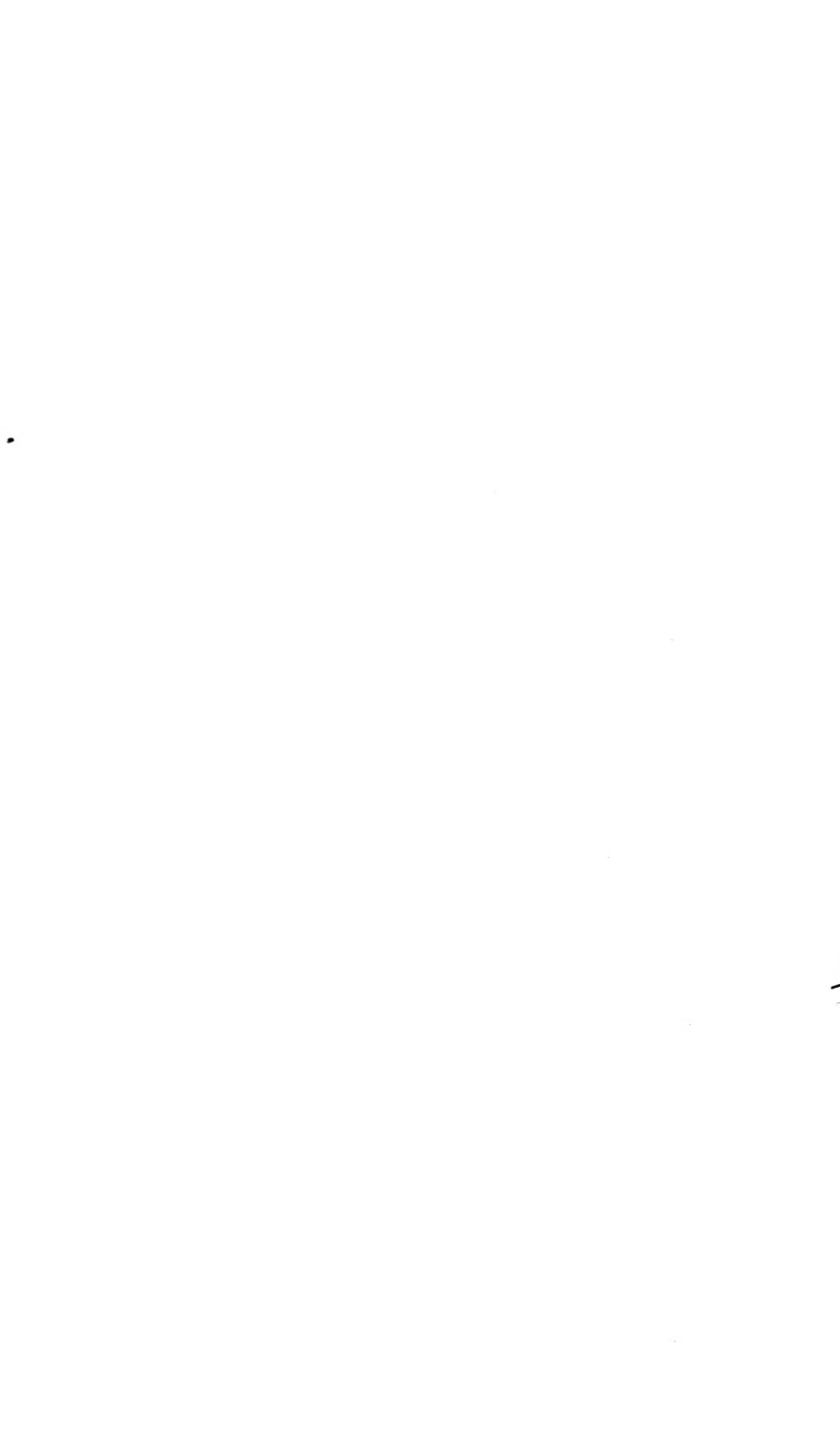


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NOTES ON TYRANT FLYCATCHERS (AVES: TYRANNIDAE)

MELVIN A. TRAYLOR, JR.

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CONTENTS

Introduction	1
<i>Tyranniscus australis</i> Olog and Contino	1
<i>Phyllomyias virescens reiseri</i>	1
<i>Zimmerius vilissimus</i>	2
<i>Sublegatus</i>	4
<i>Suiriri suiriri</i> / <i>affinis</i>	10
<i>Elaenia albiceps</i> and <i>E. parvirostris</i>	12
<i>Hemitriccus iohannis</i> and <i>H. striaticollis</i>	15
<i>Ochthodiaeta signatus</i> Taczanowski, 1874	18
Summary	20
Acknowledgments	20
Literature Cited	21

LIST OF ILLUSTRATIONS

1. Wing length of <i>Zimmerius vilissimus</i>	3
2. Distribution of <i>Sublegatus</i>	6
3. Localities of <i>Suiriri suiriri suiriri</i> and <i>S. s. affinis</i>	11
4. Breeding records of <i>Elaenia albiceps chilensis</i> and <i>E. parvirostris</i>	14
5. Distribution of <i>Hemitriccus striaticollis</i> and <i>H. iohannis</i>	17

LIST OF TABLES

1. Comparative measurements of wing and bill length in <i>Sublegatus obscurior</i> , <i>S. modestus</i> , and middle Amazon variable population	9
2. Measurements in <i>Elaenia</i> spp.	13

Introduction

During the preparation of the manuscript of the Tyrannidae for Volume 8 of Peters' *Check-list of Birds of the World* (Traylor, 1979, pp. 1-228), a number of problems arose which required further study. Ideally, these problems should have been resolved and the results published before the appearance of Volume 8. However, in order to avoid any further delay of the volume, I included my tentative conclusions there and am publishing the justifications here. Unfortunately, in the case of *Sublegatus*, subsequent studies have caused me to revise the classification presented in Peters' *Check-list*. The nomenclature used in this paper is that of Peters' *Check-list*, the rationale for which was explained in Traylor (1977).

Tyranniscus australis Olrog and Contino

Olrog & Contino (1966, p. 113) described *Tyranniscus australis* from a single female from Yuto, Jujuy, Argentina. They considered it most closely related to *Tyranniscus* (= *Phyllomyias*) *cinereiceps*, from which it differed in having the throat and breast clear gray, not yellow washed with olive, and the belly pale yellowish, not intense yellow as in *cinereiceps*. The latter species occurs in the subtropical zone of the Andes south to Cuzco, Peru, so that there was a gap of some 1,000 km between the ranges of *cinereiceps* and *australis*.

Olrog & Contino also included measurements of the type in their description. The proportion of tail:wing (53:59 or 90%) differed so much from the proportions of our single male of *cinereiceps* in Field Museum (tail:wing = 44:61 or 72%) that I questioned the identification. Through the kindness of Dr. Olrog, I have been able to examine the type. It proves to be a specimen of *Phyllomyias sclateri sclateri*, a species previously known from Jujuy. The type matches *sclateri* in both color and size. Comparison of my measurements (in mm) of the type with those of four females of *sclateri* in Field Museum are as follows: *australis* (type)—wing 62, tail 54.5, culmen 11, tarsus 16.5; *sclateri* 4 ♀—wing 61-65 (63), tail 54-60 (56.8), culmen 11-11.5 (11.3), tarsus 17-17.5 (17.3).

The name *Tyranniscus australis* Olrog and Contino becomes a synonym of *Phyllomyias sclateri* Berlepsch.

Phyllomyias virescens reiseri

Zimmer (1955, pp. 21-23) considered that *Phyllomyias reiseri* would have to be treated as a species distinct from *P. virescens*, since it occurred in Piauí and Goiás and in northern Paraguay, with *virescens* appearing in eastern Mato Grosso, between the two populations. He pointed out differences in coloration

as well as the very short wing length, which is the salient character of *reiseri*. I have examined Zimmer's material in the American Museum, as well as that in Field Museum, and do not see that two taxa segregate out on either color or measurements.

With 25 specimens from Piauí south through eastern Mato Grosso and Paraguay to Misiones, the wing measurements are distributed as follows: 11 males—(1) 54, (1) 58, (2) 59, (1) 60, (2) 61, (1) 62, (2) 63, (1) 65; 14 females—(1) 56, (2) 57, (2) 58, (5) 59, (1) 60, (2) 61, (1) 62.

Only the single male with wing length 54 can be separated on size; it is from Piauí, a topotype of *reiseri*. The spread of measurements at some localities almost encompasses the total spread for the remainder of the species. Four males from the vicinity of Villa Rica, southern Paraguay, have wings 59–65, whereas 10 females from Misiones measure 57–62. I consider *reiseri* to be a subspecies of *P. virescens*, with its range restricted to southern Piauí.

Zimmerius vilissimus

There are two generally recognized races of *Zimmerius* (olim. *Tyranniscus*) *vilissimus* in Central America: nominate *vilissimus* from Guatemala and adjoining Chiapas and El Salvador and *parvus* from Honduras south through Nicaragua, Costa Rica, and Panama to northwestern Chocó, Colombia. As expressed in its name, *parvus* is markedly smaller than *vilissimus* and has the whitish forehead and superciliaries less developed, the crown paler and more slaty, less brownish gray, and the yellow edgings on the flight feathers and coverts darker and brighter. The color characters are constant between the two races, with slight overlap due to individual variation, but there is considerable size variation in *parvus*, which caused Ridgway (1907, p. 409) to say, "If all the birds of this species from Nicaragua, Costa Rica and Panama are really of one subspecies the individual variation in size is very remarkable." An examination of 197 specimens from Central America shows that this remarkable variation in size is not individual, but is due to an abrupt increase in size with altitude over a comparatively small geographic range.

Nominate *vilissimus* is found over a wide altitudinal range, from 500 to 2,600 m among specimens examined, without any size variation correlated with altitude. Wing lengths of nine males are 57–64 (av. 60.0) and of 15 females 52–57 (av. 54.4). The northern populations of *parvus* in Honduras and Nicaragua, all in the lowlands below about 500 m, are strikingly smaller, with wings of six males 49–51 (av. 49.5) and wings of five females 43–46 (av. 44.8). These figures are fairly typical of the populations of the lowlands of Costa Rica and Panama below 600 m, where the average wing lengths, respectively, are males 51.5 and 49.7 and females 45.6 and 44.8 (fig. 1). These lowland records are from the Caribbean and Pacific slopes of both countries, although *parvus* avoids the dry Pacific slope of western Costa Rica. However, in the highlands of Costa Rica at the west end of the Cordillera de Talamanca around Santa Maria de Dota, and in the highlands of western Panama around Volcan de Chiriquí and Cerro Horqueta, both above 1,500 m, occur long-winged populations that overlap *vilissimus* in size. Wing lengths of the Costa Rican populations are 14 males 55–58 (av. 56.1) and 11 females 49–54 (av. 51.3), and those of the Panama populations are 24 males 53–59 (av. 56.1) and 12 females 48–52 (av. 50.5). Although these two populations

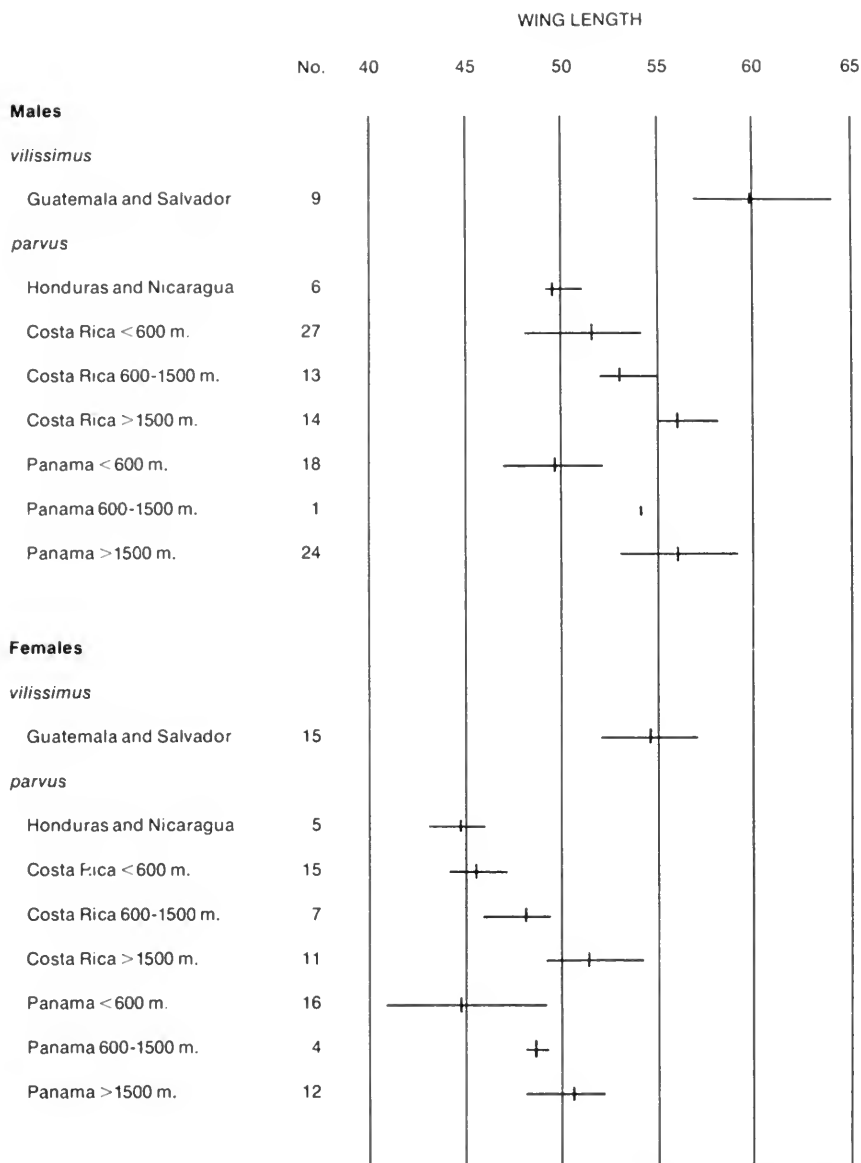


FIG. 1. Wing length of various populations of *Zimmerius vilissimus*. Wing lengths of nominate *vilissimus* are strikingly longer than those of *parvus* from adjoining Nicaragua and Honduras and from lowland Costa Rica and Panama. However, highland populations of *parvus* from Panama and Costa Rica approach *vilissimus* in wing length.

appear isolated, they are connected by continuous highlands above 1,500 m, and the range of the large populations may also be continuous.

Although the large-sized populations of *parvus* from Costa Rica and Panama overlap *vilissimus* in wing length, there is no evidence that they are biologically related. The former are identical in color with lowland *parvus*, and birds from intermediate localities, between 600 and 1,500 m, particularly in Costa Rica from which we have more extensive collections, are exactly intermediate in size (fig. 1). The large size of the highland birds appears to be the result of higher altitudes acting on the smaller birds of the adjacent lowlands. The latter, "typical" *parvus*, stretch from eastern Panama to the Caribbean coast of Honduras virtually unchanged. The only real biological break is between the northern populations of *parvus* in Nicaragua and Honduras and nominate *vilissimus* in Guatemala. Although only 320 km separate the two taxa in this area, there is no evidence of any intergradation between the two, and even the smallest females of *vilissimus* are larger than the largest males of northern *parvus*.

The present evidence strongly suggests that *vilissimus* and *parvus* have had separate evolutionary histories for some time and that their present proximity is of recent origin. Presumably, in an earlier warm, wet period, tropical forest, their primary habitat, was continuous through Central America, and proto-*vilissimus* had an unbroken range from southern Mexico to South America. In a subsequent cooler, drier period, this range was fragmented, with one population in Guatemala and a second in Costa Rica, Panama, or even northwestern Colombia. During this period of isolation, they diverged morphologically into the present *vilissimus* and *parvus*. With amelioration of conditions, the forest again became continuous, and *parvus* extended its range west and north to Honduras. However, even today, Honduras and Nicaragua are not a favored habitat for *parvus*, for the taxon is much less common there than in Costa Rica or Panama, where it is one of the most common forest-edge species.

The abrupt change between *vilissimus* and *parvus* in Guatemala and Honduras suggests that they might well behave as distinct species if they were to come in contact. However, the distinction between *parvus* and *improbis* of northeastern Colombia is said to be equally as great (Hellmayr, 1927, p. 471), and until all the related taxa can be compared, I keep them conspecific. Biological data on voice and behavior will be as important as morphological data in determining the status of the various taxa.

Sublegatus

Sublegatus is a widespread genus of small flycatchers found in open woodland, scrub, and mangroves from Costa Rica and northern Colombia east to the Guianas and south, east of the Andes, to northern Argentina. In this century it was considered monotypic with several well-marked races until Zimmer (1941b, pp. 1-7) suggested that there were two species. Since that time, treatment of the taxa has varied considerably. Meyer de Schauensee (1950, p. 861) and Phelps & Phelps (1963, p. 235) recognized Zimmer's two species and suggested that a third might have to be recognized, since two races of one of Zimmer's species occurred together in Colombia and Venezuela, respectively. Haverschmidt (1970, p. 358) also believed that the coastal and inland populations of Surinam belonged to different species, both probably resident. However, Meyer de Schauensee (1966, p. 384) and Meyer de Schauensee & Phelps (1978, p. 277)

recognized only a single species and considered the apparent cases of sympatry to be caused by wandering or migrant individuals.

The present study, based on some 200 adult skins, seems to support the recognition of two species in northern South America, although all those taxa were included in a single species by Zimmer. On the other hand, there appears to be extensive intergradation between Zimmer's two species along the lower Amazon, so that I am unable to recognize his separation of them. Unfortunately, the two species here recognized are not those accepted in Peters' *Check-list* (Traylor, 1979, p. 18). For this I can only apologize and say that I hope I have learned something in the meantime.

Within *Sublegatus*, there are three fairly well-marked entities or groups of subspecies. The first is the *arenarum* group which occurs from Costa Rica through Panama, northern Colombia, and Venezuela to coastal Guianas (fig. 2) and on most of the islands off the Venezuelan coast (not shown). It is characterized by a comparatively long bill and brighter underparts, with the pale gray breast sharply distinct from the bright yellow belly, and the throat whitish. At the extremes of its range, in Costa Rica and the Guianas, it is confined to mangroves, but from Panama to Venezuela it is also found in dry woodland and scrub. There are four mainland races recognized within this group, *arenarum* of Costa Rica and western Panama, *atrirostris* of eastern Panama and northern Colombia, *glaber* from northern Venezuela through the Guianas, and *orinocensis* in the lower Orinoco valley and in Meta, Colombia.

The second entity is the *modestus* group from southern South America, ranging from southern Peru across northern Bolivia to Mato Grosso, north in the campos region to Piauí, Maranhão, and Mexiana Island, and south to northern Argentina and western Uruguay and Rio Grande do Sul, Brazil. This group is characterized by short bills, fairly bright underparts, and in one race, clear white wing bars; its habitat is dry woodland and scrub. There are two races, *modestus* found from southern Peru through northern Bolivia to Mato Grosso and eastern Brazil, and *brevirostris* from central Bolivia and Paraguay south to western Uruguay and northern Argentina. The latter is migratory, and winter specimens have been taken in eastern Peru and central Amazonas.

The third group, *obscurior*, occupies a central position between *arenarum* and *modestus*, mostly peripheral to the Amazonian and Guianan forests. It has been taken in the north from the lowlands of eastern Colombia east through Venezuela to interior Guyana and Surinam and the coast of French Guiana, and south through eastern Ecuador and Peru to northern Bolivia; it also occurs in eastern Pará along the Tocantins and at Belém. The group is characterized by duller underparts, with the throat grayish like the breast, and the darker gray of the breast blending into the paler yellow abdomen. It is presumably a bird of forest clearings and river edges, which accounts for its rather patchy distribution around the forest. I consider *obscurior* to be monotypic, although there is considerable variation in depth of coloration; synonyms of *obscurior* are *sordidus* and *peruvianus*.

The evidence supporting the concept of two species is found in the distribution of *glaber/orinocensis* and *obscurior* in the region from eastern Colombia to French Guiana. Meyer de Schauensee (1950, p. 861) reported both *glaber* and *sordidus* (= *obscurior*) from Villavicencio, Meta, Colombia. I have examined the specimen of *obscurior*, a young unsexed bird in the American Museum, just completing its molt into adult plumage, and it is unquestionably this form. I

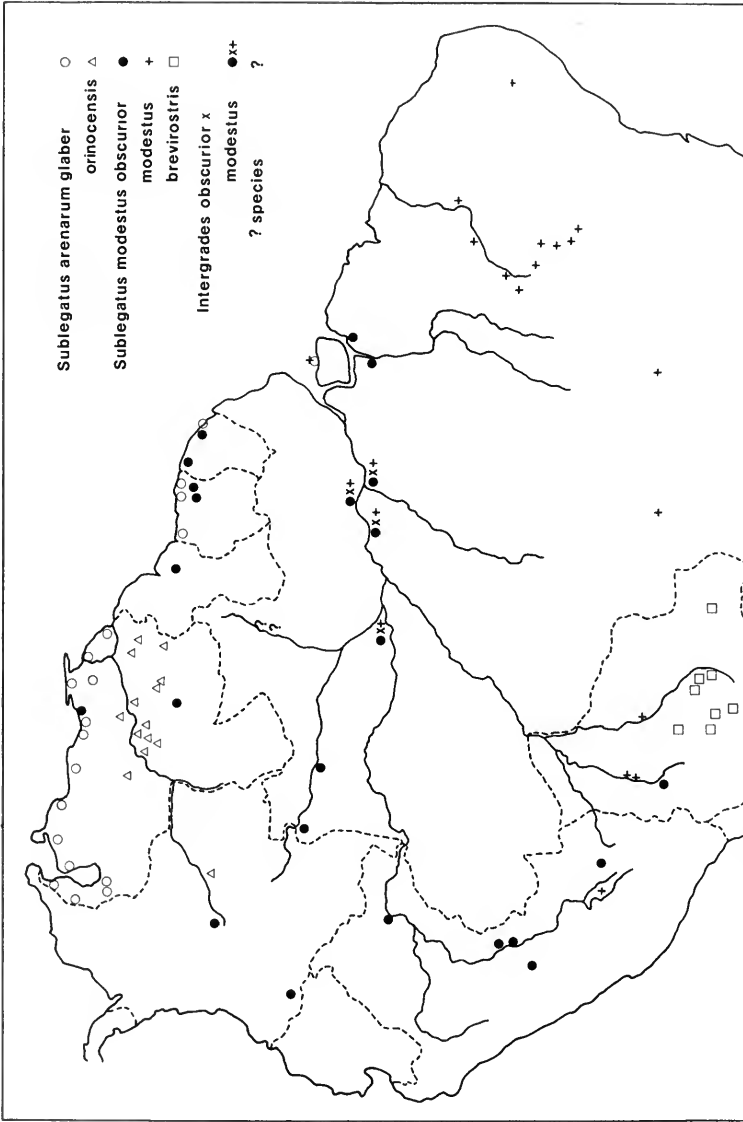


FIG. 2. Distribution of various taxa of *Sublegatus*. The points on the map refer only to specimens personally examined. The range of *obscurior* overlaps that of *glaber* and *orinocensis* in Venezuela. The populations along the middle Amazon are intergrades between *obscurior* and *modestus*. Breeding range of *modestus* extends south to Paraná, and that of *breviostris*, south to Mendoza, Argentina.

have not been able to examine the specimen of *glaber*, but there are three specimens of *orinocensis* in Field Museum from Carimagua, eastern Meta, and probably the Villavicencio bird was this subspecies. The specimen of *obscurior*, in postjuvencal molt, is almost certainly from a resident population. The Carimagua birds were in nonbreeding condition, but there is no evidence that *orinocensis* is ever migratory. There is no possibility that the dull plumage of the *obscurior* could be an immature stage of *orinocensis*. Its wing length is 74 mm, exactly the average of 19 males of *obscurior*, whereas the observed range of wing lengths of 18 males of *orinocensis* is only 66–71 mm.

From Venezuela I have two specimens of *obscurior* (Phelps Coll.), one taken adjacent to the range of *orinocensis* and the other well within the range of *glaber*. The first is a male from Salto Guaiquinima, Rio Paragua, south of the Orinoco, less than 160 km from La Paragua where *orinocensis* has been taken. It differs from *orinocensis* not only in color but in much larger size (wing 76). The second *obscurior* is a male from Los Altos, Sucre, well within the range of *glaber*. It is primarily identifiable on color, since *glaber* is much larger than *orinocensis*; wings of 14 males of *glaber* were 68–75 mm. The Los Altos male has a wing of 74 mm. Its bill length is 12.5 mm, typical of *obscurior* but outside the measurements of 14 *glaber* (13–14 mm), although the difference is not statistically significant. Phelps & Phelps (1963, p. 235) record a second *obscurior* from Guaraunos, Sucre, which I have not seen. They also list a specimen from Isla Tobeina, Amacuro, as *obscurior*. I have examined this bird, a female, and believe it to be an aberrant *glaber*. It has a paler yellow belly and somewhat darker gray breast than typical *glaber*, but it is nearer to the latter than to the two *obscurior* which have the dark gray of the breast bleeding over the belly so that the yellow is hardly apparent.

From Guyana I have examined a single specimen from Rockstone, in the interior, which is pure *obscurior*. However, Snyder (1966, p. 222) records two types of habitat for the species in Guyana: mangroves and swamp, and dry scrub and open forest. The dry scrub and forest population is *obscurior*, as shown by the Rockstone specimen; those from mangroves are presumably *glaber*, by extrapolation from adjoining Surinam. Haverschmidt (1970, p. 358) has described the distribution of the two forms in Surinam. He found *glaber* (called *obscurior* by Haverschmidt) common in coastal mangroves throughout the year and *obscurior* (called *sordidus*) in inland forest at Phedra in June, August, and October. To the latter may be added a December specimen from nearby Brownsveg, taken by Mees. The spread of dates strongly suggests that these inland birds represent a resident population. I have examined all this material, and the two series are typical of their respective taxa.

The situation in French Guiana is more confusing. The type of *obscurior* is from Cayenne, on the coast, and two other *obscurior* are from Mana, further west on the coast. However, there are four specimens from Isle Le Père, not far east of Cayenne, which more nearly resemble *glaber*. Zimmer (1941b, p. 3) noted this anomaly when he stated that "four adults, all sexed as males though two are small enough to belong to the other sex [= Isle Le Père series], are much brighter above and below, though the upper parts are not as light nor as brownish as those of most *glaber*. They are, however, not far removed from the Venezuelan form." At the time Zimmer wrote, there were no specimens of *glaber* from between Sucre, Venezuela, and French Guiana, and he was natu-

rally hesitant to assign the Isle Le Père specimens to that form. Now, however, *glaber* is known to be common in the coastal mangroves of Surinam, and I believe the Isle Le Père birds belong to that form.

When we consider the examples of parapatric and sympatric distributions of *glaber/orinocensis* and *obscurior* listed above, I believe they must be considered distinct species. The range of *obscurior* elsewhere is primarily equatorial, and there is no reason to expect that it is migratory. Certainly the wide spread of dates on which *obscurior* has been taken in inland Surinam argues for a resident population. I would make *S. arenarum* and its mainland races, *atrirostris*, *glaber*, and *orinocensis*, a species separate from *S. obscurior*.

As the map shows, *obscurior* is widely found in central South America, although there is no evidence to show that it is anywhere common. It is remarkably stable in size throughout its range, showing much less variation than that between *glaber* and *orinocensis*, or between the highland and lowland populations of *brevirostris* in Bolivia. Wing lengths of 19 *obscurior* males from southeastern Peru to French Guiana show an observed range of 70–78 mm, with a coefficient of variation (C/V) of 2.71%, comparable with the variation shown in 14 males of *glaber* from northern Venezuela (range 68–75, C/V 2.43%). Plumage variation, however, is considerable, appearing in the saturation of grays rather than in pattern. The palest, least saturated populations are found in French Guiana and adjoining Surinam, topotypical *obscurior*. The most heavily saturated specimens are from eastern Amazonia around Belém, and birds from the upper Rio Negro and Rio Vaupés are almost as dark; these are the populations called *sordidus* by Zimmer. Specimens from the eastern edge of the Andes and adjoining lowlands, from Colombia to northern Bolivia, are intermediate; this group was called *peruvianus* by Zimmer. Although these plumage differences are readily apparent, I prefer to treat all these populations as a single taxon, *obscurior*, until good series are available. The most specimens I have seen from any one locality are three, and most of the dots on the map represent single specimens.

Zimmer treated *obscurior* as conspecific with *arenarum* and allies, but considered them distinct from *modestus* because *obscurior* and *modestus* appeared to overlap in southeastern Peru. In southern Peru, *obscurior* has been taken on the middle Río Ucayali, and in Junín, Madre de Dios, and Puno, and there is a population of *modestus* in the Urubamba Valley at Sta. Ana and Maranura. I have examined all these specimens except the type of *peruvianus* from Río Tavera, Puno, and the two Maranura birds in the British Museum. They are all as Zimmer described them, and there does appear to be an overlap of the two taxa in southeastern Peru. However, along the lower Amazon the resident populations are quite variable and appear to be intergrades between *obscurior* and *modestus*. At the eastern extreme of the range of *obscurior* there is another example of apparent overlap. A single specimen from Mexiana Island at the mouth of the Amazon taken 13 November is *modestus*. Its range is separated from the nearest populations of *modestus* in Maranhão by the presence of *obscurior* in Pará. It might possibly be a vagrant or migrant from further south, but the date is quite late for a wintering bird.

Nominate *modestus* is found from the Urubamba valley in Peru east through Beni, Bolivia, to Mato Grosso, Brazil; and north in the dry interior of eastern Brazil to Maranhão, Piauí, and Pernambuco; and south to São Paulo and

Paraná. It has the shortest bill length of any form, 15 males having a range of 10–12 mm and an average of 10.8 mm. The closely related *brevirostris*, recognized by Zimmer but not by Pinto (1944, p. 283), ranges from central Bolivia through Paraguay to western Rio Grande do Sul, Brazil, and western Uruguay, and south to Buenos Aires, La Pampa, and Mendoza, Argentina. The main distinction between *brevirostris* and *modestus* is the clear white wing-barring of the former. This is important, because the wing bars of the *obscurior* and the *arenarum* groups are generally dull gray, and it is possible to distinguish wintering *brevirostris* in the breeding range of *obscurior* with a good degree of certainty. I have examined wintering *brevirostris* from Huánuco, Loreto, Junín, and Puno, Peru, and Novo Olindo, Manaus, and Villa Bella Imperatriz, Amazonian Brazil. It appears to be the only migratory taxon in the genus. Vertical distribution and size variation in *brevirostris* are unique in the genus. Specimens have been taken up to 2,300 m in Cochabamba and Tarijá, Bolivia, and populations from above 1,200 m are markedly longer-winged than lowland ones. Wing lengths of six highland males are 72–82 mm (av. 76.5 mm), while 13 lowland males measure 69–73 mm (av. 70.8 mm). The highland birds are the largest population within the genus, while the lowland are one of the smallest. The highland population is not migratory.

Along the Amazon, from Manacapuru just west of Manaus to Santarem, lives a variable population that seems to be intergrades between *obscurior* and *modestus*. There is a fine series of 11 specimens from Obidos in the Carnegie Museum which shows the full extent of variation. As a whole the series is darker gray on the breast than *modestus*, but not as dark or with as extensive a gray on the belly as *obscurior*. The color of the belly is particularly variable, going from clear pale yellow, as in *modestus*, to almost white. The extremes of variation are not far from typical *obscurior* and *modestus*, respectively. CM 84649 looks like a pure *obscurior*, with a dark gray breast extending over a pale whitish belly and the throat grayish, whereas CM 84477 has a pale breast, whitish throat, and yellow belly, only slightly darker on the breast than *modestus*. Single birds from Manacapuru and Santarem fit into this series, as does a female from Villa Bella Imperatriz in the American Museum. Bill length and wing length are also intermediate between *obscurior* and *modestus*, particularly in males; females are closer to *obscurior*. Comparative measurements are given in Table 1.

It seems, therefore, that despite the apparent geographical overlap between *obscurior* and *modestus* in southeastern Peru and near the mouth of the Amazon, the two taxa intergrade extensively along the middle Amazon, and they must be

TABLE 1. Comparative measurements (in mm) of wing and bill length in *Sublegatus obscurior* and *Sublegatus modestus* and in the middle Amazon variable population.

	♂♂	N	Wing	Bill
<i>obscurior</i>		19	70–78 (74.1)	11.5–14 (12.7)
middle Amazon		6	69–74 (71.3)	11–13 (12.0)
<i>modestus</i>		15	65–72 (68.2)	10–12 (10.8)
	♀♀			
<i>obscurior</i>		6	67–71 (68.8)	11.5–13 (12.2)
middle Amazon		7	67–73 (68.9)	11.5–13 (12.1)
<i>modestus</i>		9	65–68 (66.7)	10–11 (10.6)

considered conspecific. The classification that I presently recognize for continental South America is:

Sublegatus arenarum atrirostris
glaber
orinocensis
modestus obscurior (syn. *sordidus*, *peruvianus*)
modestus
brevirostris

Any advances in our understanding of this genus will have to come from behavioral studies rather than the amassing of more skins. The most convenient place to start would probably be Surinam, where marked ecological differences exist between *glaber* and *obscurior* and their ranges are near. If investigations using taped vocalizations and playbacks show that there are indeed two species there, then the study can be extended to include the relations between *modestus* and *obscurior* in Brazil and southeastern Peru.

Additional note: In Field Museum there are two specimens that do not fit the above pattern, and for which I have neither a name nor an explanation. They are from the upper Rio Branco in northwestern Brazil—a male taken 11 December at Boa Vista and a female taken 12 March at Serra de Lua. In coloration they are nearest *modestus*, although somewhat darker, but in size they are smaller than even the smallest *modestus* (male wing 64 mm, bill 10 mm; female wing 61 mm, bill 10 mm). They are far too small to be *obscurior*, which is where Hellmayr (1927, p. 447) placed them. They almost certainly represent a breeding population, because nominate *modestus* is on its breeding grounds in southern Brazil in December. Considering the uncertainties within the genus, it would be premature to try to name them now.

Suiriri suiriri/affinis

Suiriri suiriri suiriri and *S. s. affinis* had been treated as separate species until Zimmer (1955, p. 18) suggested that they were conspecific. Zimmer pointed out that all available specimens (19 in AMNH) from northern Paraguay were intermediate in one degree or another between typical *suiriri* and typical *affinis* and that this area was one of intergradation between the two taxa. Evidence of intergradation was found north of this area in a specimen from Companario, southern Mato Grosso. Meyer de Schauensee (1966, p. 384) followed Zimmer in treating the two as conspecific. However, Short (1975, p. 283) stated that he had failed to find any specimens showing intergradation and reverted to treating *suiriri* and *affinis* as separate species.

I have examined the Paraguayan material in the American Museum and find it exactly as described by Zimmer. The specimens are highly variable both in size and color, and none is typical of either *suiriri* or *affinis*. Average wing length is almost exactly intermediate, but bill length is more nearly like that of *affinis* rather than that of *suiriri* as stated by Zimmer. The three localities in Paraguay (fig. 3) at which these specimens were collected, La Fonciere (= San Luis de la Sierra), Zanja Moroti, and Belèn (not listed by Zimmer) form a triangle about 100 km on each side, and Companario is another 150 km to the northeast. Considering the extensive area over which intergradation occurs and the fact that the whole population is affected, I consider that *suiriri* and *affinis* are conspecific.

Zimmer also discussed five specimens of *affinis* in the American Museum which were separable from typical specimens by their short broad bills and broad pale tips to the rectrices. I have examined these birds, which were all taken from localities where typical *affinis* occurs. There is a sixth specimen, from Tranqueira Maranhão, in Field Museum, which was described by Hellmayr (1929, p. 329) and is identical with Zimmer's birds. There are other characters that correlate with the short bill and pale tips to the rectrices. In typical *affinis* the pale gray crown and nape are sharply separated from the pale olive back, but in the short-billed birds, the gray extends over the upper back and changes gradually into olive. In *affinis*, and even more in *suiriri*, the central pairs of rectrices have narrow pale edgings on both webs, but in the short-billed birds, there are no pale edgings at all, and the central rectrices are distinctly broader. On the other hand, except for the short bill, measurements of the two groups are identical.

Ordinarily the close correlation of two such discrete and unrelated characters as the short bill and the coloration and shape of the rectrices would be strong evidence that we have two sibling species. I think that eventually this will prove to be true, but the possibility that the short-billed birds may somehow be

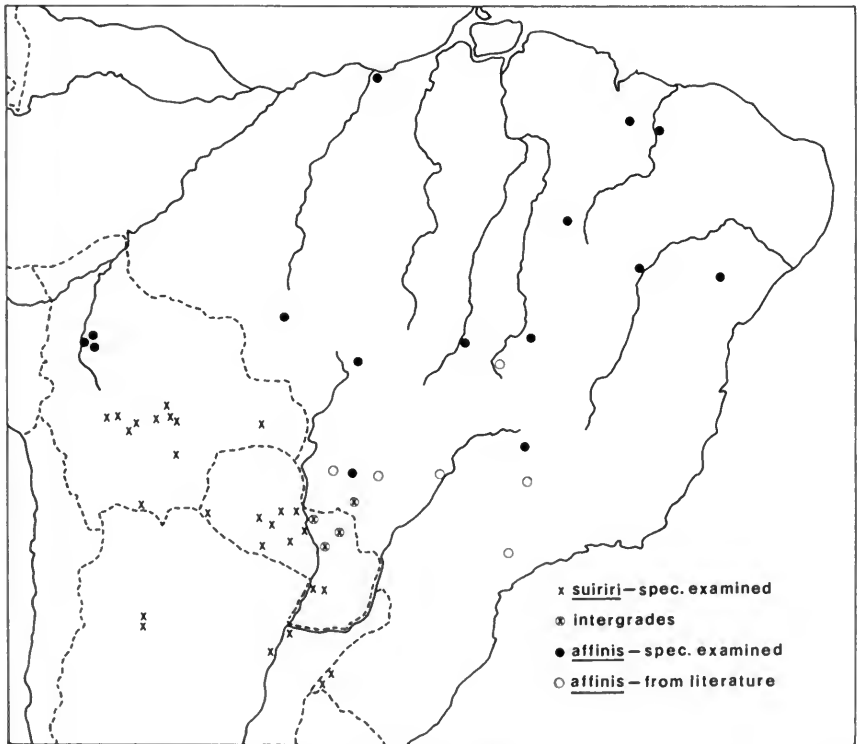


FIG. 3. Localities of *Suiriri suiriri suiriri* (crosses) and *S. S. affinis* (closed circles) from which specimens have been examined. Open circles are localities of *affinis* from the literature, to show its range in southern Brazil. The population of northeastern Paraguay and adjoining Mato Grosso is composed of intergrades between *suiriri* and *affinis*.

related to the intergradation between *affinis* and *suiriri* cannot be ignored at this time. The absolute bill length in the short-billed birds is the same as that in *suiriri*, but the width is the same as in *affinis*, giving the bill a short, broad form more like that of *Sublegatus modestus*. The broad rectrices without edgings, however, are unlike either *affinis* or *suiriri*. A further complication is the status of *bahiae*, a subspecies of *affinis* recorded from eastern Bahia, Pernambuco, and eastern Piauí. *Suiriri bahiae* is like *affinis* in having a yellow belly and long slender bill, but has the rump and upper tail coverts brown, in little contrast to the back, lacks the yellow bases to the rectrices, and has a shorter wing. Zimmer tentatively places two specimens from between PindaHYba and Gilbués, eastern Piauí, in *bahiae*, despite their peculiar coloration. They have the belly white, as in *suiriri*, but have dull outer webs to the outer rectrices and long slender bills as in *affinis*. Zimmer thought they might be lipochrome-deficient specimens of *bahiae*, but also noted that there was a typical specimen of *affinis* from Gilbués. Without adequate series of specimens, particularly of *bahiae*, and, most important, without field studies of the various taxa, it is useless to speculate.

Elaenia albiceps* and *E. parvirostris

Elaenia albiceps and *parvirostris* are two widespread species whose breeding ranges for the most part replace each other in southern South America (fig. 4). *Elaenia albiceps* is a temperate form found in the Andes from southwestern Colombia to Tierra del Fuego and in the temperate lowlands of Argentina and Chile. *Elaenia parvirostris* is a lowland species, breeding from central Bolivia east to southeastern Brazil, and south to Buenos Aires and Córdoba, Argentina. Their breeding ranges abut along the foothills of the Andes from central Bolivia to Tucuman and overlap in Santa Fe, San Luis, and Córdoba. *Elaenia parvirostris* is probably wholly migratory and is found throughout tropical South America east of the Andes in winter. The southern race of *E. albiceps*, *chilensis*, is also migratory for the most part. It breeds in southern Bolivia, in Argentina from Salta, Santa Fe, and Córdoba south to Tierra del Fuego, and in Chile, and winters commonly north to the Amazon and east of the Andes. The populations from the coastal areas of southern Chile must cross the Andes at some point on migration, since there are no known coastal wintering birds. Worn and unsexed specimens, as in any group of closely related *Elaenia* spp., may be difficult to identify, but except for Olrog (1963, p. 269), no one has suggested that *E. albiceps* and *E. parvirostris* are conspecific. However, in recent collections from southern Bolivia, there are intergrades from intermediate altitudes along the Andes, suggesting that there may be a local zone of hybridization in this region. The representatives of *E. albiceps* involved in this hybridization are a sedentary population of *chilensis* which was previously unrecognized.

Fresh specimens of *parvirostris* and *chilensis* are readily separable on a number of characters. *Elaenia parvirostris* is greener, less brownish above, and has the white crown patch smaller and more completely concealed. *Elaenia parvirostris* usually has three well-marked whitish wing bars, and *E. a. chilensis*, never more than two. The form of the wing tip is an excellent character for distinguishing migratory *chilensis*, not only from *parvirostris* but from other races of *E. albiceps* in whose ranges it winters. As pointed out by Zimmer (1941a, p. 8), in these *chilensis* the 10th primary is almost always longer than the fifth, whereas in all other taxa of this complex, it is shorter. In size, *chilensis* is larger than *parvirostris*, although there is overlap in all dimensions. The populations of *chilensis* in

TABLE 2. Measurements (in mm) in *Elaenia* spp.

Males	N	Wing	Tail	Culmen	Tarsus
<i>chilensis</i> , migrant	26	76-82 (78.7)	61-71 (64.3)	13-15 (14.2)	17.5-20.5 (19.3)
<i>chilensis</i> , Bolivia	8	77-81 (78.9)	60-75 (68.6)	13-14 (13.7)	18.5-21 (19.1)
<i>albiceps</i>	7	80-87 (83.0)	72-78 (74.1)	14-15 (14.6)	18.5-21 (19.4)
<i>parvirostris</i>	14	69-76 (73.3)	58-66 (62.6)	12-13 (12.6)	17-19 (18.0)
Females					
<i>chilensis</i> , migrant	10	71-74 (73.2)	58-63 (60.4)	13-15 (14.1)	17.5-20 (18.4)
<i>chilensis</i> , Bolivia	7	71-75 (73.1)	58-64 (61.1)	13-14.5 (13.7)	16.5-19 (17.5)
<i>albiceps</i>	6	78-85 (80.2)	71-77 (73.2)	13-14.5 (13.5)	18.5-20 (19.0)
<i>parvirostris</i>	9	68-73 (70.2)	57-62 (60.6)	12-14 (12.9)	16.5-18 (17.6)

the mountains along the eastern slope of the Andes in southern Bolivia are identical with the migratory *chilensis* in every way except that they lack the distinctive wing tip. On the assumption that the more pointed wing of Argentinian and Chilean birds is associated with their migratory habits, then the Bolivian populations are probably sedentary. The latter intergrade with nominate *albiceps* in northern Chuquisaca and adjoining Cochabamba; *albiceps* is the brownest race, with a large white crown whose lateral edges are washed with brown, and is the largest race, with a proportionately long tail. Measurements for the various taxa are given in Table 2.

These measurements point up the fact that *parvirostris* is smallest (= shortest winged), with a disproportionately short bill, and nominate *albiceps* by far the largest, with an extra long tail. Specimens from Chuquisaca and Tarija have been lumped in the Bolivian *chilensis*, but the more northern birds are slightly larger and definitely longer tailed as they approach *albiceps*.

In Argentina there is positive evidence that *E. parvirostris* and *E. albiceps chilensis* behave as distinct species. The points on the map (fig. 4) are actual breeding localities, based on personally examined specimens or on accounts in the literature. The breeding ranges overlap from Salta south to San Luis and east to Santa Fe and eastern Córdoba, and I have found no suggestion of intergradation in any specimens from that area. Not only are the species distinguishable on the morphological characters listed above, but they build different types of nests. Hoy (1971, p. 160) found *parvirostris* nesting at San Lorenzo in the Lerma Valley, Salta, where *chilensis* was common. He found *parvirostris* to be a bird of tall woodland, which reached its upper limit at 1,500 m at San Lorenzo. *Elaenia chilensis* occurred more in small trees and around agriculture, and was found from 1,500 m up to 3,500 m. The nest of *parvirostris* was a small neat cup of straw and plant fibers covered on the outside with moss and lichens, much like that of a hummingbird. It was built on a large branch or on a fork and sat up on its foundation. The nest of *chilensis* was built of dried grasses or straw and lined with feathers; it was constructed on the outer branches of low bushes, with the nest woven into their twigs. These descriptions agree with others from elsewhere. Pereyra (1942, p. 229) and Eisentraut (1935, p. 428), writing of *parvirostris*, mention the small nests covered with lichens on the outer branches of the trees, and Goodall et al. (1957, p. 193) describe the nest of *chilensis* as built of various plant fibers and lined with feathers and placed in small dense trees or most especially in young pines. Despite Olrog's suggestions, there is no evidence that *parvirostris* and *chilensis* are other than good sympatric species in Argentina.

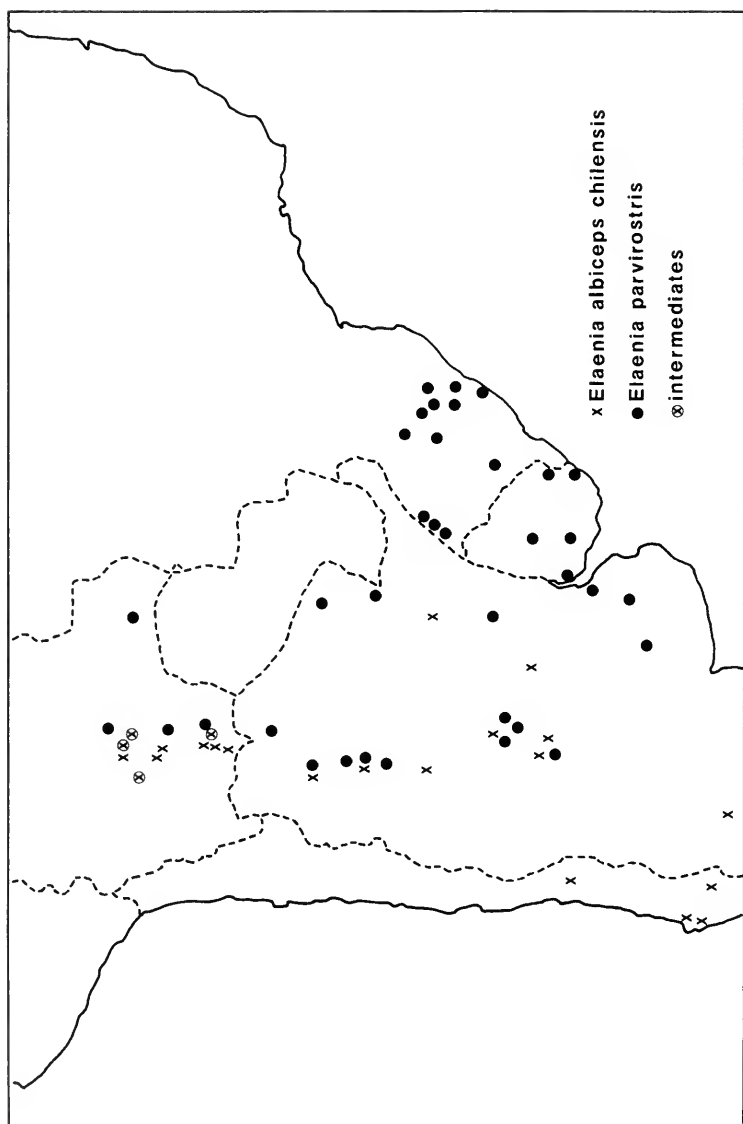


FIG. 4. Breeding records of *Elaenia albiceps chilensis* and *E. parvirostris*, based on specimens and on published records of actual nesting. The two are sympatric in Argentina with no sign of intergradation. However, in Bolivia, where *chilensis* replaces *parvirostris* at higher elevations, intermediate populations are found.

In southern Bolivia the situation appears quite different. In the lowlands, in Tarija and Santa Cruz, typical *parvirostris* is found. Above 2,000 m along the eastern slope of the Andes, *E. albiceps* occurs, represented by *chilensis* in Tarija and nominate *albiceps* in Cochabamba, the two intergrading in northern Chuquisaca. At intermediate altitudes, however, populations are found that are intergrades between *E. parvirostris* and *E. albiceps*, suggesting that the two species hybridize in this area.

In Tarija typical *parvirostris* is found at Villa Montes, 600 m, while at two localities 108 km ENE and 67 km E of the city of Tarija, at 1,950 and 2,240 m, respectively, typical *chilensis* occurs. At Entre Rios, however, at 1,400 m, the population is intermediate between *parvirostris* and *chilensis* in both color and size, and individuals may have two or three wing bars. Farther north, in western Santa Cruz, the *parvirostris* element extends higher into the mountains. Five birds from Samaipata, 1,670 m, are intermediate but generally nearer *parvirostris*, and evidence of intergradation is found as far west in Cochabamba as Aiquile and Tin-Tin, both 2,150 m, on the south side of the Mizque Valley. North of the Mizque River, at Pocona and Totorá, 2,700 and 2,900 m, respectively, typical *albiceps* is found, and *chilensis* occurs at Padilla and Tomina, Chuquisaca, south of Aiquile and Tin-Tin.

If only the evidence from Bolivia were available, we would have to consider *parvirostris* and *albiceps* conspecific. However, since the two are widely sympatric in Argentina without hybridization, I prefer to keep them distinct species. This is obviously a subjective decision, since in the somewhat similar case of *Sblegatus obscurior* and *S. modestus*, I treated the hybridizing taxa as conspecific. In *Sblegatus* the apparent overlap is based on the population of nominate *modestus* in the Urubamba Valley of Peru, within the range of *obscurior* along the eastern foot of the Andes, and on the single specimen of *modestus* from Mexiana Island, which may or may not be a breeding bird. At no locality are *modestus* and *obscurior* known to be in contact without hybridizing, and nothing is known of their comparative behavior, so the conservative course is to treat them as conspecific pending further data. On the other hand, *Elaenia albiceps* and *E. parvirostris*, which broadly overlap in northern Argentina, have been known to breed side by side without hybridization and to show different ecology and nesting habits. They seem to be good sympatric species that, for some reason, hybridize in a limited part of their range. Examination of the breakdown of the isolating mechanisms between them in Bolivia would make an elegant field study.

Hemitriccus iohannis and H. striaticollis

Hemitriccus iohannis was considered a subspecies of *striaticollis* by Hellmayr (1927, p. 313) and Zimmer (1940, p. 11). Gyldenstolpe (1945, p. 252) presented evidence that *iohannis* was a distinct species and that the remaining races of *striaticollis* also represented two species, *griseiceps* and *striaticollis*. However, Meyer de Schauensee (1966, p. 366) accepted Zimmer's treatment and united all the taxa in one species. Reexamination of most of the material available to the above authors, plus much new material from critical areas, shows that *H. iohannis* is a distinct species, and that the remaining taxa form a single species, *H. striaticollis*.

Typical *striaticollis* was originally described from Bahia, eastern Brazil. It is

characterized by a brownish wash on the crown, distinct from the green back; lores and eye ring white; wing coverts uniform with the back; throat white, clearly striped with dusky; belly clear pale yellow. Birds of this type have a continuous range from extreme southeastern Peru through northern Bolivia and northern Mato Grosso to northeastern Brazil from Maranhão to Bahia (fig. 5). There are also two isolated populations, in northern San Martín, Peru, at Moyobamba, and in eastern Meta, Colombia, at Carimagua. Despite this extensive and fragmented range, I am unable to recognize more than one race. Zimmer (1940) separated the populations of Mato Grosso and Moyobamba as *obscuriceps* because of their darker crowns and more olive wash on the sides of the breast. However, these are individually variable characters, as pointed out by Pinto & Camargo (1961, p. 259), and also ones that are associated with the age of skins; recent (1970s) skins from Meta and southeastern Peru are much more freshly colored than early (1900s) skins from Moyobamba. Within the range outlined above, I recognize only *striaticollis*, with *obscuriceps* as a synonym.

There is one isolated population of *H. striaticollis* which is a recognizable subspecies. This is *griseiceps*, which is found along both banks of the lower Tapajóz. It is characterized by a gray rather than brown pileum, and the majority of specimens are readily distinguishable, although when long series of *griseiceps* and *striaticollis* are compared, the difference between them is bridged by individual variation. This is important, because Gyldenstolpe (1945) had four typical *griseiceps* and one typical *striaticollis* from the right bank of the lower Tapajóz, and he considered that they must be treated as two distinct species. I have examined these specimens in the Royal Natural History Museum in Stockholm, and they show the distinctions Gyldenstolpe claimed for them. However, all fall within the range of variation of series of 23 *griseiceps* from the Tapajóz in the American and Carnegie Museums, and *griseiceps* must be considered a subspecies of *H. striaticollis*.

The third well-marked entity is *iohannis* of upper Amazonia. It is distinguished from *H. striaticollis* by the crown being green, uniform with the back; the lores and eye ring are dull rusty instead of white, although there is sometimes a whitish supra-loral mark; the wing coverts are edged with yellow, producing slight wing bars; the throat is washed lightly with yellow, and the dark streaking is duller and less clearcut; and the sides of the breast and flanks are washed with greenish. Typical *H. iohannis* is found from southeastern Colombia at San Antonio, Putumayo, through the lowlands of eastern Peru and western Amazonas, Brazil, to northern Beni, Bolivia. Specimens from Pebas, north of the Marañon in Loreto, Peru, were described as a separate subspecies, *amazonicus*, by Hellmayr (1914, p. 168). I have examined a specimen from Apayacu, near Pebas, in the American Museum, and do not find that it differs from *iohannis* in any significant way. The San Antonio specimen in Field Museum does differ from *iohannis* in being whiter on throat with clearer streaking, characters of *striaticollis*, but it does have the green crown, slight wing bars, and dark eye-ring of *iohannis*. Until more material from north of the Marañon is available, I shall consider *amazonicus* a synonym of *iohannis*.

The critical area where the ranges of *H. striaticollis* and *H. iohannis* come together is northern Bolivia and adjoining Peru. Gyldenstolpe (1945) had a fine series of *iohannis* and a single specimen of *striaticollis* from Victoria and Riberalta at the confluence of the Ríos Beni and Madre de Dios. Typical

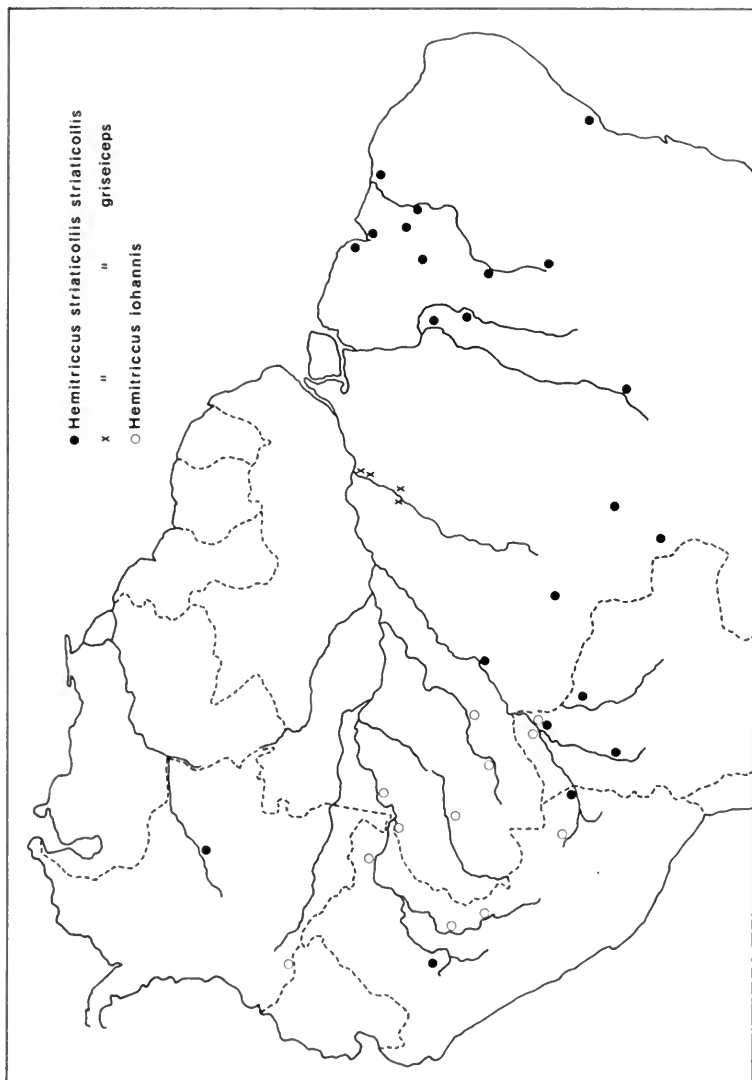


FIG. 5. Distribution of *Hemitriccus striaticollis* and *H. iohannis*. Nominate *striaticollis* occurs east and south of the Amazonian forest, with isolated populations in northern Peru and eastern Colombia. *Hemitriccus iohannis* occupies western Amazonia and overlaps *striaticollis* in northern Bolivia. Points are from specimens personally examined.

the Museum of Comparative Zoology has taken *signatus* at San Jose de Lourdes in Cajamarca, Abra Patricia on the road to Rioja in San Martín, and in the Panao region of Huánuco. Altogether there are now four adult males, three adult females, and three subadult males available for study.

Any doubt that the recently collected specimens are identical with Taczanowski's *signatus* has been removed through the kindness of Charles Munn, who made meticulous color notes, measurements, and color photographs of the Ninabamba juvenal in the Warsaw Museum. Except that it appears slightly more reddish brown on the upper parts, a character also found in juvenal *K. cabanisi*, it is virtually identical in size and color with the northern Peruvian specimens. The taxa will have to be known as:

Knipolegus signatus signatus—mountains of northern Peru from Cajamarca to San Martín and south to Junín

Knipolegus signatus cabanisi—mountains from southern Peru to northern Argentina

Wolters (1977, p. 182) has also recognized that *signatus* is a species of *Knipolegus*, and in his list of species, he placed it next to *cabanisi*. Although I include *cabanisi* as a subspecies of *signatus*, the two are quite distinct, and a case can be made for calling them two species. Either way, they certainly form a well-marked zoogeographical species, much closer to each other than to any other *Knipolegus*. In the discussion below, I compare *signatus* with the better-known *cabanisi*.

In both sexes, *signatus* is markedly darker than *cabanisi*. Males of *signatus* are uniformly black rather than dark, slate gray, but in both taxa the inner webs of the secondaries and of the proximal half of the primaries are broadly edged with white. In females the upper parts of *signatus* are a darker, warmer olive-brown than those of *cabanisi*, and the same is true of the heavy flammulations of the underparts. Subadult males are similar to females. In female *cabanisi*, the outer webs of the rectrices are narrowly edged rufous, and the inner webs are more than half rufous, this color almost reaching the shaft at the base of the feathers. In *signatus*, the edging on the outer webs is virtually obsolete, and that on the inner webs is duller and darker and occupies much less than half the web. In both taxa, females and subadult males have two well-marked wing bars that vary from white to buff. This variation is not correlated with age or sex, but seems to be dependent on wear. In two specimens that have a mixture of white and buff feathers in the wing bars, the buff feathers are fresh and the white ones worn.

There is little difference in measurements between the two taxa, except that *signatus* has a distinctly longer bill in both sexes. The 10th (outermost) primary in *signatus* is markedly shorter than that in *cabanisi*, being equal to or shorter than the first rather than about equal to the fourth. The outer primaries of *signatus* are broader than those of *cabanisi*, and the 10th lacks the slight notch that is found in *cabanisi*. There is no sexual variation in the form of the primaries. The sequence of plumages appears to be identical in *cabanisi* and *signatus*. The juvenal plumage is similar to that of the adult female, except that there is a slight rusty wash on the upper parts. The postjuvenal molt is incomplete, involving only the body feathers. Subadult females molt into a plumage that is indistinguishable from that of the adult female. Males molt into a subadult plumage that is also like that of the adult female, but they can always

be distinguished by their greater size. The subadult plumage is worn for at least a year, and the adult plumage is presumably assumed at the time of the first regular postnuptial molt. It is not known if males breed in subadult plumage, but those taken in the breeding season in Bolivia had testes as much enlarged as fully plumaged males.

Moist montane forest is the preferred habitat for both *signatus* and *cabanisi*. The former has been taken from 1,900 to 3,050 m in northern and central Peru, and the latter from 1,100 to 2,500 m in Bolivia and northern Argentina.

Berlioz (1959, p. 217) described *Knipolegus subflammulatus* on the basis of four males from Alto Palmar, Cochabamba, Bolivia. He characterized it as similar in plumage to the female of *cabanisi*, but with males retaining the female plumage at maturity, as in *K. poecilurus*, rather than assuming a gray, male-type plumage, as in *cabanisi*. I have examined three *cabanisi* from Alto Palmar, including two full-plumaged males, and I think that Berlioz described *subflammulatus* from subadult males of *cabanisi*. This was also the conclusion of Mayr (1971, p. 313), who noted that Meyer de Schauensee had examined the types. Parkes, who first suggested this identification of *subflammulatus* to Mayr, has shown me his correspondence with Berlioz, who was quite willing to accept Parkes' suggestions when he realized that young males of *Knipolegus* species have a first-year plumage similar to that of the adult female. The measurements given by Berlioz, 70–72 mm, are much too small for any age or sex of *cabanisi*. However, Dr. Christian Erard has been kind enough to remeasure the type series for me, and his wing measurements are 76, 77.5, 79, and 79.5 mm. The two smaller figures are typical of female *cabanisi*, and the two larger are smaller than my immature male *cabanisi*, but not significantly different.

Summary

Tyranniscus australis is shown to be a synonym of *Phyllomyias sclateri*. *Phyllomyias reiseri* is shown to be a race of *P. virescens*. Extensive altitudinal variation in size is demonstrated in *Zimmerius vilissimus*. The genus *Sublegatus* is shown to be composed of two species, *arenarum* and *modestus*. *Suiriri suiriri* and *S. affinis* intergrade extensively in northern Paraguay and should be considered conspecific. *Elaenia albiceps* and *E. parvirostris* are widely sympatric in Argentina, but hybridize in Bolivia. *Hemitriccus iohannis* is shown to be a good species and not a race of *striaticollis*. *Ochthodiaeta signatus* belongs in the genus *Knipolegus*, where it is conspecific with *cabanisi*.

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