. mustelina* lacks the yellow throat patch of *C. cinnamomea* they may be related.

Yellow pigment is so rarely found in the Furnariidae that it attracts attention, and it is difficult not to accord some taxonomic significance to its existence. But the significance of this pigment as an index of close relationship in *Certhiaxis* is ambiguous. This pigment exists, to a varying degree, on the upper throat of *C. gutturata, C. sulphurifera,* and *C. cinnamomea,* but nevertheless, it is probable that *C. gutturata* is more closely related to *C. mülleri* than it is to either *C. sulphurifera* and *C. cinnamomea*. It seems doubtful also that *C. sulphurifera* and *C. cinnamomea* are closely related as the structure of their nests is not at all comparable and the yellow pigment is glossy in *C. sulphurifera* and restricted to a tuft of erectile feathers, which does not exist in *C. cinnamomea*; the yellow pigment is bright as a rule in *C. cinnamomea,* but not glossy, and is distributed over virtually the whole of the upper throat and chin.

What the nearest relatives of *Certhiaxis obsoleta* and *C. vulpina* are is not clear. These two species seem "isolated," but the nearest relatives of *C. obsoleta* are probably the six species that have a red cap and that are uniform on their underparts. Hellmayr (1925) believed that *C. vulpina* is closely related to *C. pallida,* but I do not share this opinion. *Certhiaxis vulpina* seems best listed between the group consisting of *C. marcapatae, C. albiceps, C. semicinerea,* and *C. albicapilla* on the one hand, and *C. mülleri* and *C. gutturata* on the other; this is suggested by the fact that the underparts are more or less faintly and distinctly mottled in *C. vulpina,* though very far from being as distinctly and heavily patterned as in *C. mülleri* and *C. gutturata*.

Geographical Variation

Nine species vary geographically: *Certhiaxis erythrops, C. antisiensis, C. curtata, C. subcristata, C. pyrrhophia, C. albiceps, C. albicapilla, C. vulpina,* and *C. cinnamomea*. Geographical variation has been mentioned also in *C. semicinerea* and in *C. gutturata,* but it can be called important only in the case of *C. antisiensis*.

Certhiaxis antisiensis ranges in the Andes from the region of Cuenca in Ecuador, south to about 12° S. in Peru in the region east of Lima on the western slopes of the Andes; specimens were collected between 1189 and 4572 m. as far as recorded. *Certhiaxis antisiensis* is composed of two very distinct forms which also vary geographically; the oldest name for the first of these forms is *antisiensis* Sclater, 1858, based on a specimen from Cuenca, Ecuador; and the oldest name for the other is *baroni* Salvin, 1895, based on a specimen from Huamachuco, La Libertad, Peru.

The populations from the northern end of the range, from Ecuador south to Piura, northern Lambayeque, and northern Cajamarca in northern Peru are assigned to *antisiensis*. This form, which seems to be distributed between about 1180 and 2800 m., is small (see below), and its coloration can be characterized as brownish on the back, and ochraceous on the underparts. *C. a. baroni* replaces *C. a. antisiensis* farther south at generally higher elevations varying from about 1700 to 4500 m. The birds assigned to *baroni* are much larger than those assigned to *antisiensis*. The coloration of *C. a. baroni* can be characterized as gray on the back,

white or whitish on the throat and upper breast, with a grayish lower abdomen and flanks. The differences between the two forms are striking.

Taxa *antisiensis* and *baroni* were considered to be separate species until the revision of Koepcke (1961), who came to the conclusion that they are conspecific. This opinion is difficult to accept on first acquaintance, but the two forms (of which I have studied a total of 99 specimens) replace one another geographically and the geographical variation in their coloration is clinal. The larger size of *baroni* can be accounted for by higher elevations, but only to a certain extent, as the altitudinal range of the two forms overlaps and latitude seems to be a more important factor.[86]

However, a very sharp "step" exists between the two forms in coloration and size; they are not connected by an intermediate population, and a comparative study of their behavior and vocalizations is highly desirable. Nevertheless, the coloration of *C. a. antisiensis* from northern Peru (a population which was named *palamblae* by Chapman in 1923) shows a distinct approach to the coloration of *baroni*. Birds from Piura, northern Lambayeque, and northern Cajamarca, in Peru, when compared to birds from Ecuador, are more grayish on the back, less brownish, are distinctly whiter on the throat and margin of the upper breast, are less ochraceous below the upper breast, and have a better defined and whiter superciliary streak, the superciliary streak being very conspicuous and white in all the populations of *baroni*.

Birds from Chachapoyas in Amazonas and its general region, including the valley of the Huayabamba in "San Martin" (but probably taken not far to the southeast of Chachapoyas, perhaps in Amazonas) are quite incontrovertibly *baroni*, although birds from these regions were assigned to *palamblae* erroneously by Hellmayr (1925). These birds differ slightly, but appreciably, from topotypical *baroni* (and birds from the general region of Huamachuco, south to northern Ancash) by averaging somewhat more brownish, less gray, on the back, more buffy, less grayish, on the lower abdomen and flanks, and also by being less pure white on the throat. Birds from the regions of Chugur and Taulis, in Cajamarca (which were discussed as important by Koepcke) are quite similar to those of the region of Chachapoyas, in my opinion. In other words, specimens from these regions seem to represent another stage on the cline of coloration. They average smaller than topotypical *baroni*, but were collected at lower elevations and farther north.

The cline culminates farther south, in Huánuco, where specimens are distinctly whiter on the throat and upper breast, darker gray on the abdomen and flanks, and slightly darker gray on the back on an average than topotypical *baroni*. The population of Huánuco was named *capitalis* by Zimmer (1924), who mentioned also a number of other differences in coloration which are slight, however, far from constant, and of very minor importance. The increase in size (wing and tail) reaches its maximum in Huánuco.

A series of eight adult and two immature birds was collected by Koepcke in 1953–1955 between 2500 and 2900 m. on the western slope of the Andes east of Lima. These birds seem to be unusually small and were named *zaratensis* by Koepcke (1961) but the measurements she supplied cannot be compared with those listed in table 12 as males and females were combined and no average was given. One male from this series, presented by Koepcke to the American Museum of Natural History, has a wing length of 74 mm. and its coloration falls within the range of individual variation of the specimens of *capitalis* I have seen.

Koepcke (1961) stressed that the inner web of the central rectrices of her specimens of *zaratensis* is more deeply excised than in specimens of other populations she has examined and considered this difference to be an important subspecific character. I cannot agree, as the shape of the tip varies a great deal individually and to about the same extent in all the populations of the species, and, of course, is also greatly affected by wear. The shape of the tip in the specimen of *zara-*

TABLE 12
Measurements (in Millimeters) of Adult Males of *Certhiaxis antisiensis*

Region (and taxon)	Altitude (m.)	Wing			Tail			Bill		
		N	Mean	Range	N	Mean	Range	N	Mean	Range
Ecuador ("typical" *antisiensis*)	1189–2200	12	67.59	64–71	11	70.00	66–77	10	16.25	15–18
Piura, N. Lambayeque, N. Cajamarca (*antisiensis*-"*palamblae*")	1189–2804	8	67.75	64–73	7	68.86	64–73	8	16.46	16–17
S. Amazonas, Chachapoyas and environs (*baroni*)	1676–2804	8	72.94	68–70	8	74.25	67–82	7	17.67	16–18.5
Central Cajamarca (Chugur) and S. Cajamarca (Taulis) (*baroni*)	2697–2743	3	76.00	74–79	3	74.67	74–81	3	17.84	17–18.5
Extreme S. Cajamarca (Cajabamba) and L. Libertad, S. to Yánac (N. Ancash) ("typical" *baroni*)	2743–4572	10	79.70	75–84	10	81.30	76–84	10	19.55	18–20.5
Huánuco (*baroni*-"*capitalis*")	2743–3657	4	82.25	81–84	4	85.50	84–86	4	19.50	19–20
Above Lima (*baroni*-"*zaratensis*")	2800	1	—	74	1	—	77	1	—	17

tensis in the American Museum of Natural History can be matched by that of many specimens from other regions.

I believe Koepcke is probably correct in considering that *antisiensis* and *baroni* are conspecific. Her opinion is supported by the clinal variation that I have described above, but should be confirmed or refuted by a study of comparative behavior as a very sharp "step" exists between the two forms which is not bridged by true morphological intermediates.

If taxa *antisiensis* and *baroni* are conspecific (as they appear to be) it is evident to me that they should be the only two subspecies of the species *C. antisiensis*, as the recognition of the other forms which have been named (*palamblae*, *capitalis*, and *zaratensis*) would serve only to obscure the pattern of the geographical variation discussed above.[87]

The measurements of adult males that I have examined are listed in table 12, with an indication of the variation in altitude at which these specimens were collected, when recorded. I do not recognize "*palamblae*," "*capitalis*," and "*zaratensis*," and use these names, or "typical," only for reference to the discussion.

The geographical variation of the other species is much less interesting and important and I do not believe any subspecies should be recognized.

The ranges of *Certhiaxis vulpina* (map 17) and *C. cinnamomea* (map 19) are the most extensive in the genus, and Peters (1951) has recognized six subspecies in *C. vulpina* and eight in *C. cinnamomea*; an additional subspecies (*dissita*) was added to *C. vulpina* by Wetmore (1957) when he discovered the existence of an unsuspected, very isolated population in 1956 on Coiba Island, off the Pacific coast of Panama.

Examination of a large series of 222 specimens of *Certhiaxis vulpina*, representing all the forms named, shows that the geographical variation is slight and consists chiefly of variation in general coloration that is quite relative, although the populations of eastern Peru and western Brazil are better differentiated than the other populations. In these populations (which have been named *C. v. vulpecula*), the bill is generally heavier and larger as a rule, and the underparts are paler than in the other populations, especially on the throat, and more distinctly mottled. The mottling is always slight in this species, but varies irregularly and is lacking in the birds

of northeastern Brazil and of Coiba Island. The underparts are also more tawny, brighter in these two populations, and slightly more so in the birds of Coiba, but the two populations are not similar on the upperparts and wing. The birds of northeastern Brazil are quite pale and dull, whereas those of Coiba are darker, more strongly rufous.

The geographical variation is more evident in the coloration of the upperparts and upper surface of the wing. The birds of northeastern Brazil are pale and dull, as stated above, paler and duller than those of any other population; the birds of western Apure, Venezuela, are the darkest but are relatively dull; whereas the rufous coloration is rich and most bright in birds of Bolivia. Northeastern Brazil, Apure (Venezuela), and Bolivia represent the extremes in the variation, as all the other populations of the species are nondescript and only vaguely differentiated with the exception of *C. v. vulpecula* mentioned above. Wetmore (1957) believed *vulpecula* is sufficiently well differentiated to be separated specifically from *C. vulpina,* but it is evident that *vulpecula* is conspecific with *vulpina* and differs from the other populations merely to a more pronounced degree. Wetmore's opinion was expressed in his description of the population of Coiba as a new subspecies.[88]

The geographical variation of *Certhiaxis cinnamomea* is comparable to that of *C. vulpina* (although none of its populations are as distinct as *C. v. vulpecula* in the case of *C. vulpina*) and is merely a question of degree in the rufescent pigmentation of the plumage. To be sure, the extremes are well differentiated; for instance, the population of the Orinoco Valley is pale and dull, less rufescent than any other population, and the birds of Colombia and the region of Lake Maracaibo, Venezuela, are dark, strongly rufous, and bright—but, as a complete range of variability exists, including the color of the forehead which is more dusky in some populations, subspecific separation seems futile to me.

The geographical variation of *Certhiaxis pyrrhophia* is clinal from north to south. Birds from the northern end of the range (La Paz and Cochabamba in Bolivia) are more rufescent above, slightly more buffy below, and their tails are brighter and more rufous than in the populations of southern Bolivia and Argentina. In the latter, the birds become progressively more grayish above, less rufescent, more whitish below, and darker on the tail, the central rectrices of which become dusky, rather than rufous. The cline is relatively slight other than in the variation of the color of the central rectrices, and is very gradual. I cannot detect any evidence of the geographical variation which has been mentioned in the color of the crown and its streaking.

The ranges of *Certhiaxis albicapilla* and *C. albiceps* (map 18) are relatively restricted, but differences exist between populations of each species. The difference is slight in the case of *C. albicapilla* but surprisingly marked in *C. albiceps*. In the latter, birds from La Paz, Bolivia, have a white crown, whereas the crown varies from ochraceous buff to pale ochraceous orange in the birds of Cochabamba. In the case of *C. albicapilla,* specimens which are known only from the Urubamba Valley of Peru are more olivaceous, less grayish, above and below, have a slightly darker, more cinnamomeous crown, and a somewhat more conspicuous white throat.

The geographical variation of *Certhiaxis erythrops, C. curtata,* and *C. subcristata* is slight; it hardly merits taxonomic consideration. In the case of *C. erythrops,* the top of the tail is a little brighter in the populations of Costa Rica and western Panama, and, as a rule, the rufous area on the face is more extensive, or shows some tendency to be so, than in the populations of Colombia and Ecuador. These last two populations have been separated subspecifically, but seem indistinguishable to me as no constant differences exist between them. The geographical variation of *C. curtata* is even more trivial, but the population of central and southern Peru tends to be more rufous and darker than the others. In *C. subcristata* (map 17), the crown is more darkly streaked as a rule in birds from the western end of the range (Andes), but some specimens from this region are vir-

tually identical with some from northeastern Venezuela.

In 1934, Pinto and his collecting party secured one adult of *Certhiaxis semicinerea* and two young birds in "southeastern" Goiás, Brazil, which he described in 1936 as a distinct subspecies (*goyana*), stating that these specimens are darker and less uniform on the crown than those from the populations of northeastern Brazil. The three specimens were collected on the Rio das Almas in a region which seems to me more in the southern part of central Goiás than in the southeast. I have not seen specimens from Goiás, but, to the best of my knowledge the validity of *goyana* has not been confirmed. It cannot be accepted until an adequate series becomes available.

The existence of geographical variation has been claimed in *Certhiaxis gutturata*, but has been denied by Gyldenstolpe (1945). I believe this author to be quite correct because a series of 110 specimens that I have examined from every part of the range shows that their variation is purely individual.

KEY TO THE SPECIES OF *CERTHIAXIS*

1. Tail with 10 rectrices ..... *mustelina*
   Tail with 12 rectrices 2
2. Face red, a bright rusty red area surrounding the eye completely, extending also to the greater part of the malar region ..... *erythrops*
   Face not red 3
3. Breast very distinctly squamated, or spotted with dark, blackish brown 4
   Breast not squamated, nor distinctly spotted with dark brown, but uniform, or with very faint pale shaft streaks, or faint pale gray mottling 5
4. Breast squamated ..... *mülleri*
   Breast spotted ..... *gutturata*
5. Crown heavily and sharply streaked with very dark, blackish brown 6
   Crown not streaked 8
6. Ground coloration of the crown bright reddish rufous ..... *hellmayri*
   Ground coloration of the crown buffy, much obscured by the dark streaks 7
7. Underparts white or whitish; with conspicuous broad white superciliary streak, broadening greatly behind the eye ..... *pyrrhophia*
   Underparts buffy on the throat, ochraceous below the throat; superciliary streak buffy, narrow, and very poorly defined ..... *subcristata*
8. Underparts, sides of the face, and conspicuous superciliary streak orange ochraceous; virtually uniform, but paler, more buffy on chin and upper throat, and with darker, more rufous ear coverts ..... *furcata*
   Underparts whitish, pale cinereous, ochraceous, olivaceous, umbraceous, or dusky fuscous olive, but not orange 9
9. Color of the crown contrasting strongly with the color of the back 10
   Upperparts uniform, or virtually so, but with no contrast between the colors of the crown and back 16
10. Crown feathers distinctly elongated, forming a short crest; varying in coloration, but not bright reddish chestnut 11
    Crown feathers not elongated, or only very slightly so (not forming a crest), and bright reddish chestnut 13
11. Top of the crown white, ochraceous buff, or pale ochraceous orange, very sharply delimited by a very broad black superciliary and post-ocular streak ..... *albiceps*
    Crown dull white, or drab white, not delimited with black 12
12. Dull, grayish brown, or olivaceous gray-brown on the back; crown dull white ..... *albicapilla*
    Bright, back strongly rufous (reddish rufous cinnamon); crown drab white, usually with a pale yellowish gray tinge .. *semicinerea*
13. Underparts pale ashy gray ..... *demissa*
    Underparts ochraceous, or white or whitish on the throat and breast, becoming progressively more grayish, or olivaceous gray on the abdomen and flanks 14
14. Superciliary streak grayish, faint, and very ill defined, reduced to a slight trace as a rule; tips of central rectrices sharply acuminate, cuneiform in shape, with the outer web narrower than the inner web, but relatively broad ..... *curtata*
    Superciliary streak white or whitish, conspicuous as a rule, or well defined at any rate; tips of the central rectrices sharply acuminate, with the inner web more or less deeply excised concavely (not cuneiform, or very distinctly less cuneiform than in *curtata*), and with the terminal portion of the outer web very distinctly more attenuated and narrower 15
15. Forehead extensively brown or very dark

brown in all individuals; underparts ochraceous, and virtually uniform, with the exception of the chin which is paler and more buffy; restricted to southeastern Brazil ... . *pallida*

Forehead very bright rufous (not brown) in the large majority of individuals; underparts variable, ochraceous with a whitish throat, or throat and breast white or dull white, becoming progressively more grayish, or olivaceous gray on the abdomen and flanks; restricted to the Andes, from southern Ecuador south to central Peru .... *antisiensis*

16. Upper throat pale sulphur yellow, or with a tuft of glossy, erectile, bright, dark sulphur yellow feathers on the center of the throat 17

Throat white, dull white, or buffy, without any yellow pigment 18

17. Upper throat pale sulphur yellow, without a tuft of erectile glossy yellow feathers; upperparts uniformly rufous cinnamon, or cinnamon brown, with the forehead slightly more rufous, or slightly dusky, in some populations..... *cinnamomea*

Upper throat with a tuft of erectile, bright, glossy yellow feathers on its center; upperparts uniformly brownish olive; breast slightly mottled with pale gray. This species differs from all others also by having a conspicuously elongated tail..... ..... *sulphurifera*

18. Crown feathers distinctly elongated posteriorly, and crown and back uniformly and very strongly rufous, bright burnt sienna . ..... *marcapatae*

Crown feathers not elongated; crown and back strongly rufous, or pale dull olive brown 19

19. Upperparts rufous (varying from bright to dull rufous cinnamon, hazel, or russet); underparts dull and dingy, more or less faintly mottled ..... *vulpina*

Upperparts olivaceous; underparts ochraceous..... *obsoleta*

List of the Species

Certhiaxis erythrops

Description: Uniformly dark amber brown, or rufescent raw umber brown on the back; with a bright rufous crown, varying from bright reddish chestnut to pale burnt sienna, the rufous area extending irregularly; but to a large extent over the face around the eye, over the lores, and the supraorbital, malar, and auricular regions. Underparts olivaceous, but more grayish on the throat and breast, faintly whitish on the chin, and more brownish on the flanks, lower abdomen, and under tail coverts. Upper surface of the wing strongly rufous, similar to the color of the crown on the coverts, but darker, more rufous brown on the outer webs of the remiges. Tail strongly rufous, reddish chestnut or russet, with rectrices that are strongly acuminate at the tip which is cuneiform in shape.

Immature Plumage: Differs from that of the adult by being uniformly olive brown on the upperparts, without a rufous cap, and by being strongly ochraceous on the underparts, with a pronounced dull orange tinge.

Range: Mountains of Costa Rica and western Panama, between about 760 and 3150 m., and Andes of Colombia and Ecuador between about 500 and 2500 m. from the Western Andes and western slopes of the Central Andes of Colombia south to Nariño in Colombia, and south to about Azuay in Ecuador.

Specimens Examined: 107, including the types of *erythrops* in BM, and of "*rufigenis*" in AMNH.

Certhiaxis demissa

Description: Similar to *Certhiaxis erythrops* in having a bright rufous crown, but gray on the face, without the rufous area; more grayish brown on the back, and almost uniformly ashy gray on the underparts, not olivaceous, being slightly paler on the chin and upper throat, and slightly darker, more umbraceous on the lower flanks and under tail coverts. Rufous area on the upper surface of the wing restricted to the coverts, with the outer webs of the remiges dull rufous brown. Tail uniformly bright rufous, with the rectrices strongly acuminate at the tip, slightly to moderately excised in a concave fashion on the inner web.

Immature Plumage: Differs from that of

the adult by being uniformly olivaceous brown on the upperparts with a slight rufous cast (no rufous cap); and with the underparts strongly ochraceous (not gray) with a faint, very dull orange wash below the upper throat which is more whitish, less ochraceous than the breast and abdomen.

RANGE: Mountains of southern Venezuela in Amazonas and Bolívar, to neighboring Guyana (Roraima and Mount Ayanganna), and Brazil (Uei-tepui); the altitudinal range varies from about 1400 to 2100 m.

SPECIMENS EXAMINED: 26, including the type of *demissa* in BM.

Certhiaxis antisiensis

DESCRIPTION: Pale rufescent raw umber brown on the back, with or without a very slight olivaceous or grayish tinge; crown bright rufous, and with a well or relatively poorly defined superciliary and post-ocular streak, varying from buff to whitish or white. Underparts dull white on the throat, becoming ochraceous, faintly olivaceous, or pale grayish olive below the throat or border of the upper breast, but paler on the center of the abdomen, and darker, more umbraceous on the lower flanks and lower abdomen. Upper surface of the wing very strongly and extensively bright rufous. Tail bright rufous, with the tips of the rectrices strongly acuminate and moderately to well excised on the inner web.

IMMATURE PLUMAGE: Differs from that of the adult by being uniformly olivaceous brown on the upperparts, without a rufous cap, and by being slightly or well patterned on the underparts. The ground coloration of the latter varies from dingy grayish white to ochraceous with a more or less pronounced dull orange tinge, the feathers being bordered or tipped, distinctly or not, by dark or pale brown, which creates a barred or scalloped pattern which is very pronounced, rather heavy, in some individuals.

This species is composed of two forms (*antisiensis* and *baroni*) which appear to be conspecific and were discussed, together with their respective variation, in the general discussion of the geographical variation within species in this genus. The description given above is based on *Certhiaxis antisiensis antisiensis* which varies somewhat geographically. *Certhiaxis antisiensis baroni,* which also varies somewhat geographically, is a much larger bird than *antisiensis* (see discussion and tables 11 and 12) and is gray on the back, whiter below than *antisiensis,* darker and grayer below the throat, and has a very conspicuous, pure white superciliary and post-ocular streak. The immature plumage of *C. a. baroni* is similar to that of *C. a. antisiensis,* but less distinctly and heavily patterned on the underparts, which are whiter and not tinged with orange in the specimens I examined.

RANGE: Andes of southern Ecuador and of northern and central Peru, from the region of Cuenca in Ecuador, south to Pasco (and probably Junín), and about 12° S. on the western slopes of the Andes in the region east of Lima in Peru. The altitudinal range varies from about 1200 to 2800 m. in *antisiensis,* and from about 1700 to 4600 m. in *baroni.*

I recognize only two subspecies: nominate *antisiensis,* ranging from Ecuador, south to Piura, northern Lambayeque, and northern Cajamarca in northern Peru; and *baroni* replacing nominate *antisiensis* farther south.

SPECIMENS EXAMINED: 99, including the types of *antisiensis* and *baroni* in BM, and of "*palamblae*" in AMNH.

Certhiaxis pallida

Figure 4

DESCRIPTION: Pale, bright, rufescent olive brown on the back, with a bright rufous crown, broadly barred with dark brown across the forehead, a conspicuous, but usually dull white, or somewhat buffy, streak extending posteriorly from the base of the bill on the forehead and lores over the eye to the post-ocular region. Dull white on the chin, and ochraceous on the remainder of the underparts. Upper surface of the wing strongly rufous, bright pale reddish chestnut on the coverts, but hazel on the outer web

of the remiges. Tail uniformly bright rufous, bright burnt sienna verging on English Red, with the rectrices very strongly acuminate at the tip and deeply excised on the inner web.

IMMATURE PLUMAGE: Differs from that of the adult by being slightly duller and darker on the back, with a darker brown crown without rufous, and by being darker ochraceous on the underparts which are tinged more or less pronouncedly with dull orange, the feathers of the breast and upper abdomen being faintly and very narrowly bordered with brown in some individuals.

RANGE: Southeastern Brazil (chiefly in the mountains from about 1000 m., or somewhat lower, to about 2200 m.), from Espirito Santo and neighboring Minas Gerais, south through southern Minas Gerais and Rio de Janeiro, to northeastern São Paulo.

SPECIMENS EXAMINED: 25, including the type or cotype of *pallida* in AMNH.

Certhiaxis curtata

DESCRIPTION: Raw umber brown on the back, with a reddish chestnut crown, barred more or less distinctly and extensively with raw umber brown across the forehead. Underparts olivaceous gray, below the throat which is paler and more grayish, and tinged with dark ocher and very faintly streaked as a rule. Upper surface of the wing strongly rufous, reddish chestnut, but rather dull, on the coverts, hazel on the outer webs of the remiges. Tail reddish chestnut, with the rectrices sharply acuminate at the tip, which is more or less cuneiform, but not deeply excised on the inner web.

IMMATURE PLUMAGE: Differs from that of the adult by being uniformly rufescent umber brown on the upperparts, without a rufous cap, and uniform, or slightly mottled on the underparts which are strongly washed with dull orange or dark tawny ocher.

RANGE: Eastern Andes of Colombia, and from the head of the Magdalena Valley, south through eastern and southern Ecuador, to Cuzco and Puno in southern Peru. The altitudinal range seems to vary from about 1250 to 2000 m.

SPECIMENS EXAMINED: 34, including the type of "*griseipectus*" in AMNH.

Certhiaxis furcata

Figure 4

DESCRIPTION: Rufescent raw umber brown on the back, with a distinct reddish chestnut crown, the posterior border of which merges, however, into the rufous brown color of the nape; and with a distinct orange ochraceous superciliary and post-ocular streak. Face orange ochraceous, interrupted by rufous brown auriculars which emphasize the ochraceous superciliary streak. Chin and upper throat dull white, tinged with dark buff, and remainder of the underparts uniformly dark orange ochraceous, with the exception of the lower flanks which are more umbraceous. Upper surface of the wing very strongly and almost uniformly reddish chestnut. Tail strongly rufous, similar to the color of the wing, with the rectrices sharply acuminate at the tip, which is more or less cuneiform in shape, not distinctly excised on the inner web.

IMMATURE PLUMAGE: Differs from that of the adult by being darker on the upperparts, more olive brown, and uniform, without a rufous cap; less uniform on the underparts, which are faintly mottled, and more olive, less orange ochraceous, on the sides of the breast and flanks in one specimen.

RANGE: Northern Peru in southern Amazonas, and perhaps in Cajamarca, and eastern Ecuador.

This species is incompletely known and the only genuine specimen of it still in existence may be the type in the Warsaw Museum, which was examined by me and described above. This specimen (incontrovertibly adult) and an immature bird were obtained at an elevation of 1646 m. at Chirimoto in Amazonas, according to Sztolcman who collected them. Chirimoto is about 65 km. southeast of Chachapoyas, in the valley of the Huambo River (or upper Huayabamba), not in San Martín as stated by Hellmayr. The immature specimen is no longer in existence, but three other immature specimens, which I have seen and reported upon (Vaurie, 1971b), seem to represent immature *Certhiaxis furcata*. They were collected at Chaupe in Cajamarca and on the Rio Oyacachi, below Chaco, in eastern Ec-

uador. The description of the immature plumage of *furcata* given above is based to some extent on the description of the immature specimen given by Taczanowski, but chiefly on the three immature birds from Chaupe and Ecuador.

SPECIMENS EXAMINED: 1, the type of *furcata* in ZIW, and perhaps the three others mentioned above.

Certhiaxis obsoleta

DESCRIPTION: Pale brownish olive on the back, with the crown olivaceous also, but slightly more grayish than the back, not rufous, and with small buffy or dark brown streaks on the forehead; a dull white postocular streak is present. The coloration of the upperparts and underparts is nearly uniform, olivaceous on the upperparts, much paler on the underparts which are dull yellowish ocher, slightly darker on the lower flanks, and more whitish on the chin. Rufous area on the upper surface of the wing reddish chestnut, but quite restricted, chiefly to the lesser and middle coverts. Tail very strongly rufous, bright reddish chestnut, with the tips of the rectrices sharply acuminate and elongated, and very deeply excised on the inner web.

IMMATURE PLUMAGE: Similar to that of the adult on the upperparts, but darker, purer olive green, and not uniform on the underparts, patterned by narrow dark brown borders to the feathers which are best developed and most distinct on the breast.

RANGE: Southeastern Brazil, from southern Minas Gerais and Rio de Janeiro, west to eastern Paraguay, and south to Misiones and northeastern Corrientes in Argentina, and to south central Rio Grande do Sul in Brazil.

SPECIMENS EXAMINED: 102.

Certhiaxis hellmayri

DESCRIPTION: Rufescent raw umber brown on the back, with a rufous crown heavily streaked with dark brown; and with a rather poorly defined whitish superciliary and postocular streak. Underparts dingy olivaceous gray, but whitish on the chin and upper throat. Upper surface of the wing strongly and extensively rufous, bright reddish chestnut on the coverts, English Red on the remiges. Tail bright pale rufous, with the tips of the rectrices sharply acuminate, moderately excised on the inner web.

RANGE: Northern Colombia, where it is restricted to the Santa Marta Massif at elevations varying from about 1520 to 2750 m.

SPECIMENS EXAMINED: 3.

Certhiaxis subcristata

DESCRIPTION: Pale rufescent olive brown on the back, with a buffy or pale cinnamomeous crown almost completely obscured by very heavy brown or dusky streaks, the feathers being very distinctly elongated and forming a short crest in some individuals; and with a poorly defined buffy superciliary streak. Underparts pale ochraceous tawny and virtually uniform, with the exception of the chin and upper throat which are whitish. Upper surface of the wing strongly and extensively rufous, reddish chestnut but rather dull. Tail strongly rufous, similar to the color of the wing, with the rectrices sharply acuminate at the tip, but with only a shallow excision on the inner web.

IMMATURE PLUMAGE: A really young bird has not been seen by me, but in one specimen which does not seem to be fully adult, the underparts are darker than in adults, more grayish, and are very faintly mottled, the crown is grayish brown and almost uniform in coloration as the streaks are not distinct and the elongated feathers much less developed than in adults.

RANGE: Mountains of northern Venezuela, between about 700 and 2300 m. from Sucre in the northeast, west to the highlands around Lake Maracaibo, and along the lower eastern slopes of the Andes in Barinas, south to Táchira, western Apure, and along the foot of or on the lower slopes of the Eastern Andes of Colombia to Boyacá.

SPECIMENS EXAMINED: 19, including the types of *subcristata* in BM, and of "*fuscivertex*" in the Phelps Collection, deposited in AMNH.

Certhiaxis pyrrhophia

DESCRIPTION: Pale rufescent raw umber brown, or grayish brown, on the back, with a pale pinkish cinnamon crown heavily streaked with very dark brown, the feathers of which are elongated; and with a distinct white superciliary streak which broadens posteriorly over the post-ocular region. White on the throat and upper breast, whitish on the remainder of the underparts, more or less faintly tinged with pale gray and pale umber on the lower flanks and under tail coverts. Upper surface of the wing strongly rufous, bright reddish chestnut on the coverts, hazel on the remiges. Tail strongly rufous, burnt sienna, in the northern end of the range, but becoming dusky and brown on the central rectrices as the populations range farther south (see geographical variation); with the tips of the rectrices sharply acuminate, elongated, and deeply excised on the inner web.

IMMATURE PLUMAGE: Differs from that of the adult by being uniformly brown on the crown, the feathers of which are not elongated, or only slightly so; by being darker, less whitish on the breast and abdomen, the feathers of which are very faintly mottled in some individuals.

RANGE: Bolivia, from the Yungas of La Paz and Cochabamba, south through western Paraguay to Uruguay (north to neighboring southern Rio Grande do Sul in Brazil), and through northern and central Argentina to northern Neuquén and Rio Negro. The altitudinal range varies from about 600 to 3100 m. in Bolivia, and from about 400 to 1500 m. in Argentina.

SPECIMENS EXAMINED: 132, including the types of "*rufipennis*" in BM, and of "*striaticeps*" in MNHN.

Certhiaxis marcapatae

DESCRIPTION: Crown and back bright burnt sienna and uniform, with the feathers of the hind crown distinctly elongated. Sides of the head and of the nape brownish olive, with very faint whitish shaft streaks on the auriculars, and with a dull white superciliary streak, not well defined, and becoming buffy posteriorly, separated from the rufous crown by a dusky band. Chin whitish and throat buffy, with the remainder of the underparts pale grayish olive, becoming umbraceous on the upper flanks, and tawny on the lower flanks and under tail coverts. Upper surface of the wing strongly and extensively rufous, burnt sienna as on the crown and back. Tail bright reddish chestnut with the tips of the rectrices strongly acuminate, but only slightly excised on the inner web.

IMMATURE PLUMAGE: Unknown, but the only other specimen which is known of this species is not fully adult and differs from the adult by being paler rufous above, with the feathers of the crown much less distinctly elongated, and by being very distinctly more ochraceous on the underparts that are faintly mottled.

RANGE: This species is known so far only from the two specimens described above, both taken at Marcapata, Cuzco, southern Peru, at an elevation of 3307 m., which are in the collection of the American Museum of Natural History.

SPECIMENS EXAMINED: 2, including the type of *marcapatae* in AMNH.

Certhiaxis albiceps

DESCRIPTION: Upperparts very strongly rufous on the back which is pale dull burnt sienna (Sanford Brown), with the top of the crown varying from pure white to ochraceous buff and pale ochraceous orange, the feathers of which are somewhat elongated. Face sooty gray or blackish, with faint gray superciliary streak, separated from the white or ochraceous crown by a broad band of black. Chin whitish with the remainder of the underparts dark grayish olive, becoming pronouncedly olivaceous on the lower flanks and under tail coverts. Upper surface of the wing very strongly and extensively rufous, of the same color as that of the back. Tail strongly rufous, bright chestnut or auburn, with the rectrices strongly acuminate at the tip, nearly cuneiform.

RANGE: Bolivia, in the Andes of the De-

partments of La Paz and Cochabamba at elevations varying between about 2200 and 3300 m. But specimens collected very recently in Peru by John Weske and John Terborgh, which have not been reported so far, show that the range of *Certhiaxis albiceps* extends considerably farther north, to the Cordillera Vilcabamba in Cuzco, Peru.

SPECIMENS EXAMINED: 18, including the two cotypes of *albiceps* in MNHN, and the type of "*discolor*" in AMNH.

Certhiaxis semicinerea

DESCRIPTION: Dark reddish cinnamon on the back, upper surface of the wing, and tail, the tail being slightly darker and more rufous than the back and wing. Crown buffy cinnamon with a grayish cast which becomes more pronounced on the posterior part of the crown, the coloration of the crown fading into that of the nape and upper border of the mantle which are pale brownish gray. Chin and upper throat whitish, with the remainder of the underparts, which are uniformly grayish white, with a slight buffy, or "creamy" cast. The feathers of the crown are distinctly elongated, and the tips of the rectrices are sharply acuminate, slightly excised on the inner web.

RANGE: Northeastern Brazil, from Ceará south to Bahia, and west from Bahia to the Rio das Almas in south central Goiás.

SPECIMENS EXAMINED: 9, including the type of "*caniceps*" in BM.

Certhiaxis albicapilla

DESCRIPTION: Pale olivaceous grayish brown, or pale olivaceous brown on the back, with a dull whitish crown, tinged with pale pinkish cinnamon to a varying degree, and the feathers of which are distinctly elongated, forming a short "crest" in some individuals. Chin and upper throat white or whitish, with the remainder of the underparts uniformly grayish white with a very faint olivaceous cast, or more ochraceous. Rufous area on the upper surface of the wing bright reddish chestnut, restricted only to the coverts. Tail strongly rufous, reddish chestnut or somewhat duller (auburn). Rectrices sharply acuminate at the tip, which is elongated and slightly excised on the inner web.

RANGE: Andes of central and southern Peru, between about 2400 and 3300 m., from Junín south to Cuzco and Apurimac.

SPECIMENS EXAMINED: 25.

Certhiaxis vulpina

DESCRIPTION: Uniformly dull reddish chestnut, or ferruginous, reddish russet, or dark rufous cinnamon, on the crown (the feathers of which are not distinctly elongated), back, upper surface of the wing, and tail; with a dull white or buffy superciliary streak not well defined. Whitish on the chin and upper throat, and dingy, olivaceous gray, or brighter, more ochraceous or tawny on the remainder of the underparts which are more or less distinctly or faintly mottled with buff, or very pale grayish brown, in most but not in all populations. Rectrices strongly acuminate at the tips which are nearly cuneiform in shape, or only slightly excised on the inner web.

IMMATURE PLUMAGE: Similar to that of the adult, but more grayish, less rufous on the upperparts, and usually much more strongly ochraceous on the underparts, verging on dull orange in some individuals, and with narrow dark brown borders to the feathers, especially on the breast, which produce a vaguely mottled or spotted, but not very distinct pattern.

The coloration of this species varies geographically to a relative degree (see general discussion of the geographical variation), and the bill is generally heavier and larger in the populations of eastern Peru and western Brazil.

RANGE: Southern Venezuela, from the delta of the Orinoco and along its valley, west to western Apure, south through eastern Vichada in eastern Colombia, and Brazil to the Amazon Valley, west to eastern Peru, and south to the Beni and borders of Cochabamba in Bolivia, southern Mato Grosso and northwestern Paraná, east in Brazil to Piauhí, and the western parts of Bahia, Minas

Gerais (probably), and São Paulo; also Coiba Island, off the Pacific coast of Veraguas, Panama.

SPECIMENS EXAMINED: 222, including the types of "*vulpecula*" in BM, and of "*apurensis*" in the Phelps Collection, deposited in AMNH.

Certhiaxis mülleri[89]
Figure 4

DESCRIPTION: Dark rufescent olive brown on the back, with a chestnut crown which does not contrast strongly with the color of the back and is banded to an irregular extent with dark brown on the forehead; with a poorly defined, short, and narrow, buffy superciliary streak. Dull white on the chin, but dark on the remainder of the underparts, grayish or brownish olive, each feather with a dingy white or buffy subapical area, and bordered crescentically at the apical margin with very dark or blackish brown, creating a distinct, heavy, scalloped pattern which becomes progressively less well defined at the sides and on the lower abdomen, grading into uniformly brownish olive flanks. Rufous area on the upper surface of the wing very extensive, but dark, chestnut on the coverts, auburn on the remiges. Tail chestnut to auburn, with the tip of the rectrices sharply acuminate, cuneiform, not excised on the inner web.

IMMATURE PLUMAGE: Differs from that of the adult by lacking the chestnut pigment on the crown, the upperparts being uniform, or with a vague ochraceous or dull orange collar on the nape; and by having a broader "freer" pattern on the underparts, the pale subapical spots on the feathers being larger and very strongly buffy or dull orange.

RANGE: Northern Brazil, in the valley of the lower Amazon, from the lower Rio Nhamunda (or Jamunda), east to the mouth of the Amazon, including Mexiana Island and probably other islands in the mouth of the Amazon. The range seems to be restricted chiefly to the left bank, but I have seen specimens collected also on the right bank at Santarém, near the mouth of the Rio Tapajós, and at Vilarinho do Monte, near the mouth of the Rio Xingú.

SPECIMENS EXAMINED: 29.

Certhiaxis gutturata
Figure 4

DESCRIPTION: Dull and grayish olive brown on the upperparts, with a chestnut crown banded to an irregular extent with dark brown across the forehead, but not uniformly, as the brown band is stippled by dark buff or golden yellow at the center of its feathers; and with a buffy superciliary and post-ocular streak more or less well defined. Chin and upper throat dull pale yellow, and ochraceous on the remainder of the underparts which are profusely spotted with dark brown or blackish brown; the spotting is heavier and more sharply defined across the breast, and diminishes progressively, becoming paler and fainter below the upper abdomen, the ground coloration becoming then more buffy cinnamon, less ochraceous than on the breast, and acquiring a grayish tinge which becomes more umbraceous on the flanks. Rufous area on the upper surface of the wing very extensive but relatively dull, more "reddish" on the coverts, more ferruginous on the remiges. Tail bright chestnut, with the rectrices blunt at the tip, not acuminate.

IMMATURE PLUMAGE: Two types exist which seem to represent different stages in the sequence of the plumage. In both, the upperparts are uniformly grayish olive, darker, less rufescent than in the adult, not chestnut on the crown, but differ conspicuously in the coloration of the underparts. In one type (probably the more advanced stage in the sequence), the general coloration of the underparts resembles that of the adult, but is more grayish, and the spotting is less heavy, more indistinct, as the spots are much paler, grayish, less dark brown than in the adult.

In the other state, represented by two specimens in the Stockholm Museum which have been described and discussed by Gyldenstolpe (1945, 1951), the underparts are

not spotted, and the throat and breast (and also the superciliary streak and most of the face) are a strong, dark dull orange, in one bird, but paler, more ochraceous orange in the other; a tinge of orange extends irregularly over the abdomen in both specimens. The feathers of the breast have very faint, narrow, brownish margins in the two birds, and, in the paler one, a few, vague dark spots exist on the sides of the breast.

These two specimens were collected at Aruma on the lower Rio Purús in 1935, and at Santo Antonio, on the lower Rio Eiru, an affluent of the upper Rio Juruá, in 1936. They could not be identified by Gyldenstolpe, who, finally, sent the specimen from Aruma (the darker, more orange, and completely unspotted specimen) to Hellmayr, two or three years before Hellmayr died in exile in Switzerland. Hellmayr could not identify it either, and informed Gyldenstolpe "that he had never before seen anything like it." These two specimens were eventually identified by me as *gutturata* but only after I had showed them to Dr. K. C. Parkes of the Carnegie Museum, who was the first to suspect their true identity.

I have discussed these two immature specimens at some length to emphasize that the plumage sequence of the Furnariidae is virtually unknown. Any systematic conclusions based on it are suspect without thorough study.

RANGE: Southern Venezuela, from Bolívar (basin of the Rio Caura, and upper basins of the Rio Paragua and Rio Icabaru) and from Amazonas, Surinam, and French Guiana, west to Caquetá in eastern Colombia, and south through eastern Ecuador and eastern Peru, to La Paz, the Beni, and Cochabamba in Bolivia, and south, through Brazil, to the basins of the Juruá, Purús, and Madeira, and to the lower Tapajós and lower Tocantins.

SPECIMENS EXAMINED: 110, including the type of *gutturata* in MNHN.

Certhiaxis sulphurifera
Figure 4

DESCRIPTION: Uniformly brownish ocher on the upperparts, with a slight olivaceous tinge. Dull white on the underparts with a faint grayish cast, but tawny on the lower flanks, with a tuft of erectile feathers on the center of the upper throat which are bright glossy sulphur yellow, and with short, fine, inconspicuous, pale grayish brown streaks on the sides of the throat and on the breast. Rufous area on the upper surface of the wing bright reddish chestnut only on the lower and middle coverts, ferruginous on the greater coverts, secondaries, and base of the outer web of the primaries. Tail cinnamon brown with the central rectrices pronouncedly elongated; the rectrices are acuminate at the tip and not very firmly integrated, especially the terminal portion of the central rectrices.

IMMATURE PLUMAGE: Differs from that of the adult by being noticeably darker on the upperparts; also on the underparts which are ochraceous, rather than whitish, and lack the tuft of yellow feathers on the throat, and also the streaks at its sides and on the breast.

RANGE: Southeastern Rio Grande do Sul in Brazil, and Uruguay, west to southern Entre Rios in Argentina, and south through eastern Buenos Aires to the region at the mouth of the Rio Negro; chiefly in coastal regions.

SPECIMENS EXAMINED: 39.

Certhiaxis cinnamomea
Figure 4

DESCRIPTION: Upperparts uniformly reddish brown or dark rufous cinnamon, reddish chestnut on the upper surface of the wing, and somewhat paler rufous on the tail; with a faint, ill-defined grayish or whitish superciliary streak. Underparts pale, bright sulphur yellow on the upper throat, white at the sides of the throat and below the yellow area, down to about the upper border of the breast; remainder of the underparts whitish, especially on the center, but more or less faintly tinged with gray or buffy cinnamon, the pigmentation becoming more pronounced at the sides. Tips of the rectrices very sharply acuminate, becoming very finely attenuated on the central rectrices which are very deeply excised on the inner web, almost devoid of barbs.

The coloration of this species varies geographically to a relative degree (see general discussion of the geographical variation). The description given above is based on specimens from the Guianas, the mouth of the Amazon, and the lower Tocantins, which represent the nominate populations. In other parts of the range, the rufous areas are relatively paler, duller, darker, or brighter, and the underparts more or less whitish, tinged to a greater degree or not with faint gray and buffy cinnamon. In the population of Colombia, the forehead is also more or less dusky brown, not rufous as in the other populations.

IMMATURE PLUMAGE: Similar to that of the adult, but without the yellow patch on the upper throat; darker and duller, less rufous, on the upperparts, more or less whitish or cloudy on the underparts. In a few individuals, the feathers of the breast are faintly mottled, or the feathers are very narrowly margined with pale grayish brown.

RANGE: Very extensive, extending from northern Colombia (south to the valley of the middle Atrato River, and about the valley of the middle Magdalena), Venezuela, Trinidad, and the Guianas, south through Brazil (west to about the middle of the Rio Negro, the Rio Madeira, and perhaps to the right bank of the Rio Purús), to eastern Bolivia, Paraguay, Uruguay, and Argentina south to northeastern Buenos Aires, west in Argentina to eastern Salta and very probably southeastern Jujuy, central Santiago del Estero and probably northeastern Córdoba.

SPECIMENS EXAMINED: 281, including the types of "*pallida*," "*orenocensis*," and "*caudacutus*" in AMNH, and of "*valenciana*," and "*marabina*" in the Phelps Collection, deposited in AMNH.

Certhiaxis mustelina

DESCRIPTION: Strongly and uniformly rufous on the upperparts, wing, and tail, and virtually pure white on the underparts. The general coloration is similar to that of *Certhiaxis cinnamomea* but purer white on the underparts, and without the yellow patch on the upper throat of *C. cinnamomea*. The tips of the rectrices are sharply acuminate, finely attenuated, but only very slightly excised on the inner web, and the tail is composed of only 10 rectrices, not 12, as in *C. cinnamomea* and all the other species of the genus.

IMMATURE PLUMAGE: Less uniform than that of the adult. The upperparts are not uniformly rufous as in the adult, as the crown is dusky brown, contrasting well with the rufous coloration of the back. The feathers of the breast are not uniformly white as in the adult, but are slightly and very narrowly bordered with pale grayish brown at the apex, but the dark borders are usually poorly defined, not very distinct.

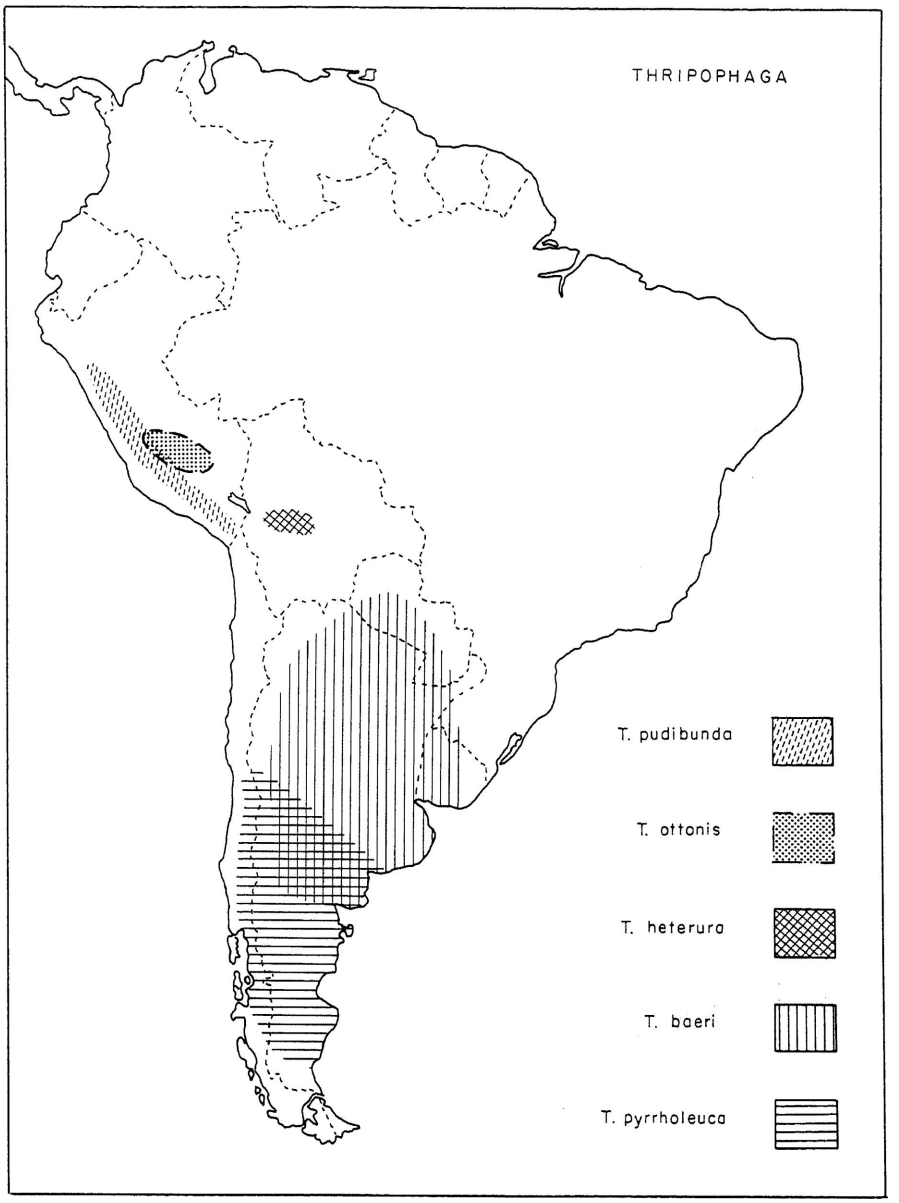
RANGE: Amazon Basin, from eastern Peru in the valley of the Ucayali and its affluents, and that of the lower Marañon, eastward through Brazil in the valleys of the Juruá, Purús, Madeira, and Amazon, to the region of Monte Alegre on the north bank of the Amazon, and to the region east of Santarém, and east of the mouth of the Tapajós, on the south bank of the Amazon. This species is also found on the lower Mamoré which suggests that it most probably occurs also in neighboring northern Bolivia, although I know of no records for Bolivia so far.

SPECIMENS EXAMINED: 66.

GENUS *THRIPOPHAGA*

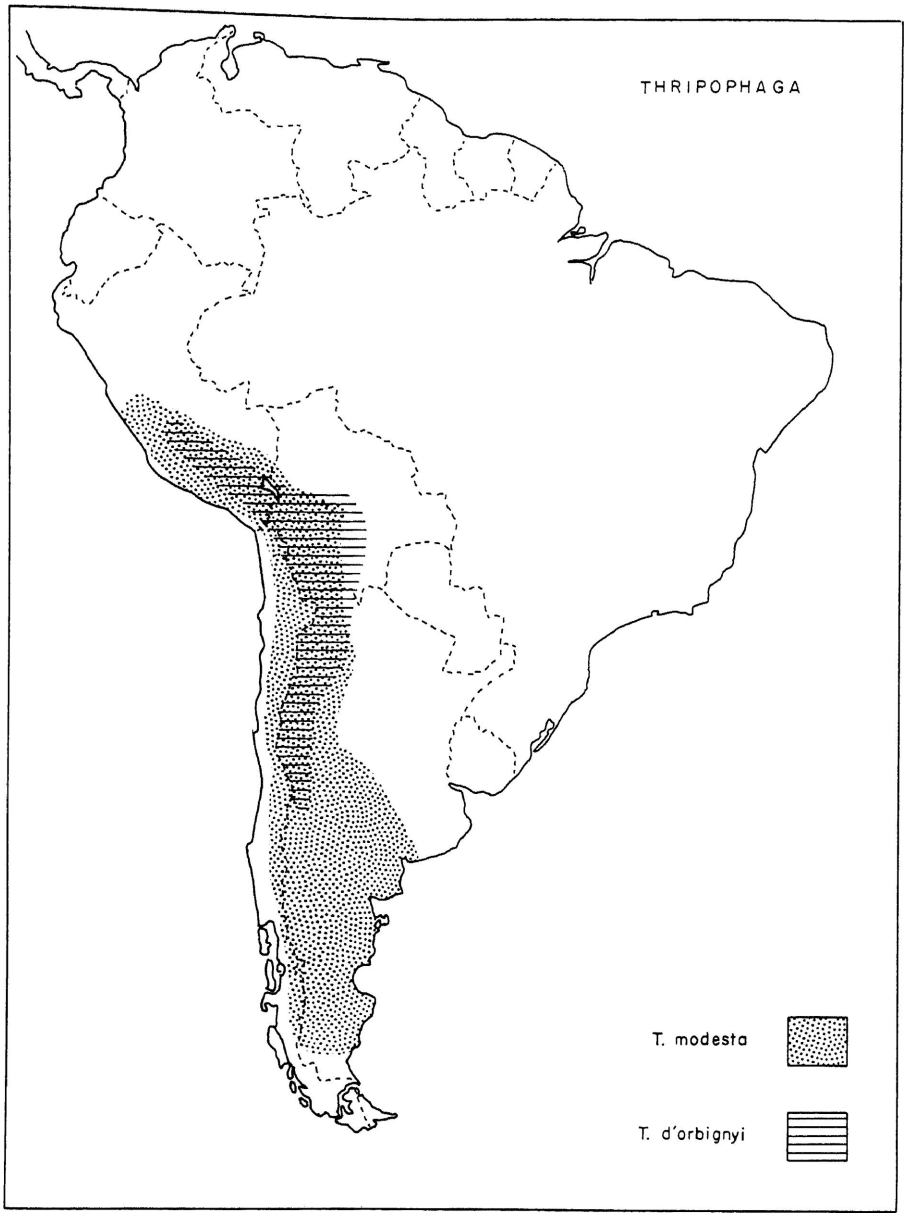
Thripophaga consists of 24 species and is related to both *Certhiaxis* and *Synallaxis* but seems less closely related to these two genera than they are to one another.

Most (21) of the 24 species of *Thripophaga* were allocated to the genus *Asthenes* Reichenbach, 1853, before my revision (1971a). But as *macroura* Wied, which is the type of the genus *Thripophaga* Cabanis, 1847, is certainly congeneric with the species which had been allocated to *Asthenes*, the correct name of the genus becomes *Thripophaga* with a well established priority of six years over *Asthenes*. Four species (*macroura, cherriei, fusciceps,* and *berlepschi*) were included in *Thripophaga* before my revision (1971a), but as I believed this grouping was not a natural one, I then transferred *fusciceps* and *berlepschi* to the genus *Phacellodomus*. The result



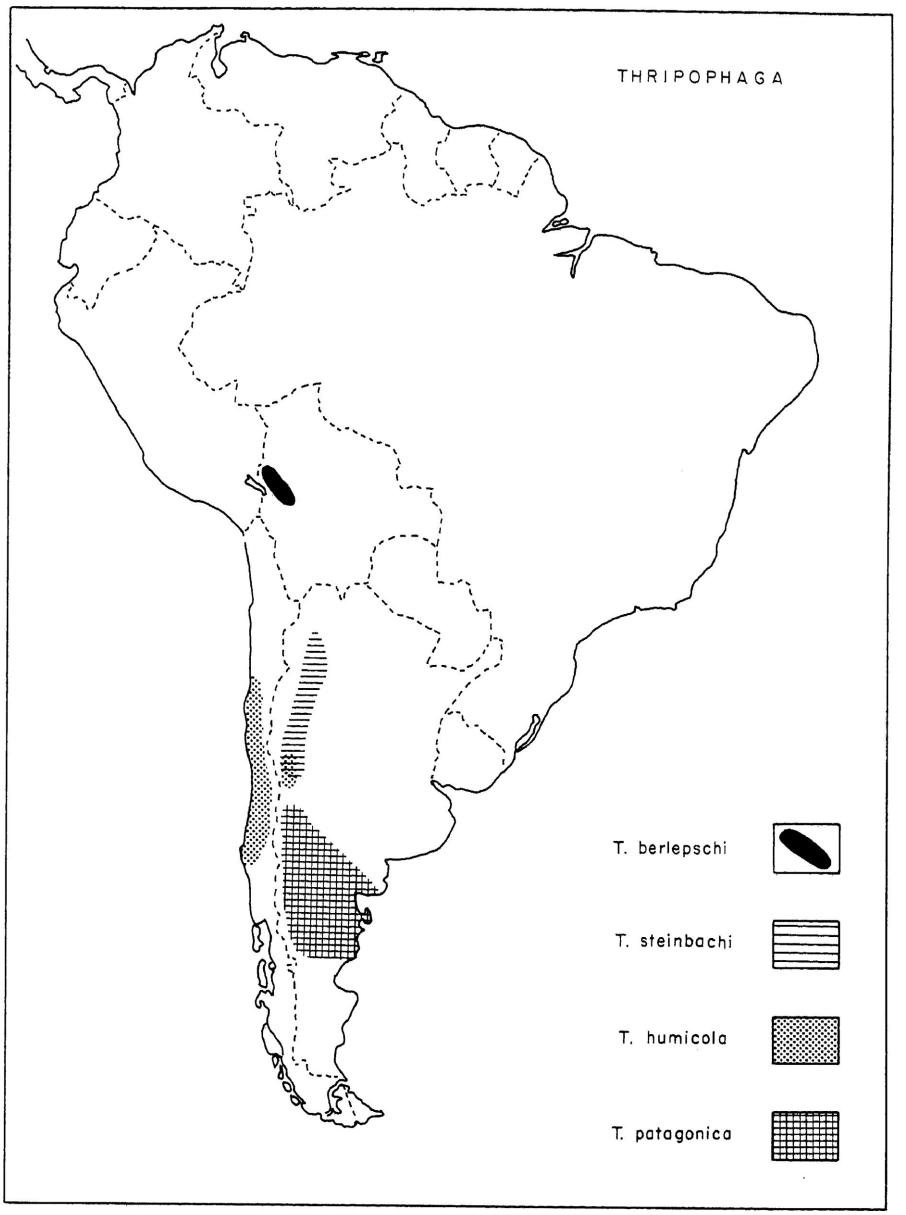
MAP 20. Geographical distribution of five species of *Thripophaga*.

is that *macroura, cherriei,* and also *hypochondriaca* form, together with the 21 "*Asthenes*," my enlarged concept of *Thripophaga*. The congeneric relationship of *macroura* and *cherriei* to the species that were allocated to *Asthenes* is strongly suggested by the fact that *macroura* and *cherriei* possess an exceptionally well-developed rufous patch on the chin and upper throat, a gular patch which is characteristic diagnostically for the genus and which is probably homologous to the black gular patch of *Synallaxis*.



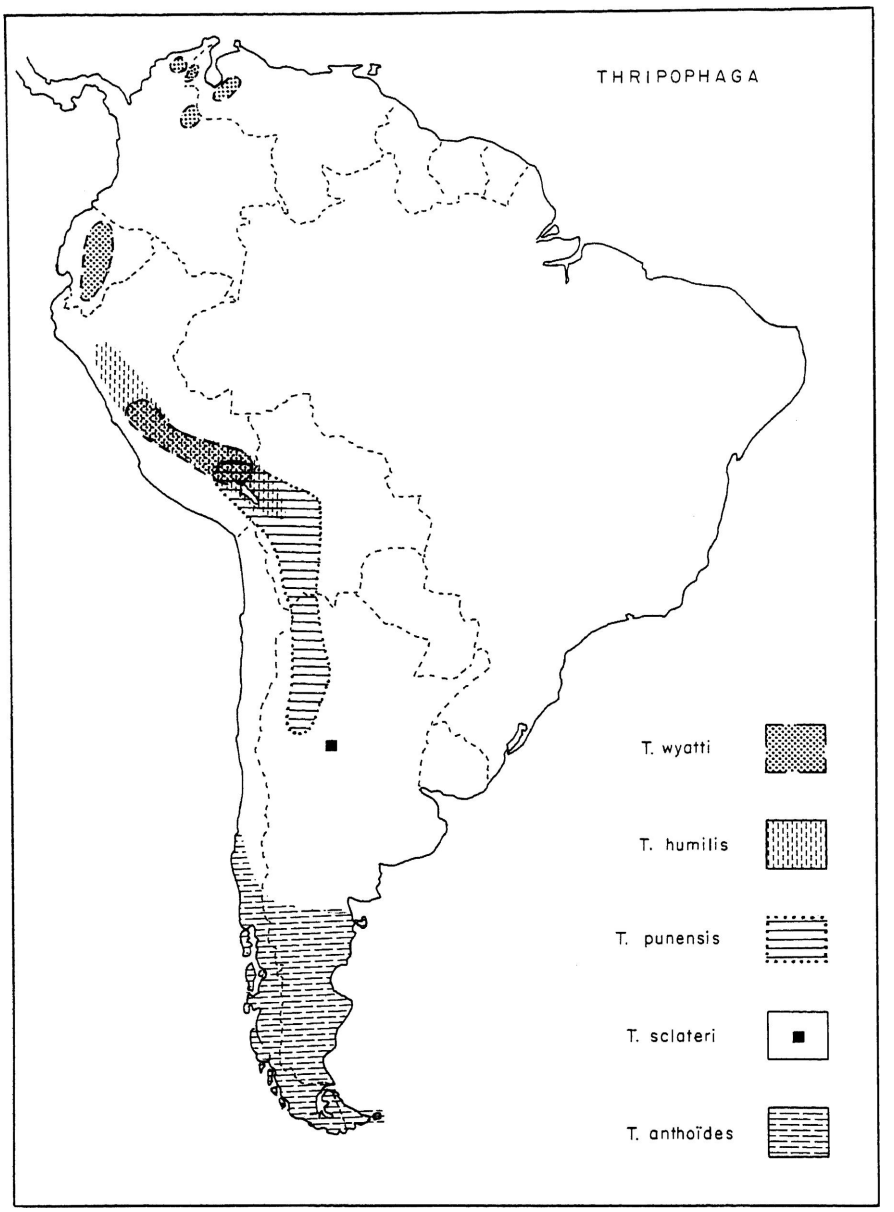
MAP 21. Geographical distribution of two species of *Thripophaga*.

Thripophaga is less widely distributed than *Synallaxis* and *Certhiaxis* and the large majority of its species are Andean and probably all were derived from the Andes (see maps 20–25). I believe this is true of species, such as *T. pyrrholeuca*, *T. patagonica*, or *T. anthoides* which are now restricted to Patagonia or southern South America, where *T. anthoides* has reached Tierra del Fuego (map 23). The Andean origin of the Patagonian species is suggested by the fact that *Thripophaga pyrrholeuca* and *T. anthoides* are



MAP 22. Geographical distribution of four species of *Thripophaga*.

partly migratory, moving north in winter, and also by the existence of *T. modesta* which is widely distributed in both the Andes and Patagonia (map 21) from central Peru south to Magallanes in southern Chile and Santa Cruz in Argentina. *Thripophaga modesta* breeds at very high altitudes which reach about 4600 m. in Bolivia and Peru, but which decrease steadily southward, to sea level in Argentina; it breeds also in the coastal hills of Peru. The origins of *T. hudsoni*, and especially those of *T. macroura* and *T.*



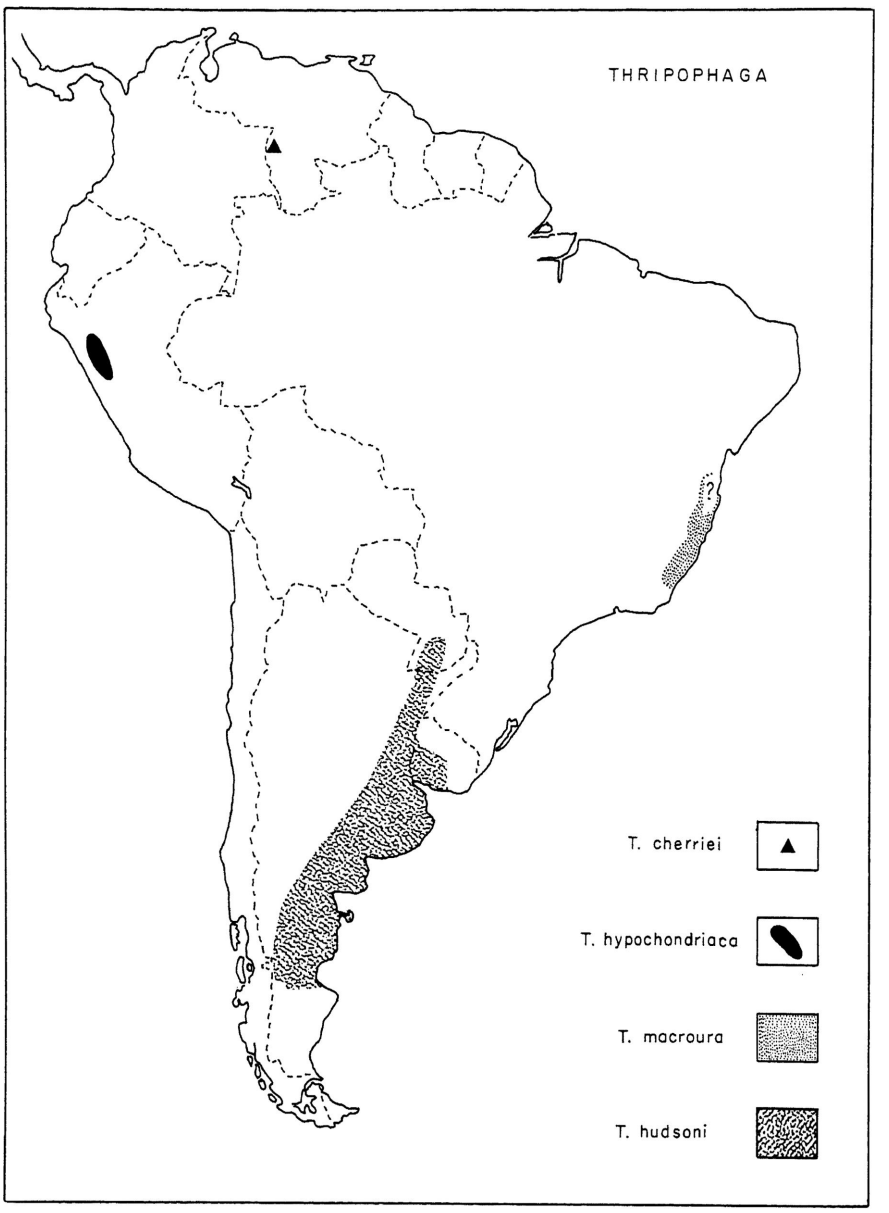
MAP 23. Geographical distribution of five species of *Thripophaga*.

cherriei (map 25), are more doubtful. *Thripophaga hudsoni* is distributed south to southern Chubut in Argentina, and, hence, is still partly Patagonian; *T. macroura* and *T. cherriei* may be relicts of forms which reached, respectively, eastern Brazil and the upper Orinoco from the Andes when the climate of South America was colder. The range of *T. macroura* is not well known but seems curiously restricted to Expirito Santo

MAP 24. Geographical distribution of four species of *Thripophaga* (the *flammulata* species-group).

and southeastern Bahia, and *T. cherriei*, known from only a single locality, is the only species which occurs in the Orinoco Basin.[90]

At the northern end of the range, *Thripophaga flammulata* and *T. wyatti* both reach northern Colombia. *Thripophaga wyatti* ranges as far north as the Sierra de Perijá, border of Colombia and Venezuela, the Santa Marta Massif, Colombia, and the Andes of Venezuela (map 23).[91] The ranges of *Syn-*



MAP 25. Geographical distribution of four species of *Thripophaga*.

allaxis and *Certhiaxis* (which are comparable) extend much farther north (into Central America) than the range of *Thripophaga*, but reach their southern limits far short (central Argentina) of the range of *Thripophaga*. In the north, *Certhiaxis* extends to Costa Rica and *Synallaxis* to southern Mexico, but the southern limit of their distribution ends in about central Argentina, whereas *Thripophaga* is represented farther south by five species in Patagonia, including Tierra del Fuego in the case of *T. anthoides*.

However, the greatest and most significant difference in the distribution of these three genera is provided by the Amazonian and Orinocan Basins, and, to a lesser extent, by the Andes. The Basins have been settled widely and extensively by species of *Synallaxis* and of *Certhiaxis*—in great contrast to *Thripophaga,* which is not represented in the Amazon Basin, but is represented in the Orinoco Valley by only a single species (*T. cherriei*), which is scarcely known and has been collected at only one locality. Relatively few species are Andean in the case of *Synallaxis* and *Certhiaxis,* and only one in each of these two genera occurs on the western slopes of the Andes south of about central Peru, whereas 17 of the 24 species of *Thripophaga* are Andean (see maps 20–25) and the remaining seven species have probably been derived from the Andes. *Synallaxis* and *Certhiaxis* have not crossed the Andes to reach Chile where *Thripophaga* is very well represented by five and possibly six species.

The seven species of *Thripophaga,* which are not found in the Andes, are *T. baeri, T. patagonica, T. anthoides, T. sclateri, T. cherriei, T. macroura,* and *T. hudsoni*; although *T. baeri, T. patagonica,* and *T. anthoides* reach their foothills into which *T. baeri* ascends to 1500 m. or more. *Thripophaga sclateri* is ambiguous as its nearest relative seems to be *T. punensis* (an Andean species) and *T. sclateri* is truly montane, restricted apparently to the higher elevations of the Sierra de Córdoba (an isolated outlier of the Andes) between about 2000 and 2900 m.

Among the Andean species, *Thripophaga wyatti* has been collected at 5500 m. in Ecuador, the highest altitude for the genus of which I have found a record, and occurs at nearly 4600 m. in the Santa Marta Massif of Colombia, and well over 4000 m. in Venezuela. But the records I have obtained are not necessarily the highest altitudes at which the birds are found; they are about 4750 m. for *T. humilis,* 4600 m. for *T. modesta* and *T. d'orbignyi,*[92] 4125 m. for *heterura.* The four related species of the *T. flammulata* group seem to ascend to altitudes which, at least, vary between 4000 and 4500 m., with the possible exception of *T. urubambensis,* for which the highest record is about 3800 m. *Thripophaga punensis* has been recorded from over 4000 m., and the records for *T. pyrrholeuca, T. pudibunda, T. ottonis,* and *T. berlepschi* vary between 3000 and 3700 m. The highest level reached by *T. steinbachi* probably falls between 2500 and 3000 m. *Thripophaga humicola,* of central Chile and Mendoza, and *T. hypochondriaca,* of the Marañon watershed of northern Peru, do not seem to ascend so high, to 2750 m. in the case of *T. hypochondriaca,* and from the coast to about 2150 m. on the lower slopes of the Andes for *T. humicola* in Chile.

The information available on the ecology and behavior is very incomplete and the nests of only the following 10 species are known: *Thripophaga pyrrholeuca, T. baeri, T. pudibunda, T. modesta, T. d'orbignyi, T. humicola, T. patagonica, T. anthoides, T. wyatti,* and *T. hudsoni.* I have found no description of the nest of *T. humilis,* but Koepcke (1964) implied it is similar to that of *T. pudibunda* and *T. modesta.*[93] The general ecology and behavior of these three species seem to be similar. Vuilleumier (1969) has described the habitat of *T. heterura* and some aspects of its behavior, but not its nest which remains unknown, to my knowledge. No information at all, or very little, exists for the other species.

All the species for which definite information exists frequent open regions and sites, not forest, although some species, such as *Thripophaga heterura,* inhabit open woodland which is best described as maquis, and some species frequent both open regions or regions with relatively thick vegetation, as in the case of *T. baeri* and *T. d'orbignyi.* The regions inhabited by *T. macroura* and *T. cherriei* are forested, but I have found no information on the habitat of *T. macroura*; *T. cherriei* has been collected on only two occasions, at or near the mouth of a stream which empties in the Orinoco River, but apparently only on the banks of this stream and of the Orinoco, not within the forest.

Grasslands are inhabited by a number of species, as in southern Patagonia, where the birds are usually to be found along or not far

from streams, or other bodies of water such as lakes, ponds, or swamps. Johnson (1967) mentioned that *Thripophaga anthoides* frequents "open meadows, damp grasslands, and well watered hillsides"; the very heavily streaked upperparts of this species suggest a close association with grasslands.[94] This is true also of *T. hudsoni,* which Hudson (in Sclater and Hudson, 1888) said, is "found exclusively on the grassy pampas, never perching on trees," and which is also "partial to marshes grown heavily with *Juncus acutus,*" according to Wetmore (1926). Other species, such as *T. flammulata,* are also very heavily streaked and Vuilleumier has written to me that he found this bird on grassy slopes in Ecuador that are generally devoid of trees, or with a few small low trees, stunted and gnarled, no more than a few meters in height at best. *Thripophaga flammulata* is related to *T. virgata* and *T. maculicauda,* which are also sharply streaked, and it is probable that the ecology of these three species does not differ significantly, although *T. virgata* occurs also in very rocky areas.

Rocky areas, and arid or semiarid slopes, are inhabited by a number of species such as *Thripophaga pyrrholeuca, T. pudibunda, T. modesta, T. humicola, T. humilis,* and *T. sclateri.*[95] Some of these species may be more or less restricted to this type of habitat, but it is clear that most of them are not, such as *T. pyrrholeuca* and *T. modesta* which inhabit grasslands in Patagonia. The vegetation on the arid, or semiarid slopes, is usually poor, consisting of clumps of thorny bushes, shrubs, or stands of cacti, separated by open areas of stony ground with or without sparse grass. Stony ravines and slopes strewn with boulders are inhabited also. The favored habitat of *T. punensis* seems to be areas where tussock grass grows on arid open slopes, and Dorst (1957) has reported that *T. d'orbignyi* is narrowly associated with stands of Puya (*Puya Raimondii*), a gigantic Bromeliaceae which grows in scattered localities on the altiplano of Peru and Bolivia, although *T. d'orbignyi* is distinctly eclectic and "is most numerous among the relatively thick vegetation of the hillsides overlooking watered valleys" in northern Chile according to Johnson.

Most of the species are reported to be shy, secretive, and reluctant to leave or to fly far from cover. Some of them seem to secure their food by feeding directly on the ground, or very close to it in the tangled underbrush, and are said often to carry their tails cocked up at a sharp angle over the back in the manner of a wren (*Troglodytes*), to which some species have been compared occasionally. However, this posture has not been noted by some observers and is not reported in the majority of the species for which information exists, notably in *Thripophaga wyatti* and *T. hudsoni* which are strictly terrestrial.[96] Some species have been compared to Old World warblers (Sylviinae), working their way, more or less deliberately, by clambering through bushes and scrub, rarely feeding on the ground. Hudson compares *T. hudsoni* to a pipit (*Anthus*), "usually being taken for one when first seen";[97] a comparison which seems to me far more apt in every way (morphologically and behaviorally) than the comparison of *T. hudsoni* to *Anumbius* (another furnariid) made by Wetmore.

The nests of 10 species[98] are known, as stated above, and consist of three different types. One type, which is characteristic for the genus, is built by eight of these species and most probably by some of the species whose nests have not been discovered or described. This nest is strongly built of well-interwoven small sticks and twigs and resembles roughly a basket (*canasta* in Spanish), hence the vernacular name (canastero) which is used widely for these birds in both Spanish and English. However, *Thripophaga wyatti* and *T. hudsoni,* and perhaps other species, do not build "baskets" for their nests.

The eight species that build "baskets," which vary somewhat but are basically similar, are *Thripophaga pyrrholeuca, T. baeri, T. pudibunda, T. modesta, T. d'orbignyi, T. humicola, T. patagonica,* and *T. anthoides.* The nest is conspicuous, built apparently without any attempt at concealment, usually

not far above the ground, in a bush, shrub, or other adequate support, and varies in size from about 20 to 65 cm. The shape varies, but is usually more or less cylindrical with an entrance that is normally situated near the top, and the material greatly preferred for its construction is thorny twigs or sticks, the more thorny and sharper-spined the better. One is tempted to say this material is used invariably, but this is not the case in some regions, perhaps because thorny vegetation is lacking. *Thripophaga modesta* builds nests of thorny twigs or not, and, at the northern end of its range seems to build its nest only among the branches of cacti, of twigs which are apparently not thorny by themselves, but the spines of the branches of the cacti substitute for thorny twigs and their spines are also incorporated in the wall of the nest.[99]

A substitute for thorny twigs is used also by *Thripophaga d'orbignyi*. The nest of *d'orbignyi* is constructed normally of thorny twigs, but when thorny bushes are probably lacking in some regions of the altiplano of Peru and Bolivia where vegetation is often scanty and very few or no arborescent plants grow, the nest is built in *Puya Raimondii* as stated above. These nests have been well described and illustrated by Dorst (1957) who stated they average between 50 and 60 cm. in height, with a diameter of about 40 cm., and are constructed of "rather large twigs . . . so perfectly interwoven that it is very difficult to separate them particularly as the whole is built around the leaves." Some of these leaves traverse the nest and the strong leaves of the puya are well armed along their edges with very sharp hooks about 15 mm. long. The twigs are not thorny but the nest is strongly armored with thorns nevertheless.

In the nests investigated by Dorst, the entrance opened at the lower part of the nest, but this was probably an adaptation to the site as the entrance is normally situated near the top. A horizontal tunnel led from the entrance into the incubating chamber. The entrance was about 6 cm. wide, the tunnel 25 cm. long and usually circular in cross section with a diameter of 6 to 7 cm., the incubating chamber was spherical, about 10 cm. in size. The tunnel and chamber were both lined and felted with soft material, consisting of feathers, wool, and vegetable down in the case of the tunnel. The chamber is described by Dorst as "quite water-tight, as could be verified after heavy daily showers . . . and is lined with a thick layer of soft materials—wool, horsehair, pappus of Compositae, feathers (even quills of doves). This layer is equally thick all around the hollow sphere of the chamber."

In other regions of Peru, *Thripophaga d'orbignyi* builds nests of thorny twigs that are usually placed in cacti, and Morrison (1939) described one from Huancavelica that was more or less globular in shape, smaller than those built in the puyas, only about 25 cm. in diameter, with "a short tunnel [leading] to the snug inner nest, warmly lined with chicken-feathers."

Morrison and also Dorst, commented on the great strength of the tightly interwoven nests of *Thripophaga d'orbignyi* which seem so disproportionate to the size of this small bird. Other authors have made similar comments about other species. For instance, Johnson (1967), who described the nest of *T. humicola* "as a miniature armoured turret" (quoting Barros), said the nests of *T. humicola* "are so elaborately and stoutly built that they survive winters and remain intact and in place for several years, even though in our experience the same nest is never used a second time."

I believe Johnson is correct. There is no conclusive evidence that any member of this family uses the same nest for two consecutive breeding seasons, no matter how elaborate it may be or how intact it may remain. But Dorst states that "it appears that [*d'orbignyi* repairs and uses its nest] for several consecutive years." The two nests mentioned by Dorst in this connection consisted of "a double nest built in an isolated Puya," and the other was a new one constructed on an old one of the same size. It seems to me, however, that the isolated and double nest represents probably utilization of a site in a

location where nesting sites were scarce, and the other nest was actually new, built on a convenient foundation. The double or multiple nests of *Furnarius* built alongside or on top of one another in favored locations are well known.

The descriptions of the largest series of nests that I have found are those of a series of 12 nests of *Thripophaga modesta* discovered by J. P. Pemberton, personally in most cases, in the Province of Rio Negro, Argentina, between September 22 and October 22, 1911. Half of these nests were situated apparently near water and all were constructed of thorny twigs in bushes, anywhere from about 1 m., or somewhat less, to a little over 2 m. above the ground. They were all more or less cylindrical as they were described as "bottle-shaped," and, although their size was not recorded, one must have been large as it had an entrance tunnel about 30 cm. long. The lining of the incubating chamber consisted of fine vegetable material with a varying amount of feathers and sheep wool. Fur from the introduced hare is also used extensively by *T. pyrrholeuca* and *T. patagonica* in the lining of the chamber.

A certain amount of variation exists in the shape, size, structure, and location of the nests for which I have given some instances, but the most interesting ones have been reported in *Thripophaga modesta,* and recorded (but not published hitherto) for *T. pyrrholeuca,* which nest under the ground, presumably when no adequate nesting site exists above it.

In 1957, Behn, Johnson, and Millie found a nest of *Thripophaga modesta* on an arid slope in Tarapacá, northern Chile, under a rock at the bottom of a hollow, about 40 cm. deep. Millie, who has written to me since about this nest, said a "sparse lining of fibers" was found, but apparently no other nesting material, as it is not mentioned by Millie, or in his published account together with Behn and Johnson. A small shrub concealed the entrance of this small "cave," a photograph of which was published, but the shrub may not have furnished adequate support for the normal type of nest.

The nests of *Thripophaga pyrrholeuca* that were situated under the ground were discovered by Pemberton in Rio Negro in December 1911 and January 1912. Two nests were found, one was placed at a depth of about 30 cm. under a flat rock and no nesting material was used other than "hair . . . small carcasses . . . mostly mice and vizcachas . . . taken from owl pellets." The other nest was also 30 cm. underground, inside the burrow of a small rodent dug in the bank of an arroyo, and was also "made entirely of hair of many kinds—mostly fine rodent hair, no doubt picked from owl pellets."

The nest of *Thripophaga modesta* was reported for the first time by Behn, Johnson, and Millie (1958). The two records for *T. pyrrholeuca* were obtained by me from the unpublished nesting records of J. P. Pemberton, which were kindly sent to me by the Western Foundation of Vertebrate Zoology, Los Angeles, through the courtesy of E. N. Harrison and L. F. Kiff.

The nests of *Thripophaga modesta* and *T. pyrrholeuca* that are located under the ground are exceptional. The normal nest is a "basket," as in the case of the other species with the exception of *T. wyatti* and *T. hudsoni.* Dorst (1963) has published a good description of the nest of *T. wyatti,* illustrated by a photograph and diagram to show its location and construction. The nest is built very near the ground, concealed in the center of a clump or large tuft of grass, and is constructed of well-interwoven dried stems and coarse leaves of Gramineae, not of twigs. It is more or less spherical, about 25 cm. in diameter, with an entrance at one side which opens directly into the incubating chamber. There is no tunnel, the entrance is about 3.5 to 4 cm. in size, and the incubating chamber, which is spherical, measures about 12 cm. The chamber is lined with finer vegetable material than is used for the exterior of the nest, and no material of animal origin, such as feathers or wool, is used.

The general behavior, ecology, and nest of *Thripophaga wyatti* approach that of *T. hudsoni,* but the nest of *T. hudsoni* is more rudimentary, distinct enough to constitute a

third type of nest in the genus. Hudson (in Sclater and Hudson, 1888) described the nest of *T. hudsoni* as a slight hollow, scooped in the ground under a tussock of grass or clump of thistles, built over with "a dome of fine dry grass, leaving a small aperture arched like the door of a baker's oven." Wetmore (1926) found one nest directly on the ground, very well concealed under a clump of *Juncus*. This nest was constructed "of bits of grass," domed over in the manner described by Hudson, "with a runway like that of some mouse leading into it." It "was warmly lined with many feathers," but Hudson reported that the lining consists only of "dry powdered horse-dung." Hudson and Wetmore both stressed the extreme degree to which the nest is concealed. In other words, the greatest contrast imaginable exists in every way between the nest of *T. hudsoni* and that of its congeners with the exception of *T. wyatti,* the nest of which tends to resemble that of *T. hudsoni.*[100]

Morphological Variation

The plumage of *Thripophaga* is streaked or unstreaked, the structure of the tail and its coloration vary, and the upper throat may be rufous or not, but many species resemble one another as *Thripophaga* is relatively homogeneous—less homogeneous than *Certhiaxis,* but much more so than *Synallaxis*.

It is difficult to describe the variation briefly because the characters tend to be more or less constant; the variation is usually subtle and many species are more or less nondescript at first glance. To be sure, abrupt differences exist but constancy in many characters is evident. For instance, the chin and upper throat are rufous in 17 of the 24 species and a trace of rufous exists in two others; the tail is rufous to some degree in 15 species and has some rufous admixture in six others; measurements of the shape of the bill vary within a narrow range.

The rufous gular patch is very characteristic. It seems homologous to the black gular patch of *Synallaxis* and the rufous feathers are probably erected or puffed out in life as in the case of the black feathers of *Synallaxis*.

The tail is brown in only three species (*Thripophaga humicola, T. urubambensis,* and *T. hypochondriaca*), but not uniformly dark as the outer rectrices, or their tips, are paler, more fuscous than brown. Species with tails that are wholly or partly rufous vary from *T. cherriei* and *T. macroura* in which the tail is wholly rufous, to other species, such as *T. d'orbignyi* and *T. punensis* in which a very extensive rufous area exists only on the outer pair of rectrices; in *T. pudibunda* and *T. ottonis* the tail is almost completely rufous, but with dusky tips on the inner pair of rectrices, or with a dusky band along the central pair. But, generally speaking, the rufous areas are more or less restricted to the three outer pairs of rectrices, and the three inner pairs are brown.

A rufous, or cinnamomeous, area exists in the wing of all the species at the base of the remiges, or on the outer edge of their inner webs, but varies a great deal from species to species in extension and intensity of the pigmentation which can be very pale or very bright. Some rufous pigmentation exists also on the upper surfaces of the wing in the large majority of the species but the variation is also very great. In some species, such as *Thripophaga pudibunda, T. ottonis, T. steinbachi, T. cherriei,* and *T. macroura,* the upper surface of the wing is almost completely rufous with the exception of the dusky tips of the remiges, but in *T. modesta, T. humicola,* and *T. hypochondriaca* it is restricted to the lesser and median coverts or only to the lesser coverts in *T. patagonica*.

The upperparts are uniform, or virtually so in 13 species, very plain and dull, more or less grayish or more rufescent "earthy" brown. The underparts of these species are pale with the exception of *T. cherriei* which is strongly olive brown, very sharply streaked with buff on the lower throat below the rufous gular patch and on the breast. The other species are buffy, dull white, dingy, more or less cinereous, with or without streaks which are faint and not well defined with the single exception of *T. hypochon-*

driaca which is heavily streaked with dark brown at the sides of the breast and on the flanks.

The 11 other species are streaked on the upperparts, although the streaks are lacking on the back of *Thripophaga urubambensis* in which the streaks are restricted to the crown and nape and are more or less well defined. The streaking is of two types: in *T. punensis, T. anthoides,* and *T. hudsoni,* the center of the feather is dark, broadly so, and is outlined by pale edges. In the other species, which consist of *T. flammulata, T. virgata, T. maculicauda,* and *T. macroura,* the center of the feather is pale, forming a narrow stripe along the shaft, on the dark ground coloration of the lateral portion of the feather. The underparts of these 13 species are pale, streaked or not, and the streaking is very heavy, flammulated in *T. flammulata* and *T. macroura.*

The tail consists of 12 rectrices in 22 of the 24 species. The exceptions are *Thripophaga cherriei* which seems to have only 10 rectrices, and *T. macroura* in which the normal number is 10 but varies from 12 to 10. Two specimens among 17 specimens in which I could count the tail feathers with assurance have 12 rectrices.

The structure of the tail varies in other respects, but in the large majority of the species, the tail is well graduated, slightly or not strongly stiffened, the webs of the rectrices are well or firmly integrated, and their tips are rounded or blunt. However, much variation exists between species, the degree of graduation and integration varies, also the width of the webs, the tail is elongated or not, and the tips of the rectrices may be more or less well rounded or blunt.

The structure of the tail is most distinct in *Thripophaga hudsoni* and *T. urubambensis,* most variable in the four species of the *T. flammulata* group which includes *T. urubambensis.* In *T. hudsoni,* the tail is strongly stiffened, the central pair of rectrices is conspicuously elongated, and its tips are much attenuated and very sharply acuminate. The stiffness of the tail varies in the *T. flammulata* group, and especially the structure of the webs. The webs are normally integrated and relatively speaking, are very broad in *T. virgata,* narrow in *T. maculicauda*; they are narrow in *T. urubambensis* and greatly decomposed. The rectrices of *urubambensis,* which are strongly stiffened, are also much attenuated for a long distance, about equal to half the total length of the feather in the case of the central pair. A similar tendency exists in *flammulata,* but the tail is less stiffened, the rectrices are less attenuated, and the webs are broader and less decomposed, although they are very loosely integrated.

The tail is distinctly longer than the wing in two-thirds of the species, about equal to or slightly shorter than the wing in the remainder. The ratio between its length and that of the wing varies from 0.89 to 1.65, with an average of 1.15. The only species with a quite distinctly shorter tail is *Thripophaga humilis* with a ratio of 0.89.

The variation in the length of the wing is relatively narrow, as the means vary from 59 to 80 mm., in round numbers, with an average of 67 mm. Many species are similar in size; for instance, the mean wing length varies from only 59 to 65 mm. in 10 species, from 71 to 75 mm. in six. The mean wing length of *Thripophaga* is similar to that of *Certhiaxis,* which measures 58 to 75 mm. (average 66); slightly bigger than *Synallaxis,* which measures 52–71 mm. (average 60). Measurements of *Thripophaga* species are given in table 13.

The shape and size of the bill is constant in most species, and the size of the feet, which are moderately strong, varies little. The bill, which averages 17.27 mm. in length, is usually slender, attenuated, slightly compressed laterally, and very slightly decurved at the tip or not. It does not seem too strong when one considers that the nests are usually constructed of twigs that are fairly large and tightly interwoven.

PHYLOGENY

Species of *Thripophaga* are or tend to be constant morphologically, as stressed above,

TABLE 13
Measurements (in Millimeters) of *Thripophaga*

Species	Wing			Tail			Bill		
	N	Mean	Range	N	Mean	Range	N	Mean	Range
pyrrholeuca									
Males	22	62.54	59–66	19	79.63	71–87	20	15.45	14.5–16
Females	14	61.00	57–64	10	75.80	68–80	12	15.21	14.2–16
Both sexes	47	62.24	57–70	36	78.44	68–87	41	15.62	14.2–18
baeri									
Males	44	63.18	57–68	33	64.15	60–68	41	14.28	13–16
Females	34	61.87	58–65	23	62.78	60–67	32	14.48	13–15.5
Both sexes	82	62.66	57–68	60	63.43	60–68	78	14.32	13–16
pudibunda									
Male	1	—	63	1	—	77	1	—	18
Female	1	—	60	1	—	74	1	—	19
Both sexes	3	61.66	60–63	3	77.00	74–80	2	18.50	18, 19
ottonis									
Males	8	60.62	59–62	8	101.37	90–108	6	16.10	15.5–17
Females	4	59.00	58–60	4	98.25	95–100	4	15.65	15.5–16
Both sexes	13	60.00	58–62	13	100.15	86–108	13	15.95	15.5–17
heterura									
Males	2	61.50	61, 62	1	—	87	2	15.50	15, 16
Female	1	—	60	1	—	87	1	—	15.5
Both sexes	5	62.00	60–64	3	87.34	87–88	4	15.62	15–16
modesta									
Males	32	69.29	60–75	28	70.25	63–77	27	17.85	16–19
Females	25	65.58	57–72	24	64.87	59–72	25	17.72	16–21
Both sexes	66	67.68	57–75	60	67.46	59–77	60	17.78	16–21
d'orbignyi									
Males	58	67.97	64–75	60	71.23	64–78	58	16.66	15.5–19.5
Females	42	66.57	62–73	40	70.82	63–80	41	16.72	15–20
Both sexes	121	67.40	62–75	121	71.08	63–80	120	16.71	15–20
berlepschi									
Males	10	69.50	67–71	9	71.00	69–73	9	19.77	19–20.5
Females	6	69.25	68.5–70	6	70.33	67–72	6	19.91	19.5–20.5
Both sexes	17	69.47	67–71	16	70.87	67–73	16	19.87	19–20.5
steinbachi									
Female	1	—	65	1	—	75	1	—	15
humicola									
Males	13	64.07	61–65	10	71.60	69–75	13	16.88	16.5–18
Females	2	64.00	63, 65	2	72.50	72, 73	2	16.85	16.5–17.2
Both sexes	29	64.13	61–67	25	71.56	67–75	28	16.83	16–18
patagonica									
Females	3	59.00	58–60	3	67.33	65–70	3	14.73	14–15.2
Both sexes	6	59.08	58–61	6	66.66	64–70	6	14.73	14–15.2

TABLE 13—(*Continued*)

Species	Wing			Tail			Bill		
	N	Mean	Range	N	Mean	Range	N	Mean	Range
humilis									
Males	31	72.25	67–76	28	64.00	58–70	26	18.67	17–20
Females	15	70.06	68–74	14	65.00	60–70	14	17.62	16.5–18.5
Both sexes	48	71.75	67–77	44	64.54	58–70	42	18.33	16.5–20
anthoides									
Males	22	72.77	67–77	20	70.35	64–75	21	17.65	16.5–19.5
Females	11	69.45	65–73	12	67.41	62–73	10	17.45	16.5–19.5
Both sexes	34	71.61	65–77	33	69.21	62–75	32	17.55	16.5–19.5
wyatti									
Males	22	71.18	62–78	19	76.15	65–85	21	18.42	16–20
Females	19	76.15	65–85	11	67.45	62–77	10	17.50	17–18.5
Both sexes	40	68.40	62–85	35	72.48	62–85	34	18.15	16–20
punensis									
Males	18	75.76	73–79	12	91.75	82–99	13	17.87	16–18.5
Females	10	72.20	70–75	9	85.66	78–92	10	17.19	16–18.2
Both sexes	28	74.53	70–79	21	89.14	78–99	23	17.58	16–18.5
sclateri									
Male, and "♂?"	2	74.50	74, 75	1♂	—	93	2	18.50	18, 19
urubambensis									
Male	1	—	60	1	—	77	1	—	17
Female	1	—	60	1	—	80	1	—	18
Both sexes	2	—	both 60	2	78.50	77, 80	2	17.50	17, 18
flammulata									
Males	43	67.32	64–71	40	72.65	62–80	40	18.03	16–20
Females	31	66.06	62–70	27	74.96	68–82	28	17.87	16–19
Both sexes	85	66.93	62–71	74	74.18	62–85	79	17.89	16–20
virgata									
Males	4	74.00	72–76	4	85.50	79–88	4	17.25	16–18
Female	1	—	69	1	—	77	1	—	17
Both sexes	5	73.00	69–76	5	84.00	77–88	5	17.20	16–18
maculicauda									
Males	3	62.00	60–64	2	—	both 85	3	15.66	15.5–16
Female	1	—	59	1	—	75	1	—	15.5
Both sexes	4	61.25	59–64	3	81.66	75–85	4	15.62	15.5–16
cherriei									
Males	3	—	all 68	3	62.34	60–65	3	16.80	16.5–17
Females	2	64.00	63, 65	2	65.00	64, 66	2	16.90	16.8, 17
Both sexes	6	66.50	63–68	6	63.25	60–66	6	16.77	16.5–17
macroura									
Males	2	80.50	80, 81	2	79.50	78, 81	2	19.25	19, 19.5
Both sexes	22	80.50	76–85	21	82.00	75–88	22	18.88	17–20
hudsoni									
Males	20	79.65	74–83	20	80.30	74–85	20	20.01	18.2–22

TABLE 13—(*Continued*)

Species	Wing			Tail			Bill		
	N	Mean	Range	N	Mean	Range	N	Mean	Range
Females	11	71.72	70–73	10	74.50	69–81	11	18.74	17.5–20
Both sexes	31	76.83	70–83	30	78.36	69–85	31	19.56	17.5–22
hypochondriaca									
Males	4	68.25	67–70	4	91.00	89–93	4	20.00	19–21
Females	6	66.08	64–68	6	89.00	87–93	6	19.40	18–20
Both sexes	10	66.95	64–70	10	89.80	87–93	10	19.65	18–21

and the geographical ranges of many species overlap. These facts furnish few clues to general phylogeny and it is difficult to divide the genus into groups of species. Nevertheless, one group of four Andean species (the *T. flammulata* group) stands out and has been reviewed by Vuilleumier (1968). These four species are *T. urubambensis, T. flammulata, T. virgata,* and *T. maculicauda,* which all differ sharply from each other in the pattern of their plumage, and, especially, the structure of their tail. Their distribution seems to be largely discontinuous but suggests these species overlap in Peru and Bolivia (map 24), although, to the best of my knowledge, species of this group have been taken together at only two localities: in the mountains near Huánuco, Peru, in the case of *T. urubambensis* and *T. flammulata,* and at Hichuloma, Bolivia, in the case of *T. urubambensis* and *T. maculicauda.*

The range of *Thripophaga virgata* is poorly known as this species is known from only a few specimens which were taken at no more than three localities: near Limbani in Puno, at Junín, and in the Rock Forest, an extensive area of peculiar rock formations situated about 25 km. west of Lake Junín; *virgata* and *maculicauda* were both taken near Limbani and it is possible that their ranges overlap or come into contact. This may be true also of *T. virgata* and *T. flammulata* in Junín and Pasco, although Vuilleumier (1968) believed the two birds are isolated geographically and concluded they are conspecific.

Thripophaga virgata and *T. flammulata* may or may not be allopatric but I cannot share the opinion that they are conspecific as I am quite confident they are distinct species, judging by my study of *Thripophaga.* Their color pattern is not similar, as *T. flammulata* is very heavily flammulated with black and white on the underparts, whereas *T. virgata* is not, and the structure of their tails—which seems to be a reliable species character in this genus—is quite different. The tail of *T. flammulata* is much better stiffened than that of *T. virgata,* and its rectrices are narrow, attenuated, and show a strong tendency to become decomposed, whereas the rectrices of *T. virgata* are much broader (about two and one-half to three times broader than those of *T. flammulata*), not attenuated, and well integrated; the tail of *T. virgata* is also distinctly longer, with a mean of about 84 mm., as against 74 mm. for *T. flammulata.*

The four species of the *Thripophaga flammulata* group, and also *T. cherriei* and *T. macroura,* share the same type of streaking (a pale stripe along the shaft, contrasting with the dark lateral portion of the feather), and it is interesting to note that the underparts of *T. macroura* are flammulated also. This similarity may denote common ancestry although I have listed *T. cherriei* and *T. macroura* apart from the *T. flammulata* group in the sequence of the species; *T. cherriei* and *T. macroura* seem more closely related to one another than to any other species, but do not appear to be very close relatives.[101]

The other two species which I have listed apart and placed at the end of the sequence are *Thripophaga hudsoni* and *T. hypochondriaca.* They are not closely related and their nearest relatives are obscure to me. *T. hud-*

soni stands quite apart; it does not seem to be closely allied to any other species, although Hartert (in Hartert and Venturi, 1909) believed it was conspecific with *T. anthoides,* but as the resemblance between the two species is very superficial, it is quite obvious that Hartert was wrong as Hellmayr (1925) stated. The problem posed by *T. hypochondriaca* is a difficult one. The behavior of this species is unknown, but I do not believe *T. hypochondriaca* should be separated from the other species as a monotypic genus (*Siptornopsis* proposed by Cory). *Thripophaga hypochondriaca* is probably quite isolated, but it certainly appears to me to be more closely related to the species allocated to *Thripophaga* than to any other member of the Synallaxinae.[102]

Relationships among the 16 species which remain are not sufficiently clear to divide them into groups of species. I had suggested in my revision (Vaurie, 1971a) that the species with plain upperparts (11), and those in which they are streaked (5), form, perhaps, two species groups, but further study has convinced me that such a division is misleading. The difficulty posed by these 16 species is demonstrated by the fact that my arrangement as well as those of Hellmayr (1925), Peters (1951), and Meyer de Schauensee (1966) conflict to a pronounced degree. The comments below concern the status of only a few species.

I believe *Thripophaga sclateri* is closely related to *T. punensis,* perhaps even conspecific. *Thripophaga sclateri,* of which a total of only four specimens seems to exist, is very poorly known and is apparently restricted only to the Sierra de Córdoba in Argentina. Its systematic status was confusing to Sclater, who, after publishing three different opinions on separate occasions, concluded finally (1890) that *sclateri* was not a distinct form but that it was merely a synonym of *T. hudsoni.* Hellmayr (1925) followed Sclater's final decision, but *sclateri* was unknown to Hellmayr. Stresemann (1948) revived this question and showed quite correctly that *T. sclateri* is valid and distinct from *T. hudsoni,* and in his opinion the nearest relatives of *T. sclateri* were *T. anthoides* and *T. humilis.* However, Stresemann (1965) realized later that he had made an error in defining the relationship of *T. sclateri* and stated that the nearest relative of *T. sclateri* was unknown to him, but was not *T. hudsoni* in any case.

The nearest relative of *Thripophaga sclateri* seems clear to me. I am convinced it is closely related to *T. punensis* because the two birds differ very slightly morphologically from one another and represent each other geographically. The differences which distinguish them are so extremely relative that the only ones I can detect are that the rufous area in the wing is somewhat more extensive in *T. sclateri,* and that its general coloration is brighter, including the rufous area at the tips of the rectrices. In addition, the general ecology of the two birds seems to be similar, stony slopes with some grassy vegetation. Nevertheless, I hesitate to combine the two taxa in one species because *T. sclateri* is so little known. It seems best to treat them as separate species provisionally, but if they prove to be conspecific, *T. sclateri,* described in 1878 by Cabanis, will have to replace *T. punensis* Berlepsch and Sztolcman, 1901, as the name of the species.

A fine photograph of *Thripophaga sclateri* was published in an article by Hoy (1965) in which he described his rediscovery of this bird. The specimen he illustrated was collected by him in July 1964, and presented by him to the American Museum of Natural History; another specimen, collected by A. Döring in 1876, is in the collection of the British Museum and is the specimen which Sclater had; the other two specimens, including the type collected by Döring, are in the Berlin Museum and are the specimens examined by Stresemann. My opinion is based on the specimens in London and New York.

Thripophaga punensis has had a checkered career. It is a very distinct species and Hellmayr (1925) was quite correct when he did not combine it with *T. wyatti,* which was done, unfortunately, by Peters (1951). Meyer de Schauensee (1966) objected to Peters's opinion, but combined *T. punensis*

with *T. anthoides,* a decision which is even more incorrect than that of Peters, although Meyer de Schauensee was probably influenced by Olrog (1963) who had combined *T. punensis* and *T. anthoides,* but with reservation. *Thripophaga anthoides, T. punensis,* and *T. wyatti* are all streaked above, but *T. anthoides* does not appear to be closely related at all to *T. punensis* and *T. wyatti*; the structure of the tail is very different and it does not resemble *T. punensis* as shown in figure 5.

Thripophaga punensis and *T. wyatti* are closely related but are distinct species that overlap in Puno, southern Peru, and have a very different tail pattern. The tail of *T. wyatti* is strongly rufous, all of its rectrices are wholly or partly rufous with the exception of the central pair, whereas the rufous area is restricted in *punensis,* only to the apical portion of the outer pair of rectrices, and, to a strongly decreasing degree, to the tips of the next three pairs. In other words, the tail of *T. punensis* is "dark," but that of *T. wyatti* is "bright," and this conspicuous difference may serve for species recognition. Other differences exist in proportion and pattern, the streaked pattern of *T. punensis* is much heavier, more distinct than that of *T. wyatti.*[103]

Bond (1945) stated that *Thripophaga heterura* of Bolivia "is closely related to, and possibly best regarded as conspecific, with *pudibunda*" of Peru, and Meyer de Schauensee (1966) has combined them. I believe this is not correct as the structure of the tail is conspicuously different in the two birds. The tail of *T. heterura* is distinctly elongated and very well graduated (figure 5), and its rectrices are narrow and distinctly acuminate at the tip, whereas the tail of *T. pudibunda* is short, less graduated that that of *T. heterura,* and its rectrices are much broader, with blunt, rounded tips. The tail of *T. heterura* is also proportionally longer than the wing with a ratio of 1.40, as against 1.24 for *T. pudibunda.* The rufous gular patch is distinct also; it is poorly developed in *T. pudibunda,* barely suggested or lacking in some individuals, but it is well developed in *T. heterura.* It seems to me that the nearest relative of *T. heterura* is probably *T. ottonis,* but not *T. pudibunda.*

Thripophaga modesta varies geographically in its great range which extends from Santa Cruz in southern Patagonia and Magallanes in southern Chile, north into the Andes to Pasco and Lima in Peru, and from the coast, or coastal hills, up to about 4600 m. The range and ecological variation of *T. modesta* is much more extensive than that of any other species.

In the coastal hills of Peru, which extend from Arequipa north to Lima, and on the lower western slopes of the Andes up to about 2500 m. this species seems to be restricted to stands of cacti, and Koepcke (1959, 1965) believed these populations, though related to *Thripophaga modesta,* are a distinct species which she named *T. cactorum* in 1959. However, *T. modesta* and *T. cactorum* differ slightly morphologically, and variations in ecology and correlated behavior do not seem conclusive when the sharp ecological variation in the great range of *modesta* is taken into consideration. It is difficult to grant that *cactorum* is a distinct species, and, at the end of 1970, I had the occasion to discuss this question personally with Koepcke. We examined specimens together and she readily agreed that the systematic status of *cactorum* required further consideration but we could not return to this question because a little over a year later she was killed in an airplane crash in Peru. My opinion is that *cactorum* and *modesta* are conspecific. I believe that all differences between *T. modesta* and the three forms named by Koepcke (1959, 1965) under the specific name *T. cactorum* are merely a question of relative degree. The most clear-cut is a difference in the bill which is longer and stronger as a rule in the populations of the coastal hills and western slopes of the Andes (*cactorum*), although the bill is identical in an occasional specimen from the region of Lake Titicaca and from Jujuy in Argentina (*modesta*). The rufous area on the rectrices tends also to be more restricted in the forms named by Koepcke (1959, 1965),

but I cannot detect any constant differences whatever in the strength of the feet and claws, or shapes of the tips of the rectrices, which Koepcke mentioned as evidence of specific distinction.[104]

Geographical Variation

Geographical variation exists, or has been mentioned, in 11 species which are: *Thripophaga pyrrholeuca, T. baeri, T. pudibunda, T. modesta, T. d'orbignyi, T. humicola, T. humilis, T. wyatti, T. punensis, T. urubambensis,* and *T. flammulata.*

The variation is most interesting and best marked in *T. d'orbignyi* in which five subspecies have been named. However, this variation presents only two trends, one form (nominate *d'orbignyi*) is strongly rufous brown on the upperparts and bright rufous on the upper surface of the wing, as against another form (*arequipae*) which differs conspicuously from nominate *d'orbignyi* by being raw umber brown on the upperparts and has a very dark wing which is sooty blackish brown, not rufous; with the exception of the lesser and median upper coverts which are more or less distinctly edged with rufous.[105] The populations with a dark back and wing (*arequipae*) inhabit Peru, the Departments of La Paz and Oruro in Bolivia, and extreme northern Chile in the Andes of Arica and Tarapacá. The rufous populations (nominate *d'orbignyi*) inhabit the remainder of the range, but as some intergradation exists in the Departments of La Paz and also Potosí in Bolivia, it is difficult to draw a sharp limit between the ranges of the two subspecies.[106] The other three forms that have been named should not be acknowledged as they represent only an intermediate in Bolivia, or very slightly differentiated local populations in Peru of which I have examined the type and series on which they are based. The bill is also bigger and distinctly heavier in the dark *T. d. arequipae.*

Thripophaga urubambensis is not well known and very few specimens seem to exist. I did not examine specimens from the northern end of the range which authors agree are quite distinctly darker and more richly colored on the upperparts, less streaked on the crown, whiter below, less buffy, than birds from Cuzco in Peru and La Paz in Bolivia which are indistinguishable and represent nominate *urubambensis.* The birds from the north have been named *T. u. huallagae.*

The geographical variation of *Thripophaga flammulata* has been discussed in great detail by Vuilleumier (1968). All the populations are more or less isolated and slightly differentiated but can be divided in two groups in my opinion. One group, which consists of the populations of Colombia, is replaced by another group in Ecuador and Peru in which the birds are distinctly less streaked on the center of the underparts, and the general ground coloration of the plumage is more blackish, less brownish. Variation exists in each group: in Colombia the birds of the Eastern Andes are more densely streaked than those of the Central Andes; in Peru, the streaks become narrowest on the upperparts and are least pronounced on the underparts where they are restricted chiefly to the upper breast and flanks.

The range of *Thripophaga wyatti* is also more or less broadly interrupted[107] but the geographical variation of this species is relatively slight and affects chiefly the streaking of the underparts which is coarser in some populations than others. In the population of Peru (which has been named *graminicola*) the streaking is least heavy and coarse, and this population is also the dullest, but the most tawny on the underparts. The population of the northern end of the Eastern Andes of Colombia (nominate *wyatti*) is coarsely and darkly streaked on the underparts, but somewhat less so than the population of Ecuador. In the Santa Marta Massif, in the Andes of western Venezuela, and in southern Ecuador, the populations, all of which have been named, are only more or less vaguely differentiated.

Thripophaga modesta has a great range and varies geographically to a distinct degree. The populations from the southern end of the range in Argentina and Chile, which

have been named *T. m. australis,* are very considerably more grayish on the upperparts, less brownish, and less buffy and ochraceous than the populations of northern Argentina, northern Chile north of southern Atacama, Bolivia, and the altiplano of Peru. The nominate race is based on a specimen believed to have been taken in Bolivia, and the bill shows also a tendency to be longer and stronger in the birds of Bolivia.

On the western slopes of the Andes of Peru up to about 2500 m., and also in some of the coastal hills of Peru, *Thripophaga modesta* seems to be restricted to stands of cacti on rocky slopes. These populations, which have been named *T. cactorum* by Koepcke (1959), were believed to be a separate species by Koepcke, but are considered by me to be part of *T. modesta,* of which they represent only a subspecies.

In *Thripophaga humicola,* the population from the southern part of the range in Chile (from Maule southward) is darker, more saturated above and below, and more heavily spotted, than the birds breeding north of Maule in Chile, and in Mendoza in Argentina; it has been named *T. h. polysticta.*

The geographical variation of *Thripophaga pudibunda* and *T. punensis* is clinal in character. In *T. pudibunda,* the populations from the northern end of the range are darker and more richly colored than birds from central and southern Peru, and their rufous gular patch is well defined. General saturation decreases from north to south, the underparts becoming more grayish at the southern end of the range, and the gular patch less distinct, paler, more cinnamomeous. The bill also becomes more slender toward the southern end of the range. In *T. punensis,* the variation is not strongly marked, but the population from the northern end of the range (nominate *punensis*) is distinctly paler and less heavily streaked on the upperparts than the populations of Argentina which have been named *T. p. lilloi*; the intervening population of Bolivia is roughly intermediate, but birds from Bolivia are more similar on the whole to the birds of Argentina.

Three "subspecies" have been recognized in *Thripophaga humilis* although the geographical variation is trivial. Birds from the northern extremity of the range (Cajamarca) are slightly paler, less buffy below, and are slightly more grayish on the upperparts, with the dark streaking somewhat better defined, than birds from other regions of Peru and from Bolivia. In southern Peru (Puno) and in Bolivia, the birds average darkest, but the difference is "negligible," as already stated by Bond (1945).

Geographical variation has been mentioned, and "subspecies" have been named in *Thripophaga pyrrholeuca* and *T. baeri* but are not confirmed by my study. In the case of *T. pyrrholeuca* the difference in coloration mentioned represents only seasonal variation in plumage. Differences in coloration and measurements have been mentioned in *T. baeri,* but I find the former does not exist, and that measurements overlap greatly throughout the range of this species.

KEY TO THE SPECIES OF *THRIPOPHAGA*

1. Tail with 10 rectrices (occasionally 12) ... 2
   Tail with 12 rectrices 3
2. Not streaked on the upperparts; tail dark chestnut; 10 rectrices ..... *cherriei*
   Heavily streaked on the upperparts; tail very pale, uniformly ochraceous orange; 10 rectrices, occasionally 12 ..... *macroura*
3. Back streaked or spotted 4
   Back uniform, not streaked or spotted ... 12
4. Forecrown russet or bright chestnut, or with very distinct rufous streaks 5
   Not rufous on the forecrown 7
5. With a dull orange gular patch 6
   Throat dull white, without a dull orange gular patch ..... *maculicauda*
6. Breast and upper flanks heavily flammulated with black and white; heavily streaked on the rump and upper tail coverts .... *flammulata*
   Upper breast slightly and not very distinctly streaked with brown, not flammulated with black and white; not heavily streaked on rump and upper tail coverts ..... *virgata*
7. Central rectrices conspicuously elongated and attenuated, becoming very sharply acuminate at the tip ..... *hudsoni*

Rectrices blunt, or relatively blunt, not sharply acuminate, or appreciably attenuated and elongated 8

8. Two outer pairs of rectrices strongly and uniformly rufous ..... *wyatti*
Two outer pairs of rectrices black with conspicuous rufous tips; or almost entirely dark brown with the exception of a poorly defined, irregular narrow rufous streak along the shaft 9

9. Two outer pairs of rectrices almost entirely dark brown, with a rufous, irregular streak along the shaft ..... *humilis*
Two outer pairs of rectrices black with very conspicuous rufous tips 10

10. Outer web of the outer pair of rectrices white; and central rectrices broadly margined with silvery gray ..... *anthoides*
Outer web of the outer pair of rectrices strongly rufous; central rectrices brown, and uniform or virtually so 11

11. Rufous area at the base of the remiges extensive and chestnut above; rufous tips of the rectrices relatively dull; restricted to the Sierra de Córdoba in Argentina .. *sclateri*
Rufous area at the base of the remiges less extensive, paler than in *sclateri*, more tawny; rufous tips of the rectrices paler rufous than in *sclateri*; distributed from southern Peru, south through western Bolivia, to Catamarca, Tucumán, and La Rioja in Argentina ..... *punensis*

12. Rectrices strongly stiffened and greatly decomposed ..... *urubambensis*
Rectrices slightly stiffened only, with the webs well integrated, or not greatly decomposed 13

13. Without a rufous (orange) gular patch ... 14
With a rufous gular patch 17

14. Throat dull white, the feathers without black bases, or black or dark brown tips; very distinctly streaked with dark brown at the sides of the breast and on the flanks ..... *hypochondriaca*
Feathers of the throat dull white, but black at the base, or tipped with black or dark brown; not streaked at the sides of the breast and on the flanks 15

15. Feathers of the throat very black at the base ..... *patagonica*
Feathers of the throat white at the base, but with distinct black or dark brown tips 16

16. Two outer pairs of rectrices very strongly and uniformly rufous ..... *steinbachi*
Two outer pairs of rectrices dark brown, but with somewhat paler, more fuscous tips .. *humicola*

17. Upper rectrices black, contrasting strongly with the upper tail coverts which are very bright reddish chestnut 18
Upper rectrices chiefly rufous, brown, or brown with rufous or pale margins, but not black, and not contrasting strongly with the color of the upper tail coverts 19

18. Second outer pair of rectrices strongly and uniformly rufous ..... *berlepschi*
Second outer pair of rectrices black on the inner web, or partly black, not uniformly rufous ..... *d'orbignyi*

19. Forecrown rufous; rectrices narrow and not very firmly integrated ..... *ottonis*
Forecrown brown; rectrices normal in width and firmly integrated 20

20. Underparts very pale gray, not streaked; under tail coverts very pale buff; margin of the outer web of the rectrices pale silvery gray; bill short and relatively stout ..... *baeri*
Underparts darker than in *baeri*, dingy, smoky gray, or strongly buffy with a tinge of cinnamon, and with very faint streaks below the gular patch; under tail coverts umbraceous, or tawny ochraceous; margins of the outer web of the rectrices rufous; bill long, attenuated, and slender ... 21

21. Underparts dingy, smoky gray; under tail coverts umbraceous 22
Underparts strongly buffy with a tinge of cinnamon; under tail coverts ochraceous or tawny 23

22. Upper tail coverts pale dull brown; central rectrices dark brown ..... *pyrrholeuca*
Upper tail coverts reddish chestnut; central rectrices chestnut also for the greater part, becoming progressively more dusky apically ..... *pudibunda*

23. Three outer pairs of rectrices strongly and uniformly rufous. In this species the tail is unusually long (averaging about 87 mm. in length), the rectrices are relatively narrow, and the tips of the central pair are moderately, but not sharply acuminate ..... *heterura*
Three outer pairs of rectrices not uniformly rufous (being blackish or very dark brown to a varying extent on the inner web). In this species the tail is unusually short (averaging about 67 mm. in length), and its

rectrices are broad with blunt tips .... *modesta*

List of the Species

Thripophaga pyrrholeuca

DESCRIPTION: Uniformly warm brown or more grayish earthy brown on the upperparts. Pale on the underparts which are very dingy, brownish or smoky gray, with very faint pale shaft streaks below the gular patch and on the breast, becoming dark brownish buff and pale umbraceous on the lower flanks and under tail coverts; gular patch pale dull orange. Rufous area in the wing dull and rather restricted. Rectrices well graduated, slightly stiffened and very well integrated, rounded or very blunt at the tip; strongly rufous, pale burnt sienna on the three outer pairs, the other rectrices being dark brown with a very narrow rufous edge on the outer web; the three outer rectrices are wholly rufous, with the exception of a restricted dusky area along the edge of the inner web of the third pair.

IMMATURE PLUMAGE: Similar to that of the adult, but lacking the rufous gular patch, and more or less squamated or mottled below the upper throat, the feathers being narrowly edged with gray or brown at the tip.

RANGE: Argentina and Chile, from Mendoza, San Luis (probably), La Pampa, and southern Buenos Aires, south to Santa Cruz in Argentina, and in Chile from Aconcagua, south to Aysén. Partly migratory, wintering north, through Argentina, to southern Uruguay, southern and southeastern Paraguay, and southern Bolivia. The breeding range ascends to about 3000 m. in the Andes (in Mendoza).

SPECIMENS EXAMINED: 81, including the types of "*flavogularis*" and "*brunnea*."

Thripophaga baeri

Figure 5

DESCRIPTION: Uniformly pale dull grayish brown on the back, with a slightly darker, more brownish, less grayish head, and with a broad, but very ill-defined grayish postocular streak. Uniformly very pale grayish brown below the gular patch and on the breast, dingy grayish white below the breast, becoming pale buff on the lower flanks and under tail coverts; gular patch dark dull orange and conspicuous. Rufous area in the wing very dull, and becoming obsolete as it is restricted only to the edge of the inner web of the remiges. Outer web of the remiges and central rectrices narrowly edged with dull silvery gray.

Rectrices well integrated and slightly stiffened, blunt, with rounded tips, and not strongly graduated, relatively speaking. The rectrices are strongly rufous with the exception of the three inner pairs which are dusky brown at the tip or subapical portion of the inner web of the fourth pair, dark brown on the inner web of the fifth pair, and wholly dark brown in the case of the central pair, with the exception of the edge of its outer web which is silvery gray as stated above. The outer web of the outer pair is whitish, and also the edge of the outer web of the next pair. The bill of this species is relatively, but quite noticeably, short and stout.

IMMATURE PLUMAGE: Similar to that of the adult, but lacking the rufous gular patch, and with the feathers of the upper breast with very faint, poorly defined grayish tips, or dingy white, without dark tips.

RANGE: Paraguay, southwestern Rio Grande do Sul in Brazil, Uruguay, and Argentina south to Neuquén and Rio Negro, but not recorded in Misiones.

SPECIMENS EXAMINED: 87.

Thripophaga pudibunda

DESCRIPTION: Upperparts earthy brown on the head, becoming progressively more rufous on the back, auburn on the lower back, chestnut on the rump, and strongly reddish chestnut on the upper tail coverts. Smoky gray on the underparts below the pale or rufous upper throat, very dingy, and with poorly defined pale streaks on the lower throat and breast; dark and umbraceous on the lower flanks and under tail coverts. The gular patch varies from pale fawn to dull or-

ange, but is barely suggested, or lacking altogether in some individuals. Rufous area in the wing reddish chestnut, rather restricted, but greater part of the upper surface of the wing, and most of the tail, strongly rufous, chestnut, with the exception of the dusky brown, blackish, distal portion of the remiges and of the dusky tips or distal portion of the inner pairs of the rectrices; the latter are moderately graduated, slightly stiffened, end in blunt, rounded tips, but their webs show a tendency to be not very firmly integrated.

IMMATURE PLUMAGE: In one specimen which has probably not assumed full adult plumage, the feathers of the underparts have faint grayish brown tips below the rufous gular patch.

RANGE: Andes of Peru, between about 2750 and 3700 m. from La Libertad south to Tacna.

SPECIMENS EXAMINED: 3.

Thripophaga ottonis

DESCRIPTION: Forecrown chestnut, and remainder of the upperparts uniformly rufous brown, with the exception of the upper tail coverts which are bright reddish chestnut; lores dull white, with a distinct cinnamomeous buff superciliary and post-ocular streak. Underparts brownish gray on the lower throat and breast, and finely streaked with buffy streaks below the gular patch which is extensive and dull pale orange; abdomen buffy white, not streaked, with ochraceous lower flanks and under tail coverts. Rufous area in the wing, and greater part of the upper surface of the wing, and also of the tail, bright chestnut, with the inner rectrices becoming dusky near the tip. The tail of this species is quite distinctive, distinctly elongated and well graduated, with blunt rectrices, the inner web of which is narrowed and not very firmly integrated; it is slightly stiffened.

RANGE: Andes of Peru, between about 2750 and 3600 m., from Huancavelica to Cuzco and Apurimac.

SPECIMENS EXAMINED: 14.

Thripophaga heterura

Figure 5

DESCRIPTION: Uniformly earthy brown on the head and nape, becoming more rufous on the back, and chestnut on the upper tail coverts; with a short and indistinct superciliary and post-ocular streak. Underparts very strongly buffy with a tinge of cinnamon, uniform on the lower throat and breast, or with an extremely faint suggestion of streaking, becoming dark, tawny ochraceous, on the lower flanks and under tail coverts. The rufous gular patch is rather restricted and dark reddish orange. The rufous area in the wing, and the greater part of the upper surface of the wing are reddish chestnut. The greater part of the tail is reddish chestnut also, but the inner webs of the two pairs of central rectrices are dark brown, and also the edge of the inner web of the next pair.

The tail of this species is also distinctly elongated and well graduated, and its rectrices are narrowed, as in the case of *T. ottonis*, but less so, and its rectrices are more firmly integrated and end in more acuminate, less blunted tips; it is only very slightly stiffened.

RANGE: Bolivia in the Departments of La Paz and Cochabamba, between about 3000 and 4150 m.

SPECIMENS EXAMINED: 5.

Thripophaga modesta

DESCRIPTION: Upperparts uniform and varying from umber brown to grayish brown, and with a poorly defined whitish or buffy superciliary and post-ocular streak. Underparts varying from dull white to pale ochraceous buff below the gular patch which is well developed and pale ochraceous orange, the lower throat and upper breast being somewhat variegated, or not, with indistinctly defined streaks or spots; darker, more ochraceous or tawny on the lower flanks and under tail coverts. Rufous area in the wing restricted, cinnamon rufous, or brighter, variable, as is also the rufous pigmentation on the upper surface of the wing, which is

restricted chiefly to the lesser and median coverts and edge of the outer web of the remiges. Rufous area in the tail variable in extent, but with the inner web of all the rectrices invaded with dark brown to a varying degree, but wholly brown, or virtually so, in the case of the three inner pairs. The tail of this species is noticeably short, not very strongly graduated, with rectrices that are well integrated, slightly stiffened, and blunt at the tip.

IMMATURE PLUMAGE: Similar to that of the adult, but lacks the rufous gular patch, and is more mottled on the whole of the underparts below the throat.

RANGE: Central Peru, from Lima and Pasco, south through Peru and Chile to northern Magallanes in southern Chile, and, through western Bolivia and western Argentina, to southern Santa Cruz, the range in Argentina extends eastward, north to Córdoba, and to coastal Argentina, north to southern Buenos Aires. The altitudinal range is also very great, from low elevations near the coast in Argentina, and coastal lomas of Peru from Lima south to Arequipa, up to about 4600 m. in the Andes and on the altiplano.

SPECIMENS EXAMINED: 89, including the type of *modesta* in BM, and those of "*proxima*" and "*monticola*" in the AMNH.

Thripophaga d'orbignyi[108]

DESCRIPTION: Upperparts vary from raw umber brown, with a somewhat darker crown to dull rufous brown, with a somewhat more cinnamon brown crown, becoming, in all instances, more rufous on the rump and being bright reddish chestnut on the upper tail coverts. Underparts uniform and very pale ochraceous buff below the gular patch which is conspicuous, ferruginous, or pale reddish chestnut, but strongly ochraceous and tawny on the lower flanks and under tail coverts. Rufous area in the wing very restricted, lacking at the base of the outer primaries, but suggested at the base of the inner primaries, and present at the base of the secondaries. Upper surface of the wing strongly rufous, including the coverts, or dark sooty, blackish brown, not rufous, with the exception of the margins of the lesser and median coverts which are rufous to a varying degree; and very rufescent, or dark sooty brown at the edges of the innermost secondaries (tertials). Tail very dark, blackish brown, with the exception of the three outer pairs of rectrices which vary in coloration, the outermost pair being wholly and strongly rufous (or with a very extensive blackish area on the inner web), and the next two pairs rufous on the outer web only (or only at the edge of the outer web, with or without a rufous edge on the third pair). The tail is moderately long, with the rectrices very firmly integrated, well graduated, slightly stiffened, and well rounded at the tip.

IMMATURE PLUMAGE: Similar to that of the adult, but lacks the rufous gular patch, and is faintly squamated with gray-brown on the underparts below the throat.

RANGE: Andes, between about 2200 and 4600 m., from Huancavelica in Peru, south through western Bolivia, and Andes of Arica and Tarapacá in Chile, and those of western Argentina south to Mendoza.

This species varies sharply geographically (see general discussion) and I recognize two subspecies: *arequipae,* with the dark back and upper surface of the wing in Peru, south to the Departments of La Paz and Oruro in Bolivia, and the Andes of Arica and Tarapacá in Chile; nominate *d'orbignyi,* with the rufous back and wing, in the remainder of the range.

SPECIMENS EXAMINED: 128, including the types of *Synallaxis humicola* d'Orbigny in MNHN on which *d'orbignyi* Reichenbach is based; and of *arequipae,* "*huancavelicae,*" and "*usheri*" in BM.

Thripophaga berlepschi
Figure 5

DESCRIPTION: Upperparts raw umber brown, becoming more rufous on the lower back and rump, and with bright reddish chestnut upper tail coverts. Underparts uniform and very pale ochraceous buff below the gular patch which is ferruginous, restrict-

ed, and partly concealed, but strongly ochraceous and tawny on the lower flanks and under tail coverts.

This species resembles some populations of *T. d'orbignyi* very much in general coloration, including the coloration of the wing and tail, but the two outer pairs of rectrices are wholly and strongly rufous, and the third pair is partly so in *T. berlepschi,* whereas the rufous area is always more restricted in *T. d'orbignyi* (*q.v.*). The structure of the tail and the shape of the rectrices are similar in the two species.

RANGE: Andes of La Paz in Bolivia between about 2600 and 3700 m.

SPECIMENS EXAMINED: 17.

Thripophaga steinbachi
Figure 5

DESCRIPTION: Upperparts cinnamon brown on the crown and upper back, but more grayish and drab on the nape, and becoming more rufous, more strongly cinnamon, on the center and lower part of the back, more chestnut on the rump, and pale burnt sienna on the upper tail coverts. Chin and upper throat dull white (not ferruginous or dull orange), with the feathers more or less narrowly tipped with dark brown at the base and sides of the whitish gular patch; soft pale gray, with a very faint and very pale vinaceous tinge, on the remainder of the underparts, with the exception of the lower flanks and under tail coverts that are tawny. Rufous area in the wing ferruginous and restricted, but upper surface of the wing almost entirely pale ferruginous.

Tail strongly rufous, pale burnt sienna, or pale bright reddish chestnut on the two outer pairs of rectrices which are entirely rufous, but with a broad dark blackish brown band along the outer part of the inner web of the next pair, the three inner pairs being also dark blackish brown, but with bright rufous edges that become very narrow and disappear almost completely on the central pair. The tail is "soft," scarcely stiffened, well graduated, with well-integrated rectrices that are rounded or blunt at the apex.

RANGE: Andes of Argentina and their foothills, from Salta south to Mendoza, between about 800 and 3000 m.

SPECIMEN EXAMINED: 1, consisting of the type of *steinbachi* in AMNH.

Thripophaga humicola

DESCRIPTION: Upperparts dull brown, or rufescent brown, on the crown, lower back, and rump; more grayish brown on the nape and upper back, with the upper tail coverts similar in coloration to the rump or more rufous. The feathers at the base of the upper bill are dull white, with or without very narrow blackish margins, and whitish feathers extend posteriorly to form a superciliary and post-ocular streak, well defined in some individuals but not in others. Chin and upper throat white or dull white, with most of the feathers tipped with dull black, especially at the sides and base of the throat. Breast and abdomen grayish, or dingy pale buffy white, with the feathers paler, more whitish along the shaft, but spotted more or less distinctly with brown laterally, creating a streaked or mottled pattern which is not very distinct as a rule; flanks and under tail coverts cinnamon brown or tawny.

The rufous area in the wing is inconspicuous, restricted to the base of the inner primaries and of the secondaries, and is only vaguely defined in some individuals; the lesser and middle upper wing coverts are dull reddish chestnut, but the upper surface of the wing is chiefly brownish. Tail dark brown, virtually uniform, but with paler, poorly defined, more fuscous tips on the two outer pairs of rectrices; the tail is "soft," scarcely stiffened, and the rectrices are well graduated and integrated, with quite broad blunt or rounded tips.

IMMATURE PLUMAGE: Very similar to that of the adult, but pattern of the underparts more diffuse.

RANGE: Central Chile from Atacama to Arauco, also northern Mendoza in Argentina. The range rises from the coastal region in Chile, up to about 2200 m. on the slopes of the Andes.

SPECIMENS EXAMINED: 33.

Thripophaga patagonica

DESCRIPTION: Upperparts uniformly cinnamon brown. Feathers of the gular patch black at the base with very conspicuous dull white tips, some of which are also faintly dull orange. Sides of the lower neck, and border of the upper breast, pale soft gray, the breast becoming paler and more buffy at the center, and then grading into pale cinnamon orange, or ochraceous tawny on the flanks, lower abdomen, and under tail coverts. Rufous area in the wing pale tawny and restricted, with the upper surface of the wing cinnamon brown, with a small and dull tawny patch restricted chiefly to the lesser coverts. Tail dark brown, wholly rufous only on the outer web of the outer pair of rectrices, but with the edges of the other pairs rufous or cinnamon brown; the structure of the tail is similar to that of *T. humicola,* but the rectrices are not quite so broad.

RANGE: Patagonia, from southern Mendoza, La Pampa, and Rio Negro south to Chubut.

SPECIMENS EXAMINED: 6, including the two cotypes of *patagonica* in MNHN.

Thripophaga humilis

DESCRIPTION: Upperparts earthy brown, with the feathers of the crown and back not uniform, but much darker brown, or blackish brown, at the center, creating a spotted pattern. Gular patch strongly ferruginous, or dark dull orange, but rather restricted in size, with the feathers at the sides of the gular patch, and beneath it on the lower throat, dark brown at the sides and pale at the center, creating a more or less sharply streaked pattern, which may or may not extend to the upper breast where it becomes very vaguely defined; the remainder of the underparts are chiefly dark buff, but more ochraceous on the lower flanks and under tail coverts. Rufous area in the wing bright chestnut and rather extensive; upper surface of the wing brown, with only vague rufous edges on the primaries and primary coverts. Tail chiefly dark brown, but with pale, dark buff or cinnamomeous edges to the feathers, and with an irregular rufous streak along the shaft of the apical portion of the two outer pairs; the rectrices are well integrated, slightly stiffened, and have blunt or slightly acuminate tips.

IMMATURE PLUMAGE: Similar to that of the adult, but pattern less distinct or lacking, and mottled with rufous spots on the nape; rufous gular patch very faint or lacking.

RANGE: Andes, between about 2750 and 4800 m., from Cajamarca in Peru, south to the Andes of La Paz in Bolivia.

SPECIMENS EXAMINED: 51, including the type of "*cajamarcae*" in AMNH.

Thripophaga anthoides
Figure 5

DESCRIPTION: Upperparts sharply and heavily patterned from the crown to the upper tail coverts, each feather being very dark, blackish brown at the center, with broad, strongly buffy edges. A pale, buffy, rather narrow, superciliary streak extends from the base of the upper bill to the postocular region, above the lores and ear coverts which are dark brown, with a few buffy streaks on the coverts. The gular patch is orange and conspicuous, bordered with narrow pale and blackish streaks, the dark markings becoming reduced to a few small spots on the upper breast; the remainder of the underparts is cinnamomeous buff on the breast, buffy on the abdomen, and ochraceous on the flanks which become streaked with dark brown posteriorly. The rufous area in the wing is extensive and very bright ochraceous orange; on the upper surface of the wing, the coverts are blackish brown with strong buffy edges, similar to the coloration of the back, but the central portion of the outer web of the outer primaries is whitish, or very pale buff, and, this pale area, together with the rufous area across the primaries and secondaries, form a conspicuous wing bar.

The tail is sharply patterned; dark brown, but with very conspicuous, large and sharply defined, rufous cinnamon or fleshy ocher api-

cal spots on the inner web of the three outer pairs of rectrices, the outer web of which is white or whitish; the inner portion of the central pair is dark brown, but the outer portion is pale and "silvery" gray. The rectrices are very well integrated, slightly stiffened, and slightly acuminate at the tip.

IMMATURE PLUMAGE: Similar to that of the adult, but lacks the rufous gular patch and is slightly mottled below.

RANGE: Central Chile, from Concepción, and Argentina, from southern Neuquén and southern Rio Negro, south to Tierra del Fuego and Staten Island; records from the Malvinas (or Falkland Islands) are probably erroneous. This species is partly migratory, and during the winter occurs north to Aconcagua in Chile.

SPECIMENS EXAMINED: 54, including the type of "*rufogularis*" in BM.

Thripophaga wyatti

DESCRIPTION: Upperparts brown and heavily patterned from the crown to the rump (but not on the upper tail coverts), each feather being very distinctly much darker brown at the center with very broad, pale rufous brown, or more grayish brown edges. A tawny superciliary streak exists, becoming more conspicuous and broader in the postocular region. Gular patch ferruginous, bordered with feathers that are dusky black at the base, the dark bases being virtually concealed by dark buff or tawny tips as a rule; the remainder of the underparts is tawny but becomes darker and more fulvous on the flanks and under tail coverts. Rufous area in the wing bright reddish chestnut and unusually extensive, extending to the apical portion (but not to the tip) on the inner primaries, and upper surface of the wing very strongly rufous also. Central rectrices uniformly dark brown, but the other pairs of rectrices wholly or partly rufous, bright reddish chestnut as in the case of the rufous area in the wing; the first and second outer rectrices are wholly rufous, and (normally) the third pair is strongly rufous also, with the exception of the base of the outer web which is brown, and also the edge of the inner web to a slight extent, the brown area increasing progressively on the fourth and fifth pairs. The tail is slightly stiffened, the rectrices are very well integrated, are blunt at the tip, and are comparatively narrow when compared to those of the related *T. punensis*.

IMMATURE PLUMAGE: Similar to that of the adult, but considerably darker brown and much less distinctly patterned on the upperparts, and lacking the ferruginous gular patch, the upper throat being merely buffy.

RANGE: Discontinuous, consisting of the Andes of western Venezuela in Mérida north to southern Trujillo, the Sierra de Perijá at the border between Venezuela and Colombia, the Santa Marta Massif and the northern end of the Eastern Andes in Colombia, the Andes of Ecuador, and the Andes of central and southern Peru from Pasco and Junín south to Puno. The altitudinal range varies between about 3000 and 5500 m.

SPECIMENS EXAMINED: 45, including the types of *wyatti* in BM; of "*aequatorialis*" and "*azuay*" in AMNH; and of "*mucuchiesi*" in the Phelps Collection on deposit at AMNH.

Thripophaga punensis
Figure 5

DESCRIPTION: Resembles *T. wyatti* but more distinctly patterned on the upperparts, and with a very different tail pattern as the brown areas are much more extensive in *T. punensis*, and much darker, more "blackish" than in *T. wyatti*. In *T. punensis* the rufous area is restricted only to the apical portion of the outer pair of rectrices, and, to a progressively decreasing degree, to the tips of the next three outer pairs, whereas the first two outer pairs are wholly rufous in *T. wyatti*, and the rufous area is very extensive on the third pair, and exists also on the fourth and fifth pairs. The structure of the tail differs also in the two species, the tail of *T. punensis* is very appreciably longer, proportionally, more strongly graduated, and its rectrices are quite distinctly broader. The feet of *T. punensis* are also quite markedly stronger and bigger than those of *T. wyatti*.[109]

IMMATURE PLUMAGE: Similar to that of the adult, but lacks the ferruginous gular patch, and with the feathers of the breast distinctly edged with gray-brown at the tip, creating a more or less distinctly mottled or squamated pattern.

RANGE: Andes, from about 2150 to over 4000 m., from Puno in southern Peru, south, through western Bolivia, to La Rioja in Argentina.

SPECIMENS EXAMINED: 38, including the types of *punensis* in ZIW; of "*rufala*" and "*cuchacanchae*" in AMNH; and the cotypes of "*lilloi*" in MNHN.

Thripophaga sclateri

DESCRIPTION: Very similar to *Thripophaga punensis* and perhaps conspecific with it, as the differences between the two taxa seem to be slight and relative only. The rufous area in the wing of *T. sclateri* is somewhat more extensive than in *T. punensis*, and its coloration (and also that of the rufous tips of the rectrices) is richer and brighter chestnut.

RANGE: Restricted to the Sierra de Córdoba in Argentina in a zone between about 2000 and 2900 m.

SPECIMENS EXAMINED: 2.

Thripophaga urubambensis
Figure 5

DESCRIPTION: Upperparts rufescent or dark auburn brown, uniform (not streaked) on the back and rump, but sharply and narrowly streaked with rufous on the forecrown, the streaks becoming obsolete and nearly vanishing on top of the crown, but reappearing on the nape and hind neck, but paler than on the forecrown and not so sharply defined. Gular patch bright orange rufous and conspicuous, with the feathers at the sides of the throat, and on the lower throat and breast heavily flammulated with dark brown. Center of abdomen dingy grayish buff, virtually uniform, but with a few vaguely indicated paler buffy streaks which become more distinct on the flanks, which together with the under tail coverts are pale raw umber. The rufous area in the wing is restricted and inconspicuous, tawny, and restricted to the base of the inner primaries and secondaries, and the upper surface of the wing is brown. The tail is brown, about similar to the coloration of the back, not rufous anywhere, but paler on the outer rectrices, more fuscous than brown. It is composed of very narrow rectrices which are strongly stiffened, greatly decomposed, and very attenuated distally for a long distance, about equal to nearly half the length of the feather in the case of the central pair, but somewhat less for the other inner pairs; the feather comes to a very narrow and sharp, "hair-like" tip or bristle, almost completely devoid of barbs.

This species varies geographically (see discussion) and the description given above is based on specimens from Cuzco, Peru.

RANGE: Probably discontinuous, but not well known; known from La Libertad, Huánuco, and Cuzco in Peru, and from the Andes of La Paz in Bolivia. The altitudinal range seems to vary from about 2750 to 3800 m.

SPECIMENS EXAMINED: 2.

Thripophaga flammulata
Figure 5

DESCRIPTION: Upperparts very dark brown and sharply streaked and heavily flammulated, the streaks are narrow and sharp on the crown and are rufous, but on the feathers of the back, rump, and upper tail coverts, the shaft of the feather is dull white, narrowly bordered with buffy white, and this pale central stripe is very broadly margined with dark brown, producing a very bold flammulated pattern. The gular patch is extensive but is pale, dull ochraceous orange, and the whole of the remainder of the underparts is very heavily flammulated with dull white and dark brown, the brown edges of the feathers decreasing, however, to a varying degree on the center of the body below the breast which becomes chiefly dull grayish white in some individuals and some populations. The rufous area in the wing is bright reddish chestnut, moderately extensive, and the edge of the outer web of the inner primaries

and secondaries is also reddish chestnut, as well as a large part of the coverts. The tail is brown, variegated with rufous, the rufous pigmentation being best developed (to an outwardly increasing degree) on the three outer pairs of rectrices, and restricted only to the edges of the other rectrices, including the central pair. The tail is well stiffened, composed of distinctly narrow rectrices that are not very firmly integrated as a rule, but not decomposed, and are more or less attenuated at the tip, but not very sharply so at the apex, except when the feather is worn, when the integration of the webs shows also a tendency to break down.

IMMATURE PLUMAGE: Differs from that of the adult only by being less distinctly and regularly patterned, and by showing only a very faint gular patch.

RANGE: Discontinuous, consisting of the Eastern and Central Andes of Colombia, the Andes of Ecuador from Nariño in Colombia, and the Andes of northern and central Peru, from Cajamarca and southern Amazonas, south to Junín. The altitudinal range varies from about 3350 to 4500 m.

SPECIMENS EXAMINED: 105, including the types of *flammulata* in BM; of "*taczanowskii*" in ZIW; of "*quindiana*" in AMNH; and of "*multostriata*" in MNHN.

Thripophaga virgata

DESCRIPTION: Resembles *Thripophaga flammulata* above, but is paler, duller brown, and is very distinctly less heavily streaked and flammulated, and the markings have also vanished, or virtually so, from the rump and upper tail coverts. Gular patch extensive and conspicuous, darker rufous, more ferruginous than in *T. flammulata,* and markings on the underparts very much more reduced than in *T. flammulata,* the breast being unstreaked, or only slightly smudged with brown in some individuals. Rufous area in the wing extensive, but duller, more tawny than in *T. flammulata,* duller also on the upper surface of the wing. Rufous areas in the tail more sharply defined than in *T. flammulata,* but rufous edges on the central pair lacking or much fainter than in *T. flammulata.*

This species is considerably bigger than *Thripophaga flammulata* (table 13) and the structure of its tail is quite different; the difference in the length of the tail is apparent at a glance, although the difference in proportions is relatively slight, and the tail is composed of less strongly stiffened rectrices that are very much broader, much more firmly integrated, not attenuated, and the tips of which are quite blunt when not worn.

RANGE: Probably discontinuous, and known from only three localities in Peru: Rock Forest which is situated about 25 km. west of Lake Junín, town of Junín or its vicinity, and region near Limbani in Puno; altitudes vary from about 3350 to 4300 m.

SPECIMENS EXAMINED: 5.

Thripophaga maculicauda

DESCRIPTION: Upperparts wholly and strongly patterned, including the tail. The forecrown is bright chestnut, uniform, but the rufous pigment is restricted to the shaft of the feathers and the central area of the feather adjacent to the shaft, behind the forecrown, and forms very well-defined streaks on the top and hind part of the crown. The back, including the rump, is sharply flammulated, the pale central stripe of the feathers being cinnamomeous buff or pale ochraceous orange; the upper tail coverts are also boldly flammulated, but some of these feathers are also slightly mottled with brown, the brown mottling becoming pronounced, on a tawny background, on the central pair of rectrices. The chin and upper throat are white, grading posteriorly into buffy white, and no trace of the "rufous gular patch" exists. The remainder of the underparts are ochraceous buff, below the white or whitish upper throat, with irregular brown mottling or "streaks," which are small and sparse on the center of the breast and of the abdomen, but become heavier and more distinct laterally, and better defined into streaks on the lower flanks and "thighs." The rufous area in the wing is bright reddish chestnut, moderately

extensive, and the rufous pigment edges also the outer web of the inner primaries and secondaries, and forms streaks on the coverts.

The tail is variegated, tawny or dull rufous and brown, the mottling being very conspicuous and abundant in the case of the central rectrices as stated above, but the apical portion or tips of the three outer pairs of rectrices are also mottled to a decreasing degree inwardly; vague, irregular, tawny spots exist on the apical portion of the outer web, or near the tips, of the next two pairs (fourth and fifth) which, otherwise, are wholly dark brown. The rectrices are moderately stiffened, very distinctly narrowed, well attenuated, with acuminate tips in the case of the inner pairs, but their webs are well integrated.

IMMATURE PLUMAGE: Similar to that of the adult, but rufous area on forecrown duller and less extensive, and underparts much more heavily mottled; variegated pattern of the tail less distinct.

RANGE: Discontinuous, consisting of Puno in southern Peru; of La Paz and Cochabamba in Bolivia, at altitudes varying between about 2250 and 4300 m.; and of northwestern Argentina in Tucumán and the Sierra de Aconquija in neighboring Catamarca where it has been collected at 4000 m.

SPECIMENS EXAMINED: 8.

Thripophaga cherriei
Figure 5

DESCRIPTION: Upperparts raw umber brown on the crown, with very faint yellowish centers to the feathers of the anterior part of the crown, the shafts of which become buffy and form very short but sharp streaks on the forehead; back rufescent brown, with a slight olivaceous cast on the upper back, but becoming distinctly more rufous on the lower back and rump, and with the upper tail coverts and the whole of the tail reddish chestnut, without any trace whatever of brown pigmentation in the tail. A narrow buffy or whitish superciliary streak exists, and the gular patch is bright orange rufous and very conspicuous. The sides of the face and neck, lower throat (below the rufous gular patch), and upper breast are raw umber brown or olive brown, and are very sharply streaked with buff, the remainder of the underparts being pale olive brown, but darker on the lower flanks, ferruginous on the under tail coverts, and, in some individuals, the streaks extend farther down onto the breast, becoming progressively more evanescent. The upper surface of the wing is almost completely bright rufous brown or chestnut, and a restricted rufous cinnamon patch exists at the base of the inner primaries and of the secondaries, or along the basal and mesial edge of their inner web.

The tail is uniformly reddish chestnut, as stated above, and composed of rectrices that are moderately well stiffened, with broad, well-integrated webs, and are blunt or very slightly acuminate at the tip.

RANGE: Known only from Capuano (or Caño Capuano) on the right bank of the Orinoco, Venezuela, which is situated about 35 km. above the mouth of the Rio Vichada.

SPECIMENS EXAMINED: 6, including the cotype of *cherriei* in AMNH.

Thripophaga macroura
Figure 5

DESCRIPTION: Upperparts strongly ferruginous brown or burnt sienna, and boldly and sharply streaked from the forehead posteriorly to the upper tail coverts. The streaks are reddish (English Red), or strongly and brightly rufous, on the crown on a dark brown ground on the center and hind part of the crown, but nearly coalesce on the forecrown, and are bright rufous cinnamon on the back. The streaks are restricted to the center of the feather, along the shaft, forming a stripe bordered with brown edges as in the case of *T. flammulata* and relatives. The rufous gular patch is conspicuous and varies from dull orange to ferruginous. There is a small, dull white spot on the lores, and the feathers of the superciliary and post-ocular streak, sides of the face, surrounding the rufous gular patch, and upper breast are brown at their edges, but broadly buffy or cinna-

momeous at the center and at their tip, creating a heavy, broadly streaked flammulated pattern; the buffy streaking becomes less distinct below the upper breast on the remainder of the underparts, including the under tail coverts. The upper surface of the wing is almost completely rufous, bright burnt sienna for the greater part, or strongly ferruginous, and there is a rufous cinnamon patch over a restricted area at the base of the inner primaries and the secondaries, or along the basal and mesial edge of their inner web.

The tail is uniformly rufous, without any trace of brown pigmentation, but is pale, bright rufous cinnamon. The rectrices are slightly or only moderately well stiffened, with firmly integrated and conspicuously broadened webs and with tips that are quite blunt when not worn.

IMMATURE PLUMAGE: Resembles closely that of the adult, but lacks the rufous gular patch; its streaked pattern is more confused, not so well defined on the upperparts, and is more mottled than streaked on the underparts.

RANGE: Eastern Brazil, from Espirito Santo, north to southeastern Bahia, but range in Bahia not known accurately.

SPECIMENS EXAMINED: 24.

Thripophaga hudsoni
Figure 5

DESCRIPTION: General coloration similar to that of *Thripophaga anthoides* which it resembles in being sharply and heavily patterned on the upperparts, in the pale coloration of the underparts which are more or less cinnamomeous buff or pale ochraceous, and in having an extensive and very bright rufous area in the wing which is ochraceous orange. *Thripophaga hudsoni* differs from *T. anthoides,* however, by having paler, more conspicuous edges to the feathers of the upperparts, which are bright hazel, rather than dull dark buff as in *T. anthoides,* and which, moreover, are outlined with silvery white on the back in *T. hudsoni,* but not *T. anthoides*; by having a very much paler gular patch which is whitish, tinged with dull yellow, but is not rufous (orange) as in *T. anthoides*; and by lacking the dark markings which border the gular patch and extend to the upper breast in the case of *T. anthoides.*

The color pattern of the tail is roughly similar in the two species, but the coloration is much paler in *Thripophaga hudsoni,* and the structure of the tail is different, as the central rectrices are conspicuously elongated in *T. hudsoni,* much attenuated, and very sharply acuminate to an extreme degree, but not in *T. anthoides* in any of these respects. The rectrices are also strongly stiffened in *T. hudsoni* (but not in *T. anthoides*), and the bill of *T. hudsoni* is also conspicuously longer than that of *T. anthoides,* very slender, much attenuated, and more compressed laterally than that of *T. anthoides.*

IMMATURE PLUMAGE: Differs distinctly from that of the adult by being heavily patterned with dark brown or blackish brown on the sides of the neck, breast, and flanks, whereas dark markings are lacking in the plumage of the adult, or exist only on the breast in individuals in intermediate plumage but less developed than in the immature plumage. The pattern of the upperparts is also less sharply defined. In *Thripophaga anthoides* (*q.v.*), the immature plumage is similar to that of the adult with the exception that it lacks the rufous gular patch and is slightly mottled.

RANGE: Southeastern Paraguay, western Uruguay, and Argentina from Entre Ríos (and probably Corrientes) and Buenos Aires, south to the Rio Senguerr in southwestern Chubut.

SPECIMENS EXAMINED: 48, including the type of *hudsoni* in BM.

Thripophaga hypochondriaca
Figure 5

DESCRIPTION: Upperparts earthy brown, including the tail, somewhat darker on the head, somewhat paler on the rump, upper tail coverts and tail, and uniform, with the exception of a few minute buffy shaft streaks on the forehead. A conspicuous and broad dull white streak extends posteriorly from the base of the bill to the region above the eye and ear coverts where it almost reaches

the nape, the lores and ear coverts being very dark brown. Underparts dull white on the whole throat, sides of the neck, and breast, and dingy white or faintly ochraceous on the abdomen and under tail coverts, but heavily streaked with dark brown at the sides of the breast, and less darkly and distinctly so on the flanks which are pale umbraceous brown. The feathers, which are streaked at the sides of the breast and on the flanks, are flammulated in appearance as these feathers are distinctly elongated and have whitish centers emphasized by the dark edges of the feather—a pattern reminiscent of *Thripophaga flammulata*.

No true rufous area exists in the wing but the basal and mesial outer edge of the inner web of the inner primaries and secondaries is pale rufous cinnamon, and the lesser and middle upper wing coverts are chestnut. No gular patch, or trace of any rufous pigmentation, exists in this species, except in the wing as described above.

The tail is distinctly elongated and composed of rather narrow rectrices that are not strongly stiffened and are firmly integrated and blunt at the tip; it is wholly brown, without any rufous pigment, as stated above, but the outer rectrices are distinctly paler and more fuscous than the inner pairs.

RANGE: Northwestern Peru in the Marañon watershed, from southern Cajamarca (and probably neighboring Amazonas), south to Ancash, at altitudes which seem to vary from about 2450 to 2800 m. or more.

SPECIMENS EXAMINED: 10, including the type of *hypochondriaca* in BM.

GENUS *PHACELLODOMUS*

Phacellodomus is composed of 10 species and its nearest relative is probably *Thripophaga*. Hellmayr (1925) included only six species in *Phacellodomus*, but this number was raised to seven by Peters (1951), and to 10 by me in my revision (1971a).

The species that was not included by Hellmayr (*erythrophthalmus*) had been separated in a monotypic genus (*Drioctistes* Ridgway, 1909). Hellmayr recognized it on the ground that *erythrophthalmus* can be distinguished generically by having a "much longer as well as slenderer tarsus, elevated, extremely compressed mesorhinium, and proportionately shorter wings." Peters quite correctly merged *Drioctistes* Ridgway, 1909, with *Phacellodomus* Reichenbach, 1853, but without giving any reason. My reasons for not recognizing *Drioctistes* are: I cannot confirm Hellmayr's conclusion as far as the tarsus is concerned, the difference in the shape of the bill is very slight and certainly of no more than specific importance, and the difference in wing proportion is trivial. The wing of *Phacellodomus erythrophthalmus* is proportionally shorter than that of any other species; when expressed as the ratio between tail length and wing length, the proportion is 1.34 in *erythrophthalmus*, 1.28 in *P. dorsalis*, and 1.23 in *P. striaticollis*; the mean wing lengths of *P. striaticollis* and *P. erythrophthalmus* are identical (65.27 and 65.26 mm., respectively, see table 14).

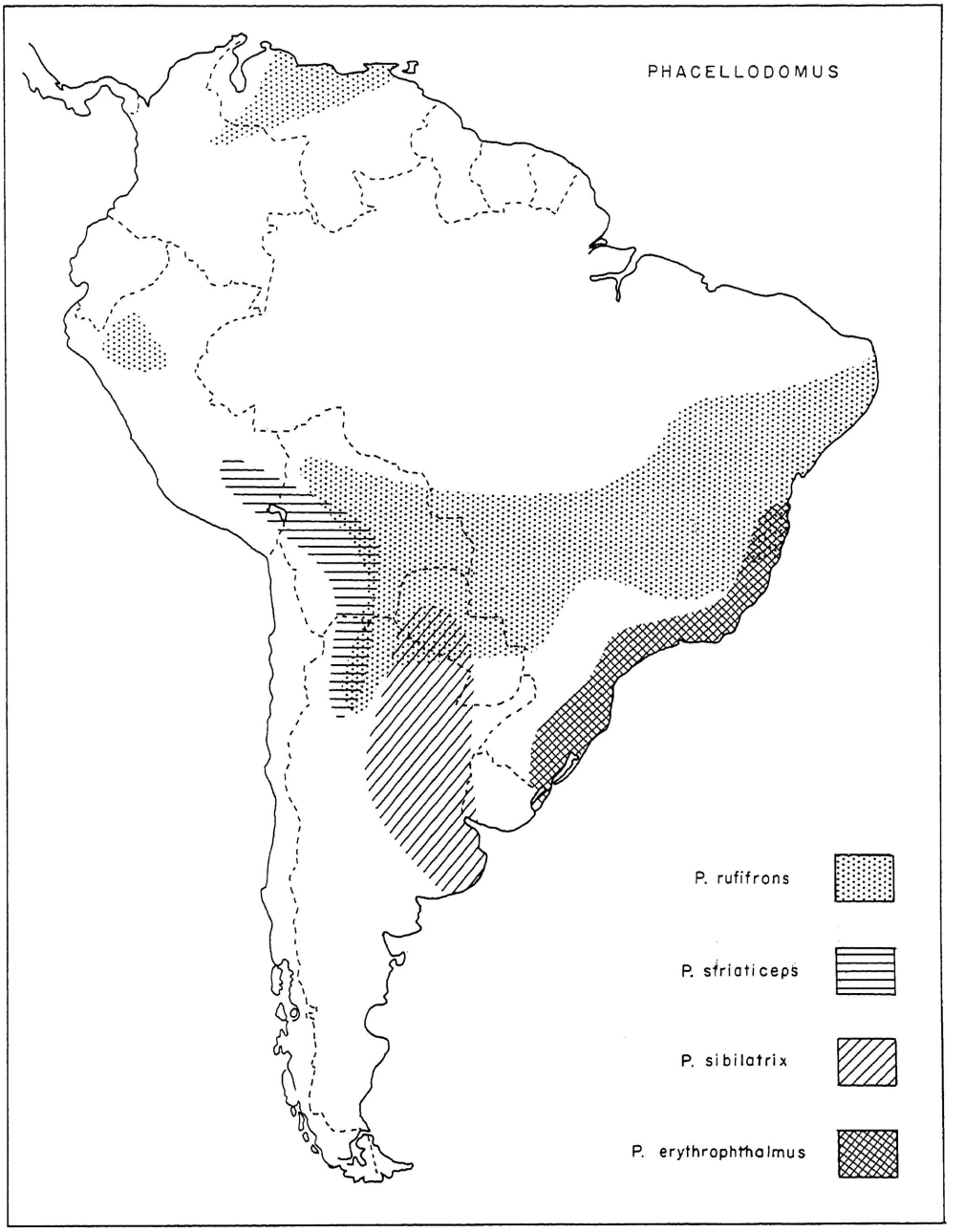
The three other species I have added to the genus *Phacellodomus* are *fusciceps*, *berlepschi*, and *dendrocolaptoides* which are discussed in the phylogeny of the genus. The first two were included in *Thripophaga* before my revision but I believe this was an error. *Phacellodomus dendrocolaptoides* was segregated in a monotypic genus (*Clibanornis* Sclater and Salvin, 1873), which was very widely separated from *Phacellodomus* and placed before my revision (Vaurie, 1971a) in the Furnariinae next to *Furnarius* or *Cinclodes*.

Information on ecology and behavior, including the nest, exists for only six species (*Phacellodomus sibilatrix*, *P. rufifrons*, *P. striaticeps*, *P. striaticollis*, *P. ruber*, and *P. erythrophthalmus*), but is very deficient in the case of *P. striaticeps*.

All these species (with the exception of *Phacellodomus striaticeps*) are birds which, generally speaking, inhabit low open country, generally arid or sparsely wooded, but some species frequent grassland as well, and some (*P. sibilatrix*, *P. striaticollis*, and *P. ruber*) are associated also with water, such as swamps and marshes, or irrigation ditches and canals. Some of them penetrate into mountainous country, but not to high alti-

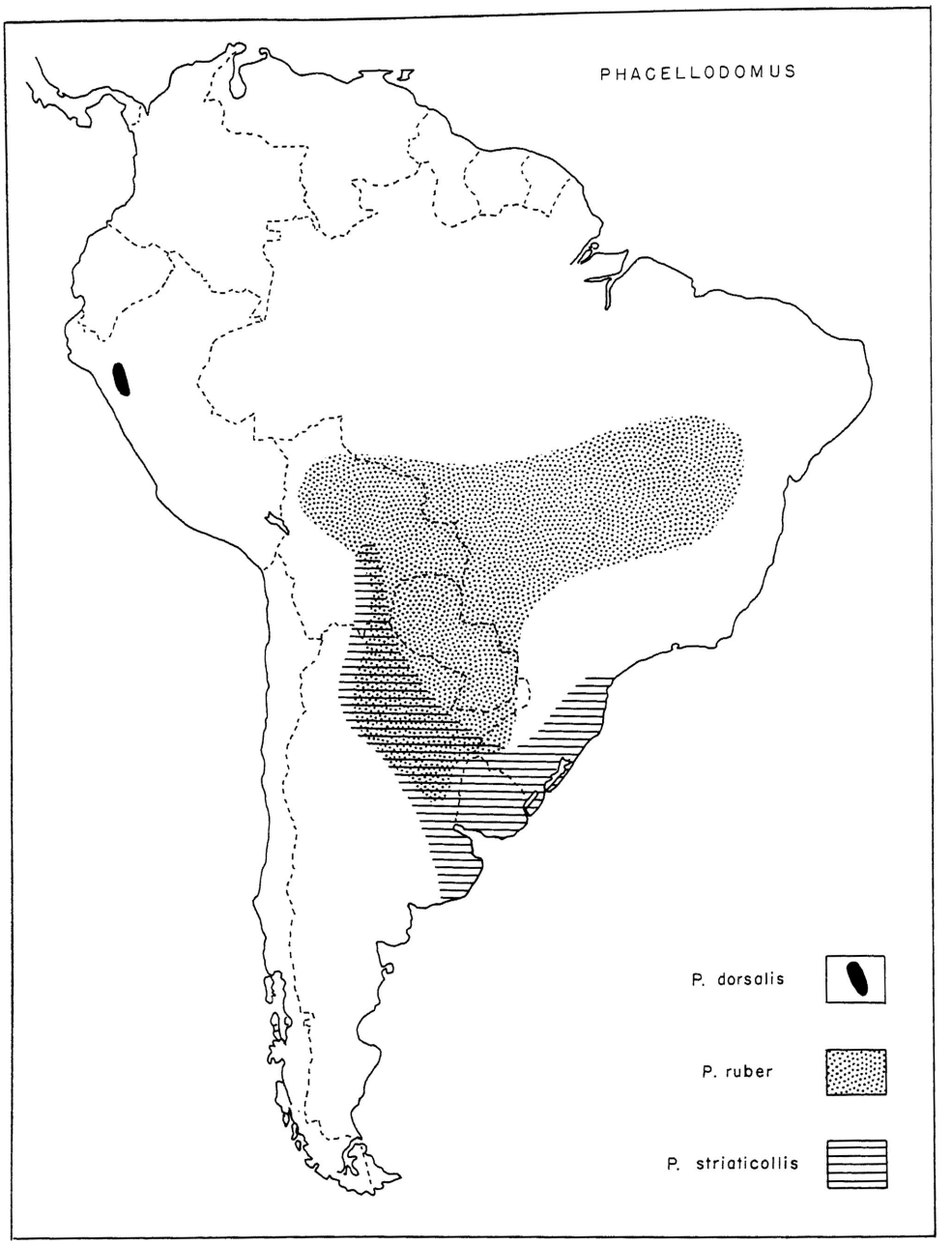
TABLE 14
Measurements (in Millimeters) of *Phacellodomus*

Species	Wing			Tail			Bill		
	N	Mean	Range	N	Mean	Range	N	Mean	Range
sibilatrix									
Males	19	58.57	55–62	18	59.61	56–65	19	14.91	14–16
Females	9	57.44	55–59	9	58.77	56–62	9	14.16	13.5–15
Both sexes	28	58.21	55–62	27	59.33	56–65	28	14.67	13.5–16
rufifrons									
Males	73	67.47	62–72	58	72.60	66–83	68	17.41	15.5–19
Females	72	66.20	62–72	64	71.16	63–81	70	17.42	16–19
Both sexes	150	67.04	62–72	127	72.00	61–83	143	17.42	15.5–19
striaticeps									
Males	41	70.15	66–74	36	70.62	64–76	41	18.86	17–21
Females	28	68.69	63–72	27	69.70	61–75	27	18.31	17–20
Both sexes	77	69.58	63–74	67	70.18	61–76	73	18.69	17–21
striaticollis									
Males	40	65.60	60–73	34	80.29	74–91	37	18.54	17–20
Females	27	64.66	60–69	24	80.33	75–86	27	18.11	16.5–20
Both sexes	68	65.27	60–73	59	80.40	74–86	65	18.36	16.5–20
ruber									
Males	56	77.93	70–83	45	91.31	80–97	47	21.32	20–23
Females	54	76.02	71–82	46	90.63	82–100	50	21.03	19–22.5
Both sexes	112	77.03	70–83	93	91.06	80–100	99	21.16	19–23
erythrophthalmus									
Males	7	64.85	62–68	6	87.50	81–92	7	19.17	18–20
Females	4	64.00	60–70	4	86.00	82–94	4	19.62	18–21.5
Both sexes	15	65.26	60–70	14	87.64	81–95	15	19.38	18–21.5
dorsalis									
Males	5	72.60	71–75	5	93.20	90–97	5	25.90	24–27
Females	2	—	72, 72	2	92.50	92, 93	2	25.50	25, 26
Both sexes	7	72.42	71–75	7	93.00	90–97	7	26.00	24–27
berlepschi									
Males	5	79.60	79–80	5	81.80	78–83	5	18.70	18–19
Females	1	—	75	1	—	81	1	—	17.5
Both sexes	6	78.84	75–80	6	81.66	78–83	6	18.50	17.5–19
fusciceps									
Males	19	75.31	67–88	17	77.00	67–89	19	17.87	17–19
Females	19	74.81	68–85	16	76.75	68–87	19	17.70	16.0–19
Both sexes	42	74.91	67–88	37	77.64	67–90	42	17.76	16.0–19
dendrocolaptoides									
Males	19	94.94	91–100	19	94.84	90–101	18	27.11	25–29
Females	11	92.54	90–95	11	93.81	89–100	11	26.31	25–28
Both sexes	33	93.96	90–100	33	94.81	89–104	32	26.81	25–29



MAP 26. Geographical distribution of four species of *Phacellodomus*.

tudes. *Phacellodomus rufifrons*, which has a very great and discontinuous range (map 26), ascends to about 2000 m. in northwestern Argentina, about 1300 m. in Peru, and over 1000 m. in Bolivia and Venezuela. *Phacellodomus striaticollis* (map 27) ascends probably to roughly the same altitudes as *P. rufifrons*. All these species build the same



MAP 27. Geographical distribution of three species of *Phacellodomus*.

general type of nest, including probably *P. striaticeps*.

This last species (*Phacellodomus striaticeps*) differs from the other five by being typically Andean (map 26), occurring at very high altitudes which seem to exceed 5000 m. in Bolivia. Some individuals have been recorded as low as 1200 m. in Argentina and

1750 m. in Bolivia but during the austral winter, and I suspect that the lowest limit of the breeding range is on the order of 3000 m., or somewhat less.

The only published record of a nest of *Phacellodomus striaticeps* that I have found was supplied by Lönnberg (1903) who described it all too briefly as "composed of small sticks, and was 150 cm. high and 40 cm. broad"; it contained three white eggs, but no other information is given. This nest was found in December at Moreno on the puna of Jujuy, a region Lönnberg described as being about 3500 m. above sea level, surrounded by mountains which rise to 6100 m. The vegetation is very poor and Lönnberg said: "There are no trees at all, but numbers of xerophilous shrubs, as a rule about a metre high, are scattered over the puna. Between them the naked sand lies bare, almost without any vegetation. In addition to the shrubs, great columnar cactuses are found in numbers in some places. The sandy plain is traversed by rivulets . . . [and] along the edges of the rivulets there is a peculiar vegetation, and Pampa grass (*Gynerium*) also grows there." *Phacellodomus striaticeps* also frequents open slopes with bushes, or other areas of the altiplano with scanty or virtually no arborescent vegetation. Dorst (1957) reported that the late Maria Koepcke wrote him that she had found this species in stands of *Puya Raimondii* near Lampa, altitude 3905 m., northwest of Lake Titicaca. In other words, the nest of *P. striaticeps*, though probably resembling that of the other species in general structure, is probably built in a low shrub, tuft of grass, or perhaps in a puya, but not in trees, as is normal for the other five species.[110]

Phacellodomus rufifrons is well known and a very thorough account of its behavior has been published by Skutch (1969a), who observed this species for a period of over four months during one breeding season in the llanos of Venezuela. The account which follows is condensed from his very lengthy report. Skutch met *P. rufifrons* in pairs or family groups of three to six or eight individuals, foraging on the ground in low, dense thickets and weedy fields, but never wandering far from their nest. He says *P. rufifrons* avoids "heavy forest and even light woodland with a closed canopy . . . [or] second-growth woods with crowded slender saplings," and normally selects an isolated tree for building its nest, or, if such a tree is not available, "one growing with only a few others," and, in such a case, the nest is built on the more exposed side of the tree. The nests observed by Skutch were built at a height which varied anywhere from about 2 to 23 m. above the ground, and the sites selected for construction were at or near the end of a slender branch at the outside of the crown of the tree and often at its bottom. The branch was horizontal or ascending, but more often it drooped, and, with the weight of the accumulating sticks, the nest often dangled vertically. Photographs of the nests were given by Skutch, who remarked that these perpendicular nests tend to give a false impression of their original location.

The nest is constructed wholly of dry interlaced sticks, crooked or not, which are gathered from the ground; some of them are branched. Many sticks were used "one only a few inches long," but sticks over 30 cm. were frequent, and one measured "21 inches," or about 53 cm., a startlingly great size for such a small bird to "handle" successfully. The thicker sticks were of about the thickness of a lead pencil, and the majority were not thorny, although *Phacellodomus rufifrons* and its congeners seem to greatly prefer thorny sticks or twigs when available.

The construction starts with the erection of a small platform, then the sides of the platform are built up, and "finally the hollow is roofed over, becoming a nearly spherical chamber," the bird continuing to "build a second, similar, chamber above the first." These two-chambered nests measured about 38–41 cm. in height and from 23 to 25 cm. in diameter, "not counting the ends of sticks which on all sides project far beyond the main mass, giving the nests a bristly, unkempt aspect." The two chambers do not communicate, according to Skutch, as "each compartment has its own opening to the outside . . . and are separated by partitions

formed of interlaced sticks." The chambers measured about 11.5 to 12.5 cm. in diameter in the nests examined by Skutch, and were both lined with soft material, such as fibers of bark or sheaths of leaves, and, near human habitations, also with a great variety of material, such as bits of paper or of plastic wrappers, tinfoil, feathers, and so on. The entrances to the chambers varied, consisting of passageways, which, in the case "of the lowest chamber, in which the brood is usually raised," may be 12.5 or 15 cm. long, by about 5 cm. in diameter, and bend in one direction or another. This passageway is "sometimes . . . shaped like the spout of a teakettle, and it may dilate inward so as to form a sort of vestibule or antechamber in front of the main chamber," an "antechamber" which has been mentioned in other species of this genus.

Some members of the Furnariidae are very strongly attached to their nests and are inveterate builders. The propensity to build superfluously seems greatly exaggerated in *Phacellodomus rufifrons* and Skutch (1969a) stated that "additional compartments are from time to time added" to the two-chambered nest. These additional compartments are constructed on top of the nest, and "nests three or four feet high, with four or five chambers are not uncommon." Skutch speculated on the significance "of the multichambered nest," and came to the conclusion that it provides dormitories, or, I may say, shelters, but is occupied by only "one breeding pair, sometimes with full-grown, nonbreeding offspring." The complexity of the nest provides also some degree of protection against predators, but its main function is to provide lodging.

Skutch stated also that "The sedentary thornbirds [*Phacellodomus rufifrons*] cling stubbornly to their chosen homesite. As long as they can, they add new chambers to their old nest rather than start a new nest"—a statement which is ambiguous if interpreted as evidence that the same nest is used by the same pair for two or more consecutive breeding seasons. His observations did not extend beyond a single breeding season, and, to the best of my belief, it has not been established with certainty that any member of this family uses the same nest the following year. Barrows, quoted in Sclater and Hudson (1888), said, in the case of *Phacellodomus sibilatrix* that the nest "may sometimes serve the same pair for two successive summers," but this requires verification. The nest may be added to, modified, rebuilt, and so on, and a second brood may be raised during one breeding season. It is also well known that favored locations are not abandoned the following year and that old nests are used as foundations for new ones, or part of their material may be used again in the case of species which build nests of sticks, but only controlled observations for more than one breeding season can settle the controversial question of whether or not the same nest is used integrally again by the same pair the following year.

The nests built by *Phacellodomus sibilatrix, P. striaticollis, P. ruber,* and *P. erythrophthalmus* are similar in general structure and location to the nest of *P. rufifrons,* but some variation exists which is most significant in the case of *P. erythrophthalmus*. Nests with only two chambers have been reported for *P. striaticollis* and *P. erythrophthalmus*; the greatest number reported for *P. sibilatrix* is three. The nest of *P. ruber* is normally composed of only two chambers, but nests with more than two chambers exist, which, however, are not built during the same breeding season if Cherrie (1930) is correct. In his description of the nest of *P. ruber,* he said, "The same site is often used for two, three, or more years in succession, a new compartment being added above the old each season."

The two compartments, or chambers, normally communicate in these four species; they are not completely sealed off by solid partitions as in the case of *Phacellodomus rufifrons,* but nests in which the two chambers did not communicate have been reported in *P. sibilatrix* and *P. striaticollis*. A drawing of a nest of *P. sibilatrix* sent to me by Sr. Samuel Narosky of Argentina illustrates the structure of the nest. There are

only two chambers and the second chamber, which had been constructed above the incubating chamber is very small, relatively speaking, only about one-third the size of the incubating chamber and is separated from it by a thick unbroken partition. This smaller chamber, which Narosky believed to be a dormitory, is apparently entered directly from the outside without any passageway, but the incubating chamber is entered by a long tunnel, curving upward. This nest is bigger at the base, the part which contains the tunnel projects outward laterally, and the entire nest resembles roughly a "retort," or "boot," in general appearance, but seems to have been constructed in the orthodox manner from a foundation resting on a branch.

The nest of *Phacellodomus erythrophthalmus* was described by von Ihering (1900) and illustrated by drawings. It resembles the nest of *P. sibilatrix,* as described above, in general outward appearance only but not in other respects. This nest is "shaped like a boot, suspended from the tip of a branch," as stated and shown by von Ihering. It has only a single entrance, at the "toe of the boot," which leads directly without a passageway, into a lower chamber in the projecting part of the boot, a small hole in the roof of this lower chamber leading up into a larger chamber where the eggs were incubated. This hole was 3 cm. in diameter, the entrance to the nest was twice as wide, and the entire nest measured 30 cm. at the base, and 40 cm. high diagonally. Von Ihering mentioned three other similar nests, and the significant differences between the nest of *P. erythrophthalmus* and that of the other species are that its nest is apparently built from the top down, suspended, not built up from a platform or foundation resting on a branch, and has only a single entrance. Von Ihering called the owners of these nests *Thripophaga sclateri* Berlepsch, but this name is a synonym of a form of *Phacellodomus erythrophthalmus.* Interlaced dry twigs were used for construction. Von Ihering did not mention whether or not they were thorny, but thorny twigs or sticks are greatly preferred by the other species, when available.

The structure, size, and location of the nests vary in all the species. Some are roughly globular, ovoid, cylindrical, or shaped like a "boot," and are relatively small or very large. Not all assume a dangling position, however, because they are built on fairly strong branches and remain more or less horizontal, or because they are built within the fork of a tree, rather than at or near the end of a slender branch at the periphery of the lower part of the crown of the tree. In the case of *Phacellodomus ruber* the nest may be built within a bush rather than in a tree. Trees of any kind are probably rarely available to *P. striaticeps*. The nesting site is also often near water, especially in the case of *P. sibilatrix* and *P. striaticollis*. The nest of the former was found by Venturi (in Hartert and Venturi, 1909) only in woods at the edge of large swamps through which a stream flows. Gibson (1885) and Hussey (1916) said that *P. striaticollis* is common along streams, or irrigation canals and ditches, building its nest directly above water in the fork, or at the end of a branch of a small tree, or in hedge rows. Wetmore (1926) did not observe *P. ruber* during the breeding season, but this sedentary species is also, or can be, closely associated with water as he found *P. ruber* "in swamps grown with saw grass, and in the cat-tails and other vegetation that bordered lagoons, particularly in the areas known as *palmares,* where low palms grew in scattered groves over marshy ground.'

No information seems to exist on the ecology, behavior, and nest of *P. dorsalis, P. berlepschi, P. fusciceps,* and *P. dendrocolaptoides,* other than a brief statement (Sztolcman, 1926) on the habitat and behavior of *P. dendrocolaptoides,* which is significant. *Phacellodomus dorsalis* and *P. berlepschi* are little known species that appear to have very restricted ranges in northwestern Peru, where they have been collected in mountainous regions, but not at very high altitudes, varying from about 2050 to 2800 m. in the case of *P. dorsalis* (map 27), and from about 3050 to 3200 m. in the case of *P. berlepschi* (map 28). It is possible that their ecology and behavior differ from that of the

other species, and this may be true also for *P. fusciceps* which seems to follow the valleys of the Amazon and of some of its larger affluents (map 28). *Phacellodomus dendrocolaptoides* is restricted chiefly to hilly southeastern Brazil (map 28), probably not in areas that are heavily forested, as the only information I have found on this species is a statement of Sztolcman (1926), quoting the field notes of Chrostowski who found *P. dendrocolaptoides* in thickets of bamboos, descending occasionally to the ground, "*Se tient dans les broussailles de la taquara, descendant quelquefois par terre.*"

Morphological Variation

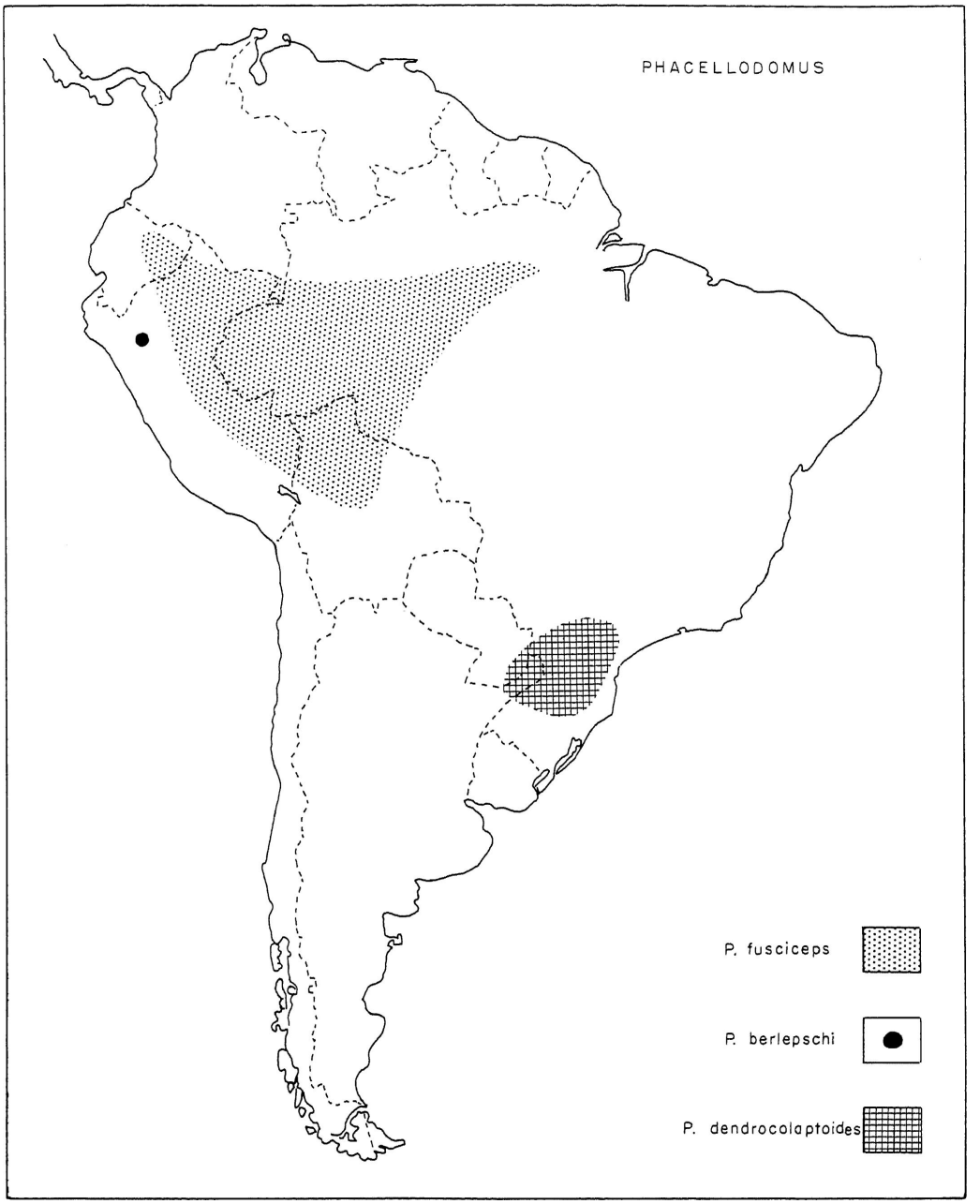
The variation in size is pronounced, as *Phacellodomus sibilatrix* is small and *P. dendrocolaptoides* is large (table 14), but, with this exception, morphological variation is relatively slight. All the species tend to resemble one another although they vary in the coloration of the upperparts, in the pattern and coloration of the underparts, and in the coloration and structure of the feathers of the crown.

The mean wing length varies, in round numbers, from 58 mm. in *Phacellodomus sibilatrix* to 94 mm. in *P. dendrocolaptoides,* but the range is narrow in the other eight species, from 65 mm. to 79 mm., with an average of 72 mm. The tail is equal to or longer than the wing, with a tail/wing ratio varying from 1.00 to 1.34, with an average of 1.12. The feet and also the bill are moderately strong. The bill is attenuated, nearly straight or slightly decurved, and is compressed laterally to a varying degree in nearly all the species.

Differences in coloration have been mentioned above but the interspecific variation is quite limited. All the species are brown above with only a slight variation in shade, or they are rufous on the back; the majority are dull white on the underparts; half of them are chestnut or strongly rufous to a varying degree on the crown. The species with a rufous back are *Phacellodomus dorsalis* and *P. berlepschi,* in which it is chestnut; and *P. fusciceps,* in which it is more rufescent amber brown than chestnut. The species that are whitish below are mottled or not across the breast, the mottling being cinnamon or pale dull rufous brown, and in *P. dendrocolaptoides* the flanks are darker than in the other species, and the feathers at the side of its whitish throat are tipped with dark brown. The underparts are rufous or very strongly ferruginous in *P. erythrophthalmus* and *P. berlepschi,* and are buffy olive in *P. fusciceps*. A rufous or cinnamomeous area exists in the internal part of the wing of all species, and the upper surface of the wing is rufous also to some degree, although the rufous area is greatly reduced in some species, only to the outer webs of the inner primaries and some secondaries, or only to the upper rows of the lesser coverts in *P. erythrophthalmus*.

The most interesting character is the structure and coloration of the feathers of the crown which is diagnostic generically for most species. The feathers of the crown, or only of its anterior portion, are slightly stiffened, somewhat elongated, more or less lanceolate in shape, and chestnut on the anterior part of the crown, or over the entire crown, with or without narrow grayish tips. These characters vary specifically; these feathers are not well developed in *Phacellodomus sibilatrix* and are only very faintly rufous on the forehead at the base of the bill; the grayish tips are best developed in *P. striaticeps* and *P. striaticollis,* but only very faintly suggested in *P. ruber,* and do not exist in *P. erythrophthalmus* and *P. dendrocolaptoides*. The feathers are most blunt in *P. dendrocolaptoides* and are only slightly stiffened on its forehead; they are sharply lanceolated and well stiffened in *P. dorsalis,* but they are brown or ochraceous, not rufous. This character is not shown by *P. berlepschi* and *P. fusciceps,* although the feathers are somewhat elongated in both species, and are slightly stiffened on the forehead of *P. fusciceps* at the base of the bill and have a distinct ferruginous cast, but, with the exception of this slight exception, the remainder of the crown is buffy olive in *P. fusciceps,* buffy olive, or ochraceous brown in *P. berlepschi*.

The tail is partly or wholly rufous in all the



MAP 28. Geographical distribution of three species of *Phacellodomus*.

species with the sole exception of *Phacellodomus rufifrons* in which it is brown, and differs very little in structure. It is composed of 12 rectrices, and, as stated above, is equal to or longer than the wing. It can be characterized also as being well graduated, with rectrices that are usually broad (sometimes exceptionally so, as in *P. erythrophthal-*

mus), blunt or rounded at the tip, and only slightly stiffened; the rectrices are also always firmly integrated. However, some degree of specific variation exists in nearly all details, such as the relative width of the webs, stiffness, degree of graduation, or shape of the tips which are, or can be, slightly acuminate in *P. erythrophthalmus* and *P. berlepschi*.

PHYLOGENY

It is difficult for me to determine the degree of interspecific relationship, but, judging by morphological variation, *Phacellodomus sibilatrix, P. rufifrons,* and *P. striaticeps* seem to be closely related to one another, also *P. striaticollis* and *P. ruber*. These five species may form a single group and I believe now that I was wrong to interrupt their systematic sequence in my revision (1971a) by placing *P. erythrophthalmus* between the first three species and *P. striaticollis* and *P. ruber*; also to separate the last two by inserting *P. dorsalis* between them. It seems best also to start the sequence with *P. sibilatrix,* rather than *P. rufifrons,* as the small *P. sibilatrix* is, perhaps, the most "primitive" species.

It is difficult to place *Phacellodomus erythrophthalmus* and *P. dorsalis* in a list; both now appear to me to be somewhat "aberrant" species, and the decision is subjective, depending on whether one accords more importance to the pattern of the breast, or to the coloration of the crown. As the coloration of the crown seems to be the most constant character, I decided to list *P. erythrophthalmus* (which has a rufous crown) ahead of *P. dorsalis,* which does not have a rufous crown. However, the breast of *P. dorsalis* is mottled (a character which it shares with *P. striaticollis* and *P. ruber*), so it is very probable that *P. dorsalis* is not too distantly related to the other two species. But the back of *P. dorsalis* is not brown as in all the other species mentioned so far; it is chestnut as in *P. berlepschi*; and *P. erythrophthalmus* (with a brown back) is strongly rufous on the underparts as in *P. berlepschi*. It seems more logical, therefore, to list *P. berlepschi* next, rather than *P. fusciceps* in which the underparts differ from the coloration of all the other species of the genus by being buffy olive, not rufous or whitish. But the structure of the feathers of the crown and their coloration (see discussion of morphological variation above) suggest that *P. berlepschi* and *P. fusciceps* are probably related to each other.

Phacellodomus berlepschi and *P. fusciceps* were included in *Thripophaga* before my revision (Vaurie, 1971a), but as I am quite certain they should be included in *Phacellodomus,* rather than *Thripophaga,* a short discussion of the concepts of *Thripophaga* and *Phacellodomus* held by Sclater (1890) seems in order, as these concepts were largely followed before my revision.

Sclater believed *Thripophaga* and *Phacellodomus* were related. I agree that they are, but the distinguishing characters mentioned by Sclater are not of generic importance in my opinion, and I do not agree about all the species he allocated to *Thripophaga*. *Phacellodomus* is characterized by Sclater as having a "short, strong, and slightly incurved bill, short wings, and long graduated tails," whereas *Thripophaga* differs from *Phacellodomus,* according to Sclater, by having "shorter wings and a longer and more graduated tail." But all these characters are very relative, they are only a question of degree, and are clearly not of generic importance in my opinion. The bill is identical in some species and the overlap in the measurements of the wing is virtually complete. The degree in the graduation of the tail is relative, and, in fact, the tail is more strongly graduated in *Phacellodomus* than in *Thripophaga*.

As far as wing measurements are concerned, the mean wing length varies, in round numbers, from 59 to 80 mm., averaging 67 mm., in *Thripophaga,* and from 58 to 79 mm., averaging 70 mm., in *Phacellodomus* (when the very big *P. dendrocolaptoides,* with a wing length of 94 mm., is excluded; the average in *Phacellodomus* rises to 72 mm. when *P. dendrocolaptoides* is in-

cluded). The variation in the ratio of tail length to wing length is pronounced, but not the average, which is 1.15 in *Thripophaga*, 1.12 in *Phacellodomus*.

Five forms were allocated to *Thripophaga* by Sclater (1890), including *striolata* Lichtenstein, 1823, which is a synonym of *macroura* Wied, 1821. Of course, no question exists about *macroura* as it is the type of the genus *Thripophaga* Cabanis, 1847, but, as I have shown in my general discussion of *Thripophaga*, the very well-developed rufous gular patch of *macroura* (fig. 5) shows conclusively that *macroura* is congeneric with the species formerly allocated to *Asthenes*, in which *macroura* is perhaps related to the *flammulata* species-group, as suggested by its peculiar streaked pattern. But as *Asthenes* Reichenbach, 1853, is younger than *Thripophaga*, the latter replaces *Asthenes* as the correct generic name.

The other four forms allocated to *Thripophaga* by Sclater were: *guttuligera* Sclater, 1864; *erythrophthalmus* Wied, 1821; *sclateri* Berlepsch, 1883; and *fusciceps* Sclater, 1889. I believe that everyone would now agree that *erythrophthalmus* is a *Phacellodomus* (see above), which also eliminates *sclateri* Berlepsch, as the latter is only a synonym of a form of *P. erythrophthalmus*. The taxon *fusciceps* does not in the least resemble *Thripophaga macroura* morphologically and is undoubtedly best allocated to the genus *Phacellodomus* in my opinion. The last of these four forms to be considered (*guttuligera*) is now generally acknowledged to be completely unrelated to either *Thripophaga* or *Phacellodomus* and has been placed by me in the separate subfamily Philydorinae.

The most interesting species to me is *dendrocolaptoides* which I believe is no more than a large and coarse *Phacellodomus*. We unfortunately know very little about its habitat and behavior, other than it inhabits stands of bamboos and their thickets, descending occasionally to the ground. *Phacellodomus dendrocolaptoides* was relegated before my revision to a monotypic genus (*Clibanornis* Sclater and Salvin, 1873) of the subfamily Furnariinae, where it was placed next to *Cinclodes* or *Furnarius*. However, *P. dendrocolaptoides* seems to have nothing in common with *Cinclodes* or *Furnarius* morphologically or, apparently, in general behavior, as *Cinclodes* and *Furnarius* are terrestrial, or very essentially so, whereas *P. dendrocolaptoides* does not appear to be so, as it is said to descend to the ground only occasionally. The rufous crown of *P. dendrocolaptoides* (the feathers of which are elongated and show a tendency to be slightly stiffened on the forehead), the general coloration and appearance, the structure of the tail, in fact all of its characters, have suggested to me that *P. dendrocolaptoides* is best allocated to *Phacellodomus*. Sclater had placed *P. dendrocolaptoides* near *Cinclodes* in his list and has been followed in this allocation by others; but to do justice to Sclater, one must quote that he had said "I am quite doubtful about its true relations"—a reservation which did not receive enough attention.

It may turn out that the nest of *Phacellodomus dendrocolaptoides* and also that of the other species (*P. dorsalis, P. berlepschi,* and *P. fusciceps*) for which we lack any information on ecology and behavior, differs importantly from the chambered nests of *Phacellodomus* described above. However, ecology and behavior are not always consistent in the Furnariidae as shown so convincingly by *Certhiaxis* where variation exists i ecology and behavior, including the struc ture and location of the nest, but not in morphology, which remains relatively very constant. Additional evidence is supplied by *Thripophaga* where the behavior of *T. wyatti* and *T. hudsoni* is quite different from that of the other species, especially their nests.[111]

I have stated above that additional study has shown the need to modify to a large degree the systematic sequence I had proposed in my first revision (1971a). The new sequence I propose for the species of *Phacellodomus* is as follows: *P. sibilatrix, P. rufifrons, P. striaticeps, P. striaticollis, P. ruber, P. erythrophthalmus, P. dorsalis, P. berlepschi, P. fusciceps,* and *P. dendrocolaptoides*.

Geographical Variation

Geographical variation exists, or has been mentioned, in five species: *Phacellodomus rufifrons, P. striaticeps, P. striaticollis, P. erythrophthalmus,* and *P. fusciceps*. The variation is most interesting in *P. fusciceps,* where it is well marked. Birds from Bolivia, which represent the nominate form *fusciceps,* are large and pale; those from the lower Rio Madeira and the middle and lower Amazon in Brazil (which have been named *obidensis*) average smaller and are very considerably darker throughout, more rufous and ochraceous than the birds of Bolivia; whereas birds from eastern Ecuador and Peru average smaller than the other two populations and are not constant in coloration, some individuals being nearly as pale as the birds of Bolivia, whereas others are nearly as dark as the birds of Brazil; in addition, specimens from Ecuador and Peru are usually distinctly more grayish on the upper and lower parts than birds from Bolivia and Brazil which are constant in coloration. The birds from Ecuador and Peru have been named *dimorpha,* and, at first glance, the contrast between a small and gray specimen of *dimorpha* from southern Peru, and a large and pale one of nominate *fusciceps* from neighboring Bolivia, is so well marked that one is led to believe that they are not conspecific. The wing length of adults I have measured is 67–78 mm. (mean 72.50) in seven of *dimorpha,* 69–80 mm. (mean 74.0) in 30 of *obidensis,* and 72–88 mm. (mean 79.60) in nine of nominate *fusciceps*.

Phacellodomus rufifrons is very widely distributed and its range is broadly interrupted (map 26). *Phacellodomus rufifrons* varies geographically and the two most distinct populations are those of Colombia and Venezuela, and of Pernambuco in northeastern Brazil. The birds of Venezuela and Boyacá in Colombia (subspecies *inornatus*) differ from all the other populations of the species in lacking the chestnut area on the forecrown entirely or virtually, a suggestion of rufous pigmentation existing in some individuals. In Pernambuco, the population (subspecies *specularis*) has a conspicuous and bright rufous area on the outer webs of the remiges which does not exist in the other populations of Brazil, of Paraguay, of Argentina, and of Bolivia, or in those of Peru. Some of these populations are more or less slightly and vaguely differentiated, being relatively more grayish, or brownish on the back and tail, or darker fulvous on the lower flanks and under tail coverts in Peru.

In the case of *Phacellodomus striaticollis* (map 27), the populations of northwestern Argentina (Jujuy, Salta, and Tucumán) and of Bolivia, which have been named *maculipectus,* differ from the other populations of the species by being mottled with rufous pigmentation on the cheeks and malar stripe, and by being darker rufous on the subapical portion of the feathers of the lower throat and breast. In these other populations, the cheeks are grayish, not mottled with rufous, and the malar stripe is buffy, not rufous.

In *Phacellodomus striaticeps* (map 26), the population of Peru has been separated nomenclaturally from those of Bolivia and Argentina, but the difference is usually slight and far from constant. When best indicated, birds from Peru are darker fulvous on the flanks and under tail coverts, and have a faint grayish vinaceous tinge on the lower throat and breast, whereas this area is normally more whitish in the populations of Bolivia and Argentina.

The populations of *Phacellodomus erythrophthalmus* have been divided into two "subspecies," but the specimens I have seen are not constant in coloration and suggest that the existence of geographical variation requires confirmation.

KEY TO THE SPECIES OF *PHACELLODOMUS*

1. Feathers at the sides of the white throat, and to some extent also at the base of the throat, or elsewhere on the throat, conspicuously tipped with dark brown .... *dendrocolaptoides*
   Feathers of the throat not tipped with brown anywhere 2
2. Breast very strongly rufous (reddish chestnut or rufous orange), uniform or virtually so ..

..... 3

Breast not rufous (whitish, buffy olive or dark ochraceous, uniform or not, mottled or not with rufous cinnamon or brownish, with very narrow faint whitish shaft streaks).. 4

3. Back reddish chestnut, crown buffy olive or pale ochraceous brown ..... *berlepschi*

Back olive brown, crown bright reddish chestnut ..... *erythrophthalmus*

4. Breast buffy olive or dark ochraceous, with or without very faint yellowish streaks .... *fusciceps*

Breast whitish, uniform, or with pale brown or cinnamomeous mottling..... 5

5. Hind neck and upper border of the mantle olive brown, contrasting strongly with the coloration of the remainder of the mantle which is strongly bright rufous ..... *dorsalis*

No contrast between the color of the hind neck and the whole of the mantle 6

6. Wing very conspicuously rufous, extensively so, internally, as well as almost completely so externally (all coverts, outer webs of primaries, and all or most of the secondaries) ..... *ruber*

Rufous area of the wing restricted (conspicuously rufous only on the lesser upper wing coverts), or with all the upper coverts brown, not rufous 7

7. Lesser upper wing coverts reddish chestnut (normally contrasting strongly with the middle and greater coverts which are brown) 8

All upper wing coverts uniform and brown, or brownish, but not rufous 9

8. Three outer pairs of rectrices strongly and uniformly rufous, without brown tips; distinctly smaller (wing length averaging about 58 mm., and tail length about 59 mm.) .... *sibilatrix*

Second and third outer pair of rectrices heavily or well tipped with dark brown; distinctly bigger (the lengths of the wing and tail average about 11 mm. longer) ... *striaticeps*

9. Breast whitish and uniform..... *rufifrons*

Breast mottled with rufous cinnamon, and finely but distinctly streaked .. *striaticollis*

List of the Species

Phacellodomus sibilatrix

Description: Uniformly dull olive brown on the back, becoming somewhat more rufous, less olive, on the rump and upper tail coverts; crown somewhat purer and darker brown than the back, with the feathers somewhat elongated on the anterior portion, slightly stiffened on the forehead and faintly rufous or ferruginous. Lores whitish and possessing a very ill-defined grayish or dingy white superciliary streak. Underparts dingy white, with the exception of the lower flanks and under tail coverts which are ochraceous tawny. The inner web of the inner primaries and of the secondaries is margined narrowly with dull cinnamon; the base and middle portion of the outer web of the inner primaries and of the secondaries is dull chestnut, forming a very poorly defined rufous area on the surface of the wing, but the lesser upper wing coverts are reddish chestnut, and contrast strongly with the middle and greater upper wing coverts which are brown. Tail moderately well graduated, slightly stiffened, and composed of relatively narrow rectrices that are firmly integrated, the four outer pairs of rectrices being reddish chestnut.

Immature Plumage: Very similar to that of the adult, but darker above and underparts more grayish.

Range: Central and southern Paraguay, south to Argentina, to Buenos Aires, west to Santiago del Estero and Córdoba, east to southwestern Uruguay, but apparently not to northeastern Corrientes and Misiones.

Specimens Examined: 29, including th type of *sibilatrix* in BM.

Phacellodomus rufifrons

Description: Uniformly pale dull oliv brown on the upperparts, with the exceptio of the anterior part of the crown, the feathers of which are reddish chestnut, and are elongated, lanceolate in shape, and slightly stiffened. Lores, post-ocular streak, and underparts dull creamy white, more whitish on throat and center of abdomen, with a very faint grayish tinge at the sides of the breast, and becoming strongly ochraceous or fulvous on the lower flanks and under tail coverts. The inner web of the inner primaries and of the secondaries is margined rather narrowly with rufous cinnamon; and the base and middle portion of the outer web of the

inner primaries and of the secondaries is more or less dull or brighter chestnut, rather than brown. Tail uniformly brown, not rufous, of the same color as the back except for the three outer pairs of rectrices which are slightly paler; composed of rectrices that are well graduated, broad, slightly stiffened, and firmly integrated.

IMMATURE PLUMAGE: The juvenal plumage differs from that of the adult by being distinctly mottled on the upperparts and faintly so on the underparts, not uniform as in the adult, and by lacking the rufous pigmentation on the front of the head, the feathers of which are not stiffened and are only slightly elongated.

This species varies geographically (see discussion) and the description of the adult plumage given above is based on specimens from eastern Brazil, other than from Pernambuco.

RANGE: Broadly discontinuous, consisting of three groups of populations; one group in northern Venezuela and the llanos, from Guárico, west to the region of Boyacá in Colombia situated east of the Andes; the other group in northern Peru in the Departments of Amazonas, Cajamarca, San Martín, and western Loreto; the third group in eastern and central Brazil, west to eastern Bolivia, Paraguay, and northwestern Argentina south to Catamarca. In Brazil, the northern limits of the range seem to extend to Pernambuco, southern Piauhí, and the central parts of Goiás and of the Mato Grosso, and south, through Bahia, to Minas Gerais, and, from the Mato Grosso, to northwestern Paraná.

SPECIMENS EXAMINED: 215, including the type of *rufifrons* in AMNH.

Phacellodomus striaticeps

DESCRIPTION: Uniformly rufous brown on the upperparts, but brighter, more rufous cinnamon on the rump, becoming chestnut on the upper tail coverts; slightly darker and purer brown on the crown, the feathers of which are elongated, lanceolate in shape, and slightly stiffened on the anterior portion and top of the crown, and are rufous at the base and edge of the forehead, but become almost entirely grayish posteriorly. Lores dark brown, and with a poorly defined superciliary streak, dull white or grayish anteriorly, but becoming cinnamomeous behind the eye. Underparts creamy white, very faintly tinged with pale gray at the sides of the breast, and tawny ochraceous on the lower flanks and under tail coverts. Color pattern of the wing similar to that of *P. sibilatrix* (with the lesser upper wing coverts reddish chestnut), but with brighter, more rufous cinnamon edges along the inner web of the inner primaries and of the secondaries.

Tail well graduated, composed of rectrices that are well graduated, broad, slightly stiffened, firmly integrated and dark brown on the central rectrices with a vague and restricted reddish chestnut area at the base of the next pair, the rufous area becoming progressively more extensive on the other pairs of rectrices, but large brown tips persisting, with the exception of the outer pair which is wholly rufous, or only very faintly tipped with brown.

IMMATURE PLUMAGE: No specimen in true immature plumage was seen by me, but in one individual that does not appear to have been a fully adult bird, the stiffened, elongated, and lanceolated feathers of the forecrown are not well developed and the underparts are more cloudy.

RANGE: Andes, between about 3000 m. or somewhat less, up to over 5000 m., from Cuzco in Peru, south through western Bolivia to Catamarca in northwestern Argentina. This species, or some individuals, move altitudinally, and, during the austral winter, have been recorded as low as 1200 m. in Argentina.

SPECIMENS EXAMINED: 82, including the types of *striaticeps* in MNHN, and of "*griseipectus*" in AMNH.

NOTE: *Phacellodomus striaticeps, P. sibilatrix,* and *P. rufifrons* seem to be closely interrelated, and are similar in general appearance. However, *P. sibilatrix* is distinctly smaller (table 14), and *P. sibilatrix* and *P. striaticeps* both differ from *P. rufifrons* in having reddish chestnut lesser upper wing co-

verts (as against olive brown in *P. rufifrons*), and having a very extensive rufous area in the tail—the rufous rectrices of which are well tipped with dark brown in *P. striaticeps* (with the exception of the outermost pair), but not in *P. sibilatrix* in which the rectrices that are rufous are not tipped with brown. Other distinguishing details between the three species exist, but they are difficult to make clear in a description.

Phacellodomus striaticollis
Figure 6

DESCRIPTION: Uniformly earthy brown, or dull rufous brown, on the upperparts, with the exception of the anterior portion of the crown which is chiefly reddish chestnut, and the feathers of which are slightly elongated and lanceolate in shape, slightly stiffened, and more or less distinctly tipped with gray. Lores dull white or buffy white and with a very poorly defined grayish or buffy superciliary streak. Throat creamy white or very pale buffy white, and breast feathers rufous cinnamon subapically; the shafts of the feathers of the throat and breast are paler and produce a very fine streaked pattern, most distinct on the breast. Remainder of underparts buffy white, with a faint cinnamomeous cast, the rufous cinnamon mottling of the breast extending vaguely to the upper flanks, the lower flanks and under tail coverts being umbraceous. Tail composed of very well graduated and very broad rectrices, slightly stiffened, firmly integrated, and the four outer pairs of which are wholly and strongly rufous.

IMMATURE PLUMAGE: No specimen in true immature plumage was seen by me but in one bird that was probably not fully adult, the general pattern of the plumage is not well defined and the abdomen is considerably darker than in the adult plumage.

This species varies geographically (see discussion) and the description of the adult plumage given above is based on specimens from southeastern Brazil, Uruguay, and from Argentina other than from Jujuy, Salta, and Tucumán.

RANGE: Eastern Bolivia, from Cochabamba and Santa Cruz, south, through Argentina, to Buenos Aires; also southeastern Brazil, from eastern Paraná, south to Uruguay and eastern Argentina. Olrog (1963) adds Misiones to the range, which is quite possible, but no records for Misiones are known to me.

SPECIMENS EXAMINED: 116, including the type of *striaticollis* in MNHN.

Phacellodomus ruber

DESCRIPTION: Uniformly rufous brown on the upperparts, with the exception of the crown which is reddish chestnut, and the feathers of which are elongated, lanceolated, and slightly stiffened, more strongly so on the forehead and anterior portion of the crown. Lores dull white; no superciliary streak, the supraorbital region, cheeks, and sides of the neck being brown and uniform. Underparts creamy white, with a pale vinaceous gray wash across the breast, on which the buffy tips of the shafts and edges of the feathers are evident or not, producing a slightly mottled or "spotted" appearance when evident, which resembles the mottling of *Phacellodomus striaticollis*, but not the finely streaked pattern of *P. striaticollis*, as the shaft streaks are not, or are much less evident than in *P. striaticollis*. Abdomen pale, creamy white as on the throat, but with the lower flanks and under tail coverts fulvous or ochraceous. The wing is almost completely rufous, internally and externally, bright chestnut, of virtually the same color as the crown, or brighter. Tail uniformly and wholly rufous, with very broad, well-graduated rectrices, the outer rectrices being brighter, more chestnut, than the central pair and the tips of the next pair (fifth) which are more dusky, more rufous brown than chestnut.

This species varies individually to a marked degree as stated by Hellmayr (1925). Some individuals are much more rufous on the back and upper tail coverts, the back and coverts being as bright rufous as the wing, whereas others are more olive brown, the

majority being rufous brown on the back and coverts to a varying degree. In some individuals, the underparts are also more whitish, including the breast which lacks the vinaceous wash.

IMMATURE PLUMAGE: Similar to that of the adult, but the rufous "cap" on the forecrown is not well defined and its feathers are not elongated and stiffened; the underparts are also distinctly mottled with brown on the breast and upper flanks.

RANGE: Brazil, from central Bahia and northwestern Minas Gerais, west to eastern Bolivia north to the Beni, south to Paraguay to extreme southwestern Rio Grande do Sul in Brazil, and northern Argentina, south to Tucumán, Entre Rios, and southern Santa Fe. Northern Buenos Aires has been mentioned also, perhaps incorrectly.

SPECIMENS EXAMINED: 132, including the types of "*rufipennis*" in BM, and of "*rubicola*" in AMNH.

Phacellodomus erythrophthalmus
Figure 6

DESCRIPTION: Uniformly olive brown on the upperparts, with the exception of the crown which is reddish chestnut, and the feathers of which are somewhat elongated and slightly stiffened; and becoming more rufous brown on the upper tail coverts. Throat and breast rufous (very strongly ferruginous), becoming progressively paler on the abdomen, more rufous cinnamon or dark ochraceous buff, and umber brown on the lower flanks and under tail coverts. The inner webs of the inner primaries and secondaries are well margined with ochraceous orange, but the upper surface of the wing is olive brown, of the same color as the back, virtually uniform, with only a slight indication of rufous pigmentation which is restricted only to the upper rows of the lesser coverts. The structure of the tail, and its coloration, are similar to the structure and coloration of the tail of *Phacellodomus striaticollis*, with the exception that a rufous area exists also at the base of the fifth (inner) pair of rectrices in *P. erythrophthalmus* and that the tips of the longer rectrices are slightly acuminate, not so blunt, or so well rounded as in *P. striaticollis*.

RANGE: Coastal region of Brazil, from southeastern Bahia to Rio Grande do Sul.

SPECIMENS EXAMINED: 17, including the types of *erythrophthalmus* in AMNH, and of "*sclateri*" in BM.

Phacellodomus dorsalis
Figure 6

DESCRIPTION: Upperparts unstreaked, but not uniform in coloration, as the posterior part of the crown, hind neck, and upper border of the mantle are olive brown and contrast well with the color of the back which is strongly rufous, burnt sienna or bright chestnut. The feathers of the crown are well elongated and well lanceolated in shape, well stiffened on the forehead and anterior portion of the crown, but are chiefly brown, rather than distinctly rufous, with dull ferruginous brown edges, and pale shaft and tips. Lores dark brown, with no superciliary streak, or streak only very vaguely suggested. Underparts dingy white with a pale olive buff cast, mottled with rufous brown across the breast, and also on the upper flanks to a decreasing degree, the lower flanks and under tail coverts becoming chestnut; on the breast, the feathers are rufous brown subapically, the tip of the shaft and border of the feather being pale buff. The wing, internally and externally, is almost completely chestnut, as brightly rufous as, or brighter than the back, with or without faint whitish tips on the middle and greater upper wing coverts. The tail is wholly and uniformly bright chestnut, and its rectrices are relatively but distinctly narrow.

RANGE: Poorly known, restricted apparently to the Marañon watershed in northern Peru, from southern Cajamarca south to northern La Libertad, but probably also in neighboring Amazonas.

SPECIMENS EXAMINED: 7, including the type of *dorsalis* in BM.

Phacellodomus berlepschi

DESCRIPTION: Upperparts, including the tail, very strongly rufous with the exception

of the crown and rump, reddish chestnut on the nape and back, burnt sienna on the tail, somewhat duller and paler on the upper tail coverts. The color of the rump is ferruginous, with a more or less pronounced olive cast, and the crown varies from buffy olive to ochraceous brown, with buffy centers to the feathers which are somewhat elongated, but not lanceolated or stiffened. Lores brown with a poorly defined ferruginous superciliary and post-ocular streak. Ear coverts brown with ferruginous streaks, throat and sides of the neck strongly ferruginous brown, with the breast strongly rufous, of virtually the same reddish chestnut color as on the back, the remainder of the underparts becoming progressively more olive brown below the breast, of somewhat the same color as the crown, but more "rusty." Wing strongly and almost completely rufous externally, chiefly bright reddish chestnut, with a rufous area internally at the edge of the inner webs of the inner primaries and secondaries. The tail is wholly and uniformly burnt sienna, as stated above, well graduated, slightly stiffened, with firmly integrated broad rectrices which are rounded at the tip, with the exception of the central pair, the tips of which are slightly acuminate.

IMMATURE PLUMAGE: Differs distinctly from that of the adult by being more olivaceous and ochraceous, less rufous throughout, with the feathers of the lower throat, breast, and abdomen edged with dark brown which produces a scalloped pattern. On the center of the crown, and on the hind neck, the feathers are orange or dark ochraceous buff at the center; these conspicuous spots are lacking in the adult plumage.

RANGE: Poorly known, but apparently very restricted and known so far only from Leimebamba and its region, southern Amazonas, not far from Chachapoyas, northern Peru.

SPECIMENS EXAMINED: 10, including the type of *berlepschi* in AMNH.

Phacellodomus fusciceps
Figure 6

DESCRIPTION: Rufescent amber brown on the back, with a strongly rufous tail which is wholly and uniformly burnt sienna, and a buffy olive crown, the feathers of which are somewhat elongated and slightly stiffened on the forehead and have a distinct ferruginous cast. Lores brown with a very faint and narrow buffy or grayish superciliary streak. Underparts buffy olive, virtually uniform, or more or less faintly and distinctly streaked with dull cadmium yellow or clay-colored streaks, becoming more ochraceous and fuscous on the lower flanks and under tail coverts. Coloration of the wing and tail similar to the coloration of *Phacellodomus berlepschi*. The tail is very strongly graduated, slightly stiffened and composed of firmly integrated rectrices, with blunt tips, which are relatively narrow.

IMMATURE PLUMAGE: Very similar to that of the adult, but faintly mottled on the throat and upper breast, and general pattern less distinct than in the adult.

RANGE: Amazonian Basin, from eastern Ecuador, eastern Peru, and northeastern Bolivia (south to the mouth of the Rio Chaparé on the border of Cochabamba), eastward in Brazil to the region of Obidos on the Amazon.

This species varies very distinctly geographically (see general discussion) and I recognize three subspecies in the material I have examined which is from the following regions: nominate *fusciceps* from Bolivia, *obidensis* from the lower Rio Madeira and lower Amazon in Brazil, and *dimorpha* from eastern Ecuador, south through eastern Peru to Madre de Dios.

The description of the adult plumage given above is based on topotypical nominate *fusciceps* from Bolivia.

SPECIMENS EXAMINED: 47, including the type of *fusciceps* in BM.

Phacellodomus dendrocolaptoides
Figure 6

DESCRIPTION: Upperparts rufous brown, but more russet on the upper tail coverts, with a strongly rufous tail, and a reddish chestnut crown, the feathers of which are somewhat elongated, but blunt at the tip, not lanceolated, and are very slightly stiffened on the forehead. Lores dark brown, ear co-

verts russet, with a narrow and indistinct superciliary streak which, however, broadens out greatly and conspicuously behind the eye, but is dull, varying from dingy white to grayish buff or dull cinnamon. Throat white, with the feathers at the sides of the throat, and, irregularly, at its base (or elsewhere on the throat) tipped with dark brown or blackish brown; the dark tips being most heavy and abundant at the sides of the lower throat where they are quite conspicuous. Breast and center of abdomen very dingy white, tinged with pale gray or buff, with the sides of the breast invaded by rufous brown, becoming ochraceous brown on the lower flanks and under tail coverts. Inner web of the inner primaries and of the secondaries edged with ochraceous orange, but upper surface of the wing almost completely rufous brown, of about the same color as the back, or brighter. Tail wholly and uniformly rufous, brighter chestnut on the outer rectrices, becoming burnt sienna on the inner rectrices, and dusky, dull chestnut on the central pair; the rectrices are firmly integrated, blunt or rounded at the tip, and are relatively narrower than in the other species of the genus, and also somewhat better stiffened.

IMMATURE PLUMAGE: Similar to that of the adult, but lacking the dark brown tips on the feathers at the sides of the throat; throat less pure white, more buffy, and with faint buffy mottling on the margin of the upper breast; abdomen more grayish on the center; and general pattern not so well defined.

RANGE: Southeastern Brazil, from southern São Paulo, south to northern Rio Grande do Sul, Misiones in Argentina, and neighboring southeastern Paraguay.

SPECIMENS EXAMINED: 33.

GENERA *SPARTONOICA, PHLEOCRYPTES,* AND *LIMNORNIS*

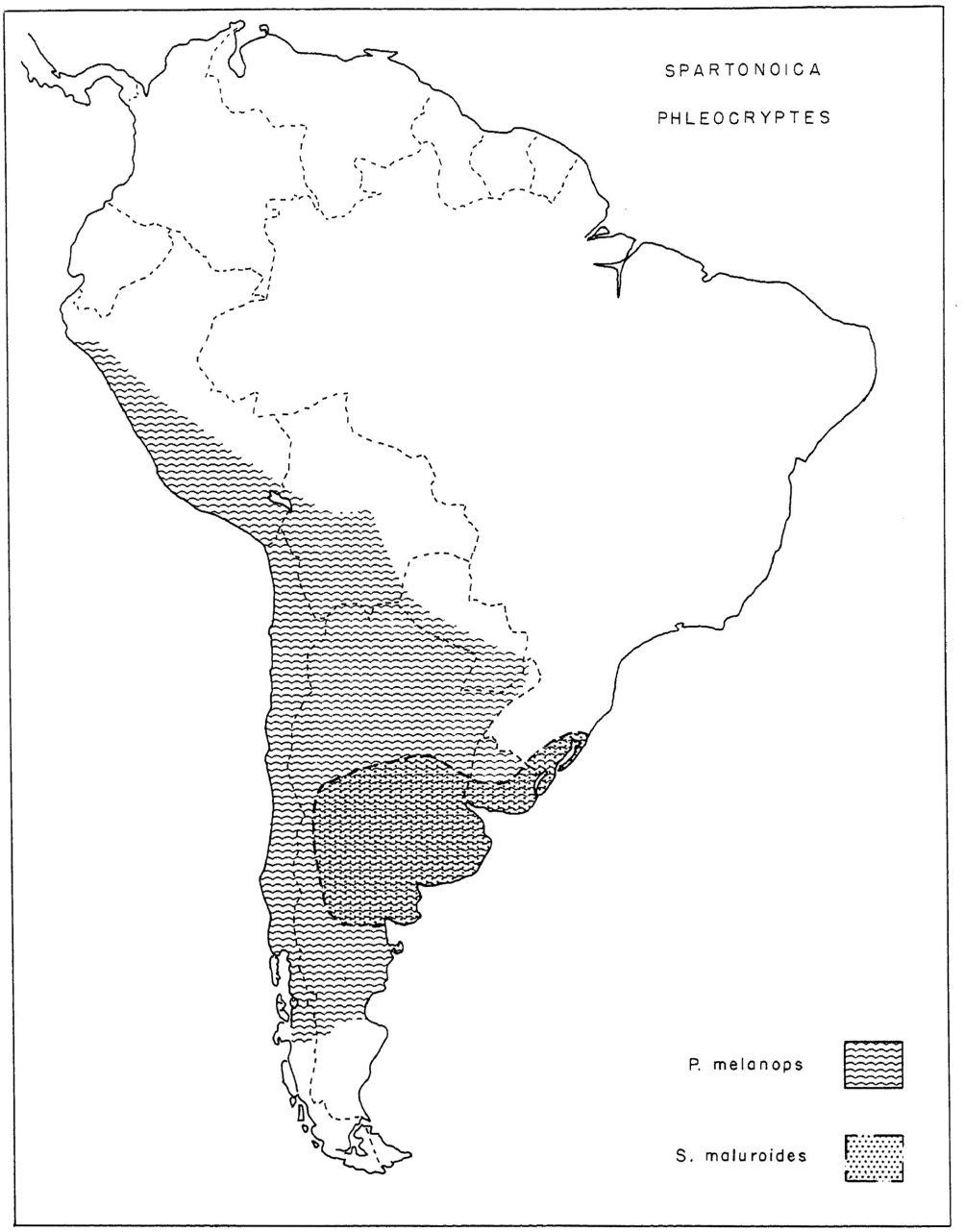
These three genera are conveniently grouped together although they are not closely related to one another. But their general ecology is similar, as the four species involved are all very narrowly associated with water or very moist areas, frequenting beds of reeds or of rushes, or also (as in the case of *Limnornis rectirostris*) bunches of spiny grass growing around swamps, lakes, or along streams.

GENUS *SPARTONOICA*

This genus is monotypic and very closely related to *Synallaxis* in my opinion. But, as it is often impossible to express relationship satisfactorily in a linear sequence, it seems best to list *Spartonoica* apart from *Synallaxis,* rather than to interrupt a satisfactory linear sequence from *Synallaxis* to *Phacellodomus,* through *Certhiaxis* and *Thripophaga.*[112]

Spartonoica maluroides was described by d'Orbigny and Lafresnaye in the genus *Synallaxis,* an allocation which is essentially correct, but when Sclater (1890) revised his earlier (1874) concept of *Synallaxis* by separating generically the species with 12 rectrices from those with 10 or fewer, he withdrew *maluroides* (which has 12 rectrices) from *Synallaxis*. The number of rectrices and their shape are certainly not generic characters in a large group of related genera. I believe I have already discussed this question sufficiently in this monograph without having to revert to it again. In the case of *S. maluroides,* it is sufficient to say that differences in the structure of the tail were invoked for placing this species in *Asthenes,* as well as for removing it from *Asthenes* (the latter was done by Peters in 1950 when he erected the new genus *Spartonoica* for *maluroides*). The structure of the tail also does not suggest that *S. maluroides* is related to *Leptasthenura,* as was apparently believed by Peters, who said that from the structure of the tail "it appears more likely that *maluroides* may be more nearly related to *Leptasthenura*" than to *Asthenes*.

In other words, I do not agree with Peters at all. Nevertheless, I believe it is probably best to recognize *Spartonoica* either as a valid genus, or possibly only as a subgenus of *Synallaxis,* but for fundamentally different reasons from those invoked by Peters: not on morphology, but on exceptionally well



MAP 29. Geographical distribution of *Spartonoica maluroides* and *Phleocryptes melanops*.

marked differences in ecology and behavior.[113] *Synallaxis* is composed of species that primarily frequent thickets or tangled vegetation on dry land, and that all build a characteristic and completely enclosed nest as far as known, whereas *Spartonoica maluroides* is very narrowly associated with marshes and is the only species of the Furnariidae

which normally builds an open nest—a most exceptional behavior for a member of this family.

Spartonoica maluroides is locally distributed (map 29), but not a rare bird, and its habitat and behavior have been described by Hudson (in Sclater and Hudson, 1888), Wetmore (1926), as well as by other authors. Hudson and Wetmore both compared *S. maluroides* to a marsh wren (*Cistothorus*), and all reports on its habitat are consistent. *Spartonoica maluroides* frequents beds of reeds or rushes (*Juncus*) in marshes, swamps, or along lagoons, and also dense grassy areas in very wet sites, but the "heavier growths of *Juncus*" seem preferred.

The nest is normally open, but varies a great deal in structure. The oldest published report of a nest that I have found was by Durnford (1878) who wrote: "this bird nests in the centre of the thick tufts of paja grass growing in water, from which the nest is only a few inches distant. It makes a very slight open structure of grass, lined with a few feathers and a little wool. Eggs quite white." Hudson said "the nest is a slight open structure of grass, lined with a few feathers, placed in a tuft of grass and reeds." More or less similar, widely open nests of dead grass, straws, shreds of reed or rushes, rootlets, or small twigs, constructed directly on the ground at the base of clumps of rushes, or very near the ground within bunches of grass, have been reported by other authors with the exception of Venturi (in Hartert and Venturi, 1909) who stated that the nest of *S. maluroides* is spherical and built at a short distance above water, which seems to imply that the nest is not opened widely and is attached to the stems of reeds and rushes.

These reports mention two very different types of nests and I have tried to obtain as much direct information as possible, most of which I have received from Sr. Samuel Narosky and Dr. Jorge R. Navas of Argentina to whom I am much indebted. Navas has described for me a nest of *Spartonoica maluroides* in the collection of the Museo Argentino de Ciencias Naturales which had been collected by Pereyra, and of which he has sent me three excellent photographs. This nest is open at the top, is more or less globular in shape, constructed of very well-interwoven strips of aquatic plants (probably chiefly *Juncus*). Navas commented that it resembles the well-known nest of *Phleocryptes melanops* somewhat in the choice of building material and in its interwoven structure, except that it is open and less compact and strong. He wrote "*El nido que tenemos esta construido con . . . hojas secas de plantas acuáticas y por el material empleado y la forma de entrelazar las hojas, este nido tiene algún parecido con el de* Phleocryptes melanops, *salvo que éste es cerrado, más compacto y fuerte.*"

This nest measures about 10 cm. in diameter, but is more flattened at the top, with a circular entrance at its center, surrounded by a very broad rim. I estimate, from the photographs, that this entrance measures about 3.5 cm. in diameter. In another letter, Navas wrote that the depth of the incubating chamber varies from 5 to 6 cm., as the rim is higher at one side. In other words, the nest is nearly "closed," if one considers that any nest has to be provided with an entrance. It seems to correspond to the "spherical" nest of Venturi.

Señor Narosky sent me information on three nests which he observed carefully very recently on my behalf. These three nests are different from the nest described above; they are "not at all" similar to it, according to Narosky, who also examined the nest of which Navas sent me a description and photographs.

One of these three nests was concealed at the bottom of a hollow in the center of a mass of dry and green weeds; the bottom of the hollow was about 10 cm. above the ground, and an irregular opening, about 4 cm. wide, led into the hollow. Narosky said that this nest was so loosely constructed that the only part of the nest he was sure had been contributed by the bird was a platform of soft cottony material about 1 cm. thick on which there were four young, and which rested on a few pieces of the stems of the rushes that may or may not have been gathered by the owner of the nest.

A second nest was found, also in a hollow,

but this one in a low clump of rushes surrounded by taller grass. Narosky said that the only nesting material which seemed to have been contributed by the bird was a low mattress ("*colchón*"), about 6 cm. in diameter, at ground level, consisting only of sheep wool. The grasses growing around the rushes formed a roof over the hollow, which was entered by an irregular opening about 4 cm. wide; the hollow was about 10 cm. deep. This nest contained three young. Narosky wrote that these two nests did not at all resemble the nests of the other species of Furnariidae he is acquainted with, and are virtually shapeless ("*carecen practicamente de forma*").

The third nest reported by Narosky has a definite and interesting shape. It was built in rushes, about 40 cm. above the ground, and, judging by Narosky's description and drawings, it is shaped somewhat like an archaic oil lamp, broadly opened, with a flattened side (at the "spout of the lamp"), but with a "handle" on the opposite side, consisting of a well raised and constructed "protecting" rim or wall, which is inclined forward at an angle of 40 degrees, and at the top curves down somewhat over the depression in which the eggs had been laid.

This rim or wall rose for about 6 cm. above the bottom of the depression, which was shallow, about 7 cm. in diameter, and lined with soft vegetal material. The "entrance" to the nest measured about 8 cm. from the inner border of the outer edge of the depression to the curving lip of the raised rim. This nest was constructed almost entirely of material obtained from the rushes and its walls were about 5 cm. thick throughout. Three young were raised from this nest which had contained a clutch of four eggs.

I have discussed the nest of *Spartonoica maluroides* at some length because it is the only species of the family Furnariidae which normally breeds in an open nest as far as known. But the descriptions of the nests given above show that it varies very importantly in structure from a "spherical" nest mentioned by Venturi and one which is globular in shape, with thick walls of well interwoven material and with a relatively small entrance, which is basically "closed"—to nests which are virtually shapeless and seem to consist only of a small pad of soft material on which the eggs are incubated, but even these rudimentary nests are well concealed in a hollow. In other words, the open nest of *S. maluroides* is not so exceptional as it may seem, and I believe that *S. maluroides* probably also bred in a closed nest, although it is evident that its nesting behavior is breaking down for reasons which escape me completely.

I emphasize again that *Spartonoica maluroides* is the only species which breeds in an open nest, to my knowledge, because the incorrect report of Hudson (in Sclater and Hudson, 1888) stating that *Certhiaxis pyrrhophia* builds an open nest of grass and hair in the fork of a tree is still perpetuated, unfortunately, in modern works as for instance in the authoritative "A New Dictionary of Birds," published in 1964 by the British Ornithologists' Union. *Certhiaxis pyrrhophia* Vieillot builds, in fact, two distinct types of tightly constructed and very well enclosed nests of thorny twigs (see *Certhiaxis*); it had been called *Synallaxis striaticeps* by Sclater and Hudson (1888).

Spartonoica maluroides
Figure 6

DESCRIPTION: *Spartonoica maluroides* is a small, slender, very graceful bird; its mean measurements, in round numbers, are 51 mm. in the case of the wing, and 70 mm. in the case of the tail (table 15). Its bill is thin, straight, very attenuated, and slightly compressed laterally; its feet are small. It is heavily streaked with black on the upperparts, with the exception of the forehead and anterior part of the crown which are uniformly bright reddish chestnut. The black streaks are very broad and sharp, well delimited by the edges of the feathers which are ochraceous orange, and extend from the center or hind part of the crown posteriorly to the upper tail coverts. On the innermost secondaries (or tertials), the outer web of the feather is black with a dull ochraceous orange edge, but the inner web is grayish. The cen-

TABLE 15
Measurements (in Millimeters) of *Spartonoica, Phleocryptes,* and *Limnornis*

Species	Wing			Tail			Bill		
	N	Mean	Range	N	Mean	Range	N	Mean	Range
S. maluroides									
Males	16	51.69	50–55	12	72.00	65–76	15	15.22	14.5–16
Females	10	49.90	48–51	6	68.34	64–70	9	14.80	14–16
Both sexes	31	50.92	48–55	22	70.14	63–76	27	15.06	14–16
P. melanops									
Males	63	60.47	56–66	55	53.43	46–62	64	18.91	18–21
Females	28	57.64	55–61	25	48.80	45–54	25	17.74	16–20
Both sexes	97	59.60	55–66	85	52.02	45–62	94	18.55	16–21
L. curvirostris									
Males	31	72.91	70–78	28	65.18	57–74	31	25.08	23.5–27
Females	18	72.80	68–76.5	15	66.86	63–73	18	24.70	23.5–26
Both sexes	57	72.77	68–78	50	65.90	57–74	57	24.93	23–27
L. rectirostris									
Male	1	—	64	1	—	65	1	—	25
Females	2	—	60, 60	1	—	67	2	25.75	25, 26.5
Both sexes	7	61.80	59–66	3	64.00	60–67	5	26.00	25–27

tral tail feathers have a broad stripe of brownish black along the shaft, but the remainder of the feather is pale ochraceous grayish brown. A small white spot is present on the lores, and also directly behind the eye; a vague, narrow, buffy streak extends posteriorly behind the whitish spot. The underparts are white, with the exception of the upper breast, across which extends a broad band of pale ochraceous brown, and also of the flanks and under tail coverts which are more or less pale ochraceous brown, or very pale buffy brown.

The tail is strongly graduated, slightly stiffened, and composed of 12 relatively narrow rectrices. The distal portion of the central rectrices is strongly attenuated, for a distance of about 25 mm., and tapers to an acute point, and, when the feathers are at rest and not disturbed, the attenuation produces a very distinct "fork." The other five rectrices are attenuated also, have acute tips, and are excised shallowly at the tip of the inner web, the degree of attenuation and excision decreasing greatly from the center of the tail outward. All the rectrices are rufous (with the exception of the central pair mentioned above), but to a varying degree, as the tip of the feather, or its inner web, is more or less invaded by dark brown.

IMMATURE PLUMAGE: Similar to that of the adult, but brown, not rufous on the forecrown, lacking the bright reddish chestnut "cap" of the adult; underparts more buffy, less whitish, and slightly mottled with brown at the sides of the breast; the streaked pattern is also less sharply defined than in the adult.

RANGE: Southeastern Rio Grande do Sul in Brazil, south through central and southern Uruguay, to Argentina, from Entre Ríos and southern Santa Fe, south to Rio Negro, and west to Mendoza, La Pampa, and probably eastern Neuquén.

SPECIMENS EXAMINED: 39, including the two cotypes of *maluroides* in MNHN.

GENUS *PHLEOCRYPTES*

The nearest relative of the monotypic *Phleocryptes melanops* is uncertain. Modern authors such as Hellmayr, Peters, and Meyer de Schauensee all place *Phleocryptes* between *Aphrastura* and *Leptasthenura* in sys-

tematic lists, but I believe this is certainly wrong because *Aphrastura* and *Leptasthenura* are closely related to each other, in my opinion, but not to *Phleocryptes*. I do not know to which genus *Phleocryptes* is most closely related, but I believe it is likely to be *Synallaxis*. I have stated in my account of *Spartonoica* that *S. maluroides* appeared to me to be closely related to *Synallaxis*, implying that *S. maluroides* was derived from common ancestors, but modified for a different type of habitat. I think this may very well be true also for *Phleocryptes melanops*, an instance of radiative adaptation, probably over a different time-scale, which gave rise, first to *P. melanops*, and later to *S. maluroides*.[114] Morphological differences are greater in the case of *P. melanops* and it seems to be far more abundant than *S. maluroides*, and certainly over a much greater range which extends from northern Peru south to southern Chile and southern Argentina, and from sea level up to the puna, where it breeds at 4300 m. or more (map 29). These considerations suggest that *P. melanops* is probably an older form than *S. maluroides*.

The ecology and general behavior of *Phleocryptes melanops* and of *Spartonoica maluroides* are quite evidently exceedingly similar (though not the nests), but it is possible that *P. melanops* is even more narrowly associated with reed beds, and especially rushes, than *S. maluroides*. Both species are "true marsh wrens" (*Cistothorus*) in one sense, though not systematically. Wetmore (1926) commented that "in general appearance, notes, and haunt this frequenter [*P. melanops*] of cat-tail and rush-grown marshes is [strikingly] similar to the oscinine long-billed marsh wren [*Cistothorus palustris*]," and continued to describe the general behavior of *P. melanops* as follows:

> As one approaches the rushes of some cañadon in the eastern pampas, a small wrenlike bird may come near to hop about excitedly among the rushes to the accompaniment of clicking notes like those made by striking two pebbles together, and in a short time half a dozen of these *Phleocryptes* may be gathered about. Their alarm is soon over and it is not unusual to have them come almost within reach to look about confidingly. Where the aquatic vegetation is composed of large-leaved floating forms the birds hop about on the stems and leaves, frequently with feet and tarsi immersed in the cold water, while they seize eagerly any insects or other life that appears on the plants in the water. At other times they cling to the stalks of vertical reeds and reach out as far as possible to dig with their bills among the small floating plants, resembling duckweed, that cover the surface.

Hudson (in Sclater and Hudson, 1888) added that though *P. melanops* "seldom ventures out of its rush-bed [it] is occasionally seen feeding in the grass and herbage a few yards removed from the water."

The nest of *Phleocryptes melanops* is well known and has attracted much attention as it is a remarkable structure. The nest is firmly attached to several stems of *Juncus* which grow in water, and vary in number from three to seven, but usually consist of four or five. The nest is constructed from about a half to a little over a meter above water, and is more or less globular, oval, or shaped like an inverted pear, measuring anywhere from about 12 to 18 cm. in height, by about 15 cm. or less at its greatest diameter. In a very careful drawing of a nest sent to me by Gunnar Hoy, the nest is pear-shaped, 16 cm. high and 10 cm. wide below the entrance. The bird begins by binding the stems very tightly with narrow strips of dry tough grass. On this firm support the nest then is built up, starting with the base of broader grass leaves and strips of aquatic plants that are first liberally daubed with wet clay, and then tightly interwoven and firmly molded. The nest is very strong, impervious to water when finished and is provided with a relatively small, circular or roughly oval entrance near the top. This entrance was circular in the drawing sent to me by Hoy and had a diameter of 3.5 cm. The inside of the nest is constructed of finer material and thickly lined with feathers. The eggs are bright blue or greenish blue, a rare color in the Furnariidae which lay white eggs as a rule. *Phleocryptes melanops* is such an industrious builder that it is called "*Trabajador*" in some countries of

South America, such as Peru and Chile, but the Argentine name "*Junquero*" for it is very apt.

The nest possesses some unusual features which are either constant or exceptional. A constant feature is a small sloping "awning," built above the entrance and curving down partly at its sides. This awning is apparently designed to protect the entrance, and is constructed of finer material than the rest of the nest which is carefully matted, according to MacDonagh (1933), who has published a long description of the construction of the nest.

Milton W. Weller, Iowa State University, wrote me that he has found nests provided with a small, shallowly depressed platform of clay, built on top of the roof of the nest from which the bird sings or calls. This feature seems exceptional but the most curious feature of all, which may have been unique, is a hinged trap door which closes the entrance perfectly, according to Hudson (in Sclater and Hudson, 1888) who described this structure in a nest that was brought to him. This feature constructed of the same material as the nest was apparently authentic, but Hudson said he "never found another nest like it, nor have I heard of one being found by any one else; and that one nest, with its perfectly-fitting stopper, has been a puzzle to my mind ever since I saw it." Hudson believed the trap door (or "stopper") had been provided, perhaps, to prevent intrusion by small frogs or small birds; small reed frogs, numbering "sometimes as many as three or four," take up the nests in winter as a favorite shelter, according to Hudson.

MacDonagh (1933) mentioned nests which seem double ("*que parecen dobles*"), but he said one of these is an abandoned nest, at least one year old, on top of which the bird started to build a new nest ("*en realidad se trata de un nido abandonado, del año anterior por lo menos, sobre el cual se ha iniciado la construcción de uno nuevo*"). This observation is interesting because it is relevant to the reports of "multiple nests" which I have briefly discussed above in the case of *Furnarius rufus, Thripophaga d'orbignyi,* and *Phacellodomus* spp.

Geographical Variation

Phleocryptes melanops has a great range (map 29) and varies somewhat geographically. Birds from coastal Peru, which have been named *brunnescens,* are generally more brownish, less blackish, on the upperparts than the populations from the remainder of the range, and, on the whole, the rufous area on their primaries is slightly paler and more restricted, but these differences in coloration are not strongly marked; the wing length is also shorter, or averages shorter, than in the other populations. The populations from the highlands of Peru, of Bolivia, and of Jujuy in northwestern Argentina have distinctly longer wings and have been named *schoenobaenus*. With this exception, geographical variation is slight and of little significance.[115] Other populations have been separated nomenclaturally, but I cannot detect any other evidence of geographical variation, including shape and length of the bill. Wing length (in mm.) of 10 males in each case: coastal Peru, 57–60 (mean, 58.60); highlands of Peru and of Jujuy, 62–67 (mean, 64.70); Argentina (other than Jujuy), Chile and Paraguay, 57–62 (mean, 60.35); Rio Grande do Sul, Brazil, 57–62 (mean, 60.0).

Phleocryptes melanops
Figure 6

Description: *Phleocryptes melanops* is a small, rather stocky bird, with a short tail, a long, thin, straight bill, relatively long legs, and feet that are quite strong in proportion to the small size of the bird. Mean measurements, in round numbers, are 60 mm. in the case of the wing, 52 mm. for the tail, and 18.5 mm. for the bill. The coloration of the upperparts, wings, and tail is variegated. The forehead and forecrown, and a broad band across the nape are chiefly pale ochraceous brown or ochraceous tawny, with some admixture of dull black. The crown is chiefly sooty black, behind the forehead or forecrown, with some admixture of ochraceous brown. The upper back is chiefly black, purer black than on the crown, but variegated to a varying degree by white or whitish shaft streaks, and by grayish or ochraceous edges

to the feathers; the lower back, and the unusually long upper tail coverts, are almost uniformly pale ochraceous brown, with the main exception that some of the coverts have black edges. A broad buffy superciliary streak reaches posteriorly to about the anterior border of the brown band across the nape. The underparts are white, purer on the throat, more cloudy with buff or pale umber below the breast which is crossed by an ill-defined grayish or ochraceous band; the flanks are umbraceous, the under tail coverts buffy; much individual variation exists in the coloration of the underparts below the throat.

The wings are black, variegated with white, ochraceous brown, and very bright reddish chestnut. The rufous area forms a broad band at the base of the remiges or at their centers on the primaries. The middle and greater upper wing coverts are or tend to be bright rufous at the tip and base, but not on the center of the feather which is black; some rufous exists also on the lesser coverts, and these rufous markings form ill-defined bars that are most distinct on the greater coverts.

The tail is rounded, soft (not stiffened), and composed of 12 relatively broad rectrices, which are rounded at the tip, but the shaft of the feather is prolonged as a soft hairlike filament, which is longer on the inner pair of rectrices. The tail is chiefly black, but all the rectrices, with the exception of the central pair, have whitish tips which are larger on the three outer pairs. The central rectrices are almost entirely tawny, but a fusiform blackish brown band exists along the shaft of their apical portion.

IMMATURE PLUMAGE: The immature plumage differs from that of the adult by being much less sharply patterned; by having distinct rufous shaft streaks on the crown; and, especially, by being much less white below, as all the feathers are more or less narrowly edged with dark brown; the dark edges are broader on the breast and upper abdomen, but very narrow on the throat.

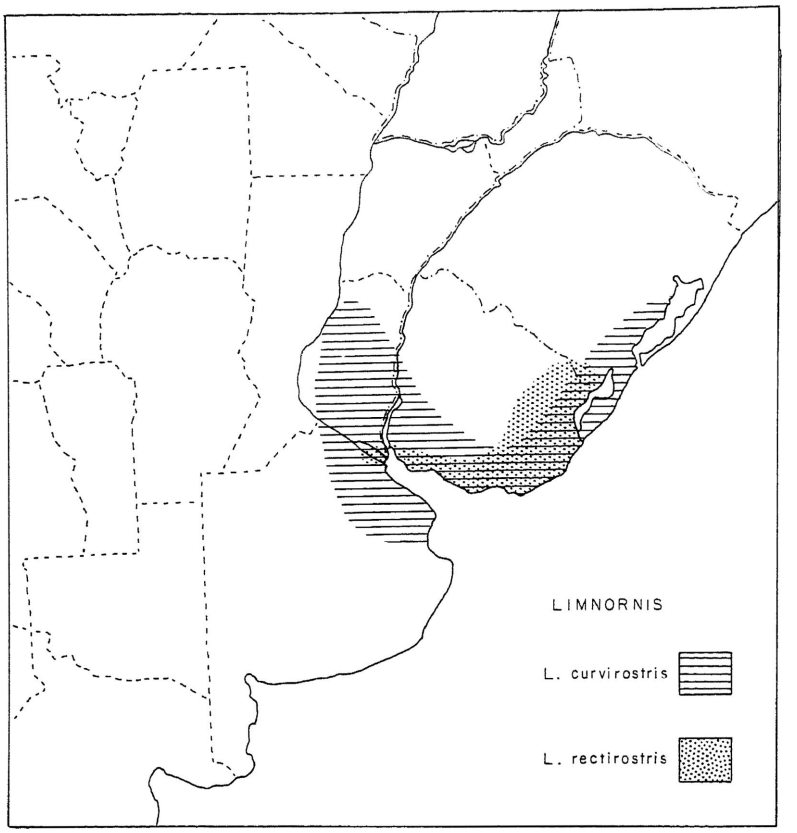
RANGE: From Lambayeque in northern coastal Peru, south through coastal Peru and the Andes, to Aysén in southern Chile, and through western Bolivia (where it has been recorded so far from La Paz, Oruro, Cochabamba, and western Santa Cruz), Paraguay, and Uruguay, to southern Chubut and perhaps Santa Cruz in Argentina; and, north from Uruguay, to southeastern Rio Grande do Sul in Brazil. One individual has been collected at Ushuaia in southern Tierra del Fuego, but this species is very probably only accidental in Tierra del Fuego. No valid records seem to exist in Brazil north of southeastern Rio Grande do Sul, although São Paulo and Rio de Janeiro have been mentioned. The altitudinal range ascends from the coast to at least 4300 m. in the Andes, but probably rises still higher.

SPECIMENS EXAMINED: 187, including the types of "*dorsomaculata*" in MNHN, and of "*brunnescens*" in AMNH.

GENUS *LIMNORNIS*

Limnornis is composed of two species (*L. curvirostris* and *L. rectirostris*) with restricted ranges (map 30), which were both discovered by Charles Darwin in 1832 in southern Uruguay at or near Maldonado. They were described by Gould in 1839, who erected the new genus *Limnornis* for them. The two species are closely related, but they are quite distinct morphologically, and Hellmayr (1925) decided to separate them generically, proposing the new genus *Limnoctistes* for *rectirostris*. Hellmayr mentioned, however, that the two species are "allied," which is certainly very evident, and which renders Peters's (1951) subsequent systematic treatment of these two birds quite incomprehensible. Peters (1951) separated them by no fewer than 12 genera in his list. Meyer de Schauensee (1966) brought the two species back together, but retained *Limnoctistes*, although the existing differences are only of specific importance in my opinion. I believe very strongly that *Limnoctistes* should be suppressed and merged with *Limnornis*.

The information available on the ecology, general behavior, and nests of *Limnornis curvirostris* and *L. rectirostris* is not abundant, but the ecology and behavior of these two birds seem to be similar, and are similar



MAP 30. Geographical distribution of the two species of *Limnornis*.

also to the ecology and behavior of *Spartonoica maluroides* and *Phleocryptes melanops*, although *L. curvirostris* and *L. rectirostris* do not appear to be closely related to either *S. maluroides* or *P. melanops* and their nearest relatives are uncertain. Convergence is very strong in the ecology and general behavior of the four species, but the nests are different in the three genera. *Limnornis curvirostris* is very narrowly associated with dense beds of reeds and rushes which grow in the water, "and is not found in any other situation," according to Hudson. *L. rectirostris* shares the same habitat, but its requirements are less rigid, as it frequents also high grasses which grow on the edge of swamps and marshes or along lagoons, especially the spiny, prickly grass called "caraguata" (*Eryngium*). Gerzenstein and Achaval (1967) reported that they found *L. rectirostris* only in spiny grass, mostly "caraguata," in the valleys of the little creeks and small tributaries of the upper Tacuari River, not in reed beds, in a rocky upland region of the Department of Cerro Largo, northeastern Uruguay, "far from great lakes or swamps," but, in other regions, no essential difference seems to exist in the ecological requirements of the two species. They were both collected at or near Maldonado by Darwin, but it does not seem to be known whether or not they actually associate in the same locality. They may, because Gerzenstein and Achaval report that their vocalizations are very distinct.

Limnornis rectirostris is rare in collections

and has been difficult to observe because it seems to be secretive and lives in very dense growth in inaccessible marshes, but Gerzenstein and Achaval (1967) found it abundant in the more open grassy habitat of Cerro Largo. They did not find a nest, but Daguerre (1933) found one at Paranacito in southernmost Entre Ríos, Argentina, along a lagoon. This nest had been built in a clump of *Eryngium* grass, about 20 cm. above the ground. It was globular in shape, but ovoid vertically, according to Daguerre, with a small entrance at the side, and constructed of leaves of *Eryngium* and of flexible stems of other plants. The egg is white according to Daguerre. Pereyra (1938) said that he also found a nest in *Eryngium,* similar to the one described by Daguerre, near Campana, northern Buenos Aires, along a small stream emptying in the Paraná. That is all I have been able to find on the nest of *L. rectirostris*.

Limnornis curvirostris is better known. Its nest is built in the same location as the nest of *Phleocryptes melanops,* attached to the stems of the reeds which grow in water, and roughly at the same height, from about one-half to over 1 m. above water. The nest of *L. curvirostris* resembles also that of *Phleocryptes melanops* in general shape and size, and is built of the same material. However, the resemblance is superficial as no clay is used by *L. curvirostris* with the result that its nest is less neat, compact, and strong than the nest of *P. melanops,* and its entrance is at one side, near the center of the nest, not near the top as in the case of *P. melanops*. Narosky wrote me that the two nests of *L. curvirostris* he found were constructed 1.80 m. above water, were oval in shape, but somewhat broader at the top, and that one of them was provided with a small "awning" over the entrance, "well pronounced and constructed in the same manner as *P. melanops*" (translation). The eggs of *L. curvirostris* are blue, similar to those of *P. melanops* in color, whereas those of *Spartonoica maluroides* and *Limnornis rectirostris* are white, but the systematic significance of the differences in coloration of the eggs of these four species—if any—is obscure to me.

Morphological Variation

Limnornis curvirostris is a larger, very distinctly more corpulent bird than *L. rectirostris,* with much bigger, stronger feet, shorter tail, and more decurved bill. The ratios between the lengths of the tail and of the wing are 0.90 in *L. curvirostris* and 1.03 in *L. rectirostris*; and the means of the lengths of the wing and tail, in round numbers, are, respectively, 73 and 66 mm. in *L. curvirostris,* as against 62 and 64 mm. in *rectirostris* (see also table 15). The scientific names selected by Gould call attention to the difference in the shape of the bill, which is distinctly more decurved in *L. curvirostris,* whereas it is nearly straight in *L. rectirostris,* but nevertheless, the difference in the shape is not so pronounced as these names seem to indicate. The tail of the two species is composed of 12 rectrices which are well stiffened at the base in *L. curvirostris,* but only slightly so at the apical portion, whereas the rectrices of *L. rectirostris* are about equally well stiffened at the base and apex; they are broad, firmly integrated, and rounded or blunt at the tip in *L. curvirostris,* but much narrower in *L. rectirostris,* less firmly integrated, and are moderately acute at the tip, or tend to be so.

In short, the structural differences between the two species are well marked, but their coloration and its pattern "bears a remarkable likeness," as expressed by Hellmayr. *Limnornis curvirostris* is browner on the upperparts and surface of the wing than *L. rectirostris,* less grayish on the upperparts, less rufous on the wing, and has also a more distinct streak behind the eye, but only the difference in the color of the upper surface of the wing is very appreciable. The tail is wholly and strongly rufous in both species.

KEY TO THE SPECIES OF *LIMNORNIS*

Upper surface of the wing distinctly bright rufous, especially on the coverts; bill nearly straight; legs and feet relatively weak ..... *rectirostris*

Upper surface of the wing brown, virtually uniform; bill distinctly decurved; legs and feet markedly heavy and strong ..... *curvirostris*

List of the Species

Limnornis curvirostris
Figure 6

DESCRIPTION: Warm bister brown on the head and nape, and rufous brown on the back and upper tail coverts, the rump and coverts being brighter rufous than the back. Lores whitish, with a broad, but not well defined, whitish post-ocular streak. Underparts almost uniformly white, more creamy white on the abdomen, and with a faint, very pale ochraceous wash across the breast, becoming more ochraceous and umbraceous on the flanks and under tail coverts. Upper surface of the wing rufous brown, of about the same color as the back, virtually uniform, but more strongly rufous on the outer webs of the inner primaries. Tail strongly and wholly rufous, dull reddish chestnut, virtually uniform, but somewhat brighter rufous on the outer webs of the four outer pairs of rectrices, more dusky on their inner webs, as also on the central pair of rectrices. Bill strong and long, attenuated, compressed laterally, and distinctly decurved.

IMMATURE PLUMAGE: In one bird, which may not have been fully adult, the underparts are slightly buffy, not pure white, as in the adult, and very faint, small buffy spots exist on the forecrown.

RANGE: From southeastern Rio Grande do Sul in Brazil (region of Lagos dos Patos southward), south through eastern and southern Uruguay, to Entre Ríos and northern Buenos Aires in Argentina (south to about 36° S.).

SPECIMENS EXAMINED: 68, including the type of *curvirostris* in BM.

Limnornis rectirostris

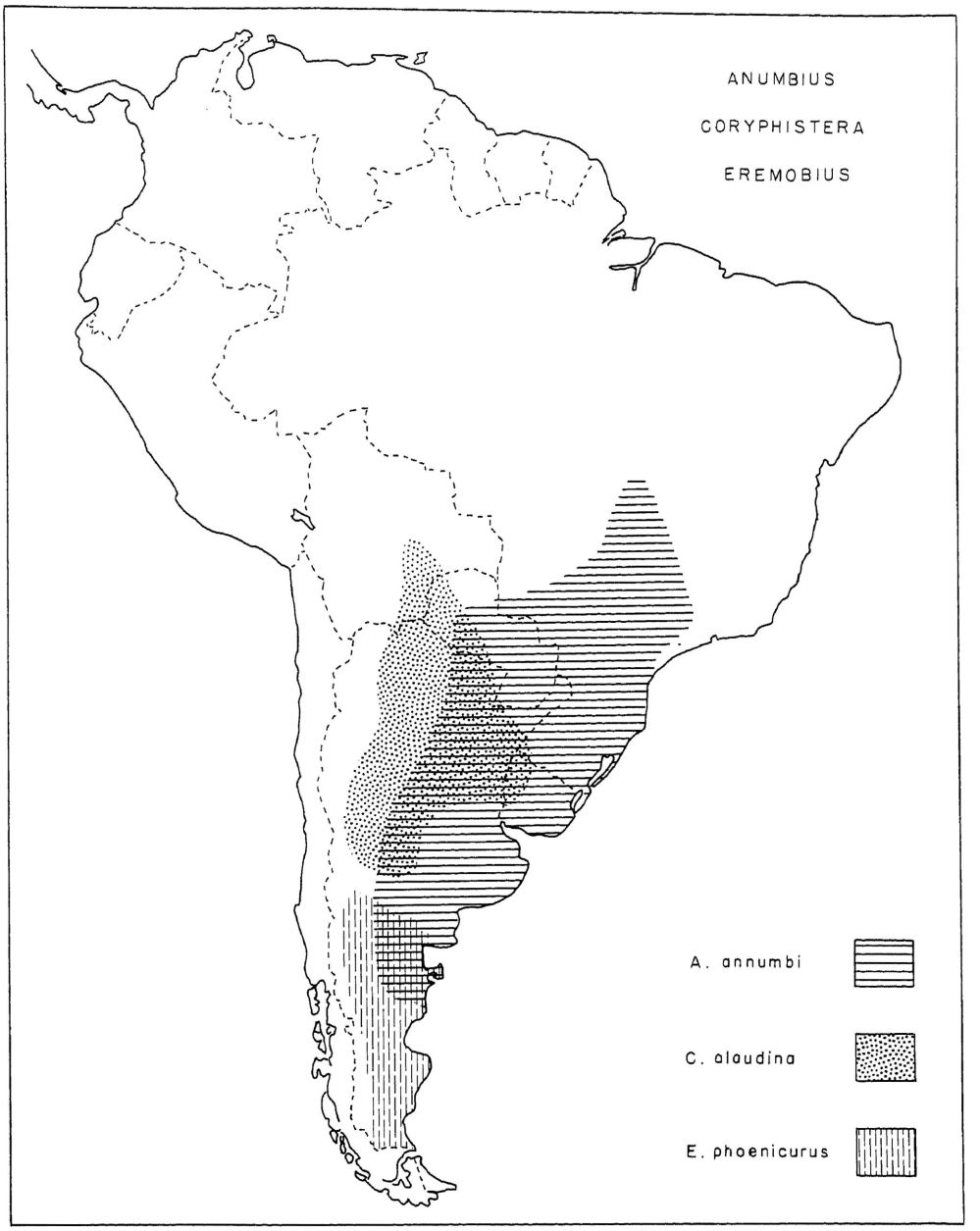
DESCRIPTION: Upperparts grayish brown, with a faint olivaceous cast in fresh plumage; with an ill-defined whitish spot on the lores, and a small, short, and rather narrow whitish post-ocular streak. Underparts almost uniformly white, with a faint, cinereous wash across the upper breast and on the upper flanks, but more ochraceous, or pale umbraceous on the lower flanks and under tail coverts. Upper surface of the wing bright reddish chestnut on the coverts, rufous also, especially on the outer webs of the inner secondaries, but duller than on the coverts, and dull rufous also on the outer webs of the other secondaries, and on those of the inner primaries. Tail strongly and wholly rufous, nearly uniform, but brighter on the three outer pairs of rectrices, and paler on the central pair. Bill very long, strongly attenuated, compressed laterally, and nearly straight.

RANGE: From extreme southeastern Rio Grande do Sul (lower Rio Jaguarão) in Brazil on the border of Uruguay, south through eastern Uruguay (basin of the Rio Tacuari in Cerro Largo, and Departments of Treinta y Tres and Rocha), and through southern Uruguay, to the marshes of the delta of the Paraná in extreme southern Entre Ríos and neighboring Buenos Aires in Argentina.

SPECIMENS EXAMINED: 7, including the type of *rectirostris* in BM.

Genera *Anumbius, Coryphistera,* and *Eremobius*

These three monotypic genera do not appear to be closely related to one another. Their nearest relatives are uncertain, but the three genera are best considered and listed systematically together, as much similarity exists in their general ecology and behavior, including the structure of their nests. The three species are *Anumbius annumbi, Coryphistera alaudina,* and *Eremobius phoenicurus*. Their distributions overlap in part (map 31), and they inhabit low open brushy country and savannas, spending much time on the ground although *A. annumbi* and *C. alaudina* are also arboreal. *Eremobius phoenicurus* is said to run along the ground with the tail cocked at an angle over the back, and this posture has been reported also in *C. alaudina,* but not in *A. annumbi,* which is more deliberate when active on the ground than *C. alaudina,* and especially than *E. phoenicurus*. All three species build voluminous nests of thorny twigs in shrubs and bushes in the case of *E. phoenicurus*; in low isolated trees, usually not far above the ground, in the case of *C. alaudina* and *A.*



MAP 31. Geographical distribution of *Anumbius annumbi*, *Coryphistera alaudina*, and *Eremobius phoenicurus*.

annumbi, although the nest of *A. annumbi* may be built higher and in tall trees.

The three species are coarse, or rather coarse birds, with big feet, but they are very distinct morphologically in other regards and have been very widely separated systematically. *Coryphistera* and *Eremobius* were included in the Furnariinae by Hellmayr

TABLE 16
Measurements (in Millimeters) of *Anumbius, Coryphistera,* and *Eremobius*

Species	Wing			Tail			Bill		
	N	Mean	Range	N	Mean	Range	N	Mean	Range
A. annumbi									
Males	38	84.57	79–90	37	82.81	74–92	35	20.07	18.5–22
Females	40	82.32	78–87	35	81.14	74–87	38	19.72	18–22
Both sexes	83	83.51	78–90	77	82.00	74–93	78	19.93	18–22
C. alaudina									
Males	46	76.15	70–81	34	67.90	62–74	45	17.55	16.5–19
Females	43	74.79	69–79	35	67.70	63–73	41	17.35	16–19
Both sexes	90	75.52	69–81	70	67.75	63–74	87	17.47	16–19
E. phoenicurus									
Males	14	75.28	71–78	14	66.64	60–70	14	25.21	23–27.5
Females	4	73.50	72–78	4	68.75	65–74	4	24.62	24–26.5
Both sexes	22	74.95	71–78	22	66.95	60–74	22	24.88	23–27.5

(1925), separated by several genera, and *Anumbius* was placed in the Synallaxinae. This was a great departure from the treatment of Sclater (1890), who had decided to place *Coryphistera* in the Philydorinae, followed by *Anumbius,* although he was not sure these two genera were related and suggested that *Coryphistera* "might . . . be better placed in the Furnariinae,"—a remark which may have influenced Hellmayr in transferring *Coryphistera* to the Furnariinae. In my opinion *Coryphistera* and *Anumbius* do not belong in the subfamily Philydorinae. The nest of *Coryphistera,* which is built of sticks and twigs above the ground, suggests that *C. alaudina* should be included in the Synallaxinae. This reason (structure of the nest) was mentioned by Esteban (1951) when he transferred *Coryphistera* back to the Synallaxinae, but I do not agree with Esteban that *Coryphistera* and *Anumbius* resemble one another morphologically. *Coryphistera alaudina* and *Anumbius annumbi* have big feet, as these birds spend a great deal of time walking on the ground, but, contrary to the statement of Esteban (1951), they do not resemble one another morphologically in other respects, as shown quite clearly by the descriptions of these two birds given in this monograph. It is also evident at a glance that *C. alaudina* is less "heavy," sturdy, and compact in general appearance than *A. annumbi.* Peters (1951) also brought back *Coryphistera* and *Anumbius* together, independently from Esteban.[116]

GENUS *ANUMBIUS*

Anumbius annumbi is very well known and second only to *Furnarius rufus* in the interest it attracts. *Anumbius annumbi* is not restricted to a single habitat, but is primarily a bird of thinly wooded districts, or other open country, such as acacia savannas, thorny thickets, or open brush which is often very scanty, Wetmore (1926) reported that he found *A. annumbi* also "far into the open where heavy growths of thistles afford low coverts." Hudson (in Sclater and Hudson, 1888) said *A. annumbi* feeds "exclusively on the ground," where it is said to walk sedately about on open ground, low sward, or in the shelter of tussocks and clumps of weeds, carrying its body horizontally. *Anumbius annumbi* is said to be tame.

The nest is voluminous, constructed of large or rather large sticks that are often thorny and are gathered on the ground. These sticks are laboriously flown up to the nest, the bird dropping a great many, and Hudson said that "frequently as much fallen material as would fill a barrow lies under the

tree. The fallen stick is not picked up again . . . [the bird going] far afield in quest of a fresh one, and having got one to its liking, carefully takes it up exactly by the middle, and, carrying it like a balancing-pole, returns to the nest, where, if one end happens to hit against a projecting twig, it drops like the first." *Anumbius annumbi* is known by many vernacular names, and one of the most commonly used is "*leñatero,*" from its habit of gathering so much "wood," but the Argentine name "*Añumbí,*" adopted by Olrog (1963), is more desirable, as other Furnariidae which build nests of sticks are also called "*leñateros*." *Añumbí* has the merit of being a native name (in Guaraní), and also that of having been adopted as the scientific name (though slightly misspelled) by Vieillot when he described this species.[117]

The sticks are firmly interwoven, but the finished nest is more or less irregular in shape and varies a great deal in size. A nest of average size is about 50 or 60 cm. high by 30 or 40 cm. broad, but some are nearly twice as large, whereas others are somewhat smaller than the measurements mentioned. A great variety of material is incorporated among the sticks, such as roots, bones, wires, bits of broken china or glass, and, according to Renard (1918), even old rinds of cheese; in fact, any kind of scrap which has caught the fancy of the bird. Wilson (1926) reported that he recovered one kilogram of metal from one nest, consisting of bits of wire, old springs and nails, and "various other metallic objects."

The location of the nest varies, but the site that is normally preferred is a low or stunted isolated tree with scanty foliage, often thorny, where the nest is constructed at a low or moderate elevation above the ground in the branches of the tree or within one of its forks. But the nest may be constructed in a variety of other sites, and among those which have been reported are the cross arms or braces of utility poles, supports of sheds or shelters on ranches, top of stakes in corrals, unused or abandoned farm machinery, or within a bush and clump of thistles. Occasionally or locally nests can also be built quite high. Durnford (1877) reported that *Anumbius annumbi* nests in tall poplars in the region of Buenos Aires, as high as about 21 to 24 m. above the ground. Wetmore (1926) observed one nest "in the head of a railroad semaphore . . . [where] the birds had filled a space between iron uprights 4 feet long [1.20 m.] and were still engaged in carrying sticks up to 10 meters in the air, though lower nesting sites abounded."

The entrance of the nest is at the top, and an irregular tunnel with bends, or which is roughly spiral in shape, leads down to the bottom of the nest where the incubating chamber is situated. The latter is lined with soft material, such as wool or fine grass, but a great variety of other material is used also, among which feathers, horse hair, straw, bits of rags or paper, threads, shoe laces, and the wing cases of beetles have been mentioned. A very curious behavior described by Daguerre (1927) is the "adornment" of the entrances to the nest when it has been completed. At this time, according to Daguerre, the bird searches for something which is conspicuous in coloration and places it at the side of the entrance or above it ("*busca . . . un objeto de color llamativo y lo coloca a un costado de la puerta, o sobre ella*"), and he mentioned colored wool, bright rags or paper, metal discs from labels, and a tuft of black and white fur. He believed this signifies the nest has been completed, a signal which is usually soon destroyed by the weather: "*pues según creo, ello es señal de su terminación y la intemperie casi siempre lo destruye prontamente.*"

Some nests are large and bulky, and, sometimes, several nests are joined together or are built in the same tree, as many as six according to Azara, quoted by Hudson. Barrows (1883) stated that "the same nest is used for several seasons in succession," and that multiple nests are "all occupied at the same time." However, no proof exists, to my knowledge, that *Anumbius annumbi* breeds in the same nest again for more than one season, or that multiple nests are occupied by more than one breeding pair. It is highly probable that *A. annumbi* (as in the case of *Furnarius rufus,* or other species which build stick nests, such as *Phacello-*

domus rufifrons) is strongly attached to a favorite breeding site and uses the old nest as a convenient foundation for a new one, with the result that the structures become very large, or builds a new, more distinct nest touching the old one. *Anumbius annumbi* is strongly territorial. Wetmore (1926) said "males fight savagely in defense of their chosen territory, battling with intruders until exhausted," but are accompanied in family parties by their grown young. These observations suggest to me that only a single breeding pair occupies the same breeding site during one season, and that the multiple nests which are occupied are only shelters or dormitories for non-breeding members of the same family—as in the case of *Phacellodomus rufifrons,* well studied by Skutch (1969a).

Anumbius annumbi
Figure 6

DESCRIPTION: Pale ochraceous brown on the upperparts, with the exception of the forehead, or forecrown, which are chestnut, with heavy dark brown streaks on the remainder of the crown and back, but not on the rump or shorter upper tail coverts; the longer coverts, which are unusually prolonged, are darker brown, with narrow but pronounced darker shaft streaks. Lores white, with a well-defined buffy superciliary and post-ocular streak; cheeks dull pale chestnut or tawny. Throat white, bordered on all sides by small black spots, with the remainder of the underparts very pale ochraceous brown on the breast, the feathers of which are paler, more buffy at the center along and near the shaft; the abdomen and under tail coverts are paler than the breast, pinkish buff, or pale cinnamomeous ocher and uniform or virtually so, the lower flanks being more umbraceous. The wings are brown, with very pale cinnamomeous buff axillaries and under wing coverts; with a darker, more rufous cinnamon area on the edge of the inner web of the secondaries and inner primaries, and, on the upper surface of the wing, the outer web of the greater coverts and secondaries is dull rufous.

The tail is about equal to the length of the wing, composed of 12 rectrices that are well stiffened and more or less acute at the tip, especially the central pair, the tips of which are very finely attenuated. The rectrices are blackish, with the exception of the central pair and outer web of the next pair (fifth) which are earthy brown, and all the rectrices, with the exception of the central pair, are very conspicuously tipped with creamy white with a faint cinnamomeous tinge; these whitish tips are very large, but decrease progressively in size, inwardly, from the outer pair of rectrices to the fifth. Bill relatively short and stout; tarsus relatively short, thick and heavy, as well as the toes which have strong claws.

IMMATURE PLUMAGE: Similar to that of the adult, but not chestnut on the forehead, less sharply patterned throughout, and considerably darker on the underparts, as the throat is not white, but ochraceous (also not so distinctly bordered with spots which are more brownish than black), and the remainder of the underparts are also much more ochraceous or umbraceous below the throat than in the adult plumage.

GEOGRAPHICAL VARIATION: The range of *Anumbius annumbi* was extended very considerably farther north in 1956 (by about 500 miles) when three specimens were collected in Brazil in central Goiás. These specimens, two of which were kindly lent to me by the Los Angeles County Museum, differ from birds from the other populations of the species in having the black spots surrounding the throat more reduced in number and size; these specimens were assigned to a new subspecies, *A. a. machrisi.* The other characters mentioned for this new form fall, however, within the range of individual variation of the other populations.

RANGE: Brazil, from the upper Rio Tocantins in central Goiás, western and southern Minas Gerais, southward through southern Brazil, Paraguay, Uruguay, and Argentina to Chubut, west, in Argentina, to central Formosa, Santiago del Estero, Córdoba, San Luis, La Pampa, and Rio Negro.

SPECIMENS EXAMINED: 152, including the types of "*anthoides*" in MNHN, and of "*major*" in BM.

GENUS *CORYPHISTERA*

The ranges of *Coryphistera alaudina* and *Anumbius annumbi* overlap to a large extent (map 31), but, generally speaking, *C. alaudina* is a bird of more arid regions, whereas *A. annumbi* frequents open scrub and open "woods" of low thorny trees (*Prosopis*). *Coryphistera alaudina* apparently feeds only or chiefly on the ground where it is said to forage in small family parties of six or seven individuals, walking, hopping, or running about on open, sandy or barren areas, among the thorny bushes, occasionally cocking the tail over the back. But *C. alaudina* is also arboreal according to Friedmann (1927), who said that "at the slightest sign of danger . . . they take to the trees and taller bushes, where they hop and flit and clamber about with the greatest rapidity and ease," the rather long crest being erected when the bird is wary.

Coryphistera alaudina is not as well known as *A. annumbi* and its nest has attracted less attention, but I get the impression that its nest resembles that of *A. annumbi* in general structure, size, and location, being constructed not far above the ground in trees. Wetmore (1926) reported that the nests he found "were strongly made with thorny, crooked twigs so [tightly] interwoven that it was difficult to open them for examination. The twigs used were often 300 mm. or over long and as large around as a pencil." These nests "were 300 mm. in diameter, globular in form, with an entrance through a small tunnel that led into one side."

The dimensions of the nest given by Wetmore seem smaller than those of the nests described by Masramon (1971) who said that the globular nest of thorns ("*globo de espina*") varies from 120 to 130 cm. in "circumference," or well over 1 m. Masramon did not mention the location of the entrance, but described the tunnel as cylindrical, curving [down] to the incubating chamber which is oval in shape, 18 by 14 cm., lined with much soft vegetal material and with a bed of dry fibers matted with feathers. A curious feature of the entrance tunnel mentioned by Masramon seems to correspond to the "adornment" applied by *Anumbius annumbi* to the entrance of its nest, which was reported by Daguerre and mentioned by me above. Masramon said that pieces of broken glass of different colors shine ("*relumbran*") in the entrance tunnel of the nest of *Coryphistera alaudina,* as well as other odd objects, such as the skeletons of small toads and desiccated remains of small snakes, which, no doubt, are applied to the walls of the tunnel.

Masramon said also that *Coryphistera alaudina* may "repair" the nest it used the year before, rather than build a new one, and that "perhaps" two breeding pairs may use the same nest in rotation during the same breeding season. But these observations were not made under controlled conditions and seem doubtful to me.

GEOGRAPHICAL VARIATION

Coryphistera alaudina varies distinctly geographically, the variation affecting the streaking of the plumage, especially the density of the streaks and their pigmentation on a more or less buffy or whitish background. No two populations that I have examined are identical, but as the variation is only relative, and usually slight between any two populations, it is difficult to describe it briefly. Generally speaking, birds from Bolivia and Tucumán, Argentina, are relatively pale and not heavily streaked. Birds from Bolivia are distinctly brighter, with dull brown streaks on a strongly buffy or pale cinnamomeous ground on the upperparts, and with rufescent (pale tawny) streaks on the underparts on a creamy white ground, whereas birds from Tucumán are duller, with more umbraceous streaks on a pale ground above, and with less rufescent (more hazel) streaks below.

Birds from Salta, Santiago del Estero, and Córdoba, Argentina, are all distinct; specimens from the first two of these provinces are heavily streaked above. The streaks are dark brown on a strongly buffy ground in the case of the birds of Salta, but on a pale buffy ground in the case of those from Santiago del Estero; the streaking is very heavy on the underparts of the birds of Salta, and the

streaks are cinnamon brown, but birds from Santiago del Estero are less densely streaked and the streaks are paler. Birds from Córdoba are dull, not very heavily streaked above, relatively speaking, but are about as densely but not so darkly streaked below as the birds of Salta. Series from Entre Ríos and Corrientes are also different from one another and all the other series mentioned above. They are both heavily streaked above, but the streaks are darker in the birds of Entre Ríos, more "blackish" than in any other populations of the species I have examined. The streaks on the underparts are very dense in birds from Entre Ríos and Corrientes, but somewhat darker, more rufescent in the birds of Entre Ríos, less so than in birds from Salta and about similar to the coloration of the streaks in the birds from Santiago del Estero. The saturation of the chestnut area in the tail is correlated with the general degree of saturation and density of the streaked pattern.

In short, the distinct geographical variation of *Coryphistera alaudina* is of the type common in many birds that are terrestrial, like the Alaudidae, or that spend much or most of their time foraging on the ground in open country—a type of geographical variation that is not satisfactorily expressed by the subspecies concept, in my opinion.

I have taken into consideration the view of Olrog (1963), who questioned the validity of *campicola* named by Todd from Bolivia. Olrog believed that this form probably represents only the winter plumage, as he stated that *C. alaudina* is only a winter visitor in Uruguay, Paraguay, and Bolivia. This statement requires confirmation, and I have not accepted it in defining the range of the species. I am grateful to Dr. K. C. Parkes from the Carnegie Museum for lending me the five paratypes of *campicola* to add to my material from Bolivia.

Coryphistera alaudina
Figure 6

DESCRIPTION: Upperparts chiefly warm dark brown, or blackish brown but not uniform, as the feathers, including the inner secondaries (tertials) and upper surface of the tail, are well edged with buff or pale rufous cinnamon, which produces a very heavy, massive, streaked pattern. These pale edges are only faintly indicated on the crown and hind neck, and the forehead is somewhat more rufous brown than the back; and above the forehead, and on the center of the crown, grow long, plumelike feathers which form a conspicuous crest, and are very dark blackish brown. Lores and an incomplete "eye-ring" white; the "ring" is narrow above the eye, completely interrupted with brown posteriorly, but broadens greatly below the eye into a conspicuous white crescentic patch; the ear coverts are hazel behind and below the crescent. The ground coloration of the underparts is whitish, but the feathers have broad pale fulvous brown centers which produce a very conspicuous, thickly streaked pattern. Wing dark brown, with the under wing coverts, axillaries, and edges of the inner web of the secondaries and inner primaries vinaceous cinnamon, and, on the upper surface of the wing, with the coverts conspicuously well edged with dull white with a faint pinkish buff cast, and with pale brown edges on the secondaries and primaries.

Tail rounded and distinctly shorter than the wing, composed of 12 rectrices that are slightly stiffened and blunt or rounded at the tip, and are bright chestnut on the basal two-thirds, or more, of the five outer pairs of rectrices, the tips of which are blackish brown. Bill relatively short, rather broad at the base, becoming compressed laterally anteriorly and slightly, but appreciably, decurved at the tip. Tarsus relatively short, thick and heavy, as well as the toes which have strong claws.

IMMATURE PLUMAGE: Similar to that of the adult, but crest much shorter, less developed, usually quite short, and streaked pattern more confused, less regular and distinct.

This species varies distinctly geographically (see discussion), but I do not believe any subspecies should be recognized. The description of the plumage given above is based chiefly on birds from Entre Ríos.

RANGE: Eastern Bolivia (Santa Cruz, Chu-

quisaca, and Tarija), western Paraguay and Argentina, south to Mendoza, San Luis, Córdoba, La Pampa, Santa Fe, and Entre Ríos (not recorded for Misiones); also western Uruguay, and extreme southwestern Rio Grande do Sul (Uruguaiana) in Brazil.

SPECIMENS EXAMINED: 122.

GENUS *EREMOBIUS*

Eremobius phoenicurus is a Patagonian genus and species distributed from the Rio Negro and Neuquén south to Santa Cruz (map 31), and for which less information exists than for *Coryphistera alaudina* and *Anumbius annumbi*. Peters (1923) observed *E. phoenicurus* in Rio Negro, and Wetmore (1926) in Neuquén. Sr. Samuel Narosky kindly sent me information on its ecology, behavior, and nest.

All the available information suggests that *Eremobius phoenicurus* is restricted to arid or semidesert regions with low sparse vegetation consisting of a few low trees or arborescent plants ("*arbustos*") and more or less widely spaced bushes and shrubs, many of them thorny, with bare sandy or stony ground between them. *Berberis* and cacti have been mentioned, and especially the "*Mata de Sebo*" bush (*Monttea*) of the family Scrophulariaceae, with which *E. phoenicurus* seems to be closely associated. A photograph of the habitat of *E. phoenicurus* was published by Wetmore (1926, pl. 17), which shows a flat plain with patches of low brush and isolated clumps of low bushes, but Wetmore also found *E. phoenicurus* on the slopes of rolling hills. The bird walks, hops, or runs rapidly on the ground with the tail erected or cocked at an angle over the back.

Peters (1923) found "a nest built on the ground in the middle of a *Chupa de Sangre* cactus . . . nicely made and arched over," but did not describe it further. This situation may have been unusual, because Narosky wrote me that he did not find nests in cacti, and because the five nests found by Pemberton in Rio Negro had all been built in the "*Mata de Sebo*" bush, from 3 to 6 feet (about 0.91 to 1.83 m.) above the ground. These five nests were "bottle-shaped," constructed of well interwoven thorny twigs, and the incubating chamber was lined with fine grass, matted in most instances with wool and feathers. Pemberton did not mention the size of the nest, its position, or the location of the entrance which, presumably, was at one side, at the mouth of the "bottle." I am indebted to the Western Foundation of Vertebrate Zoology, Los Angeles, for the unpublished field notes of Pemberton.

Narosky found two occupied nests in Chubut which were situated in the "*Mata de Sebo*" bush also, respectively, 1.20 and 1.50 m. above the ground. They were pear-shaped, horizontal, with the entrance at the side at the top of the "pear," and constructed also of interwoven thorny twigs. These twigs were 2 to 2.5 mm. thick at the entrance to the nest, but were coarser and thicker, 4 to 6 mm., on the roof of the nest. The long axis of the nest measured 50 to 55 cm., the shorter axis was 30 cm. high, and a tunnel, with an entrance 5 cm. wide, and 25 cm. long, which was slightly curved, led to the incubating chamber which was lined with many feathers, some wool, threads, and thistle down in one of the two nests. Narosky did not mention the shape or size of the incubating chamber, but it seems to be circular, with a diameter of roughly 12 or 13 cm., judging from the drawing of the nest he sent me. The eggs are white.

Eremobius phoenicurus

Figure 6

DESCRIPTION: Upperparts uniformly earthy grayish brown, with a narrow, but distinct, whitish superciliary streak, hazel ear coverts, and slight brownish streaks above and in front of the lores and at the gape. Underparts dingy white on the chin and throat which are faintly streaked with pale brownish gray, the breast and upper abdomen becoming pale brownish gray with dull, not sharply defined buffy white streaks, whereas the lower abdomen and under tail coverts are ochraceous. The under wing coverts and axillaries are partly buff, creamy white, and brown, and an ochraceous buff or cinnamomeous area exists at the basal portion and

edge of the inner web of the secondaries and inner primaries; the upper surface of the wing is brown, with pale, narrow buffy edges on the outer web of the primaries and secondaries.

The tail is rounded, distinctly shorter than the wing, composed of 12 rectrices that are slightly stiffened and blunt or rounded at the tip; the central rectrices are brown, darker and more dusky apically, more rufous at the base to a varying degree or wholly brown, but all the other five pairs of rectrices are strongly reddish chestnut at their basal half, or more, and are blackish brown at the distal half, or less, the reddish area being more extensive on the outer rectrices, decreasing progressively in size inwardly. Bill relatively long, strongly compressed laterally, and straight or virtually so. Tarsus relatively short, thick, and heavy, including the toes which have strong claws.

IMMATURE PLUMAGE: Very similar to that of the adult, but with faint pale tips to the feathers of the forecrown, and streaked pattern on the underparts very vague, scarcely evident on the breast, and lacking on the throat.

RANGE: Patagonia, from the Rio Negro and Neuquén south to southern Santa Cruz in Argentina, and probably neighboring eastern Magallanes in Chile.

This species is said to be occasional in Mendoza and La Rioja, but these records are doubtful; the authenticity of one specimen from Tierra del Fuego is also very questionable, as this specimen probably was taken in Santa Cruz; see also Olrog (1963).

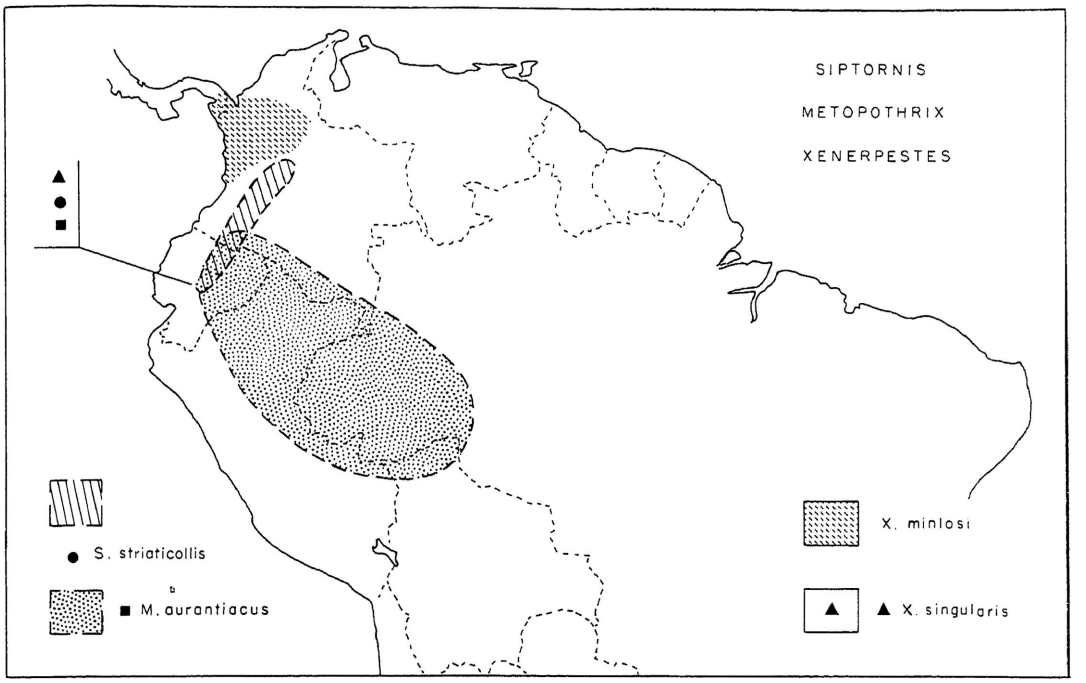
SPECIMENS EXAMINED: 22, including the type of *phoenicurus* in BM.

GENERA *SIPTORNIS, METOPOTHRIX,* AND *XENERPESTES*

I have listed these three genera together at the end of the Synallaxinae, following Hellmayr (1925) and Peters (1951), but it seems clear that they are not closely related. Their nearest relatives are most uncertain, but I believe *Siptornis* is related to the "*Cranioleuca*" species of *Certhiaxis,*[118] that *Metopothrix* belongs in the Synallaxinae without any doubt, and that *Xenerpestes* is best included in this subfamily also. *Siptornis* and *Metopothrix* are monotypic; *Xenerpestes* consists of two closely related species (*X. minlosi* and *X. singularis*) which I have reviewed in detail (1971b). In the case of *Siptornis* and *Metopothrix,* the species are respectively, *S. striaticollis* and *M. aurantiacus.*

The four species inhabit forested regions in northwestern South America (map 32), and are probably more or less highly arboreal, especially *Xenerpestes minlosi* and *X. singularis.* The nest of *Siptornis striaticollis* is probably built above the ground, but no other information exists on the ecology, behavior, and nests which might furnish clues to systematic relationships. I found that the nest of *S. striaticollis* is probably constructed above the ground only from two words, "building nest," written by the collector on the label of one specimen; no information at all exists for the other species, other than that a specimen of *X. minlosi,* collected by Wetmore (1951), "was shot high up in a tall tree."

The systematic affinities of *Xenerpestes* and *Metopothrix* have been considered to be extremely doubtful. Sclater (1890) included *Xenerpestes* in the Synallaxinae, but not *Metopothrix,* which he included (1888) in the Pipridae, though not without much doubt as he said that *M. aurantiacus* "is a very abnormal and singular form, which may perhaps belong elsewhere." Berlepsch (1903) removed *Metopothrix* from the Pipridae with prescience, saying it should be "placed in the family Dendrocolaptidae [Furnariidae] not far from *Xenerpestes.*" Hellmayr (1925) followed the opinion of Berlepsch, placing *Metopothrix* and *Xenerpestes* in the Furnariidae, as did Peters (1951) also, but with much reservation, saying "I retain *Metopothrix* and *Xenerpestes* in the Furnariidae with misgivings; nothing is known of their anatomy or life history, and their colors and color-pattern are not consistent with those exhibited by other Furnariidae." However, the skull of a recently collected specimen of *M. aurantiacus* was studied by Feduccia (1970), who placed this taxon incontrovert-



MAP 32. Geographical distribution of *Siptornis, Metopothrix,* and *Xenerpestes.*

ibly in the Furnariidae; see also Vaurie (1971a).

Berlepsch believed that *Metopothrix* "is closely allied to *Xenerpestes,*" and Hellmayr went further, stating "*Xenerpestes* is so closely related to *Metopothrix* that the propriety of its generic separation may well be questioned." I cannot agree with Berlepsch and Hellmayr, as the only morphological characters shared by these two genera (and also *Siptornis*) are that the birds are very small (table 17) and have a short tail which is distinctly shorter than the wing. The bills of *Metopothrix* and *Xenerpestes* are roughly similar in shape also, but it seems impossible to me to draw conclusions from these characters, which I believe are only an instance of convergence. In fact, the systematic position of *Xenerpestes* is still as doubtful as ever, but nothing seems to be gained by removing *Xenerpestes* from the position it presently occupies: "*On avait suggéré les Pipridés pour* Metopothrix *avant Feduccia [1970]. Les Formicariidés sont suggérés pour* Xenerpestes*; mais, après l'exemple de* Metopothrix, *il est plus sage de conserver* Xenerpestes *dans les Furnariidés en attendant qu'il puisse être étudié anatomiquement*" Vaurie (1971b, p. 125). As stated above, it seems best included in the subfamily Synallaxinae.

GENUS *SIPTORNIS*

Siptornis striaticollis
Figure 7

DESCRIPTION: Crown chestnut, with a small tuft of buffy white feathers at the base of the bill; hind neck pale raw umber, and back and rump pale rufous brown, with more rufous, chestnut, upper tail coverts; the feathers of the crown are slightly elongated, and those of the neck and mantle have very faint and very narrow dark brown edges. An incomplete pure white "eye-ring" exists; this ring is very narrow, palpebral for the greater part, but is very broad, though short, above the eye where it forms a conspicuous

TABLE 17
Measurements (in Millimeters) of *Siptornis*, *Metopothrix*, and *Xenerpestes*

Species	Wing			Tail			Bill		
	N	Mean	Range	N	Mean	Range	N	Mean	Range
S. striaticollis									
Male	1	—	67	1	—	48	1	—	11
Females	4	64.50	63–69	4	46.50	44–50	4	13.35	13–14
Both sexes	17	65.64	62–70	13	47.30	42–52	14	13.32	11–14.5
M. aurantiacus									
Males	4	59.50	58–61	4	44.75	42–46	4	12.62	12–13
Female	1	—	56	1	—	45	1	—	12.5
Both sexes	8	59.12	56–61	8	45.37	42–49	8	12.71	12–13
X. minlosi									
Males	3	59.16	58–61.5	3	45.33	43–47	3	13.83	13.5–14
Females	4	55.87	55–57.5	4	44.25	43–45	4	13.87	13–14.5
Both sexes	7	57.28	55–61.5	7	44.71	43–47	7	13.85	13–14.5
X. singularis									
Male	1	—	60	1	—	50	1	—	14.5

spot; the ear coverts and most of the face are chestnut. The underparts are pale olivaceous gray-brown on the throat and breast, the shaft of the feathers being dull white and creating a streaked pattern, the remainder of the underparts being ashy gray, with a brownish cast, and very faintly mottled with dull buffy white on the abdomen and under tail coverts, but umbraceous ocher on the lower flanks. The under wing coverts and axillaries are very bright pale orange, and a duller orange area exists along the edge of the inner web of the secondaries and inner primaries, whereas the upper surface of the wing is white at the upper edge of the wing, bright reddish chestnut on the coverts, and rufous brown (of about the same shade as the back) on the innermost secondaries (tertials), and edge of the outer web of the other secondaries and of the primaries.

Tail distinctly shorter than the wing (tail/wing ratio: 0.71), moderately graduated, composed of 12 rectrices which are slightly stiffened, acuminate at the tip, and wholly and uniformly bright pale reddish chestnut. Bill short, nearly straight; feet noticeably weak, as the tarsus is short and thin, weak, as well as the toes.

RANGE: Colombia, in the upper and middle Magdalena Valley and along its slopes; also eastern Ecuador in the region east of Baños. The range is unknown between Colombia and Ecuador and may be interrupted.

SPECIMENS EXAMINED: 17.

GENUS *METOPOTHRIX*

Metopothrix aurantiacus

Figure 7

DESCRIPTION: Dull olive on the upperparts, with the exception of the forecrown which is reddish orange and bright golden yellow, and the feathers of which are plush-like and reddish orange at the base of the bill and forehead, becoming elongated posteriorly, slightly stiffened, semi-erect, and bright glossy golden yellow. A faint, not well defined, buffy superciliary streak, and narrow, buffy palpebral "eye-ring" exists. Chin and throat glossy golden yellow or yellowish orange, with the feathers of the upper throat slightly stiffened, the yellowish pigment invading the upper breast to a slight and irregular extent, the remainder of the underparts being dingy pale gray with a slight olivaceous cast. The under wing coverts and axillaries are very pale lemon yellow, and a whitish

area extends along the edge of the inner web of the secondaries and of the inner primaries; on the upper surface of the wing, the innermost secondaries (tertials) are olivaceous, and the other remiges and coverts are fuscous, with narrow, dingy, pale edges on the outer webs.

Tail distinctly shorter than the wing (tail/wing ratio: 0.76), slightly graduated, composed of 12 rectrices that are slightly stiffened and which are rounded, blunt, or very slightly acuminate at the tip, and are wholly and uniformly olivaceous gray. Bill short, somewhat broad at the base, but becoming compressed laterally anteriorly and slightly decurved. Tarsus and feet well developed, very pale, buffy orange in specimens, probably yellowish or the color of flesh in life.

IMMATURE PLUMAGE: Differs from that of the adult by having the yellow pigment reduced only to a slight trace at the base of the feathers of the forehead, these feathers and those of the forecrown being normal in structure, not plushlike, elongated, or stiffened. The yellow pigment is lacking also on the chin and throat which are dull olivaceous buff, and the whole of the underparts is more dingy, darker than in the adult, with the feathers tipped and bordered more or less narrowly and faintly with dusky gray. See also Traylor (1972) for a description of this plumage and of the postjuvenal molt.

NOTE: The rectrices of *Metopothrix aurantiacus* are fully webbed and normally integrated, not decomposed, although Feduccia (1970) stated that the tips of the rectrices lack barbs in the specimen he has examined, a fact to which he attaches systematic importance. However, it is probable that the tips of the rectrices were abraded by wear, frayed, in the specimen concerned, as they do not lack barbs and are well integrated, when fresh or not badly worn, in the specimens I have seen, and also in the larger series studied by Traylor.

RANGE: Southeastern Colombia (Umbria and Rio Pilcomayo), south through eastern Ecuador, and eastern Peru, to northern Bolivia (Riberalta), east to western Brazil (upper Solimões and upper Purús).

SPECIMENS EXAMINED: 9, including the type and cotype of *aurantiacus* in BM.

GENUS *XENERPESTES*

Xenerpestes is composed of two species, *X. minlosi* in eastern Panama and Colombia, and *X. singularis* in eastern Ecuador (map 32), which I have reviewed and discussed in detail (Vaurie, 1971b). These two species are not well known, especially *X. singularis*, which is very probably the rarest and the least known of all the Furnariidae, known so far from only a single specimen in the Warsaw Museum. About a dozen specimens of *X. minlosi* seem to have been collected, but no information exists on the ecology and behavior of this species, other than that one specimen was collected from a tall tree, high above the ground. No information of any kind exists for *X. singularis*.

I had not seen the specimen of *Xenerpestes singularis* when I wrote my first revision (1971a) and had been misled by the remarks of Berlepsch (1903) in believing that *X. minlosi* and *X. singularis* were probably conspecific, as the two birds represent one another geographically and Berlepsch had stressed they were very similar. However, I found that Berlepsch was not correct when I compared directly the type of *X. singularis* (which is in perfect condition) to *X. minlosi* during my visit to the Warsaw Museum.

It seems unnecessary to repeat my observations (1971b) as the two species are described below. They are very distinct morphologically, in structure and in coloration and its pattern. *Xenerpestes singularis* has a very well graduated tail, is strongly rufous on the forecrown, yellow and heavily and regularly streaked on the underparts, and its wing is not barred with white; whereas *X. minlosi* does not have a well graduated tail, is blackish on the forecrown, whitish below with a few, not very distinct gray spots, and has two regular, conspicuous white wing bars. A number of other differences exist also. In other words, *X. singularis* and *X. minlosi* are very distinct from one another morphologically, although it is clear that they are closely related and congeneric.

KEY TO THE SPECIES OF *XENERPESTES*

Forecrown strongly rufous; underparts yellow and regularly and heavily streaked; tail well graduated ..... *singularis*

Forecrown blackish; underparts dingy white with a slight yellowish cast, with a few, indistinct grayish spots on the upper breast and sides; tail not well graduated ..... *minlosi*

Xenerpestes minlosi

Figure 7

DESCRIPTION: Upperparts olivaceous gray, with a darker, blackish crown, which is uniform, or has very narrow yellowish shaft streaks, the feathers on the anterior part of the crown are somewhat elongated and lanceolate in shape, and slightly stiffened. Lores and slightly elongated and stiffened feathers at the base of the sides of the forehead, and in front of the eye, buffy white, and forming "eyebrows," these pale "eyebrows" merging posteriorly into a whitish superciliary and post-ocular streak. Underparts very pale, dingy white, with a slight yellowish cast, and with a few, not very distinct gray or dusky spots on the upper breast and at its sides; the lower flanks becoming pale olivaceous gray as well as the under tail coverts. Under wing coverts, axillaries, carpal edge of the wing, and edges of the inner web of the secondaries and inner primaries whitish with a faint yellowish cast; whereas the upper surface of the wing is fuscous or blackish brown, with distinct, regular, white tips on the middle and greater coverts which form two conspicuous wing bars.

Tail distinctly shorter than the wing (tail/wing ratio: 0.78), not well graduated as the three inner pairs of rectrices are equal in length or subequal, and the outer pair is long, projecting far beyond the under tail coverts; composed of 12 rectrices that are not stiffened, are blunt or rounded at the tip, and are wholly fuscous gray, uniform with the exception of a narrow whitish edge along the inner web of the three outer pairs of rectrices. The bill is relatively big and strong, broader at the base, but becoming compressed laterally anteriorly and slightly decurved. Feet moderately strong.

IMMATURE PLUMAGE: Differs from that of the adult by being ashy gray on the face and underparts, by having a very indistinct superciliary streak, and by lacking altogether the white spots at the tips of the middle and greater upper wing coverts. The underparts are almost uniformly gray, although the feathers of the throat, breast, and upper abdomen are faintly edged with darker gray. The immature specimen described and figured by Berlepsch (1903, pl. 6) is not in true juvenal plumage, but in one that appears to be an intermediate stage between the adult plumage and the first juvenal plumage described here.

This species seems to vary slightly geographically as specimens from Panama and from the Pacific slope of Colombia south to the lower Rio San Juan, are somewhat darker on the upperparts, and more blackish and uniform on the forecrown than specimens from the remainder of the range in Colombia; in the latter, the forecrown is very slightly streaked as a rule, but the difference is not constant.

RANGE: Eastern Panama near the border with Colombia, and northwestern Colombia (map 32).

SPECIMENS EXAMINED: 8.

Xenerpestes singularis

DESCRIPTION: Upperparts slaty gray with a very faint olivaceous cast (more grayish and "ashy" than in *Xenerpestes minlosi*), and differing also from *X. minlosi* by being strongly rufous on the forecrown rather than blackish; the feathers on the anterior part of the crown are better elongated in *X. singularis* than in *X. minlosi,* more lanceolated, better stiffened, burnt sienna on the forehead, becoming considerably brighter rufous posteriorly. Lores grayish, superciliary streak yellowish, broader and better defined than in *X. minlosi,* and prolonged farther back to the nape as a post-ocular streak. Underparts dark chrome yellow, very regularly and heavily streaked with dark gray from the up-

per throat to the lower abdomen, with broad, dark ochraceous or fulvous edges, lacking in *X. minlosi*. Under wing coverts and axillaries yellowish, with a somewhat paler edge along the inner web of the secondaries and inner primaries; upper surface of the wing gray (and of the same color as the back, but without an olivaceous cast), with two or three very small, hardly distinct, whitish spots at the tips of the coverts, lacking the conspicuous white wing bars of *X. minlosi*, and also the conspicuous white carpal edge on the wing of *X. minlosi*.

Tail shorter than the wing (tail/wing ratio: 0.83), very well graduated (see Vaurie, 1971b, fig. 2 which compares the graduation of the tail in *Xenerpestes singularis* and in *X. minlosi*), composed of 12 rectrices that are not stiffened, are blunt or rounded at the tip, and are wholly and uniformly slaty gray. Bill and feet similar to those of *X. minlosi* but the bill is somewhat more slender, less thick in *X. singularis*.

RANGE: Eastern Ecuador, where it is known only from Mapoto, east of Baños.

SPECIMEN EXAMINED: 1, consisting of the type of *X. singularis* in ZIW, the only specimen collected to date.

SUBFAMILY PHILYDORINAE

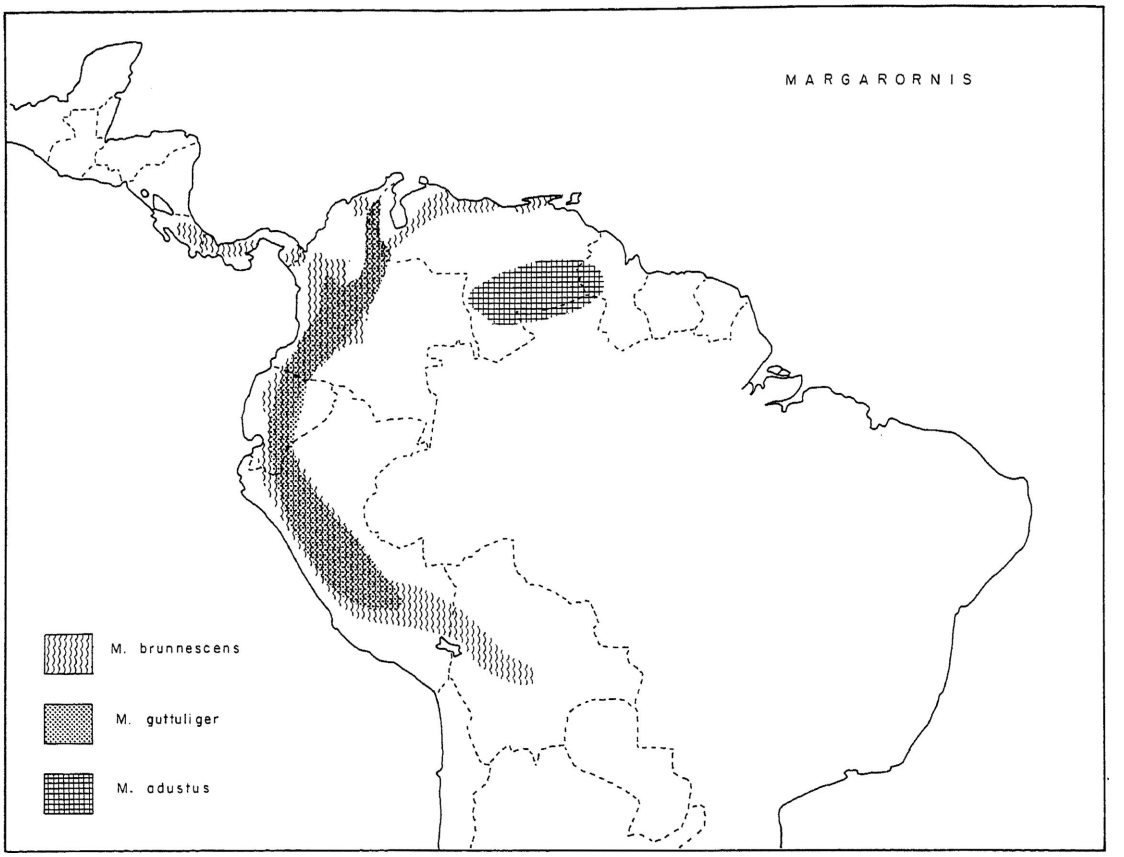
GENUS *MARGARORNIS*

Margarornis is composed of six species: *M. adustus, M. guttuliger, M. brunnescens, M. rubiginosus, M. stellatus,* and *M. squamiger*. Two more forms (*M. tatei* and *M. bellulus*) were included provisionally in the list of the species of *Margarornis* in my first revision (1971a), but after more study I concluded that *tatei* is conspecific with *M. brunnescens* and *bellulus* with *M. squamiger*; this opinion confirms the reservations that I had made in 1971 about the status of *tatei* and *bellulus*.

All six species, with the exception of *Margarornis adustus,* were quite correctly considered to be congeneric before Cherrie proposed a new genus (*Premnoplex*) for *brunnescens* in 1891, and Ridgway another new genus (*Premnornis*) for *guttuliger* in 1909. Taxon *adustus* was believed to be a member of the genus *Synallaxis* until Chapman demonstrated in 1929 that *adustus* "agrees with *Premnoplex* and *Margarornis*" in some characters. Chapman stated, however, that *adustus* is "not typical of this group," and he proposed the new genus *Roraimia* for it, although he granted that *Roraimia* lacks "structural characters that are distinctively its own."

Thus three of the six species (*Margarornis adustus, M. guttuliger,* and *M. brunnescens*) have been separated as monotypic genera although it seems quite clear that all six species are probably closely related. They are not uniform, to be sure, but all the variation in structural characters (such as general size, shape of the wing, or relative proportions of the lengths of the tarsus and toes), and in characters of coloration and of pattern seem to me of no more than specific importance. Mayr and Phelps (1967) concluded independently that "*Roraimia, Premnornis,* and *Premnoplex* certainly appear to be congeneric," and that, together with *Margarornis,* they form a single "complex." I believe that all the four genera should be merged, *Margarornis,* 1853, possessing a very long priority.

Wetmore (1972), commenting upon this opinion (first expressed by me in 1971), believed that *Premnoplex* should be retained "pending further information" because the wing of *brunnescens* is more rounded than that of *Margarornis rubiginosus* and *M. squamiger* and is supported by weaker bones, *brunnescens* being also a smaller bird. These differences are only species characters in my opinion, as stated above, and I am more impressed by a great similarity of the unusual spotted pattern of the un-

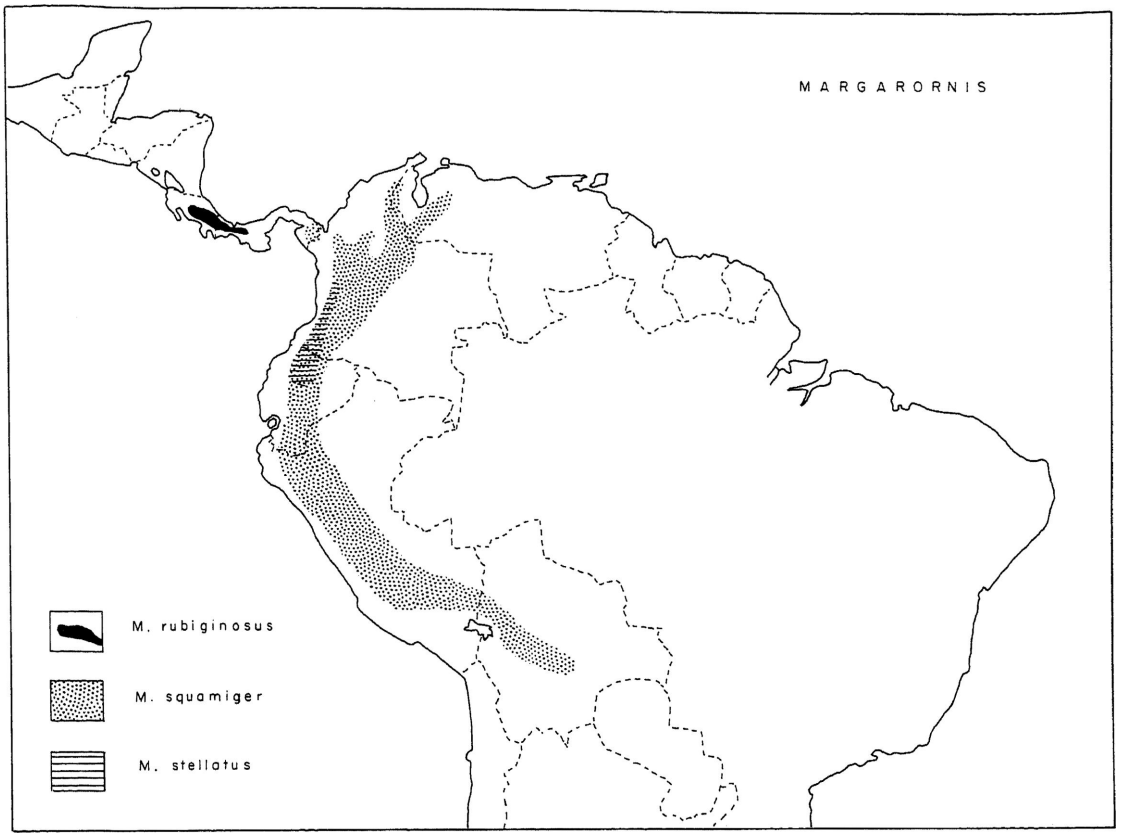


MAP 33. Geographical distribution of three species of *Margarornis*.

derparts, and a general similarity in geographical distribution, in ecology, and in behavior (see below).

The systematic position of *Margarornis* within the family is uncertain and has varied widely in different treatments of the Furnariidae. It seems to me (Vaurie, 1971a) that *Margarornis* is best placed, on the whole, in the Philydorinae at the head of the sequence of their genera, but Sclater (1890) believed that *Margarornis* was allied to *Sittasomus*, a member of the family Dendrocolaptidae. Sclater and other authors, such as Taczanowski (1884), who considered that *Margarornis* was a dendrocolaptid, were probably influenced by the scansorial habits of *Margarornis*, but climbing forms exist in the Furnariidae, which show no evidence of close relationship, as well as in many of the other passerine families. *Margarornis* was transferred to the Furnariidae when it became better known and when the family division between the Furnariidae and Dendrocolaptidae was adopted. Ridgway (1911) supported this division into two families and listed *Margarornis* after *Xenops*, perhaps because he described both genera as "small scansorial Furnariidae."

A few years later, Chapman (1917) listed *Margarornis* and *Xenops* not far apart, in a sequence consisting of *Xenops*, *Sclerurus*, and *Margarornis*, although *Sclerurus* is almost entirely terrestrial and a much larger bird. Hellmayr (1925) recognized a separate subfamily, the Margarornithinae, for *Margarornis* and also *Premnornis* and *Premno-*



MAP 34. Geographical distribution of three species of *Margarornis*.

plex. I believe *Premnornis* and *Premnoplex* should be merged with *Margarornis* as stated above, and this subfamily (which thus becomes monogeneric) is ranked by Hellmayr between the Synallaxinae and Philydorinae. Feduccia (1973) stated that "the margarornithines [*Margarornis, Premnornis* and *Premnoplex* are recognized by Feduccia] are clearly 'ovenbirds' and are probably closely allied to the synallaxines, at least in cranial osteology. I would recommend their placement at the end of the Synallaxinae." However, I do not believe that *Margarornis* is closely related to the typical Synallaxinae and it seems best included in the Philydorinae, most genera of which are scansorial and have developed a foot structurally adapted for climbing, as is the case for *Margarornis*.

All the species of *Margarornis* are montane and are distributed from Costa Rica to Bolivia, with an outlying colony (*M. adustus*) in the highlands of southern Venezuela and neighboring Guyana, which were reached probably from the ranges of northern Venezuela and the Andes (maps 33 and 34). The altitudinal range varies from about 1000 m. up to timberline; *M. squamiger* has been recorded higher than the other species, to nearly 3900 m. in Colombia.[119] The lowest altitude at which any species of this genus seems to have been encountered is about "2000 feet" (about 609 m.) in Costa Rica in the case of *M. brunnescens* according to Skutch (1967), who quotes a report of Carriker. However, this low altitude is probably unusual, as Skutch remarks that *M. brunnescens* in Costa Rica is not common below about 1524 m., except on the Caribbean

slope where it is abundant down to about 1067 m.—but *M. brunnescens* also ascends to the timberline on the high volcanoes. The highest records that I have found are about 1850 m. for *M. adustus,* about 2200 m. for *M. stellatus,* about 2750 m. for *M. guttuliger, M. brunnescens,* and *M. rubiginosus,* and about 3900 m. for *M. squamiger.* The latter is widely distributed and the altitude to which it ascends reaches or exceeds 3500 m. throughout its range, except in the case of its isolated population (*bellulus*) of eastern Darién, Panama, which Wetmore (1972) said has been collected at altitudes varying from 1370 to 1580 m.

The information on ecology and behavior is very far from complete, but, as far as known, *Margarornis* seems to frequent dense and cool humid forests where moss and epiphytes grow on the trunks or branches of the trees. I have found no definite information for *M. adustus* and *M. guttuliger,* but, in the case of *M. adustus,* the vegetation in which this species has been collected was described as densely matted and humid "brush-forest," or "rich subtropical forest," near streams or not.[120] Meyer de Schauensee (1970) described the habitat of *M. guttuliger,* and also that of *M. stellatus,* as "wet, mossy forest."

All the species of *Margarornis* seem to be arboreal and more or less scansorial. In the case of *M. brunnescens,* for which the most complete published information exists, Slud (1964) described the habitat and general behavior of this species in Costa Rica as follows. "This inconspicuous furnariid is at home in the dark dank understory of the cool and misty highland forests. Occasionally it visits an opening with densely foliaged trees and stumps covered with moss and epiphytes. It climbs trunks and creeps along limbs, sometimes on their under sides, like a spurting little woodhewer and clings to twigs like a xenops. Nervously active, it explores the vegetation rising from the ground cover up to medium heights in the trees. Generally it occurs alone."

Skutch (1967) described the habitat and behavior of *Margarornis brunnescens* in very similar terms but made some remarks on the function and structure of the tail which gave a false impression of its structure. Skutch said "Although this ovenbird sometimes works up vertical trunks with its body upright and its tail pressed against the bark, in the manner of a woodcreeper, on the whole it seems to depend little upon its strongly barbed tail feathers for support."

However, the tail of *Margarornis brunnescens* is not strongly barbed. It is not "barbed" in any member of the genus and is not adapted for true bracing against bark as in the woodhewers and woodpeckers. The rectrices are soft, but flexible, with the tip more or less sharply attenuated, the rachis being prolonged beyond the vane to a degree varying with the species, and nearly bare of barbs. That the tail is not used as a brace and probably does not provide firm support in climbing is suggested by the fact that the tips of the feathers are more or less intact and very little worn in most specimens.

The only other species for which I have found some published information are *Margarornis rubiginosus* and *M. squamiger.* Slud (1964) and Wetmore (1972) compared *M. rubiginosus* to a wren. Slud stated that *M. rubiginosus* "frequents thickety, overgrown edges, clearings with trees, and woodland. It hitches itself lightly up the trunks in the manner of a little woodhewer but with the erratic side-to-side spurts of a trunk-climbing wren. The pointed soft tail provides little support in climbing, yet sometimes serves as a stationary prop. The bird also creeps along branches and clings to thickety, bamboo-like growth. Rarely, it drops to the ground. It either accompanies traveling mixed bands or forages alone. Constantly searching for food, the bird shows a special interest in the moss clinging and hanging everywhere."

Wetmore (1972) said "In my few encounters [with *Margarornis rubiginosus*] I have found these quiet little birds in heavy forest on the higher mountain slopes, ranging alone or occasionally in pairs. Some have worked over dead leaves lodged among parasitic plants, or through the mossy growth covering the branches. Others have climbed up vertical tree trunks, with the tail braced,

woodpecker-fashion as a support. In this they resemble wood-creepers, though it will be noted that the tail tip is more flexible. Their actions on the whole, however, except for this use of the tail, are more those of a wren."

I have discussed the structure and function of the tail above. I agree with Slud, not Wetmore, that the tail does not provide much support to *Margarornis* when climbing.[121]

In a very short note on *Margarornis squamiger* Sztolcman (in Taczanowski, 1884) said [translation]: "Its habits resemble those of xenops. It searches for food by climbing up vertical tree trunks [but] sometimes it hangs down also at the ends of fine twigs, in the manner of a tit-mouse."[122]

The nest has been described only in the case of *Margarornis brunnescens*. Skutch (1967) found one nest that had been built within a niche, and was partly covered by a flap of bark, on a steeply inclined rotting log that had fallen across a small stream. The log was "verdant with mosses and ferns and other epiphytic growths," and the bulky and compact nest was constructed of "mosses, liverworts, and fine, dark-colored rootlets, evidently of epiphytic plants." It was entered from the bottom by a vertical tube, about 4 cm. in diameter and about 8 cm. long. This tubular entrance led into a chamber where the two eggs had been laid in a shallow depression on top of the main mass of the material of which the nest was constructed. The chamber was about 5.5 cm. in diameter, by about 7.5 cm. high, "and its ceiling was the rotting wood of the supporting log, with no covering." A drawing of the nest was given by Skutch.

Skutch also mentioned roosting nests constructed of moss and similar in shape to the breeding nest described above, but less massive, that he observed attached "to the uneven rock-face of a vertical highway cutting, in the heavy, humid forest of the coastal range" near Rancho Grande, Venezuela.

F. Gary Stiles has told me he found a nest of *Margarornis brunnescens* in Costa Rica which was basically similar to the breeding nest described by Skutch. Stiles said this nest was built largely of moss, into which a few leaves and twigs had been incorporated, and was constructed at the bottom of a crotch on a fallen log which was about 50 cm. in diameter. The nest was roughly spherical in shape, about 30 cm. in diameter, with the entrance at the bottom.

G. V. N. Powell told me he found two nests, also in Costa Rica, built chiefly of moss. One was built within a depression, or some hollow of a tree trunk, about 9 m. or a little more above the ground. The other was built within a hanging cluster of broken branches, covered with moss, about 5 m. above the ground.

It is believed that the nests of the other species are constructed also of moss, or largely so, on appropriate support on the limbs or trunks of trees.

Morphological Variation

All six species of *Margarornis* are small (table 18). The means of the wing length vary in round numbers from only 63 to 82 mm., with an average of 73 mm. The tail is somewhat shorter than the wing in all the species, the mean lengths in round numbers, varying from 59 to 72 mm., with an average of 67.5 mm. The ratio between the length of the tail and of the wing varies from 0.87 to 0.96, with an average of 0.93.

The tail is composed of 12 rectrices that are more or less graduated. In some species, such as *Margarornis squamiger*, graduation is relatively unpronounced. The integration of the webs varies from relatively firm to relatively loose, but the webs are not decomposed. The tips of the rectrices are sharply acuminate, and in most of the species the rachis is prolonged conspicuously beyond the vane to a varying degree as a thin filament which is nearly bare of barbs. The feathers are soft in texture, but the tail is elastic and slightly stiffened when palpated and flexed somewhat as a whole. The middle toe is long and the basal phalanges of the front toes are more or less united, as in all the other members of the Philydorinae.

The plumage is brown, rufous, or reddish brown on the upperparts, with or without some contrast between the coloration of the

TABLE 18
Measurements (in Millimeters) of *Margarornis* and *Lochmias*

	Wing			Tail			Bill		
Species	N	Mean	Range	N	Mean	Range	N	Mean	Range
M. adustus									
Males	11	68.09	62–72	10	63.30	59–67	11	15.90	15–16.50
Females	12	65.50	63–70	10	63.20	60–67	11	16.13	15.50–17.50
Both sexes	27	66.81	62–72	24	63.66	59–72	25	16.04	15–17.50
M. guttuliger									
Males	15	70.46	67–75	14	68.42	64–74	14	16.69	16–17.50
Females	10	68.40	66–75	10	63.40	58–68	10	16.25	15.50–17.50
Both sexes	33	69.60	66–75	31	67.09	58–74	31	16.57	15.50–17.50
M. brunnescens									
Males	70	63.70	60–70	63	59.22	54–68	67	17.56	15.50–20
Females	41	62.43	59–68	38	57.89	50–66	41	17.41	15.50–20
Both sexes	125	63.31	59–70	113	59.03	50–68	122	17.47	15.50–20
M. rubiginosus									
Males	20	77.42	71–83	20	73.45	64–82	20	15.04	14–16
Females	18	74.88	70–79	17	70.88	67–74	15	14.89	14–16
Both sexes	41	76.32	70–83	40	72.45	64–82	38	14.98	14–16
M. stellatus									
Males	5	81.40	79–85	5	72.40	67–75	5	16.00	15–17
Female	1	—	78	1	—	68	1	—	16.5
Both sexes	13	82.23	76–87	13	71.46	67–75	13	16.17	15–17.50
M. squamiger									
Males	65	80.79	73–86	60	73.10	61–81	64	14.96	14–17
Females	48	78.97	73–84	47	70.67	61–79	48	15.00	14–17
Both sexes	126	79.98	74–86	119	72.30	61–81	125	14.98	14–17
L. nematura									
Males	42	71.83	66–81	40	48.70	45–55	42	22.94	21–26
Females	37	69.28	65–78	36	47.50	43–53	38	22.18	20–25
Both sexes	87	70.86	65–81	84	48.19	43–55	87	22.67	20–26

crown and mantle, and with or without pale buffy spots or short streaks on the feathers of the hind neck or scapulars. The underparts are heavily flammulated or spotted beyond the pale clear throat, or the spots are much reduced, only to the base of the throat and upper breast. The spotting is very distinctive; in *Margarornis squamiger* and *M. brunnescens,* where the spots are best developed, the pattern consists of large white, whitish, or buffy spots which are narrowly edged with black and are teardrop-like, or pearl-like in shape (hence the name *Margarornis* which means a pearly bird). These pearly spots are developed to a varying degree and this very unusual pattern exists only in this genus and in the monotypic genus *Lochmias.*

The coloration of the tail is uniform in all six species, darker and browner in *Margarornis brunnescens,* brighter and chestnut in the other species.

Phylogeny

The three species, which appear to be the most closely related, are *Margarornis rubiginosus, M. stellatus,* and *M. squamiger,*

although the spotted or pearly pattern is much better developed in *M. brunnescens* than in *M. stellatus* and especially in *M. rubiginosus* in which the spots are obsolete and very imperfectly developed. However, the structure of the tail suggests that the most closely related species are *M. rubiginosus, M. stellatus,* and *M. squamiger*; the structure of the tail is identical or virtually so in these three species.

The other three species (*Margarornis adustus, M. guttuliger,* and *M. brunnescens*) share a common origin, but are perhaps more evolved than the other three species.

Geographical Variation

Geographical variation exists or has been described in four species (*Margarornis adustus, M. brunnescens, M. rubiginosus,* and *M. squamiger*), but it is well indicated in *M. brunnescens* and *M. squamiger* only.

The range of *Margarornis brunnescens* (map 33) is interrupted and a number of subspecies have been named. One form (*tatei*) is quite distinct, but some of the populations that have been separated as "subspecies" differ only slightly, if at all. For instance, Wetmore (1972) rejected the validity of one of the three "subspecies" that have been named from Panama, and characterized a second from these three of Panama as only "very slightly browner above; buff of throat faintly paler," although I cannot distinguish at all the form concerned. Moreover, individual variation is well marked in *M. brunnescens,* especially in the populations of South America, a fact which has not been taken sufficiently into consideration.

However, the populations of northeastern and coastal Venezuela are quite distinct and are separated by some authors as a distinct species which was named *tatei* by Chapman in 1925. *Margarornis brunnescens tatei* differs from the other populations of *M. brunnescens* by having some small whitish spots and streaks on the nape; by having more whitish, less buffy or ochraceous, spots on the underparts which are less regularly defined than in the other populations of *M. brunnescens,* tending to coalesce in *M. b. tatei*; and also by having a distinctly longer bill than most of the populations of *M. brunnescens*. But Chapman was not misled by these differences and was well aware that *tatei* was closely related to *M. brunnescens*. Chapman mentioned that the long bill of *tatei* is matched by the nearest geographical representative of *M. brunnescens,* and that the difference in the "markings of the underparts may be considered a difference of degree [only]," but, nevertheless, he thought that the small spots and streaks on the nape of *tatei* warranted its recognition as a distinct species. Chapman was not aware, however, that these spots exist to some degree in individuals of *brunnescens,* especially from the southern extremity of its range, and later Peters (1951) combined *tatei* with *M. brunnescens* (as well as another population named from the Paria Peninsula of Venezuela which does not merit consideration as it is virtually indistinguishable from *tatei*). I had recognized *tatei* provisionally as a separate species in my first revision (1971a), with the reservation that it might be conspecific with *M. brunnescens*. After examining more material I now agree with Peters that *tatei* is conspecific with *M. brunnescens*.

The range of *Margarornis squamiger* is interrupted (map 34) and the population (*bellulus*) of eastern Darién, Panama, and probably neighboring Colombia, is quite distinct morphologically from the birds from the remainder of the range which extends from western Venezuela and Colombia to Bolivia. *Margarornis squamiger bellulus* is normally considered to be a separate species closely allied to *M. s. squamiger,* but as the difference is one of degree only and the two forms are incontrovertibly very closely related geographical representatives it seems more candid to me to admit only one species. *Margarornis squamiger bellulus* differs from *M. s. squamiger* by being duller in coloration on the upperparts, more dull rufous brown on the mantle, rather than chestnut, and, especially, by being less spotted on the underparts; in *M. s. bellulus* the spots are distinctly much reduced in size and in number, on a duller, browner ground coloration than in *M. s. squamiger*.

In the remainder of the range (the Andes) a distinct cline in coloration runs from north to south. Birds from the northern end of the range (Venezuela and Colombia to roughly northern Peru) have a more brownish crown, a white or more whitish post-ocular streak, and the "pearly" spots on their underparts are also white or whitish, and these populations have been named *perlatus*. The color of the crown becomes more rufous farther south in Peru, and the post-ocular streak and pearly spots of the underparts become very slightly tinged with yellow. In view of this clinal variation and the fact that *M. s. bellulus* clearly represents a separate evolutionary line, I believe it is not constructive to admit subspecies, other than *M. s. bellulus* in eastern Darién, and nominate *M. s. squamiger* in the remainder of the range.

The populations of *Margarornis adustus* which inhabit the isolated mountains of southern Venezuela and western Guyana are not perfectly uniform. For instance, the birds of Mount Duida tend to be somewhat brighter, less dark, than those of Roraima (on which *M. adustus* was based by Salvin and Godman) and of other mountains such as Auyán Tepui, Cerro Paraque, and several others. However, the geographical variation is slight, not of taxonomic importance.[123]

The geographical variation of *Margarornis rubiginosus* is the most trivial, but the birds of the highlands of western Panama tend to average somewhat brighter throughout, and less spotted on the breast, than those of the highlands of Costa Rica.

KEY TO THE SPECIES OF *MARGARORNIS*

1. Underparts very heavily streaked, flammulated, or spotted over the whole of the breast, and on the center and lower abdomen ... 3
   Underparts not streaked, flammulated, or spotted on the abdomen, but with or without small buffy spots on the breast with very small blackish centers 2
2. Underparts strongly rufous, burnt sienna, or reddish chestnut; with or without extremely faint and small dusky or blackish spots .... *rubiginosus*
   Underparts tawny ochraceous; with small, but distinct, buffy spots on the breast that have very small blackish centers ..... *stellatus*
3. Sides of neck spotted or streaked with buff, whitish, or white; and post-ocular streak buff or whitish, and more or less interrupted 4
   Sides of neck uniformly strong, rich reddish chestnut, not spotted or streaked; post-ocular streak conspicuous and broad, not interrupted, and of the same color as the sides of the neck, broadening into the reddish area on the sides of the neck ..... *adustus*
4. Mantle and whole back very bright reddish chestnut; crown rufous brown; nape and hind neck uniform, not streaked or spotted. Underparts, below the pure white throat, very profusely spotted with teardrop-like or pearl-like white spots that are margined with black ..... *squamiger*
   Mantle and back dark rufous brown, or mahogany; crown blackish; nape and hind neck more or less spotted or streaked with pale buff. Underparts heavily streaked, flammulated, or spotted with dull white or buff below the throat which is buffy or dull white 5
5. Tail dark dull brown; outer edge of the inner web of the remiges dark brown, or with an ill-defined pale edge ..... *brunnescens*
   Tail bright chestnut; outer edge of the inner web of the remiges cinnamomeous, as well as the bases of most remiges, the pale area being well defined ..... *guttuliger*

LIST OF THE SPECIES

Margarornis adustus

DESCRIPTION: Crown and ear coverts very dark raw umber brown with a rufous cast, uniform on the crown, but with a few faint and very small cinnamon shaft streaks on the coverts which are darker, more blackish than the crown. The dark crown and ear coverts are conspicuously divided by a broad, well developed, post-ocular streak which is a rich, strong reddish chestnut, and merges posteriorly into an area of the same color at the sides of the neck and across the nape; the reddish post-ocular streak is prolonged, more or less distinctly, anteriorly over the eye to the base of the forehead. Back, upper tail coverts, and exposed webs of the remiges and their upper coverts, red-brown, but less bright than on the nape, sides of neck, and post-ocular streak.

Throat white, becoming more creamy white and slightly tinged with cinnamon posteriorly at the sides, and flammulated with dark brown on the lower throat. The feathers of the lower throat, breast, and center of abdomen are broad, somewhat elongated, and are buffy or cinnamomeous, but more or less narrowly edged with very dark brown at the sides, but not at the apex of the feather; the result is a heavily flammulated appearance. The flanks are dark raw umber brown, the under tail coverts are red-brown with pale ferruginous shafts and tips. The wing is brown, without a pale area, and the tail is uniformly chestnut, graduated, slightly stiffened, and the webs of the rectrices are normally, but not very firmly integrated. The apex of the longer rectrices is very sharply acuminate, the rachis being well prolonged beyond the vane, and becoming nearly bare of barbs distally.

IMMATURE PLUMAGE: Differs from the adult plumage by having a more confused, much less distinct pattern, especially on the underparts, the breast and abdomen being mottled, rather than flammulated. The throat is also less white and its feathers are very narrowly, but distinctly, tipped and margined with dark gray-brown. On the upperparts, the crown is dull blackish brown, the back plain brown, and the strong rufous cast of the adult is lacking, as well as its rufous post-ocular streak, or this streak is only very poorly indicated.

RANGE: Mountains of southern Venezuela to those in neighboring Guyana and on the border of Brazil. The altitudinal range recorded is from about 1432 to 1850 m.[124]

SPECIMENS EXAMINED: 31, including the types of *adustus* in BM; of "*duidae*" in AMNH, and of "*obscurodorsalis*" in the Phelps Collection, on deposit at AMNH.

Margarornis guttuliger

DESCRIPTION: Upperparts dark raw umber brown, more blackish brown on the crown than on the back, with small buff centers to the feathers of the forecrown; these buffy centers become less distinct on the remainder of the crown, but reappear at the sides of the neck, nape, and upper back, and more or less abundant and well defined along the shaft of the feathers, forming small streaks. The rump is reddish brown, with faint, dusky edges to the feathers; the upper tail coverts are bright reddish chestnut and uniform. The buffy spots at the sides of the neck coalesce more or less behind the eye to form a poorly defined post-ocular streak. The upper throat is buffy yellow, becomes darker, more pale chamois posteriorly; the feathers of the lower throat, breast, and from the center of the abdomen are chamois also at their center and most of their surface, edged with dark raw umber brown. These dark edges are more regular and complete than in *Margarornis adustus*, as they extend also to some extent around the apex of the feather, at least on the lower breast and abdomen, with the result that the pattern of *M. guttuliger* is more regular and spotted, less flammulated than the pattern of *M. adustus*.

The flanks are dark raw umber brown; the under tail coverts red-brown, as in *Margarornis adustus*, but less sharply streaked and spotted. The exposed remiges and their external edges are chestnut, and a well-defined, broad, cinnamomeous area is present at the base or mesial portion of most of the remiges and along the outer edge of their inner web. The tail is uniformly bright chestnut, well graduated, and slightly stiffened with the webs well integrated. The apex of the longer rectrices is sharply acuminate, but the rachis is not prolonged beyond the vane as in *M. adustus*, or, at the most, for barely 1 mm. or so.

IMMATURE PLUMAGE: Differs distinctly from that of the adult by being very heavily spotted with buff over the whole of the mantle, and also with pale centers to the feathers of the lower back and rump, whereas the lower back and rump are uniformly brown in the adult, not spotted. The underparts are also more heavily spotted, with darker chamois spots than in the adult.

RANGE: Mountains of extreme western Venezuela (Sierra de Perijá, and southwestern Táchira near the border of Colombia), south, through the Andes, through Colombia (west to the eastern slopes of the Western

Andes), Ecuador, and Peru to Cuzco. The altitudinal range recorded is from about 1650 to 2743 m.

SPECIMENS EXAMINED: 48, including the types of *guttuliger* in BM; of "*guttata*" in AMNH; and of "*venezuelana*" in the Phelps Collection, on deposit at AMNH.

Margarornis brunnescens
Figure 7

DESCRIPTION: Upperparts dull brown, rufous brown, or mahogany on the back, with dark, dusky edges and shaft spots. Crown and hind neck darker, more dark olive brown, or blackish, than the back, with small buffy centers to the feathers of the forecrown, and with the feathers of the central and posterior part of the crown, paler at the center, with dark, dusky, blackish edges. Buffy or whitish spots and short streaks coalesce more or less distinctly behind the eye to form a post-ocular streak which is not well defined. These buffy or whitish spots, or shaft streaks, are present to a variable degree at the sides of the neck, on the nape, and upper border of the mantle. Wing dark brown, with or without an ill-defined pale edge along the outer edge of the inner web of the inner remiges; upper wing coverts and exposed parts of the remiges rufous brown, with a few buffy spots on the coverts in some individuals.

Chin and throat dingy creamy white, buff, or dull pale orange buff with faint, dark, dusky edges to the feathers. The remainder of the underparts is heavily flammulated, or spotted with creamy white, buff, or dull orange buff. When spotted, the feather which is broad and somewhat elongated, is whitish or buff at the center and most of its surface and is edged completely with dull black, creating a heavily, profusely spotted pattern; the spots, at their most regular, are large and teardrop-like or pearl-like in shape. When the spotting is not regular (as in *M. b. tatei*), the pattern is more flammulated than spotted, and the pale centers of the feathers (which are dull white) coalesce more or less on the upper breast. The tail is uniformly dark dull brown, graduated, slightly stiffened, with the webs of the rectrices not very firmly integrated. The apex of the longer rectrices is strongly acuminate, with the rachis well prolonged beyond the vane and virtually hairlike.

IMMATURE PLUMAGE: Similar to that of the adult, but much better spotted on the upperparts, with distinct buffy spots on the center of the back and also at the tips of the greater wing coverts; the pattern of the underparts is also more confused, less regular than in the adult.

RANGE: Central highlands of Costa Rica, of Panama (Chiriquí to Veraguas and also eastern Darién), and mountains and Andes of Colombia, of western and northern Venezuela, south through the Andes, through Ecuador and Peru, to the eastern slopes of the Andes of La Paz and Cochabamba in Bolivia. In Colombia, the range includes the Santa Marta Massif, and in Venezuela, the Sierra de Perijá, the Andes, and the northern and coastal ranges, east to the Peninsula of Paria. The altitudinal range varies from about 610 to 2743 m.

SPECIMENS EXAMINED: 184, including the types of *brunnescens* in BM; of *tatei* in AMNH; of "*albescens*" and "*distinctus*" in AMNH; and of "*pariae*" in the Phelps Collection, on deposit at AMNH.

Margarornis rubiginosus
Figure 7

DESCRIPTION: Upperparts very rufescent, reddish chestnut or russet, darker, more chestnut brown on the crown. Ear coverts, sides of the neck, and underparts, below the throat which is dull white, tawny ochraceous, becoming more rufous and ferruginous on the flanks and under tail coverts. A rather poorly developed pale buff post-ocular streak exists. On the breast, the feathers are buffy subapically, with a dusky or blackish area along the shaft which is very small. This results in a curious, "pearly," spotted pattern which becomes less distinct and tends to vanish below the lower breast.

The exposed surface of the upper wing is very bright reddish chestnut; the pattern of the under surface is similar to that of *Mar-*

garornis guttuliger, that is, conspicuously cinnamon along the outer edge of the inner web of the remiges and at the base or mesial portion of the remiges. The tail is uniformly bright reddish chestnut, moderately well graduated, slightly stiffened, with the webs of the rectrices firmly integrated. The apex of the rectrices is sharply acuminate with the inner web deeply "cut in" to the rachis which is well prolonged as a virtual filament beyond the vane.

IMMATURE PLUMAGE: Similar to that of the adult but pattern less distinct.

RANGE: Central highlands of Costa Rica and of western Panama (Chiriquí and Veraguas) at altitudes varying from about 1219 to 2743 m.

SPECIMENS EXAMINED: 51, including the type of "*boultoni*" in AMNH.

Margarornis stellatus
Figure 7

DESCRIPTION: Upperparts strongly rufous, burnt sienna, or reddish chestnut; nearly uniform, with the crown slightly darker than the back; an indistinct dark rufous cinnamon post-ocular streak is present. Throat dull white, with the feathers at its lower border and on the adjacent border of the upper breast elongated, somewhat lanceolated, and bordered with black. Remainder of underparts strongly rufous, as on the back, but paler. The feathers of the breast (below the white lanceolated feathers bordered with black) and the feathers of the center of the abdomen, are somewhat paler at the center and show a tendency to be blackish along the shaft, but these black "spots" are minute in size, and the pattern is much less distinct than in *Margarornis rubiginosus* although basically similar. The color pattern of the under surface of the wing is similar to that of *M. rubiginosus*.

The coloration and structure of the tail is similar to that of *M. rubiginosus*, but the rectrices are not quite so firmly integrated, and the tail has a tendency to be slightly better stiffened.

RANGE: Colombia, in the western Andes and in Nariño, south to the Andes of northern Ecuador, at altitudes varying from about 900 to 2194 m.

SPECIMENS EXAMINED: 14, including the type of *stellatus* in BM.

Margarornis squamiger
Figure 7

DESCRIPTION: Crown and hind neck rufous olive brown, with slight dusky edges to the feathers, and very small dull white spots on the forehead. Remainder of upperparts strongly rufous, bright burnt sienna or bright reddish chestnut; a dull white, not very sharply defined post-ocular streak is present. The feathers at the sides of the neck, and on the underparts (below the uniformly white throat) are olive brown, but the distal part of the feather is dull white or pale yellow, and is edged narrowly but conspicuously with black. The pale spots are elongated, shaped like a "tear" or "drop," or an oval "pearl" tapering at the top.

The under tail coverts are olive brown, conspicuously streaked with white or pale yellow (along the shaft) and then black. Greater upper wing coverts, exposed webs of the innermost remiges, and edge of the outer web of the primaries, reddish chestnut as on the back. The color pattern of the under surface of the wing is similar to that of *Margarornis guttuliger* and of *M. rubiginosus*, but the under wing coverts and axillaries are white or creamy white, virtually pure, in *M. squamiger*, whereas they are chiefly strongly buff, more or less invaded by dusky, in the other two species. The color and structure of the tail are similar to those of *M. rubiginosus*.

IMMATURE PLUMAGE: Similar to that of the adult, but the coloration of the crown tends to be less uniform; the spotted pattern of the underparts is less regular, and the color of the throat is not uniformly white, as the feathers are tipped more or less with dusky or blackish brown.

RANGE: Eastern Panama (eastern Darién and probably neighboring Colombia), northwestern Venezuela (Sierra de Perijá, and Andes north to Trujillo), south, in the Andes, through Colombia, Ecuador, and Peru, to La

Paz and Cochabamba in Bolivia. The altitudinal range varies from about 1371 to 3870 m.[125]

SPECIMENS EXAMINED: 219.

GENUS *LOCHMIAS*

The systematic position of *Lochmias* has always been very uncertain and this monotypic genus has been shifted about widely within the family. It was formerly placed in the Furnariinae, Sclater (1890) and other authors, such as Goeldi (1894), believing that "*Lochmias* seems to be somewhat related to *Furnarius*." However, Hellmayr (1925) decided to place *Lochmias* at the very end of the generic sequence in the family, in a separate subfamily, the Sclerurinae, consisting only of *Sclerurus* and *Lochmias*.

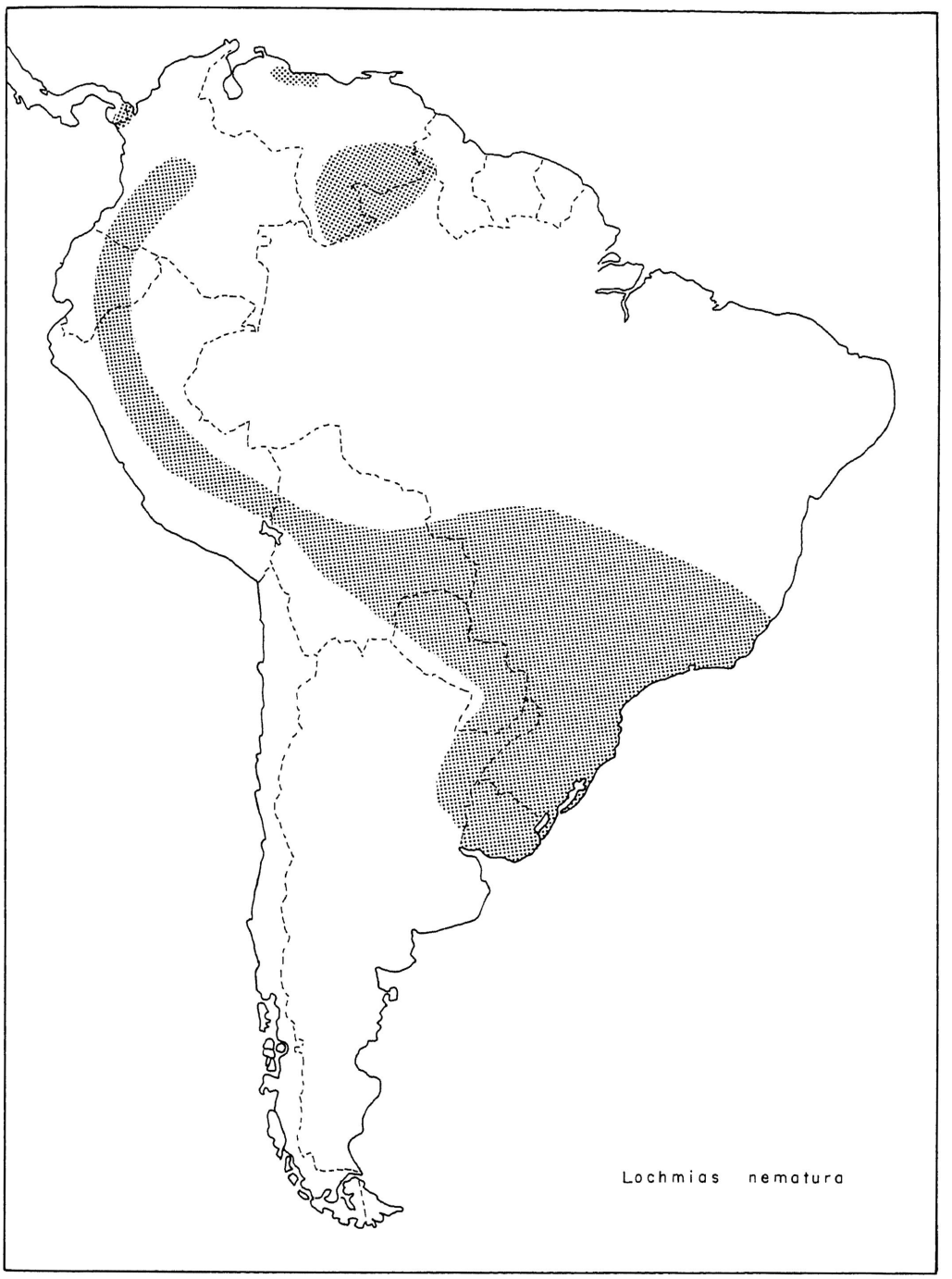
I have discussed the systematic position of *Lochmias* in my classification (1971a), stating that Hellmayr's opinion, which has been followed by modern authors, does not seem to be acceptable because *Lochmias* and *Sclerurus* differ strongly in every morphological character and also in nesting habits. I pointed out, on the other hand, that *Lochmias* and *Margarornis* share some morphological characters and that the basic structure of the nest is similar, though not its location. The morphological characters shared seem important as they consist of the spotted, guttate, or "pearly" pattern of the plumage which is very unusual and exists only in these two genera; and also of a general similarity in the structure of the tail. The tails of *Lochmias* and *Margarornis* are slightly stiffened only, their general structure is "soft," and in each the rachis is prolonged beyond the vane as a thin filament which is nearly bare of barbs; whereas the tail of *Sclerurus* is strongly stiffened, exceptionally so, its general structure is "hard," and the shaft of the feather is very wiry, "spiny," but not prolonged beyond the vane.

The structure of the tail, and the pattern of the plumage, are characters which are normally of taxonomic importance in the Furnariidae, and the basic structure of the nest is also significant as a rule. No similarity exists between *Lochmias* and *Sclerurus*, other than that they are chiefly terrestrial, but since very definite similarities exist between *Lochmias* and *Margarornis*, it seemed logical to divorce *Lochmias* from *Sclerurus* and to place it next to *Margarornis* in my classification (1971a). The actual degree of relationship between *Lochmias* and *Margarornis* is uncertain, but, at any rate, these two genera certainly appear to be much more closely related to one another than they are to *Sclerurus*.

A short discussion of my opinion seemed to be called for again because it may be questioned by some workers, such as Wetmore (1972), who, however, misrepresents my argument by giving the false impression that I have taken only *Margarornis* (not *Sclerurus* as well) into consideration in advancing my view.

Lochmias nematura is very widely distributed (map 35) from eastern Panama and Venezuela south to northeastern Argentina and Uruguay and inhabits regions that are heavily wooded or where there is a thick and tangled growth of tall bushes and shrubs. It is montane in the northern half of its range but becomes a species of the lowlands in the south. The altitude reached by *L. nematura* is never very high and varies from about 725 to 1525 m. in Panama, about 1350 to 2100 m. in Colombia, and about 1000 to 2430 m. in Venezuela. The same altitudes are roughly occupied in Ecuador, Peru, and Bolivia, but, in Brazil, it is found from well over 2000 m. in the mountains, down to very low elevations, only a few meters high, and on the coast; low regions are inhabited also in Paraguay, Argentina, and Uruguay.

This species is preeminently terrestrial, and in appearance and actions *Lochmias nematura* has been compared to a large wren, or more often, to a dipper (*Cinclus*). It follows the banks of streams in shady ravines or hollows, walking about deliberately on the ground under the tangled vegetation or the undergrowth into which it ascends to perch from time to time, not high above the ground; it lives in the shadows but is not truly secretive. The streams followed can be very small and sluggish, or be replaced by ponds, but *L. nematura* is not restricted to



MAP 35. Geographical distribution of *Lochmias nematura*.

this habitat and is usually well known locally. In some parts of the range, such as Brazil, *L. nematura* is well known for its predilection for sites described by Mitchell (1957) as "wet and often filthy places, such as small sewage outlets, where flies, beetles, and larvae are found in concentration." This attachment to unsavory sites has earned *L. nematura* the uncomplimentary name of "Presidente da porcaria" (president of filth) in Brazil, but the English names are not much happier in my opinion, though not pejorative, as remarked by Mitchell. These names, the older "Sharp-tailed Creeper," "improved" by Eisenmann to "Sharp-tailed Streamcreeper," are inept, as the tail of *L. nematura* is exceptionally soft (see below), not sharp, although pointed; it is not a creeper in any sense; and it is not restricted to streams. Hudson (in Sclater and Hudson, 1888) had adopted the scientific name *Lochmias* for the English name as well. It is best to follow him or to borrow the Spanish name "*Macuquiño,*" generally used in Argentina and Uruguay, which is appropriate as it denotes a small bird that walks on the ground; the Brazilian form "*Macuquinho*" is used also very widely.

Lochmias nematura nests under the ground at the end of a burrow dug in a bank or slope. The location and structure of the nest have been well described and illustrated by Goeldi (1894). The nest described by Goeldi was dug into a slope about 30 m. from a brook. The entrance to the burrow, which had a diameter of 3.5 cm., was under the root of a small tree, about 30 cm. above the bottom of the slope where it met level ground, and led into "a more or less horizontal gallery," about 60 cm. in depth, which "ended in a spacious cavity and contained a wonderfully large nest," which Goeldi removed carefully and photographed. He said this nest reminded him of those of *Cinclus* [*cinclus*] *aquaticus* with which he was acquainted and was similar to them in being "a vaulted globe with a lateral entrance. The exterior is made of small roots and branches; the interior lining consists of regularly crossed dry bamboo leaves. The walls of the central cavity especially are very well made, and consist of crossed bamboo-leaves woven in a really artistic manner." The nest was roughly globular in shape with a diameter varying from about 12.5 to 13.5 cm., and "the thickness of the walls is everywhere less than 3 cm."

Goeldi believed apparently that *Lochmias* and *Furnarius* were closely related and his remarks are of interest—although it seems certain that the two genera are not as closely related as Goeldi suggested. He wrote that *L. nematura* was "an architect by no means inferior to *Furnarius* [*rufus*]. There is a striking resemblance between the shape and dimensions of the Ovenbird's [*F. rufus*] nest . . . and that of *Lochmias,* and the simple comparison of the two nests would lead us to believe in the consanguinity of their builders . . . . The difference of the material is of no importance, and we may very well define the loam-nest of *Furnarius* as an overground nest of *Lochmias,* or the leaf-woven nest of *Lochmias* as a subterranean building of *Furnarius*."

I believe that the well woven type of nest of *Lochmias* is a conclusive argument for considering that *Lochmias* is not closely related to *Sclerurus,* and, hence, must be removed from the end of the generic sequence of the Furnariidae, the opinion of Wetmore (1972) notwithstanding. *Sclerurus* also nests under the ground at the end of a gallery, but does not construct a nest in the normal sense, being content with a mere flat and open platform of leaf debris. The morphological differences between *Lochmias* and *Sclerurus* were briefly discussed above.

Geographical Variation

The range of *Lochmias nematura* is interrupted and this species varies geographically, but slightly only, although seven "subspecies" have been admitted by Peters (1951). But the recognition of any subspecies seems unnecessary as the variation consists only in the relative development of the white spots on the sides of the face and on the underparts and saturation of the "blackish" plumage which is relatively darker (more dusky or dark dull brown on the upperparts, or purer black on the underparts), in some

populations than in others. The populations in which the white spots are least well developed, and the general coloration is more blackish, are those ranging from central Peru south to Bolivia which have been named "*obscurata*."

Lochmias nematura
Figure 7

DESCRIPTION: Upperparts dark dull brown, or dusky brown, somewhat more blackish on the crown, and with a more or less pronounced dark blackish chestnut tinge on the back, rump, and upper surface of the wing. Sides of the head and ground coloration of the entire underparts very somber, dusky or blackish brown, profusely spotted with white or dull white. The white spots are large and tend to coalesce on the upper throat; the spotted pattern of the sides of the head and underparts is similar to that of *Margarornis squamiger,* as the spots are guttate (shaped like a "drop," or "tear") and are narrowly edged with black. As in *M. squamiger,* the white markings at the sides of the head tend to coalesce and form a rather poorly defined post-ocular streak; and the spots are transformed into streaks on the lower flanks and under tail coverts. The under surface of the wing is uniformly blackish, without a pale area at the base or mesial portion of the inner webs of the remiges, or a pale outer edge to the inner webs; but the under wing coverts and axillaries are more or less spotted, streaked, or tipped with dull white.

The tail is uniformly black, slightly stiffened, but at its base or near it only, as the greater part of the tail is exceptionally soft in texture. The tips of the rectrices are acuminate, the rachis being prolonged beyond the vane for a short distance as a very loose, thin, "hair-like" filament, bare of barbs distally. The tail is noticeably short, as the ratio of its length to that of the wing is only 0.68. The feet are not as heavy and strong as one would expect for a bird which is very preeminently terrestrial, but the tarsus is relatively long and the toes well-developed.

IMMATURE PLUMAGE: Very similar to that of the adult, but the spotted pattern of the underparts is less regular, and the white spots tend to be more "cloudy."

RANGE: Eastern Panama (mountains of eastern Darién); Venezuela in the coastal ranges of the north from Yaracuy to the region of Caracas; Venezuela in the mountains of the south and in those of neighboring Guyana and on the border of Brazil; Andes from Colombia, south through Ecuador, Peru, and Bolivia, and lower regions from Bolivia to southeastern Brazil (from the Mato Grosso, Goiás, and Minas Gerais, to Rio Grande do Sul), Paraguay, northeastern Argentina (Misiones to Entre Ríos), and Uruguay.

The range is not continuous in the north and the altitudinal range varies also (see text above); this species is montane in the north (south to Bolivia), but not in the south.

SPECIMENS EXAMINED: 130, including the types of "*castanonota*" and "*sororia*" in BM, of "*sancti-hilarii*" in MNHN, and of "*chimantae*" in the Phelps Collection, on deposit at AMNH.

GENUS *PSEUDOSEISURA*

Pseudoseisura is composed of three species (*P. cristata, P. lophotes,* and *P. gutturalis*) and is quite distinct from any other genus in the family. As I stated in my classification (1971a), "The position of the genus *Pseudoseisura* is doubtful . . . although structurally—at any rate—its three species seem to belong to the Philydorinae. These large, noisy, and crested birds resemble the jays in their appearance and actions much more than they do the ovenbirds, and they also differ very conspicuously from the Philydorinae by building a truly huge nest of sticks in trees, the extreme culmination of the Synallaxine nest. The position of this very aberrant genus is uncertain . . . ."[126]

The comparison of *Pseudoseisura* to a jay or small corvid is apt and has been stressed. The three species are not homogeneous, but can be characterized as large and coarse birds, with very large feet, a very strong bill, and a conspicuous crest. They have a jerky, undulating flight, but move chiefly by hopping on the ground and in branches, and are restless and very wary, but they become

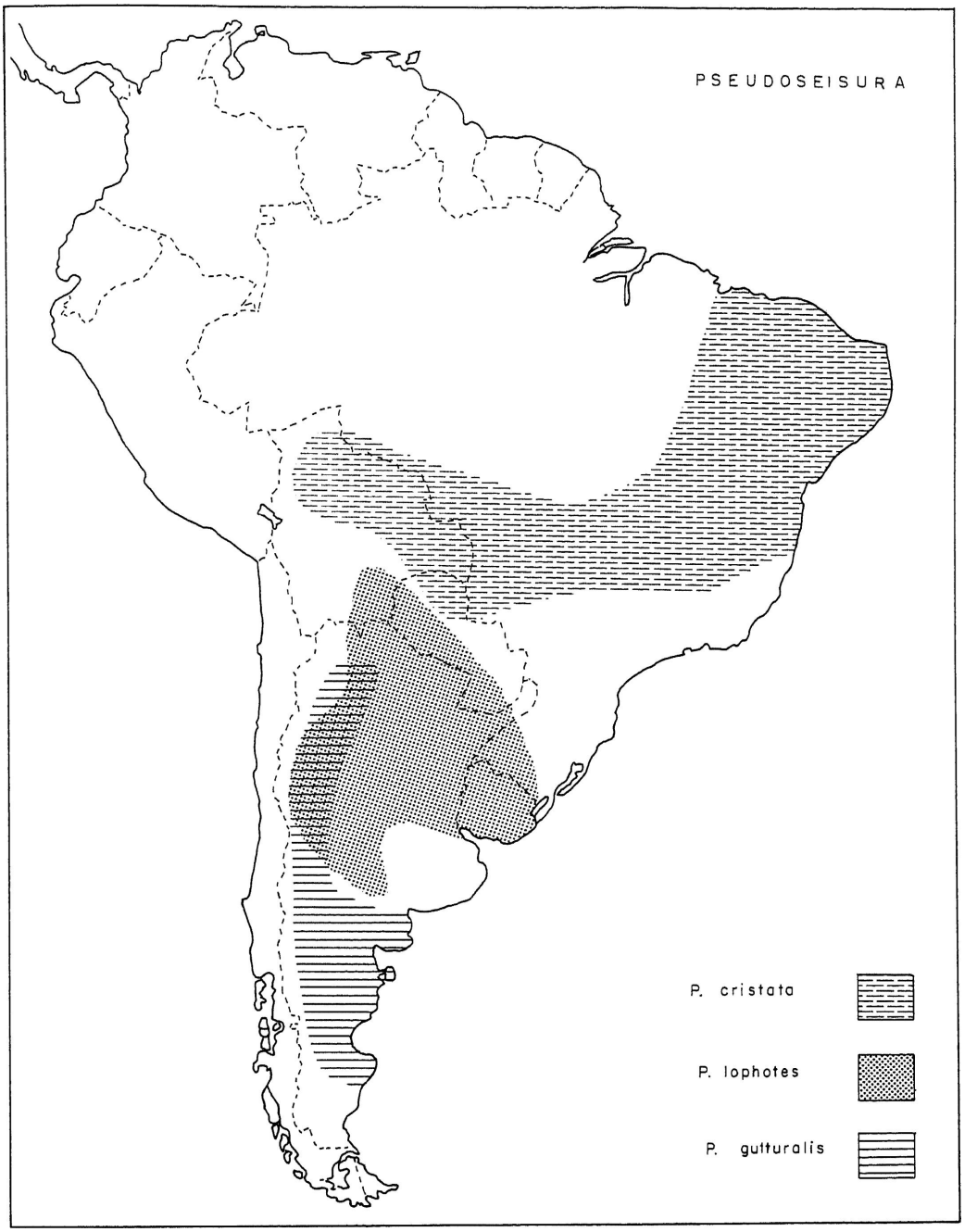
truculent at times, and are very noisy, the loudest members of the family. Barrows (1883) characterized *P. lophotes* as follows: "a bird the size of a Blue-jay, with uniform rufous plumage, a respectable crest, an outrageous disposition and voice, and a nest the size of a barrel, is a bird that cannot be overlooked, especially if, as is his custom, he comes attended by a score or so of his immediate relatives and friends."

Pseudoseisura lophotes also resembles corvids by its habit of robbing the nests of other birds for food, eating the eggs, not excepting those of the domestic fowl. The habit of invading barnyards has been reported by several observers, including Rodriguez (1918) who said he witnessed a successful attack on a hen sitting on its nest inside the corner of a chicken coop. This attack was carried out by *P. lophotes* with loud screams and flashing wings until the terrorized hen abandoned its nest and its egg was then broken and cleaned out by *P. lophotes,* with "great satisfaction," according to Rodriguez. This habit of stealing eggs for food is apparently prevalent in some regions as the bird is called there "*Comehuevos,*" the egg-eater, but in other regions it may be known as "*Copetón*" or "*Coperote,*" or big-crest, "*Casero*" or "*Caserote,*" house-builder, or "*Cachalote*";[127] this last name has been adopted as the English name for all the three species with a qualifier to their coloration. The Uruguayan "*Urraca marrón,*" or brown magpie, shows that a certain resemblance to a corvid has not escaped the people of that country.

The three species are widely distributed from northeastern and central Brazil south to Patagonia (map 36) and their ecology varies somewhat but remains basically similar. The species of *Pseudoseisura* are birds of flat or hilly open country. In Brazil, *P. cristata* frequents the "caatinga" (or low open spiny "forest") or savannas with isolated groves or clumps of trees; and the extremely flat and open swampy and marshy country of the southern Mato Grosso and neighboring eastern and northern Bolivia. The habitat of *P. lophotes* in Argentina includes also grasslands, or any type of savannas, away from or near human habitations, corrals, screens of trees along rivers, river bottoms, and acacia dotted ravines. The habitat of *P. gutturalis* becomes more arid and may include few trees, if any. In Rio Negro and Neuquén, the habitat is described by Wetmore (1926) as arid regions, the bird frequenting "the denser growths of low, thorny brush that grows over the dry, barren slopes of stony, sandy hills"; stands of tall cacti have been mentioned also.[128]

Hudson (in Sclater and Hudson, 1888) was "strongly impressed with [the] personality [of *Pseudoseisura gutturalis*], if such a word can be applied to a bird," and believed *P. gutturalis* was probably "the loudest screamer and greatest builder" in a family noted for birds which "as a rule [are] builders of big nests and very noisy." Male and female *P. gutturalis* "live together in the same locality all the year; the young, when able to fly, remain with their parents till the breeding-season, so that the birds are found occasionally in pairs, but more frequently in families of five or six individuals. When feeding they scatter about, each bird attaching itself to a large bush, scraping and prodding for insects about the roots; and at intervals one of the old birds, ascending a bush, summons the others with loud shrill cries, on which they all hurry to the place of meeting, and from the summits of the bushes burst forth in a piercing chorus, which sounds at a distance like screams of hysterical laughter . . . after each performance they pursue each other, passing from bush to bush with a wild jerky flight, and uttering harsh angry notes." The "extravagant cries," or "song," can be heard from a distance of "over a mile and a quarter" (about 2 km.) on a quiet day, according to Hudson.

The general behavior of *Pseudoseisura lophotes* seems to be very similar to that of *P. gutturalis*. Little information exists for *P. cristata,* other than on its nesting habits, but there is no reason to suspect that its behavior differs significantly from that of *P. lophotes* and of *P. gutturalis*. These two species are said to be "shy" by some observers, but a better description of their behavior is "wary," as birds which are so extremely strident and noisy are social to some extent,



MAP 36. Geographical distribution of the genus *Pseudoseisura*.

and which plunder the nests of other birds for eggs, attacking birds very much larger than themselves (see above), cannot be said to be truly "shy."

Some aspects of the behavior of *Pseudoseisura gutturalis* have been mentioned above. The wariness of *P. gutturalis* and *P. lophotes* has been noted by Wetmore and Hudson. Wetmore said that *P. gutturalis* "is difficult to approach . . . [and is] seen occasionally running swiftly on the ground, with the tail erect, taking advantage of any cover that may offer. When excited they may come out to rest on some low branch with jerking wings and tail, while they peck nervously at the branches near at hand. They are found in pairs or family groups that remain near their huge stick nests placed in the low bushes."[129] Wetmore's remarks on the behavior of *P. lophotes* noted that this bird "flies up [from the ground] with chattering calls . . . at the slightest alarm . . . and hops about in the shelter of the limbs as alertly as a jay, pausing to peer out or to peck nervously at the limbs." Wetmore said that *P. lophotes* is "usually so shy and retiring that it may be difficult to find," but added that it "may come familiarly into dooryard trees," and is accused of robbing the eggs of the domestic hen. Hudson said that *P. lophotes* does not fly away when approached "but runs swiftly to the nearest tree, behind the trunk of which it hides, then scuttles on to the next tree, and so escapes without showing itself"; the greater part of Hudson's notes on the behavior of *P. gutturalis* were quoted above.

Meyer de Schauensee (1970) has characterized the three species as "climbers." However, climber is not accurate in the case of *Pseudoseisura* and is actually misleading in a family in which "climbing," or scansorial habits, characterizes some genera. *Pseudoseisura* is not scansorial, its species do not ascend the trunks of trees and their branches, or investigate them, by climbing or creeping along them. They clamber and hop among bushes or trees in the manner of a jay, and, of course, nest in them, but otherwise seem to spend their time on the ground in search of food, secured by rummaging and digging among fallen leaves, bark, or other promising debris. Their food consists of animal matter, as in the case of all Furnariidae, but not exclusively so as *P. lophotes* eats seeds also. This species is reported to tear at buds and bark with its powerful bill, rip the buds and bark off with its claws, and then investigate the material secured by "handling" it with its big feet; *P. gutturalis* has been reported behaving "like a woodpecker," digging holes into columnar cacti. The birds are presumably searching for larvae, but their eclectic feeding habits are worthy of note—also the fact that *P. lophotes* is said to be easily tamed and raised on scraps of raw meat; its fondness for eggs and "shy" behavior were discussed above.

The nests of the three species are well known and are similar, differing only in size and location. Large sticks, preferably thorny ones, are used, some of which may exceed 60 cm. in size ("two feet or more long") and are frequently as thick as a finger. A favorite site is not deserted from year to year and three to four huge nests may exist in the same tree. These nests are so strongly made that they survive the winter intact, but are not used again, although they can be adapted for nesting by other species and are a bonanza of material for *Anumbius* or other Furnariidae which also construct large nests of thorny sticks.

Cherrie (1930) described the nest of *Pseudoseisura cristata* as "an enormous stick nest, many of the sticks and twigs employed being fully two feet in length . . . irregular in outline . . . [but resembling] roughly a huge powder flask, lying on its side, fully three feet [about 91 cm.] in diameter, and half that much in thickness." The nest described by Cherrie was located in the fork of a tree, supported by twigs and branches of the tree incorporated into it, and had a breeding chamber, which was nearly spherical in shape with a diameter of about 20 cm., and which was reached by an entrance tunnel, opening directly down into the chamber, and the external orifice of which was at one end of the nest. Cherrie reported that "the nest-cavity was lined with bits of bark and several pieces of cast snakeskin, also throughout the entire

nest-mass were interspersed many long quill feathers (from black vultures, ibises, and hawks), some snail shells, land-crab shells, and pieces of bone. The eggs are a lusterless white, ovate in form."

Cherrie said also that "in order to get at the eggs [he] had to tear away the entire top of the nest . . . [but] had scarcely dropped to the ground and retreated for a half a dozen yards when the parent birds who had remained in the immediate neighborhood returned. After an inspection of the wreck and ruin the intruder had wrought . . . they immediately set to work to repair the damage, industriously carrying up the sticks and twigs [he] had thrown to the ground." Rodriguez (1918), who had also torn a nest apart for inspection of its contents said that *P. lophotes* also repairs its nest "perfectly."

The nest of *Pseudoseisura lophotes* is similar to that of *P. cristata,* but some nests are larger, attaining a size of about "five feet" (about 1.52 m.) with a diameter of about 75 to 90 cm., and some are more cylindrical, or "barrel"-like in shape. The breeding chamber is somewhat larger than in *P. cristata* as a rule (about 24 cm.), and only bits of vegetable material have been reported so far in its lining. The nest is built in an isolated and rather low tree, as in the case of *P. cristata,* and placed in or near its crown, about 4 to 6 m. above the ground.

The nest of *Pseudoseisura gutturalis* is the largest nest built by an ovenbird and is more spherical in shape than the nest of the other two species. It differs also by being constructed inside a strong, spreading bush, not in a tree, but its location, shape, and other modifications (a more elaborate entrance gallery) seem to be dictated by the habitat which is normally without trees. Hudson stated that the nests of *P. gutturalis* he has examined were "perfectly spherical and four to five feet [about 1.21–1.52 m.] deep, the chamber inside being very large," but Hudson does not mention the size of the chamber. The latter was entered "at the side near the top . . . by a narrow arched gallery, neatly made of slender sticks resting along a horizontal branch, and about fourteen inches long [about 35.5 cm.]." Hudson believed this "arched gallery" was probably a protection against predation, and, commenting on the strength of the nest and its general structure, added that "so strongly made is the nest that I have stood on the dome of one and stamped on it with my foot without injuring it in the least, and to demolish one I had to force my gun-barrel into it [to] prize it up by portions."

Morphological Variation

The three species are large (table 19), crested, and coarse birds, with exceptionally big feet and very strong bills, much compressed laterally, but the three species are not homogeneous. The mean wing length varies, in round numbers, from 102 to 126 mm., with an average of 112 mm.; *Pseudoseisura lophotes,* with a mean wing length of 126 mm., is exceeded in size among the Furnariidae only by *Cinclodes palliatus,* in which the mean wing length measures 133 mm.

The tail is composed of 12 rectrices and is shorter than the wing, with a ratio varying from 0.86 to 0.94, and averaging 0.89. It is not strongly graduated, and the width of the webs of the rectrices, which are firmly integrated, varies specifically. The shaft of the longer rectrices is prolonged somewhat beyond the vane, but is not completely denuded of barbs, and the tip of the rectrix is not truly acuminate and is best described as apiculate (fig. 8). The tail is stiffened, but the degree of stiffening varies in each species and is not correlated with the habitat (with more or less abundant trees or with none). The tail is most stiffened in *Pseudoseisura gutturalis,* although it is doubtful that it is much used for support, for *P. gutturalis* runs on the ground and seems to inhabit only bushes, as very few, if any, trees exist in the regions it inhabits.[130] The tail is well stiffened in *P. lophotes,* but only at the base, as the apex of the rectrices is "soft," although this species is more "arboreal" than *P. gutturalis*; and the tail is least stiffened in *P. cristata,* the most "arboreal" of the three species.

The plumage of *Pseudoseisura cristata*

TABLE 19
Measurements (in Millimeters) of *Pseudoseisura*, *Pseudocolaptes*, and *Berlepschia*

Species	Wing			Tail			Bill		
	N	Mean	Range	N	Mean	Range	N	Mean	Range
Pseudoseisura cristata									
Males	21	103.23	97–109	20	96.75	89–109	21	24.57	22–27
Females	20	100.70	95–106	20	94.35	86–102	20	24.07	22–29
Both sexes	47	102.27	95–111	44	96.00	86–109	46	24.45	20.5–29
Pseudoseisura lophotes									
Males	29	128.65	120–134	30	111.53	105–121	29	27.03	25–29
Females	27	123.03	116–135	27	109.40	102–120	26	26.36	24–28
Both sexes	59	125.94	116–135	60	110.70	102–121	58	26.76	24–29.5
Pseudoseisura gutturalis									
Males	10	109.20	103–114	10	93.80	88–101	10	28.80	25–31
Females	9	107.66	102–111	8	91.87	85–100	9	28.61	27–29
Both sexes	21	108.33	102–114	20	92.65	85–101	21	28.66	25–31
Pseudocolaptes boissonneautii									
Males	91	113.26	97–130	92	96.97	85–115	93	24.60	21.5–31
Females	47	107.59	95–123	44	92.88	82–103	47	28.01	21–32
Both sexes	149	110.88	95–130	147	95.47	82–115	151	25.74	21–32
Berlepschia rikeri									
Males	15	98.56	92–104	15	84.80	79–92	15	30.41	28–32
Females	14	95.65	92–100	13	83.30	75–88	14	29.78	26–32.5
Both sexes	34	97.25	92–104	32	84.59	75–92	34	30.42	26–32.5

and *P. lophotes* is rufous, but *P. gutturalis* is earthy gray above, paler below, and lacks any trace of rufous pigmentation. *Pseudoseisura gutturalis* has a large, pure white throat patch, bordered with black at its base, but *P. cristata* and *P. lophotes* do not have a throat patch, the throat being rufous, uniform with the breast in the case of *P. cristata*, darker than the breast in *P. lophotes*. Finally, the crest is long, very well developed in *P. cristata* and *P. lophotes*, but more bushy in the latter, and is short in *P. gutturalis*.

Phylogeny

The rufous pigmentation, common lack of a throat patch, and very well-developed crests of *Pseudoseisura cristata* and *P. lophotes* certainly suggest that these two species are more closely related to one another than they are to *P. gutturalis*.[131]

Geographical Variation

In *Pseudoseisura cristata*, the population which inhabits the northeastern end of the range in Brazil, is, generally speaking, somewhat paler and brighter than the birds of southwestern Brazil, northern Paraguay, and Bolivia. In *P. lophotes* birds from Bolivia are generally somewhat paler than birds from Paraguay, Uruguay, and Argentina; presumably, birds from southern Rio Grande do Sul in Brazil resemble those of Paraguay, Uruguay, and Argentina, but I have not examined specimens from Brazil. Geographical variation has been described also in *P. gutturalis* but is not confirmed by specimens in comparable plumage that I have seen from

the regions (Tucumán and Patagonia) from which the two alleged subspecies have been described.[132]

KEY TO THE SPECIES OF *PSEUDOSEISURA*

1. Throat pure white ..... *gutturalis*
   Throat strongly rufous 2
2. Back, including the rump, and whole of the underparts, uniformly reddish cinnamon; crest feathers edged with pale gray; distinctly smaller, the wing length averaging 102 mm. ..... *cristata*
   Coloration of back, rump, and underparts not uniform; crest feathers blackish; distinctly larger, the wing length averaging 126 mm. . ..... *lophotes*

LIST OF THE SPECIES

Pseudoseisura cristata
Figure 8

DESCRIPTION: Plumage reddish cinnamon and virtually uniform, with the exception of the inner webs of the remiges and of the greater upper wing coverts which are dusky, and of the lores and feathers of the crest. The inner webs of the remiges are dusky, as stated, but are well edged with reddish cinnamon along their outer border. The lores are cloudy gray; and the distal half, or more, of the longer crest feathers has grayish edges, and is brown or brownish at its center or along the shaft, the base of the crest feathers being rufous. The tail is well stiffened only at the base, and its rectrices are relatively narrow, apiculate, or somewhat more acuminate in the case of the central pair. The crest feathers are well elongated and slender.

IMMATURE PLUMAGE: Differs from that of the adult by being less uniform in coloration, the feathers of the throat being faintly barred with gray, and the feathers of the back, breast, and abdomen being somewhat paler at the tip than in the adult. The crest is also distinctly shorter, not so well developed.

RANGE: Eastern Brazil, from Maranhão, south to Bahia and Minas Gerais, west to the Mato Grosso, northern and eastern Bolivia, and northern Paraguay.

SPECIMENS EXAMINED: 59, including the type of "*unirufa*" in MNHN.

Pseudoseisura lophotes
Figure 8

DESCRIPTION: Back brownish, with a drab, vinaceous or rufous cast, the rufous cast becoming more pronounced posteriorly, whereas the rump is strongly rufous, and the upper tail coverts and the whole of the tail are reddish chestnut, uniformly so in the case of the tail, but not the coverts which have grayish or drab tips. The crest is long as in *Pseudoseisura cristata,* but more bushy, and the feathers of its lower levels are strongly rufous, but not those of the upper and exposed levels of the crown which are blackish brown. Upper wing coverts dull chestnut, with blackish shafts, and pale gray tips. Under wing coverts and axillaries reddish cinnamon, a narrow edge of reddish cinnamon existing also along the outer border of the inner webs of the remiges. Sides of the face and whole throat dark reddish cinnamon, virtually uniform, and distinctly darker than the breast and abdomen which are fawn with a vinaceous cast. The feathers of this area, and the under tail coverts also, are paler at the tip, buffy pink, and also grayish subapically, with the result that the underparts have a faint "barred" pattern below the throat. The tail is slightly better stiffened than that of *P. cristata* on the whole, and its rectrices are unusually broad, and very distinctly apiculate.

IMMATURE PLUMAGE: Differs from that of the adult by having the feathers of the breast and abdomen more or less distinctly margined with dull grayish brown. The crest is less well developed than in the adult and its feathers are broader.

RANGE: Eastern Bolivia, from southern Santa Cruz, Paraguay, southern Rio Grande do Sul in Brazil, and Uruguay, to Argentina, south to Mendoza, La Pampa, and Entre Ríos, to neighboring Buenos Aires along the Plata River.

SPECIMENS EXAMINED: 70.

Pseudoseisura gutturalis
Figure 8

DESCRIPTION: Upperparts brownish earthy gray, with ear coverts darker brown, and a narrow, interrupted, white eye-ring. Chin and throat pure white, bordered with feathers that are black at the lower border of the throat, but not uniformly black as a rule, as their shafts and tips are more or less buffy white. Underparts pale grayish olive, more drab, and distinctly paler than the upperparts. Under wing coverts chiefly drab gray, and axillaries chiefly creamy with a faint cinnamon tinge. The tail, other than the central pair of the rectrices, is dark brown and well stiffened, with the apex of the two central pairs of rectrices more acuminate, less apiculate than that of the other rectrices. Crest relatively short (very distinctly shorter than those of *Pseudoseisura cristata* and *P. lophotes*), with the center of the feathers darker and browner on the anterior part and top of the crown.

IMMATURE PLUMAGE: Similar to that of the adult, but the feathers of the breast and abdomen have narrow margins which are faintly darker than the remainder of the feather.

RANGE: Argentina south to Patagonia, from southeastern Salta, south through Tucumán, La Rioja, Catamarca, San Juan, San Luis (probably), and Mendoza, and from Neuquén, and the valley of the Rio Colorado to southernmost Buenos Aires, south to northern Santa Cruz.

SPECIMENS EXAMINED: 22, including the type and cotype of *gutturalis* in MNHN.

GENUS *PSEUDOCOLAPTES*

This monotypic genus is related to the genus *Philydor*. *Pseudocolaptes boissoneautii* is a more slender and larger bird than *Philydor* and differs from all other members of the family by having a very conspicuous tuft of elongated soft feathers growing from the posterior part of the malar region at the base of the cheek on each side of the face. These feathers are white or buffy, and the wing length averages about 111 mm. in *P. boissonneautii* (table 19), as against about 85 mm. in all the species of *Philydor*, with one exception consisting of *Philydor ucayalae* in which the wing length averages about 104 mm. The color pattern of the underparts is different, more or less distinctly squamated in *P. boissonneautii*, rather than flammulated, streaked, or uniform in *Philydor* spp.

Foraging and nesting habits seem to be similar in both genera, but *Pseudocolaptes boissonneautii*, though arboreal, is apparently not a bird of dense forest, as in the case of *Philydor*. Slud (1964) stated that in Costa Rica he did "not recall seeing this species well inside forest but at the borders of woodland and frequenting the trees . . . in parklike pastures." He added that the relative abundance of *P. boissonneautii* on the partially deforested volcanoes suggests that it may not be a forest species. Skutch (1969) has observed *P. boissonneautii* "occasionally in the heavy, epiphyte-burdened forest about 5500 feet [about 1676 m.]" in central Costa Rica. In Ecuador, *P. boissonneautii* is apparently found both in forest and above it, as Goodfellow (1902) found it in "Both stony ground and the paramo grass regions," at high altitudes varying from about 3660 to 4420 m.[133]

The general foraging behavior of *Pseudocolaptes boissonneautii* seems to be similar to that of *Philydor*, consisting in the case of *P. boissonneautii* of an active search of leafy clumps and tangles of vines, clumps of moss on the trunks of trees or their branches, and especially, busy probing and rummaging of bromeliads or other epiphytes with its long and straight, attenuated wedge-shaped bill. During this search, the bird clings, hops, or creeps along branches or the trunks of trees in all sorts of attitudes. *Pseudocolaptes boissonneautii* is said to be very active and noisy, but Skutch said he "rarely heard it utter a sound." Vuilleumier has told me that once when he observed a bird of this species, it was sitting quietly on a branch with its "cheek" tufts conspicuously spread out. These tufts probably play a role in some as-

pects of behavior other than mere recognition which are not known; they are developed to the same degree in the two sexes.

Another interesting behavior which has been reported only by Goodfellow (1902) is that *Pseudocolaptes boissonneautii* retires at night "to holes in the banks or quebradas, or under tufts of grass [on the paramos]".[134] It is possible that *P. boissonneautii* nests also in such holes as very few, or no trees at all, would be present at the very high altitudes where Goodfellow found it. If indeed it nests in holes in the earth as well as in trees, this behavior parallels that of *Philydor rufus* which nests in both locations, holes in trees, and burrows in the earth or holes in man-made structures, such as walls.

The only nest of *Pseudocolaptes boissonneautii* of which I have found a description was located by Skutch at about 1676 m. in Costa Rica in "a cavity, apparently an old woodpecker's hole, in a barkless, decaying trunk that stood in a narrow clearing in the heavy forest." This hole was about 9 m. above the ground, but the trunk was too decayed to support a ladder to permit inspection of the inside of the hole and eggs. Before occupying the hole, the bird cleaned it out by removing particles of decaying wood with its bill, and "while incubating [done by apparently only one parent] the bird carried in for the nest's lining a number of billfuls of large brown scales, apparently the ramentum [membranous scales] of tree ferns [and] was not seen to take any other kind of nest material into the cavity."

The nest found by Skutch was at an exceptionally low altitude, because *Pseudocolaptes boissonneautii* seldom descends below about 2000 or 1900 m. This montane species is said to become more common as altitude increases, according to Slud; the highest altitude recorded for a specimen which I have seen was 14,500 feet [or about 4419 m.] in Ecuador, and seems to be also the highest altitude reported.

The populations of *boissonneautii* form two isolated groups (map 37). One group, called *lawrencii,* inhabits the higher mountains of central Costa Rica and western Panama; the other group (nominate *boissonneautii*) is Andean and is distributed from Venezuela south to Bolivia. The birds of the two groups are very similar morphologically and were considered to be conspecific by Hellmayr (1925) and most of his contemporaries, but Zimmer (1936c) decided that "perhaps it is well" to recognize two species. I followed Zimmer's opinion in my preliminary "Classification of the ovenbirds" (1971a), but after reinvestigating the question (1974), I agreed with Hellmayr. Only one species seems to exist, as the belief that there might be two was occasioned by a misinterpretation of the plumage sequence.

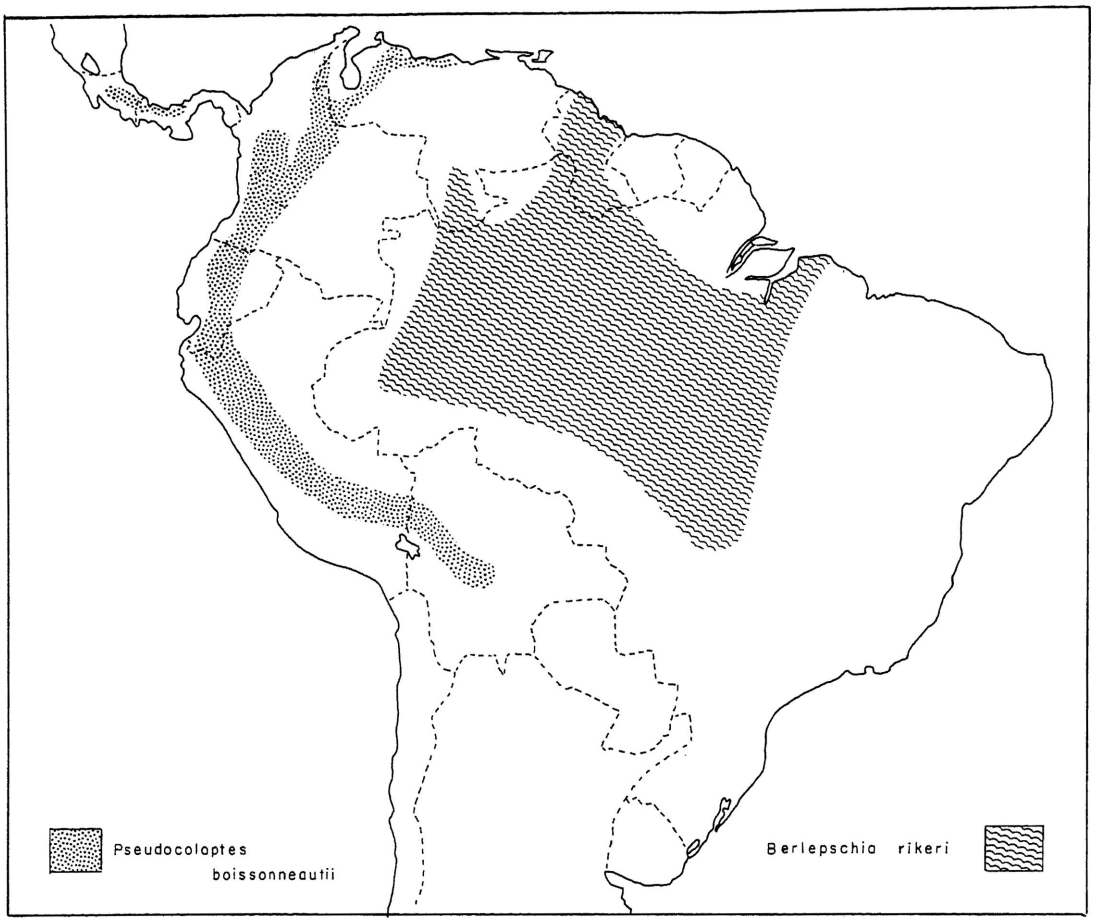
Geographical Variation

Peters (1951), who followed Zimmer's division into two species, had recognized no fewer than 12 "subspecies," three in *P. b. lawrencii,* and nine in *P. b. boissonneautii.* However, it seems sufficient to me to recognize only two, *P. b. lawrencii* in Central America and nominate *P. b. boissonneautii* in South America. *P. b. lawrencii* differs from nominate *P. b. boissonneautii* only in some details: less heavily streaked on the upperparts, as the streaks do not extend below the upper border of the mantle; by having a somewhat more regular pattern on the breast, and buffy, rather than white cheek tufts; and the outer web of its primaries is also less "rufous," blackish, rather than rusty brown.

The other "subspecies" recognized by Peters are forms that were either based on individual variants, or on trivial differences between populations, some of which have very restricted ranges; and at least two of these "subspecies" are based on a misconception of the plumage sequence.

Pseudocolaptes boissonneautii
Figure 8

Description: Crown, nape, and upper border of mantle dark brown, streaked narrowly with dark rufous cinnamon, or russet; the streaks become broader posteriorly and



MAP 37. Geographical distribution of *Pseudocolaptes boissonneautii* and *Berlepschia rikeri*.

extend to the whole of the mantle where they are quite broad, on a paler brown ground than on the crown and nape. Rump and upper tail coverts uniformly bright rufous, and tail uniformly reddish chestnut with darker shafts to the feathers. A dark buff superciliary streak, which is not well defined, extends from the base of the bill posteriorly to the nape. The ear coverts are very dark, of the same color as the crown, but below them, a large and very conspicuous tuft of soft feathers, which are usually pure white, extends posteriorly along the malar region, elongated from the cheek by about 15 mm. The chin and throat are dull white, and the feathers at the base of the throat and on the upper breast, which are whitish also, or pale buff, have dusky or dark brown narrow margins which create a more or less regular squamated pattern. The feathers below the upper breast become progressively darker buff, more ochraceous and tawny, and have also dark but more irregular margins. The flanks and under tail coverts are very tawny, brownish orange or brownish cinnamon.

The exposed surface of the wing is chiefly tawny brown or russet, with dark, dusky concealed centers to the coverts, which are more or less distinctly tipped with rufous, and the inner webs of the remiges are dark

also, but have a rufous cinnamon outer edge. The axillaries and under wing coverts are pale ochraceous buff or buffy orange.

The tail is composed of 12 moderately well-graduated rectrices that are very well stiffened (almost rigid) at the base, but which become progressively more elastic distally and only slightly stiffened at the tip. The rectrices are broad, firmly integrated, moderately acuminate at the tip. The tarsus and toes are strong with large claws. The bill is long and strong, straight or virtually so, wedge-shaped at the base, but becoming compressed laterally and sharply attenuated at the tip. It is very distinctly longer in females (table 19).

The description of the coloration of the adult plumage given above is based on nominate *P. b. boissonneautii*; for differences from *P. b. lawrencii,* see geographical variation above.

IMMATURE PLUMAGE: This species has at least two immature plumages (Vaurie, 1974) which have been misinterpreted, one of them as an adult plumage by Zimmer (1936c). In one immature plumage, which is probably an earlier stage in the sequence of plumages, but which Zimmer believed was an adult plumage, the crown is well streaked on a dark brownish ground (as in the adult) but the streaks are usually finer, and extend posteriorly only to the nape or upperpart of the mantle, not farther down to the center of the back, which is not streaked, and the feathers of which are usually dusky at the margins and tip. The underparts are very dark below the pale throat (the dull white feathers of which have dark margins or tips, occasionally up to the chin), being rusty brown below the throat, much darker than in the adult, but with a large buffy white spot or shaft streak on the breast. The cheek tufts are buffy, rather than white; the coloration of these tufts, and the lack of streaks on the center of the back are about similar to the adult plumage of *P. b. lawrencii.*

In the other immature plumage, the crown and nape are dull black or blackish, wholly so, not streaked, or are slightly streaked, but much less distinctly so than in the adult. The center of the back (or mantle) is streaked as in the adult plumage, and the cheek tufts are white also, but, in this other immature plumage, the coloration of the bird differs from that of the adult on the underparts by having dark margins to the feathers of the throat and chin (as in the first of the immature plumages described above); by having considerably darker or broader margins on the feathers of the breast; and by being generally darker, more tawny, but less dark than in the first of the immature plumages.

In both of these immature plumages, immaturity is denoted also by structural details, such as the general texture of the plumage, which is looser; narrower and blunter rectrices that are less firmly integrated; blunter and paler primaries, and, as a rule, a distinctly shorter bill.

RANGE: Higher mountains of central Costa Rica and of western Panama to eastern Veraguas; Venezuela in the northern and coastal ranges from Aragua and Miranda westward, Sierra de Perijá, and Andes, south through the Andes of Colombia, Ecuador, Peru, to La Paz and Cochabamba in Bolivia. The altitudinal range varies from about 2000 m. (normally) to about 4400 m., but the species descends lower occasionally and a nest was found at 1676 m. in Costa Rica. The highest records I have obtained reach about 2750 m. in Costa Rica, 3125 m. in Panama, 3000 m. in Venezuela, 3700 m. in Colombia, 4419 m. in Ecuador, and a little over 3300 m. in both Peru and Bolivia.

SPECIMENS EXAMINED: 236, including the types of "*costaricensis*" in MNHN, of "*johnsoni*" in NRS; and of "*panamensis,*" "*orientalis,*" "*carabayae,*" "*meridae,*" "*flavescens,*" "*pallidus,*" and "*intermedianus,*" all in AMNH.

GENUS *BERLEPSCHIA*

This monotypic genus is related to *Philydor,* but *Berlepschia rikeri* differs from the many species of *Philydor* and from the single species of *Pseudocolaptes* (*boissonneautii*) in its morphology, in its rigid ecological re-

quirements, and very probably also in its nesting and other behavior.

Berlepschia rikeri is very elegant, more so than *Philydor* and than *Pseudocolaptes* or any other member of the family, with its beautiful coloration and graceful proportions; it is bright burnt sienna with a sharp pattern of pure black and white. *Berlepschia* is strictly and highly arboreal, apparently associated only with tall palms, and its wing is distinctly more pointed than those of *Philydor* and *Pseudocolaptes*; its tail is also more graduated (especially when compared to *Philydor*) and the tips of its rectrices are more acuminate.

The range of *Berlepschia* seems strange (map 37), consisting almost entirely of widely isolated localities[135] in Guyana, southern Venezuela, and in the Amazon Basin south to Goiás, but, no doubt, it follows the range of the taller species of the genus *Mauritia,* such as *M. flexuosa,* which are native to the Amazon Basin. These palms, which often grow in marshes in very extensive groves, or along rivers and other bodies of water, have very large crowns of heavy palmate leaves that are frequented by *Berlepschia*. The palms are slender and tall, rising to between about 18 and 25 m. from the ground, and may even reach 45 m. or more in height on the lower Amazon. *Berlepschia* is a good flyer and is said to fly only from the top of one palm to another, not alighting in other trees.

The nest of *Berlepschia* is unknown, but is most probably constructed within the fronds of the palms, perhaps in the dead hanging leaves, which if true, would suggest that its nest is woven, rather than placed in a cavity or hole as in *Philydor* and *Pseudocolaptes*. The food is gleaned from leaves as in the case of the other two genera.

Berlepschia rikeri
Figure 8

DESCRIPTION: Back, rump, upper tail coverts, and exposed surface of the wing, bright burnt sienna, with the exception of the primaries which are blackish; blackish centers or bases exist also in the coverts but are concealed. Head, nape, upper border of the mantle, and the whole of the underparts are pure black, very well and regularly streaked or barred with pure white, but the white markings predominate on the upperpart or center of the throat which may be almost entirely white in some individuals. The white streaks are modified into cross bars on the lower abdomen, flanks, and under tail coverts. The under wing coverts and axillaries are white, barred by black, and no rufous bar or area exists in the wing, although the inner web of the inner remiges is faintly paler along its outer edge.

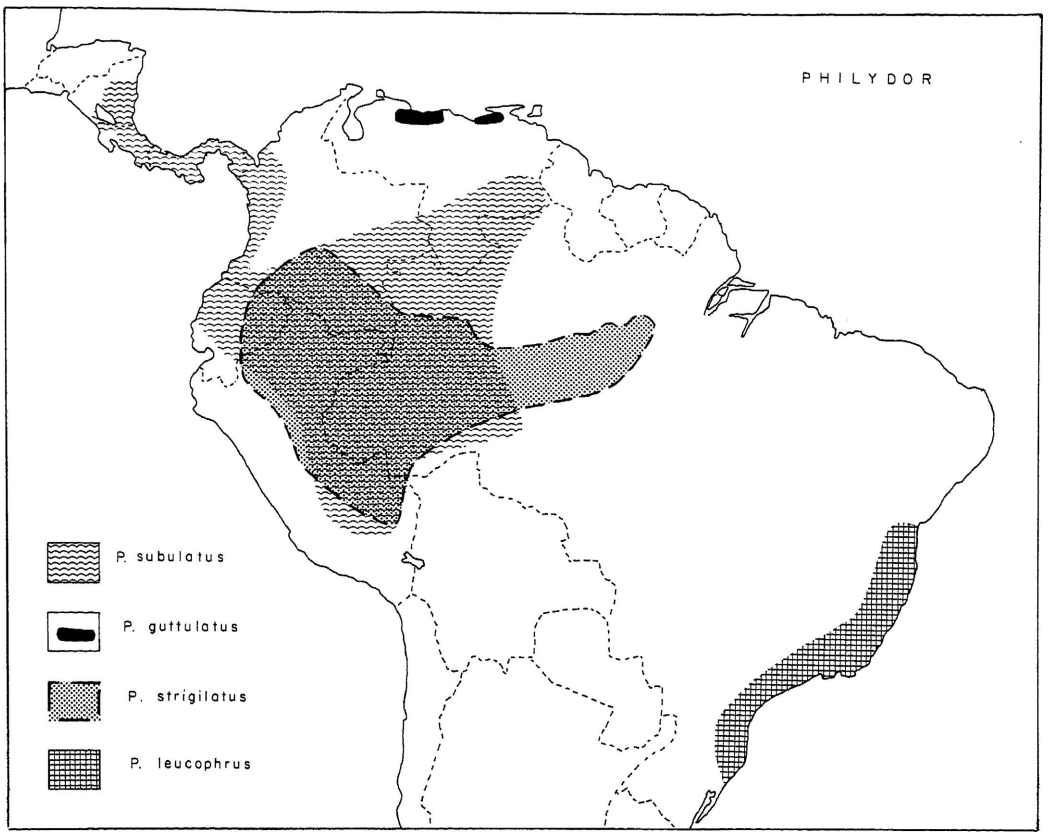
The tail is uniformly reddish chestnut, well graduated and composed of 12 stiffened rectrices, with very firmly integrated webs that are relatively narrow, and are sharply acuminate at the tip. Bill long and nearly straight, very strongly compressed laterally, and finally attenuated at the tip to an exceptional degree. Tarsus and toes relatively weak, but with strong claws.

RANGE: Not well known, but most probably corresponds to the range of the taller species of palms of the genus *Mauritia,* with which this species is very narrowly associated. Records are from Guyana, southern Venezuela (base of Mount Duida), and Brazil (region of Pará, lower Tocantins, region of Santarém and lower Tapajós, Manáos and lower Rio Negro, upper Rio Juruá and upper Rio Araguaya).

SPECIMENS EXAMINED: 34.

GENUS *PHILYDOR*

Eight generic names were merged with *Philydor* Spix, 1824, in my preliminary classification (1971a) and I now add another: *Cichlocolaptes* Reichenbach, 1853.[136] I had retained *Cichlocolaptes* in my first study, but only as a monotypic subgenus and with much reservation. After reopening the study of *Philydor* I cannot see any reason for retaining *Cichlocolaptes* even as a subgenus and have reached a firmer conclusion about the number of species which can be included in *Philydor*. After examining material of four forms which were not available to me when preparing my preliminary classification, I

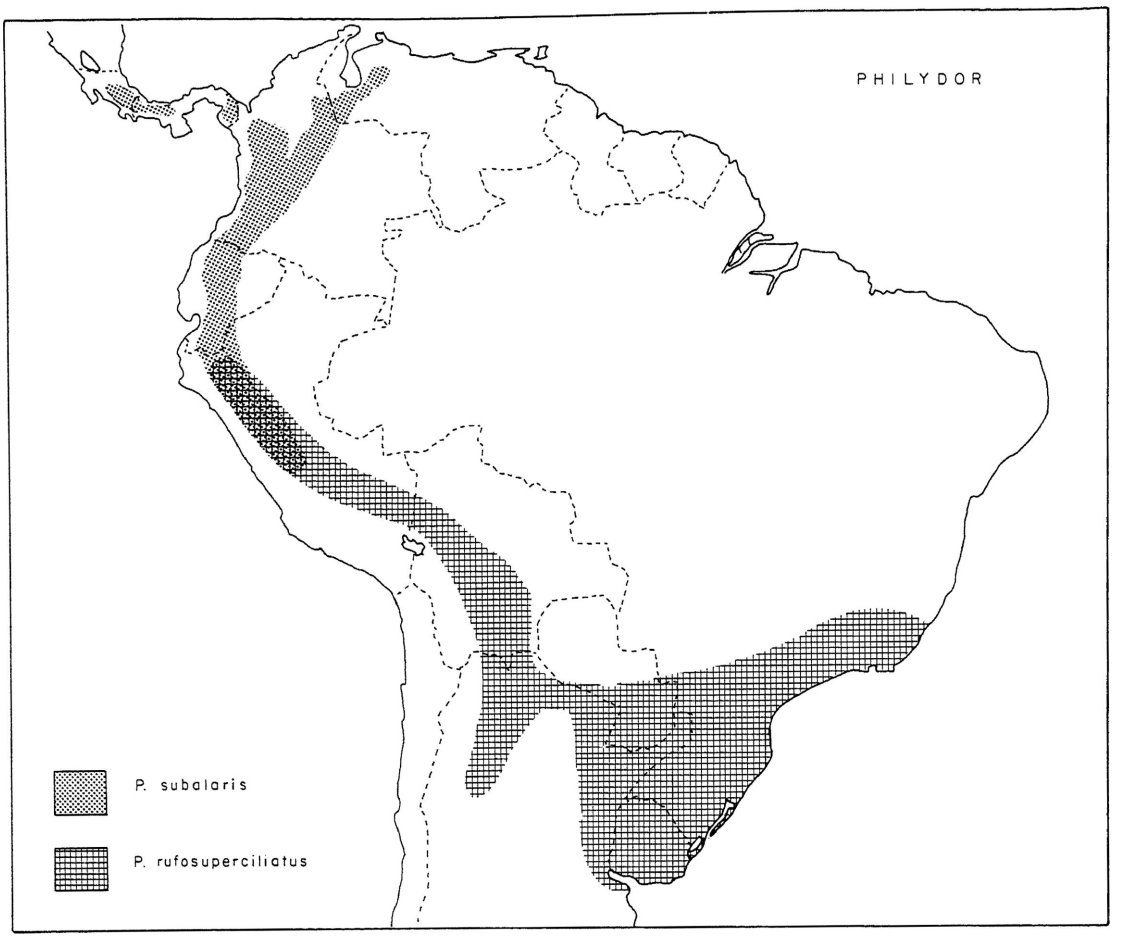


MAP 38. Geographical distribution of four closely related species of the genus *Philydor*; the distribution of a fifth species, related to these four (*P. subalaris*), is depicted on map 39.

now include 20 species in *Philydor*. These include *leucophrus* Jardine and Selby which I had placed apart from the other species, admitting for *leucophrus* the monotypic subgenus *Cichlocolaptes*. One other species was added and one was deleted. *Philydor striatus* Carriker, 1935, was added. I originally thought *striatus* was probably conspecific with *P. ucayalae* Chapman, 1928, and it is quite possible that this conclusion may be correct, but until specimens are collected in an intervening region, it seems best to treat *P. striatus* as a separate species. I have deleted *P. erythronotus* reluctantly from my first list; this form is combined with *P. erythrocercus* in the present arrangement, but the complex of forms of which *erythrocercus* and *erythronotus* are a part requires further consideration.

Philydor is distributed from southern Mexico (southern Veracruz and central Guerrero) south to northern Argentina (see maps 38–43), usually in heavy forest or very dense thickets, a type of habitat which makes observation difficult as a rule. On that account, *Philydor* is poorly known, generally speaking, for such a large genus. The nests of only 3 of its 20 species are known, and the nest has not been adequately described for any species.

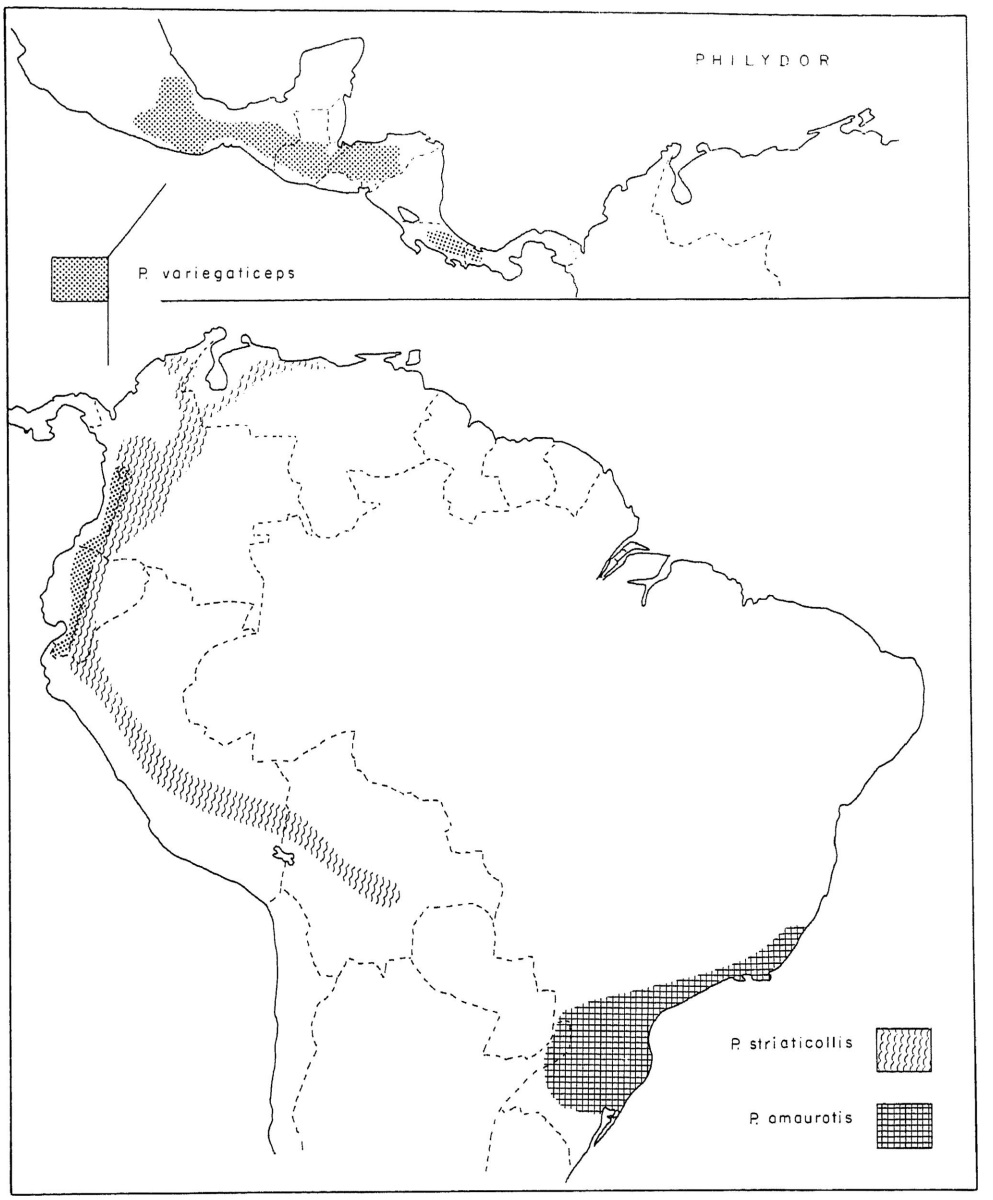
Some species are restricted to lowland forests, or occur chiefly in this type of forest, but well over half of the 20 species ascend humid forested mountain slopes to a fair el-



MAP 39. Geographical distribution of two species of the genus *Philydor*.

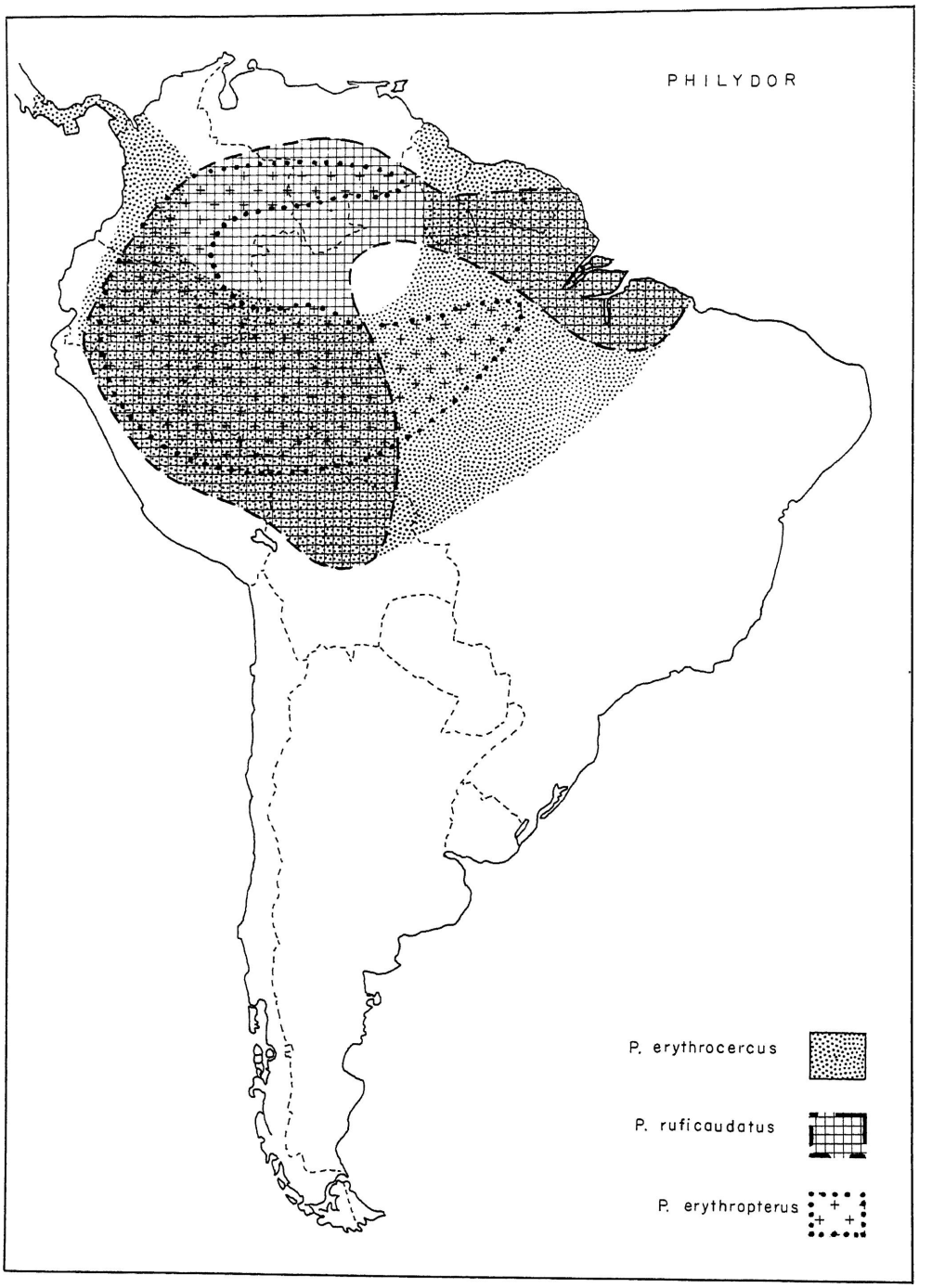
evation, and some species are perhaps best characterized as species of middle altitudes. This is especially true of the five species which inhabit Central America and Mexico (*Philydor subulatus, P. subalaris, P. variegaticeps, P. erythrocercus,* and *P. rufus*). Among these, *P. subalaris* and *P. variegaticeps* ascend to about 2800 m., exceeding well over 2000 m. in the case of *P. rufus,* but seem to reach only to about 1500 m. for *P. subulatus* and *P. erythrocercus*. About the same altitudes are reached by these five species in South America. Among the South American species not represented in Central America, *P. guttulatus* reaches about 2100 m. in coastal Venezuela; *P. rufosuperciliatus* breeds from the coast of Brazil and the delta of the Paraná, to about 2200 m. in the mountains of coastal Brazil, and to about 2800 m. on the slopes of the Andes in Bolivia and Peru; the range of *P. striaticollis* varies between about 1000 and 2600 m. A group of four South American species (*P. leucophrus, P. ruficaudatus, P. lichtensteini,* and *P. atricapillus*) reach altitudes varying between about 1400 and 1850 m.

The best known species are the five from Central America and Mexico mentioned above. They are all birds of dense, heavy, humid forest and their ecology and general

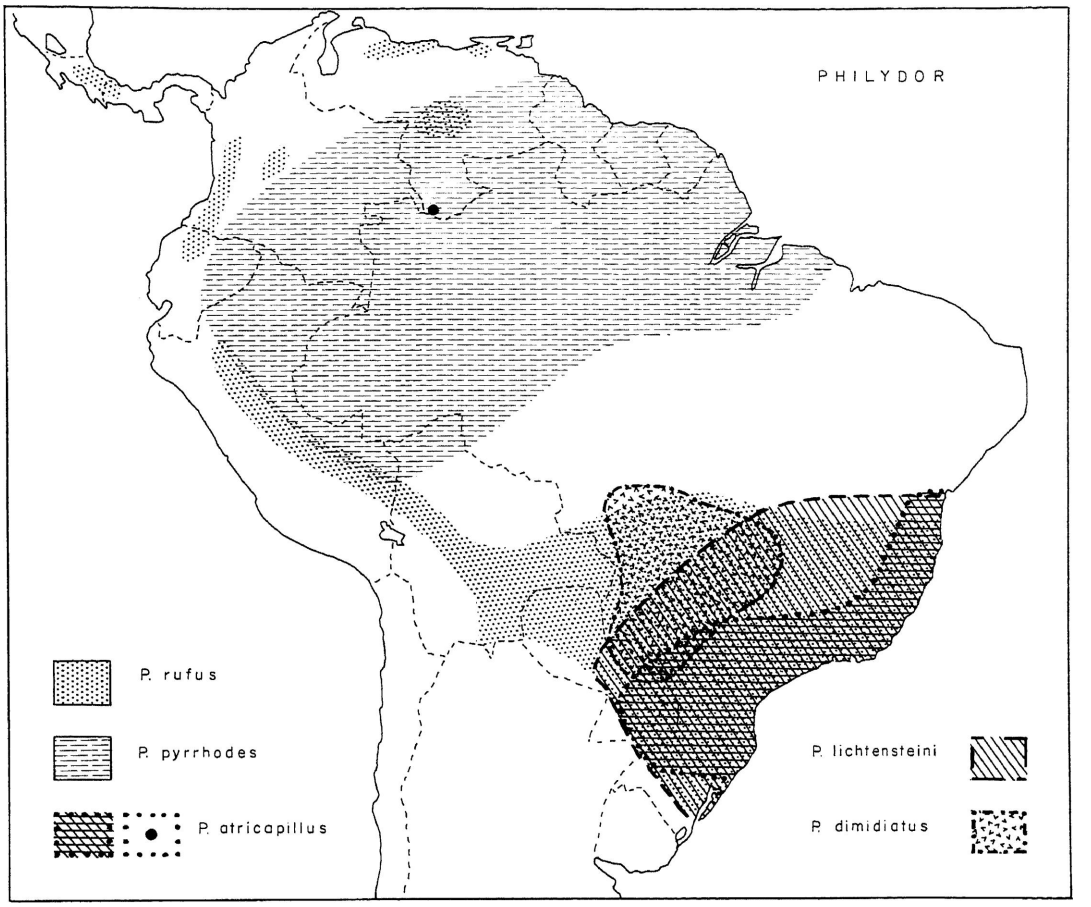


MAP 40. Geographical distribution of three species of the genus *Philydor*.

behavior seem to be essentially similar. They are all arboreal and very active, climbing over branches, and foraging in the foliage, tangles of vines, accumulation of dead leaves or other vegetable debris, and also searching and probing epiphytes. They assume many attitudes as they hunt actively for food, clinging to the sides or under surfaces of branches, occasionally dangling down from fronds like a large titmouse, or pecking and tearing at rotten twigs, or at the stems of epiphytes.



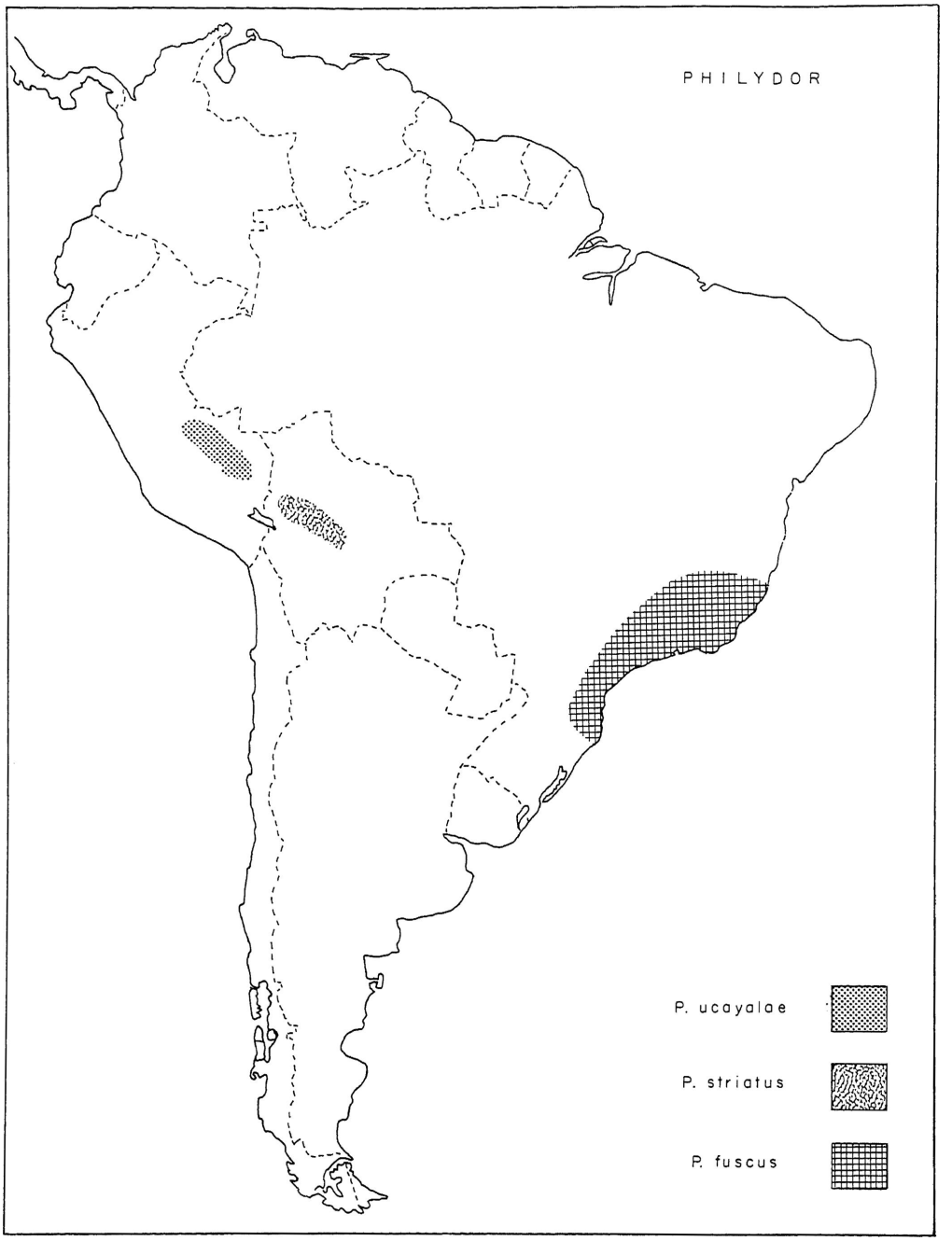
MAP 41. Geographical distribution of three species of the genus *Philydor*.



MAP 42. Geographical distribution of five closely related species of the genus *Philydor*; the distribution of a sixth species (*P. amaurotis*), related to these five, is depicted on map 40.

Wetmore (1972) described the behavior of *Philydor erythrocercus* as follows: "These are birds of the heavy forests . . . climbing actively over branches, particularly those that are broken and dead, to search among the epiphytes. While their method of climbing may suggest that of a woodpecker, they are quicker and more active in much of their movement. To the eyes of a naturalist trained in the north they seemed completely strange, unlike any northern species." In the case of *P. subalaris*, Wetmore said he has observed this species braced against a branch with its tail: "once I saw one climbing a vertical tree trunk, woodpecker fashion, bracing with the tail so that I thought that it was a woodcreeper until I had it in hand."

However, any mention of the woodpeckers (Picidae), or woodhewers (Dendrocolaptidae), is quite misleading when discussing the behavior of *Philydor*, as even the most superficial examination of its tail shows that its tip is not at all adapted for bracing against bark when climbing. The tail of *Philydor* is stiffened, to be sure, but its stiffening decreases progressively distally and its apex is soft, or relatively so. The rachis is not prolonged beyond the web, as a "spine," or "wire," in the manner of the Picidae or Den-



MAP 43. Geographical distribution of three species of the genus *Philydor*; *Philydor ucayalae* and *Philydor striatus* are very closely related to each other, but *Philydor fuscus* is a taxonomically isolated species.

drocolaptidae, in any species of *Philydor*. The tips of the rectrices are blunt or only slightly acuminate, and, in the only species (*P. rufus*) in which they are markedly acuminate, the tips are particularly soft, softer than in any species with blunt tips. *Philydor* may rest the tip of its tail against branches or the trunks of trees to some extent when climbing, but cannot derive much support from this action as it lacks a "bracing tool" entirely. Moreover, the small amount of wear shown at the tip of the tail in specimens suggests that this organ is not used much for support.

The four species that occur in Costa Rica (*Philydor subulatus, P. subalaris, P. variegaticeps,* and *P. rufus*) seem to have about the same geographical distribution, but differ somewhat in their ecology and behavior, judging by the report of Slud (1964). *Philydor variegaticeps* and *P. rufus* seem to be more active than the other two species (especially *P. variegaticeps*), and to forage higher above the ground than *P. subalaris* and *P. subulatus,* in the middle or upper strata of the forest in the case of *P. variegaticeps* and *P. rufus,* whereas *P. subulatus* is active from the upper undergrowth to a medium level in trees, and *P. subalaris* is usually found lower down than the other three species, "low along the periphery of or at breaks in the forest, mostly in the dense growth rising from the almost impenetrable ground cover, rather than inside the forest. It forages in the undergrowth and perhaps to a greater extent, low in the trees, rarely to medium heights from the ground," according to Slud.

The pronounced variation in the shape and size of the bill suggests that these species take somewhat different prey. The bill of *Philydor subulatus* is distinctly longer than that of the three other species, straight and thin, strongly attenuated, apparently well adapted for probing; whereas that of *P. subalaris* is shorter, thicker, more massive; and the bill of *P. variegaticeps* is small and strongly compressed laterally. The bill of *P. rufus* is about similar to that of *P. subalaris* in length, but not in shape, as the bill of *P. subalaris* is about twice as thick. The length of the bill, consisting of the average for both sexes (in round numbers) is: 25 mm. for *P. subulatus,* 22 mm. for *P. subalaris,* 19 mm. for *P. variegaticeps,* and 21 mm. for *P. rufus*.

An interesting aspect of behavior reported in the four species in Costa Rica is their association with birds of other families in mixed insect-hunting parties which wander through the forest. This behavior is mentioned by Slud, but the species with which *Philydor* associates are mentioned by Slud only in the case of *P. subulatus*; they are antbirds (Formicariidae). Slud (1964) said *P. subulatus* "is met singly, sometimes in two's, usually in the company of antwrens and antvireos circulating immediately above the forest understory," but *P. variegaticeps* is apparently associated with parties traveling higher above the ground, as Slud said this species was "a component of a mixed insect eating bird party sweeping noisily through the trees, at middle or higher levels."

Little or no information exists for the 15 other species, which are all restricted to South America, with the exception of four species (*Philydor strigilatus, P. rufosuperciliatus, P. striaticollis,* and *P. atricapillus*), for which some information can be found.

The information on record for *P. strigilatus, P. striaticollis,* and *P. atricapillus* is brief. In the case of *P. strigilatus,* Sztolcman (in Taczanowski, 1884), stated that this species formed part of mixed hunting parties wandering through the forest, was highly arboreal, active, hopping from branch to branch, but did not cling (climb?) to the vertical trunks of trees ("*ne s'accroche jamais aux troncs verticaux des arbres*").

A roughly similar remark was made by Carriker (in Todd and Carriker, 1922) about *Philydor striaticollis* in field notes from Santa Marta, Colombia; *P. striaticollis* is "an active, noisy bird, continually scrambling and hopping about among the branches of the trees, but unlike the stiff-tailed species doing little real climbing. It is fond of rummaging about in the bromelias for insects." The "stiff-tailed" species cited are most probably of the family Dendrocolaptidae.

Mitchell (1957) found *Philydor atricapillus* in very dense forest "where it always advertised its presence by its loud harsh cells and by its ceaseless activity. Its movements can best be described as scrambling, for it climbs about in the thickets it inhabits, over, under, and around branches and twigs, balancing with its long, bright cinnamon-brown tail. It is not particularly shy and allows a close approach before flying off to the next bit of shrubbery."

The information on *Philydor rufosuperciliatus* is more extensive. This species has a great range from the slopes of the Andes of northern Peru to southeastern Brazil, northwestern Argentina, Uruguay, and the delta of the Paraná, and varies ecologically more than the other species. On the slopes of the Andes it inhabits dense humid forest, but forages chiefly in the undergrowth or in low trees, according to Sztolcman (in Taczanowski, 1884) who said "*Il habite les forêts humides, où il cherche sa nourriture dans les fourrés des buissons et des arbrisseaux de la forêt, sur les branches basses et les feuilles sèches, en produisant quelquefois un bruit assez fort.*"

In Argentina and Uruguay, *Philydor rufosuperciliatus* is also a bird of dense forest, but frequents also thickets in low flat country or on slopes, gallery forest along water, such as the Paraná and its delta, and thick high vegetation in swamps. Wetmore (1926) found *P. rufosuperciliatus* in Tucumán "on the lower forested slopes . . . in dense growths of bushes and herbaceous vegetation," where it kept well under cover; and in Uruguay "in dense thickets, usually in lowlands, where it was more or less wet and swampy . . . [and] worked deliberately in the dense plant growth, often somewhat awkwardly, clambering about like large titmice, always well under cover."

Pereyra (1938) also stated that *Philydor rufosuperciliatus* behaves like the Paridae and inhabits densely wooded or forested localities, but his account indicates he found this species to be much more alert and less diffident than did Wetmore. Pereyra said *P. rufosuperciliatus* is very active and lively ("*alegre*"), curious, investigating holes and crevices, hopping, dangling down from branches, and climbing, but not climbing in the manner of a woodpecker or woodhewer.

The nests of only three species of *Philydor* are known: *P. guttulatus, P. striaticollis,* and *P. rufus*; they have not been adequately described for any species. Paul Schwartz wrote me that a nest was found in a cavity, the size and depth of a normal concrete block, in a wall of the biological station of Rancho Grande, Venezuela. This cavity, which Schwartz compared to a "box" opened on only one side, had been "filled" with twigs, undoubtedly by a furnariid, and provided with an entrance near the bottom of what had been the open side of the box. The nest was not found and examined by Schwartz himself, but Schwartz and the discoverer of the nest who described it to Schwartz, both believed it was the nest of *P. guttulatus*.

Ernst Schäfer wrote me that he once found and photographed a nest of *Philydor striaticollis* within the broken trunk of a thorn-studded *Bactris* palm, but Schäfer could not locate the photograph at the time he wrote and gave me no additional information.

I have obtained data on the nest of *Philydor rufus* from four independent correspondents; this information shows that it is located within a cavity, but in quite different sites. Claes C. Olrog wrote me he found four nests of *P. rufus* in Misiones, Argentina, all within holes in trees. C. J. Marinkelle reported finding one in Colombia constructed of fine grass at the end of a burrow under the ground about 20 cm. deep. This burrow had apparently not been excavated by the bird, as Marinkelle described it as "an animal burrow."

Ernst Schäfer and Paul Schwartz have found the nest in a tunnel dug in a bank of earth, but Schwartz told me that most of the nests he had found were in holes in walls. Schäfer believed that *Philydor rufus* digs its own burrow, but Schwartz said he had no proof that it does so. According to Schwartz, if *P. rufus* does not dig its own burrow, it appropriates one dug by some other species of bird or by a species of small mammal. As the wording of the report pub-

lished by Schäfer (1953) on the nest of *P. rufus* is ambiguous, I wrote him for elucidation. Schäfer's report could be misinterpreted as indicating that *P. rufus* digs a hole into "virgin wood"; Schäfer replied that *P. rufus* "breeds in burrows in the earth, mostly alongside roads or man-made earth walls near buildings in the forest, but in ecological niches which are drier than the surrounding virgin woods," thus confirming the information received from Schwartz that I had transmitted to Schäfer.

A very large nest, built of thorny twigs (*Acacia*), constructed about 2 m. above the ground in a low tree overhanging water, photographed and reported by Fiebrig (1921) as the nest of *Philydor rufus*, was undoubtedly misidentified, in my opinion.

Morphological Variation

The plumage of *Philydor* is streaked or not, and the variation of the bill is pronounced, but, with this reservation, *Philydor* is homogeneous, or relatively so, and most of its species are not sharply differentiated.

The species are of medium size, but are relatively large for the Furnariidae as their mean wing length, in round numbers, averages 89 mm., as against 64 mm. in a large group of 81 species of three genera (*Synallaxis, Certhiaxis,* and *Thripophaga*) in the Synallaxinae. The tail, which is composed of 12 rectrices, is shorter than the wing, and the ratio between its length and that of the wing averages 0.85. However, in *Philydor rufosuperciliatus,* with a ratio of 0.98, and in *P. rufus* with one of 0.97, the tail is almost as long as the wing.

The tail is moderately graduated as a rule, but in some species the graduation is less pronounced than in others and becomes slight, especially in the case of *Philydor erythrocercus,* in which the tip of the tail could be described as more rounded than graduated. The rectrices are normal in width, or somewhat narrow, their webs are firmly integrated, and their tips are blunt or slightly acuminate, with the single exception of *P. rufus* in which they are quite distinctly acuminate. The acuminate tip of the rectrices of *P. rufus* is soft, however, not stiffened, contrary to expectation, as, normally, the tips are more stiffened when more acuminate in the Furnariidae. The tail is elastic but not rigid when flexed and manipulated. The degree of stiffness varies somewhat specifically but, generally speaking, the upper third of the tail is well stiffened, the middle third less so, and the stiffening decreases gradually on the distal third, the tips of the rectrices being soft in some species, such as *P. rufus.*

The tarsus is of moderate length and strength and the toes and their claws are well developed, but not unusually so; the species with the strongest feet are *Philydor ucayalae* and *P. striatus.*

The most pronounced structural variation is in the shape of the bill, although the difference in size is well indicated also; the mean length in both sexes varies from about 17.50 to 28 mm., with an average of 21.50 mm.

In some species, the bill is "normal" in shape, of average length, moderately compressed laterally, with the culmen slightly decurved and slightly hooked at the tip, and the mandible is nearly or quite straight, with the gonys ascending only very slightly and only near the apex. But the shape of the bill is not identical in any two species and the major variations have been reflected in the separation of no fewer than seven "genera," four of them monotypic, which were based exclusively or chiefly on adaptive variations in the shape of the bill. For instance, *subulatus* was separated from *Philydor* as a distinct "genus" (*Hyloctistes*) because its bill is "relatively much longer"; *Ancistrops* was proposed for *strigilatus* because its bill is strongly hooked and has a quite distinctly ascending gonys. But all the variation is very clearly, in my opinion, of no more than specific importance taxonomically, a question I discussed in my preliminary classification (1971a); in a second paper (1971b) I studied the species with a "xenops-type" of bill.

Species with a "xenops-type" of bill exist in unrelated genera of the Furnariidae, or in other bird families such as the Formicariidae. In these species the bill is very strongly compressed laterally, the culmen is straight

or virtually so (not decurved), and the gonys ascends very strongly, giving the impression that the bill is turned or tilted-up, which is false, as the culmen is straight. This type of bill exists in several species of *Philydor*, such as *P. guttulatus, P. ucayalae,* and *P. striatus* in which it is the most pronounced. But variations in this type of bill are shown also by *P. strigilatus, P. rufosuperciliatus, P. dimidiatus,* and *P. fuscus*. Variations among these six species have led to the separation of three monotypic "genera" (*Ancistrops* for *strigilatus, Simoxenops* for *ucayalae,*[137] and *Anabazenops* for *fuscus*).

A slight, curious modification of the throat feathers is shown by *Philydor ucayalae* in which these feathers are probably erectile, as the feathers are somewhat squamate in shape, slightly but distinctly elongated, arranged in vertical rows, and are or seem to be slightly stiffened. This modification of the feathers of the throat is suggested in a few other species, among them *P. striatus* which is a close relative of *P. ucayalae*.

The variation in coloration and pattern is slight although some species are streaked and some are not. Streaks can exist on both the upper and underparts, or only on the underparts. The species which are streaked both above and below are *Philydor strigilatus, P. leucophrus, P. subulatus, P. guttulatus,* and *P. subalaris,* in addition to *P. striatus*. The first five of these six species are brown on the upperparts with buffy or ferruginous streaks on both the crown and back; the buffy streaks on their underparts vary a great deal in their development. The streaks are only more or less vague in *P. subulatus*; narrow, but quite distinct in *P. subalaris*; and very broad, but with dark edges that are broad also, in *P. guttulatus* and *P. leucophrus,* these broad dark and buffy streaks producing a flammulated appearance. In *P. strigilatus,* the greater part of the feather has become buffy, and the dark edges have become so pale, that the underparts of *P. strigilatus* are chiefly buffy or dull pale yellow (Naples Yellow). The underparts are strongly ferruginous in *P. striatus,* with paler streaks that are not sharply defined; *P. striatus* is not a close relative of the other five species.

The species that are streaked on the underparts only, or not completely uniform, are more numerous than the five species mentioned above that are streaked on both the upper and underparts. The streaking varies from quite distinct, heavy and broad in *Philydor rufosuperciliatus,* to very faint in other species. Other species, such as *P. lichtensteini, P. rufus, P. atricapillus,* and *P. pyrrhodes* are uniformly dark ochraceous or ochraceous orange on the underparts, without any trace of streaking. In most species, the throat is distinctly or slightly paler than the breast and abdomen, and, in virtually all the species, a superciliary and/or post-ocular streak exists, or some suggestion of it. The tail is uniformly rufous in all the species with only the partial exception of *P. lichtensteini* in which the central pair is more pale buffy brown than rufous, which is true also of the outer web of the other rectrices to a variable extent.

The crown and mantle are usually uniform in their coloration, but a contrast exists in some species which have a darker crown, such as *Philydor rufus, P. atricapillus,* and *P. fuscus*. In a few species, of which the best example is *P. amaurotis,* the crown feathers are not uniform. The greater part of the exposed area of the feather is brown, but the concealed portion of the feather is black or blackish and prolonged as a narrow exposed subapical band, with a white area, narrowly guttate in shape which follows the shaft of the concealed portion of the feather.

The under surface of the wing, or rather the axillaries, under wing coverts, and an area variable in extent along the outer edge of the inner web of the remiges, are normally very bright in coloration. It is the most colorful area of the entire plumage, generally speaking; and, I suspect, this bright coloration plays a role in the behavior of *Philydor* in its heavy and dark forest habitat.

Phylogeny

The close relationship of some species seems to be clear; certain groupings are sug-

gested by the morphological variation mentioned above.

The five species (*Philydor strigilatus, P. leucophrus, P. subulatus, P. guttulatus,* and *P. subalaris*) which are streaked on both the upper and underparts probably form one group. These species are also coarser than all the other species with the exception of *P. ucayalae, P. striatus,* and *P. fuscus,* but the plumage of these three species suggests they are not related to the other five. *P. ucayalae* and *P. striatus* are very closely related to each other (if not actually conspecific), but the nearest relative of *P. fuscus* is totally obscure to me, and, for this reason, I have listed it last in the sequence of the species, apart from the others.

Another group of four species (*Philydor lichtensteini, P. rufus, P. atricapillus,* and *P. pyrrhodes*) can be recognized, to which *P. dimidiatus* and *P. amaurotis* can be added. In these six species the underparts are strongly pigmented, dark ochraceous or ochraceous orange, with the exception of *P. amaurotis,* and uniform with the exception of *P. dimidiatus.* In the latter species, very faint and slight, very narrow pale shaft streaks can be discerned on the breast, and the center of its feathers shows also a very slight tendency to be paler, but I think Hellmayr (1925) was correct when he stated that *P. dimidiatus* was "most nearly related to" *P. pyrrhodes.* But quite distinct differences in the bill and in proportions show that the two birds are not conspecific, in my opinion. The bill of *P. dimidiatus* is slender, with the culmen nearly straight, and with the gonys ascending moderately but quite distinctly; whereas the bill of *P. pyrrhodes* is much thicker, with the culmen decurved and the gonys normal in shape. *P. dimidiatus* has a considerably longer tail, proportionally, as well as in actual measurements.

The underparts of *Philydor amaurotis* are pale brownish olive, heavily and broadly, but not sharply streaked with dull white on the breast, and are narrowly streaked on the abdomen. This fact suggests, at first, that *P. amaurotis* is not related to the other five species that have very strongly ochraceous underparts that are also uniform or virtually so (not streaked). However, evidence of relationship is suggested by the coloration of the crown and the pattern of its feathers. The color of the crown is not stable in this group of six species. In *P. amaurotis,* as stated above, only the exposed portion of the feather is brown with the exception of the narrow black or blackish subterminal band; the remainder of the feather is black or blackish with a white area. This unusual pattern exists also in *P. lichtensteini,* though not so well developed, and is suggested in *P. atricapillus.* The color of the crown varies geographically in *P. atricapillus,* from rufous brown to brownish black and dull black; the crown is ashy gray in *P. rufus,* and bronzy in *P. pyrrhodes* and *P. dimidiatus,* where it is uniform with the mantle.

In the first paragraph of the section on the genus *Philydor* I stated that I now include 20 species in this genus, but more than one species may be involved in the *P. erythrocercus* "complex of forms," whereas *P. ucayalae* and *P. striatus* may turn out to be conspecific (see Vaurie, 1971b). It will be necessary to collect fresh material to reopen the study of these birds.

Three other taxa, the status of which seemed controversial to me, and of which I had then seen no specimens, were listed in my preliminary classification (1971a). They are *hylobius* Wetmore and Phelps, 1956, from southern Venezuela; *baeri* Hellmayr, 1911, from Minas Gerais, Brazil; and *dimidiatus* Pelzeln, 1859, from Mato Grosso, Brazil.

It was necessary for me to compare *baeri, dimidiatus,* and *pyrrhodes* directly to one another, as Hellmayr had given the impression these three birds might be conspecific. For the loan of specimens of *baeri* and *dimidiatus,* which are very rare in collections, and for the loan of the only two known specimens of *hylobius,* I am very grateful to the institutions and persons named below.

The type and paratype of *Philydor baeri,* and two additional specimens, were lent by the Museum of Natural History of Munich through the recommendation of Dr. G. Dies-

selhorst, and the three cotypes of *P. dimidiatus* by the Natural History Museum of Vienna through the courtesy of Dr. H. Schifter. Direct comparison shows that *baeri* is somewhat paler than *dimidiatus* but is certainly conspecific with it as Pinto and Camargo (1955) had already concluded, whereas *P. dimidiatus* is distinct specifically from *P. pyrrhodes,* but, in my opinion (see above), probably related to it.

The two specimens of *Philydor hylobius* known so far were lent by the United States National Museum and consist of one immature bird and one mutilated adult (without the tail). My comparison of this rather inadequate material to specimens of *P. atricapillus* from Bahia in comparative plumage, suggests *hylobius* is only an isolated population of *P. atricapillus,* but not a distinct species as concluded by Wetmore and Phelps (1956), who had compared their two specimens to *P. atricapillus. P. hylobius* is probably more rufescent than *P. atricapillus* from the greater part of its range, but birds from Bahia match or approach closely the two specimens of *P. hylobius,* including the color of the crown (the most conspicuous character) which is rufous brown and about similar. Birds from Espirito Santo are more similar to those of Bahia, but farther south the crown becomes darker, less brown, more blackish and, eventually, dull black. The variation is apparently clinal.

Geographical Variation

Fifteen of the 20 species of *Philydor* vary geographically, or are said to vary geographically, but the variation is of really major importance in only a single species (*P. erythrocercus*), and quite distinct in three more (*P. leucophrus, P. rufosuperciliatus,* and *P. variegaticeps*), and possibly also *P. atricapillus,* for which adequate material of an isolated population has not been collected.

The geographical variation of *Philydor erythrocercus* (map 41) is strongly marked and puzzling. The variation has been discussed by Zimmer (1935) and I follow him in recognizing only one species, although I disagree with him factually and in his interpretation of the geographical variation. The populations can be divided in three groups, in my opinion.

In one group, composed of two forms (*P. e. fuscipennis* in western Panama, and *P. e. erythronotus* in eastern Panama and in the Andes of Colombia south to northwestern Ecuador), the coloration is dark and the remiges are dusky gray. The underparts are darker in western Panama, more brownish cinnamon, and the upperparts are slightly darker on the crown and back, which are dusky rufous on the crown, chestnut on the back. The ear coverts are dark brown with rufous streaks, and the rufous post-ocular streak is not sharply defined in these populations which I had considered to be a separate species in my first revision (1971a), calling it *P. erythronotus* in error, as *fuscipennis* Salvin, 1866, is older than *erythronotus* Sclater and Salvin, 1873, though much less well known.

The second group of populations occupies the remainder of the range, with the exception of the region extending from central Peru south to northwestern Bolivia, which is inhabited by the strongly differentiated *P. e. ochrogaster* (see below). This second group is composed of three slightly differentiated forms: nominate *erythrocercus* Pelzeln, 1859, in the Guianas and lower Amazon west to about the Rio Negro; *lyra* Cherrie, 1916, in eastern Peru and in Brazil south of the Amazon to the Beni in Bolivia; and *subfulvus* Sclater, 1862, in southeastern Colombia and in eastern Ecuador, south to the region north of the Amazon in Peru. The geographical variation is not uniform in the great range occupied by this second group. Other populations could be distinguished taxonomically, as stated by Gyldenstolpe (1951), but I agree with him that no further subdivision is necessary. An additional form (*suboles* Todd, 1948) that I have not seen may belong to this second group.

This second group of populations can be characterized by having the wings more brownish than the birds of the first group, and by having a body plumage which is distinctly olive or olivaceous, "greenish" on the upperparts, not very strongly rufous as

in the populations of the first group. Birds of this second group are also much paler on the underparts, which are washed thinly by pale gray, buff, or dull yellow, but are not cinnamon brown or rufous as in the first group; the post-ocular streak is better developed, and, in some cases, extends forward to the region above the eye, or in front of the eye to the base of the bill. The ear coverts are much darker and more conspicuous; the throat is much paler, whitish; and the coloration of the upperparts is uniform, whereas the color of the crown contrasts well with the mantle in the populations of the first group (*P. e. fuscipennis* and *P. e. erythronotus*). In other words, the populations of the second group are quite distinct from those of the first group, and, at first glance, appear to be a distinct species, but they are probably conspecific as the juvenal plumage of *P. e. subfulvus* (the darkest of the three forms of the second group) is strongly rufous and resembles the coloration of *P. e. erythronotus,* the paler and duller form of the first group.

The third group of populations consists of a single form (*P. e. ochrogaster* Hellmayr, 1917) which is strongly distinct from the populations of both the first and second groups. This form inhabits central and southern Peru and northwestern Bolivia, as stated above, and is the most strongly differentiated form of the entire complex—"it certainly appears to be specifically distinct," as noted by Bond (1945). Zimmer (1935) stated that *P. e. ochrogaster* is "intermediate between *lyra* and *subfulvus*" of the second group, and that it "approaches the condition of true *erythrocercus,*" the third member of the second group. However, this is not evident to me, judging by my examination of the material he had seen and of many other specimens as well. I find his long discussion to be confusing, when not irrelevant; and I did not see a specimen that was truly intermediate between the three groups, although some similarity exists between some forms of the first and second groups.

Philydor erythrocercus ochrogaster is a bright, richly colored bird, strongly ochraceous buff or pale amber brown on the underparts which are almost uniform. It is much more rufous, less greenish, on the back than the populations of the second group, but is not chestnut as in the populations of the first group. Its wing is cinnamomeous, not dusky gray (as in the first group), or brown (second group); its post-ocular streak is much better developed; and its ear coverts are paler and more variegated than in all the populations of the two other groups. It is possible that this complex of three very distinct forms represents three separate species, but until the birds can be studied carefully in the zones of contact in Colombia, Ecuador, Peru, and Bolivia, it seems best to follow Zimmer's treatment and admit only a single species; *P. e. ochrogaster* poses the greatest problem in the complex.

Pinto (1941) has discussed the geographical variation of *Philydor leucophrus* and shown that two quite distinct forms can be recognized. Specimens from the northern end of the range—from Bahia south to eastern Minas Gerais and the border of Rio de Janeiro and São Paulo—are large, coarsely streaked, and have a pale rufous tail (Light Red or English Red); whereas the populations which exist farther south—through Santa Catarina and Paraná to Rio Grande do Sul—consist of smaller birds that are less coarsely streaked and have a much darker rufous tail, bright reddish chestnut in color. These smaller birds with dark tails were named *P. l. holti* by Pinto. In adults that I have measured, seven specimens of *holti* have a wing length of 85–91 mm. (average 89), as against 88–108 mm. (average 102.3) in eleven of nominate *leucophrus,* the type locality of which is Minas Gerais. The trend of geographical variation is a clinal one, and birds taken on the border between the states of Rio de Janeiro and of São Paulo are intermediate, according to Pinto.

The geographical variation in the coloration and its general saturation in *Philydor rufosuperciliatus* (map 39) are distinct. The populations of Peru and of La Paz and Cochabamba in Bolivia are rufous brown above and the ground coloration of their underparts is umbraceous, whereas birds from southeastern Bolivia and western Argentina

(which have been named *P. r. oleagineus*) are paler and duller above than the more rufous birds of Peru and of La Paz and Cochabamba, and their underparts are distinctly olivaceous gray rather than umber. The birds of Brazil (north of Santa Catarina) are darker and more olivaceous above and below than the birds of southeastern Bolivia and western Argentina, and represent nominate *P. r. rufosuperciliatus* if subspecies are recognized. The darkest form (which has been named *P. r. acritus*) is strongly olive on the upperparts and inhabits Santa Catarina and Rio Grande du Sul in Brazil, Uruguay, Paraguay, and eastern Argentina. Two forms, called *P. r. similis* and *P. r. cabanisi* have been named from Peru to La Paz and Cochabamba. Some differences exist in the streaking but they are trivial and very relative, and also not constant as much individual variation exists in the streaking.

The range of *Philydor variegaticeps* is interrupted (map 40) and the two groups of its populations differ quite distinctly. The underparts in *P. v. temporalis* of South America are much more richly colored than in nominate *P. v. variegaticeps* of Central America, heavily spotted with buff on an ochraceous orange ground, whereas nominate *variegaticeps* is poorly streaked and duller, olive brown, rather than ochraceous orange. In *P. v. temporalis*, the crown is darker also, the back is more rufous, and the post-ocular streak is much better developed.

The geographical variation of *P. atricapillus* (map 42) has been briefly mentioned above in the section on phylogeny. A cline of increasing color saturation runs from north to south in Brazil—to which no attention seems to have been called hitherto—and "*hylobius*" (a form known from only one adult and one young taken on the border of Venezuela and Brazil) represents probably a more rufescent and well-isolated population which, however, requires further study.

The other 10 species of the genus *Philydor* which show some evidence of geographical variation or in which geographical variation has been mentioned are: *P. strigilatus, P. subulatus, P. guttulatus, P. subalaris, P. striaticollis, P. ruficaudatus, P. erythropterus, P. rufus, P. dimidiatus,* and *P. ucayalae*. The variation affects the coloration or streaking of the plumage in all these species with the exception of *P. ucayalae*. In the latter species, which I have discussed in another publication (1971b), the bill and feet appear to be bigger in birds from the basin of the Madre de Dios River, southern Peru, than in birds from the basin of the Ucayali River, but this difference requires confirmation as only a single specimen is known so far from the Ucayali. In the other nine species, the variation in the coloration, saturation, or streaking of the plumage is usually slight or quite trivial, and is so relative as a rule that all the many forms that have been named differ only to a question of degree. In some cases (such as *P. rufus*, in which about eight "subspecies" have been named) the variation is also clinal for the greater part; in *P. rufus* the variation affects the width and distinctness of the ochraceous band across the forehead as well as the relative brightness of the coloration of the plumage. The populations of *P. rufus* from Brazil have been reviewed by Novaes (1961a), but in *P. rufus*, and all the other nine species listed above, no subspecific separation seems necessary to me, with the possible exception of *P. ucayalae*.

KEY TO THE SPECIES OF *PHILYDOR*

1. Crown and mantle streaked 2
   Crown and mantle not streaked 7
2. Breast and abdomen heavily or conspicuously streaked with buff on an olive brown ground 3
   Breast and abdomen not heavily or conspicuously streaked 5
3. Upper tail coverts rusty brown, or dark hazel, with fine yellowish shaft streaks; post-ocular streak broad, sharply defined, very conspicuous ..... *leucophrus*
   Upper tail coverts reddish chestnut, uniform, not streaked; post-ocular streak very narrow, indistinct, very poorly defined 4
4. Bill straight, with gonys strongly ascending; streaks on mantle relatively broad, edged with dull black laterally; buffy streaks on breast exceptionally broad, with dark olive brown edges, resulting in a flammulated appearance ..... *guttulatus*

Bill slightly decurved, "normal" in shape, with gonys not ascending; streaks on mantle quite fine and without dark edges; buffy streaks on breast narrow and without dark edges ..... *subalaris*

5. Underparts strongly ochraceous and tawny; gonys of the bill ascending strongly ..... *striatus*

Underparts buffy, or pale dull brown with an olive tinge; gonys normal, or ascending moderately or slightly toward tip 6

6. Upper tail coverts olive; culmen slightly decurved and gonys ascending moderately, or slightly but quite distinctly .... *strigilatus*

Upper tail coverts reddish chestnut; bill straight, attenuated, with gonys normal... *subulatus*

7. Crown and nape separated by a conspicuous nuchal band of dull white ..... *fuscus*

Crown and nape not separated by a dull white nuchal band 8

8. Rump and upper tail coverts olive, yellow ocher, or ochraceous 9

Rump and upper tail coverts reddish chestnut or rufescent 13

9. Rump and upper tail coverts olive 10

Rump and upper tail coverts yellow ocher .. 12

10. Greater upper wing coverts and outer webs of remiges reddish ..... *erythropterus*

Greater upper wing coverts and outer webs of remiges dark dull brown..... 11

11. Underparts dull pale olive brown, very heavily streaked with pale buff ..... *rufosuperciliatus*

Underparts dull pale yellow (Naples Yellow) with a faint cinereous wash, and very faint, vague streaks ..... *ruficaudatus*

12. Crown ashy or olivaceous gray, with a broad, conspicuous, ochraceous buff band across the forehead; and feathers of the crown uniform from the base to the tip, not black or blackish on their concealed portion .... *rufus*

Crown pale grayish olive, lacking completely an ochraceous frontal band; and with its feathers not uniform in coloration as the concealed portion is black or blackish .... *lichtensteini*

13. Breast and abdomen pale brownish olive, distinctly streaked with buff; and contrasting strongly with the throat, which is paler... 14

Breast and abdomen burnt sienna, ochraceous, cinnamomeous, olive or dingy buff, with only very faint streaks, or uniform; not contrasting or contrasting only very slightly with the throat 16

14. With broad and very distinct supra-auricular streak and eye-ring which are deep cadmium yellow ..... *variegaticeps*

Supra-auricular, or post-ocular streak dull white or pale buff; with or without an indistinct pale buff eye-ring 15

15. Post-ocular streak dull white, very distinct and broad; no eye-ring ..... *amaurotis*

With a very narrow and indistinct buffy supra-auricular streak and eye-ring..... *striaticollis*

16. Upper tail coverts reddish chestnut 17

Upper tail coverts dull or bright orange.. 19

17. Bill "normal" in shape, with culmen decurved and gonys not modified ..... *erythrocercus*

Bill modified in shape, culmen straight or virtually so; gonys ascending very strongly or quite distinctly so 18

18. Very richly pigmented (dark reddish chestnut above, bright burnt sienna below); bill massive, with gonys ascending to an exceptionally pronounced degree; large, wing length averaging about 104 mm. ..... *ucayalae*

Less richly pigmented (rufous or olive brown above, dark ochraceous below); bill slender, with gonys ascending but to a moderate degree only; smaller, wing length averaging about 87 mm. ..... *dimidiatus*

19. Superciliary streak not sharply defined; ear coverts ochraceous and similar to the throat in coloration; crown and mantle uniformly bronzy brown ..... *pyrrhodes*

Superciliary streak very conspicuous, broad and sharply defined; ear coverts dark and not similar to the color of the throat; crown dark (varying from dark or rufous brown to blackish) and contrasting with the paler mantle ..... *atricapillus*

List of the Species

Philydor strigilatus

Figure 9

Description: Upperparts dark olive, very distinctly streaked with buff or pale yellow with an indistinct superciliary streak of the same color. Underparts buffy, indistinctly streaked, the center or greater part of the feather being buffy, with the sides or edges more or less pale olive gray. Exposed sur-

face of the wing dull Venetian Red or burnt sienna; with the axillaries, under wing coverts, and a very large area on the inner web of the remiges salmon orange. Tail uniformly Light Red, slightly graduated only, with the tips of the rectrices slightly subacuminate or nearly blunt. Bill strongly compressed laterally, slightly but distinctly hooked, and gonys ascending moderately, or slightly but distinctly.

IMMATURE PLUMAGE: Similar to that of the adult, but streaked pattern less regular on the upperparts, and heavier on the underparts as the dark streaks are darker and more abundant on the throat and breast, more diffused on the abdomen. Rectrices narrower and more acuminate.

RANGE: Southeastern Colombia, and eastern Ecuador and Peru, eastward in Brazil, apparently south of the Amazon only, to the lower Rio Tapajós.

SPECIMENS EXAMINED: 56, including the type of "*lineaticeps*" in BM.

Philydor leucophrus
Figure 9

DESCRIPTION: Crown blackish brown and remainder of upperparts rusty brown with the crown and back well and sharply streaked with yellowish (raw sienna) streaks; and with a buffy or dull yellow streak, irregular and narrow in front of and above the eye, but becoming very conspicuous behind the eye, and very broad to the nape. Lores and auricular streak dark brown or blackish. Throat uniformly buffy or dull yellow, but remainder of the underparts very heavily and broadly streaked with buff and dark brown; the streaks are broad, rather regular, and produce a flammulated appearance. Upper surface of the wing chiefly dark brown, with strongly buffy axillaries and under wing coverts, and relatively narrow cinnamon edges to the inner web of the remiges. Tail uniformly Light Red, moderately graduated, with the tips of the rectrices subacuminate. Bill slender, markedly long, and well attenuated. This species varies geographically (see general discussion) and the description given here is based on specimens from the northern end of the range which represent nominate *P. l. leucophrus*.

IMMATURE PLUMAGE: Similar to that of the adult, but streaked pattern less sharp and well defined, distinctly more confused on the underparts.

RANGE: Coastal region of eastern Brazil from Bahia south to Santa Catarina and Rio Grande do Sul.

SPECIMENS EXAMINED: 24, including the type of *leucophrus* in BM and the two cotypes of "*ferruginolentus*" in AMNH.

Philydor subulatus
Figure 9

DESCRIPTION: Upperparts dark rusty brown, more sooty or blackish on the head, more rufescent on the rump with reddish chestnut upper tail coverts; and with the crown and mantle narrowly, but distinctly streaked with dull yellow or dark buff. The sides of the head are dusky brown with small ocher spots and streaks which show a tendency to form a very vague post-ocular streak. Upper throat uniformly dull ochraceous buff, the feathers of the lower throat becoming edged with pale brownish olive; the brownish olive pigmentation extends from the lower throat to the whole of the breast, and, below the latter, the abdomen to the under tail coverts becomes progressively duller brown, less olive, more rufescent; the breast and abdomen are streaked more or less distinctly with ochraceous buff. Upper surface of the wing chiefly dull reddish brown, but under surface of the wing much brighter, chrome orange on the axillaries, under wing coverts, and along the edge of the inner web of the remiges. Tail uniformly reddish chestnut, moderately graduated, with the tips of the rectrices nearly blunt. Bill slender and long, sharply attenuated.

IMMATURE PLUMAGE: Very similar to that of the adult but streaked pattern less sharp on the upper and underparts; and with the coloration of the breast and abdomen generally paler than in the adult. Also, the feathers of the upper throat are not uniformly ochraceous buff as in the adult, but have

brownish olive edges that are more or less well indicated.

RANGE: Eastern and southern Nicaragua, and Costa Rica, with the exception of the Pacific lowlands, south through Panama and western Colombia (Córdoba to Nariño), and from Caquetá in eastern Colombia, and southern Venezuela (Amazonas and southern Bolívar), south to Ecuador, eastern Peru to Puno, and upper Amazon Basin in Brazil (upper Rio Negro, and, south of the Amazon, to the upper Rio Madeira).

SPECIMENS EXAMINED: 124, including the types of "*nicaraguae*" in AMNH, and of "*lemae*" in the Phelps Collection, deposited in AMNH.

Philydor guttulatus

DESCRIPTION: Upperparts rusty brown, becoming reddish chestnut on the rump and upper tail coverts, spotted and streaked on the head, nape, and mantle. The forecrown is spotted with pale rust, and the nape with dark buff; the remainder of the crown is narrowly streaked with pale rust, but the streaks on the mantle are relatively broad, dark buff, and the spotted or streaked feathers of the nape and mantle are edged more or less distinctly with dull black. The sides of the head are dark brown with small ocher spots, narrow buffy streaks on the ear coverts, and with a rather poorly defined superciliary streak, which is dull orange in front of the eye and above it, but becomes buffy behind it. Upper throat uniformly yellowish, the feathers of the lower throat becoming edged with dark brown, and the breast and abdomen heavily and boldly streaked with dark buff and dark brown, thus creating a very conspicuous and heavily flammulated pattern. Lower abdomen more umbraceous, and under tail coverts strongly rufous. Upper surface of the wing chiefly dark rufous brown, with bright chrome orange axillaries, under wing coverts, and over a broad area along the edge of the inner web of the remiges. Tail uniformly reddish chestnut, very moderately graduated, with blunt rectrices. Bill modified, very strongly compressed laterally, with the culmen straight or virtually so, and the gonys ascending strongly.

RANGE: Mountain ranges of northern Venezuela, between about 900 and 2100 m., from Yaracuy to Aragua, and from northern Anzoátegui to Sucre and northern Monagas.

SPECIMENS EXAMINED: 11, including the type of "*pallida*" in the Phelps Collection, deposited in AMNH.

Philydor subalaris

DESCRIPTION: Crown and mantle rusty brown, divided by a broad band of dull black across the nape, with narrow pale buffy shaft streaks on the crown, nape, and mantle. The rump and upper tail coverts are not streaked, the rump is more rufescent than the mantle, and the upper tail coverts are bright reddish chestnut. Sides of head dark brown with small buffy streaks and with a vague, poorly defined superciliary and post-ocular streak. Throat uniformly buffy, and breast and abdomen with rather narrow but quite distinct streaks on an olive brown ground; under tail coverts strongly ferruginous. Coloration of the wing similar to that of *P. guttulatus* above and below (bright chrome orange below, including axillaries). Tail uniformly reddish chestnut, with the rectrices somewhat more graduated than in *P. guttulatus,* and subacuminate at the tip. Bill "normal" in shape, with culmen decurved, and gonys unmodified.

IMMATURE PLUMAGE: Differs distinctly from that of the adult by being pale rufous orange, or chrome orange, on the throat, sides of the neck, and breast, not streaked, or with only a few streaks on the breast. The orange pigmentation suffuses also most of the underparts to a varying degree, but is duller below the breast and some feathers of the abdomen have pale, buffy, not very distinct shaft streaks. The orange pigmentation tips also the feathers of the nape irregularly, forming a broken collar. Birds in immature plumage are also more rufous throughout than the adult, but not on the head, the crown of which is dull black as on the nape (but not the crown) of the adult.

RANGE: Mountains of Costa Rica and

western Panama (ascending to about 2800 m.), eastern Panama (Darién) and probably neighboring Colombia, and Andes of Venezuela (up to about 2000 m.), south through the Andes of Colombia and Ecuador (ascending to about 2400 m.), to Junín in central Peru.

SPECIMENS EXAMINED: 140, including the types of *subalaris* in BM; of "*mentalis*" in ZIW; of "*tacarcunae,*" "*columbianus,*" and "*colligata*" in AMNH; and "*olivacea*" in Phelps Collection, deposited in AMNH.

Philydor rufosuperciliatus
Figure 9

DESCRIPTION: Upperparts (with exception of the tail) uniformly olive brown. Sides of the head olive brown with small buffy spots and streaks, and a narrow, but distinct yellow ochre superciliary streak. Throat creamy white, or pale buffy white, uniform (not spotted) on the chin, but with small olive brown tips to some of the feathers of the upper throat, the tips of the feathers of the lower throat becoming more regularly and more broadly margined with olive brown. The underparts below the throat are olive brown also, but profusely and heavily streaked with very pale buff or cloudy white. Upper surface of the wing raw umber brown, with the axillaries, under wing coverts, and a broad edge of the inner web of the remiges pale bright orange. Tail uniformly reddish chestnut, moderately graduated, with subacuminate tips to the rectrices. Bill modified, with culmen nearly straight, and gonys slightly, but quite distinctly ascending.

This species varies geographically and the description above is based on nominate *P. r. rufosuperciliatus*.

IMMATURE PLUMAGE: Similar to that of the adult, but streaked pattern of the underparts more confused; more spotted than streaked.

RANGE: Peru and Bolivia (the range ascending to about 2800 m. on the slopes of the Andes), from Cajamarca, Amazonas, and San Martín in Peru, south through Peru, and Bolivia (in La Paz, Cochabamba, western Santa Cruz, Chuquisaca, and Tarija) to La Rioja in western Argentina; also from northern Argentina, east to southeastern Paraguay and southeastern Brazil (north to Espirito Santo, and from sea level up to about 2200 m), south to Uruguay, and northeastern Argentina to the delta of the Paraná in northern Buenos Aires; in eastern Argentina, the range extends west to eastern Formosa, eastern Chaco, and Santa Fe.

SPECIMENS EXAMINED: 351, including the types of "*oleagineus*" in BM, and of "*similis*" in AMNH.

Philydor striaticollis

DESCRIPTION: Crown olive brown with dusky bases to the feathers; mantle, rump, and upper tail coverts amber brown with a rufescent cast. Sides of the head and neck olive brown, with darker, more dusky ear coverts, and with small buffy spots and streaks, and a narrow, post-ocular streak that is not very distinct. Upper throat buffy or dingy white, uniform (not spotted) or virtually so on the chin, but with dusky margins which are faint, but become more pronounced and more pale olive brown below the chin and on the lower throat. On the feathers of the latter, the buffy white centers are well surrounded by pale olive brown, producing a spotted appearance, and, below the throat, the buffy white centers become modified into streaks on the breast and upper abdomen, on a pale olive brown ground. Upper surface of the wing chiefly amber brown; with the axillaries, under wing coverts, and edges of the inner web of the remiges buffy. Tail uniformly Light Red, very moderately graduated, and with the tips of the rectrices subacuminate. Bill "normal" in shape.

IMMATURE PLUMAGE: Differs very distinctly from that of the adult by having the underparts much more heavily and broadly streaked with dull orange (rather than relatively narrow buffy streaks) on a more rufous, less olive and brownish, ground; and by having a very broad and most conspicuous deep cadmium yellow post-ocular streak reaching well back to the nape. The crown

is also very dusky, almost blackish, with very fine but distinct yellowish shaft streaks, and contrasts well with the color of the mantle which is chestnut brown, distinctly more rufescent than in the adult plumage.

RANGE: Venezuela, between about 950 and 2300 m., in the mountains of the north from Miranda and Aragua westward, Andes, and Sierra de Perijá; Colombia in the Santa Marta Massif and in the Andes, south through Ecuador and Peru, to La Paz and Cochabamba in Bolivia. The altitudinal range varies between about 1000 and 2400 m. in Santa Marta, and in the Andes from Colombia to Bolivia, from about 1400 to 2600 m.

SPECIMENS EXAMINED: 163, including the types of "*montanus*" in ZIW; of "*yungae*" in AMNH; and of "*perijana*" in Phelps Collection, deposited in AMNH.

Philydor variegaticeps

DESCRIPTION: Crown and nape chiefly dusky, but with very fine yellowish shaft streaks on the forecrown, and olive brown centers and tips to the feathers from the top of the crown back to the nape, the crown and nape contrasting from the coloration of the mantle, rump, and upper tail coverts, which are rufescent amber brown. Ear coverts dark brown, with buffy streaks at the center, contrasting strongly with a broad eye-ring and short, but broad, post-ocular streak, which are deep cadmium yellow. Sides of the lower neck pale olive brown mottled with dark buff. Upper throat uniformly pale yellowish buff, or buffy white, the feathers becoming darker buff on the lower throat and acquiring pale olive brown margins; the buffy centers of the feathers become modified into poorly defined streaks on the breast, which, together with the abdomen and under tail coverts, are pale olive brown. Upper surface of the wing chiefly amber brown, with the axillaries, under wing coverts, and edges of the inner web of the remiges, pale cadmium orange. Tail reddish chestnut, slightly graduated only, with the tips of the rectrices nearly blunt or slightly subacuminate. Bill "normal" in shape.

The description given above is based on nominate *P. v. variegaticeps* from Central America. The color in *P. v. temporalis* from Colombia and Ecuador is richer; its breast and abdomen are much more heavily spotted with buff on an ochraceous orange ground, whereas nominate *variegaticeps* is poorly streaked on an olive brown ground. The conspicuous cadmium yellow post-ocular streak is much better developed, extending well back to the nape; the back is distinctly more rufous, strongly rufous brown, rather than amber; and the crown is darker, more blackish.

Nominate *P. v. variegaticeps* resembles *P. striaticollis* rather closely in a general way, but differs from it by being darker on the crown and nape, and, especially, by having a conspicuously distinct facial pattern (broad and richly colored eye-ring and post-ocular streak). The coloration of the under surface of the wing is brighter also in *P. variegaticeps*. In *P. v. temporalis*, the range of which comes into contact and overlaps slightly with that of *P. striaticollis* in Colombia and Ecuador (map 40), some of the species characters of *P. variegaticeps* are emphasized (much greater development of the conspicuous post-ocular streak), or new ones have been developed (ochraceous orange underparts, as against olive brown in nominate *P. v. variegaticeps* and *P. striaticollis*). This fact seems to me to represent a clear instance of character displacement.[138]

IMMATURE PLUMAGE: Closely similar to that of the adult, but general pattern less distinct, and crown and nape more brownish, less dusky, in nominate *P. v. variegaticeps*; general pattern less distinct in *P. v. temporalis*, and breast and abdomen much more rufous (bright rust), less ochraceous orange than in the adult plumage.

RANGE: Central America (nominate *variegaticeps*), from southern Mexico (region of Jalapa in central Veracruz, and central Guerrero), south to western Chiriquí in western Panama, but apparently lacking in Nicaragua; and (subspecies *temporalis*) in Pacific region of Colombia (Cauca to Nariño), south through western Ecuador to Loja. The alti-

tudinal range in Mexico and Central America varies from about 1000 to 2750 m., and between about 1000 to 2100 m. in Colombia and Ecuador; altitudes prevailing in Nicaragua may not be high enough for this species.

I have also seen specimens that had been collected by von Sneidern, presumably at Morelia and Belén, Caquetá, Colombia; and by Goodfellow, presumably at Baeza, eastern Ecuador, but the authenticity of these localities has been challenged.

SPECIMENS EXAMINED: 134, including the types of *variegaticeps* and *temporalis* in BM.

Philydor ruficaudatus

DESCRIPTION: Upper parts olive green, somewhat paler on the rump and upper tail coverts than on the mantle and crown. Sides of the head brown, streaked with buff, including a not very well-defined post-ocular streak. Underparts dull pale yellow (Naples Yellow) with a faint cinereous wash, more or less pronounced, on the breast and abdomen, and faint vague streaks best indicated on the breast; the cinereous wash becomes darker and uniform and acquires an olive tinge on the flanks. Upper surface of the wing chiefly dull brown, with the axillaries, under wing coverts, and edges of the inner web of the remiges cinnamomeous buff. Tail uniformly reddish chestnut, nearly rounded or slightly graduated only, with rectrices that are nearly blunt at the tip. Bill "normal" in shape.

IMMATURE PLUMAGE: Similar to that of the adult, but dull brown rather than olive on the upperparts, with the underparts darker, less yellowish, more buffy olive; and with a more conspicuous post-ocular streak, better developed and more richly colored, dark raw sienna rather than buff as in the adult.

RANGE: Inland districts of the three Guianas, west through southern Bolívar and Amazonas in Venezuela, to eastern Colombia (north to Meta), eastern Ecuador, eastern Peru, northern and eastern Bolivia (Beni, La Paz, Cochabamba, and Santa Cruz), eastward through Brazil to Rondônia and upper Madeira River in the west, and in the north and east, to upper Rio Negro and south to Amapa, lower Tocantins, and region east of Pará, to northern Maranhão.

SPECIMENS EXAMINED: 74, including the types of *ruficaudatus* in MNHN; and of "*flavipectus*" in the Phelps Collection, deposited in AMNH.

Philydor erythrocercus

DESCRIPTION: Crown and mantle uniformly dull olive green, contrasting strongly with the rump and upper tail coverts which are bright reddish chestnut. Sides of the head dark dull olive brown, with fine buffy shaft streaks on the ear coverts, and with a buff or ochraceous streak above and behind the eye which is distinct, but rather poorly defined. Throat and upper breast uniformly dull white or pale yellowish buff, with thin washes of very pale gray and dull yellow on the remainder of the underparts, with the exception of the under tail coverts which are cinnamomeous, the flanks becoming pale brownish olive. Upper surface of the wing chiefly dull brown or russet brown, with the axillaries and edges of the inner web of the remiges bright ochraceous buff, but with the under wing coverts somewhat darker, more orange. Tail uniformly reddish chestnut, nearly rounded, with the tips of the rectrices subacuminate. Bill "normal" in shape.

IMMATURE PLUMAGE: Similar to that of the adult, but rufescent brown on the crown and mantle, rather than olive; less washed with yellow below; and with a more conspicuous streak above and behind the eye, better developed and more richly colored than in the adult, rufous orange, rather than buff or ocher; this streak is broader than in the adult and extends farther back, well onto the nape, where it merges with a vague nuchal band of the same color; the rufous orange pigmentation extends also to the sides of the neck behind the ear coverts, and, irregularly, to the posterior part of the malar region.

The descriptions given above are based on nominate *P. e. erythrocercus* from the Guianas and Brazil, but this species either varies strongly geographically, or the forms included represent more than one species

(see discussion of the geographical variation). The range defined below, and specimens examined, apply to the entire complex.

RANGE: Panama, southward through Colombia, Ecuador, and Peru, to La Paz and Cochabamba in Bolivia, and, eastward (but not north of Caquetá in Colombia) through Brazil, to eastern Pará and northern Maranhão, and also northeastern Brazil, from the lower Rio Negro, eastward to Amapá, and north to the Guianas. This species is not montane, but ascends the slopes of the Andes to about 1800 m., and in Panama to about 1250 m.

SPECIMENS EXAMINED: 297, including the types of "*guianensis*," "*subfulvus*," "*fuscipennis*," and "*erythronotus*" in BM; and of "*lyra*" in AMNH.

Philydor erythropterus
Figure 9

DESCRIPTION: Upperparts dull grayish olive, darker on the crown and upper mantle, becoming progressively paler and more olive, less grayish, from the center of the back to the upper tail coverts. Feathers of the forecrown with small rusty spots, with a few fine and pale shaft streaks on the center and back of the crown, and with a conspicuous dark ochraceous orange streak extending from the base of the bill back to the front of the eye. Throat uniformly pale ochraceous buff, with the remainder of the underparts very soft pale gray with a distinct pale cinnamon cast, and with very fine dark buff or cinnamomeous shaft streaks on the breast. Exposed surface of the upper wing reddish, including the coverts, varying from bright burnt sienna to dull red; axillaries and under wing coverts bright salmon orange, and with a dull reddish edge on the inner web of the remiges. Tail bright burnt sienna, uniformly rufous, but darker on the exposed pair of central rectrices; slightly graduated only, with the tips of the rectrices nearly blunt. Bill slightly but distinctly "hooked," "normal" in shape otherwise.

IMMATURE PLUMAGE: Very similar to the adult but somewhat paler and duller, more grayish on the upperparts; throat darker buff, and without, or with only very faint shaft streaks on the breast.

RANGE: Southern Venezuela, from southern Bolívar, westward to southeastern Colombia, southward through eastern Ecuador and Peru, to the Beni in northern Bolivia, and eastward through Brazil, south of the Amazon, to the lower Tapajós.

SPECIMENS EXAMINED: 36, including the type of *erythropterus* in BM.

Philydor amaurotis

DESCRIPTION: Upperparts tawny brown, becoming more rufescent on the rump, and rufous orange on the upper tail coverts. The feathers of the crown are not uniform in coloration, the greater part of the exposed feather is tawny, but the concealed portion of the feather is black or blackish and prolonged as a narrow exposed subapical band, the black or blackish area having a small, but conspicuous pure white guttate stripe along the shaft on the concealed portion of the feather. The ear coverts are dark brown, below a very conspicuous broad post-ocular streak, which is dull white or pale buff, and extends to the nape, broadening posteriorly, and breaking down into a few small buffy spots on the nape which, together with similar spots behind the ear coverts, tends to form a very vaguely defined nuchal band, very broadly interrupted at its center.

The throat is uniformly dull white, the white area invading the pale dull olive brown breast as broad, not sharply defined, streaks, which become progressively narrower and fewer on the abdomen, which is of the same color as the breast, pale dull olive brown with an ochraceous cast. The upper surface of the wing is rufous brown, with the axillaries, under wing coverts, and edges of the inner web of the remiges pale orange. Tail uniformly dark orange rufous, moderately graduated, with the tips of the rectrices subacuminate. Bill attenuated distally, but "normal" in shape.

RANGE: Southeastern Brazil from southern Espirito Santo, south to Rio Grande do Sul, and Misiones in Argentina.

SPECIMENS EXAMINED: 12.

Philydor lichtensteini

DESCRIPTION: Crown and mantle pale grayish olive, with the concealed portion of the feathers of the crown black or blackish with very fine pale shaft streaks; the center of the back becomes more ochraceous than gray, and the ochraceous pigmentation progressively purer and paler to the lower rump and upper tail coverts which are yellow ocher. The remainder of the body plumage is dark ochraceous buff, with a faint orange cast, including a broad superciliary and postocular streak, emphasized by a broad dark brown streak along the upper ear coverts; on the underparts, the throat is slightly paler, and the lower abdomen and under tail coverts somewhat darker, more umbraceous. The upper surface of the wing is chiefly pale orange brown, with orange brown, but brighter axillaries, under wing coverts, and a broad area on the inner web of the remiges, extending inward from the edge. The tail is orange brown also, but not completely uniform, as the exposed central rectrices, and edge of the outer web of some of the other rectrices are more dusky, more hazel, to a varying degree. The tail is moderately to slightly graduated, with subacuminate rectrices; and the bill is not quite "normal" in shape as the distal portion of the gonys ascends slightly.

IMMATURE PLUMAGE: Very similar to that of the adult, but coloration of the underparts less uniform than in the adult, cross-barred with narrow grayish brown tips to the feathers of the throat, breast, and abdomen.

RANGE: Eastern and southeastern Brazil from Bahia south to Rio Grande do Sul, and west to Goiás and southern Mato Grosso, eastern Paraguay, and Misiones in Argentina.

SPECIMENS EXAMINED: 208.

Philydor rufus
Figure 9

DESCRIPTION: Crown ashy gray or olivaceous gray, with a broad band across the forehead which is dark ochraceous buff, as well as a broad streak above and behind the eye, which joins the frontal band and extends back to the nape. Lores, and a streak through the ear coverts, dark gray-brown. The back is cinnamon brown with an olivaceous cast, or ochraceous brown, the pigmentation becoming progressively paler and purer ocher posteriorly to the upper tail coverts. In the population of Brazil in which the crown is purer gray and the back more ochraceous, a good contrast exists between the coloration of the crown and that of the back. Underparts and sides of the face (other than the dark streak through the ear coverts) uniformly ochraceous orange. Upper surface of the wing chiefly dull red, with the axillaries and under wing coverts ochraceous orange, as on the underparts, but richer, purer orange, and with the edge of the inner web of the remiges reddish cinnamon. Tail dark reddish cinnamon, darker, more dusky, on the exposed central rectrices; moderately or well graduated, with acuminate rectrices. Bill "normal" in shape.

IMMATURE PLUMAGE: Very similar to that of the adult, but with a narrower ochraceous band of buff across the forehead; the ashy crown is paler, but the underparts are somewhat darker, more orange and rufous than in the adult.

This species resembles *Philydor lichtensteini* superficially, but is distinctly larger (table 20), with a much bigger bill, the gonys of which does not ascend as it does in *P. lichtensteini* to a slight but distinct degree. *Philydor rufus* is characterized also by a broad and very conspicuous ochraceous band across the forehead, no trace of which exists in *P. lichtensteini*.

RANGE: Broadly interrupted, consisting of mountains of Costa Rica to western Chiriquí in western Panama, to about 1550 m. in Costa Rica and between about 1650 and 2130 m. in Panama; mountains of northern Venezuela, between about 1000 and 1800 m. in Sucre-Monagas (Caripe) and from Miranda to Yaracuy, also southern Venezuela in Amazonas and northwestern Bolívar; Colombia, in the Eastern Andes, and on the Pacific slope from the upper Rio San Juan, south through Nariño, to northwestern Ecuador; eastern Peru

TABLE 20
Measurements (in Millimeters) of *Philydor*

Species	Wing			Tail			Bill		
	N	Mean	Range	N	Mean	Range	N	Mean	Range
strigilatus									
Males	27	97.85	90–104	26	76.50	71–83	27	23.40	22–25
Females	21	92.14	88–97	21	71.90	65–77	21	23.42	22–25
Both sexes	56	95.23	88–104	55	74.22	65–83	56	23.35	21–25
leucophrus									
Males	7	99.42	90–108	7	84.57	79–90	7	26.57	25–28
Females	9	92.22	85–104	9	80.11	76–88	9	28.33	26–32
Both sexes	22	96.36	85–108	21	82.71	76–90	21	27.83	25–32
subulatus									
Males	56	83.51	78–90	56	67.50	62–74	55	25.14	22–28
Females	35	81.60	78–86	34	65.76	60–72	34	25.10	23–28
Both sexes	94	82.72	78–90	93	66.77	60–74	92	25.11	22–28
guttulatus									
Males	5	91.60	88–94	4	77.00	76–79	5	22.50	22–24
Females	3	89.66	89–90	3	77.33	76–79	3	22.16	21.5–23
Both sexes	10	91.30	88–94	8	77.62	75–81	10	22.30	21–24
subalaris									
Males	32	90.21	84–96	28	79.57	72–88	33	22.03	21–23
Females	29	87.51	83–93	28	78.14	73–85	28	22.20	20–24
Both sexes	68	89.00	83–96	64	78.65	72–88	69	22.11	20–24
rufosuperciliatus									
Males	148	79.13	71–86	139	77.16	69–85	140	19.98	17.50–22
Females	122	77.94	71–85	111	76.78	70–83	114	19.75	18–22
Both sexes	280	78.52	71–86	259	77.04	69–85	262	19.88	17.50–22
striaticollis									
Males	49	91.46	81–98	49	72.87	69–78	48	18.47	17–20
Females	39	84.38	79–92	38	69.00	57–75	39	18.57	17.50–19.50
Both sexes	109	87.82	79–98	105	71.00	57–78	105	18.94	17–20
variegaticeps									
Males	58	88.53	82–96	51	69.96	69–74	55	18.72	17–20
Females	36	85.52	80–94	33	67.06	62–74	35	19.00	18–20
Both sexes	112	87.08	78–96	101	68.86	62–77	108	18.75	17–20
ruficaudatus									
Males	30	93.26	83–98	26	72.11	64–78	29	19.38	18–20
Females	21	85.42	83–88	19	66.10	63–69	21	19.28	18–21
Both sexes	58	90.08	82–98	50	69.70	63–78	57	19.39	18–21
erythrocercus									
Males	101	90.57	80–96	94	68.74	58–76	101	19.95	18–21
Females	76	85.14	79–93	74	65.30	57–71	75	19.48	18.50–21
Both sexes	189	88.33	79–97	177	67.33	57–76	189	19.75	18–21
erythropterus									
Males	13	96.76	91–101	12	71.66	67–75	13	22.47	20.50–24
Females	11	89.36	83–94	12	68.50	64–74	11	22.17	20.20–23

TABLE 20—(*Continued*)

Species	Wing			Tail			Bill		
	N	Mean	Range	N	Mean	Range	N	Mean	Range
Both sexes	33	92.55	83–101	31	70.25	64–75	33	22.27	20.20–24
amaurotis									
Males	5	78.80	73–83	5	70.20	68–72	5	17.80	16.50–19
Females	5	75.00	73–78	4	72.00	68–76	5	18.00	all 18
Both sexes	12	77.00	73–83	11	70.72	68–76	12	18.00	16.50–19
lichtensteini									
Males	96	81.58	73–91	92	73.58	67–82	93	17.53	16–20
Females	71	75.33	72–83	70	70.94	63–75	72	17.47	16–19
Both sexes	172	79.82	72–91	167	72.49	63–82	170	17.51	16–20
rufus									
Males	62	91.15	81–107	47	88.65	82–99	60	21.83	20–24.50
Females	38	89.82	80–97	33	87.60	80–97	41	21.23	20–23
Both sexes	111	90.88	80–107	92	88.14	78–99	111	21.46	20–24.50
atricapillus									
Males	15	85.00	80–89	15	76.13	71–80	15	19.23	18–20
Females	17	78.58	75–84	17	73.29	69–80	17	19.42	18–20.50
Both sexes	38	82.15	75–91	37	74.86	69–80	38	19.45	18–20.50
pyrrhodes									
Males	34	88.32	81–95	29	65.10	59–71	33	20.71	19–22
Females	24	82.97	78–90	23	61.65	58–68	22	20.66	18–22.50
Both sexes	70	85.97	78–95	61	63.54	58–71	65	20.70	18–22.50
dimidiatus									
Males	3	88.33	87–89	3	74.00	72–77	2	20.75	20.5, 21
Female	1	—	81.50	1	—	69	1	—	22
Both sexes	4	86.62	81.50–89	4	72.75	69–77	3	21.16	20.5–22
ucayalae									
Males	2	106.50	106, 107	2	84.50	84, 85	2	25.50	25, 26
Females	2	101.00	100, 102	2	79.50	78, 81	2	27.75	27.5, 28
Both sexes	4	103.75	100–107	4	82.00	78–85	4	26.62	25–28
striatus									
Females	2	96.00	95.5, 96.5	2	78.50	77, 80	2	22.00	21, 23
fuscus									
Males	12	96.00	91–100	12	82.00	76–87	12	25.54	24–27
Females	8	84.00	79–95	7	76.00	73–81	8	24.25	23–25
Both sexes	22	91.45	79–100	21	79.61	73–87	22	25.10	23–27

from northern San Martín south to eastern Bolivia, to the Argentina border in Tarija, and eastward (through Tarija, Chuquisaca, and Santa Cruz), to Brazil (north to central Mato Grosso, Goiás, and Bahia), south to Paraguay, Misiones in Argentina, and Rio Grande do Sul in Brazil. The upper altitudes reach about 1800 m. in Colombia, about 1500–1600 m. in Ecuador and Peru, about 1400 m. in Bolivia, and about 1200 m. in Brazil.

SPECIMENS EXAMINED: 167, including the

types of "*riveti*" in MNHN, of "*panerythrus*" in BM, of "*chapadensis*" in AMNH, and of "*cuchiverus*" in the Phelps Collection, deposited in AMNH.

Philydor atricapillus

DESCRIPTION: The color of the crown varies geographically from dark rufous brown, to blackish brown, and dull black, contrasting strongly with the coloration of the back which varies from rufous brown to warm cinnamon brown, the lower back becoming progressively brighter, grading into orange-brown on the rump, and brighter, more orange rufous on the upper tail coverts. A bright tawny, or rufous orange, superciliary and post-ocular streak broadens out posteriorly where it merges into a darker rufous (more orange-brown) nuchal band, which is rather vaguely defined, and joins the sides of the lower neck, which are also orange-brown behind the very dark ear coverts and a dark malar streak. This malar streak and the ear coverts are blackish brown, the ear coverts interrupted by buff or not.

The underparts, including the sides of the lower neck (see above) are wholly and uniformly orange rufous, but slightly paler on the throat (the feathers of which have concealed whitish bases), and are somewhat darker on the flanks and under tail coverts. The upper wing coverts and outer webs of the remiges are rufous brown, the axillaries, under wing coverts, and edge of the inner web of the remiges are pale ochraceous buff. The tail is uniformly bright orange rufous, well graduated, with subacuminate tips to the remiges. The bill is attenuated, but "normal" in shape.

IMMATURE PLUMAGE: Similar to that of the adult, but not uniform, the feathers of the underparts having dark brown edges or tips.

RANGE: Cerro de la Neblina on the border between southern Amazonas, Venezuela, and Brazil ("*hylobius*"); and Brazil from Bahia south to Rio Grande do Sul, eastern Paraguay, and Misiones in Argentina; in Brazil, the range extends west to southern Minas Gerais, and to São Paulo and extreme southern Mato Grosso.

SPECIMENS EXAMINED: 56, including the cotypes of *atricapillus* in AMNH, the types of "*pallidior*" in BM, and of "*hylobius*" in USNM.

The status of "*hylobius*" has been discussed in geographical variation; "*hylobius*" needs more study, but seems to represent only an isolated population of *Philydor atricapillus*.

Philydor pyrrhodes

DESCRIPTION: Crown and back "bronzy" brown, becoming strongly rufous on the rump, and bright orange rufous, or rufous orange on the upper tail coverts. Ear coverts dark ochraceous brown; superciliary streak (not sharply defined), sides of face below the ear coverts, of the neck, and whole of the underparts uniformly orange rufous, or deep rufous orange, slightly paler on the throat, somewhat darker on the lower flanks and under tail coverts. Upper surface of the wing almost uniformly dark dusky brown, almost "blackish," with the axillaries and under wing coverts bright, orange rufous as on the underparts, but with virtually no pale edge on the inner web of the remiges, only the extreme edge of the feathers being very faintly paler than the dark remiges. Tail rufous orange, virtually uniform, as only the upper surface of the central rectrices is slightly duller and duskier than the bright outer rectrices; it is slightly graduated only, with blunt rectrices. Bill "normal" in shape, but with the culmen well decurved.

IMMATURE PLUMAGE: Similar to that of the adult but upperparts are browner, or olive brown, not "bronzy" brown as in the adult, and the underparts are very slightly paler, especially on the chin and throat, which are more buffy white, less orange rufous.

RANGE: Guianas and southern Venezuela (Bolívar and Amazonas), west to southeastern Colombia, south through eastern Ecuador and Peru to the Beni in Bolivia, eastward through Brazil to the coast of Pará.

SPECIMENS EXAMINED: 80.

Philydor dimidiatus
Figure 9

DESCRIPTION: Similar superficially to *Philydor pyrrhodes* in being brown above with a poorly defined superciliary streak, and strongly dark rufous orange on the face, sides of the neck, and the whole of the underparts, but not quite uniform on the breast and upper abdomen, the feathers having very faint, very narrow, minute pale shaft streaks, and very faint dusky edges that are barely discernible. The brown pigmentation of the upperparts is also more rufous brown in *P. dimidiatus,* especially the exposed upper surface of the wing which is entirely rufous (russet or dark rufous cinnamon) in *P. dimidiatus,* not blackish as in *P. pyrrhodes*. The axillaries and under wing coverts are more reddish in *P. dimidiatus,* which has also a very conspicuous, unusually extensive, bright ferruginous area on the inner web of the remiges, which is entirely lacking in *P. pyrrhodes* (*q.v.*). Tail uniformly reddish chestnut, slightly graduated, with blunt or virtually blunt rectrices. Bill distinctly modified in shape, long and attenuated distally, with a straight culmen, and a very distinctly ascending gonys.

IMMATURE PLUMAGE: Differs from that of the adult by having a very distinctly paler throat, dull white or buffy white, the feathers of which have small brown apical spots, whereas the throat is uniformly rufous orange in the adult. In the immature plumage, the feathers of the breast and abdomen have very distinct brown tips, forming bars; the feathers of the forecrown have also dark brown tips, lacking in the adult; the rectrices are distinctly narrower and acuminate; and the bill is shorter.

RANGE: Brazil, from central Mato Grosso and Goiás, south to northeastern Paraguay.

SPECIMENS EXAMINED: 7, including the three cotypes of *dimidiatus* in NMW, and the type of "*baeri*" in ZSM.

Philydor ucayalae
Figure 9

DESCRIPTION: Mahogany, or dark reddish chestnut on the crown and mantle, becoming more and brighter rufous (reddish chestnut) on the rump and upper tail coverts. The feathers of the crown have small, slightly paler centers on the forecrown, and faint and narrow, barely discernible, pale shaft streaks on the front and center of the crown. Lores very dingy, grayish white, with a narrow, poorly defined superciliary and post-ocular streak. Ear coverts brown, with faint buffy shaft streaks. The whole of the underparts is uniformly darkly and strongly ferruginous; dull red or reddish burnt sienna on the throat, the feathers of which are somewhat squamate in shape, arranged in vertical rows, are or seem to be slightly stiffened, and are probably erectile. The breast and abdomen are somewhat paler than the throat, but the lower abdomen and under tail coverts are slightly darker, more mahogany, less brightly ferruginous than on the breast.

The exposed surface of the upper wing is reddish brown, with the axillaries, under wing coverts, and a broad area at the edge of the inner web of the remiges reddish ferruginous, of the same color as the breast and upper abdomen. Tail uniformly reddish chestnut, with a vinaceous cast, slightly graduated, with subacuminate rectrices. Bill strongly modified, massive, but extremely compressed laterally, with a straight culmen, and a very strongly ascending gonys.

IMMATURE PLUMAGE: Differs quite distinctly from that of the adult as the crown and nape are blackish, well spotted with ferruginous buff, and the mantle is darker, browner, less rufous than in the adult. The underparts are also paler than in the adult, ochraceous buff, with narrow, but regular blackish edges to the feathers of the throat which emphasize strongly their squamate appearance. These black borders exist also on the feathers of the breast, but usually not at the tip, but on the feathers of the abdomen the dark pigmentation is restricted narrowly to the tip of the feather, producing a barred pattern. Rufous spots exist on the sides of the lower neck, that are not present in the adult, and the superciliary and post-ocular streak is also brighter and better developed than in the adult, and the lores are whitish.

RANGE: Eastern Peru, where it is known

so far from the upper Ucayali River, and the regions of Quincemil in Cuzco, and Manú in Madre de Dios.

SPECIMENS EXAMINED: 5; these are the only specimens in existence to date and consist of the type of *ucayalae* in AMNH, and of the type of "*ferrugineus*" and three other specimens in MNHN.

Philydor striatus
Figure 9

DESCRIPTION: Similar to *Philydor ucayalae* in general appearance and coloration, but with the plumage spotted and streaked, whereas *P. ucayalae* is virtually uniform in coloration. In *P. striatus,* the underparts are streaked with pale orange rufous below the throat, but not very sharply or distinctly so; on the upperparts, the small ferruginous spots are better developed on the forecrown; the superciliary streak is more distinct; and distinct ferruginous spots (on the nape and sides of the lower neck) and streaks (on the mantle) exist, which are completely lacking in *P. ucayalae*. The coloration of the upper and lower surface of the wing; coloration and structure of the tail; and the modification in the shape of the bill are all similar in the two species, but the bill of *P. striatus* is less massive than that of *P. ucayalae*.

IMMATURE PLUMAGE: No specimens in immature plumage have been collected to date, but I suspect that this plumage is about similar to the immature plumage of *Philydor ucayalae* (*q.v.*).

RANGE: Bolivia, in the Yungas of La Paz and Cochabamba, where it has been collected between about 670 and 800 m.

SPECIMENS EXAMINED: 2.

Philydor fuscus
Figure 9

DESCRIPTION: Crown uniformly dark raw umber brown, vary well outlined by a white, broad superciliary and post-ocular streak, which merges into a quite distinct, but less pure white nuchal band, which rejoins the white sides of the lower neck behind the dark brown ear coverts. Back paler than the crown (Brussels Brown rather than dark raw umber), becoming progressively more rufous on the rump and upper tail coverts. Throat uniformly white, becoming slightly buffy at its posterior border and joining the pale ochraceous center of the breast, the abdomen becoming progressively darker with washes of pale gray and pale raw umber; the flanks and lower abdomen darker, and the under tail coverts dull pale brownish orange. Exposed surface of the upper wing brown, similar to the coloration of the mantle, with pale cadmium orange axillaries, under wing coverts and broad edge to the inner web of the remiges. Tail uniformly pale burnt sienna or dull Light Red, moderately graduated, with subacuminate rectrices. Bill modified in shape, very strongly compressed laterally, with culmen nearly straight, much attenuated at the tip, and with the gonys ascending distinctly over a long distance.

IMMATURE PLUMAGE: Very similar to that of the adult, but the color pattern of the head is somewhat less sharp, and the throat is somewhat buffy, less pure white than in the adult.

RANGE: Southeastern Brazil, from Espirito Santo and southeastern Minas Gerais, to Santa Catarina.

SPECIMENS EXAMINED: 29, including the type of *fuscus* in MNHN.

GENUS *THRIPADECTES*

The genus *Thripadectes* seems to be closely related to the genera *Automolus* and *Sclerurus*; I briefly discussed its systematic relationships in my preliminary classification of the Furnariidae (1971a). *Thripadectes* is composed of seven species which can be characterized as coarser, more sturdy, less specialized, and with bigger bills and feet than those of *Automolus* and of *Sclerurus*. The color pattern is also quite different: *Thripadectes* is streaked, coarsely so in the majority of its species, whereas *Automolus* and *Sclerurus* are not streaked, generally speaking.

The seven species of *Thripadectes* are: *T. ignobilis, T. rufobrunneus, T. virgaticeps, T. melanorhynchus, T. holostictus, T. scrutator,* and *T. flammulatus*. All seven species

inhabit the undergrowth of dense, cool, and humid mountain forests, usually at fairly low or middle altitudes; and all are Andean, with the exception of *T. rufobrunneus,* which is restricted to Costa Rica and Panama at elevations that vary from about 760 to 2350 m. Much sympatry is characteristic. For instance, the following five of the seven species occur in Colombia and Ecuador (with the altitudinal records I have obtained from Colombia): *T. ignobilis,* from about 800, or more usually 1000, to about 1850 m.; *T. virgaticeps,* from about 1000 or 1200 to 2350 m.; *T. melanorhynchus,* from about 1230 to 1400 m.; *T. holostictus,* from about 1300 to 3100 m.; and *T. flammulatus,* from about 1000 to 3150 m. The altitudinal ranges are roughly similar in Ecuador.

Three species occur in Peru: *Thripadectes melanorhynchus, T. holostictus,* and *T. scrutator,* the records of which are not numerous enough to determine their ranges accurately. However, these records suggest that *T. melanorhynchus* and *T. holostictus* are broadly sympatric in the same regions and occur at roughly the same elevations, from about 760 to 1300 m. in the case of *T. melanorhynchus,* and from about 760 to 1800 m. for *T. holostictus.*[139] These two species reach Peru from Colombia and Ecuador, but *T. scrutator* has been collected only in central Peru, to which it may be restricted at elevations indicated as varying from 2100 to about 3650 m.; *T. scrutator* is rare in collections, known only from about nine specimens, most of them caught in nets. In fact, no really large series of any species of *Thripadectes* exists, a fact which is probably explained by the behavior of these birds: they are not gregarious at all and keep well concealed in dense undergrowth.

Bolivia represents the southern extremity of the range, reached only by *Thripadectes holostictus,* in the Yungas of La Paz and Cochabamba where it is recorded between about 1200 and 2500 m.

All seven species of *Thripadectes* seem to inhabit the dense undergrowth of humid forests and probably differ little in their ecology and general behavior, including nesting, but the only information available for the genus as a whole is provided by *T. rufobrunneus* of Central America, with the exception of a very brief remark on the behavior of *T. flammulatus.*

Slud (1964) and Skutch (1969b) reported that *Thripadectes rufobrunneus* inhabits dense undergrowth, or, according to Skutch, "dense stands of small trees and bushes, especially those in deep ravines and along mountain streams, which bear an abundance of moss and larger epiphytes," among which it searches vigorously for its food which consists of animal matter, such as insects, and apparently many small frogs, lizards, and salamanders; *T. rufobrunneus* also "rummages noisily in low-hanging trash and clusters of dead leaves," climbing vines, according to Slud. The individuals which Skutch observed were always solitary except during the nesting season, but Slud said that although he "generally encountered [*T. rufobrunneus*] singly," he observed also two and three individuals calling to one another and climbing "about low in the same tree." In other words, *Thripadectes* is arboreal, but does not seem to ascend much above the level of the undergrowth, and then probably only in low trees with much growth of moss and epiphytes. It searches in moss and epiphytes for food, tearing apart the bases of the bromeliads "to disclose the creatures that hide in the imbricated leaves," according to Skutch, and which include small frogs, lizards, and salamanders, which seem to form an important part of the diet of *T. rufobrunneus.* The hooked and strong bill of *Thripadectes* would seem to be an efficient tool, well adapted for tearing stems and killing prey.

Thripadectes rufobrunneus nests at the end of a burrow dug in a steep bare bank of soft earth along a path, or other cut in the forest. Nests were found and have been reported upon by Skutch (1969b), Worth (1939), and Hartman (1957). All three nests described by these authors had been dug in a bank of soft volcanic soil or ash, at heights varying from nearly 2 to about 6 m. above ground level. The tunnel was about 10 cm. in diameter (when indicated) and varied from about 48 to 66 cm. in depth, slanting upward,

TABLE 21
Measurements (in Millimeters) of *Thripadectes*

Species	Wing			Tail			Bill		
	N	Mean	Range	N	Mean	Range	N	Mean	Range
ignobilis									
Males	4	92.25	84–98	4	81.50	77–85	4	24.50	24–25
Females	9	91.33	84–102	8	80.12	72–85	9	24.50	22.5–26
Both sexes	14	92.00	84–102	13	80.53	72–85	14	24.50	22.5–26
rufobrunneus									
Males	15	94.13	91–98	15	88.86	82–94	15	26.40	25–29
Females	8	91.50	89–94	7	87.57	84–93	7	26.50	25–28
Both sexes	31	93.06	89–98	29	88.80	82–94	30	26.25	24–29
virgaticeps									
Males	12	100.08	92–106	12	91.50	88–95	11	28.54	25.5–32
Females	8	98.50	92–106	7	91.00	85–96	8	28.50	26–30.5
Both sexes	21	99.48	92–106	20	91.45	85–97	20	28.45	25.5–32
melanorhynchus									
Males	13	94.42	88–99.5	13	86.47	83–91	13	26.88	25–28
Females	5	94.10	92–97	5	85.60	85–87	5	26.66	26–27
Both sexes	21	93.67	87–99.5	21	86.24	80–92	21	26.64	25–28
holostictus									
Males	16	90.31	85–98	15	92.00	87–97	16	25.53	23.5–28
Females	6	88.83	87–92	6	92.33	87–100	6	25.16	24–26
Both sexes	30	89.80	85–98	28	92.32	87–101	30	25.25	23.5–28
scrutator									
Males	6	98.17	91–102	6	102.84	100–111	6	26.33	26–29
Females	2	99.50	99, 100	2	105.50	105, 106	2	27.50	27, 28
Both sexes	8	98.25	91–102	8	104.00	100–111	8	27.37	26–29
flammulatus									
Males	20	97.85	93–107	19	102.57	94–113	19	27.96	27–29
Females	6	95.50	90–104	7	100.00	95–105	7	27.79	26–29
Both sexes	40	97.00	90–107	35	102.31	94–114	40	27.68	25–29

and in an incubating chamber with a diameter of 15 or 20 cm. The nest itself was an open shallow cup, or "almost flat" platform about 3.5 cm. thick, by about 15 cm. in diameter, constructed of fibrous rootlets in all three nests. Skutch said the tunnel was "barely wide enough to admit my arm," and believed this relatively large width suggested that the burrow had not been dug by the bird itself. However, the report of Hartman [and the only information recorded for any other species (*Thripadectes flammulatus*), see next paragraph] does suggest that *Thripadectes* probably digs its own burrow. In the case of the nest reported by Hartman, not one, but two burrows of the same width had been dug only 12 inches [about 30 cm.] apart, and at the same height above the road. One tunnel (about 66 cm. deep) led to the incubating chamber, but the other tunnel "was about 10 inches deep [about 25.5 cm.] and had no enlargement. It may have been a 'trial' hole. Whether it was used for roosting was not learned." A good photograph of the nesting site and entrances to the burrows is supplied by Hartman.

In the case of *Thripadectes flammulatus*, L. Söderström, quoted by Lönnberg and

Rendahl (1922), said this species "makes holes in the hill-sides, comes out and suns itself. Is supposed to sleep in the burrows at night."

Morphological Variation

Thripadectes is an exceptionally homogenous genus. All seven species are of medium size, with heavy bodies, big bills and feet (table 21), and have a plumage which is reddish brown on the upperparts, paler and more tawny on the underparts. In all species the rump and upper tail coverts are rufous and, as is the case in the genus *Philydor,* the axillaries, under wing coverts, and an extensive area along the inner webs of the remiges are very bright in coloration, normally chrome orange, varying slightly in hue and intensity interspecifically. This bright area is the most colorful area of the entire plumage (as in the genus *Philydor*), but does not necessarily denote close relationship between *Thripadectes* and *Philydor.* I believe that the possession of this character in common probably represents only parallel adaptation in these two genera to the dark dense undergrowth of forest where the very bright coloration plays, I suspect, a role in behavior.

The tail of *Thripadectes* is composed of 12 rectrices, is uniformly reddish chestnut or bay, and is moderately graduated; the rectrices are not firmly integrated and are well stiffened at the base, but not at the tip which is soft or relatively soft and more or less subacuminate in shape. Virtually no interspecific variation exists, except that the webs of the rectrices are somewhat better integrated as a rule in *T. holostictus,* and that the rufous pigmentation is slightly brighter, or duller, in some species than others.

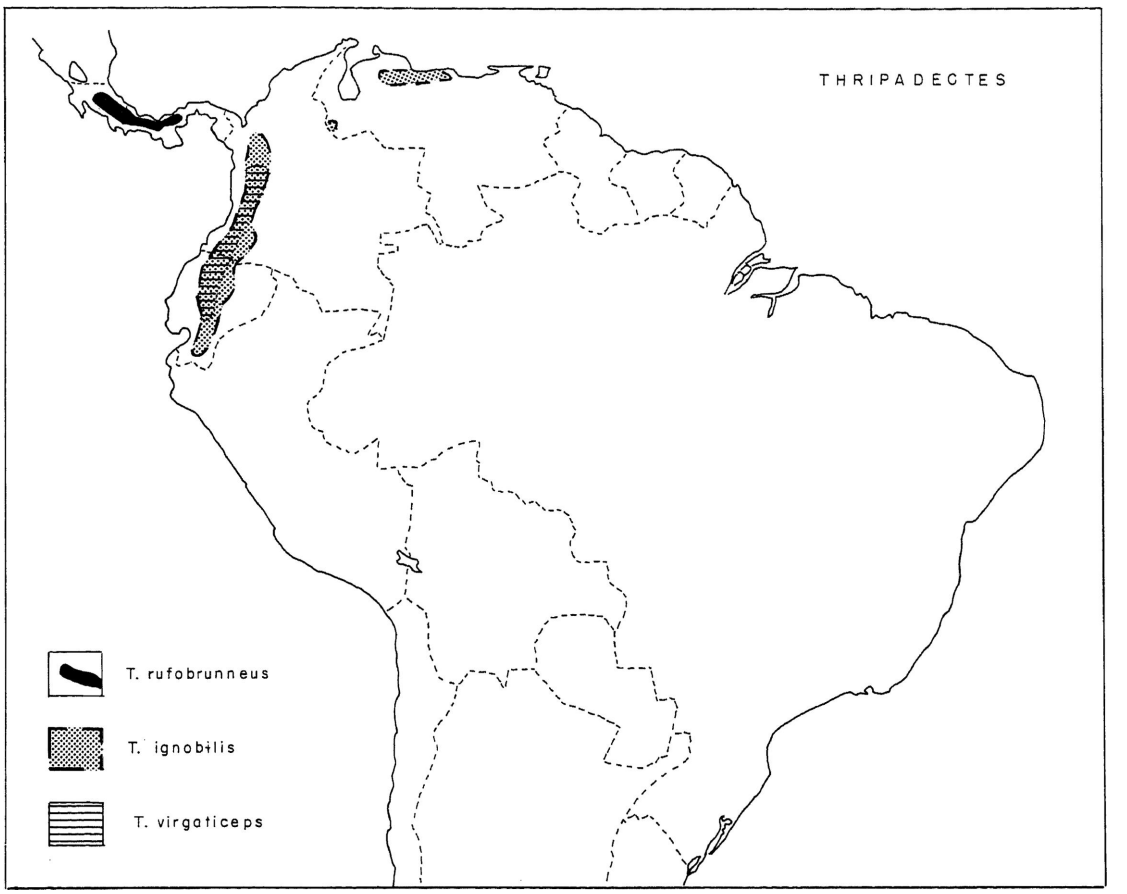
The variation in measurements is slight. The mean wing length varies in round numbers from only 90 to 99.5 mm., with an average of 94.5 mm. The variation in the case of the tail is somewhat greater, the means varying from 80 to 104 mm., with an average of 92 mm. The tail may be slightly longer, or slightly shorter, than the wing, but averages very slightly shorter; the ratio between its length and that of the wing varies from 0.88 to 1.06, average 0.97. The bill is very strong, slightly or well hooked, and the variation in its length is moderate, 24.50 to 28.45 mm., with an average of 26.59 mm. The feet, toes, and claws are strong.

The plumage is streaked in all seven species of *Thripadectes* and the streaking is the only character which varies conspicuously, but within a very definite range as the species are either heavily streaked or not, on both the underparts and mantle, or only on the underparts. The species that are not streaked on the mantle are: *T. ignobilis, T. rufobrunneus,* and *T. virgaticeps.* The species that are streaked on both the mantle and underparts are *T. melanorhynchus, T. holostictus, T. scrutator,* and *T. flammulatus,* but *T. melanorhynchus* is less streaked than the other three species, and, thus, is roughly intermediate between them and the three that are not streaked. In the streaked species, the streaking is very heavy in *T. scrutator,* and even more highly developed in *T. flammulatus.*

Phylogeny

The great morphological homogeneity and the geographical distributions of the seven species (maps 44 and 45) give no definite clues to relationships. All seven species seem to be closely interrelated, but if the degree of streaking and the areas involved denote relationship, the sequence I have adopted here is logical. *Thripadectes ignobilis* and *T. flammulatus* represent the opposite ends of the sequence, and the bill of *T. ignobilis* is also somewhat shorter and weaker than that of the other species, but it is certainly not stouter as Hellmayr (1925) said and added that *T. ignobilis* "should perhaps be separated generically." This suggestion was echoed by Meyer de Schauensee (1966), but fortunately was never implemented.

Thripadectes scrutator and *T. flammulatus* replace one another geographically (map 45) and perhaps are quite closely related. But the two birds are probably not conspecific as their color patterns differ to about the same degree as in the case of the other species.



MAP 44. Geographical distribution of three species of the genus *Thripadectes*.

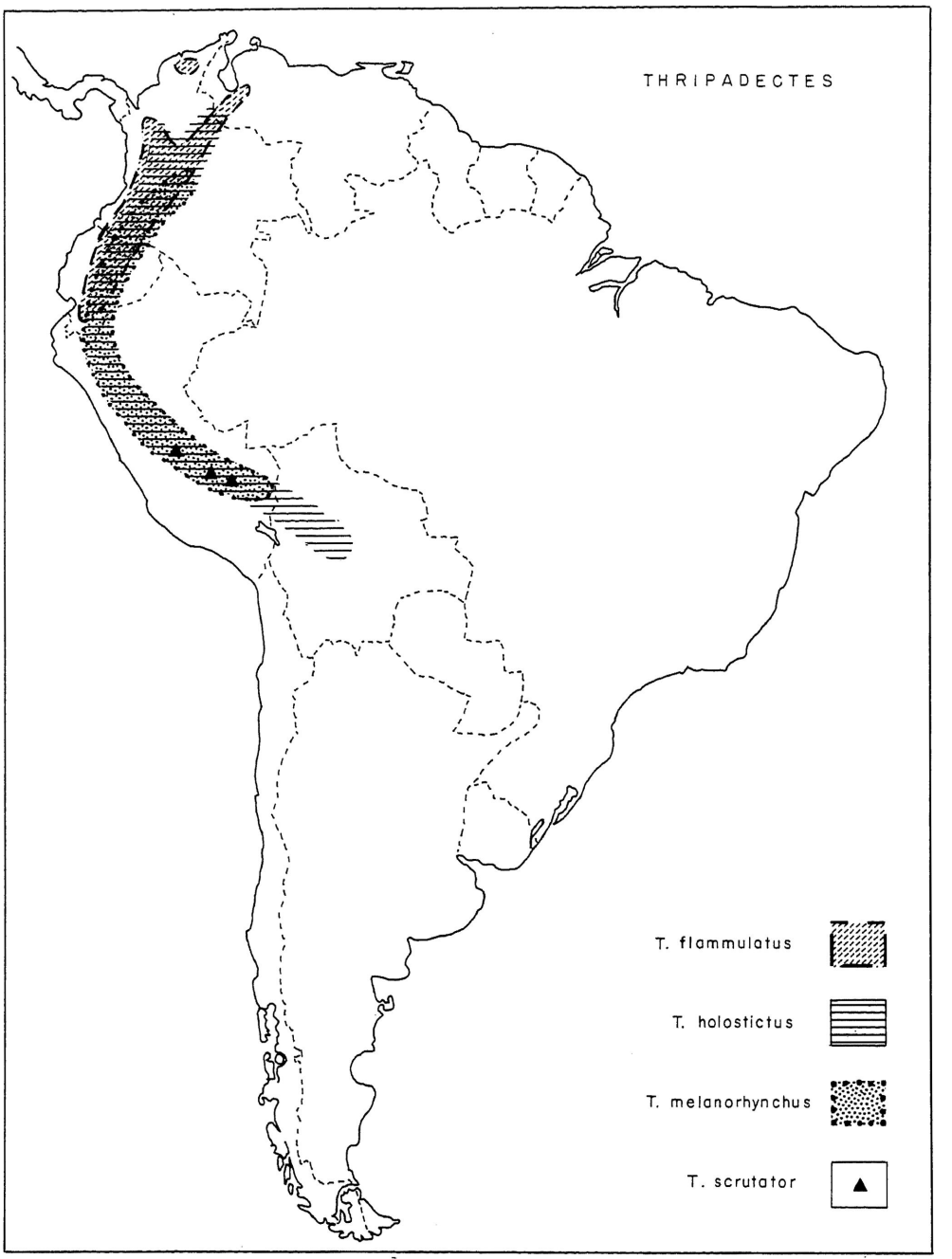
Thripadectes flammulatus is much more heavily and regularly flammulated on the underparts than *T. scrutator* and is very heavily streaked on the mantle, whereas the streaking is faint only on the central and lower parts of the mantle in *scrutator* and virtually obsolete in some individuals.[140]

GEOGRAPHICAL VARIATION

The geographical variation is distinct only in *Thripadectes flammulatus* and very slight or dubious in the three other species (*T. virgaticeps, T. melanorhynchus,* and *T. holostictus*) in which "subspecies" have been recognized.

In *Thripadectes flammulatus,* the population of the Andes of western Venezuela, which was named *bricenoi* by von Berlepsch in 1907, is distinctly paler on both the upper and underparts than the population from the remainder of the range in Colombia and Ecuador. This difference is best shown by the dark margins of the feathers which are less blackish and more reduced and create a paler appearance.

In *Thripadectes virgaticeps* the geographical variation is trivial and only relative differences exist in the color saturation of the plumage and in the degree of its streaking; "differences" in measurements of the wings and bill exist, but are not at all constant.



MAP 45. Geographical distribution of four species of the genus *Thripadectes*.

Nevertheless, a division into no fewer than six "subspecies" has been proposed.

The geographical variation in *Thripadectes melanorhynchus* has been discussed by Zim-

mer (1936c), and briefly mentioned also by Bond (1945). The comparative material that I have examined is more abundant than that seen by Zimmer or Bond, and does not supply any satisfactory evidence of geographical variation; I therefore believe the existence of this variation is dubious.

The geographical variation of *Thripadectes holostictus* is so slight that the recognition of subspecies is certainly an abuse of the subspecies concept. However, the streaking is somewhat more reduced on the breast of the birds of Peru and Bolivia which were separated subspecifically by Zimmer; and another "subspecies" was proposed by Peters in 1951 from southwestern Colombia and western Ecuador because birds from this area are allegedly more heavily streaked, but this "fact" is not at all evident to me.

KEY TO THE SPECIES OF *THRIPADECTES*

1. Mantle streaked 2
   Mantle not streaked 5
2. Abdomen streaked 3
   Abdomen not streaked ..... *melanorhynchus*
3. Whole mantle very heavily streaked, with broad rufous or fulvous shaft streaks, outlined by dark brown or blackish edges to the feathers 4
   Mantle not heavily streaked below its upper border, but with only pale and very narrow, fine shaft streaks ..... *scrutator*
4. Whole of the underparts, including under tail coverts, heavily flammulated with black, cinnamon, or bright ochraceous buff ..... *flammulatus*
   Breast well spotted (rather than flammulated) with black, and cinnamon or ochraceous buff, the feathers being somewhat squamate in shape; abdomen not flammulated but streaked with buff ..... *holostictus*
5. Crown narrowly, but very distinctly and sharply streaked with dull white or buff, on feathers which are dull black ..... *virgaticeps*
   Crown not streaked, or with only very faint and very vague pale shaft streaks, on feathers that are rufous brown, or grayish brown, with more or less faint and narrow dull black edges and tips 6
6. Feathers of the throat dark chrome orange and squamate in appearance; feathers at the sides of the lower neck somewhat elongated, chrome orange, as also an area along the shaft of the feathers of the breast which have tawny olive sides. Bill powerful, well elongated, and black ..... *rufobrunneus*
   Feathers of the throat ochraceous buff, not distinctly squamate; with narrow, ochraceous buff streaks on the breast, and pale ferruginous spots at the tip of the feathers at the sides of the lower neck. Bill strong, stout, not markedly elongated, and brownish ("horn") in color ..... *ignobilis*

LIST OF THE SPECIES

Thripadectes ignobilis

DESCRIPTION: Upperparts uniformly reddish brown, somewhat darker and more dusky on the crown, somewhat brighter and more rufous on the rump and upper tail coverts. Lores cloudy white, ear coverts brown with a few fine pale shaft streaks, and feathers at the sides of the neck tawny brown, with small, brighter ferruginous spots which tend to form a very vague, irregular postocular streak. Underparts chiefly burnt umber, paler and more ochraceous on the throat, darker and with a vague olivaceous cast on the lower abdomen and flanks. The centers of the feathers of the throat are pale, dull ochraceous orange, bordered by the brown edges of the feather, and, progressively and posteriorly, the pale area becomes more restricted to the shaft, resulting in a streaked pattern which dwindles and disappears on the center of the abdomen; the streaked pattern of *Thripadectes ignobilis* is relatively indistinct. Bill slightly shorter and weaker than that of the other species, see discussion of phylogeny.

RANGE: Colombia, in the Pacific region, and south to Nariño, and to northwestern and central Ecuador. The altitudinal range varies from about 800 m., or more usually 1000, to about 1850 m.

SPECIMENS EXAMINED: 14, including the type of *ignobilis* in BM.

Thripadectes rufobrunneus
Figure 10

DESCRIPTION: Back uniformly reddish brown, becoming brighter on the rump and reddish chestnut on the upper tail coverts. Crown and hind neck brown, but with the feathers edged and tipped with dull black. Lores grayish, and dark chrome orange on the feathers at the sides of the lower neck which are somewhat elongated; and dark chrome orange also on the feathers of the throat which are squamate in appearance. On the feathers at the base of the throat, and on the feathers of the upper breast, the orange pigmentation is restricted to the center of the feather along the shaft, and these shaft streaks decrease in width and number gradually posteriorly to dwindle and disappear on the center of the abdomen. The dark edges of the feathers that have orange centers or streaks, as well as the ground coloration of the entire underparts, are chiefly dark tawny olive. The streaked pattern of *Thripadectes rufobrunneus* is more distinct, sharper than that of *T. ignobilis*. Bill strongly hooked.

IMMATURE PLUMAGE: Very similar to that of the adult, but streaks on the upper breast not so well defined, and black tips and edges of the feathers of the crown and hind neck less distinct, or lacking.

RANGE: Central highlands and mountains of Costa Rica, south to eastern Veraguas in Panama; the altitudinal range varies between about 760 and 2350 m.

SPECIMENS EXAMINED: 31.

Thripadectes virgaticeps

DESCRIPTION: Crown and hind neck dull black, or blackish, with fine, dull white shaft streaks; back uniformly reddish brown, becoming more rufous on the rump, and reddish chestnut on the upper tail coverts. Sides of the face blackish or dark sepia, with very fine buffy streaks. Upper and central portions of the throat with feathers that are somewhat squamate in shape, cinnamon buff with dark brown edges. The feathers are normal in shape on the lower throat, lack the dark brown edges, and the buffy area becomes progressively more restricted; these streaks become very fine and dwindle and disappear on the center of the upper breast; the ground coloration of the entire underparts is dark ochraceous tawny below the paler throat. Bill long, powerful, and strongly hooked.

IMMATURE PLUMAGE: Similar to that of the adult, but squamated pattern of the throat less distinct, only barely suggested, or absent.

RANGE: Venezuela, in the coastal mountains of the north, between about 1900 and 2000 m. from Aragua and the Distrito Federal, west to southern Lara, also Andes of southern Táchira between about 1250 and 2100 m.; and Colombia, from the headwaters of the Rio San Juan in the Pacific region, and from the upper Magdalena Valley, south to the region of Loja in southern Ecuador; the altitudinal range in Colombia and Ecuador varies between about 1000 and 2350 m.

SPECIMENS EXAMINED: 24, including the types of *virgaticeps* and that of "*sumaco*" in AMNH, of "*tachirensis*" in the Phelps Collection on deposit at AMNH, and of "*brooki*" in BM.

Thripadectes melanorhynchus

DESCRIPTION: Crown dull black and back dark dusky brown, the crown and mantle being well, but not very heavily, streaked with pale or ochraceous buff; sides of the head and neck with small buffy spots or streaks. Feathers of the whole throat, which are squamate, ochraceous buff at the upper portion of the throat, but more ochraceous orange below the upper throat, and distinctly edged with dark or blackish brown. Breast ochraceous brown with an olive gray cast in some individuals, and streaked, more or less faintly and distinctly, with fine pale shaft streaks.

IMMATURE PLUMAGE: Very similar to that of the adult but streaked pattern of the upperparts and squamated pattern of the feathers of the throat less distinct.

RANGE: Eastern Andes of Colombia, from region south and near Bogotá, south through eastern Ecuador, to Puno in southeastern Peru; the normal altitudinal range seems to vary between about 900 and 1400 m.

SPECIMENS EXAMINED: 21, including the type of "*striaticeps*" in BM.

Thripadectes holostictus
Figure 10

DESCRIPTION: Crown dull black and back very dark dusky brown, the feathers having broad buffy or fulvous shaft streaks, outlined by the blackish or dark dusky brown edges to the feathers, producing a heavy streaked pattern. Sides of head and neck with small spots or streaks of buff. Feathers of the throat somewhat squamate, with pale ochraceous buff, or cinnamon buff centers to the feathers which are well edged with blackish brown. The "spotted" pattern of the throat extends to the upper breast, but becomes less distinct on the center of the breast, as the dark edges of the feathers gradually disappear, and the pale buff center of the feather becomes progressively more restricted to the shaft, thus producing a streaked appearance on the lower breast and abdomen which becomes gradually fainter and less distinct on the lower abdomen.

IMMATURE PLUMAGE: Similar to the adult, but streaked pattern of the upperparts less sharp and distinct; the streaks are finer on average. On the underparts, the streaked pattern becomes confused on the lower breast and disappears, or tends to disappear, from about the center of the lower breast down, the feathers becoming tipped or margined with dark brown, creating a mottled rather than streaked pattern.

RANGE: Andes, from southwestern Táchira in extreme western Venezuela, south through Colombia, Ecuador, and Peru, to La Paz and Cochabamba in Bolivia. The altitudinal range varies between about 800 and 3100 m.

SPECIMENS EXAMINED: 34, including the types of *holostictus* in BM, and of "*moderatus*" in AMNH.

Thripadectes scrutator
Figure 10

DESCRIPTION: Crown and nape to the upper border of the mantle dull black, very heavily and broadly streaked with fulvous or cinnamon streaks. The back is rufous brown below the upper border of the mantle, with very faint, or more distinct, but very fine pale fulvous shaft streaks. The underparts are more olivaceous, less rufous brown than the back, and are very heavily streaked with very broad fulvous or cinnamon streaks, emphasized by the blackish or very dark brown edges to the feathers. The fulvous streaks are also very broad below the upper breast, but less conspicuous, as the dark edges of the feathers gradually disappear, and the streaks become gradually finer and less distinct on the lower abdomen and under tail coverts.

IMMATURE PLUMAGE: In one specimen which, perhaps, is not quite fully adult, the streaked pattern is a little more diffuse than in birds which appear to be adult.

RANGE: This species is rare in collections, known only from about nine specimens taken in Junín, Ayacucho, and Cuzco in central Peru, where it may be restricted geographically. These specimens consist of the type from Maraynioc, Junín, which has been lost and probably destroyed during the First World War, or its aftermath in Russia; one specimen from Yuraccyacu, Ayacucho, and seven specimens from Cuzco, taken at Lucma in the Urubamba region, and in the Cordillera de Vilcabamba. The description of the specimen of *Thripadectes scrutator* from Lucma given by Hellmayr (1925, p. 229, footnote b) is not correct and gives a false impression of the characters of this species. This specimen, the only one seen by Hellmayr, was reexamined by me through the courtesy of the United States National Museum. The altitude at which the specimens were taken varied from 2100 to about 3650 m.

SPECIMENS EXAMINED: 8.

Thripadectes flammulatus
Figure 10

DESCRIPTION: Crown dull black and back rufous brown; the feathers of the crown and of the whole of the mantle are heavily and broadly streaked with ochraceous buff, cinnamon buff, or bright cinnamon, the broad cinnamomeous or buffy streaks being strongly emphasized on the mantle by the black

edges of the feathers. These cinnamomeous and blackish streaks extend also, though fainter and smaller, to the rump but not to the upper tail coverts which are uniformly rufous in all the species of *Thripadectes*. The whole of the underparts from the chin to the under tail coverts are very heavily but beautifully flammulated, with black bright ochraceous buff or bright cinnamon. The flammulated pattern is most regular on the lower throat and on the breast, the black edges of the feathers becoming gradually less distinct and regular on the lower abdomen, whereas the pale and bright centers of the feathers become more extensive. On the under tail coverts, however, the dark edges of the feathers are well defined, and the pale center is darker, richer than on the feathers of the abdomen, distinctly more ferruginous.

IMMATURE PLUMAGE: Similar to that of the adult, but streaked pattern less distinct and heavy.

RANGE: Andes of Mérida in western Venezuela, Santa Marta Massif in northern Colombia, and Andes of Colombia and Ecuador south to Loja in southern Ecuador. The normal altitudinal range seems to vary from about 1000 to 3260 m.

SPECIMENS EXAMINED: 42, including the type of *flammulatus* in BM.

GENUS *AUTOMOLUS*

Automolus is composed of 11 species distributed in heavily forested regions and also in campos in Brazil, from southeastern San Luis Potosí and from Guerrero in Mexico, south to Bolivia, Paraguay, and southeastern Brazil.

Automolus seems to be closely related to *Thripadectes* and *Sclerurus*; its systematic position has been discussed earlier in the section on *Thripadectes*, and in my preliminary classification of the Furnariidae (1971a). However, Sclater (1890) and Hellmayr (1925) believed that *Automolus* was closely related to *Philydor*, which it resembles morphologically in a general way. Sclater separated *Automolus* and *Philydor* only on the basis of relative size, and Hellmayr on a difference in the shape of the bill and "slightly lengthened crown feathers, suggesting a sort of crest" in *Automolus*, but no constant morphological differences exist between the two genera. Nevertheless, they do differ in their behavior, whereas the distinct similarities of behavior which exist suggest that *Automolus* is related to *Thripadectes* and *Sclerurus*, rather than to *Philydor*.

Thripadectes, *Automolus*, and *Sclerurus* nest only in burrows dug under the ground, as far as known, whereas the preferred nesting site of *Philydor* seems to be above the ground in a cavity, such as a hole in a tree, although *P. rufus* is reported also to nest in a burrow under the ground, as well as in cavities in walls and holes in trees. *Philydor* is noted for being actively arboreal, climbing over branches or along the trunks of trees, from the upper level of the undergrowth to the middle or the upper levels of trees, whereas *Thripadectes* and *Automolus* are birds of the low and densely tangled undergrowth and *Sclerurus* is almost strictly terrestrial, frequenting the forest floor where it tosses about the fallen leaves with its bill in search for food. In general behavior and also in morphological aspects, *Automolus* seems "closer" to *Sclerurus* than to *Thripadectes*, which is the least specialized of the three genera, whereas *Sclerurus* is quite clearly the most specialized morphologically and behaviorally—a question of degree which suggests that *Automolus* is best listed systematically between *Thripadectes* and *Sclerurus*.

The three genera can be easily distinguished morphologically. *Thripadectes* are heavy, coarse birds, with big bills and feet, and their plumage is streaked, very coarsely in some species; the long tail, with rectrices that are not firmly integrated, varies in length from slightly longer, to slightly shorter, than the wing, with a ratio averaging 0.97. In *Automolus*, the tail is always distinctly shorter than the wing, with a tail/wing ratio of 0.87, and the web of its rectrices is well integrated; only one of its 11 species is streaked, but not heavily and on the breast only; the feet are very distinctly weaker than in *Thripadectes*; and the bill of *Automolus* is also weaker and more attenuated. The tail of *Sclerurus* is proportionally very short, as the ratio between

its length and that of the wing decreases to only 0.69, and it is strongly modified, as the rachis of its rectrices (that are normally integrated as a rule) is strongly stiffened throughout the entire length of the feather. The apex of the rachis is "wire-like" and usually protrudes somewhat beyond the web, whereas the apex of the rachis is soft, or relatively so, in *Thripadectes* and *Automolus,* and does not normally protrude beyond the web. Other differences exist: *Sclerurus* is not streaked and has a black tail (as against strongly rufous in the two other genera); the feet are big, but are relatively slender, and the bill of *Sclerurus* is very markedly long and attenuated.

All the species of *Automolus* inhabit rain forest or other dense humid forest, where they are active in the densest tangles of the undergrowth, usually near or not far above the ground, to which they regularly or occasionally descend to forage for food—or, as in the case of *A. rectirostris,* they inhabit drier regions, the campos of Brazil, where they frequent the very dense tangles of lianas or other creepers. *Automolus* species are not truly montane birds and can be characterized as typical of the lowland rain forests; nevertheless, the majority of species ascend to the lower altitudes (or higher) of montane rain forests. For instance, *A. ruficollis* (maximum altitude: 2865 m.), *A. dorsalis* (2134 m.), *A. albigularis*[141] (2200 m.), and *A. rubiginosus* (2438 m.), all ascend to over 2000 m. Three other species have not been recorded so high; the records I have obtained are 1650 m. in Mexico and nearly 1500 m. in Honduras for *A. ochrolaemus*; 1300 m. in Venezuela for *A. infuscatus*; and 1981 m., or nearly 2000 m., for *A. erythrocephalus* in Peru. The other four species (*A. leucophthalmus, A. melanopezus, A. rufipileatus,* and *A. rectirostris*) do not seem to occur much over 600 m., usually much less.

The best known species (*Automolus ochrolaemus*) is also the most widely distributed, and the one about which Skutch (1952, 1969b) has written extensively after having observed it in Central America. Skutch wrote (1969b) that *A. ochrolaemus* "is primarily an inhabitant of the rain forest, but in regions where this forest is shrinking before the inroads of man, it adapts itself to life in the taller secondary vegetation and shady plantations." The food consists of insects, or other small animals, such as spiders and little lizards secured chiefly by searching assiduously "among curled or clustered dead leaves, sometimes those lodged in the undergrowth near the ground, sometimes those caught among vine tangles," which are investigated by clinging in any position the situation demands, an inverted position if necessary. The leaves may be on or near the ground and "the dead foliage of the prostrate crown of a great fallen tree is a fertile hunting ground"; "apparently [*A. ochrolaemus*] . . . never forage[s] in the high canopy of the forest," and "sometimes it descends to the ground to push aside fallen leaves with its bill."

This manner of foraging may be occasional only in *Automolus ochrolaemus,* but more regular in *A. rubiginosus* which Marshall (1943) said forages on the ground among fallen logs and overhanging roots. Marshall's observations were made in El Salvador. In Santa Marta, Colombia, Carriker (in Todd and Carriker, 1922) described *A. rubiginosus* as being "partial to the heavy forest or thick second-growth, and . . . fond of dark tangles and ravines. It does little climbing, but keeps hopping about on or near the ground."

The nests of *Automolus ochrolaemus, A. infuscatus, A. leucophthalmus,* and *A. rubiginosus* are known. They are broad shallow cups of plant fibers constructed at the end of a burrow dug in a bank of earth, often along a small stream, but other convenient sites which may be used are cuts along paths and small roads, in clearings, ravines, or walls of pits. *Automolus ochrolaemus* digs its own burrow, or uses and adapts old burrows that may have been excavated by members of its own or other species, or they may be "natural" tunnels caused by the decay of thick roots that were exposed when the cut was made. Skutch, who has observed about a dozen nests of *A. ochrolaemus,* said the depth of the burrow usually varies between about 60 and 75 cm., but may be as short as 46 cm. The tunnel is about 5 to 7 cm. wide,

nearly horizontal and straight, expanding at the end into a low chamber wide enough to hold the nest which consists "almost wholly of a single kind of vegetable material, usually the curving brown rachises of compound leaves," which at El General, Costa Rica, are chiefly the slender "secondary rachises of the twice-pinnate, acacia-like leaves of a thorny liana, *Mimosa myriadena,*" the rachises of which have lost their "many tiny leaflets [and are] covered with fine pubescence."

The nest of *Automolus infuscatus* was briefly described by Snethlage (1935) and Pinto (1953), and that of *A. leucophthalmus* by Euler (1867) and Novaes (1961b). The location of the nest (at the end of a burrow underground), and the material used (rachises of compound leaves, or other soft plant material), are the same as in the case of *A. ochrolaemus,* except that the burrow mentioned by Snethlage was considerably deeper, "about 2 meters."

Laurence C. Binford has written to me that he observed *Automolus rubiginosus* active at a burrow, the entrance of which was 8 feet [about 2.40 m.] up on the face of a clay bank formed by a road cut, but he could not examine the nest itself, the only description of which seems to be by Rowley (1966). The latter found a nest at the end of a burrow about 2 m. deep, dug into a low vertical bank of earth along a stream about 1.20 m. above the stream bed. The nest itself was described by Rowley as "rather compactly constructed, with fine rootlets as a base and the sides and lining composed chiefly of soft, fine yellowish-brown plant fibers. The greatest diameter of this quite shallow nest was approximately 155 mm., and the slightly depressed cup in which the two unmarked white eggs were laid averaged about 30 mm. deep."

On another occasion, about one month later, Rowley observed another pair of *Automolus rubiginosus,* and one of the two birds (which Rowley called a female) entered a hole dug into a bank of earth along a road cut and was observed pushing out particles of earth from the entrance, which suggests that *A. rubiginosus* digs its own burrow, or adapts an existing one, at least occasionally.

Morphological Variation

Automolus is a less homogenous genus than *Thripadectes* but the range of its variation is narrow and consists chiefly of variations in coloration and its general saturation. The bill of some species is also more slender and distinctly longer than in others, and in most species, the feathers of the crown are or tend to be more or less elongated, as mentioned above and noted by Hellmayr (1925), but not to the point of forming a true crest.

Nine species are rufous brown on the crown and mantle; the two exceptions are: *Automolus infuscatus* which is or tends to be grayish olive or umbraceous, less rufescent, and *A. erythrocephalus* in which the bright rufous crown contrasts with the pale grayish brown mantle. The hue, shade, and intensity of the rufous pigmentation vary, but the rump is normally paler than the mantle, and the upper tail coverts are uniformly chestnut or reddish chestnut, as well as the tail, in all the species. In *A. rubiginosus,* however, which varies a great deal geographically, the upper tail coverts can be bay, and the tail dark dull mahogany, or nearly black. The crown and mantle are uniform in coloration, or they are not, but they are not streaked. The axillaries, under wing coverts, and an extensive area along the outer edge of the inner web of the inner remiges, are normally very bright ("orange," or chrome orange) as in the case of *Thripadectes* and *Philydor.* They are the brightest parts of the plumage, with the exception of the exposed upper surface of the wing which is also very bright rufous in *A. rectirostris* and *A. erythrocephalus.*

The coloration of the underparts is more variable than that of the upperparts, especially in *Automolus rubiginosus* which varies geographically from bright rufous to olive brown and sooty or raw umber brown, with the throat, breast, and abdomen uniform in coloration or not. *Automolus ruficollis* is

TABLE 22
Measurements (in Millimeters) of *Automolus*

Species	Wing			Tail			Bill		
	N	Mean	Range	N	Mean	Range	N	Mean	Range
ruficollis									
Males	14	87.92	85–91	14	78.78	74–84	12	23.87	23–25
Females	12	84.33	82–87	11	76.45	70–82	10	23.70	23–24.5
Both sexes	28	86.39	82–91	27	77.96	70–84	24	23.77	23–25
ochrolaemus									
Males	126	92.74	84–101	119	77.00	71–84	123	25.51	23–28.5
Females	105	88.94	83–95	94	74.67	68–82	103	24.88	23–29
Both sexes	244	91.02	83–101	225	75.95	68–84	239	25.23	23–29
infuscatus									
Males	103	93.97	85–104	84	75.26	66–82	100	23.72	21–26
Females	69	90.34	83–95	61	73.36	65–78	69	23.06	21–25
Both sexes	177	92.51	83–104	149	74.44	65–82	174	23.46	21–26
dorsalis									
Males	10	97.65	92–105	9	79.88	75–85	9	23.95	22.2–25.5
Females	8	88.00	86–89	7	70.42	66–80	8	22.77	21–24
Both sexes	22	93.11	85–105	20	75.20	62–85	21	23.41	21–25
leucophthalmus									
Males	25	90.04	83–97	23	81.65	75–88	25	24.48	22.5–26
Females	14	86.96	82.5–95	14	80.57	74–84	14	23.77	23–25.2
Both sexes	46	89.07	82.5–99	44	81.02	74–88	46	24.31	22.5–26
melanopezus									
Males	8	88.12	83–91	8	75.25	73–78	8	22.81	21–23.5
Females	4	83.75	82–86	4	73.00	68–77	4	22.62	22–23
Both sexes	16	86.62	82–91	16	74.87	68–78	16	22.81	21–23.5
albigularis[a]									
Males	15	85.26	81–89	14	77.92	73–81	15	22.14	21–23
Females	14	81.78	79–83	12	75.25	70–79	14	22.26	21–24
Both sexes	32	83.87	79–89	29	76.72	70–81	32	22.30	21–24
rubiginosus									
Males	45	90.57	83–98	44	79.81	70–92	42	26.88	24–29
Females	25	88.40	80–95	25	78.16	70–87	24	26.27	23–28
Both sexes	81	90.09	80–98	80	79.63	70–92	75	26.66	23–29
rufipileatus									
Males	37	91.67	84–98	36	79.80	75–86	33	25.42	23.5–27
Females	22	88.36	83–93	21	77.52	74–83	20	24.85	23.5–27
Both sexes	61	90.26	83–98	59	78.71	70–86	55	25.12	23–27
rectirostris									
Males	3	99.33	95–103	3	84.33	81–87	3	27.66	26.5–29
Females	2	98.00	95, 101	2	83.00	78, 88	2	27.50	26, 29
Both sexes	8	99.50	95–104	8	85.87	78–90	8	27.93	26–30
erythrocephalus									
Males	2	99.00	98, 100	2	89.00	88, 90	2	32.50	32, 33
Females	8	92.75	90–96	8	84.00	81–89	8	32.00	31–34
Both sexes	10	94.00	90–100	10	85.00	81–90	10	32.10	31–34

[a] See note 143 about nomenclature (E. Eisenmann).

streaked on the breast, and *A. ochrolaemus* is more or less distinctly mottled on the lower throat and upper breast, but not streaked. In the other nine species, the throat and breast may be uniform in coloration, or not, but are not streaked or mottled. In three species (*A. infuscatus, A. dorsalis,* and *A. leucophthalmus*), which are probably related, the throat and breast are very pale, whitish, and nearly uniform. *Automolus rufipileatus* is uniformly ochraceous, and *A. rectirostris* is cinnamomeous and ochraceous buff, nearly uniform; in *A. erythrocephalus,* however, the bright rufous throat contrasts strongly with the pale olive gray of the breast and abdomen, although *A. rectirostris* and *A. erythrocephalus* are probably close relatives.

The structural variation is very slight. Some species, to be sure, have a longer and more attenuated bill, which is also more compressed laterally than in other species. These species are *Automolus rubiginosus* and especially *A. rectirostris* and *A. erythrocephalus.* In *A. ochrolaemus,* the bill tends to be long also, attenuated and compressed, and *A. ochrolaemus* together with *A. rubiginosus* are intermediate between *A. rectirostris* and *A. erythrocephalus* and the other seven species in which the bill varies very little in shape and length, the mean length varying from only 22 to 25 mm., with an average of about 23.5 mm. in the seven species.

The tail is composed of 12 rectrices that are slightly or moderately graduated, are broad, well integrated, and end in subacuminate tips. The distal third of the tail is elastic, but not stiffened. It must be emphasized again that the apex of the tail is soft or relatively soft in *Automolus,* as well as in *Thripadectes* and *Philydor.* It is *not* stiff, as is often stated erroneously in the literature, and hence, the tip of the tail in these birds does not constitute an efficient brace for support in climbing as in the case of the woodhewers and woodpeckers. The variation in the length of the tail is remarkably slight, from only 74 to 86 mm., with an average of about 79 mm., and the tail is distinctly shorter than the wing, the length of which measures 84 to 99 mm., with an average of about 90.5 mm.; these measurements are means stated in round numbers. The mean ratio between the lengths of the wing and tail is 0.87.

Automolus is usually characterized as having "noticeably large, strong feet" (Wetmore, 1972). This is correct relatively speaking, as the feet of *Automolus* though of good size are not unusually large and strong when compared, for instance, to the really large and strong feet of *Thripadectes.*

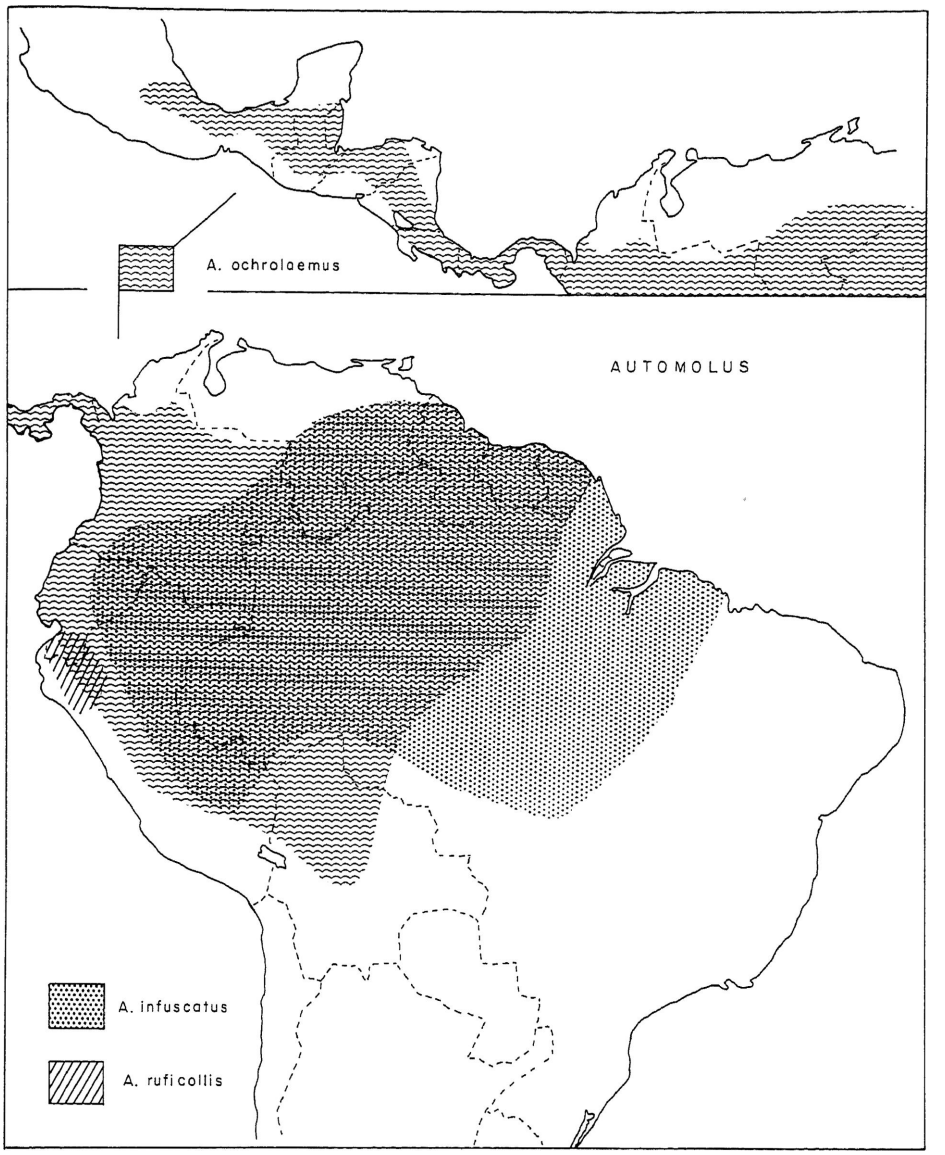
Phylogeny

All the species seem to be more or less closely related, but their degree of relationship is uncertain except for *Automolus rectirostris* and *A. erythrocephalus,* which seem to be closely related, and of a group consisting, perhaps, of the species *A. infuscatus, A. dorsalis,* and *A. leucophthalmus.* I started the sequence of the species with *A. ruficollis,* followed by *A. ochrolaemus,* only because *A. ruficollis* is streaked and *A. ochrolaemus* is mottled on the underparts, a plumage which one can consider, perhaps, as "primitive" in a genus in which a streaked or mottled plumage is exceptional. But the relationships of *A. ruficollis, A. ochrolaemus,* and also *A. albigularis* (which Mayr and Phelps, 1967, connect to the other two species) are too uncertain to permit speculation on the degree of relationship.

The only two species which seem to be quite clearly closely related are *A. rectirostris* and *A. erythrocephalus.* It has been suggested that these two birds may be conspecific, but this suggestion is not well founded, in my opinion, and I also believe that it would be certainly most unwarranted to accept a separate "genus" (*Hylocryptus,* Chapman, 1919) for these two species on the ground that the bill of *A. erythrocephalus* is longer than that of the other species and "proportionately more slender" than most.[142]

Geographical Variation

Geographical variation exists or has been mentioned in eight of the 11 species of *Automolous*; it is dubious in one species (*A. erythrocephalus*), slight in three (*A. ruficol-*

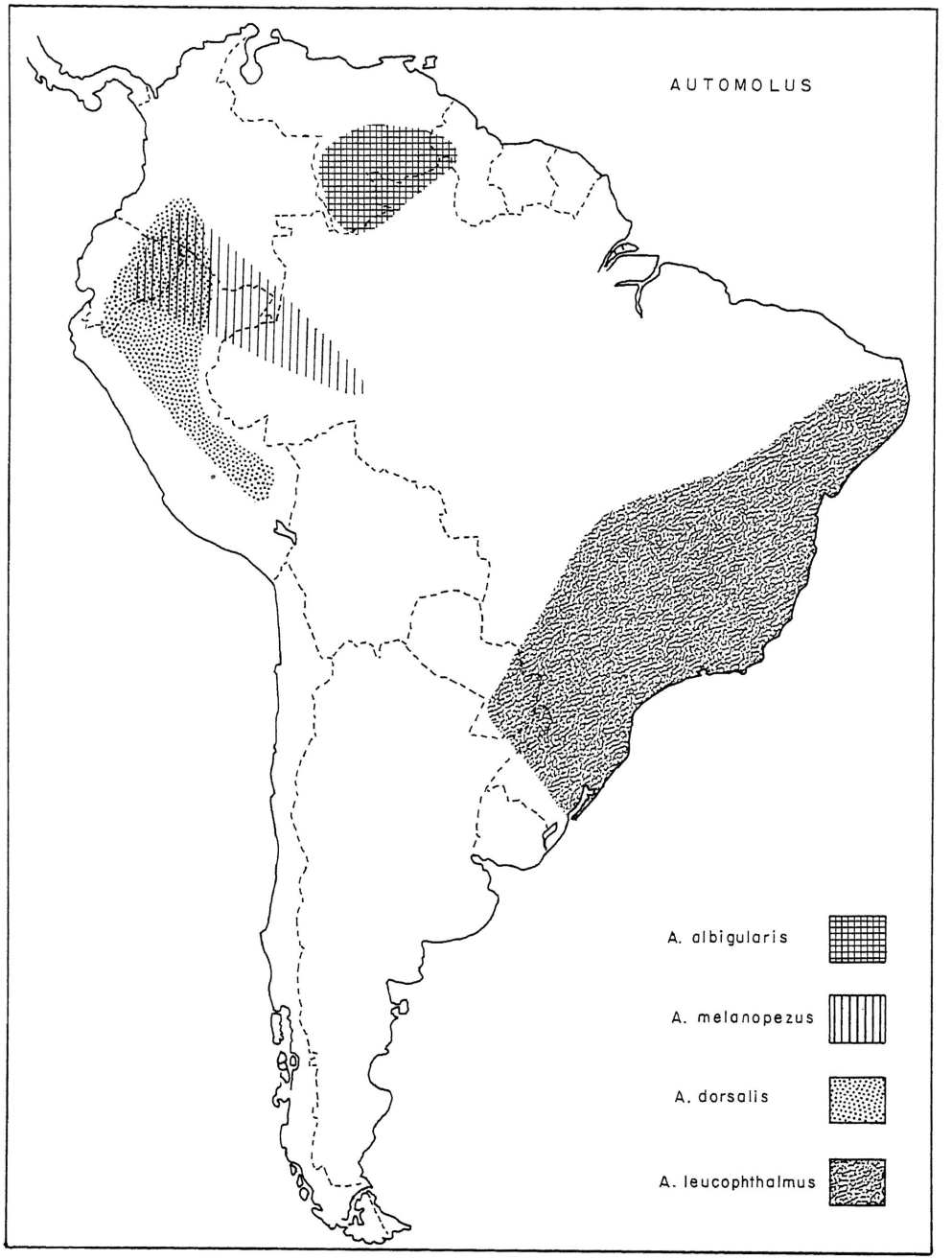


MAP 46. Geographical distribution of three species of the genus *Automolus*.

lis, *A. infuscatus*, *A. leucophthalmus*), and distinct in four species (*A. ochrolaemus*, *A. albigularis*, *A. rubiginosus*, and *A. rufipileatus*).

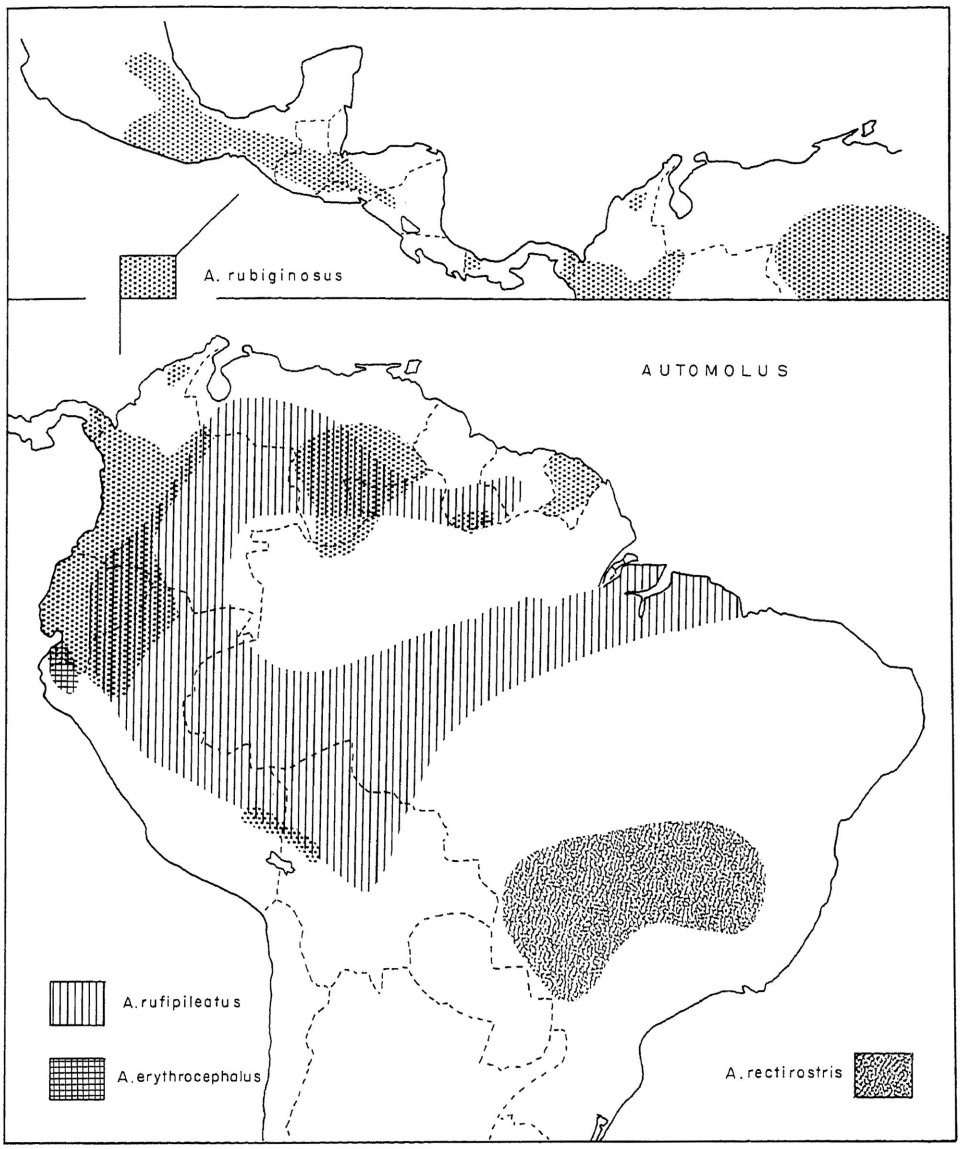
The variation is very strongly indicated in *Automolus rubiginosus* and 16 subspecies have been recognized by Peters (1951), a large number for the Furnariidae. The variation affects the general coloration and also size in one case. Some populations are extremely dark and others not, and it is evident that the variation reflects the distribution of this species which is greatly interrupted (map 48).

The darkest populations of *Automolus rubiginosus* form a group distributed from ex-



MAP 47. Geographical distribution of four species of the genus *Automolus*.

treme eastern Panama south through western Colombia and the Magdalena Valley to western Ecuador, and the most saturated taxon in this group is *A. r. saturatus* of eastern



MAP 48. Geographical distribution of four species of the genus *Automolus*.

Panama and Antioquia which is so very dark chestnut and dark maroon on the upperparts that it is blackish in general appearance, has a black tail, is dark ferruginous on the breast, and very dark raw umber below it. Another taxon in this complex, called *A. r. nigricauda,* is almost as dark as *saturatus,* but somewhat more rufescent.

Along the eastern base of the Andes on the other hand, from Colombia south to northern

Peru, the populations are rufescent on the upperparts, ochraceous brown on the underparts, and have a chestnut tail. A rather slight degree of variation exists in this group and the oldest form which has been named is *Automolus rubiginosus cinnamomeigula* which is based on specimens from Colombia.

The population of the Santa Marta Massif (which is called *Automolus rubiginosus rufipectus*) does not resemble at all the birds of the two groups which have been characterized above, as *rufipectus* is a very bright bird, the brightest and palest form of all. *A. r. rufipectus* is uniformly warm amber brown on the upperparts, with a bright rusty breast, and amber brown below the breast, but paler on the underparts than on the upperparts; its tail is bay.

It is not practical to describe all the other forms of *Automolus rubiginosus*. The oldest name in the group of populations which is distributed from Mexico to Nicaragua is nominate *Automolus r. rubiginosus* Sclater, 1857, which is based on specimens from Mexico and is described in detail below in the description of the species. A very distinct form (*A. r. formosus*) is restricted to the base of the Volcán de Chiriquí in western Panama. Another is *A. r. watkinsi* which is greatly isolated from Puno in southern Peru to La Paz in Bolivia. I have not seen a specimen of *watkinsi,* unfortunately, but Bond (1945) said it is "a strikingly marked form" chiefly characterized, apparently, by the fact that its crown and nape are chestnut and contrast strongly with the brown back. *A. r. venezuelanus* is the name of the form isolated in southern Venezuela and in the mountains on the border of Venezuela and Brazil.

One of the most interesting and least known forms of all is *Automolus rubiginosus obscurus* from French Guiana. In *A. r. obscurus* the upperparts are uniformly rufous brown and the underparts are chiefly burnt sienna and nearly uniform below the darker, more "reddish" upper breast. Its coloration resembles that of some of the other populations of *A. rubiginosus* in a general way, but *obscurus* is a smaller bird, with weaker feet, and a smaller, more slender bill, which suggests, perhaps, that it is a distinct species. Only a few specimens of *A. r. obscurus* seem to exist and the wing length of five adults, seen by me or recorded in the literature, is 77–83 mm. (mean 80.60), as against 84–97 mm. (mean 89.40) in 25 specimens of the other populations of *A. rubiginosus* taken at random. The identity of specimens reported by Snyder (1966) as *obscurus* from the Acary Mountains of southern Guyana requires confirmation. She credits this record to "Blake, 1938," although Blake's report (1950) on the collection he made in the Acary Mountains in 1938 does not mention *obscurus* or any form of *A. rubiginosus.*

The recognition of subspecies in *Automolus rubiginosus* is a matter of opinion, but it is quite certain that most of the "subspecies" in some of the isolated groups differ only slightly from one another and were proposed without a concept and study of the geographical variation of the species as a whole. At least half of the 16 "subspecies" listed and recognized by Peters (1951) should not be acknowledged in my opinion and the most satisfactory solution is probably to recognize only one subspecies for each isolated group of populations, in addition to single isolates such as *formosus, rufipectus, watkinsi,* and *obscurus* that are quite distinct, which is not true of *venezuelanus* which is slightly differentiated only. The forms have been named above although two (*saturatus* and *nigricauda*) were mentioned in the first group of very dark populations. In the case of these two, *nigricauda* Hartert, 1898, has priority, which is somewhat unfortunate despite the quite appropriate name, as the dark extreme in this group is represented by *saturatus* Chapman, 1915.

Eight "subspecies" have been recognized in the case of *Automolus ochrolaemus* by Peters (1951), which is an excessive amount as the geographical variation of this species is relatively slight though distinct. The variation seems to follow only three trends. One of these three forms occupies the northern end of the range, from Mexico south to northwestern Panama, and consists of birds that are dark above and below. A distinct contrast exists on the upperparts between the coloration of the crown and back; the

crown is dusky, darker than the back. The underparts are strongly ochraceous and umbraceous, and the throat is paler than the back. These populations are darkest at the northern end of their range and become slightly paler clinally from north to south. Three "subspecies" have been recognized in this dark northern form by Peters, but the validity of one has been rejected quite correctly by Monroe (1968) and it seems quite sufficient to me to recognize only *A. o. cervinigularis* Sclater, 1857, which was based on Mexican specimens and is the oldest name in this complex. For reviews see Monroe (1968) and also Howell (1957).

In the region which extends from southwestern Costa Rica and adjacent Pacific region of western Panama south through central and western Colombia to northwestern Ecuador, the dark northern form (*Automolus ochrolaemus cervinigularis*) is replaced by a distinctly paler and less ochraceous form in which the coloration of the upperparts is uniform and the throat is paler than in *cervinigularis*. The populations which occupy nearly all of the range of this second form with uniform upperparts are called *A. o. pallidigularis* Lawrence, 1862, and it seems quite sufficient to me to recognize only *pallidigularis*, so-called because the throat of this form is pale and whitish, less buffy than in birds which range from Costa Rica to about the Canal Zone.

In the remainder of the range of *Automolus ochrolaemus*, the populations vary somewhat geographically but are only vaguely differentiated. Three forms have received names but I believe that only one should be accepted and the oldest name is *ochrolaemus* Tschudi, 1844, based on specimens from Peru. The birds of this third group can be characterized by the uniform coloration of their upperparts as in the birds of the second form (*A. o. pallidigularis*), and by the strongly ochraceous coloration of their underparts as in the first and northern form (*A. o. cervinigularis*); their throat is buffy, not whitish as in *A. o. pallidigularis* (in the strict sense).

Some of the populations of *Automolus albigularis* that are more or less isolated on the mountains of southern Venezuela (map 47) differ geographically from one another, but only two forms are distinguishable in my opinion. These are *A. a. duidae* Chapman, 1939, based on birds from Mount Duida, which are distinctly brighter, more rufous and tawny than those of Roraima and Auyán-Tepui, the correct name of which is *A. a. albigularis* Salvin and Godman, 1844, based on specimens from Roraima; not preoccupied by *albogularis* Spix, 1824, despite the belief of Hellmayr who proposed the substitute name *roraimae* for it in 1917.[143] Hellmayr has been followed uncritically by a number of authors, because *albigularis* Salvin and Godman and *albogularis* Spix [=*A. leucophthalmus*] were both proposed in the genus *Philydor* and both are currently placed in *Automolus*.[144] A third "subspecies" proposed by Phelps and Phelps (1947) from Mount Paraque is not valid in my opinion; its type, which I have seen, falls within the range of individual variation of *A. a. duidae*.

Two distinct forms exist in *Automolus rufipileatus*. The nominate form, which is based on specimens from Pará, inhabits Brazil south of the Amazon, and is paler, less ochraceous and brownish on the underparts than *A. r. consobrinus* which is based on specimens from Colombia and occupies the remainder of the range of the species. Nominate *rufipileatus* is also duller, more olivaceous on the mantle, less rufescent or cinnamon brown than *consobrinus*.

The geographical variation of *Automolus ruficollis*, *A. infuscatus*, and *A. leucophthalmus* is slight; some populations are somewhat brighter than others, but as all the differences are quite relative they are not significant to me. The question of recognizing "subspecies" becomes a matter of taxonomic judgment; I do not share the point of view of authors (such as Zimmer) to whom any perceptible difference is of "subspecific importance," no matter how trivial. For instance, the validity of a "new subspecies" of *A. erythrocephalus* described by Zimmer in 1936 requires confirmation as it is based on only four specimens from Palambla, Piura, Peru, which vary individually, but which, Zimmer said, "are not quite identical" with a few other specimens he had seen

from Paletillas, Piura, and neighboring southwestern Ecuador.

KEY TO THE SPECIES OF *AUTOMOLUS*

1. Breast and upper abdomen distinctly streaked ..... *ruficollis*
   Breast and abdomen not streaked 2
2. Underparts pale grayish olive, contrasting conspicuously with the color of the throat and sides of the neck, which is strongly ochraceous orange ..... *erythrocephalus*
   Underparts not pale grayish olive below the throat, the color of which may or may not contrast with that of the breast and abdomen 3
3. Throat and upper breast strongly ferruginous ..... *rubiginosus*
   Throat ochraceous buff, white, or whitish 4
4. Throat ochraceous buff, with the feathers of the upper breast (and sometimes sides of the throat also) more or less distinctly mottled ..... *ochrolaemus*
   Feathers of the upper breast and sides of the throat not mottled 5
5. Crown and nape strongly rufous (chestnut or rufous orange), contrasting with the color of the mantle 6
   Upperparts uniform in coloration 7
6. Crown chestnut; underparts relatively dark (tawny ochraceous with an olive cast); bill distinctly shorter, averaging about 25 mm. in length ..... *rufipileatus*
   Crown rufous orange; underparts relatively pale (ochraceous orange with a cinnamomeous cast); bill distinctly longer, averaging about 28 mm. in length ... *rectirostris*
7. Upperparts grayish olive brown .... *infuscatus*
   Upperparts rufous brown 8
8. With a distinct, well defined whitish superciliary and post-ocular streak 9
   Without a superciliary and post-ocular streak, or streak buffy, and so poorly defined it is scarcely distinct 10
9. Underparts very pale, white or nearly white on the throat and with a very pale cinereous wash on the breast ..... *dorsalis*
   Underparts quite dark, tawny olive beneath a pale throat which is pale buff in coloration ..... *albigularis*[145]
10. Underparts very pale; throat and upper breast creamy white, lower breast and abdomen pale creamy buff, and ochraceous tawny on the lower flanks, lower abdomen, "thighs," and under tail coverts .. *leucophthalmus*
    Underparts quite distinctly darker; throat ochraceous buff at the center, but ochraceous orange laterally, with washes of ochraceous tawny, pale raw umber, and pale gray on the remainder of the underparts, with the exception of the lower flanks, lower abdomen, "thighs," and under tail coverts which are dark cinnamon brown ..... *melanopezus*

Note that *Automolus ruficollis* (number 1 in key) is quite distinctly streaked with buff on the breast and upper abdomen, the ground coloration of which is grayish brown with an olive cast; whereas in *A. ochrolaemus* (number 4 in key), the feathers of the upper breast (and sometimes also those at the sides of the throat) are darker at their edge than at the center, to a varying degree. The result is a more or less distinct mottled pattern in *ochrolaemus*, as against a clearly defined streaked pattern in *ruficollis*.

LIST OF THE SPECIES

Automolus ruficollis

Figure 10

DESCRIPTION: Upperparts dark tawny ocher or hazel, with the crown (the feathers of which are somewhat elongated) darker, more raw umbraceous brown. A pronounced well-defined, superciliary streak extends from the base of the bill posteriorly to the nape, and is paler, yellowish or ochraceous buff in front of the eye, but is darker, chrome orange in the post-ocular region. The ear coverts are dark brown, with buffy shaft streaks, and the sides of the lower neck are dark ochraceous orange behind the ear coverts. This ochraceous orange area shows a vague tendency to extend posteriorly to the nape, and extends anteriorly to the base of the throat, the feathers of which have narrow dark brown edges, whereas the center of the throat is wholly clear, not spotted, and is ochraceous buff.

The underparts below the lower throat (where the dark edges of the feathers tend to form a jugular band) are pale grayish brown, with an olive cast, streaked distinctly with buff, the streaks becoming narrower and

vanishing gradually on the center of the abdomen. The flanks are darker, more tawny and olive, and the under tail coverts are strongly ferruginous or dark cinnamon rufous. The axillaries, under wing coverts, area at the outer edge of the inner webs of the remiges, and also carpal edge of the wing are very bright, chrome orange.

IMMATURE PLUMAGE: Similar to that of the adult, but duller throughout; less brown, more dusky on the crown; and with the feathers of the upper throat with narrow dark brown edges.

RANGE: Southern Ecuador and northern Peru, south to Lambayeque and Cajamarca, and the Marañon watershed in Amazonas.

SPECIMENS EXAMINED: 32, including the type of "*celicae*" in AMNH.

Automolus ochrolaemus

DESCRIPTION: Upperparts dark rufous brown (varying geographically from more rufescent brown to darker and duller brown), with narrow blackish edges to the feathers of the crown and nape which are somewhat elongated, the blackish edges being better defined in some populations than others, and causing the crown and nape to be darker than the mantle. The lores are partly buff, and a few, small buffy feathers at the base of the bill and in front of the eye create a poorly defined streak, which becomes a more distinct, but rather poorly defined buffy postocular streak. The ear coverts are dark brown with buffy streaks. The center of the throat is whitish, buff, or cinnamomeous, uniformly clear, but the feathers at the side of the throat, and at its base, have dark or dusky edges which produce a more or less distinct and regular mottled pattern. This character varies geographically, is better defined in some populations than others, and the mottling exists also to some degree on the upper breast, the feathers of which are dark also at the edge, but less dark than the feathers at the base and sides of the throat. The coloration of the underparts varies, below the upper breast, from ochraceous, dull grayish buff, tawny, or rufescent raw umber brown to olive brown, is much darker on the lower flanks, and the under tail coverts are ferruginous. The axillaries, under wing coverts, and pale area at the outer edge of the inner web of the remiges, vary geographically in coloration from rich and dark chrome orange to ochraceous buff. This species varies geographically; see general discussion.

IMMATURE PLUMAGE: The immature plumage is not very distinct from that of the adult, but is duller throughout, generally speaking; less patterned, and shows little or no contrast between the color of the mantle and crown, the feathers of the latter being distinctly elongated in the adult.

RANGE: Mexico, from the region of Orizaba and Córdoba, south through Veracruz and northern Oaxaca, to Tabasco, southern Campeche, and Chiapas, south through Central America, including British Honduras but not El Salvador, to Colombia (but not the Santa Marta Massif), east to Venezuela south of the Orinoco and the Guianas, and south through Ecuador, and central and eastern Peru, to Bolivia (in the Beni, La Paz, and Cochabamba), and Brazil, east to the region of Obidos, the Tapajós, and the basin of the Madeira.

SPECIMENS EXAMINED: 504, including the cotypes of "*cervinigularis*" (one in BM, the other in MNHN); the types of "*macconnelli*" in BM; and of "*auricularis,*" "*pallidigularis,*" and "*albidior,*" all three in AMNH.

Automolus infuscatus

DESCRIPTION: Upperparts varying geographically from dull grayish olive to raw umber and rufescent olive brown, somewhat darker on the crown (the feathers of which are slightly elongated), and rufescent on the rump in all the populations. Underparts pale and dingy, more or less white or whitish on the throat and upper breast, becoming increasingly "soiled" posteriorly with washes of pale gray, buffy gray, and ocher down to the under tail coverts, and on the flanks. The axillaries, under wing coverts, and the pale area at the outer edge of the inner web of the remiges varies geographically from chrome orange to ochraceous buff.

IMMATURE PLUMAGE: The immature plumage is very similar to that of the adult but darker and duller throughout, with the feathers of the crown less distinctly elongated than in the adult.

RANGE: Guianas, and Venezuela south of the Orinoco, west to Caquetá and eastern Nariño in southeastern Colombia, south through eastern Ecuador and eastern Peru to Cuzco, and through Brazil to the upper Madeira and tributaries of the upper Xingú in northern Mato Grosso, east to Amapá, eastern Pará, and northern Maranhão.

SPECIMENS EXAMINED: 239, including the types of *infuscatus* and of "*cervicalis*," both in BM; and of "*paraensis*" and "*badius*," both in AMNH.

Automolus dorsalis
Figure 10

DESCRIPTION: Crown and mantle uniformly reddish brown, with the feathers of the crown of normal length, not elongated. Lores dull white, with a few buffy small feathers at the base of the bill and in front of the eye, but which do not form a distinct streak; however, a distinct and well-defined buffy white streak extends posteriorly from the region above the eye to the nape. The ear coverts are raw umber, uniform or virtually so. The underparts are pale, white or whitish on the throat and upper breast, the latter being tinged faintly with pale sulphur yellow, and washed with pale gray olive at the sides of the breast and on the flanks, the olive gray tinge becoming progressively darker, more umbraceous, on the lower flanks and on the under tail coverts. The axillaries, under wing coverts, and the area on the outer edge of the inner web of the remiges is bright chrome orange.

IMMATURE PLUMAGE: Differs from that of the adult by being more rufous on the upperparts; and by being washed very distinctly with pale ocher on the underparts below the whitish throat, rather than with pale grayish olive (or pale sulphur yellow) in the adult.

RANGE: Southeastern Colombia, from Caquetá, south through eastern Ecuador and eastern Peru to Puno.

SPECIMENS EXAMINED: 23, including the type of *dorsalis* in BM.

Automolus leucophthalmus

DESCRIPTION: Crown and mantle warm pale rufous brown or dark rufous hazel, with the feathers of the crown slightly elongated and very faintly edged with darker, more dusky brown, showing also a few fine pale shaft streaks. Lores buffy white, with a few small ferruginous feathers at the base of the bill and in front of the eye, forming a vague streak, restricted to the region in front of the eye (lacking in the post-ocular region). Ear coverts dark rufous brown. Underparts very pale, with the throat and upper breast creamy white, whereas the lower breast, abdomen, flanks, and under tail coverts become progressively more tinged with cinnamon buff, ochraceous buff, and cinnamon rufous on the coverts. The rufous tail is also quite bright, more Light (or English) Red than reddish chestnut. The axillaries, under wing coverts, and pale area on the inner web of the remiges are also bright chrome orange, as in most species.

IMMATURE PLUMAGE: Similar to that of the adult but coloration of the crown and mantle more uniform with the feathers of the crown less elongated than in the adult; and with the sides of the breast and flanks more darkly washed with brown, the coloration of the underparts being generally less pale and pure than in the adult.

RANGE: Eastern Brazil from Paraíba south to Rio Grande do Sul, west to central Goiás, eastern Mato Grosso, eastern Paraguay, and Misiones in Argentina.

SPECIMENS EXAMINED: 75, including the two cotypes of *leucophthalmus* in AMNH, and the type of "*rufus*" in MNHN.

Automolus melanopezus

DESCRIPTION: Crown, mantle, and sides of the face uniformly dull rufous brown, with the feathers of the crown showing a tendency to be slightly elongated. No superciliary or

post-ocular streak exists, but the lores are pale, very dingy white. Throat pale ochraceous buff at the center, but dull orange at the sides. The pale ochraceous buff area of the center of the throat invades slightly the center of the upper breast, but at the sides of the latter, and below it, the underparts become progressively darker, more "earthy," tawny ochraceous with pale grayish washes, but strongly umbraceous brown on the flanks and under tail coverts. The axillaries, under wing coverts, the pale area at the outer edge of the inner web of the remiges, and also the carpal edge of the wing are rich, strong chrome orange.

IMMATURE PLUMAGE: Similar to that of the adult but underparts darker, and with the feathers of the crown, breast, and abdomen very narrowly tipped and marginated with gray-brown to a varying degree, producing a somewhat irregular barred pattern.

RANGE: Southeastern Colombia (Caquetá and eastern Nariño), and eastern Ecuador, east through northern Loreto in Peru, to the middle Rio Purús in Brazil.

SPECIMENS EXAMINED: 20, including the type of *melanopezus* in BM.

Automolus albigularis[146]

DESCRIPTION: Crown, mantle, and sides of the face uniformly dark rufescent brown, but somewhat darker, less rufescent, on the crown and face. The feathers of the crown are of normal length, not elongated, and a narrow, but quite distinct, white or whitish post-ocular streak exists. The throat is creamy white or very pale buff, and the underparts, below the throat, are uniformly dark, varying from dark hazel to dark ochraceous brown, and becoming darker on the lower flanks and under tail coverts. The axillaries, under wing coverts, and pale area at the outer edge of the inner web of the remiges is more bright tawny, or pale burnt sienna, than chrome orange. This species varies geographically; see general discussion.

IMMATURE PLUMAGE: Differs from the adult plumage by the color of the post-ocular streak which is ochraceous orange rather than white or whitish; by being much more rufous on the underparts; and by the fact that the feathers of the lower throat, breast, and upper and central parts of the abdomen are very narrowly tipped and marginated with dark gray brown.

RANGE: Venezuela, south of the Orinoco, including mountains on the border of Venezuela, Brazil, and Guyana, such as Roraima, Uei Tepui, and Cerro de la Neblina.

SPECIMENS EXAMINED: 36, including the two cotypes of *albigularis* in BM; the types of "*duidae*" in AMNH; and of "*paraquensis*" in the Phelps Collection, deposited in AMNH.

Automolus rubiginosus

DESCRIPTION: Crown (the feathers of which are somewhat elongated), and sides of the face, dark bay or liver brown, darker than the mantle which is dull dark rufous brown. No superciliary or post-ocular streak exists, but the lores are tawny, dull, but paler than the crown. Upper throat strongly ferruginous, somewhat paler than the center of the throat, the paler area grading into bright burnt sienna, which becomes darker and richer posteriorly as far as the border of the upper breast, and duller below that, more dull orange rufous, more ochraceous, darker tawny, and dull chestnut or somewhat olivaceous brown on the lower flanks which are quite dark; but is more ferruginous on the under tail coverts than on the abdomen and flanks. The axillaries, under wing coverts, and the pale area on the outer edge of the inner web of the remiges are dark chrome orange. The tail, and also the upper tail coverts, are dark, bay, rather than reddish chestnut.

This species varies strongly geographically (see discussion) and the description given above is based on specimens of nominate *A. r. rubiginosus* from Mexico, chiefly from Chiapas.

IMMATURE PLUMAGE: Differs from the adult plumage by having the feathers of the lower throat, breast, and upper abdomen very narrowly tipped and marginated with

dark gray-brown. In *A. r. saturatus,* the upper throat is dark buff, much paler than in the adult, the feathers have dark tips and margins, and the central part of some of the feathers of the breast is pale along the shaft, ochraceous orange, whereas these feathers are uniformly chestnut in the adult.

RANGE: Not continuous, consisting of Central America from southeastern San Luis Potosí and Guerrero in Mexico, south to northwestern Nicaragua and including northwestern El Salvador; Panama in western Chiriquí and also eastern Darién; Colombia, in the Santa Marta Massif, region of the Pacific, Andes north to northwestern Antioquia, and from the east slope of the Eastern Andes to western Apure in western Venezuela; also Venezuela south of the Orinoco to the mountains on the border of Venezuela and Brazil; Acari Mountains in southern Guyana; French Guiana; Ecuador to western Loreto and south to northern San Martín in northern Peru; also southern Peru in Puno, south to La Paz in Bolivia.

SPECIMENS EXAMINED: 103, including one cotype of *rubiginosus* in BM and the other in MNHN; the types of "*umbrinus,*" "*fumosus,*" "*guerrerensis,*" and "*verae-pacis*" in BM; of "*brunnescens*" in MNHN; and of "*saturatus,*" "*nigricauda,*" "*venezuelanus,*" "*cinnamomeigula,*" and "*moderatus*" in AMNH.

Automolus rufipileatus

DESCRIPTION: Crown (the feathers of which are slightly elongated) dull reddish chestnut, contrasting distinctly but moderately only, with the color of the mantle which is rufescent cinnamon brown. The lores are ochraceous tawny and a poorly defined postocular streak of the same color exists, but this streak and the tawny spot of the lores are not distinct. The underparts are ochraceous buff on the throat and ochraceous tawny below the throat, becoming darker, more russet on the lower flanks and under tail coverts. The axillaries, under wing coverts, and the pale area on the outer edge of the inner web of the remiges are dark chrome orange. This species varies geographically (see general discussion). The description given above is based on specimens of *A. r. consobrinus,* chiefly from Colombia and Venezuela.

IMMATURE PLUMAGE: Similar to that of the adult, but duller and darker on the upperparts, and with the feathers of the underparts narrowly edged with dark brown from the chin to the lower abdomen.

RANGE: Central Surinam and southern Guyana, westward through Venezuela (south of the Orinoco, and western Venezuela in Apure, Barinas, Mérida, and Táchira), and south through eastern Colombia, eastern Ecuador, and eastern Peru, to Cochabamba in Bolivia, and then east through Brazil (south of the Amazon), and north from the Beni in Bolivia, to eastern Pará and northern Maranhão.

SPECIMENS EXAMINED: 82, including the type of "*consobrinus*" in BM.

Automolus rectirostris

Figure 10

DESCRIPTION: Crown (the feathers of which show a tendency to be slightly elongated) Light (or English) Red, as well as the exposed surface of the upper wing, whereas the mantle and rump are cinnamon rufous. Lores tawny, with no superciliary or postocular streak. Throat pale cinnamon or pinkish buff, paler than the remainder of the underparts which are ochraceous buff, but become hazel on the lower flanks and ferruginous on the under tail coverts. The axillaries, under wing coverts, and the pale area on the outer edge of the inner web of the remiges (which is unusually extensive) are bright chrome orange.

RANGE: Campos of eastern and south central Brazil, from "Campos Geraes" (equals border of the States of Bahia and of Minas Gerais), to southern Goiás, southern Mato Grosso, Paraná, and western São Paulo.

SPECIMENS EXAMINED: 8, including the types of *rectirostris* in AMNH, and of "*rubidus*" in BM.

Automolus erythrocephalus
Figure 10

DESCRIPTION: Crown (the feathers of which show a tendency to be slightly elongated) Light (or English) Red, as well as the exposed surface of the upper wing, contrasting well with the color of the mantle which is pale grayish brown or grayish olive; the nape is Light Red also, as well as the upper border of the mantle. The sides of the face are rufous also, but slightly paler than the crown, the rufous pigmentation spreading to and merging with the rufous coloration of the throat and border of the upper breast, which is somewhat paler, brighter, and more ochraceous orange than the sides of the face. The underparts are dull pale grayish olive below the rufous throat with which they contrast well, becoming paler on the center of the abdomen, darker and browner, more umbraceous, on the lower flanks, whereas the "thighs" and under tail coverts are strongly ferruginous. The axillaries, under wing coverts, and the pale area on the outer edge of the inner web of the remiges are strong dark chrome orange. The bill of *A. erythrocephalus* is decidedly longer than that of the other species of *Automolus*.

IMMATURE PLUMAGE: Similar to that of the adult plumage but with the reddish feathers of the crown, and those of the entire underparts, more or less narrowly tipped and marginated with dark gray-brown.

RANGE: Restricted to southwestern Ecuador (El Oro and Loja), south to neighboring eastern Piura in northern Peru.

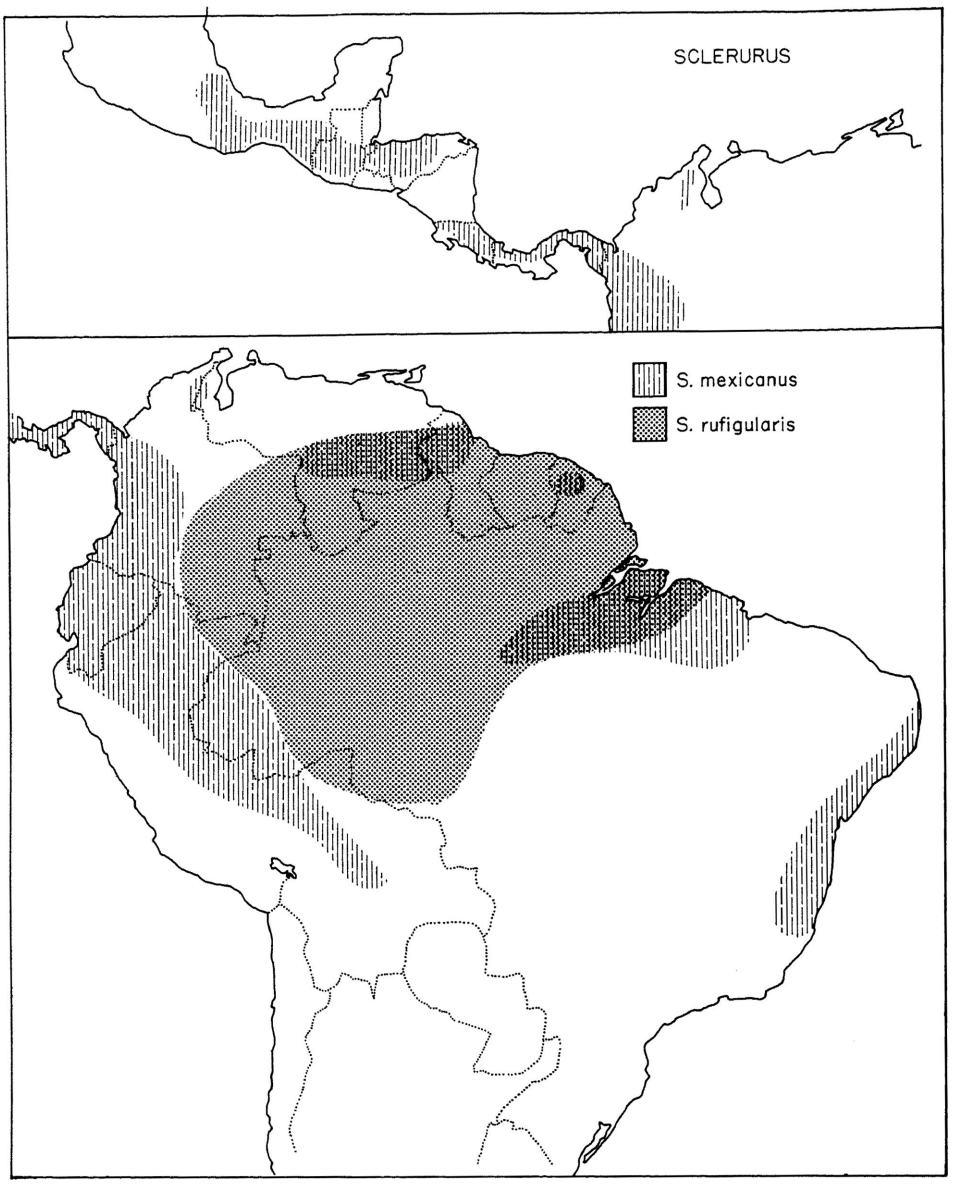
SPECIMENS EXAMINED: 11, including the types of *erythrocephalus,* and of "*palamblae,*" both in AMNH.

GENUS *SCLERURUS*

Sclerurus consists of six species that are extremely uniform: *S. mexicanus, S. rufigularis, S. albigularis, S. caudacutus, S. scansor,* and *S. guatemalensis.* They are uniform morphologically (except for the bill which varies markedly in length and slenderness), and their general behavior and ecology are also very similar. These birds are almost entirely terrestrial and live on the floor of the forest where they are relatively unencumbered, or in small paths in the denser and most shady parts of the forest, hopping about investigating litter and especially fallen and decaying leaves for food. In their search for insects or small animals leaves are tossed or flicked vigorously aside with strokes of the closed bill, unlike fowls that scratch or "scrape" with the feet. This suggests that the English name "leaftosser," as used by Skutch (1969b) is more appropriate than "leafscraper," commonly used for *Sclerurus*. The small storm of leaves briskly rained by *Sclerurus* is most often the first way in which this retiring and usually solitary bird reveals itself; as it is difficult to see in the deep shade, it easily escapes attention when not foraging.

Sclerurus is reported to rise to a low branch or fly to the base of a tree only occasionally where it clings briefly to the trunk sometimes fluttering its wing and then erratically dashing away. But *Sclerurus* apparently rises and flies to a branch or the trunk of a tree only when alarmed. It does not climb. Skutch described this aspect of the behavior of *S. guatemalensis* as follows: "I have never seen a leaftosser climb up a trunk or forage elsewhere than on the ground. It seems to cling to trees only when alarmed, and if it chooses a tree with brown bark, the bird blends with its background and is not easy to detect. Yet it is not evident that the leaftosser is safer in this position than it would be if it took refuge in a bush in the dim undergrowth of the forest."

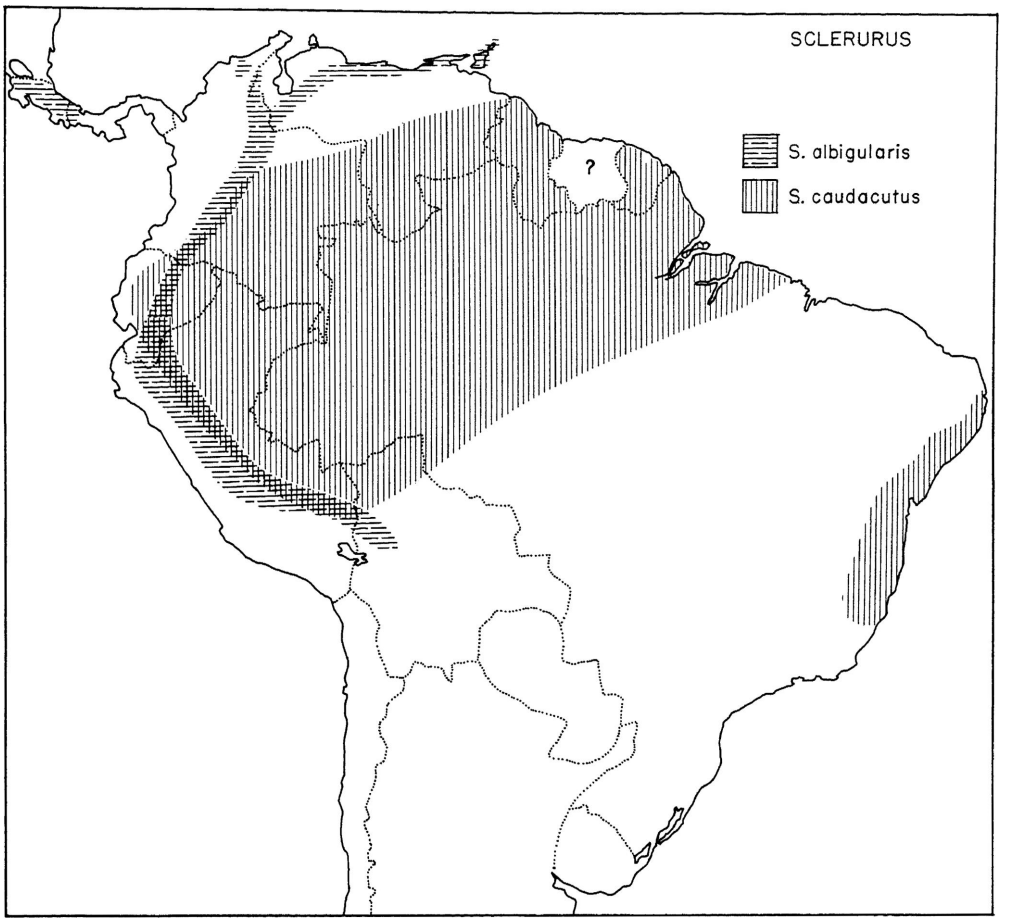
The shaft of the tail feathers is stiff and its tip is very sharp, and when pressed against hard bark would give support. The tip of the tail may also function when the bird is on the ground, for the stance adopted by *Sclerurus* is notably low and Slud (1964) said that "the tail, continuing the long axis of the body, touches the ground at its tip and seems to function as a prop." However, the adaptive function of the tip of the tail is not clear because Skutch and Slud agree that *Sclerurus* rarely clings to a tree, and it seems doubtful that the very sharp rachis can be a good



MAP 49. Geographical distribution of *Sclerurus mexicanus* and *Sclerurus rufigularis*.

"prop" against the soft, damp, often muddy floor of the humid forests frequented by *Sclerurus*. The webs of the feathers are actually quite soft—certainly not "stiff" or "harsh" as some authors state—only the shaft is stiffened and the rachis (or distal portion of the shaft) becomes very sharp and projects, needle-like, very slightly beyond the webs (or vane) of the feathers when they are worn.

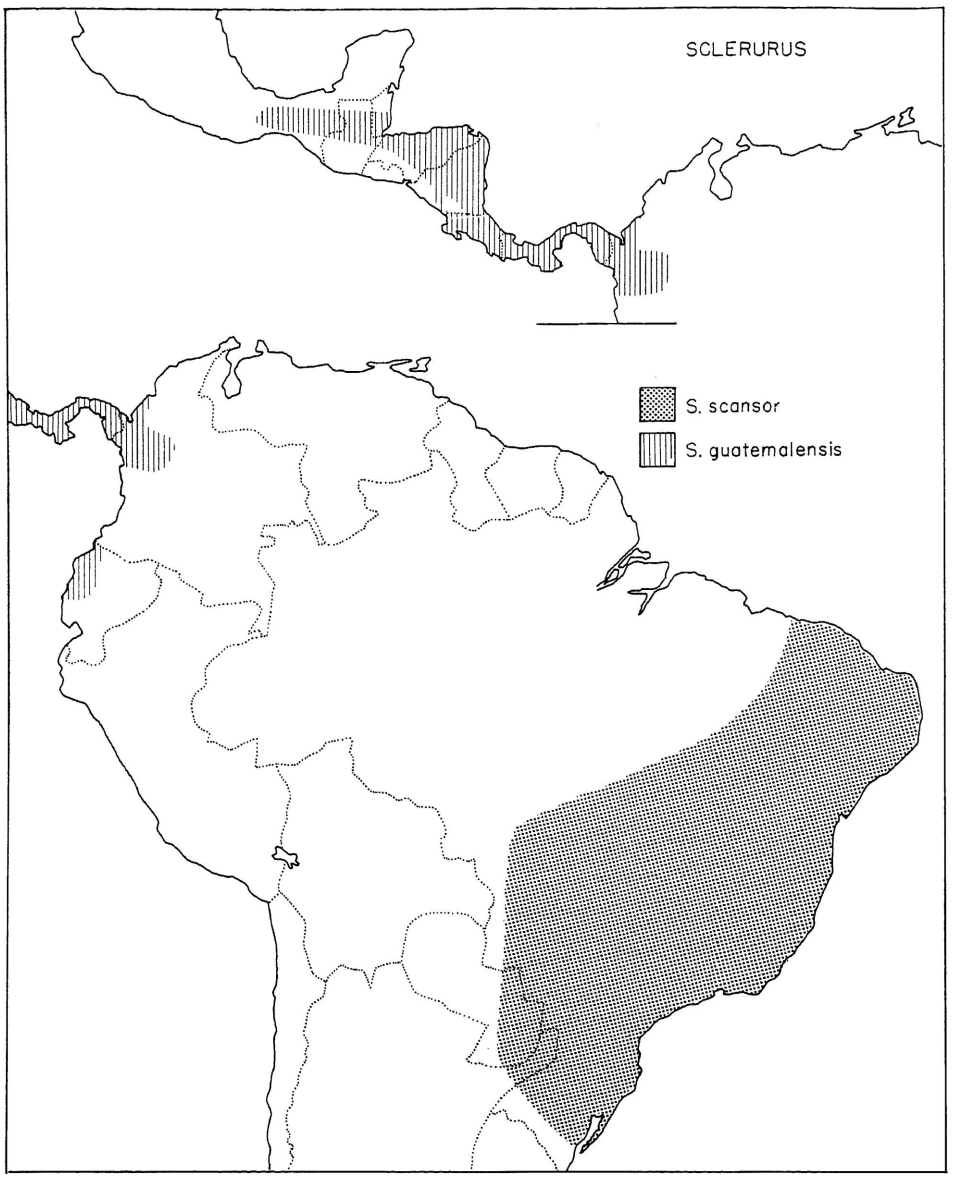
It seems important to dwell to some extent upon the structure and possible function of the tip of the tail because they have occasioned misconceptions, some of which seem to me to have been unfortunate from a sys-



MAP 50. Geographical distribution of *Sclerurus albigularis* and *Sclerurus caudacutus*.

tematic point of view. The least disturbing misconception was that *Sclerurus* is scansorial, as witness the scientific name, *scansor*, of one of its species. The most disturbing one has been that the structure of the tip of the tail led Sclater (1890) to provide a distinct subfamily (Sclerurinae) for the genus *Sclerurus* which, he believed, provided the link between the ovenbirds (Furnariidae) and the woodhewers (Dendrocolaptidae). According to Sclater, *Sclerurus* "combines . . . the spiny tail of the Dendrocolaptinae [which are strictly scansorial] . . . with . . . the longer tarsi and habits of a terrestrial bird." In other words, the Sclerurinae were intermediate between the ovenbirds and the woodhewers, according to Sclater, and the central point in his thesis was that these two groups are only distinct at the subfamily level—an opinion which has been revived by some authors but which I believe is incorrect.

Sclerurus is better represented in Central America and Mexico than any other genus of the Furnariidae, with three of its six species living there (maps 49 to 51). It inhabits preferably very humid forests, in Central America and western South America, but is not restricted to this habitat as it also occupies the coastal forests of eastern Brazil where humidity varies,[147] also savannas (such as *S. rufigularis* in Venezuela), and



MAP 51. Geographical distribution of *Sclerurus scansor* and *Sclerurus guatemalensis*.

even the arid "caatinga" of eastern Brazil, but no doubt only favored sites that are well wooded. Skutch described the habitats of *S. guatemalensis* as "the lowest and darkest levels of the heavy lowland forest" in Costa Rica. Slud, who stated that the habitats of *S. guatemalensis* and of the other two species of Costa Rica (*S. mexicanus* and *S. albigularis*) are "much alike," said that the birds "prefer relatively uncluttered portions of the damp and muddy floor in very humid forest, from which they occasionally enter contiguous tall second growth." *Sclerurus* is also said to be fond of water, following small

streams, also "splashing long and vigorously in the shallow water" of these streams or small pools.

The altitudinal range of *Sclerurus* species varies from sea level up to at least 2200 m. in Central America and also some regions of South America, where *S. mexicanus* and *S. albigularis* have been recorded at about the same altitude in Colombia and Venezuela as in Central America. According to Slud, *S. guatemalensis* does not ascend as high as *S. mexicanus* and *S. albigularis* in Costa Rica, although its range overlaps somewhat that of the other two species.

The breeding habits of five of the six species of *Sclerurus* are known and are very similar. The nest is located at the end of a burrow dug by the birds in a bank of firm earth or clay, or any similar firm earthy wall; banks along small streams or a path in the forest are favored. Skutch, who has studied *S. guatemalensis* extensively, said that the nests he found were at the end of deviating burrows which were from about 54 to 81 cm. in depth and had a roughly circular entrance measuring about 6.5 by 8.5 cm. The tunnel expanded at the end of the burrow to form a rounded chamber where the eggs were laid on a "thick mat," or in a "loose, shallow" nest, constructed "of the naked rachises of compound leaves from which the leaflets had become detached. As far as I could learn by removing a sample of the loosely matted material, the structure was composed wholly of these rachises." He also mentioned that "when the eggs were laid, this mat was at times so thin that the eggs touched the earth beneath them," but the bird continues to add material while incubating. Burt L. Monroe, Jr. wrote to me that he found *S. guatemalensis* nesting in a burrow that was about 1 m. deep, with an entrance of about 10 cm. in diameter, but remarked that although the burrow had been dug by a bird, he could not ascertain it had been done by *S. guatemalensis* itself.

The nest of *Sclerurus scansor* described by Goeldi was at the end of a deviating burrow dug in a steep bank of earth beside a forest path and the nest was also constructed of only the dry rachises of leaves, "flat and open . . . somewhat intricately woven [but not] . . . a masterpiece." The diameter of the burrow was 5 cm., and its depth, though not indicated, may have been about 50 cm., judging by the diagram of the burrow supplied by Goeldi in his account. Incidentally, *S. scansor* was called *umbretta* incorrectly by Goeldi in his account, as shown by Hellmayr (1925, p. 246). The nest of *S. albigularis*, described by Herklots (1961) from Trinidad, is similar in its location to the nests of *S. guatemalensis* and *S. scansor*, but its construction is even more rudimentary. In the case of *S. albigularis*, the deviating burrow varies from about 30.5 to 46 cm. in depth, and the incubating chamber is floored with only "a few mid ribs of leaves placed side by side." Skutch, commented that "apparently the leaves were all of one kind in any given nest, and they were loose and independent of each other rather than interwoven."

I have found no information on the nest of *Sclerurus rufigularis*, but it is probably similar to that of the other five species. This is suggested by the fact that the location and simple structure of the nest (more or less rudimentary) seem to vary little in *Sclerurus* when known.

Morphological Variation

The six species of *Sclerurus* are remarkably uniform structurally with the exception of the bill, which varies in length and slenderness. They are birds of moderate size or somewhat smaller, with a tail distinctly shorter than the wing, a relatively long and slender bill, and relatively short legs (for measurements, see table 23). In round numbers, the mean wing length varies from 80 to 93 mm., with an average of about 87.5 mm.; and the mean tail length from 56 to 67 mm., averaging about 60.5 mm. The ratio between the averages of the wing and tail lengths varies from 0.65 to 0.73, average 0.69.

The tail of *Sclerurus* is composed of 12 rectrices with soft webs that are well integrated and rounded at the tip. The webs are not stiffened in any way, but the shaft is strongly stiffened, becomes attenuated dis-

TABLE 23
Measurements (in Millimeters) of *Sclerurus*

	Wing			Tail			Bill		
Species	N	Mean	Range	N	Mean	Range	N	Mean	Range
mexicanus									
Males	43	81.69	75–88	41	56.19	50–66	40	26.56	24.5–31
Females	39	80.89	76–85	37	55.40	49–62	36	26.31	24–29
Both sexes	89	81.52	75–88	83	56.02	49–66	81	26.50	24–31
rufigularis									
Males	19	80.42	76–84	18	57.94	52–65	17	20.71	20–23
Females	17	78.82	75–82	17	56.35	50–61	16	20.25	19–21
Both sexes	37	79.70	75–84	36	57.08	50–65	34	20.50	19–23
albigularis									
Males	22	90.31	86–95	24	61.08	54–65	22	24.70	23–27.5
Females	20	91.05	83–96	17	60.47	56–64	19	24.94	24–26
Both sexes	52	90.34	83–96	51	61.05	54–67	51	24.78	22.5–27.5
caudacutus									
Males	37	93.56	90–99	36	64.61	58–70	37	24.50	23–27
Females	45	92.15	86–99	42	62.47	52–68	45	23.21	23–26
Both sexes	87	92.79	86–99	83	63.55	52–70	86	23.86	23–27
scansor									
Males	18	91.83	85–98	17	67.17	60–74	17	26.23	24.5–28
Females	22	90.86	88–93	21	66.23	62–73	22	26.73	25–28
Both sexes	46	91.73	85–99	44	67.04	60–74	44	26.53	24.5–28
guatemalensis									
Males	42	90.45	84–97	35	59.37	54–68	42	25.26	24–28
Females	27	89.11	85–92	24	57.79	54–66	24	25.20	24.5–26.5
Both sexes	76	89.94	84–97	66	58.74	53–68	73	25.30	24–28

tally and normally projects very slightly beyond the web of the feather, as a very sharp "needle," when the feather is worn. The tip of the tail thus feels "spiny" although this impression is actually produced only by the shaft. But the adaptive significance of this character, which would seem to have been developed to produce support, is not clear and was briefly discussed earlier.

The bill of all species of *Sclerurus* is slender and well compressed laterally, but it is more slender in some species than in others and becomes more or less slightly decurved at or near the tip. In mean length, in round numbers, it varies from 20.5 to 26.5 mm., with an average of 24.6 mm. In the three species that are sympatric in some regions of Central America, such as Costa Rica, there is interspecific variation in bill size and shape. The bill is longer, most slender and attenuated in *S. mexicanus*; shorter and relatively thick, especially at the base, in *S. albigularis*, and straighter than in *S. mexicanus*; whereas the bill of *S. guatemalensis* is about intermediate between those of *S. mexicanus* and *S. albigularis*. The first two species (*S. mexicanus* and *S. albigularis*), which have the most distinct bills, are very definitely sympatric, whereas *S. guatemalensis* largely replaces them at lower altitudes and probably does not compete ecologically with them to an appreciable extent. *Sclerurus* not only searches for insects beneath decaying leaves or other litter on the floor of the forest, but also probes the ground for insects or for any other animal matter. It

is quite possible, therefore, that *S. mexicanus* exploits somewhat different food sources than *S. albigularis* does, smaller insects, or insects not reached or seized by *S. albigularis* with its shorter, coarser bill.

The tarsus of *Sclerurus* species was not measured by me, but can be described as relatively short and not appreciably thick or "strong." This is true also of the toes and claws. They are "competent," but not unusually developed in any way. The feet of *S. caudacutus* and *S. guatemalensis* are somewhat bigger than those of the other species.

The coloration is nearly uniform within *Sclerurus,* although variation exists in the coloration of the throat, breast, rump, and upper tail coverts. The plumage is chiefly dark brown, somewhat duller on the upperparts, and with or without a rufous tinge. This rufous tinge may not exist on the back, and the rump and upper tail coverts are dark brown in two species (*S. caudacutus* and *S. guatemalensis*), whereas they are reddish chestnut in the other four, a little brighter or duller from one species to another. The tail is wholly black in all the species, or brownish black to some extent, as the outer webs of the rectrices are more brownish than blackish in *S. scansor,* especially nearer the base of the feathers, and *S. scansor* is also the species in which the back is browner, less dull. The underparts are brown also but with a strong rusty or dark rufous tinge on the breast, which may extend also over the abdomen (in *S. rufigularis*), or is present over the whole of the underparts, including the throat, in *S. mexicanus*. The throat is paler than the breast in all the species with the exception of *S. mexicanus*. In the other five species the ground coloration of the throat is white or whitish, but strongly tinged with pale rufous in *S. rufigularis*; with a broad grayish border surrounding the dull white center of the throat in *S. albigularis,* and with brown edges to the feathers in the remaining three species (*S. caudacutus, S. scansor,* and *S. guatemalensis*). These edges are darkest, most regular, and best developed in *S. guatemalensis,* giving to the throat a "scaly" appearance. These dark edges exist also on the feathers of the breast in *S. guatemalensis* in which only the center of the feather is rufous, with very fine pale shaft streaks, a few of which are also faintly indicated in an occasional specimen of *S. scansor.*

The coloration of the rump and upper tail coverts normally alternates in species the ranges of which overlap, and may serve for species recognition. Thus brown *Sclerurus caudacutus* is sympatric with reddish *S. mexicanus* and *S. scansor* in eastern Brazil, and elsewhere also with *S. mexicanus,* as well as with *S. rufigularis* and *S. albigularis* which have reddish rumps and coverts; the range of the brown *S. guatemalensis* overlaps that of the reddish *S. mexicanus* and *S. albigularis*. The only exceptions are in the case of *S. caudacutus* and *S. guatemalensis* in western Ecuador, which are brown; and between *S. mexicanus* and *S. albigularis* which are reddish, in Costa Rica and western Panama. However, in the case of the last two, the similarity in the coloration of the rump and coverts is compensated for by a conspicuous difference in the color of the throat (very strongly rufous in *S. mexicanus,* white with a gray border in *S. albigularis*). In western Ecuador, the overlap of *S. caudacutus* and *S. guatemalensis* appears to be slight and the birds may not come together, for the birds appear to be rare. The overlap, or contact, between the ranges of these two species is restricted to the region of Balzar, where both have been collected. Brosset (1964) stated that *S. guatemalensis* was rarely seen; he did not see *S. caudacutus*; indeed, to the best of my knowledge, only a single specimen of *S. caudacutus* has been collected in this region and the whole of western Ecuador.

Phylogeny

All the species of *Sclerurus* differ morphologically to about the same extent, except that *S. mexicanus* is somewhat better differentiated (wholly rufous underparts and long, most compressed and attenuated bill), and that the scaly pattern of the throat and breast of *S. guatemalensis* is the culmination of a character state which exists also in *S. cau-*

dacutus and *S. scansor*. I have therefore listed *S. mexicanus* at the start, and *S. guatemalensis* at the end of the sequence of the species, but the phylogeny is not clear. Nevertheless, the very extensive and widely interrupted distribution of *S. mexicanus* (map 49), together with the fact that it has penetrated farther north and is the most distinct species morphologically suggests that it is "older" and best listed apart at the head of the sequence. The phylogenetic significance of the coloration of the rump and upper tail coverts, if any, is difficult to assess. The alternate difference (dark brown versus reddish chestnut) in species the geographical distributions of which overlap has been briefly discussed in the previous section; such a difference may serve for species recognition.[148]

KEY TO THE SPECIES OF *SCLERURUS*

1. Rump and upper tail coverts dark brown .. 2
   Rump and upper tail coverts reddish chestnut 3
2. Feathers of throat and breast with distinct dark brown tips and margins, very regular on throat to which it gives a scaly appearance ..... *guatemalensis*
   Feathers of throat with faint, more or less irregular pale brown tips and margins, lacking on breast ..... *caudacutus*
3. Throat and breast reddish chestnut, virtually concolorous; bill very distinctly slender ... . *mexicanus*
   Throat very distinctly paler than breast, pale salmon or dull white; bill not markedly slender 4
4. Throat pale dull salmon ..... *rufigularis*
   Throat dull white 5
5. Center of throat dull white, the white area surrounded by a broad band of gray at the sides and base ..... *albigularis*
   Throat dull white, with ill-defined brownish tips and margins to the feathers; white area not surrounded by gray ..... *scansor*

LIST OF THE SPECIES

Sclerurus mexicanus

Figure 10

DESCRIPTION: Upperparts dark warm brown, somewhat darker on the crown and nape, less tinged with rufous, becoming progressively more rufous on the lower back and grading into reddish chestnut on the rump, the upper tail coverts are reddish chestnut but somewhat more "reddish" than the rump. Tail wholly dull black, with the exception of the edge of the outer webs of the rectrices which is dark sepia brown. Underparts reddish chestnut, somewhat paler on throat, especially the chin which sometimes is rufous tawny; and brown below the breast but strongly tinged with reddish chestnut or burnt sienna on abdomen and under tail coverts. Under wing coverts and axillaries are bright, orange rufous in coloration.

IMMATURE PLUMAGE: Duller than that of the adult on the upperparts, including the rump and upper tail coverts, much less rufous, more sooty brown on the underparts; much duller on throat and much darker brown below the breast, with the feathers of the lower throat, breast, and abdomen faintly, and more or less indistinctly edged and bordered with dull black.

RANGE: Broadly interrupted, consisting of Mexico from Puebla, region of Jalapa in Veracruz, and Oaxaca, south through Chiapas to Honduras; Costa Rica south through Panama, Colombia (in Andes and also Sierra de Perijá), Ecuador, and Peru, to Cochabamba in Bolivia; also Venezuela in Sierra de Perijá and region south of the Orinoco to Guyana; French Guiana; eastern Brazil, south of the Amazon, from Pará and Maranhão, west to the Tapajós; and also coastal forests from Alagoas south to Espirito Santo.

SPECIMENS EXAMINED: 112, including types of *mexicanus*, "*certus*," "*macconnelli*," "*peruvianus*," and "*bahiae*," in BM; and of "*andinus*" and "*obscurior*" in the AMNH.

Sclerurus rufigularis

DESCRIPTION: General coloration similar to that of *S. mexicanus* (*q.v.*) with the exception of the color of the throat. In *S. rufigularis*, the throat is pale ochraceous salmon, very much paler than that of *S. mexicanus* which has a reddish throat, and

the chin is almost "white," cinnamon buff. The rump and upper tail coverts are somewhat less bright chestnut, and the rufous coloration of the underparts is also duller in *S. rufigularis*.

IMMATURE PLUMAGE: Generally similar to that of immature *S. mexicanus*, but dusky edges of the feathers are less distinct and are apparently restricted to the throat, not present on the breast and abdomen. The rump and upper tail coverts are also more brown than rufous.

RANGE: Guianas, and Venezuela south of the Orinoco, west to the base of the Macarena Mountains in Colombia, south through eastern Loreto in Peru (not recorded so far from eastern Ecuador, to the best of my knowledge), and Brazil south to northern Beni in Bolivia, Rondônia in western Brazil, and region east of Pará in the east.

SPECIMENS EXAMINED: 47.

Sclerurus albigularis

DESCRIPTION: Upperparts dark warm brown, somewhat darker and more sepia on the crown, and with chestnut rump and upper tail coverts. Tail dark brown, becoming blackish distally. Underparts dull white on chin and center of throat, with the throat surrounded with a broad, diffuse band of mouse gray at the sides and base; breast dull reddish chestnut, the remainder of the underparts below the breast more or less brownish slate, but purer brown on the under tail coverts. Under wing coverts and axillaries bright, pale vinaceous gray.

IMMATURE PLUMAGE: Similar to that of the adult, but duller throughout.

RANGE: Discontinuous, consisting of Costa Rica to Chiriquí in western Panama; Trinidad and Tobago; coastal ranges and Andes of Venezuela, and Sierra de Perijá in Venezuela and Colombia, south through Colombia, Ecuador, and Peru to the Department of La Paz in Bolivia; also Santa Marta Massif of Colombia.

SPECIMENS EXAMINED: 43, including the types of *albigularis* in BM, and of "*zamorae*" in AMNH.

Sclerurus caudacutus

DESCRIPTION: Upperparts dark warm brown, including the rump and upper tail coverts. Underparts dark warm brown also with the exception of the throat which is white or dull white and the feathers of which are more or less darkly and regularly tipped and bordered with pale brown. The breast is also, or tends to be, more rufescent than the abdomen. Under wing coverts and axillaries pale rufescent brown.

IMMATURE PLUMAGE: Similar to that of the adult but much darker and duskier throughout; with the white area of the throat smaller, less distinct, more cloudy, with darker margins on the feathers, and with faint, very ill-defined dusky or blackish apical margins on the feathers of the breast and abdomen.

RANGE: Interrupted, consisting of French Guiana, Guyana, and Venezuela south of the Orinoco, west to the lower Eastern Andes of Colombia from Caquetá to Meta (also "Bogotá"), south through Ecuador, and eastern Peru, to northern Beni in Bolivia, and in Brazil to Rondônia, and Pará to the region east of Pará; also coastal forests from Alagoas south to Espirito Santo.

SPECIMENS EXAMINED: 151, including types of "*brunneus*" in BM, and of "*pallidus*," "*insignis*," "*lawrencei*," and two cotypes of "*fuscus*" in AMNH.

Sclerurus scansor

Figure 10

DESCRIPTION: Upperparts warm brown (brownish burnt sienna, warmer and paler brown than the other species), with bright reddish chestnut rump and upper tail coverts. Brown coloration of the underparts is generally similar to the coloration of the upperparts but slightly duller, and the throat is dull white and the breast chestnut. The feathers of the throat are tipped and bordered with brown as in *Sclerurus caudacutus*, but these dark margins are better defined and somewhat darker, as a rule, than in *S. caudacutus*. The tail is blackish or blackish brown with the exception of the mesial and central

portion of the outer web of the rectrices which is dark warm brown. Under wing coverts and axillaries pale rufescent brown.

IMMATURE PLUMAGE: Similar to that of the adult but darker, more dusky.

RANGE: Eastern and southern Brazil, from Ceará south to Rio Grande do Sul, west to Goiás and the Mato Grosso, eastern Paraguay, and Misiones in Argentina.

SPECIMENS EXAMINED: 51, including syntype in MNHN.

Sclerurus guatemalensis
Figure 10

DESCRIPTION: Upperparts dark dull brown, including rump and upper tail coverts. Underparts white or whitish on the throat, ferruginous on breast, and dark brown below the breast, but slightly paler and warmer brown than on the back. The white feathers of the throat tend to be acuminate and their tips and margins are very dark brown; these dark edges are regular and relatively broad and give a "scaly" appearance to the throat. These dark edges exist also on the feathers of the breast, but are paler brown than on the throat, and are broader, more diffused, and only the center of the feather is rufous, with very fine pale shaft streaks, a few of which occasionally exist also on the abdomen. Under wing coverts and axillaries are ferruginous with brown margins.

IMMATURE PLUMAGE: Similar to that of the adult, but generally darker, and with the white area of the throat more cloudy and less regularly squamated or scaly in appearance.

RANGE: Southern Mexico from southern Veracruz, Oaxaca, Chiapas, and Tabasco, south through Central America (in northern Guatemala, British Honduras to ?Quintana Roo, and Honduras, Nicaragua, Costa Rica, and Panama), to northwestern Colombia (east to the Sinú River and left bank of the Magdalena in middle Magdalena Valley, south to the Baudo Mountains in the Chocó); and also northwestern Ecuador south to Manabí and Balzar Mountains in northern Guayas.

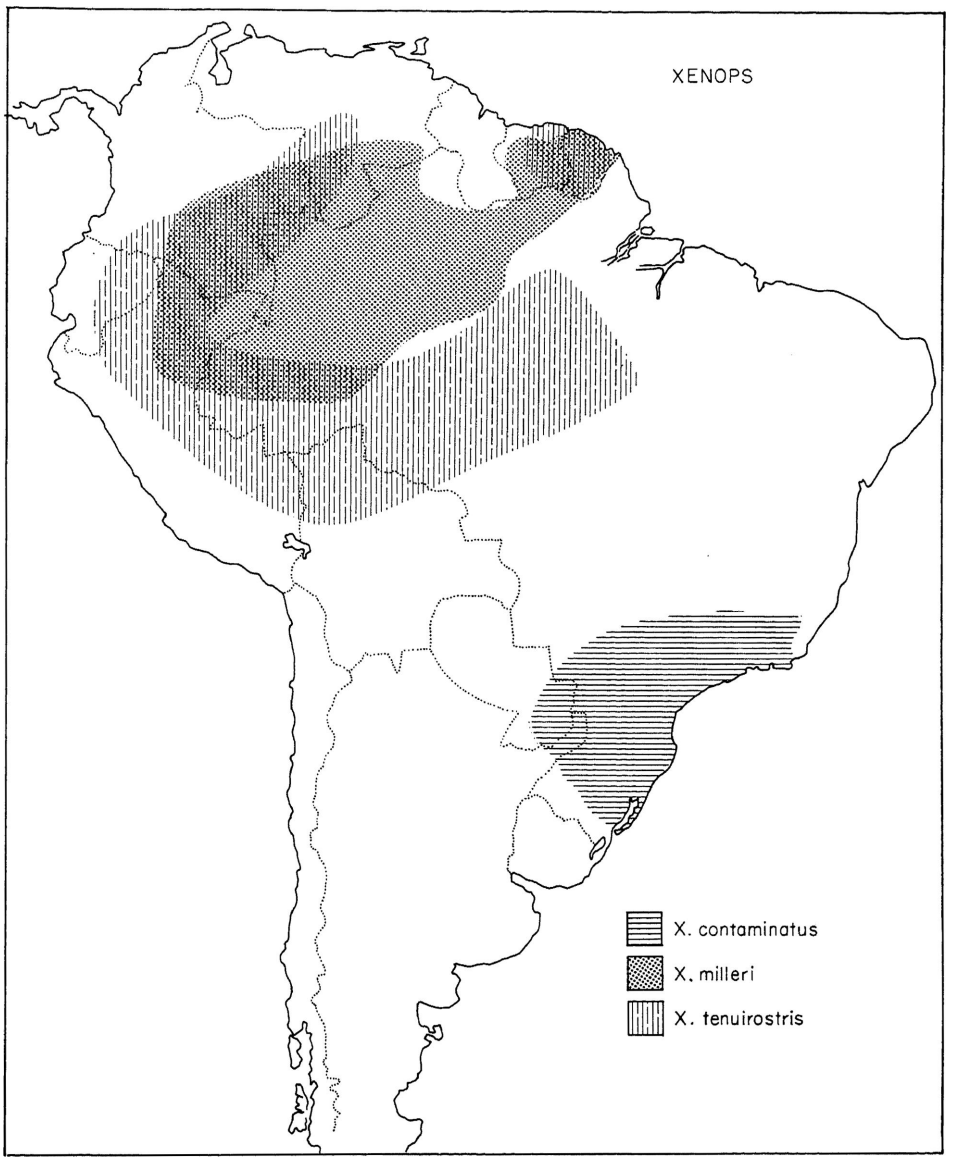
SPECIMENS EXAMINED: 84.

GENUS *XENOPS*

This small and distinctive genus consists of five species and is widely distributed, as a whole, in forests or woodlands from southern Mexico south to northern Argentina and Paraguay. The five species are *Xenops contaminatus, X. milleri, X. tenuirostris, X. minutus,* and *X. rutilans,* and the ranges of the first three (map 52), though extensive, are restricted when compared to the great ranges of *X. minutus* (map 53) and *X. rutilans* (map 54), which extend from South America north into Central America, to central Veracruz in the case of *X. minutus,* but only to Costa Rica for *X. rutilans.* The range of *X. minutus* does not cover "the entire length of tropical America," as stated by Skutch (1969b), as it is interrupted by a huge gap in Brazil, but Skutch expresses a common impression.

Xenops minutus and *X. rutilans* are very closely related to each other. They are also virtually identical in most respects, their distributions overlap a great deal and the two birds may be associated with one another. Slud (1964) reported that "both species may be found in the same mixed band" of small arboreal birds that hunt through the forest in Costa Rica and that no difference exists in their foraging behavior. However, *X. minutus* tends to be more common than *X. rutilans* and its altitudinal and ecological range is normally greater. Slud said that in Costa Rica *X. rutilans* is "restricted to tall humid forest and its borders," whereas *X. minutus,* though common in the same type of forest, inhabits also "maturing second growth [and] shows up regularly in partially shaded plantations, sometimes down to eye level, and it even strays into tree-scattered clearings." In Venezuela, the two species inhabit forest, as well as some regions of the llanos. Little or no information exists for the other three species, but all three are apparently birds of lowland forests or wooded hillsides.

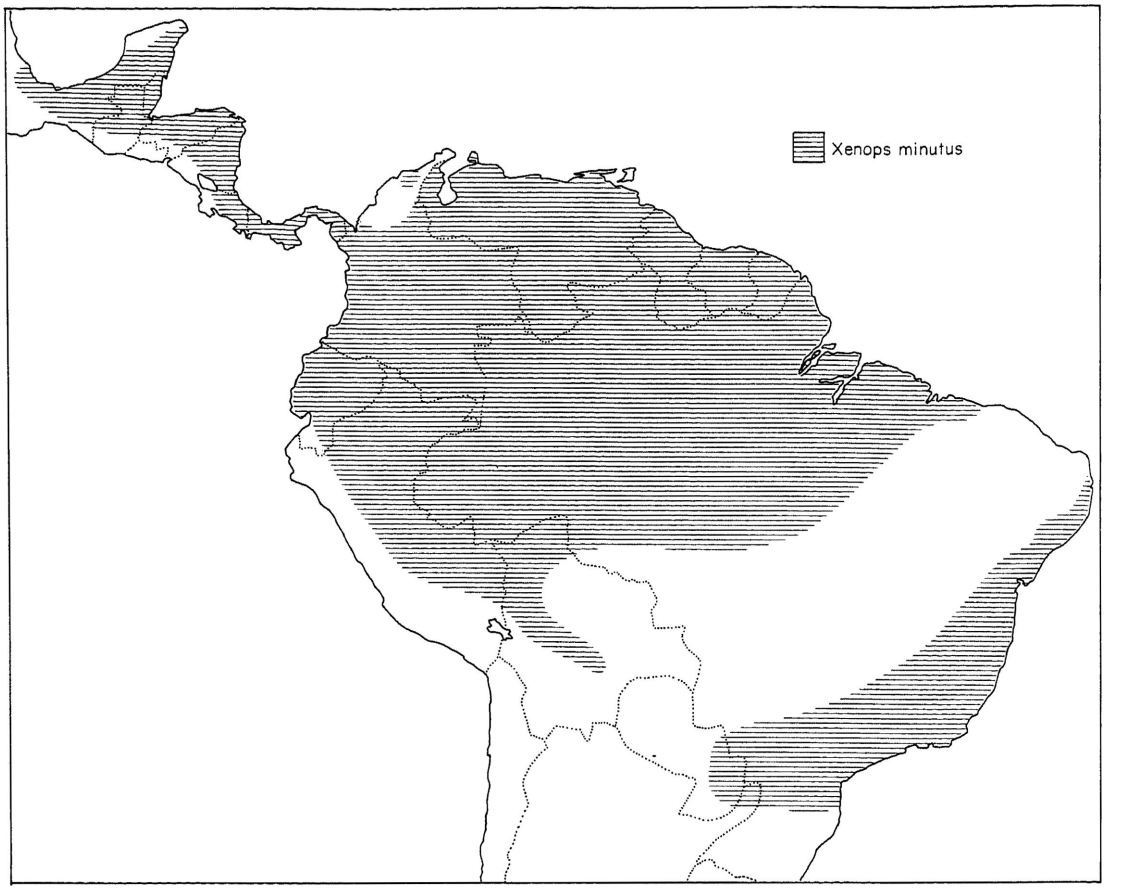
The altitudinal range of *Xenops* species seems to vary from sea level up to about 2750 m. with the probable exception of *X. milleri* and *X. tenuirostris,* which have been collected only at low elevations. In the case of



MAP 52. Geographical distribution of three closely related species of the genus *Xenops*.

X. contaminatus, the highest record known to me is about 1830 m. in the Serra do Caparão in Minas Gerais; this species ascends to about the same level in the Serra do Itatiaia, a level which corresponds to the upper limit of the forest on the slopes of the Itatiaia according to Pinto (1954). *Xenops minutus* and *X. rutilans* ascend to 2200 to 2300 m. in Venezuela, and the highest record I have found for any species of *Xenops* is 2743 m. in Colombia in the case of *X. rutilans*.

Xenops minutus is the only species of *Xenops* the behavior of which is well known. However, the behavior of *X. rutilans* seems

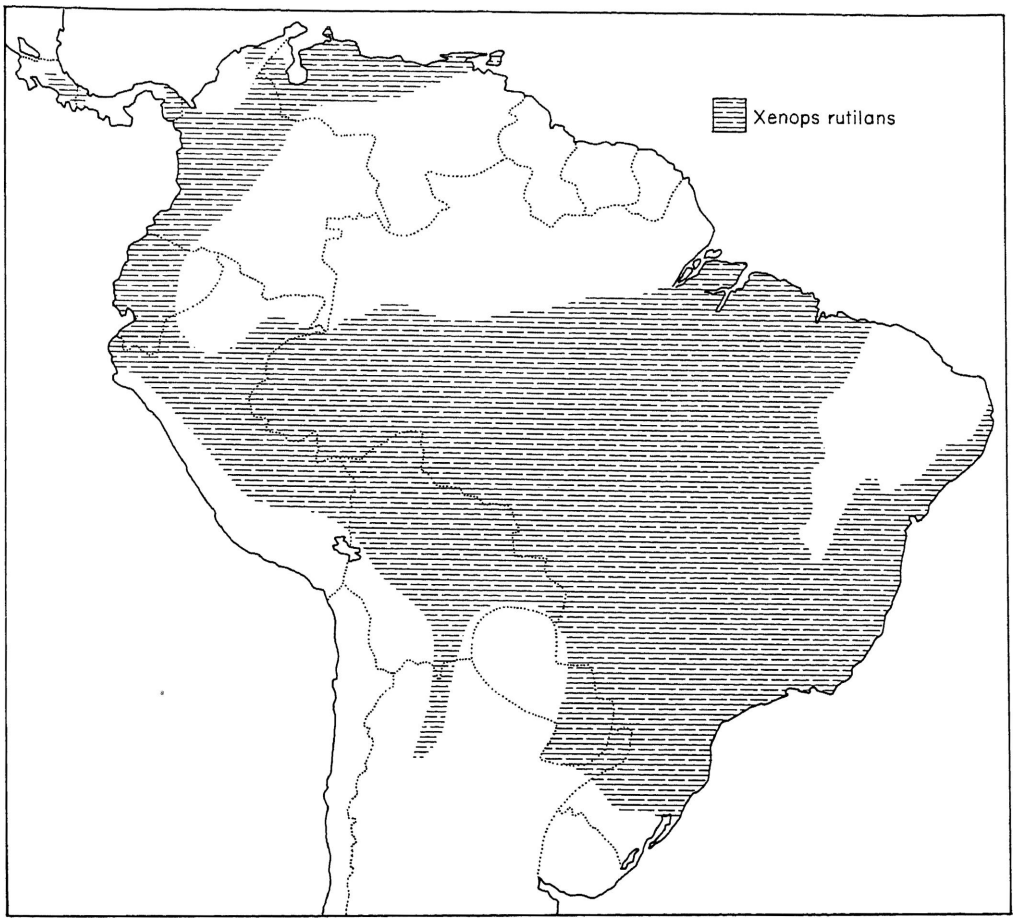


MAP 53. Geographical distribution of *Xenops minutus*.

to be similar to that of *X. minutus* in all respects, and the little that is known of *X. contaminatus* and *X. tenuirostris* agrees in the main with what is known for *X. minutus* and *X. rutilans*. No information seems to be available for *X. milleri* but it is probable that its general behavior does not differ significantly from that of the other species.

Xenops minutus is a curious and active little bird which forages among tangles of vines, in the crowns of the smaller trees, lower branches of the big trees, and also in shade trees on plantations or clearings, usually or often wandering in mixed hunting parties of small birds of other families which may include antwrens (Formicariidae), tanagers (Thraupidae), flycatchers (Tyrannidae), and other kinds. Slud (1964), who has observed *minutus* in Costa Rica, said "the bird explores branches and twigs along which it habitually moves sideways like a clinging tit, hangs from curled dry leaves like an antwren or greenlet [Vireonidae], and often, like a piculet [Picidae], loudly pecks woody branchlets and dead leaf clusters. In the forest it is apt to occur together with the little Wedge-billed Woodhewer, *Glyphorynchus spirurus,* which also pecks, but the latter is a relatively sedentary, stiff-tailed bird that creeps on trunks." The tail of *Xenops* is typically soft, not at all adapted to be used as a brace or prop in climbing.

Skutch (1969), who has also observed *Xenops minutus* in Costa Rica and published a



MAP 54. Geographical distribution of *Xenops rutilans*.

detailed account of its behavior, said that although *X. minutus* has been compared to some species of *Parus* [Paridae] and *Sitta* [Sittidae], the comparison to a nuthatch (*Sitta*) "is wide of the mark, for the nuthatch creeps over thick trunks and boughs, whereas the xenops hunts chiefly on slender dead branches and vines . . . [and] resembles [closely] its neighbor the Olivaceous Piculet [*Picumnus olivaceus*], smallest of the Central American woodpeckers—smaller even than itself. Like the piculet, the xenops climbs over slender twigs without using its tail as a prop in the manner of the larger woodpeckers and woodcreepers [Dendrocolaptidae]; like the tiny woodpecker, it hammers vigorously on decaying branches and extracts food from their pith . . . To complete the similarity, the xenops carves holes which resemble those of the piculet, and at times it nests in cavities made by the latter." The acrobatic foraging habits of *Xenops*, suspended *Parus*-like from the ends of twigs or small branches, has been reported also in *X. rutilans* and *X. tenuirostris*, and the vigorous pecking also in *X. rutilans* and *X. contaminatus*.

The nesting habits of only *Xenops minutus* and *X. rutilans* are known. These two species nest in a hole or within a natural cavity in a tree. When a hole is used, the hole may be dug by the bird or may be an old hole

adapted from some other species. In the case of *X. minutus,* Skutch (1969) said this species "nests in a neatly carved hole in soft, decaying wood. Four of the five nests that I have found were in slender, upright dead trunks, but the fifth was in an erect dead branch of a living burío (*Heliocarpus excelsior*), a rapidly growing tree with very soft wood. The sites of these nests were, respectively, at the woodland's edge, a short distance within primary forest, in tall second-growth woods, and in a clearing close beside the forest. The lowest nest was only 5 feet [about 1.5 m.] up in a decaying burío stump standing in a weedy, abandoned potato patch, 25 feet [about 7.6 m.] from heavy forest. Some months earlier, a family of [*Picumnus olivaceus*] had used this hole as a dormitory, and without much doubt these woodpeckers had carved it themselves, as I have watched them carve similar holes. The other nests were all considerably higher, from 15 to 30 feet up [about 4.5 to 9.1 m.]. Two of these were excavated by xenops as I watched, and possibly all four were the work of the occupants themselves." Skutch mentioned that Van Tyne reported a nest from Guatemala "12 feet [3.65 m.] up in a tree overhanging a dry stream bed in the heavy forest. It was 90 mm deep and had a doorway about 35 mm in diameter." The measurements of the five nesting holes were not mentioned by Skutch, other than stating "The nest cavity which had been carved by piculets and taken over by the xenops had a round doorway slightly less than an inch [25 mm.] in diameter."

The nest is lined with soft vegetable fibers. Skutch (1969) said that "after carving a hole or taking possession of one which has been abandoned by piculets, the xenops lines the bottom with soft, shredded bast fibers, such as one never finds in holes of woodpeckers, whatever size they may be. The burío, whose soft wood often provides a favorable nest site, likewise yields in its inner bark fibers suitable for lining the cavity. The xenops continue to increase their lining while they incubate, and at this time I have seen both members of the pair bring fibers as they come to take their turns on the eggs."

The only report on the nest of *Xenops rutilans* that I have found is from Trinidad and was published by Belcher and Smooker (1936). Two nests were found; one "was in a natural cavity of a tree at about 10 feet [about 3 m.], and was composed of a few leaf-stems and root-fibres"; the other "formed by a few root-fibres [was] placed in a hole in a dead stump at 8 feet [2.43 m.] above the ground."

Morphological Variation

The morphological variation is relatively slight in *Xenops*. All five species are small brown birds (measurements in table 24) with wing lengths the means of which vary, in round numbers, from 63 to 70 mm., with an average of 66 mm. The tail is distinctly shorter than the wing, its mean length varies from 35 to 55 mm., with an average of 46 mm., and the ratio between the lengths of the tail and wing varies from 0.55 to 0.78. The tail is composed of 12 rectrices that are very well integrated, rounded at the tip, and not stiffened with the exception of the basal portion of the shaft which is slightly stiffened, somewhat better so in *X. contaminatus* than in the other species. One specimen of *X. minutus* from a total of 574 examined has one additional pair of well-developed rectrices, or 14 rectrices in all.

Xenops climbs and clings acrobatically to its support in whatever position is most convenient, erect or inverted, but does not use its tail as a prop (see earlier). Its soft tail is not adapted structurally for this purpose, but as Mitchell (1957) has compared *X. contaminatus* to a dendrocolaptid, it is possible that this species derives some degree of support from its better stiffened tail, though I believe not from the tips of its rectrices which, though slightly acuminate, are soft.

The tail is also more graduated in some species than others, but the most evident structural variation which exists in *Xenops* is the variation in the shape of its bill, which I discussed in an earlier publication (Vaurie, 1971b), and illustrated by the profile of the bill in all five species. The bill of *X. contaminatus* is "normal" in shape, similar to that

TABLE 24
Measurements (in Millimeters) of *Xenops*

Species	Wing			Tail			Bill		
	N	Mean	Range	N	Mean	Range	N	Mean	Range
contaminatus									
Males	35	70.68	67–73	32	55.71	51–61	35	15.15	14–16
Females	16	68.25	65–73	16	53.43	50–56	16	15.07	14–16
Both sexes	58	69.82	65–73	55	54.90	50–61	58	15.13	14–16
milleri									
Males	10	64.20	60–70	9	36.00	34–40	10	14.15	13–15.5
Females	7	61.85	61–63	7	34.14	32–37	7	14.25	13.5–15
Both sexes	17	63.23	60–70	16	35.18	32–40	17	14.19	13–15.5
tenuirostris									
Males	10	64.10	60–66	9	42.00	37–48	10	13.44	13–15
Females	13	61.84	58–64	12	41.16	36–46	13	13.72	13–15
Both sexes	25	62.72	58–66	23	41.43	36–48	25	13.57	13–15
minutus[a]									
Males	188	65.68	55–71	175	49.74	42–56	181	14.64	12–16
Females	108	62.94	54–69	99	46.25	42–54	102	14.58	12–16
Both sexes	323	64.68	54–71	289	48.51	42–56	297	14.60	12–16
rutilans									
Males	87	69.33	63–75	84	49.13	44–55	86	14.08	13–15
Females	55	67.70	62.5–74	56	48.30	44–52	53	14.23	13–15
Both sexes	166	68.69	62.5–75	163	48.81	44–55	161	14.14	13–15

[a]The measurements of the population isolated in eastern Brazil, eastern Paraguay, and Misiones in Argentina are distinctly smaller than measurements given here for the species taken as a whole (see text).

of a large number of small insectivorous birds of different families, although, as noted by Sclater (1890), the gonys of its mandible ascends slightly, a tendency more pronounced in some individuals than others. Its culmen is slightly arched, not straight, and the bill of *X. contaminatus* is also less compressed laterally than it is in the other four species. In *X. rutilans,* on the other hand, the culmen is perfectly straight (rectilinear), the gonys ascends very strongly, and the bill is extremely compressed laterally. The bill of *X. rutilans* is shaped like a wedge and appears "up-turned." *Xenops minutus* and *X. tenuirostris* have bills of the same type, but less pronounced, especially *X. tenuirostris* in which it is distinctly less "up-turned," or wedge-shaped, than in *minutus* and *X. rutilans,* markedly slender and attenuated. The bill of *X. milleri* is more similar to the bill of *X. contaminatus,* but its gonys shows a definite tendency to ascend more strongly and is better compressed laterally. A complete and subtle graduation exists in the shape of the bill, from *X. contaminatus* to *X. rutilans,* where the climax of the variation is reached, via *milleri, tenuirostris,* and *minutus* in that order.

This modification of a bill of the "normal" type to one of the "*Xenops*-type" has no phylogenetic importance in my opinion (Vaurie, 1971b) as it exists in heterogeneous genera of the Furnariidae, as well as in other families, such as the Formicariidae. It is probably an instance of parallelism as suggested by Chapman (1928), an adaptation for extracting insect food from the soft stems of plants (such as *Heliconia*) or decayed twigs and small branches. Information on the feeding behavior of *X. minutus* and of *Clytoc-*

tantes alixii (a formicariid with a most pronounced "*Xenops*-type" of bill) was supplied to me by E. O. Willis who has observed it. With the sharp tips of their wedge-shaped bills the two birds slit the soft stems of *Heliconia* or other plants (*Clytoctantes*), or decayed twigs and small branches (*Xenops*), from which they apparently extract insects. After breaking into the stem or branch and inserting the bill, the birds then extend the opening by forcing it upward with the sharp ridge of the bill, used as a lever (or "can-opener"), according to Skutch who has observed also the feeding behavior of *X. minutus*.

The feet of *Xenops* are small or relatively small but do not seem weak and have large strong claws.

The coloration varies only slightly. The plumage is dull raw umber brown or rufescent brown on the upperparts, dull grayish brown on the underparts with a pale throat, and is well streaked or not, the streaking being much reduced in *Xenops minutus*. The crown is darker than the back, streaked in all five species and in all a well-developed whitish or buffy superciliary and post-ocular streak exists also. Three species (*X. tenuirostris, X. minutus,* and *X. rutilans*) are distinguished by a conspicuous pure white stripe of slightly elongated feathers below the dusky brown feathers of the auricular region lacking in *X. milleri* and *X. contaminatus*. In these three species with the white stripe, the tail is rufous cinnamon with extensive black areas, and the central portion of the remiges is crossed obliquely by a broad rufous, tawny, or warm ochraceous band which dwindles rapidly in width externally to vanish gradually on the inner web and its outer edge of the three or four outer primaries. In *X. milleri,* which lacks the white stripe, the entire basal half of the secondaries and inner primaries is rufous, but not in *X. contaminatus* in which the rufous band or rufous base of the feathers is lacking, replaced by conspicuous buffy edges along the outer edge of the inner web of the remiges. The tail of *X. milleri* and *X. contaminatus* is wholly rufous, more reddish and chestnut than in the other three species. It lacks the black areas which exist to a varying degree in the tail of *X. tenuirostris, X. minutus,* and *X. rutilans,* best developed in *X. minutus,* most reduced in *X. rutilans* but always lacking from the central pair of rectrices. It is curious to note that in *X. milleri* and *X. contaminatus,* which lack the black areas, the base of the shaft of one or two feathers is blackish in occasional specimens.

Phylogeny

The five species of *Xenops* were formerly divided among three genera, two of them monotypic: *Heliobletus* Reichenbach, 1853, for *X. contaminatus, Microxenops* Chapman, 1914, for *X. milleri,* and *Xenops* for the other three species. Behavioral information is lacking or not sufficient for some species, but as I have stated in my first revision (1971a), all five species appear to be congeneric—from a morphological point of view at any rate. Peters (1951) had already decided that the recognition of *Microxenops* was not warranted. I merged *Heliobletus* with *Xenops* in 1971.

The sequence of species that I have adopted is based chiefly on the progressive modification of the bill (see section on morphological variation), but it seems clear that *Xenops tenuirostris, X. minutus,* and *X. rutilans* are closely related as suggested by their color pattern (white stripe on the face, banded wing, and black areas in the tail); the "*Xenops*-type" of bill is also best developed in these three species. The degree of relationship is uncertain in the case of *X. contaminatus* and *X. milleri,* but *X. milleri* seems to occupy a position roughly intermediate between *X. contaminatus* and the other species, combining some of their characters.[149]

KEY TO THE SPECIES OF *XENOPS*

1. Tail wholly rufous 2
   Tail not wholly rufous 3
2. Basal half of the secondaries and inner primaries rufous ..... *milleri*
   Secondaries and primaries not rufous ..... *contaminatus*
3. Abdomen not streaked; and with only faint and vague buffy white streaks on upper breast ..... *minutus*

Abdomen and breast conspicuously streaked 4

4. Bill of "*Xenops*-type" but markedly slender and attenuated; tail with more extensive black areas as a rule..... *tenuirostris*
Bill very much stronger, of very pronounced "*Xenops*-type"; black areas in the tail more reduced as a rule..... *rutilans*

Note that *Xenops tenuirostris* and *X. rutilans* (number 4 in key) resemble each other superficially, but the difference in the shape of their bill is very conspicuous. Furthermore in *X. tenuirostris* the third and fourth rectrices (from the outside) are almost wholly black, and the base of the inner web of the second, and sometimes even of the outermost rectrix, is black or blackish to a restricted extent. The under tail coverts of *X. tenuirostris* are chiefly grayish olive, less distinctly rufous than those of *X. rutilans*, and the buffy markings on the mantle are much better developed as a rule in *X. tenuirostris*. In *X. rutilans* the base of the outer rectrix is usually rufous, rarely dusky, the base of the second is dusky or blackish as a rule, and the black areas on the third and fourth are normally more restricted.

List of Species

Xenops contaminatus
Figure 7

DESCRIPTION: Upperparts dull pale raw umber brown with darker, more dusky crown, the darker appearance of the crown being caused by the margins of the feathers which are dusky or blackish; the crown and mantle are also conspicuously streaked with buff, but the streaks are sharper, better defined on the mantle, whereas the buffy area is diffused on the crown away from the pale shaft of the feather. Lores grayish; a narrow buffy, or dull pale yellow streak exists over the eye which is prolonged far back behind the eye as a broad and conspicuous streak reaching the nape. Throat pale and clear, chiefly dull pale yellow (Naples Yellow), but more ochraceous at the sides. The pale yellowish area of the throat invades the center of the breast irregularly, becomes more diffused below the upper breast and at the sides of the upper breast, and forms conspicuous streaks on a dull grayish brown ground, but on the under tail coverts the streaks are dull orange, rather than yellowish. The axillaries, under wing coverts, and the outer edge of the inner web of the remiges are bright and vary from buffy yellow or ochraceous buff to cinnamomeous buff. Tail wholly and uniformly chestnut, slightly stiffened, with the tips of the rectrices slightly acuminate but soft; the webs of the rectrices are well and firmly integrated. Bill with culmen slightly arched, moderately compressed laterally, and with the gonys ascending slightly or not.

IMMATURE PLUMAGE: Similar to that of the adult, but pattern less distinct, and with the streaks (including superciliary and postocular streak) of the entire plumage more ochraceous, less buffy or pale yellow than in the adult.

RANGE: Southeastern Brazil from Serra do Caparão (collected in Minas Gerais but probably occurs in neighboring Espirito Santo), south to Rio Grande do Sul, eastern Paraguay, and Misiones in Argentina.

SPECIMENS EXAMINED: 118.

Xenops milleri
Figure 7

DESCRIPTION: Upperparts raw umber brown, darker and more dusky on the crown, chestnut on the rump and upper tail coverts. The crown and mantle are heavily and conspicuously streaked with pale cinnamon, buff, or buffy white; but not the lower back, which is not streaked, and becomes gradually rufous. Lores grayish, a well-defined pale buff streak extends from the lores, or region above the eye, posteriorly to the nape. Underparts rather dingy and patterned; the throat is dingy white with small pale brown streaks, and the remainder of the underparts dingy buffy white, more ochraceous on the lower abdomen, not very sharply patterned with streaks of dull pale gray-brown that are most distinct and best defined on the breast, but become very diffused below the breast.

The axillaries, under wing coverts, and a

very extensive area at the base of the remiges are strongly but brightly rufous (chiefly bright and reddish pale burnt sienna). This rufous area extends over most of the surface of the inner secondaries, and then forms an oblique band across the wing which dwindles rapidly in width and becomes restricted to the inner web of the three or four outer primaries, and eventually only to their outer edge. Tail uniformly chestnut as in *X. contaminatus,* very slightly graduated only, and composed of firmly integrated rectrices that are soft, not stiffened (except slightly so at the base), and are very blunt and rounded at the tip. Bill similar in general shape to that of *X. contaminatus,* but with the culmen slightly straighter, slightly better compressed laterally, and with the gonys slightly, but definitely ascending more than in *X. contaminatus* as a rule.

IMMATURE PLUMAGE[150]:

RANGE: French Guiana and Surinam (but not recorded from Guyana), westward through Venezuela south of the Orinoco (southern Bolívar and Amazonas), to the Sierra de la Macarena in Colombia, Loreto in Peru, and south through Brazil to the upper Purús and Madeira rivers, basin of the Rio Negro, and east on the north bank of the Amazon to the mouth of the Jamunda River.

SPECIMENS EXAMINED: 18, including the type of *milleri* in AMNH.

Xenops tenuirostris
Figure 7

DESCRIPTION: Upperparts dusky on the crown, raw umber brown on upper mantle, grading into rufescent brown on center of the back, and bright chestnut on the rump and upper tail coverts. The crown and mantle are streaked, the streaks are narrow and whitish on the crown, but are buffy and become much broader on the mantle and tend to form spots, rather than streaks, that are more or less lanceolate in shape. A distinct, but relatively narrow and short whitish or buffy superciliary and post-ocular streak exists, and also a very conspicuous and broad stripe of pure white, slightly elongated feathers, below the cheek which is dusky or dark raw umber brown, more or less distinctly and narrowly streaked with dull white or buff. The chin and upper throat are whitish but this pale area is rather restricted in size and not pure white as the tips and margins of its feathers are grayish. The remainder of the underparts is dull grayish brown (somewhat more ochraceous or olivaceous on the under tail coverts), and is well and distinctly streaked with dull white.

The coloration of the axillaries, under wing coverts, and wing is similar to that of *X. milleri* (*q. v.*), but with the exception that the base of the inner remiges which is rufous in *X. milleri,* is black in *X. tenuirostris,* thus narrowing the rufous area to a true band on these feathers. The tips of the secondaries are also more extensively and brightly rufous in *X. tenuirostris.*

The structure of the tail is similar to that of *X. milleri* (*q.v.*), but not its coloration which is a strong reddish cinnamon, with bold black areas in *X. tenuirostris* (and also to a varying degree in *X. minutus* and *X. rutilans*). The individual variation in the pattern of the tail is strong in these three species, but the central pair of rectrices is always reddish cinnamon, without any black. In the other rectrices (counted from the outside), the first, in the case of *X. tenuirostris,* may, or may not, have a small black or blackish wedge at the base of its inner web. The second had a black wedge at the base of its inner web in all the specimens examined, and this wedge is bigger than the wedge on the outer (first) rectrix when present. The third and fourth rectrices are almost entirely black on both webs, and, on the fifth, the black area is restricted to the outer web to a highly variable extent. The bill is of the "*Xenops*-type" (culmen rectilinear and gonys ascending) but is markedly slender and attenuated.

IMMATURE PLUMAGE[151]:

RANGE: French Guiana and Surinam, and from northwestern Bolívar and Amazonas in Venezuela, west through Colombia to the base of the Andes in Caquetá, and south through eastern Ecuador and eastern Peru to the Beni in Bolivia, and Brazil on the upper Purús and Madeira rivers, in Rondônia, on

the lower Tapajós, and to the Rio Fresco, an affluent of the Rio Xingú; also probably northern Amapá and upper Rio Negro and Rio Vaupés.

SPECIMENS EXAMINED: 27, including the type of "*acutirostris*" in AMNH.

Xenops minutus
Figure 7

DESCRIPTION: Crown sepia with very narrow indistinct pale shaft streaks, mantle chiefly cinnamon brown, or raw umber, more russet in some populations, not streaked, and grading into cinnamon rufous on the rump and upper tail coverts. Lores vary from dark brown to dull white. Facial pattern similar to that of *X. tenuirostris* (*q.v.*, with whitish or buffy superciliary and post-ocular streak better developed in some populations than others, and with conspicuous stripe of pure white below the brown cheek). Throat white, or whitish (indistinctly spotted with grayish brown in some populations), and remainder of the underparts dull grayish brown, more or less faintly and indistinctly streaked with dull pale buff on the upper breast.

Coloration of the axillaries, under wing coverts, and wing similar to that of *X. tenuirostris* (*q.v.*); also the coloration of the tail but patterned more heavily with black. In *X. minutus*, the first or outer rectrix has normally a very distinct black or blackish wedge at the base of its inner web; the second is about half black on the inner web and has a smaller black wedge on the outer web; the greater part of the third is black on both webs; and the fourth and fifth are entirely black. The tail is somewhat better graduated than in *X. tenuirostris*, and the bill of *X. minutus* is much stronger than that of *X. tenuirostris*, of a strongly developed "*Xenops*-type."

IMMATURE PLUMAGE: Similar to that of the adult, but general pattern less distinct, and pale area of the throat less pure, more cloudy with gray brown.

RANGE: Mexico from south-central Veracruz, south through Central America, to the greater part of South America (east of the Andes in Peru and Bolivia, and including the Santa Marta Massif in Colombia), south to southeastern Cochabamba in Bolivia; then, after being interrupted by a huge gap in distribution (map 53), extends from Paraíba in northeastern Brazil, south to eastern Paraguay, northern Misiones in Argentina, and the Uruguay River forming the border between Santa Catarina and Rio Grande do Sul in Brazil. The southern limit of the range, north of the gap, is not sufficiently well known but probably follows the southern limit of the humid Amazonian forest, including some gallery forest such as on the lower Rio Paraíba forming the border between Maranhão and Piauhí. The northern limit, south of the gap, seems to extend more or less to the western limit of the eastern tropical forests. In Mexico, the range on the Yucatán Peninsula includes Campeche and Quintana Roo.

SPECIMENS EXAMINED: 574, including the types of "*mexicanus*," "*cayoensis*," and cotypes of "*littoralis*" in BM; of "*remoratus*" and "*ridgwayi*" in AMNH, and of "*olivaceus*" in Pons collection, deposited in AMNH.

Xenops rutilans
Figure 7

DESCRIPTION: Crown dark warm sepia with narrow but distinct pale brownish buff streaks which become broader and more cinnamon on the nape; mantle rufescent brown streaked with a few ill-defined buffy or cinnamomeous streaks on its upper portion, rump and upper tail coverts burnt sienna or dark cinnamon rufous. Lores brownish and facial pattern similar to that of *X. tenuirostris* (*q.v.*) and *X. minutus*, with conspicuous pure white stripe below the brown cheek. Chin and throat dull white, and remainder of the underparts very well and conspicuously streaked with dull white on a grayish brown ground, which, however, is more ochraceous and tawny on the under tail coverts; the streaks are broadest on the breast.

Coloration of the axillaries, under wing coverts, and wing similar to that of *X. tenuirostris* (*q.v.*) and *X. minutus*; also the col-

oration of the tail, but patterned less heavily with black than that of *X. tenuirostris* (*q.v.*) and especially *X. minutus* (*q.v.*). In *X. rutilans,* the first rectrix is usually entirely rufous, rarely dusky at its base; the base of the inner web of the second is normally dusky, but the dark area is restricted and dusky or blackish but not true black; the inner web of the third rectrix is mostly black in about two-thirds of the specimens, but the black area is much reduced in the other third; the inner web of the fourth rectrix is almost entirely black, and, sometimes, a black, but smaller area exists also on the outer web; the fifth rectrix is often entirely rufous, or has a narrow, usually quite restricted, blackish or dusky shadow on the outer or inner web. The bill is of the "*Xenops*-type," very strongly developed.

IMMATURE PLUMAGE: Very similar to that of the adult, but general pattern less distinct; black areas in the tail more dusky, less deep black, and pale area of the throat more cloudy and more restricted.

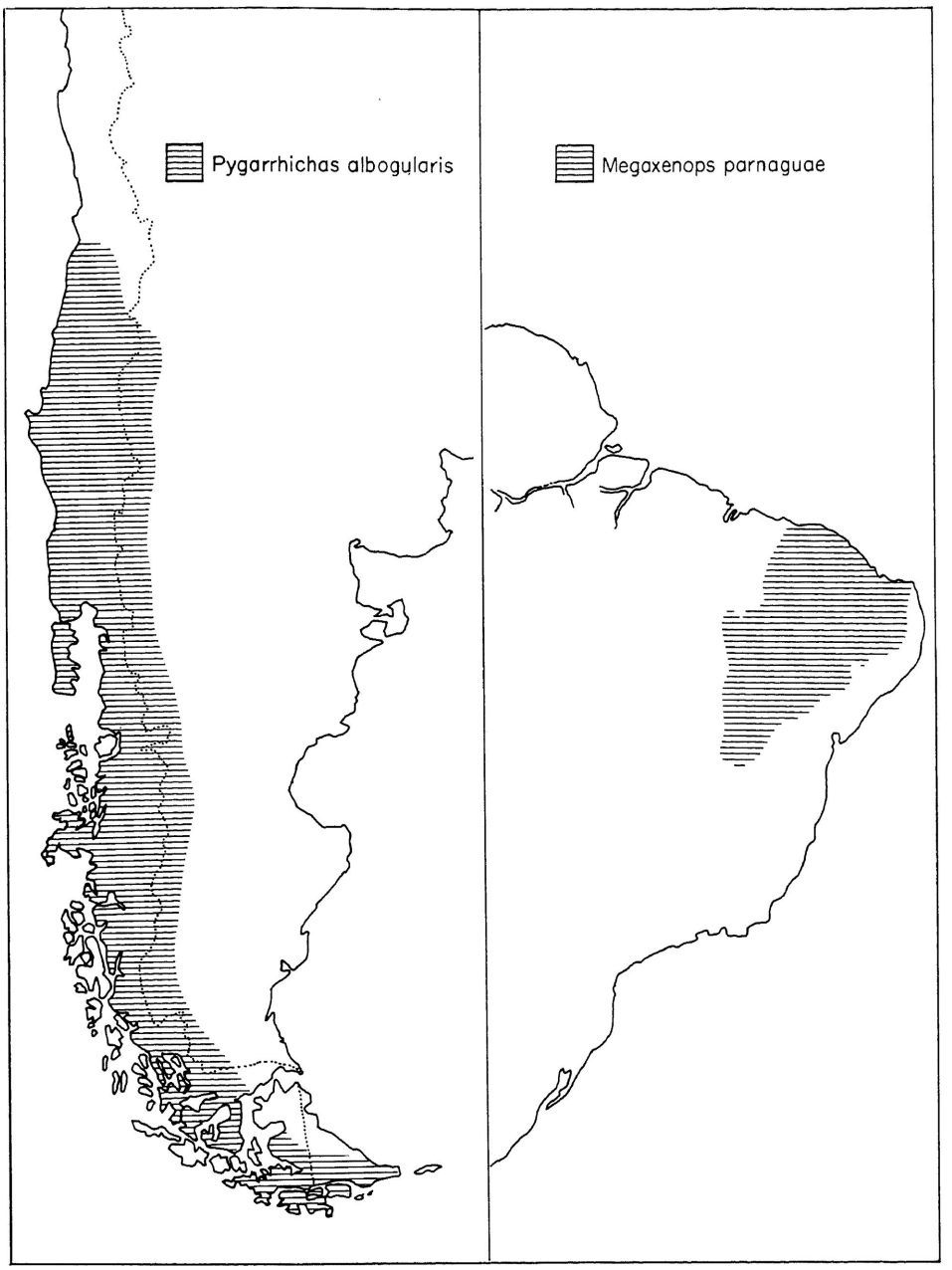
RANGE: Costa Rica and western Chiriquí in western Panama,[152] and from eastern Darién in eastern Panama, south to northern Argentina, Paraguay, and southeastern Brazil. In South America the range extends from Colombia in the Santa Marta Massif, and the Sierra de Perijá on the border of Colombia and Venezuela, east through the Andes and mountains of northern Venezuela to Sucre, and also the island of Trinidad, including also the llanos of northern Portuguesa and northern Guarico in Venezuela; western half of Colombia; Ecuador; Peru and Bolivia east of the Andes (with the exception of Piura in extreme northern Peru); Salta, Jujuy, and Tucumán in northwestern Argentina; Brazil south of the Amazon to Rio Grande do Sul; eastern Paraguay; Misiones in Argentina. In Brazil, this species is lacking also from the arid northeast, and the northernmost record seems to be from Mamanguape in coastal Paraíba.

SPECIMENS EXAMINED: 282, including the types of "*chapadensis,*" "*connectens,*" and "*peruvianus*" in AMNH, and of "*perijanus*" in the Phelps Collection deposited in AMNH.

GENUS *MEGAXENOPS*

Megaxenops is monotypic and *M. parnaguae* is a curious bird without near relatives although it has always been assumed that *Megaxenops* and *Xenops* are very closely related. For instance, in 1925, Hellmayr stated that "*Megaxenops* . . . [is] nearly allied to *Xenops,* but of gigantic proportions, with much more powerful bill and stronger feet"; and, in 1929, referred again to *M. parnaguae* by characterizing it as a "gigantic Xenops of peculiar coloration." However, the belief that *Megaxenops* and *Xenops* are closely related is based entirely on the shape of the bill. In fact, *Megaxenops parnaguae* shows no other morphological resemblance to *Xenops,* and differs much from it ecologically and very probably in behavior also.

Megaxenops parnaguae is known from fewer than two dozen specimens. The first two were collected by O. Reiser on June 3, 1903, in southern Piauí when he apparently encountered a flock in the caatinga near a small pool of cool water at the base of a Buriti Palm, the only water in the region. Reiser could conserve only two specimens from a number that he shot and it is unfortunate that he gives no information on the number of birds seen, associated or not. The next specimen was collected by Dr. H. E. Snethlage on the border of Piauí and Ceará in 1925. All the other specimens were taken by H. E. Kaempfer in 1927 in southern Piauí and in northern and central Bahia for Mrs. Naumburg (1928) who has said that the "rediscovery" of *Megaxenops parnaguae* was one of her main reasons for sending Kaempfer to collect birds in northeastern Brazil. All the known specimens were collected in the arid caatinga to which *M. parnaguae* may be mainly restricted (map 55) although (see below) it has been observed also in fairly dense woodland. Kaempfer said he has also seen, but he did not collect, *M. parnaguae* near Orobo, which is about 200 km. west of the city of Bahia, and to where the caatinga may



MAP 55. Geographical distribution of *Pygarrhichas albogularis* (left) and *Megaxenops parnaguae* (right).

not extend although the photograph (pl. 22) of Orobo in the itinerary of Kaempfer, published by Naumburg (1935), shows an arid and very scrubby forest.

Nothing is known of the behavior of *Megaxenops parnaguae* other than two short notes in the unpublished correspondence between Kaempfer and Mrs. Naumburg. To be sure, Reiser (1926) had published a colored plate in which a scansorial bird with zygodactyl feet is shown ascending the trunk of a tree, bracing its tail against the bark in the manner of a woodpecker. But the attitude shown is wrong; the texture of the tail of *M. parnaguae* is unusually soft, certainly not adapted for support when climbing, and its foot is anisodactyl, with three forward toes, the middle toe being well united to the first phalanx and most of the second of the outer toe as in all Philydorinae.

That *Megaxenops parnaguae* does little, if any, climbing is made quite clear by Kaempfer's unpublished notes. In the first note, Kaempfer said: "Reiser [who] pictures the bird like a woodpecker going up a tree and the toes like woodpecker toes . . . is all wrong the bird never climbs as a woodpecker does but jumps around like a formicaridae [*sic*] and the toes even in a freshly killed bird cannot be bent to stay as he pictures them. The bird picks ants and other insects just as any Formicaridae [*sic*] does."

This first note was written after Kaempfer said he had the occasion to observe *Megaxenops parnaguae* better, after collecting most of his series. In the second note from Orobo, Bahia, he said "I wish to come back again to *Megaxenops* that to find here I was rather surprised because I can hardly understand how such a very conspicuous bird could have been overlooked by former collectors. Indeed it is rather difficult to see the small *Xenops* that climb the trees . . . . But *Megaxenops* whose behavior is that of a perching bird is seen from far and the bright color makes it easily seen. The very perfect state of conservation of the *soft* [underlined in the original] tail feathers proves indeed that *Megaxenops* has not woodpecker habits." The notes of Kaempfer are not sufficiently informative, but suggest that *Megaxenops* is not scansorial and moves chiefly by hopping or clambering, frequenting apparently thickets or low trees, and is not oversecretive.

The nest of *Megaxenops parnaguae* seems to be unknown so far, unfortunately.

After this account of the behavior of *Megaxenops* was written, I received a letter from my colleague and friend E. O. Willis which adds valuable information, especially about the manner in which *Megaxenops* uses its strange bill in feeding. Willis said he observed briefly an individual in "fairly dense woodland" in the Chapada de Araripe which was "clambering around on medium-sized branches about 3–5 m. up . . . it hung under twigs or perched low across them in the usual ovenbird stances, and to feed inserted its bill under flakes of bark—especially peeling ones at the tips of stubs of limbs or twigs—to separate the bark from the trunk and there peck out little insects hiding under. It did not force the bark off, just wedged the bark flakes outward while looking to see what was uncovered. It had some loud calls and songs . . . more like those of a *Sclerurus* than those of a *Xenops*." The bird was observed "in the forest reserve" of the Chapada de Araripe where trees "are perhaps 8–15 m. tall," according to Willis.

Megaxenops parnaguae

Figure 7

DESCRIPTION: Entire plumage orange rufous except where noted. The coloration of the head, back, and upper surface of the wing is dark and rich, but the underparts are paler, more rufous cinnamon below the white throat, and the tail is uniformly reddish chestnut. Exceptions to the strongly rufous plumage consist of the following: the color of the chin and throat, which is pure silky white; a small blackish spot in front of the eye, and also behind it, which is not feathered; and the greater part of the remiges which are dark dusky brown. A very faint post-ocular streak exists, but is not conspicuous as it is strongly rufous also, only slightly paler than the crown. On the under surface of the wing, the axillaries, under wing coverts, and broad borders to the outer edge of the inner web of the secondaries and inner primaries are very bright rufous cinnamon. It is interesting to note that the silky texture

of the plumage is characteristic of the entire body plumage, not only of the throat.

The tail is slightly graduated, composed of 12 rectrices that are soft in texture (not stiffened, except at the very base), with firmly integrated webs and rounded tips. The bill is very strong, of the most pronounced "*Xenops*-type." The feet and claws are normally developed for a perching bird, not noticeably strong or weak.

IMMATURE PLUMAGE: Unfortunately not known to date.

MEASUREMENTS: In 18 specimens, the wing length varies from 75 to 83 mm. (average 79.0 mm.); among these seven males measure 78–83 mm. (81.07), and eight females 75–79 mm. (76.87). The tail length of 18 specimens measures 58–68 mm. (62.94); of these seven males measure 62–68 mm. (63.85), and eight females 58–66 mm. (61.37). The bill length of 18 specimens measures 18–20.5 mm. (19.30); of these seven males measure 18–20.5 mm. (19.14), and eight females 18–20 mm. (19.18).

RANGE: Probably all the caatinga region of northeastern Brazil. Has been collected so far at Varzea Formosa, western Ceará on the border of Piauí; near Parnaguá, southern Piauí; at Parnaguá; at Santa Rita do Rio Preto, northern Bahia, about 80 km. directly south of Parnaguá; and at Sincora, eastern-central Bahia. It has been observed also at Orobo, about 200 km. west of the city of Bahia, and in the Chapada de Araripe in "fairly dense woodland."

SPECIMENS EXAMINED: 18.

GENUS *PYGARRHICHAS*

Pygarrhichas is monotypic and another curious genus the systematic position of which is obscure. *Pygarrhichas albogularis* was considered to be a woodhewer (Dendrocolaptidae) at one time, probably because the structure of its tail associated with scansorial habits is similar to that of the woodhewers, but as the skull of *P. albogularis* is typically schizorhinal, the bird was removed to the Furnariidae. The structure of its foot suggests that it is best included in the subfamily Philydorinae.

Pygarrhichas albogularis is strictly arboreal and scansorial, "and resembles superficially a woodpecker or a large *Sitta* in behavior and appearance. It resembles a woodpecker in using its stiffened tail with rigid rachis as a brace when climbing the trunk or a branch of a tree, and also resembles the woodpeckers in excavating its nesting hole in the trunk, branch, or stump of a decaying tree. . . . But, with these two exceptions, *Pygarrhichas* is much more similar to *Sitta* in colour pattern (though not pigmentation as *Pygarrhichas* is chocolate brown above, rather than gray), general form and appearance, including the position of the head and bill" (Vaurie, 1971a). *Pygarrhichas albogularis* has been compared also to the tree creepers (*Certhia*), and is a bird of the forest, typical of the *Nothofagus* forests where, according to Johnson (1967) "it is usually seen near small clearings, tirelessly searching for grubs up and down the trunks and along the branches."[153]

The nest is at the bottom of a hole apparently excavated by the bird itself in decaying wood. But as the bill of *Pygarrhichas albogularis* is decidedly more frail than that of a woodpecker or nuthatch, my colleague, L. L. Short has suggested to me that *P. albogularis* uses its bill "more as a chisel in prying into the decayed wood than as a hammer or drill in excavating, as in the woodpeckers." The nests reported by Johnson from Chile were "generally at a height of 12 to 20 feet [about 3.65 to 6 m.] from the ground, perfectly cylindrical in shape and from 12 to 16 inches in depth [about 30.5 to 40.5 cm.]." No lining is used, but Johnson and other observers who have described the nest say the eggs rest on a bed of "sawdust" (probably small chips produced during excavation).

Pygarrhichas albogularis
Figure 7

DESCRIPTION: Upperparts uniformly chocolate brown, with the exception of the rump and upper tail coverts which are reddish chestnut. A band of darker, blackish brown extends posteriorly through the eye to the

nape, broadening behind the bill and resembling the facial mask characteristic of *Sitta*; four or five very small white feathers exist laterally on the forehead. The chin, throat, and the whole of the breast are uniformly pure white. The feathers of the abdomen are white, or more cloudy, but have dark brown borders which produce a guttate pattern on the abdomen, these spots becoming streaks on the under tail coverts which are faintly cinnamomeous. The axillaries and under wing coverts are white, and, to a slight extent, the outer edge of the inner web of the inner remiges is dull white.

The tail is uniformly reddish chestnut, with 12 rectrices that are strongly stiffened and the rachis of which becomes increasingly rigid, and prolonged as a "spine" beyond the web, progressively from the outer rectrix inward; the spine averages about 7 mm. in length on the central pair where it is best developed. The bill is of the general "*Xenops*-type," but very much longer than in *Xenops*, more compressed laterally, and much more attenuated. The feet are very strong with big toes and claws.

MEASUREMENTS: Wing length of 55 specimens: 78–87 mm. (mean 83.00 mm.); among these 30 males measure 79–87 mm. (mean 83.60 mm.), and 20 females 78–87 mm. (mean 82.40 mm). The tail length, minus the spine, of 55 specimens measures 45–62 mm. (mean 52.72 mm.); among these 30 males measure 45–62 mm. (mean 53.73 mm.), and 20 females 45–62 mm. (mean 51.40 mm.). The bill length of 52 specimens measures 22–28 mm. (mean 25.32 mm.); among these 28 males measure 22–28 mm. (mean 24.62 mm.), and 19 females 24–28 mm. (mean 26.65 mm.).

IMMATURE PLUMAGE: Differs from that of the adult by being heavily streaked above, on the crown and back.

RANGE: Chile, from Santo Domingo in the Province of Santiago; and western Argentina, in forest or woodland along the Andes, from southern Mendoza, south to Tierra del Fuego and forested islands to the south, such as Hoste and Navarino, but lacking from open and unforested regions of Tierra del Fuego.

SPECIMENS EXAMINED: 65.

APPENDIX I: CHECKLIST OF SPECIES OF FURNARIIDAE

This list was compiled by P. Vaurie; annotations are by F. Vuilleumier, extracted from manuscript of monograph by C. Vaurie.

SUBFAMILY FURNARIINAE (four closely related genera, and one genus with no close relatives: *Furnarius*)

Genus *Geositta*

G. poeciloptera
G. cunicularia
G. maritima
G. peruviana
G. punensis
G. saxicolina
G. isabellina
G. antarctica
G. rufipennis
G. crassirostris
G. excelsior
G. tenuirostris

Genus *Upucerthia* (one isolated species and three species-pairs)

- *U. certhioides* (isolated)
- *U. ruficauda* / *U. andaecola* (species-pair)
- *U. serrana* / *U. dumetaria* (species-pair)
- *U. albigula* / *U. validirostris* (species-pair)

Genus *Cinclodes* (four groups of species; relationships between groups are uncertain)

Group 1
- *C. fuscus*
- *C. comechingonus*
- *C. pabsti*

Group 2
- *C. oustaleti*
- *C. patagonicus*

Group 3
- *C. taczanowskii*
- *C. nigrofumosus*
- *C. antarcticus*

Group 4
- *C. atacamensis*
- *C. palliatus*

Genus *Chilia* (monotypic)
- *C. melanura*

Genus *Furnarius* (five closely related species)

dark-capped species
- *F. minor*
- *F. figulus*
- *F. leucopus*

species without cap
- *F. rufus*
- *F. cristatus*

SUBFAMILY SYNALLAXINAE (17 genera)

Genus *Sylviorthorhynchus* (monotypic)
- *S. desmursii*

Genus *Aphrastura* (closely related to *Leptasthenura*; one continental and one insular species)
- *A. spinicauda*
- *A. masafuerae*

Genus *Leptasthenura* (nine closely related species, with various degrees of closeness)

- *L. fuliginiceps* / *L. yanacensis* (species-pair)
- *L. platensis* / *L. aegithaloides* (related species)
- *L. striolata* (isolated species)

species group
- *L. pileata* / *L. striata* (species-pair)
- *L. andicola*
- *L. setaria* (isolated species)

Genus *Schizoeaca* (related to and intermediate between *Leptasthenura* and *Synallaxis*; two species)

S. fuliginosa
S. moreirae

Genus *Synallaxis*

Subgenus *Schoeniophylax* (monotypic)

S. phryganophila

Subgenus *Synallaxis* (36 species, placed into four groups; each believed to be a single phylogenetic assemblage)

Group 1 (16 species with a rufous "cap")

subgroup 1 (closely related)
- *S. ruficapilla*
- *S. superciliosa*
- *S. frontalis*
- *S. azarae*
- *S. elegantior*

subgroup 2 (closely related)
- *S. albigularis*
- *S. albescens*
- *S. spixi*

subgroup 3 (somewhat heterogeneous)
- *S. hypospodia*
- *S. infuscata*
- *S. brachyura* } (closely related)
- *S. courseni* }

subgroup 4
- *S. moesta* } (closely related)
- *S. cabanisi* }
- *S. macconnelli* }
- *S. subpudica* (position uncertain)

Group 2 (seven species with a brownish or grayish crown)

(± distantly related)
- *S. tithys* (transitional between Group 1 and Group 2 species)
- *S. cinerascens*
- *S. maranonica*
- *S. propinqua*
- *S. hellmayri* (position uncertain)

(closely related)
- *S. gujanensis*
- *S. albilora*

Group 3 (six closely related species that are rufous on the underparts)
- *S. rutilans* } (very closely related pair)
- *S. cherriei* }
- *S. unirufa* } (closely related pair)
- *S. castanea* }
- *S. fuscorufa* (probably related to *unirufa*)
- *S. zimmeri*

Group 4 (seven species, not all of which are very closely related)
- *S. erythrothorax* } (three isolated species)
- *S. cinnamomea* }
- *S. stictothorax* }
- *S. candei* } (related, but not very closely)
- *S. kollari* }
- *S. scutata* }
- *S. gularis* (no close relative [isolated species])

Genus *Certhiaxis* (20 species, heterogeneous in behavior and ecology, uniform morphologically; close to *Synallaxis*)

(red capped; closely related)
- *C. erythrops*
- *C. demissa*
- *C. antisiensis*
- *C. pallida*
- *C. curtata*

C. furcata (isolated?)
C. obsoleta (isolated)

- *C. hellmayri*
- *C. subcristata* (related)
- *C. pyrrhophia*

(related?)
- *C. marcapatae*
- *C. albiceps*
- *C. semicinerea*
- *C. albicapilla*

C. vulpina (isolated)
C. mülleri (isolated)
C. gutturata
C. sulphurifera

(related?)
- *C. cinnamomea*
- *C. mustelina*

Genus *Thripophaga* (24 species, related to *Certhiaxis* and *Synallaxis*, but not so close to either as *C.* is to *S.*, closely related to *Phacellodomus*)

T. pyrrholeuca
T. baeri
T. pudibunda

(closely related)
- *T. ottonis*
- *T. heterura*

T. modesta
T. d'orbignyi
T. berlepschi
T. steinbachi
T. humicola
T. patagonica
T. humilis

(closely related)
- *T. anthoides*
- *T. wyatti*

(closely related)
- *T. punensis*
- *T. sclateri*

species group
- *T. urubambensis*
- *T. flammulata*
- *T. virgata*
- *T. maculicauda*

T. cherriei (isolated?)
T. macroura (isolated?)
T. hudsoni (isolated)
T. hypochondriaca (isolated)

Genus *Phacellodomus* (10 species, nearest relative is probably *Thripophaga*)

closely related, species group
- *P. sibilatrix*
- *P. rufifrons*
- *P. striaticeps*
- *P. striaticollis*
- *P. ruber*

P. erythrophthalmus (isolated)

(probably related)
- *P. dorsalis* (isolated)
- *P. berlepschi*
- *P. fusciceps*
- *P. dendrocolaptoides* (isolated)

Genus *Spartonoica* (closely related to *Synallaxis*; monotypic)
- *S. maluroides*

Genus *Phleocryptes* (isolated, perhaps related to *Synallaxis*)
- *P. melanops*

Genus *Limnornis* (nearest relatives uncertain)
- *L. curvirostris*
- *L. rectirostris*

Genus *Anumbius* (near relatives uncertain)
- *A. annumbi*

Genus *Coryphistera* (near relatives uncertain)
- *C. alaudina*

Genus *Eremobius* (near relatives uncertain)
- *E. phoenicurus*

Genus *Siptornis* (relatives uncertain)
- *S. striaticollis*

Genus *Metopothrix* (relatives uncertain)
- *M. aurantiacus*

Genus *Xenerpestes* (relatives uncertain)
- *X. minlosi*
- *X. singularis*

SUBFAMILY PHILYDORINAE (12 genera)

Genus *Margaroronis* (six species, closely related)
- *M. adustus* (isolated?)
- *M. guttuliger* (isolated?)
- *M. brunnescens* (isolated?)

(closely related)
- *M. rubiginosus*
- *M. stellatus*
- *M. squamiger*

Genus *Lochmias* (monotypic, rather closely related to *Margarornis*)
- *L. nematura*

Genus *Pseudoseisura* (isolated genus)

(closely related)
- *P. cristata*
- *P. lophotes*
- *P. gutturalis*

Genus *Pseudocolaptes* (monotypic, related to *Philydor*)
- *P. boissonneautii*

Genus *Berlepschia* (monotypic, related to *Philydor*)
- *B. rikeri*

Genus *Philydor* (20 species)

one group of closely related spp.
- *P. strigilatus*
- *P. leucophrus*
- *P. subulatus*
- *P. guttulatus*
- *P. subalaris*

P. rufosuperciliatus
P. striaticollis
P. variegaticeps
P. ruficaudatus
P. erythrocercus (a "complex" of forms)
P. erythropterus

a group of species:
- *P. amaurotis*
- *P. lichtensteini*
- *P. rufus*
- *P. atricapillus*
- *P. pyrrhodes*
- *P. dimidiatus*

- *P. ucayalae*
- *P. striatus* (perhaps conspecific)

P. fuscus (isolated species)

Genus *Thripadectes* (closely related to *Automolus* and *Sclerurus*)

T. ignobilis
T. rufobrunneus
T. virgaticeps
T. melanorhynchus
T. holostictus

(closely related):
- *T. scrutator*
- *T. flammulatus*

Genus *Automolus* (seems closely related to *Thripadectes* and *Sclerurus*)

A. ruficollis (relationships uncertain)
A. ochrolaemus (relationships uncertain)

?group of related spp.:
- *A. infuscatus*
- *A. dorsalis*
- *A. leucophthalmus*

A. melanopezus
A. albigularis (relationships uncertain)
A. rubiginosus
A. rufipileatus

(closely related):
- *A. rectirostris*
- *A. erythrocephalus*

Genus *Sclerurus* (closely related to *Thripadectes* and *Automolus*)

S. mexicanus
S. rufigularis
S. albigularis
S. caudacutus
S. scansor
S. guatemalensis

Genus *Xenops*

X. contaminatus
X. milleri

(closely related):
- *X. tenuirostris*
- *X. minutus*
- *X. rutilans*

Genus *Megaxenops* (no near relatives, monotypic)

M. parnaguae

Genus *Pygarrhichas* (no clear relative, monotypic)

P. albogularis

APPENDIX II: SYNONYMIZED GENERA

GENERA SYNONYMIZED	NOW INCLUDED IN:
Geobates Swainson, 1837	*Geositta* Swainson, 1837
Ochetorhynchus Meyen, 1834	*Upucerthia* Geoffroy Saint-Hilaire, 1832
Dendrophylax Hellmayr, 1925	*Leptasthenura* Reichenbach, 1853
Oreophylax Hellmayr, 1925	*Schizoeaca* Cabanis, 1873
Gyalophylax Peters, 1950	*Synallaxis* Vieillot, 1818
Poecilurus Todd, 1917	*Synallaxis* Vieillot, 1818
Hellmayrea Sztolcman, 1926	*Synallaxis* Vieillot, 1818
Cranioleuca Reichenbach, 1853	*Certhiaxis* Lesson, 1844
Asthenes Reichenbach, 1853	*Thripophaga* Cabanis, 1847
Siptornopsis Cory, 1919	*Thripophaga* Cabanis, 1847
Drioctistes Ridgway, 1909	*Phacellodomus* Reichenbach, 1853
Clibanornis Sclater and Salvin, 1873	*Phacellodomus* Reichenbach, 1853
Limnoctistes Hellmayr, 1925	*Limnornis* Gould, 1839
Premnoplex Cherrie, 1891	*Margarornis* Reichenbach, 1853
Premnornis Ridgway, 1909	*Margarornis* Reichenbach, 1853
Roraimia Chapman, 1929	*Margarornis* Reichenbach, 1853
Cichlocolaptes Reichenbach, 1853	*Philydor* Spix, 1824
Anabazenops Lafresnaye, 1840	*Philydor* Spix, 1824
Anabacerthia Lafresnaye, 1840	*Philydor* Spix, 1824
Ancistrops Sclater, 1862	*Philydor* Spix, 1824
Hyloctistes Ridgway, 1909	*Philydor* Spix, 1824
Simoxenops Chapman, 1937	*Philydor* Spix, 1824
Syndactyla Reichenbach, 1853	*Philydor* Spix, 1824
Xenicopsoides Cory, 1919	*Philydor* Spix, 1824
Xenoctistes Hellmayr, 1925	*Philydor* Spix, 1824
Hylocryptus Chapman, 1919	*Automolus* Reichenbach, 1853
Heliobletus Reichenbach, 1853	*Xenops* Illiger, 1811
Microxenops Chapman, 1914	*Xenops* Illiger, 1811

APPENDIX III: LIST OF SPECIES FOR WHICH NO OR VERY LITTLE INFORMATION ON NESTS EXISTS

Geositta crassirostris
Geositta excelsior
Geositta tenuirostris
Upucerthia andaecola
Upucerthia serrana[20]
Cinclodes palliatus
Aphrastura masafuerae
Leptasthenura striolata
Leptasthenura pileata
Leptasthenura striata
Leptasthenura setaria
Synallaxis hypospodia
Synallaxis infuscata
Synallaxis courseni
Synallaxis moesta
Synallaxis cabanisi
Synallaxis macconnelli
Synallaxis subpudica
Synallaxis tithys
Synallaxis cinerascens
Synallaxis maranonica
Synallaxis propinqua
Synallaxis hellmayri
Synallaxis cherriei
Synallaxis unirufa
Synallaxis castanea
Synallaxis fuscorufa
Synallaxis zimmeri
Synallaxis candei
Synallaxis kollari
Synallaxis scutata
Synallaxis gularis
Certhiaxis demissa
Certhiaxis curtata

Certhiaxis furcata
Certhiaxis obsoleta
Certhiaxis hellmayri
Certhiaxis marcapatae
Certhiaxis albiceps
Certhiaxis semicinerea
Certhiaxis albicapilla
Certhiaxis mülleri
Certhiaxis gutturata
Thripophaga ottonis
Thripophaga heterura
Thripophaga berlepschi
Thripophaga steinbachi
Thripophaga humilis[93, 100]
Thripophaga punensis[93]
Thripophaga sclateri
Thripophaga urubambensis
Thripophaga flammulata
Tripophaga virgata
Thripophaga maculicauda
Thripophaga cherriei
Thripophaga macroura
Thripophaga hypochondriaca
Phacellodomus dorsalis
Phacellodomus berlepschi
Phacellodomus fusciceps
Phacellodomus dendrocolaptoides
Siptornis striaticollis
Metopothrix aurantiacus
Xenerpestes minlosi
Xenerpestes singularis
Margarornis adustus
Margarornis guttuliger
Margarornis rubiginosus
Margarornis stellatus
Margarornis squamiger
Berlepschia rikeri
Philydor strigilatus
Philydor leucophrus
Philydor subulatus
Philidor subalaris
Philydor rufosuperciliatus
Philydor striaticollis
Philydor variegaticeps
Philydor ruficaudatus
Philydor erythrocercus
Philydor erythropterus
Philydor amaurotis
Philydor lichtensteini
Philydor atricapillus
Philydor pyrrhodes
Philydor dimidiatus
Philydor ucayalae
Philydor striatus
Philydor fuscus
Thripadectes ignobilis
Thripadectes virgaticeps
Thripadectes melanorhynchus
Thripadectes holostictus
Thripadectes scrutator
Thripadectes flammulatus
Automolus ruficollis
Automolus dorsalis
Automolus melanopezus
Automolus albigularis
Automolus rufipileatus
Automolus rectirostris
Automolus erythrocephalus
Sclerurus rufigularis
Xenops contaminatus
Xenops milleri
Xenops tenuirostris
Megaxenops parnaguae

NOTES

[1]The generic names were left out of Vaurie's manuscript, but are suggested in parentheses on the basis of my knowledge and Vaurie's indications in the generic accounts (F.V.).

[2]Although the problem of intercontinental convergences in birds of taxonomically unrelated families has not been studied in the Furnariidae, this has been started with the Tyrannidae (see casual remarks in Smith and Vuilleumier, 1971, and analysis by Keast, 1972) (F.V.).

[3]The text on Furnariidae in the "New Dictionary of Birds" (Thomson, 1964) was contributed by Stephen Marchant (F.V.).

[4]*Sclerurus* puts its nest at the end of a burrow; *Pseudoseisura* builds a huge nest of sticks in bushes; *Sylviorthorhynchus* constructs a globular nest with a side entrance in low bushes; and *Phleocryptes* builds a pear-shaped, closed nest attached to reeds close to water (F.V.).

[5]Vaurie referred presumably to the lists of Hellmayr (1925), Peters (1951), and Meyer de Schauensee (1966) (F.V.).

[6]Vaurie's text contains descriptions of 214 species. Two new species, *Schizoeaca perijana* (Phelps, 1977a) and *Cinclodes olrogi* (Nores and Yeurieta, 1979, see note 22b), have been described since his monograph was completed (F.V.).

[7]Since this was written by Vaurie, field guides to birds of Panamá (Ridgely, 1976) and Venezuela (Meyer de Schauensee and Phelps, 1978) have appeared, in which a number of Furnariidae are illustrated (F.V.).

[8]This diagnosis is based on manuscript notes left by Vaurie, which have not been emended as to content, but only editorially (F.V.).

[9]This discussion is based on manuscript notes left by Vaurie, who did not "intend to study the Dendrocolaptidae to the same extent" as the Furnariidae. These taxa have at times been merged into one family, and Vaurie wished to indicate his reasons for keeping them separate (F.V.).

[10]For the validity of the species name *G. peruviana*, see note 18 (F.V.).

[11]If Vaurie had had field experience with several species of *Geositta* he would probably have favored the view that these furnariids are most convergent toward larks (Alaudidae), less so toward pipits (Motacillidae), and least so toward wheatears (Turdidae), at least as far as general attitudes and general behavior go. Tyrannidae of the genus *Muscisaxicola*, on the other hand, are more convergent toward *Oenanthe* (wheatears) (F.V.).

[12]Wing and tail patterns differ among these three species and congeners or other furnariids sympatric with them. Thus *G. excelsior* is often sympatric with *Cinclodes fuscus*, which it resembles in color; *G. saxicolina* is sympatric with *G. cunicularia*; and *G. maritima* is sympatric with *G. peruviana*. Since wing and tail patterns appear to be used in displays, such interspecific differences are perhaps of biological significance (F.V.).

[13]*G. poeciloptera* differs from other species of *Geositta* in the coloration of the axillaries, which are deep pinkish chestnut with conspicuous white tips. In other species of *Geositta* the axillaries are plain-colored, varying from whitish to chestnut (F.V.).

[14]On morphological grounds, taking all color and pattern characters into account, one could argue that *Geositta maritima* is more closely related to *G. saxicolina* and *G. isabellina* than to *G. peruviana*, which in turn might be more closely related to *G. cunicularia* (F.V.).

[15]Had Vaurie been able to observe species of the genera *Geositta*, *Upucerthia*, and *Cinclodes* in the field, he would probably have put the species *excelsior* in *Cinclodes* because of its general behavior (locomotion, foraging) and displays (vocalizations, wing-raising displays). A case could be made for merging *Upucerthia* with *Cinclodes* because *U. dumetaria* is somewhat intermediate but I believe that *Geositta* and *Geobates* (minus *excelsior*) are composed of a close-knit group of closely related species (F.V.).

[16]High Andean birds (subspecies *frobeni*) seem geographically separated by a hiatus from western Andean, coastal and foothill birds (subspecies *deserticolor*), and a zone of contact may occur near Arequipa, southern Peru, at intermediate altitudes. The possibility of incipient altitudinal speciation exists. Furthermore, *G. peruviana* and the coastal populations of *G. cunicularia* are allopatric, as already discussed by M. Koepcke (1965). They may form a superspecies. The disjunction within *G. cunicularia* is not shown on map 1, but the replacement of *G. peruviana* by *G. cunicularia* can be seen on map 1. The great morphological similarity between *G. cunicularia* and *G. antarctica* and their sympatry are not mentioned by Vaurie. From the point of view of speciation, *G. antarctica* can be thought of as a former peripheral isolate of proto-*cunicularia* (F.V.).

[17]Continuity of range between Colombian populations in the Western Andes and those of Nariño, southern Colombia, is not certain; continuity is more probable, however, between Nariño and Ecuador (F.V.).

[18]This is now the valid species name. The International Commission on Zoological Nomenclature (Bull. Zool. Nomencl., 34 (4), 1978: 205) has suppressed *Anthus paytensis* Lesson, 1837, considered by Zimmer (1953, pp. 26–27) a senior synonym of *Geositta peruviana paytae* Ménégaux and Hellmayr, 1906, which, if correct, would have given *G. paytensis* priority over *G. peruviana* Lafresnaye, 1847, as the specific name. Lafresnaye's name was conserved (Eugene Eisenmann).

[19]A more complete discussion of similarities and differences between *Upucerthia*, *Geositta*, and *Cinclodes* is given in the section on the genus *Cinclodes* (F.V.).

[20]In October 1975 I found a nest of *Upucerthia serrana* at about 4000 m. in the Cordillera Blanca of Peru. The nest, containing two unfeathered young (weights 15.0 and 15.5 gr.), was at the end of a 35 cm. deep, 10 × 6 cm. wide, gently sloping hole in the ground. The hole was on a west facing, pebbly slope, not well hidden in short bunch grass, a few m. from tall *Puya Raimondii* plants (F.V.).

[21]An additional character that seems to differentiate *Upucerthia albigula* from *U. validirostris* is the shape of the tip of the bill, which is slightly broader, more spatulate in *albigula* than in *validirostris*. These two species could be called sibling species (F.V.).

[22a]Besides the four specimens cited by Vaurie, there are four additional specimens: at the American Museum of Natural History (1), Louisiana State University Museum of Zoology (2), and at the Museum of Comparative Zoology (1), bringing the total number of specimens to eight (F.V.).

[22b]An eleventh species, *Cinclodes olrogi*, was described by Nores and Yzurieta (1979), una nueva especie y dos nuevas subespecies de Aves (Passeriformes), Acad. Nac. Cienc., Côrdoba, Argentina, Misc. no. 61, pp. 4–8).

[23]I am not certain of the validity of the comparison between *Cinclodes* and *Motacilla*. Wetmore (1926, p. 252) compared *Cinclodes* to *Seiurus* (Parulidae); Morrison (1939, p. 474) and Goodall et al. (1957, p. 200) compared *Cinclodes* to *Cinclus*. From my own experience, I cannot conclude that there is convergence be-

tween *Cinclodes* and *Motacilla*, but I can do so in part for the convergence between *Cinclodes* and *Cinclus* or *Seiurus* (F.V.).

[24]On the basis of field experience with *Cinclodes fuscus* (in many parts of its range), *C. oustaleti* (central part of its range), *C. patagonicus* (northern part of its range), *C. taczanowskii* (northern part of its range), *C. nigrofumosus* (northern part of its range), and *C. atacamensis* (most of its range), I would judge those species not to be especially confiding, although their flight distances appear to vary both intra- and interspecifically. *C. fuscus* behaves often as a near commensal of man, but its boldness does not approach that of *C. antarcticus* as mentioned by Cawkell and Hamilton (1961), although I cannot make a direct comparison, having not observed the last species (F.V.).

[25]In my experience with *C. nigrofumosus* (near Arica, Chile) and *C. taczanowskii* (north of Lima, Peru), I found that both species have a very similar "maritime" habitat, that of the rocky intertidal zone in areas where the surf breaks on the algae-covered rocks (F.V.).

[26]I have observed migrating flocks of *G. tenuirostris* in the Sierra de Aconquija on April 14, 1965; Olrog (1949, p. 150) wrote, for the same species and the same region: "En mayo se observaron bandadas migrando entre El Infiernillo y Tafi del Valle" (F.V.).

[27]It is not clear whether Vaurie meant to mention the phenomenon of "character displacement" in this sentence. It seems to me that *C. fuscus* living on isolated mountaintops in Venezuela, Colombia and Ecuador (map 3) resembles the mountaintop isolate *C. comechingonus* of the Sierra de Córdoba (F.V.).

[28]Although Vaurie states that taxa *C. comechingonus* and *C. fuscus* coexist in the isolated mountains of Córdoba, this "fact" does not appear to be well-established. Until definite proof of breeding of both taxa in the same area has been offered, one must remain skeptical of alleged sympatry. The evidence for sympatric breeding is at best unconvincing. Olrog's observations that *comechingonus* and *fuscus* can be distinguished in the field on the wintering grounds is no proof that they are specifically distinct. Geographically differentiated populations of the same species that winter together may be told apart by experienced observers (F.V.).

[29]In the field, *C. taczanowskii* and *C. nigrofumosus* recall *C. atacamensis* in general aspect and in general behavior. Although there is no doubt that *taczanowskii* and *nigrofumosus* are very closely related to each other, and probably are allospecies of a superspecies, it is possible that they are related to *C. atacamensis* of the high Andes. Unlike Vaurie, I would not put *C. antarcticus* near *C. taczanowskii* and *C. nigrofumosus*, but near *C. patagonicus* and *C. oustaleti* (F.V.).

[30]I submit the hypothesis that *C. palliatus* may show some convergences towards *Podoces*, the Old World ground jay (Corvidae). *Pseudoseisura* also would appear to show some convergence toward ground jays (F.V.).

[31]The remark about *C. atacamensis* is surprising. Indeed, there is little geographical variation in the Andean populations of that species, but the isolated population living in the Sierra de Córdoba in western Argentina (subspecies *schocolatinus*) seems well marked to me. It parallels remarkably the differentiation and isolation of *C. comechingonus* vis-à-vis *C. fuscus* (F.V.).

[32]I am not sure of the significance of these three records. December and February dates from Bolivia and Jujuy, Argentina, are probably in the breeding season, especially the Bolivian record. A March record from Tucumán, Argentina, could be post-breeding. Whether these records mean an altitudinal movement is far from clear (F.V.).

[33]On the basis of field and museum experience with *Chilia melanura*, six species of *Cinclodes*, and five of *Upucerthia*, I would judge *Chilia* to be much closer to *Upucerthia* than to *Cinclodes*. In particular, *Chilia melanura* resembles *Upucerthia serrana*, *U. ruficauda*, and *U. andaecola* in several respects, including general behavior, habitat, and displays (F.V.).

[34]*Furnarius leucopus* occurs rather high up in the valleys of the rivers draining into the upper Marañon Valley, for instance up to about 2200 m. in the Chotano Valley. Thus the distribution shown on map 5, which does not include the upper Marañon, is incomplete, and does not show the correct position of the gap between the two isolated populations of *F. leucopus*. In view of the low altitude of passes in this region (dry *Porculla* at only about 2250 m.), it is unlikely that passage between the two disjunct populations of *F. leucopus* took place "before the rise of the Andes." It would be very easy for these birds to cross today (F.V.).

[35]The text does not mention *F. tricolor* Giebel, 1868, from Bolivia (*hauxwelli* of Pebas, Peru, being a synonym), which Vaurie (1971a) listed tentatively as a valid species. In a later paper (1973) he concluded that it was a pale variant of *torridus* and belonged in the species *F. leucopus* (Eugene Eisenmann).

[36]*Scelorchilus rubecula* (Rhinocryptidae) is a common species living in the same or similar habitats to those of *Sylviorthorhynchus*, and in which they are often found together (F.V.).

[37]The resemblance between the South American *Sylviorthorhynchus* and the Australian *Stipiturus* had been pointed out as long ago as 1890 by Sclater (Catalogue of the birds in the British Museum, vol. xv, Taylor and Francis, London, 1890, p. 31) (F.V.).

[38]The same sort of obsolescent barring on the underparts of immatures of *Sylviorthorhynchus* can be found in the immatures of some *Thripophaga* species (e.g., *T. pyrrholeuca*) (F.V.).

[39]Vaurie does not say anything about geographical variation in *Sylviorthorhynchus*. According to my own study of this species, there is no geographic variation,

either on the mainland or in the insular populations, (F.V.).

[40]This comment is slightly incomplete. *Aphrastura spinicauda* is a forest bird, but it occurs from sea level to timberline up to about 2000 m. It does not, however, occur above timberline, a habitat characteristically inhabited by *Leptasthenura* spp. I have found *Aphrastura spinicauda* in various kinds of forest, and it is not confined to deep forest, although it is slightly more common there. For example, the estimated number of individuals/40 ha was 80 in rainforest and 64 in mesophytic forest (Vuilleumier, 1972) (F.V.).

[41]*Aphrastura spinicauda* can be said to resemble tits of the genus *Parus* (Paridae) as well as treecreepers (Certhiidae) of the genus *Certhia* (description of this behavior in Vuilleumier, 1967). I agree that *Leptasthenura* spp. can be compared to *Aegithalos* spp. (Timaliidae), especially because when foraging for food, birds in both genera often hang from twigs upside down, probing the undersides of the foliage for food. However, *Aphrastura spinicauda* often forages hanging upside down too. The resemblance between *Leptasthenura* and *Aegithalos* appears more marked simply because both have long tails, whereas the tail of *Aphrastura* is much shorter (F.V.).

[42]The social behavior of *Aphrastura spinicauda*, including a description of its various vocalizations and its association in mixed species flocks, has been described by Vuilleumier (1967) (F.V.).

[43]*Aphrastura spinicauda* (continent and neighboring continental islands) and *A. masafuerae* (Juan Fernández Islands) can be considered allospecies of a single superspecies (F.V.).

[44]It should be noted that the Mocha Island subspecies was named by Chapman (1934) on the basis of only two specimens, a very inadequate population sample (F.V.).

[45]This is true in study skins, but less so, or not at all when observing birds in the field (experience with *L. fuliginiceps, L. yanacensis, L. aegithaloides, L. pileata,* and *L. andicola*). In the field the tail of *Leptasthenura* spp. appears simply long, or tapered (F.V.).

[46]See note 40 (F.V.).

[47]*Leptasthenura aegithaloides* reaches such altitudes only north of the range of *Aphrastura*. Within the range of *Aphrastura spinicauda* the Andes are much lower and the alpine zone between timberline (where *A. spinicauda* is found) and mountain tops or permanent snow does not reach 4000 m. In southern South America (from about 41° S southward), *Leptasthenura aegithaloides* is chiefly found in open steppes below the Andean forest in the steppes of Patagonia (F.V.).

[48]Vuilleumier and Ewert (1978, pp. 70, 78) recently published information on the distribution and ecological preferences of *L. andicola* in Venezuela (F.V.).

[49]On November 1, 1975 I found a nest of *Leptasthenura andicola* near Lagunas Queshque, Ancash, in the Cordillera Blanca of Peru at 4100 m. The location of the nest, also in a giant *Puya Raimondii*, was almost identical to that mentioned by Dorst (1957). The nest I found was made of wool-like material, and very "cozy." A similar nest, found at 3650 m. at Páramo del Aguila, Mérida, Venezuela, on March 12, 1975, in a *Hesperomeles* shrub, made similarly of wool-like material, was most likely to be of this species, because of its resemblance to the nest of *L. andicola* found later that year in Peru. The Venezuelan nest is simply referred to as "nest of an unidentified Furnariidae in a low shrub" in Vuilleumier and Ewert (1978, p. 79) (F.V.).

[50]I found *L. yanacensis* and *L. fuliginiceps* together in a *Polylepis* woodland near Cochabamba at 3720 m. (Vuilleumier, 1969, p. 602) (F.V.).

[51]The general behavior (locomotion, foraging, vocalizations) of *L. fuliginiceps, L. yanacensis, L. aegithaloides, L. pileata,* and *L. andicola* is very similar in all these species, but there are some differences in vocalization and habitat selection. Usually no more than two species appear to occur sympatrically in the same habitat, and the ranges of *L. andicola* and *L. aegithaloides* appear to be complementary. A comparative study of all species in this genus would be rewarding (F.V.).

[52]According to map 6, the range of *L. yanacensis* in Bolivia is in fact entirely enclosed in that of *L. fuliginiceps*. I believe that the overlap in range is not nearly so broad. *L. fuliginiceps*, although locally sympatric with *L. yanacensis*, is found in drier habitats and seems to occur chiefly in dry intermontane basins. *L. yanacensis*, on the other hand, is found in wetter habitats along the eastern edge of the Andes. Thus on map 6 the ranges of *L. fuliginiceps* and of *L. yanacensis* extend too far to the west, but that of *fuliginiceps* more so than that of *yanacensis*. There should be a strip where only *yanacensis* occurs, then one where both occur, and then another where only *fuliginiceps* occurs. The details of distributions of these two species, and the exact extent of their sympatry and habitat co-occupation are problems for further fieldwork (F.V.).

[53]It is not clear whether vocalizations are similar in allopatry, but different in sympatry. In any case, this potential case of character displacement is worthy of further field study. For a critical discussion of character displacement, see Grant (1972), who suggests that the phenomenon may not be as widespread as once thought, and can be interpreted in terms other than competition in the zone of overlap (F.V.).

[54]The altitudinal range of *L. andicola* in Venezuela is from 3400 to 4400 m. (Vuilleumier and Ewert, 1978, p. 70) (F.V.).

[55]In 1977 Phelps (1977a, pp. 47–50) described *Schizoeaca perijana*, new species, on the basis of six specimens collected at about 3000 m. in the Sierra de Perijá, Zulia, Venezuela, at the foot of Cerro Tetari. Type deposited at AMNH. This new taxon extends the range of the genus northward. The new taxon, like all other taxa in this genus, shows that they are closely related, allo-

patric forms. In some ways *S. perijana* is "intermediate" between other taxa in *Schizoeaca*, especially *coryi* and *fuliginosa*, its closest geographic neighbors. Phelps (*op. cit.*, p. 49) maintained specific distinctness of *coryi* and *fuliginosa*, contra Vaurie et al. (1972). Although Vaurie did not see this taxon before his death, I feel pretty confident, from his previous treatment and his treatment in the present monograph (and personal discussions) that he would have merged *S. perijana* with *S. fuliginosa*. Without altering the text, faithful to the guideline explained in the introduction, I have nevertheless inserted mention of *perijana* where appropriate, in order to bring the account up to date. Furthermore, I have inserted measurements (from Phelps, 1977a) in table 7 and color characters in table 8 (F.V.).

[56]Paragraph supplied by F.V.

[57]A discussion of *Schizoeaca coryi*, and of *S. fuliginosa* (altitudinal range, distribution, habitat requirements, voice) in Venezuela can be found in Vuilleumier and Ewert (1978, pp. 70–78). I have also seen nominate *S. fuliginosa* in Ecuador (Pambamarca, near Volcán Cayambe) in moist pure grassland at about 4000 m. (F.V.).

[58]As a complement to this discussion, the following quote might be useful: "The voice of *S. fuliginosa* is very reminiscent of that of *S. coryi*. Call notes, which are either contact or alarm calls can be transcribed as "vĭh" or "pĭh," just as in *S. coryi*. The song is a trill, consisting of a series of high-pitched notes, which increase in tempo and slightly in pitch. The trill resembles that of *Asthenes wyatti*, although it is longer" (Vuilleumier and Ewert, 1978, p. 70). Several species of *Cinclodes, Asthenes, Schizoeaca, Oreophylax moreirae*, and *Leptasthenura*, among various high altitude, open-country furnariid taxa, all emit trills as songs. But so do several high Andean tyrannids (*Ochthoeca*), or fringillids (*Phrygilus*). Thus, the problem of determining relationships through vocal characters will necessitate precise research into the problem of convergence versus homology (F.V.).

[59]If only two species are included in *Schizoeaca*, they should probably be included as allospecies of a superspecies. If several taxa of *Schizoeaca* (without *moreirae*) are kept as species, then *S. fuliginosa* (sensu Vaurie) is really a superspecies with several allospecies; some of the allospecies show geographical variation of a subspecific kind (F.V.).

[60]I have observed *Synallaxis unirufa* at Páramo de Tamá, Venezuela, in March 1975 in wet montane forest at 2890 m.; the forest was almost like elfin-woodland at that altitude, the trees being rather small on average (although some isolated trees were tall), and covered with epiphytic growth. *S. castanea*, studied in March 1975 at Colonia Tovar, Coastal Range of Venezuela, was seen in disturbed and second-growth montane forest at about 2100 m., alone or in a mixed flock of tanagers, *Catamblyrhynchus, Diglossa*, flycatchers, furnariids, and dendrocolaptids. The forest there is partly open, partly dense, broken up by stretches of bamboo growth and of shrubbery. Trees are covered by bromeliads and other epiphytes. Near Hotel Humboldt, El Avila, above Caracas, Venezuela, *S. castanea* was seen in a bamboo thicket, pecking at the nodes, presumably for insects (F.V.).

[61]*Synallaxis albescens* evidently is an ecologically plastic species; I have also observed it at about 1450 m. near Cerro Venamo in SE Venezuela, in an area consisting of open glades interrupted by islands of extremely dense vegetation. *Synallaxis albescens* occurred within such islands, usually keeping well out of sight (F.V.).

[62]In a more general way perhaps, it can be said that several species of *Synallaxis* behave (locomotion, attitudes, foraging, scolding intruders, etc.) like some species of Old World warblers of the genus *Sylvia* (sylviidae). Parenthetically, *Sylvia* spp. and *Chamaea* are each other's ecological counterparts in Mediterranean macchia and California chaparral, respectively (F.V.).

[63] A characteristic habit of *Synallaxis* spp. seems to be to scold the intruder approaching them. As they scold, they move back and forth in the vegetation, keeping more or less hidden or visible as they fly from denser to more open vegetation rather near the intruder (F.V.).

[64]I agree with Slud as to Panamá song (Eugene Eisenmann).

[65]Vaurie unfortunately did not make it clear what he meant evolutionarily by "reduction in the number of tail feathers." From his text, it would appear that he considered a high number (12) to be a "primitive" or "ancestral" condition, and a lower number an "advanced" condition (see p. 111, discussion of *S. hellmayri*). I would guess he thought that 12 rectrices was the primitive number, and that the reduction took place independently in several species within *Synallaxis, Thripophaga, Certhiaxis*, and *Leptasthenura*, rather than in sequence. It might be interesting to attempt to correlate the number of rectrices with environmental factors (including the nature of the habitat, for example whether it is predominantly grassland or shrubbery, whether it is mesic or xeric, etc., and including the material of the nest, possibly the size of the nest chamber), and with behavioral factors (for instance, whether the tail is held upright or not in locomotion, whether it is used in displays, etc.) (F.V.).

[66]Sick's impressions (*in litt.*) were that "as I saw [*Gyalophylax hellmayri*] for the first time, I thought of an *Asthenes*. As I held it in the hand I saw that it was very different from both genera [*Synallaxis* and *Asthenes*]. Peters was just correct to call attention on this" (*in litt.*, quoted with permission from Dr. Sick) (F.V.).

[67]Vaurie had used here, and subsequently within the 16 species of "Group 1," the terms "the first group,"

the "second group," the "third group," and "the fourth group," respectively. Because of potential confusion, I have replaced the terms with "subgroup" instead, a term used by Vaurie himself, although only as a penciled note on the maps (F.V.).

[68]See note 67.

[69]See note 67.

[70]See note 67.

[71]*Synallaxis moesta, S. cabanisi,* and *S. macconnelli* can probably be considered allospecies of a single superspecies (F.V.).

[72]According to my experience with *S. azarae* in Peru and Bolivia, this is a characteristic species of elfin woodland or its second-growth replacement in areas sharply disturbed (cut and planted) by man, along steep slopes in wet areas. Thus *S. azarae* can be found in dense thickets of trees and bushes, all covered with epiphytes, in the patchwork areas of wooded islands and tall grassland that compose the natural timberline. Or it can be found in tangles of *Stevia,* Melastomes, thorny shrubs that grow along roads at comparably montane altitudes. The call notes, a bitonal "pü-hip," or "pü-yp," are more often heard than the bird is seen (see also Niethammer, 1956, p. 97) (F.V.).

[73]Distant geographical distribution is not, by itself, a good criterion of taxonomic relatedness. Examples of closely related, allopatric (and geographically quite separated) species having a distribution pattern somewhat similar to *S. maranonica* and *S. cinerascens* would be *Phytotoma raimondii–P. rutila–P. rara* (Phytotomidae), and *Melanopareia elegans–M. maranonicus–M. maximiliani* (Rhinocryptidae) (F.V.).

[74]H. Sick (*in litt.*) has recently observed this species in northeastern Brazil (see note 66.) (F.V.).

[75]Indeed in the field when the birds are observed through binoculars the black gular patch is conspicuous in *S. castanea,* and invisible in *S. unirufa.* This difference could be of importance in species-specific displays, and hence would act as part of an isolating mechanism, but the two taxa are entirely allopatric (F.V.).

[76]I would consider *S. fuscorufa, S. unirufa,* and *S. castanea* three allospecies of the same superspecies (F.V.).

[77]*Synallaxis candei, S. kollari,* and *S. scutata* could perhaps be considered three allospecies of a single superspecies (F.V.).

[78]It is a pity that Vaurie did not investigate this distribution and its parallel geographical variation closer, in order to check whether, indeed, populations taxonomically assigned to *S. s. chinchipensis* in the Marañon basin are isolated from other populations across the Western Andes. Although the passes in the Western Andes of northwestern Peru are low, and some are furthermore dry (e.g., Porculla), in my experience *S. stictothorax* does not reach altitudes high enough for direct contact across such passes, unlike other species having a similar kind of distribution (e.g., *Furnarius leucopus, Campylorhynchus fasciatus*) (F.V.).

[79]The precise habitat of *S. gularis* at very high altitudes, of 3500–4000 m., should be ascertained. At such altitudes in the Andes of Venezuela, Colombia, and Ecuador, one finds oneself usually in páramo vegetation, an open type of habitat in which I have never encountered any species of the genus *Synallaxis* (F.V.).

[80]See note 89.

[81]*Cranioleuca antisiensis* occurs, mostly in tree tops, in a variety of types of montane forests, from dense and wet mid-montane forests at about 2300 m. up to elfin woodland not far from timberline. They also occur in much dryer types of montane woodlands. This species was seen climbing up and down tree trunks, even head down, and reminded me, by the latter behavior, of nuthatches of the genus *Sitta* (F.V.).

[82]From my limited field experience with *C. albiceps* in Cochabamba, Bolivia, I would judge this species to behave very much if not exactly like *C. antisiensis,* which is arboreal, and so perhaps also like *C. erythrops* (which I have not seen in the field) (F.V.).

[83]The problem of convergence in morphology, but divergence in behavior or habitat, and/or vice versa, does not seem to have been posed by Vaurie when he undertook his revision. One wonders whether Vaurie's genus *Certhiaxis* is a mixture of groups of rather unrelated taxa, in other words a polyphyletic assemblage, not a monophyletic genus. The great ecological diversity Vaurie cites might reflect taxonomic diversity rather than an exception to the rule that "behavior and ecology have been quite consistent . . . in the polytypic genera . . . in this monograph" (p. 137). Morphological similarity could mask genetic diversity, but unfortunately I have had enough field experience with too few forms of *Certhiaxis* (*sensu* Vaurie) to have an opinion based on interspecific comparisons of general behavior and habitat preferences. It is unfortunate that Vaurie did not write up a section on character analysis, in which we would have discovered how he used behavioral and ecological characters (F.V.).

[84]*Cranioleuca demissa* (Pantepui) and *C. curtata* (Andes) can be considered either semi-species or allospecies of a superspecies. *C. erythrops* and *C. antisiensis* could also be allospecies of a superspecies (F.V.).

[85]One could suggest that these three species (*C. hellmayri, C. subcristata,* and *C. pyrrhophia* are allospecies of the same superspecies. The distribution of *C. subcristata* includes far more than the "coastal mountains of Venezuela," and that of *C. pyrrhophia* far more than the "Chaco" (see map 17) (F.V.).

[86]What Vaurie means, I think, is that the trend of increase in size from north to south within *C. antisiensis* as a whole is correlated with both an increase in altitude and an increase in latitude. In other words, the birds tend to get progressively larger partly "because" they

live at both higher altitudes and higher latitudes. However, Vaurie does not say why or how this trend "can be accounted for." An analysis of altitudinal variation in Andean birds was published by Traylor (1950) (F.V.).

[87]In Peru, taxon *antisiensis* occurs on the Western Andes, and taxon *baroni* on the Eastern Andes. It is possible that the "step" in color and size between the two forms, and the "approach to the coloration of *baroni*" shown by the population called *palamblae* by Chapman, indicate, respectively, that speciation is far along in this pair of taxa, and that secondary contact and hybridization are taking place. The contact, one could postulate, occurred after *baroni* colonized the Western Andes in Cajamarca and La Libertad, where barriers to E–W inter-Andean crossing are few. One could also hypothesize that the size and color cline is a trend superimposed independently on both taxa, not truly evidence of close relationships. In any event, as Vaurie said, this group deserves intensive field study (F.V.).

[88]What is remarkable about the Coiba Island population of *C. vulpina* is its geographical isolation away from all other populations of the species (see map 17), yet its very small level of morphological differentiation. This distribution pattern is rare, if not unique, in Neotropical birds (F.V.).

[89]Vaurie spelled the name of this species "*mülleri.*" Under the International Code of Zoological Nomenclature, the original spelling "*mülleri*" ought to have been emended to *muelleri,* or a footnote should have been included, as required by the International Code of Zoological Nomenclature. But Vaurie purposely disregarded this because he disapproved of the Code (Eugene Eisenmann).

[90]Vaurie seems to imply that he believes the concentration of species of *Thripophaga* in the Andean realm is a fact militating in favor of an Andean origin for the majority of species. The fact of an important adaptive radiation of *Thripophaga* in the Andes is not, however, by itself compelling evidence of origin in the Andes. It is curious that Vaurie did not cite Chapman's well-known views (e.g., 1926, p. 1, which was not included in Vaurie's bibliography) that many páramo and puna species (i.e., Andean) were ultimately derived from southern South America (i.e., Patagonia). Although Chapman did not include only *Thripophaga* species as examples, his reasoning would seem to apply to this genus, or at least to those species living at high altitudes in the Andes and/or in Patagonian steppes (F.V.).

[91]Phelps (1977a, pp. 50–52) described *Asthenes wyatti perijanus* on the basis of 13 specimens collected in 1974 in the Sierra de Perijá, at the border between Colombia and Venezuela, altitudes 2750 and 3100 m. This record extends the known range by providing an additional locality between Santa Marta (Colombia), the Eastern Colombian Andes, and the Venezuelan Andes. Mention of this population has been inserted in the appropriate places in the text, to update what Vaurie had written (F.V.).

[92]Under the International Code of Zoological Nomenclature (1961), Arts. 26 and 27, the original spelling, preferred by Vaurie, must be emended to *dorbignyi,* without apostrophe (Eugene Eisenmann).

[93]I found a nest of *T. humilis* in the Cordillera Negra of Peru (see note 100), and Hoy (1975) described a nest of *T. punensis* he found in Salta, Argentina (F.V.).

[94]However, I have observed *T. anthoides* in a vegetation best described as open scrub near Bariloche, Rio Negro, Argentina, and Hoy (1975, p. 191) calls this species "non-terrestrial," a behavior contrary to that of other streaked species that are terrestrial (*wyatti, punensis, humilis*) (F.V.).

[95]Both *T. modesta* and *T. humilis* also occur in tussock-grassland growing on rocky or gravelly soil (F.V.).

[96]*T. wyatti* is not strictly terrestrial (see Vuilleumier and Ewert, 1978, pp. 71–72). There is generally much more geographical variation in habitat preferences in *Thripophaga* spp. than Vaurie suspected. Terrestrial spp. are often hard to observe: they run fast, and keep concealed. See Koepcke's (1954) diagrams in her Birds of Lima (F.V.).

[97]Peters (1923, p. 318), and Wetmore (1926, pp. 273–274) stressed the resemblance to *Anthus,* not so much in habits as in coloration (F.V.).

[98]Twelve now, see note 93 (F.V.).

[99]The variability of nest material within *T. modesta* may not be "taxonomic." Vaurie (see later) merges *T. modesta* (essentially a high Andean and Patagonian species) with *T. cactorum* (living exclusively in cactus-steppes of western Peru). *Thripophaga modesta,* the nest of which I do not know, occurs more often than not in areas devoid of cactus (at least tall cacti) and/or of thorny shrubs. I would expect the nest of Andean *T. modesta* to be made of small, non-thorny twigs, or of grass stems, because locally *T. modesta* lives in open tussock-grassland. The nest of *T. cactorum,* however, as far as known (Koepcke's observations; and my own), is always built *in* the tall, columnar cacti that form the major vegetal structure of the landscape (F.V.).

[100]The nest of *T. humilis* I found in Peru resembled greatly the nest of *T. wyatti* described by Dorst (1963) quoted by Vaurie. It was in a clump of bunch-grass built on a NE facing slope, on the ground. The nest opened by a round hole facing W, thus shaded from the sun a 0900 (when it was found). The nest was 15 cm. in diam eter, about 12 cm. in depth. The outside was made o grass stems of the same species as the sparse bunch grass on the rocky and bare soil. Inside we found *Nothoprocta* feathers, wool, and vegetal material. It contained two young. The nest of *T. punensis* described by Hoy (1975) was also built on the ground of grass. It differed from the nests of *T. wyatti* described by Dorst

and of *T. humilis* (above) in having a tunnel "formed of straws folded back upon themselves, to which have been added softer vegetal fibers." Until *series* of nests of a variety of species of *Thripophaga* have been found and described, I would not want to say whether some of the apparent variability is species-specific or not. For the one species of which I have seen a variety of nests (*T. dorbignyi*) I can say that they all have something in common ("basket" of twigs with a side entrance), but that they all differ, both in construction and size, and in material and location (F.V.).

[101]The species of the *T. flammulata* species-group generally live in moist high Andean grasslands above timberline or at timberline in the ecotone between elfin woodland and páramo-grassland. By contrast, *T. cherriei* and *T. macroura* live in lowland, forested areas (although their habitats are not known). Is similarity of pattern here an indication of relationships in these geographically distant species? Are *T. cherriei* and *T. macroura* correctly placed in the same genus with the *flammulata* group? Having had no field experience with *T. cherriei* or *T. macroura* I would not venture a guess (F.V.).

[102]"*Siptornopsis*" *hypochondriaca* seems to me to be as isolated from other *Thripophaga* species as "*Schoeniophylax*" *phryganophila* is from other *Synallaxis* species. In the latter case, Vaurie chose to make *Schoeniophylax* a subgenus of *Synallaxis*. A satisfactory parallel solution would have been to make *Siptornopsis* a subgenus of *Thripophaga*. I am surprised that Vaurie did not suggest it (F.V.).

[103]I wish that Vaurie had been more specific and had cited precise evidence for the overlap between *T. wyatti* and *T. punensis* in Puno, Peru. The three outermost rectrices are entirely or largely rufous in birds from Venezuela to southern Ecuador; the outermost four rectrices have only the tips rufous in birds from central Bolivia to northwestern Argentina. Birds from central Peru to western Bolivia are intermediate between these two patterns. From my own field and museum study of this group I would conclude: (1) that birds with an intermediate kind of tail pattern exist in southern Peru and western Bolivia, (2) that there is no overlap between the two taxa, and (3) possibly that we are dealing here with a case of secondary intergradation or hybridization. The *wyatti-punensis* complex shows, like the *flammulata-maculicauda* complex, evidence of replacement of taxa, with or without hybridization, in the Puno area of southern Peru (F.V.).

[104]I must confess that the taxonomic relationships of *T. cactorum* puzzle me, even after having observed it and *T. modesta* in the field. I would remain on the conservative side here and maintain them as distinct species (F.V.).

[105]Another trend, of altitudinal variation in size, has been described by Traylor (1950) for birds from Bolivia (F.V.).

[106]In my opinion, the problem is not so much whether "to draw a limit between the ranges of the two subspecies," but whether one is dealing, in the species *T. dorbignyi*, with primary intergradation (or a stepped cline), or with secondary intergradation (and hybridization) in western Bolivia. I collected series of these birds in western Bolivia in 1967–1968 but do not find them adequate to solve the question. A further problem posed by *T. dorbignyi* is how closely *T. berlepschi* is related to it. Niethammer (1956, p. 98) suggested that *berlepschi* was a small population isolated from *T. dorbignyi*, and Bond and Meyer de Schauensee (1942, p. 332) considered them conspecific (F.V.).

[107]This is an understatement: the species occurs in the Venezuelan and northern Colombian Andes, then is missing from the rest of the Colombian Andes, reappears in Ecuador, is absent again from northern Peru, and reappears only in central Peru (see Chapman 1926, p. 437) (F.V.).

[108]Under the International Code of Zoological Nomenclature, this name should be spelled *dorbignyi* without apostrophe. See note 92 (Eugene Eisenmann).

[109]In my experience, *T. punensis* is more terrestrial than *T. wyatti* (F.V.).

[110]For the simple reason that trees are scarce in its habitat (F.V.).

[111]The relative inconsistency of Vaurie, when it comes to the problem of "weighting" morphological characters against behavioral (nest) or ecological (habitat) ones, can be seen again here. In the case of *Thripophaga wyatti* and *T. hudsoni*, the "different" behavior may be due to the incapacity of these two species, respectively, (1) to build a nest of sticks (they are rare or absent in their preferred, grassy habitats); (2) to build a nest in shrubs (there are few or none of these in their habitats) (F.V.).

[112]I am puzzled by this statement. I fail to see why *Spartonoica* could not have been placed near *Synallaxis* in Vaurie's sequence, the more so when he says, a little later, that *Spartonoica* could be "possibly only . . . a subgenus of *Synallaxis*" (F.V.).

[113]Similarity in morphology, but differences in behavior or ecology, did not prevent Vaurie from maintaining a variety of species in *Certhiaxis* (see also note 111) (F.V.).

[114]Vaurie uses the term "radiative adaptation" in this sentence, but probably meant "adaptive radiation," although the latter term is usually employed in a different meaning. What Vaurie seems to imply is that from a common, *Synallaxis*-like stock, two offshoots evolved adaptations to marsh-dwelling, one leading to the modern genus and species *Spartonoica maluroides*, the second to *Phleocryptes melanops* (F.V.).

[115]This altitudinal trend of a larger altiplano or puna series of populations, when compared with lowland or foothills ones, is of significance for speciation. It is found, among other taxa, in *Gallinula chloropus* (*garmani*) and in *Lessonia rufa* (*oreas*). In each case, the altiplano taxon is in parentheses (F.V.).

[116]The relationships of the genera *Coryphistera* and *Anumbius* to other Furnariidae are indeed unclear. It seems to me that *Eremobius phoenicurus*, in spite of its building a nest of twigs, as do most other members of the Synallaxinae, resembles in general morphology and in general behavior such taxa of the Furnariinae as *Chilia* and some species of *Upucerthia* (e.g., *U. ruficauda* and *U. andaecola*) (F.V.).

[117]This was not a misspelling. It was the accepted practice at the time to latinize the Spanish "ñ" by doubling the letter "n" (Eugene Eisenmann).

[118]I do not understand why *Siptornis* was placed at the end of the sequence of genera of Synallaxinae, and why it was not placed immediately before *Certhiaxis* (F.V.).

[119]*Margarornis squamiger* occurs higher still in Colombia, Ecuador, and probably also elsewhere (e.g., Venezuela, see Vuilleumier and Ewert, 1978, p. 72). Furthermore, *M. squamiger* occurs above the normal timberline in isolated woodlands of *Polylepis* sp. (Rosaceae) (F.V.).

[120]I have collected *Margarornis adustus* at 1450 m. at the foot of Cerro Venamo in SE Venezuela. This area consists of a patchwork of open, grassy areas surrounding "islands" of densely forested vegetation, with a "pseudosoil" of tree trunks and branches elevated above the level of the true forest floor. *M. adustus* was caught low down in a mist net erected in one of these forest patches (F.V.).

[121]This comment appears largely academic in view of our scant knowledge of the locomotory behavior of any species of *Margaronis*. There might be interspecific variation (individual and geographic) as well as interspecific variability in the way these birds use their tail as a brace when clinging to branches on tree trunks (F.V.).

[122]See Vuilleumier and Ewert (1978, p. 72) for a brief description of one kind of habitat in Venezuela, and a note on behavior. *M. squamiger* often travels about montane forests or elfin woodlands in flocks of several bird species, as well as alone. Sztolcman's description of behavior seems very apt, and corresponds to my own observations (F.V.).

[123]Phelps (1977b, pp. 24–30) has described a new subspecies of *Margarornis adustus, mayri*, from the Meseta de Jaua, altitude 1800 m., Bolívar, Venezuela (F.V.).

[124]The altitudinal range extends from about 1200 m. to 2500 m. (see Phelps, 1977b, p. 29) (F.V.).

[125]Definitely higher, see note 119 (F.V.).

[126]Another instance of Vaurie's difficulty in dealing with conflicting morphological and behavioral (nest) evidence. Morphologically they resemble Philydorinae, but behaviorally they are more like Synallaxinae. Vaurie opts in favor of morphology, as he did in the case of *Certhiaxis*, for instance. The nests of *Pseudoseisura* spp. are larger, but since these birds are giant compared to the small *Synallaxis* spp., the nests of either genus do not appear extraordinarily sized: they are large in both genera, and scaled to the size of their maker (F.V.).

[127]Contreras (1977, p. 15) mentions a variety of vernacular names, including these and others as well (F.V.).

[128]In my own experience in N.W. Argentina, *P. gutturalis* would appear to be a species of open mesquite (*Prosopis*) woodland growing on barren, or nearly barren soil. Contreras (1977) wrote that *P. lophotes* is more arboreal than *P. gutturalis*, the latter being found in the Monte Phytogeographic Province and in the Patagonian steppe. As for *P. cristata*, he wrote that it is a characteristic species of the caatinga, the cerrado and the northern chaco. Contreras hypothesized about the Pleistocene climatic and vegetational fluctuations that might have produced differentiation and habitat preferences within *Pseudoseisura* (F.V.).

[129]Wetmore's observations agree very well with my own (F.V.).

[130]This would be true in the steppes of Patagonia, but *Prosopis* trees are rather common in the northern part of the range of *P. gutturalis* (F.V.).

[131]*P. cristata* and *P. lophotes* could be considered allospecies of a single superspecies (F.V.).

[132]Contreras (1977) discusses geographical variation in *P. gutturalis*, and maintains two subspecies, Patagonian *gutturalis*, and northern *ochroleuca*. His distribution map shows that a hiatus exists between the two subspecies, whereas Vaurie's map (map 36) shows a continuous distribution (F.V.).

[133]See note 134 (F.V.).

[134]Goodfellow's observations of *Pseudocolaptes boissonneautii* in páramos, up to 4420 m., and of its retiring at night under tufts of grass might be due to an error of identification. In my own experience, *P. boissonneautii* is a montane forest or elfin woodland species, not a páramo species. My observations thus agree fully with those of Skutch. *P. boissonneautii* searches for its food, presumably insects, in tufts of epiphytes, especially bromeliads. This foraging may be done in low shrubs all the way up to treetops. Most often the birds move on branches by hopping, with the body maintained horizontally and perpendicularly to the branch. Once or twice only have I seen *P. boissonneautii* climb up a tree trunk as a Picidae or a Dendrocolaptidae would, but that behavior was of a short duration. The calls emitted by this species can be transcribed as a loud and dry "tick,"

which recall the calls of the Thraupidae *Chlorornis riefferii*. Goodfellow's observations appear most unusual (Vuilleumier, 1970, pp. 713-714) (F.V.).

[135]In spite of this remark, Vaurie drew the distribution as a continuum (F.V.).

[136]The other eight are: *Anabazenops* Lafresnaye, 1840; *Anabacerthia* Lafresnaye, 1840; *Ancistrops* Sclater, 1862; *Hyloctistes* Ridgway, 1909; *Simoxenops* Chapman, 1937; *Syndactyla* Reichenbach, 1853; *Xenicopsoides* Cory, 1919; and *Xenoctistes* Hellmayr, 1925 (F.V.).

[137]This species and the very similar *Simoxenops striatus* have always been treated as congeneric (see Meyer de Schauensee, 1966, p. 260). Chapman originally named *ucayalae* in a new genus *Anachilus*, which, when found to be homonymous, he replaced in 1937 by *Simoxenops*. Meanwhile Carriker had described *striatus* in *Anachilus* (Eugene Eisenmann).

[138]About character displacement, see the critical paper by Grant (1972) (F.V.).

[139]Terborgh (1971, fig. 9, p. 33) showed that in the Cordillera Vilcabamba of eastern Peru, the three *Thripadectes* species are allopatric altitudinally (F.V.).

[140]*Thripadectes scrutator* and *T. flammulatus* are probably allospecies of a single superspecies (F.V.).

[141]See notes 143 and 144 (Eugene Eisenmann).

[142]*Automolus rectirostris* and *A. erythrocephalus* could be allospecies of a superspecies. A geographical pattern like these two is not so unusual (e.g., also in *Melanopareia*) (F.V.).

[143]*Automolus roraimae* seems to be the correct name of this species (*A. albigularis*) under the International Code of Zoological Nomenclature (see note 144) (Eugene Eisenmann).

[144]Under the International Code of Zoological Nomenclature Art. 58 (8) these two names are homonymous variable spellings and under Arts. 57 and 59(a) primary homonyms, so Hellmayr was correct and Vaurie was wrong; *A. roraimae* Hellmayr would seem the correct name of the species (Eugene Eisenmann).

[145]For nomenclature see notes 143 and 144 (Eugene Eisenmann).

[146]For nomenclature see notes 143 and 144 (Eugene Eisenmann).

[147]Some localities occupied by *Sclerurus* within the belt of coastal forest in Brazil are as humid as some in Central America or western South America (F.V.).

[148]There was no write-up on geographical variation in the genus *Sclerurus* (F.V.).

[149]There was no write-up on geographical variation in the genus *Xenops* (F.V.).

[150]There was no section on immature plumage of *Xenops milleri* (F.V.).

[151]There was no section on immature plumage of *X. tenuirostris* (F.V.).

[152]In Costa Rica and Panama it seems to be restricted to the highlands ("Subtropical Zone") (Slud, 1964; Wetmore, 1972) (Eugene Eisenmann).

[153]Notes on the habitat, vocalization, and behavior (including social behavior in mixed flocks) were published by Vuilleumier (1967), and relative density in *Nothofagus* forest by Vuilleumier (1972, tables 1 and 2) (F.V.).

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