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Geographic Variation and Evolution in South American *Cistothorus platensis* (Aves: Troglodytidae)

Melvin A. Traylor, Jr.

A Contribution in Celebration of the Distinguished Scholarship of Robert F. Inger on the Occasion of His Sixty-Fifth Birthday

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MURRA, J. 1946. The historic tribes of Ecuador, pp. 785–821. *In* Steward, J. H., ed., Handbook of South American Indians. Vol. 2, The Andean Civilizations. Bulletin 143, Bureau of American Ethnology, Smithsonian Institution, Washington, D.C.

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Geographic Variation and Evolution in South American *Cistothorus platensis* (Aves: Troglodytidae)

Abstract

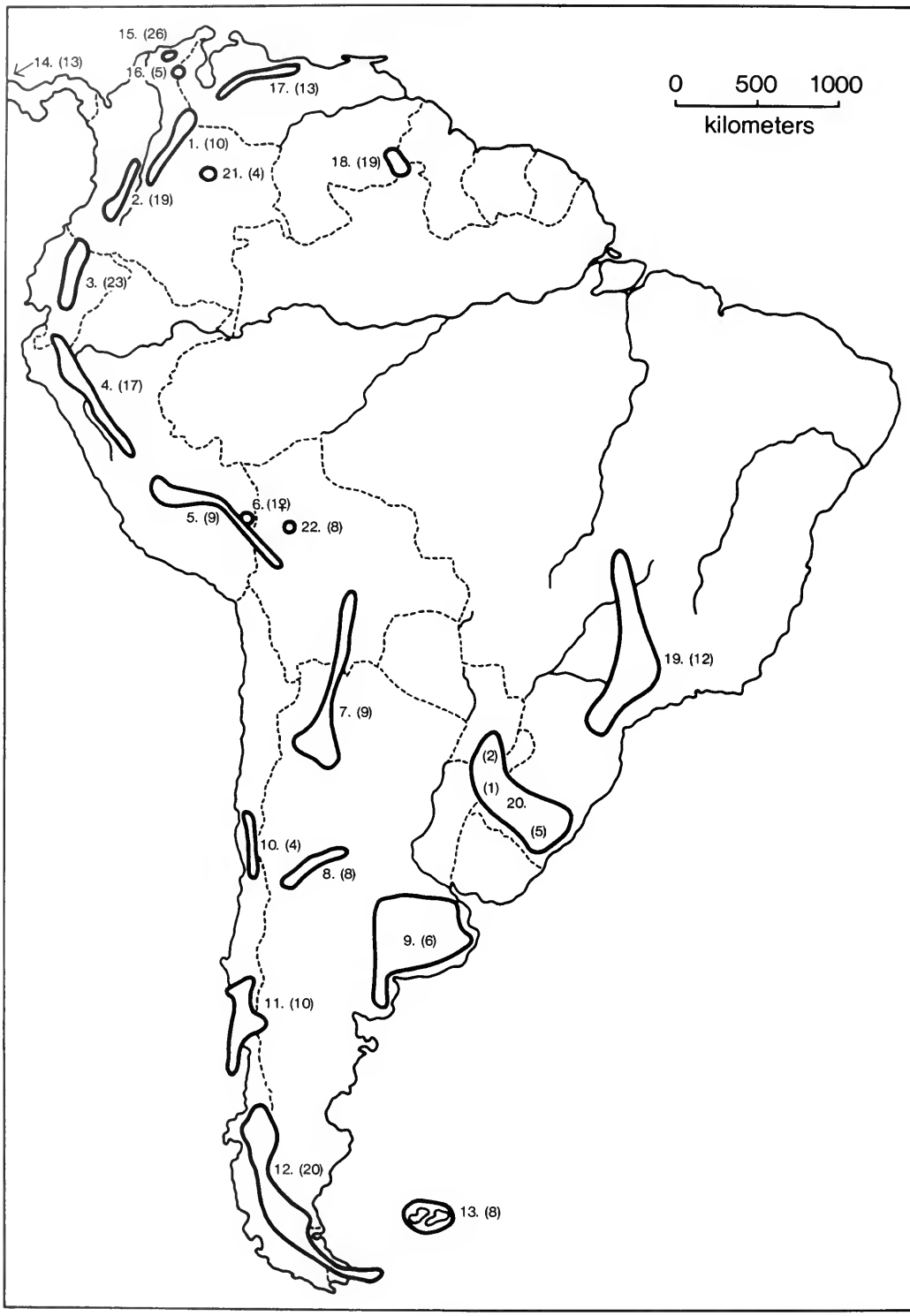
The sedge wren, *Cistothorus platensis*, occurs in eastern North America and locally in Central and South America south to Tierra del Fuego, Argentina, and the Falkland Islands. The South American populations are divisible into two groups. The first group is found in the high Andes from northern Colombia and adjoining Venezuela south to Tierra del Fuego and in the lowlands of central Argentina east to Buenos Aires Province. The second group occurs at subtropical elevations in the Sierra Nevada de Santa Marta, Colombia, and locally in the highlands of Venezuela, reappearing in southeastern Brazil and in three isolated populations in the llanos of Colombia, the lowlands of northern Bolivia, and the highlands of southeastern Peru. The respective northern populations of the two groups differ in size and proportions and show no intergradation across a geographical gap of only 200 km. However, in Paraguay, northeastern Argentina, and southern Brazil, the two groups interbreed extensively. The Andean group is extremely variable geographically, but the eastern group shows practically no variation within a range from northeastern Colombia to southern Brazil. This pattern is considered the result of two separate invasions from the north. The earliest population colonized the Andes and central Argentina, where it has undergone much variation; the second colonized the northern highlands and eastern lowlands and is so recent that it has undergone only modest changes. The two groups must be considered a single species because they still interbreed freely in southeastern South America.

Introduction

This study of *Cistothorus platensis* in South America was stimulated by the receipt of four specimens collected by Sean Furniss in 1976 from Carimagua in the llanos of eastern Colombia. They were the first specimens from a lowland locality north of the Amazon, and it was of great interest to determine whether they were related to one of the northern highland races or to the lowland race of southeastern Brazil. The solution to this question eventually involved the study of all available specimens from South America. The patterns of variation revealed by this study suggest three conclusions:

1. *Cistothorus platensis* made two separate invasions of South America from the north. One followed the high Andes south to Tierra del Fuego and the Falkland Islands (Islas Malvinas) and east to Buenos Aires Province, Argentina. The other spread through intermediate altitudes in the Sierra Nevada de Santa Marta, Colombia, and the Venezuelan mountains, then south through the lowlands east of the Andes to Paraná and Rio Grande do Sul, Brazil. Where the Colombian/Venezuelan representatives approach each other, they are strikingly different and show no signs of intergradation; however, where the respective representatives meet in southern Brazil and northeastern Argentina, there is complete intergradation.

2. The Andean populations of *Cistothorus* show a great deal of geographic variation both in size and plumage pattern, and two of them, *apolinari* and *meridae*, are actually considered separate species, but the regions of change in the different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characters are nonconforming. This suggests that the populations have been subjected to a number of climatic or geographic vicissitudes that have acted selectively on different characters and that the presence of *platensis* in the Andes and temperate South America is a comparatively old one.

3. The populations from Santa Marta through Venezuela to southeastern Brazil are remarkably uniform, showing only ill-defined clinal color changes and one variation in proportions. At some recent date, the species must also have been much more widespread, for there are still two essentially unchanged relict populations in lowland eastern Colombia and lowland eastern Bolivia and a slightly modified population that has penetrated to 2750 m in Puno, Peru. The relative uniformity among isolated populations separated by thousands of kilometers suggests that this must be a much more recent invasion than that of the Andes.

Materials and Methods

Altogether, 387 specimens of South American *C. platensis* were examined. Of these, 229 adult or adult-plumaged males were used in the study of variation (Appendix A; fig. 1). Dickerman (1975) considered sexual dimorphism to be so slight in Central American *platensis* that he lumped the measurements of both sexes in his comparisons. However, among the South American populations, female wing length varied from 95% to 101% of male wing length. In three populations this difference was statistically significant ($P < .01$), and in others it was nearly so. For this reason measurements of the sexes were kept separate. In the following discussion of variation, only males were considered, because within some populations, the series of females was too small.

The geographical groupings of populations for statistical and comparative purposes are based on uniformity of characters within groups and the apparent presence of real geographic gaps between groups. In a few cases, where specimens are sparse, a number of isolated populations are grouped together to boost sample sizes to permit quantitative analysis (fig. 1). Figure 2 shows the inclusive altitudes within which specimens were taken in each group. The groupings are based only on specimens that I have personally examined. The only published records that I have found that would fall outside these groupings are two from Minas Gerais, Brazil (Hellmayr, 1934, p. 118), which extend the southeastern Brazil group to the east.

Seven characters, three mensural and four plumage, were used to analyze the pattern of variation within *platensis*. Each was plotted on a map of the population groups, and the areas of clinal change or abrupt discontinuity were determined. These areas of change or discontinuity were plotted together on a summary map which gives a graphic representation of the areas of major differentiation between groups. The characters used were wing length; relative tail and tarsal lengths (tail/wing and tarsus/wing ratios); crown pattern (streaked or plain); extent of streaking on back; rump and lower back (called "rump" for convenience) pattern (plain, barred, or streaked); and rectrices, (whether the inner webs of pairs 2–5 are barred or washed with black).

As noted by James (1970), "the least variable and most valid indicator of body size for intraspecific comparisons in birds is generally considered to be wing length," and that measure is used here. However, the relative tail and tarsal lengths are better indicators of variation in proportions. The Student's t test was used to determine the statistical significance of differences between absolute measurements, and the Mann-Whitney U test was used for ratios. Values of $P \leq .05$ were considered statistically significant.

Character Variation

Wing Length

Figure 3 gives the variation of wing length means among South American *C. platensis*. The most

Opposite Page:

FIG. 1. Geographical groups of *Cistothorus platensis*: **1,** northern Eastern Andes; **2,** Central Andes; **3,** northern Ecuador (including adjoining Colombia); **4,** northern Peru (including southern Ecuador); **5,** south-central Peru and La Paz, Bolivia; **6,** Oconeque, Puno, Peru; **7,** southern Andes (Santa Cruz, Bolivia, to Tucumán, Argentina); **8,** west-central Argentina; **9,** Buenos Aires Province; **10,** north-central Chile; **11,** south-central Chile (and adjoining Neuquén, Argentina); **12,** southern Chile and Patagonia, Argentina (including Tierra del Fuego); **13,** Falkland Islands (Islas Malvinas); **14,** Costa Rica (including Chiriquí, western Panama) just off map; **15,** Sierra Nevada de Santa Marta; **16,** Sierra de Perijá, Venezuela; **17,** Coastal Range, Venezuela; **18,** Mt. Roraima and vicinity; **19,** southeastern Brazil; **20,** zone of intermediacy, Paraguay; Corrientes, Argentina; and Rio Grande do Sul, Brazil; **21,** Meta, Colombia; **22,** El Beni, Bolivia. The figures in parentheses are the number of adult males in each group that were used in this study.

FIG. 2. Altitudinal range (in meters) within which specimens of *Cistothorus platensis* were collected.

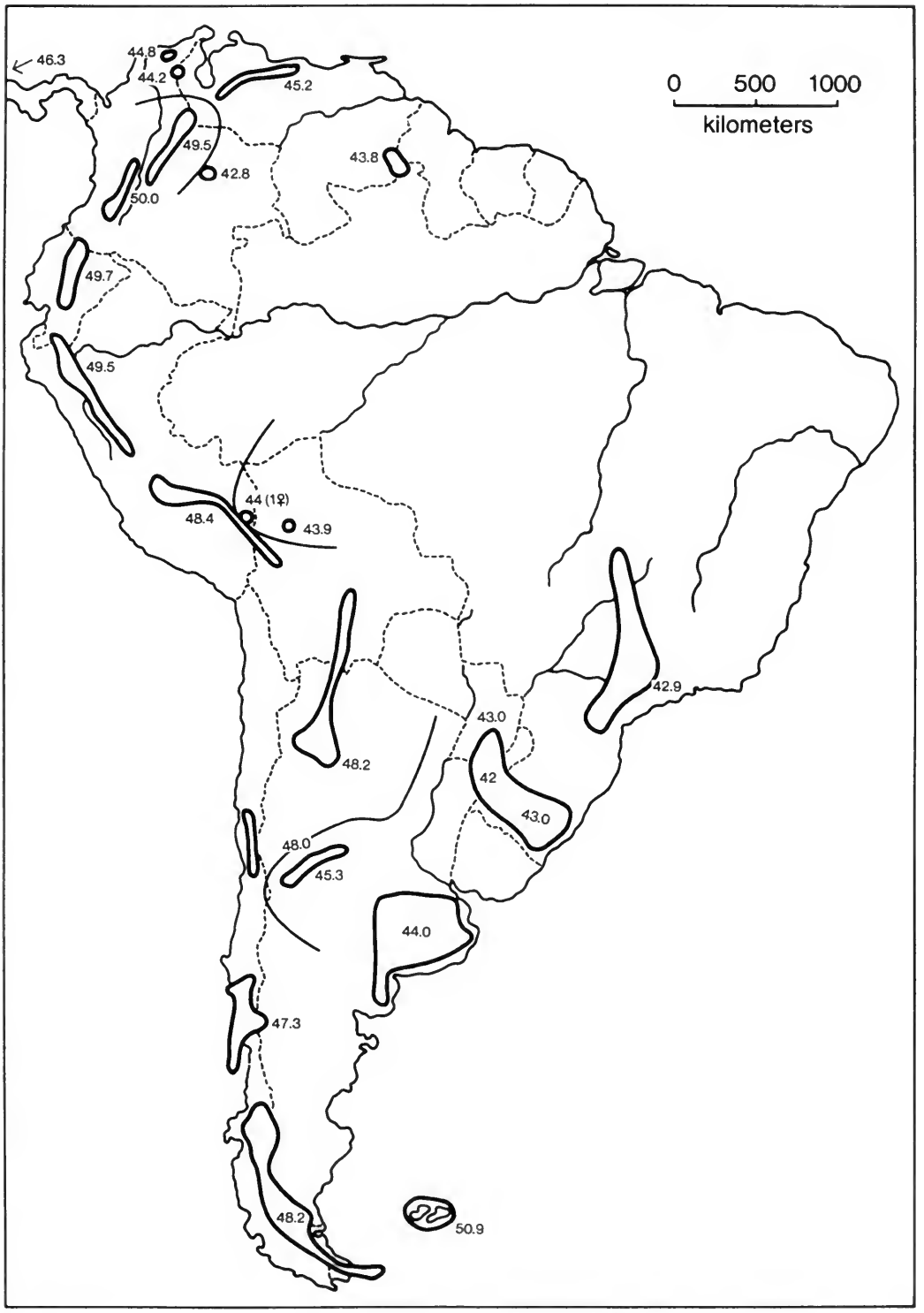


FIG. 3. Mean wing length of adult males for each population group.

obvious pattern to emerge is the series of long-winged populations (means 47.3–50.9 mm) along the spine of the Andes from the northern Eastern Andes, including the Páramo de Tamá of Venezuela, south to Tierra del Fuego and the Falkland Islands (Islas Malvinas). The remaining populations, from the mountains of Santa Marta and of Venezuela south through the lowlands to central Argentina, are consistently smaller (mean wing lengths 42.8–45.3 mm).

There are three areas where the change in wing length is abrupt, of the type expected where there is a secondary meeting of different taxa, but apparently no genetic exchange.

The first area is between the northern Eastern Andes in Colombia (group 1) and the adjoining populations to the north (Santa Marta, Colombia, group 15; Sierra de Perijá, Venezuela, group 16; and the Coastal Range in Venezuela, group 17). These differences between the population of the Eastern Andes and those to the north are all highly significant statistically ($P < .001$).

The second area is in Puno, southern Peru, where the small population at Oconeque (group 6) intrudes into the large group of southern Peru/La Paz, Bolivia (group 5). Unlike individuals of other small-sized populations south of the Amazon, those of group 6 have been taken at 2745 m, as high as some individuals of the large population. The small birds of group 6 are known from a male and female collected by Carriker; I have had to use the female's measurements, because the male type was not seen. Compared to 11 females from the southern Peru/La Paz group, the female from Oconeque is significantly smaller ($P < .01$).

The third area where small and large populations approach each other is in west-central Argentina. Here the change in wing length is not so abrupt: 48.2 mm in Tucumán (group 7), 45.3 mm in west-central Argentina (group 8), and 44.0 mm in Buenos Aires (group 9). The differences between groups 7 and 8 are statistically significant ($P < .01$), but those between groups 8 and 9 are not ($P \cong .10$).

Although there appears to be a modest cline of decreasing size from north to south along the Andes in the long-winged populations, there is actually no significant difference between the geographical extremes (groups 1 and 12; $P \cong .4$). The only significant difference is between the birds from Patagonia (group 12) and those from the Falkland Islands (group 13); the latter are longer-winged ($P < .01$).

Within the short-winged groups, birds from above 30°S in Argentina, or from the mountains of Colombia and Venezuela, usually have wing lengths above 44.0 mm, whereas those from more tropical regions have wings shorter than 44.0 mm. However, there are no sharp breaks in the size cline.

Relative Tail Length

Figure 4 shows the proportional tail lengths for each group. There are two fairly well-defined areas in which the tail is comparatively short (tail/wing ratio < .880).

The first area is in the northern Andes, comprising the northern Eastern Andes through Ecuador (groups 1–3), and the lowlands of Meta, Colombia (group 21). To the north and east, the populations of Santa Marta and the Venezuelan highlands (groups 15–17) are moderately long-tailed (tail/wing ratios .919 to .949), although the Roraima population in Venezuela (group 18) is intermediate (.893). Going south through the Andes, the change between northern Ecuador (group 3) and southern Ecuador/northern Peru (group 4) is quite abrupt (.876 and .948, respectively), and ratios remain high as one goes south, actually reaching parity in west-central Argentina. The only Andean exception to these high tail/wing ratios is again the single specimen from Oconeque, Puno (group 6), which has a ratio of only .886. With only the single specimen, however, the ratio is less dependable than absolute measurements.

The second area of short-tailed birds is in the extreme south, from south-central Chile (group 11) to Tierra del Fuego (group 12) and the Falkland Islands (group 13). Here the discontinuity is abrupt (tail/wing ratio of 1.003 in group 8 of west-central Argentina vs. only .845 in group 11). The north-central Chile (group 10) populations are intermediate in form (ratio .911), although not in geographic location. Even with the more variable ratios, there is no individual overlap between the populations of west-central Argentina and Buenos Aires on the one hand, and those of south-central and southern Chile and Argentina and the Falkland Islands on the other.

The remaining major lowland population in southeastern Brazil (group 19), has a fairly high tail/wing ratio of .954. The birds (group 20) from the area of intermediacy between southeastern Brazil and Buenos Aires, where the ratio is .968 (group 9), are variable but shorter-tailed, with ratios of .833 to .930. The isolated lowland population in El Beni, Bolivia (group 22), has a ratio of .978, similar to that of the Brazilian birds.

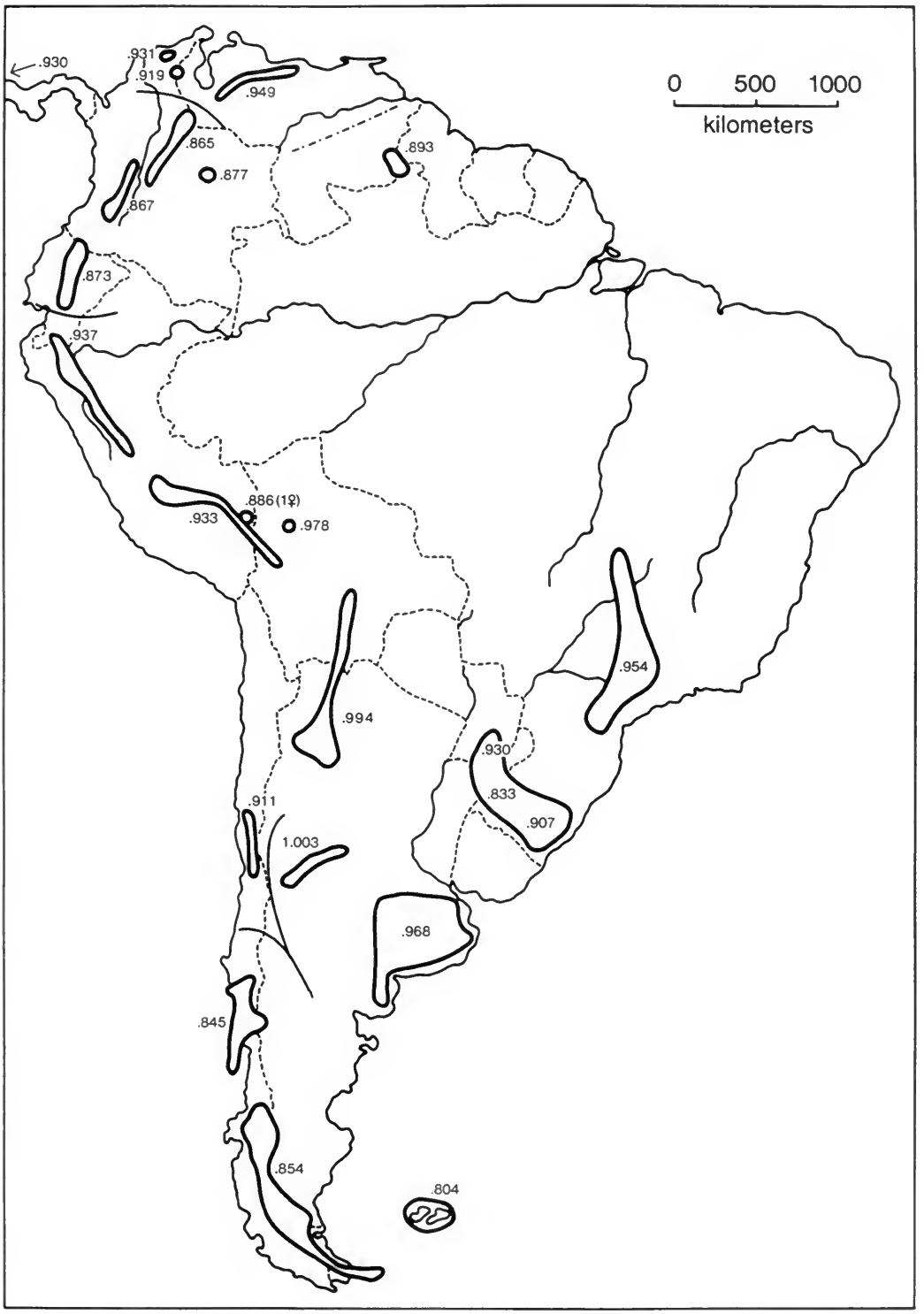


FIG. 4. Relative tail length (tail/wing ratio) for each group.

Relative Tarsal Length

Relative tarsal length shows few consistent geographic trends (fig. 5), except for one group of populations that is sharply set apart by its long tarsi. From the northern Eastern Andes (group 1) south to La Paz, Bolivia (group 5), all populations have a relative tarsal length of .392 to .414. At the north end of the range, between the Eastern Andes and the mountains of Santa Marta and of Venezuela (groups 15–17), the change in relative tarsal length is moderate, from .402 to .378, and to .380 in the lowlands of Meta (group 20). The statistical significance of these differences varies from $P < .001$ (for n = 26) to $P < .10$ (for n = 4). Since the probability was greater than .05 only for the smallest sample, I consider the differences biologically significant for all groups. However, at the south end of the range, between southern Peru/La Paz (group 5) and the southern Andes (group 7, Santa Cruz, Bolivia, to Tucumán, Argentina), there is an abrupt change (.414 to .357). This difference is highly significant statistically ($P < .001$). The ratio from the southern Andes is typical of the southern populations from north-central Chile and Buenos Aires to Tierra del Fuego and the Falkland Islands (groups 8–13). The single female from Oconeque (group 6) also has a relatively short tarsus, .375 compared to .399 for 10 females from southern Peru/La Paz, including one from Valcón, Puno, only 55 km from Oconoque. This difference does not prove to be significant statistically ($P \cong .3$) for the single specimen, but a longer series might show that it actually is.

Crown

There are basically two types of crown pattern, plain or streaked (fig. 6). Among the plain-crowned populations, there is often enough pale tipping or suggested pale streaking to give a distinctly mottled appearance, as is indicated in the figure. However, there does seem to be a quantitative change between the populations of the northern Andes (groups 1–4) and those of central and southern Peru (group 5) (fig. 7). While the former have plain crowns, the crown feathers of the latter are pale buffs and browns with variable blackish edgings, giving the effect of pale streaks on a blackish ground. The general effect varies greatly, depending on the original extent of the blackish edgings, the degree of wear, and the amount of bleaching of the pale streaks. Where the blackish edges are confined to the proximal half of the feather, the effect is of pale buff streaks on a darker brown ground. As the blackish extends distally, the background becomes more nearly blackish, and the pale streaks more contrasty. Within the area of streaked crowns, a cline of increasing contrast runs from southern Peru to western Argentina and Buenos Aires (groups 8–9) (fig. 7). In the latter region, the effect is of pale buff streaks on a black background, covering the whole crown, including the nape and blending into the back. Going south from central Argentina, the background again becomes more brownish, starting with the nape, and the crown of Tierra del Fuego birds is much like that of southern Peru birds. Throughout all the populations, the buff streaks become much paler with wear and may be almost white by the end of the breeding season.

All the groups of the northern Andes, highlands of Venezuela, and eastern lowlands are essentially plain-crowned, but those from the area of intermediacy (group 20) show graded steps to the heavily streaked crowns of Buenos Aires birds (fig. 7). The crowns of typical southeastern Brazil (group 19) specimens are uniform mouse brown, but the pair from Paraguay have a much darker background, with faint, deep buff streaking. The birds from Corrientes, Argentina, and Rio Grande do Sul, Brazil, have blackish crowns as do those from Buenos Aires, but the streaks are narrower, occasionally reduced to fine shaft streaks.

Back

Geographic variation in the streaking of the back is shown in Figure 8. Variation is apparent in both the contrast of the streaks and their topographic extent (fig. 7). In all populations there is streaking on the interscapular region or mantle, and in heavily streaked birds, the scapulars and lower back and also the lesser wing coverts, which are otherwise plain, are also marked (fig. 7).

The dorsal stripes are similar to the coronal stripes, that is, there is a pale center stripe, buff to whitish, bordered laterally with dark brown to blackish. In the sparsely striped birds ("O" on fig. 8), the dark borders may occasionally be replaced by the ground color of the back, either as a stripe between the pale center and dark edging or completely replacing the dark edging on one web. The general effect in these sparsely striped birds is of a mantle with pale and dark stripes on a ground color of dull brown like the remainder of the upperparts. The next stage is the intensification of the dark edgings to fuscous or blackish and the

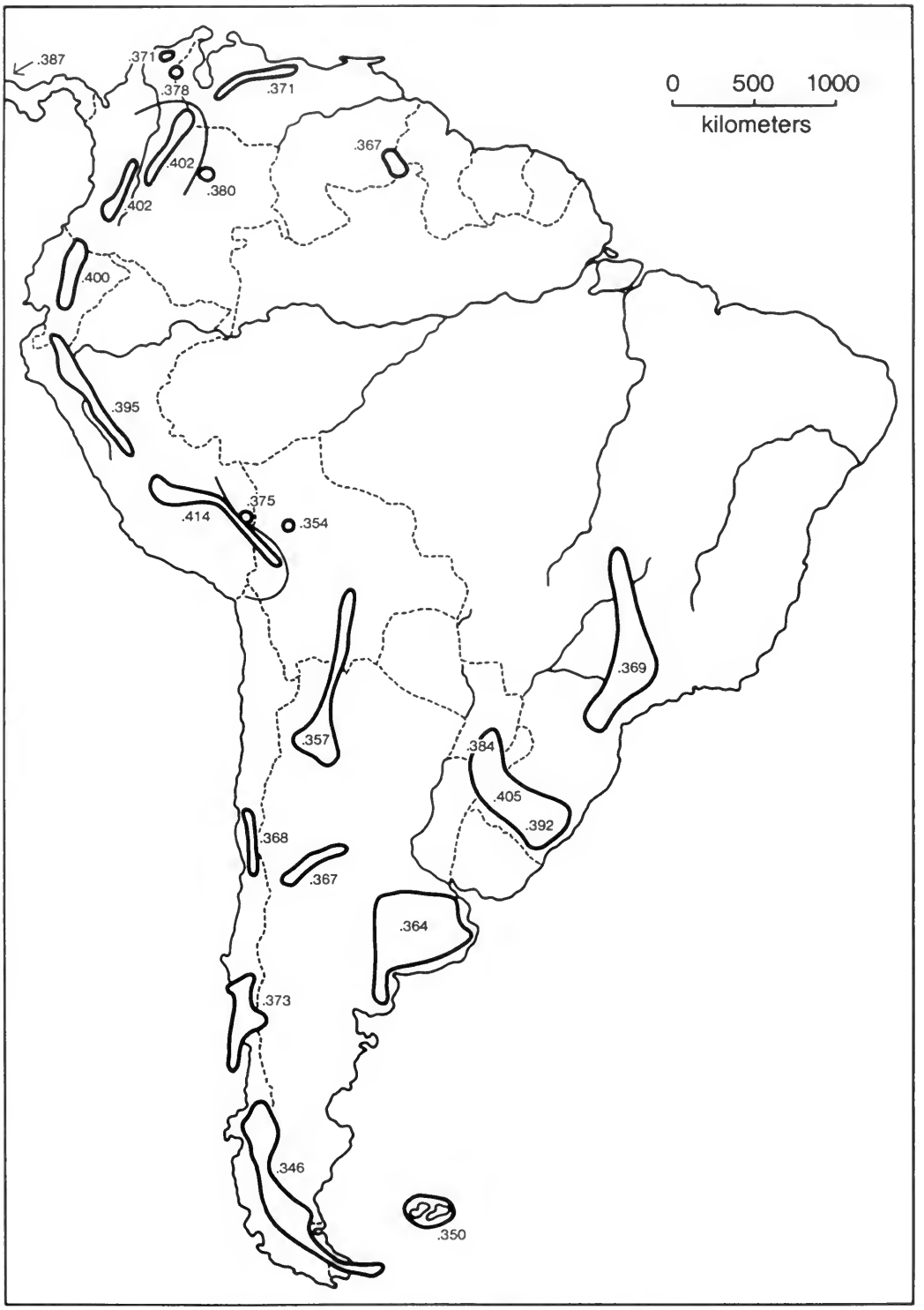


FIG. 5. Relative tarsal length (tarsus/wing ratio) for each group.

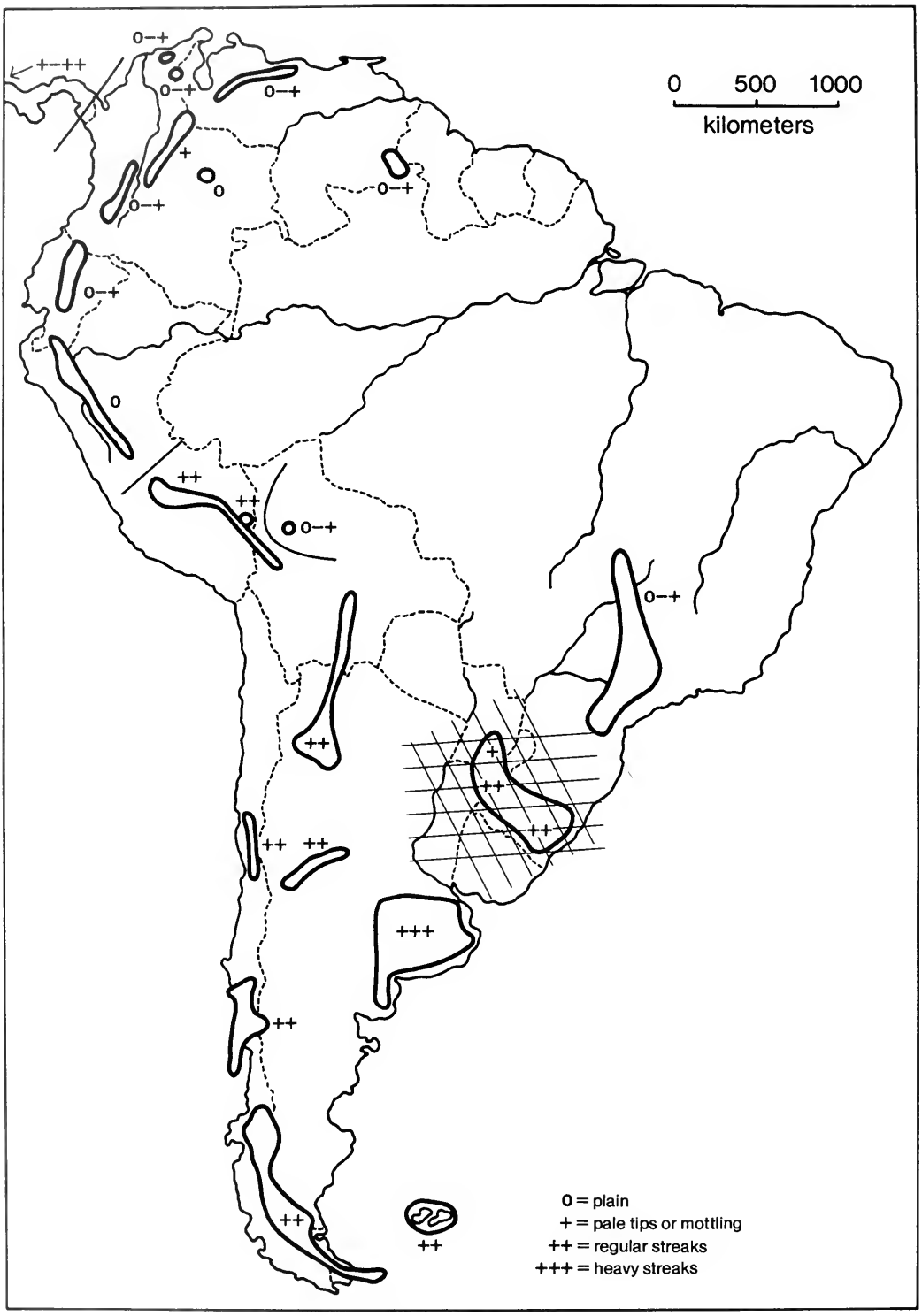


FIG. 6. Geographic variation in crown pattern.

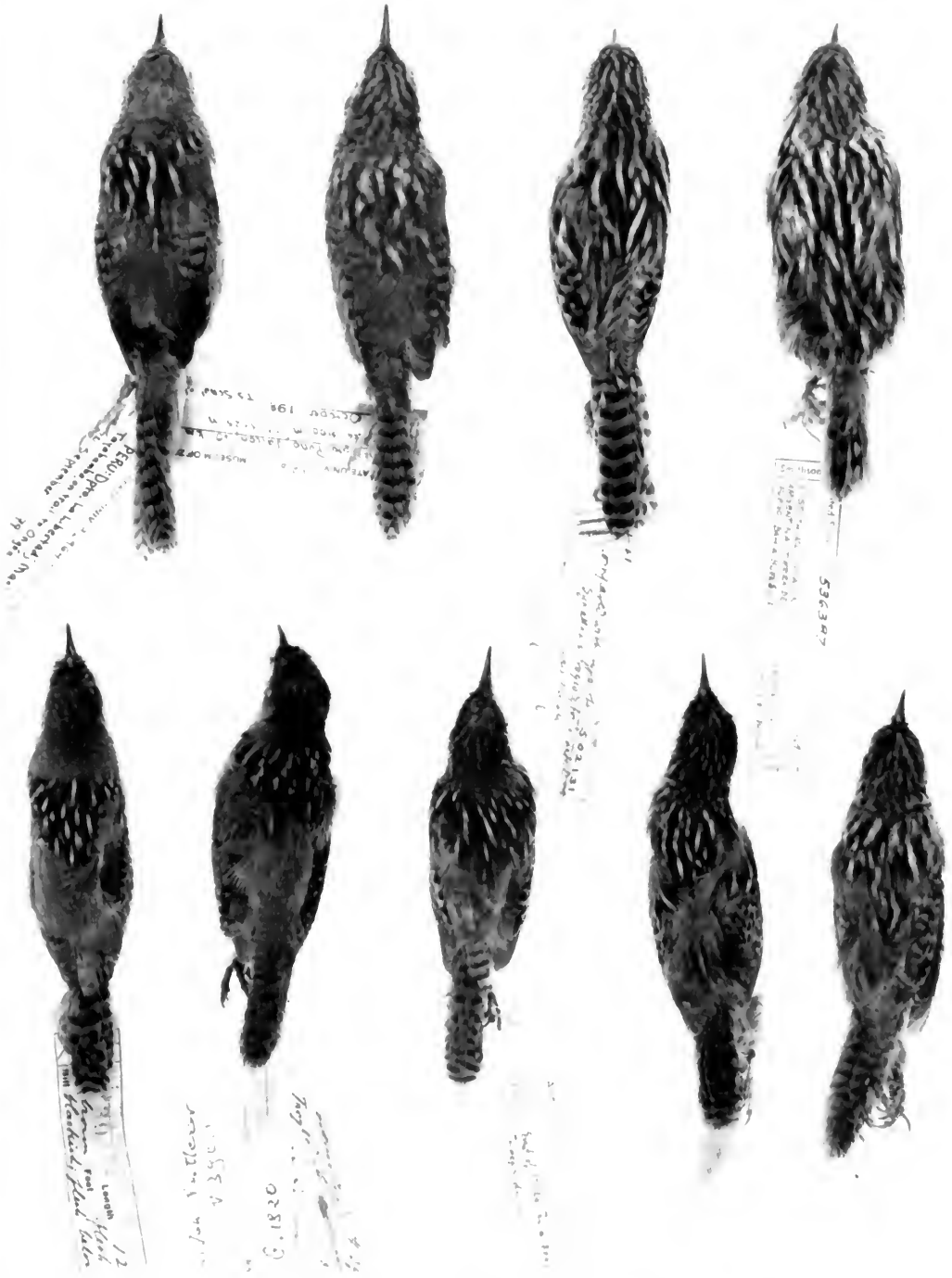


FIG. 7. Variation in dorsal plumage (from left to right): **top,** ♂, La Libertad, N Peru (group 4); ♀, Valcón, Puno, S Peru (group 5); ♂, Bahia Blanca, Buenos Aires, Argentina (group 9); ♂, Tierra del Fuego (group 12); **bottom,** ♂, Sierra Nevada de Santa Marta (group 15); ♂, Curytiba, Paraná, SE Brazil (group 19); ♀, Colonia Independencia, Paraguay (group 20); unsexed, Rio Grande do Sul, Brazil (group 20); ♀, Oconeque, Puno, S Peru (group 6).

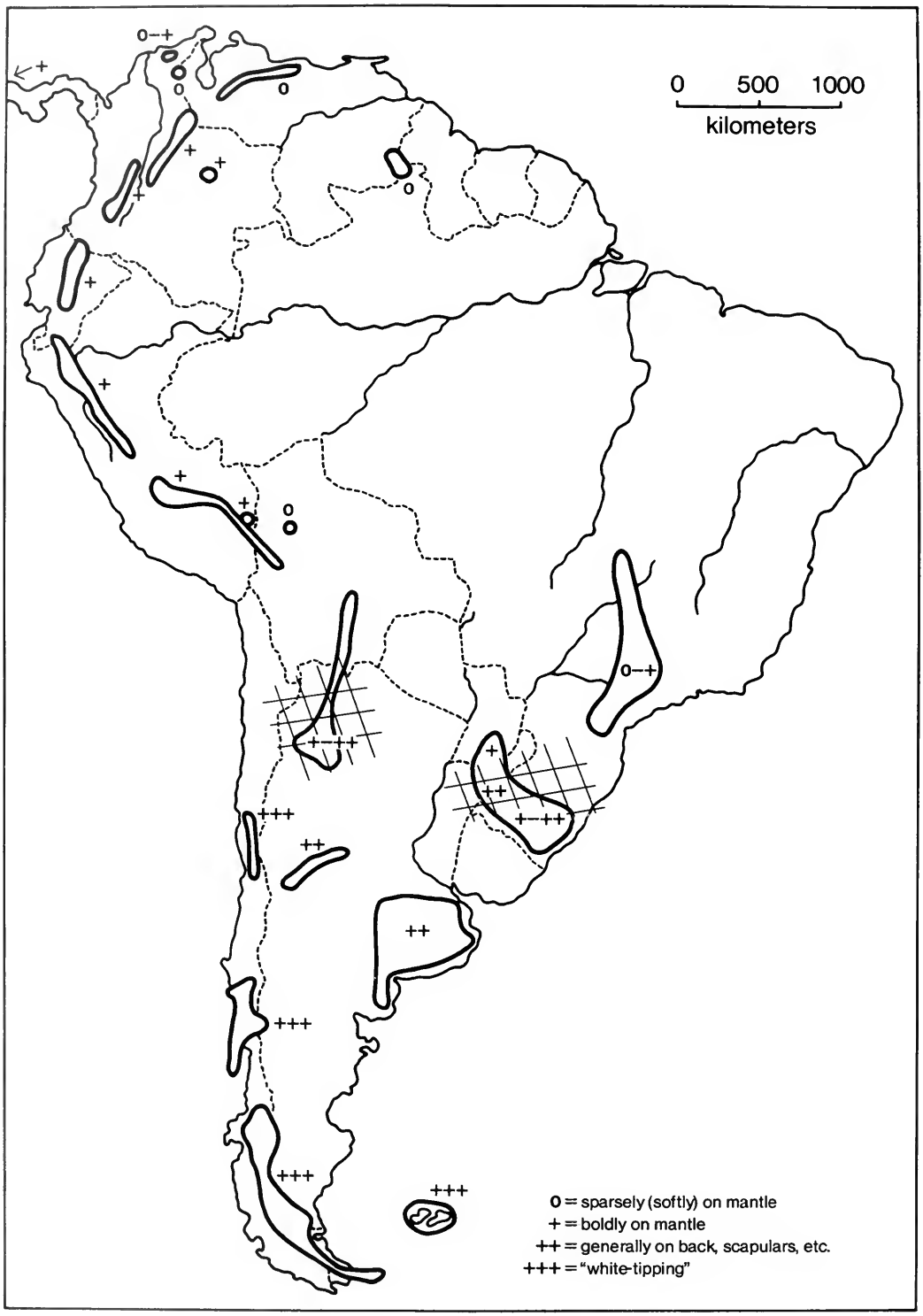


FIG. 8. Geographic variation of streaking on back.

loss of the brownish ground color, so that the general effect is of a blackish mantle with pale streaks. In the next stage, the streaking extends to the rest of the dorsal feathers, the scapulars, lower back and rump, and also the lesser wing coverts. The general effect is of a bird wholly streaked above, buffy on a blackish ground.

There is a fairly simple geographic distribution to these patterns. The dullest and most sparsely streaked birds are found from Santa Marta and the Venezuelan mountains to southeastern Brazil. Coming south through the Andes, the streaking is bolder, but through southern Peru and La Paz (group 5), it is still confined to the mantle. However, within the southern Andes region (group 7), there is a cline of increasing streaking, with the scapulars becoming marked in Tucumán (one bird from there even having streaking on the rump). In the remaining southern populations, all specimens are fully streaked above (fig. 7). In populations from central Chile (groups 10–11), far southern Argentina (group 12), and the Falkland Islands (group 13), the streaks in fresh-plumaged birds are pale buffy tipped with white, giving almost a spangled effect. In other populations the stripes turn white only with bleaching and age.

In the region of intergradation (group 20) from southern Paraguay to Rio Grande do Sul, the extent of dorsal streaking varies irregularly from the sparsely marked pattern typical of southeastern Brazil to the bold and extensive pattern of Buenos Aires. The Paraguay pair and two birds from Candiota, Rio Grande do Sul, have comparatively limited streaking, but the Corrientes specimen, almost on the Paraguay border, and three birds from Casino, Rio Grande do Sul, ca. 200 km from Candiota, have extensive streaking.

Rump

Figure 9 shows the distribution of types of markings on the lower back and rump, here called "rump" for brevity. The basic pattern is more clearly marked than that for most characters, with unstreaked rumps north and streaked rumps south of Tucumán and Rio Grande do Sul (fig. 8). In Tucumán and Rio Grande do Sul, there is intergradation.

For the most part, the unstreaked rumps are completely plain, but in southern Peru and Bolivia, there may be fine, dark barring. This barring occurs on less than half the specimens in southern Peru and La Paz, Bolivia, but all specimens from Santa Cruz, Bolivia, have it, as do those which are unstreaked from Tucumán, Argentina. However, I do not believe that this barring has much significance as a "new" character. From half to all specimens in all populations have fine, dark barring on the tail coverts. The appearance of this barring on the rump seems to be merely an extension from the coverts rather than the appearance of a new character.

Tail

Figure 10 shows the distribution of the various patterns of tail coloration in *Cistothorus platensis*. There are basically two types of tail pattern (fig. 11).

In the first, each rectrix is evenly barred dark and light, with the barring on the central rectrices being finer and more regular. This pattern is found through the main Andes, from Páramo de Tamá south to Tierra del Fuego and in the Falkland Islands. There is some variation within this range. From Ecuador south the barring on the inner webs of the 2nd to 5th rectrices becomes heavier and more irregular, but it nevertheless is clearly barring.

In the second pattern, the central and outermost rectrices and the outer web of the others are barred as in the first, but the inner webs of the 2nd to 5th rectrices are solidly black except at the tip. This pattern is found from Santa Marta and the Venezuelan highlands south through Meta and El Beni and eastern Brazil to Rio Grande do Sul. The population from Buenos Aires Province, however, is intermediate, two of eight having barred rectrices, and the other six having the inner webs of one or more feathers solidly black. One population that unexpectedly shows the blackish tail pattern is that at Oconeque, Puno, Peru (group 6), which is at 2745 m, the same elevation as the barred-tail Andean birds. The single specimen examined from Oconeque has the whole inner web of the 2nd rectrix black, except for the tip, and the proximal half of the 3rd to 5th rectrices.

Underparts

Variation in the color of the underparts is clinal and does not lend itself to numeric or graphic representation. This is true of the background color of the upperparts as well, since the general coloration varies as a whole. The basic pattern of the underparts is a whitish background, invariably

FIG. 9. Geographic variation of rump marking.

FIG. 10. Geographic variation of tail patterns.

FIG. 11. Tail patterns: **left,** barred throughout, ♀, El Crucero, Cauca, Colombia (group 2); **right,** barred with black inner webs on middle rectrices, ♂, Carimagua, Meta, Colombia (group 21).

washed with pale brown, or buff, or rusty on the flanks and crissum. In darker birds the flank color extends up along the sides and may form a faint breast band; in the darkest populations, even the throat and middle of the abdomen are washed darker.

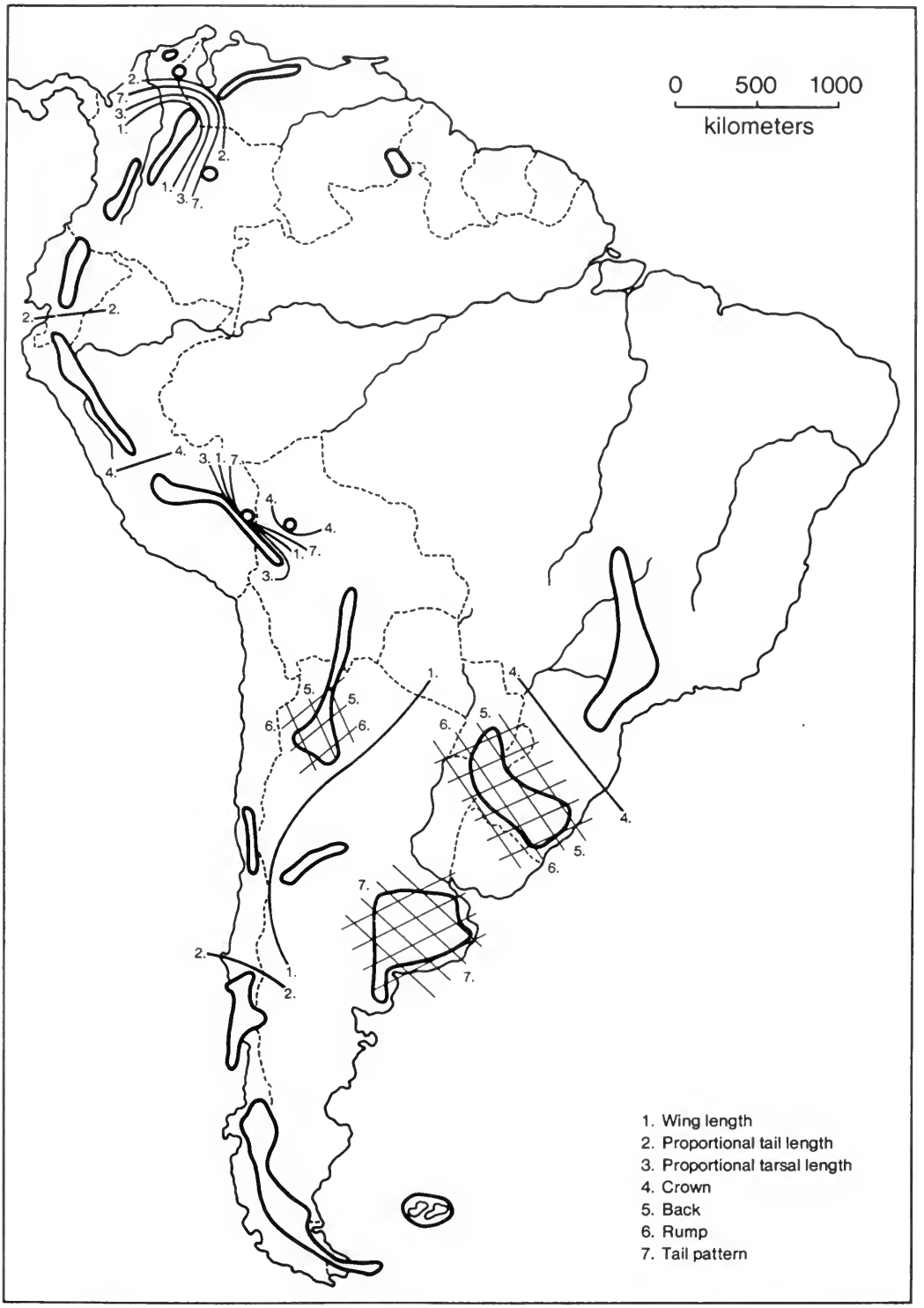
The darkest and most rusty populations are found in the Páramo de Tamá and the Eastern Andes of Colombia. There is a gradual cline of decreasing intensity and duller, less reddish hue as one goes south along the Andes, with the palest underparts being found in birds from west-central Argentina; those from north-central Chile south are somewhat darker again. The non-Andean birds are generally paler below and are much more uniform; only the Meta and El Beni birds stand out as being almost pure white.

Summary

Figure 12 summarizes the geographical distribution of the various mensural and plumage characters, emphasizing the areas of discontinuities among them. One major area of change, where

Opposite Page:

FIG. 12. Summary map showing the regions in which various mensural and plumage characters of *Cistothorus platensis* show abrupt changes or gradual intergradation. The most marked coincidence in character changes occurs in the northwest between group 1 (see fig. 1) and groups 15–17, 22; the next most marked area is between groups 5 and 6 in southeastern Peru. Areas of intergradation are in Tucumán, the southern part of group 7; in Buenos Aires Province (group 9) and in southern Paraguay/Corrientes Province/Rio Grande do Sul (group 20). For further discussion see text.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kilometers
1. Wing length
2. Proportional tail length
3. Proportional tarsal length
4. Crown
5. Back
6. Rump
7. Tail pattern

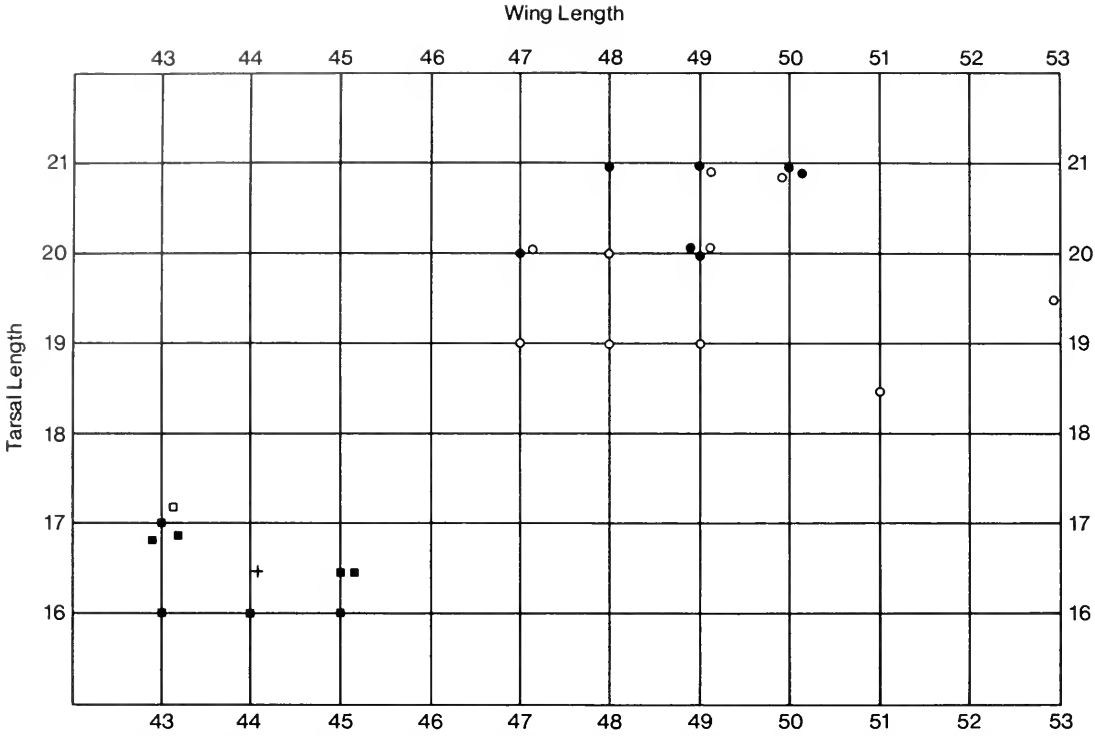

FIG. 13. Graph comparing wing and tarsal measurements of the female from Oconeque, Puno, Peru (group 6), with those of populations from Andean southern Peru and northern Bolivia (group 5) and lowland northern Bolivia (group 22). Closed circles = ♂♂, group 5; open circles = ♀♀, group 5; closed squares = ♂♂, group 22; open square = ♀, group 22; cross = ♀ from Oconeque.

there is a concordance of abrupt discontinuities in four characters, immediately catches the eye; that is, the gap between the Eastern Andes of Colombia, including the Páramo de Tamá, Venezuela, and Santa Marta and the Venezuelan highlands. Across this gap there is a major decrease in wing length, increase in proportional tail length, decrease in proportional tarsal length, and change in tail pattern. There is also a change in color, from rich, reddish brown to dull, mouse brown. Changes of this magnitude over a span of barely 200 km strongly imply that the present geographical proximity is secondary.

A second major area of discontinuity is found in southern Peru and northern Bolivia between the populations from Junín to Cuzco in Peru and La Paz in Bolivia and the adjoining population from Oconeque, Puno, 2745 m. The latter is known only from a pair of birds (I have seen the female), but the differences are so striking that I believe they are real. The Oconeque bird has much shorter wings, proportionately shorter tarsi, and a distinctive tail pattern. This bird differs much more from the contiguous Andean populations (the nearest being at Valcón), with which it shares the same habitat, than it does from the population in El Beni in the tropical lowlands 280 km away. Size is particularly convincing. In Figure 13 I have plotted wing and tarsus (absolute) measurements for all individuals (both sexes) of group 5 (southern Peru/La Paz, Bolivia) and group 22 (250 km to the east in El Consuelo and San Borja, El Beni), as well as for the single ♀ from Oconeque. The last individual clearly belongs with the lowland El Beni taxon rather than the adjacent taxon of the Andes. The Oconeque bird differs from those from El Consuelo only in having a streaked crown.

South of Peru there are no sharp discontinuities involving several characters. Populations from north-central Chile, west-central Argentina, and Buenos Aires Province south are all characterized by heavily streaked upperparts, which can almost be treated as a single character. In the west the streaking of rump and back is reduced in a clinal way through the populations from Tucumán to central Bolivia, but in the east, from southern Paraguay through Rio Grande do Sul, there appears to be an area of hybridization. Both plain and

streaked rumps occur together in Paraguay and Rio Grande do Sul, crown streaking is reduced but still present in Paraguay birds, and back streaking is fairly intense in Paraguay. The remaining plumage pattern that is distinctive of the populations of southeastern Brazil (group 19)—the black inner webs on the rectrices—extends south from Brazil into Buenos Aires, where it still predominates but is mixed with the barred condition.

Although the plumage patterns of the southern populations are uniform across the southern part of the continent, there are two size changes that are unrelated to them. The long wing length that characterizes the Andean forms is continued through central Chile to Patagonia and Tierra del Fuego. However, the population of west-central Argentina is distinctly smaller, and that of Buenos Aires smaller yet, at about the level of the Brazilian populations. Another change, also within the uniform highly streaked plumage pattern, is the abrupt reduction in proportional tail length between west-central Argentina and south-central Chile. These sudden, single character changes are not confined to the south, but are found randomly along the spine of the Andes. There is an abrupt increase in proportional tail length in southern Ecuador and a sharp decrease in proportional tarsal length between northwestern and central Bolivia.

In contrast to the situation in the Andes and the south, there are no marked character changes within the populations from Santa Marta (Colombia) and from the Venezuelan highlands to Meta (Colombia), El Beni (Bolivia), and southeastern Brazil. The only statistically significant difference is found in the populations of Roraima and Meta, which have proportionately shorter tails than any of the others. Plumage pattern is identical throughout. The birds from Carimagua are darker and grayer above and whiter below than populations from Venezuela and Brazil, but specimens from the latter localities are from 35 to 150 years old, and it is hard to know to what extent they are comparable.

Other Species

Discussion so far has dealt with the variation found among the populations of *C. platensis*. There are two other species of *Cistothorus* in South America, both with very local distribution in the northern Andes (fig. 14), and both almost certainly derived from *platensis*. The first of these is *meridae*, found in the páramos of Mérida and adjoining Trujillo at altitudes from 3000 to 4100 m. Its most striking characteristic is the strongly barred flanks, unique in the genus. A single specimen of *platensis* was taken at 3000 m on the Páramo de Escorial, northeast of Mérida, within the general range of *meridae*; otherwise, the two species are allopatric. The Escorial bird belongs to the smaller, lower elevation population of the coastal range and Perijá, which otherwise is not known from such high elevations, and may be a stray from lower levels. *Cistothorus meridae* has not been taken at Escorial, so the two species are at most parapatric, not sympatric.

The second localized species of *Cistothorus* is *apolinari*, which is found in Colombia in the high Eastern Andes from northern Boyacá to Bogotá and on the Páramo de Sumapáz (*fide* Meyer de Schauensee, 1964). It is broadly sympatric with the Eastern Andean *platensis*, although I am unable to find any record of the two from the same locality. The main character of *apolinari* is its great size compared to *platensis*; average wing length of males 56.8 mm compared to 49.6 mm in sympatric *platensis* (table 1).

When the measurements of *C. meridae* and *apolinari* are compared to those of the adjoining populations of *platensis* (table 1), it is clear that the two localized species are much more nearly related to the Eastern Andean *platensis* than to the populations of northern Venezuela. They are all at the large end of the spectrum, *apolinari* being the extreme in this respect, and with proportionately long tarsi. On the other hand, they have proportionately short tails, *meridae* being the most extreme. There is only one plumage character that separates the Eastern Andean *platensis* from those of the Venezuelan highlands: the wholly barred tail of the former compared to the black inner webs of the middle rectrices in the latter. Both *meridae* and *apolinari* have wholly barred tails as in the Andean form. They also have preference for altitudes above 3000 m, similar to the Andean birds and unlike the mid-altitude Venezuelan birds.

Analysis

From the summary discussion of variation within the species *C. platensis*, it is evident that there are two taxa that, in northern South America at least, (1) are clearly distinct morphologically, (2) show no evidence of genetic exchange across a

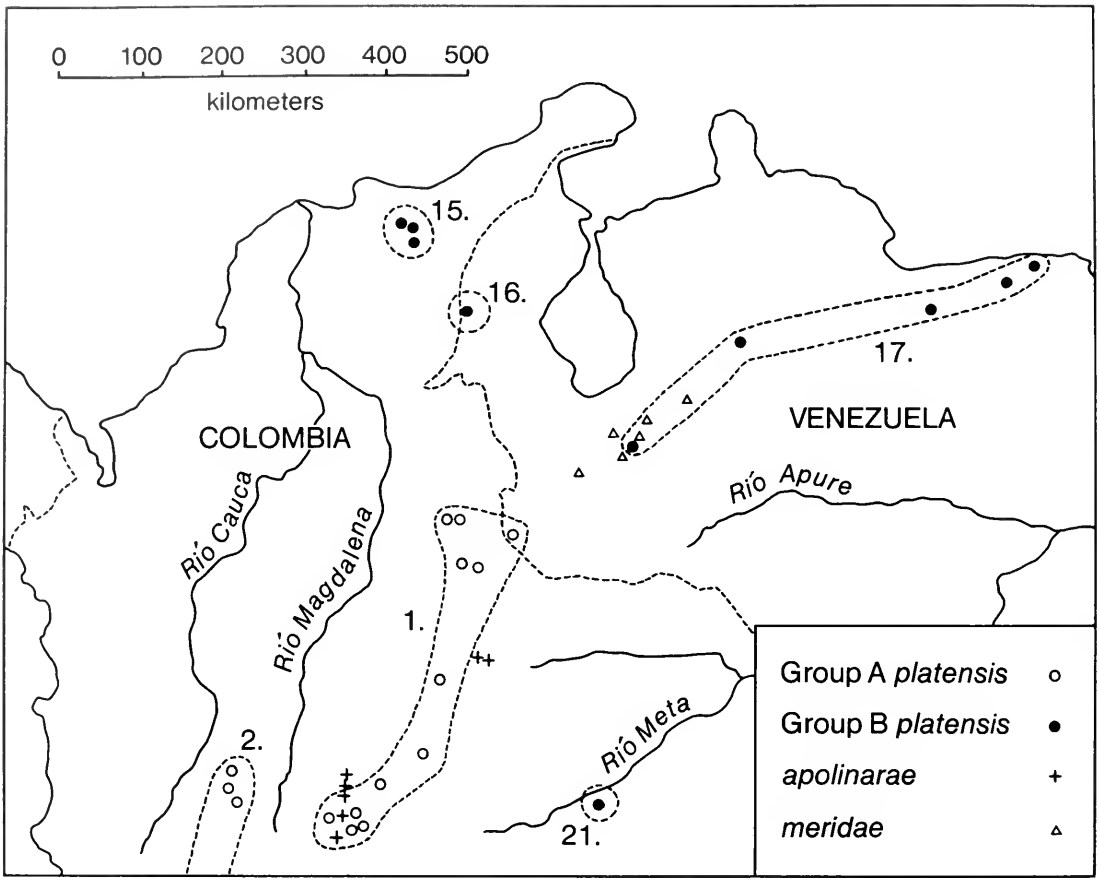

FIG. 14. Distribution of the two geographically restricted species, *Cistothorus apolinari* and *C. meridae*, and their apparently parapatric relationship to *C. platensis*.

gap of only 200 km, and (3) possibly would behave as distinct species if they met. On the other hand, as one follows the two taxa south through eastern and western South America, respectively, they intergrade or hybridize extensively in southern Brazil and northeastern Argentina. For ease of discussion, the western taxon, ranging from Páramo de Tamá through the Andes and Patagonia to Tierra del Fuego and the Falkland Islands and east to Buenos Aires, is called group A (groups 1–5, 7–

TABLE 1. Comparison of *Cistothorus platensis, apolinari* and *meridae*.

Species	N	Wing length	Tail length	Culmen length	Tarsus length	Tail/ wing ratio	Culmen/ wing ratio	Tarsus/ wing ratio
MALES								
Eastern Andes *platensis*	9	49.6	42.5	15.2	19.9	.861	.306	.403
apolinari	1	59	...	...	23	...	...	.390
meridae	8	48.9	35.8	14.9	19.3	.732	.306	.392
Coastal range *platensis*	13	45.2	42.8	13.2	16.7	.949	.293	.370
FEMALES								
Eastern Andes *platensis*	11	48.1	41.7	14.5	19.6	.867	.301	.407
apolinari	4	56.8	45.0	15.8	23.5	.793	.281	.414
meridae	3	47.0	34.8	14.7	19.2	.731	.312	.408
Coastal range *platensis*	4	43.5	42.3	12.9	16.0	.972	.296	.368

13) (fig. 15). The taxon ranging from Santa Marta through the highlands of Venezuela to, very locally, eastern Colombia, southeastern Peru, northern Bolivia, and southeastern Brazil to Paraná is called group B (groups 6, 15–19, 21–22). Populations from Rio Grande do Sul, southern Paraguay, and northern Corrientes (group 20) are intergrades between group B and the Buenos Aires population of group A. Because of the great variation within group A, there is no single character of plumage or measurements that can be said to characterize either group. The barred tail of group A comes closest to being such an identifying character, but in the Buenos Aires population, black inner webs predominate. Similarly, the majority of population groups in group A are characterized by longer wing length than any of the group B populations, but the two A populations from central Argentina (groups 8–9) are small, well within the range of group B. There is a possibility that the group A birds are large relative to the group B birds because they are found at higher elevations, and this type of intraspecific variation is known in South America (Traylor, 1950). However, the group B Santa Marta and Venezuelan populations are also montane, and more convincingly, the Oconeque population of group B birds, found at 2750 m and almost parapatric with group A populations, is identical in size with lowland group B populations (cf. fig. 13).

Evolution

The only congener of the *Cistothorus platensis* group of species is *C. palustris* of North America. It ranges throughout the temperate parts of the continent and is sympatric with *platensis* over the eastern half. There are no South American wrens that appear at all closely related to *Cistothorus*. The genus is apparently of northern origin, as is the family (Mayr, 1946, 1964). This suggests that the two distinct taxa in South America (or four when *apolinari* and *meridae* are included) may be traced to two separate invasions by the northern *platensis*. That there might have been two invasions was first suggested by Vuilleumier (1980) to account for the sympatry between *meridae* and *platensis* and between *apolinari* and *platensis*. At present *platensis* is found locally in Central America, where it has evolved a number of distinct subspecies (Dickerman, 1975). Since the plumage pattern of the northern populations of both groups A and B is the same, it is tempting to try to select a common ancestral form from among the Central American races. However, there is evidence for a considerable difference in time between the two invasions, and there is little reason to believe that the ancestor of the earlier invasion would now be recognizable.

Evidence for the much greater age of group A is found in the extensive geographic variation within the group, particularly in several proportional changes that occur nonconformingly with the plumage changes. There are two plumage types: a pattern of unmarked crown, lower back and rump, and moderately streaked back in the northern Andes; and fully streaked upperparts from central Argentina and central Chile south. The change to a streaked crown occurs in central Peru, but the major shift to fully streaked upperparts is found in northwestern Argentina. From central Argentina and Chile south to Tierra del Fuego and the Falkland Islands, the streaked plumage pattern is remarkably uniform. In the north, except for the variable crown streaking, the sparsely streaked pattern is uniform from the northern Andes to central Bolivia.

Within these two more or less uniform plumage patterns, there are a number of mensural changes that geographically lie unconformably on the plumage changes. One is the sharp change in tail length in southern Ecuador (fig. 4). The population to the north has a tail/wing ratio of .873, whereas that of the population to the south is .937. This difference is highly significant ($P < .001$), but is not correlated with any other change in plumage or measurements. Similarly, there is a marked decrease in proportional tarsal length between La Paz in northwestern Bolivia and Santa Cruz in central Bolivia (fig. 5). Here the tarsus/wing ratio is .414 in the northern population and .357 in the southern, again a highly significant difference ($P < .001$). The change in tarsal length is correlated with a significant, but not so abrupt, change in tail length, but with no plumage characters. Absolute tarsal lengths are 18 ♂♂♀♀, 18–21 (20.0) for the northern populations, and 11 ♂♂♀♀, 16–18 (17.3) for the southern ones. However, there is a single unsexed bird, taken at Khapaguaia, La Paz, in the range of the northern populations, which has a tarsus of only 17 mm. Unfortunately, Khapaguaia has not been located (Paynter et al., 1975), and its altitude is not known; the exceptionally short tarsus might be an approach to the condition in the southern populations or the result of hybridization with a small lowland population like that at El Consuelo, El Beni.

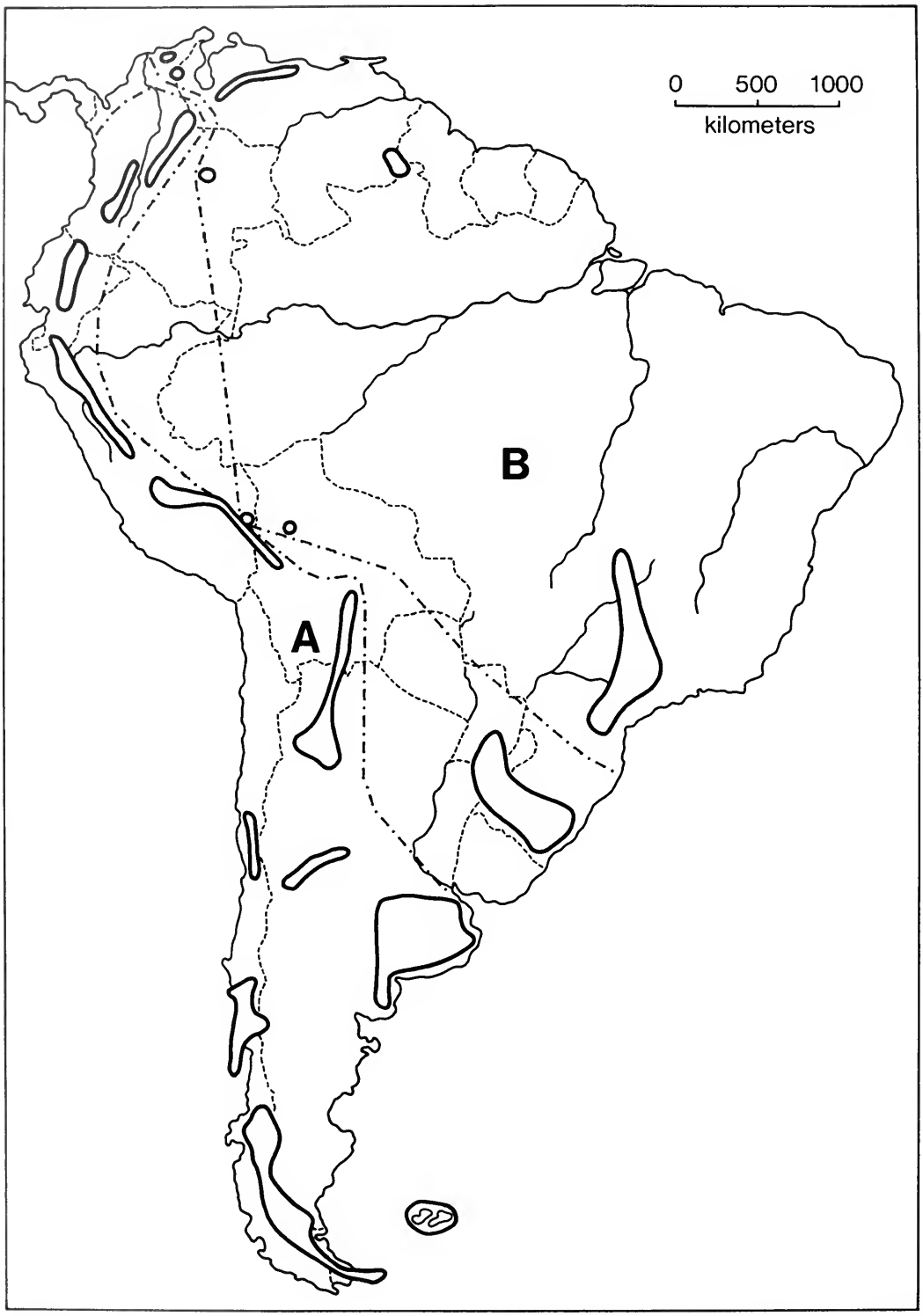

FIG. 15. Ranges of groups A and B, representing the two different invasions. The area in extreme southern Brazi and northeastern Argentina is one of intergradation.

Two uncorrelated mensural changes also occur in the region of uniformly streaked plumage. The first is in wing length, which is otherwise remarkably uniform throughout group A; there are no significant differences in wing length from western Venezuela to Tierra del Fuego except in central Argentina. In the west-central region (group 8) and in Buenos Aires Province (group 9) (fig. 3), wing lengths are significantly shorter than those in the populations to the north, west, and south (groups 7, 10–11; $P < .02$). The difference between wing lengths in Buenos Aires Province and those in western Argentina is not statistically significant ($P \cong .1$), but is probably biologically significant, because the Buenos Aires measurements approach those of group B with which the Buenos Aires birds hybridize freely. The second marked mensural change within the uniformly streaked group is the short relative tail length in the two southern populations compared to those in the north (fig. 4). The tail/wing ratios in west-central Argentina and Buenos Aires are 1.003 and .968, respectively, while those of south-central Chile and Patagonia/Tierra del Fuego are .845 and .854; the differences are highly significant ($P < .001$); this difference is apparent when the specimens are compared (fig. 8). The relative tail length of birds from north-central Chile is almost exactly intermediate, at .911, even though the area is not geographically intermediate.

The presence of these nonconforming changes in size and proportions on a fairly simple pattern of plumage variation suggests that the group A populations must have undergone considerable geographic or climatic vicissitudes since the basic plumage pattern was evolved. There is, however, no such variation in either plumage pattern or measurements among the populations of group B. The same pattern of unstreaked crown, lower back and rump, and moderately streaked back is found throughout its range from Santa Marta, Colombia, to Paraná, Brazil, and in the isolated populations of Meta, Colombia, and El Beni, Bolivia. Actually, all the populations of group B south of the coastal range of Venezuela are isolated from each other by distances an order of magnitude greater than those found among the group A populations. Yet there are no plumage differences among them and only one significant size difference, which is the shorter tail length in populations from Roraima and Meta. Essentially, a single, uniform taxon occupies isolated regions on the periphery of Amazonia and in the Venezuelan highlands.

The one population of group B not included in the above discussion is that at Oconeque, Puno, Peru (group 6). I have included it in group B on the strength of its small size and the black inner webs on the rectrices. It does, however, have a streaked crown, characteristic of the group A birds. It is certainly a highly localized population, because birds from Valcón, 55 km northwest, are typical of Andean group A populations. Geographically, the presence of a group B representative at 2745 m in southeastern Peru is not as startling as it appears at first glance. The population in the lowlands at El Consuelo, El Beni, is only ca. 250 km east, and the populations in Venezuela and Santa Marta regularly reach elevations of 2745 m. The presence of a streaked crown suggests that there might have been some interbreeding with group A birds, but there is no evidence of intergradation in measurements (fig. 13).

For group B, the only explanation of its present distribution is that it is the result of a recent explosive expansion of range throughout the eastern lowlands. As Haffer (1974) has shown, during glacial periods the climate of Amazonia was cooler and dryer, the forest was broken up and reduced in extent, and grassland became more extensive and continuous. During the most recent such period, considering the lack of differentiation among the isolated populations, group B *platensis* must have expanded throughout the Venezuelan highlands and the eastern lowlands. With the subsequent return of more humid conditions, the forest again became continuous, and the range of the species was reduced to isolated populations in Santa Marta and the Venezuelan highlands, an extensive population in southeastern Brazil, and small, isolated populations in El Beni and Meta and in the highlands in Puno.

During this period of expansion or shortly thereafter, the advancing group B birds met the group A representatives, probably in the Rio Grande do Sul area. These group A birds were fully streaked above, but presumably small in size, more or less like the Buenos Aires population. I say "presumably" because the small size of Buenos Aires birds may represent introgression from hybridization with group B, just as is their possession of black on the inner web of the rectrices. Unlike the situation in Colombia and Venezuela where there is no evidence of interbreeding between groups A and B, there has been complete hybridization in the southeast. All specimens examined, from southern Paraguay, northern Corrientes, and Rio Grande do Sul, show mixed characters. All have black inner webs to the rectrices, a group B char-

acter that has reached even to Buenos Aires. A pair from Colonia Independencia, Paraguay, has uniform dark crowns with only a trace of streaking (the darkness is group A, the uniformity group B), the back is black with white streaks (group A), while the lower back and rump are plain or barred (mostly group B). A northern Corrientes, Argentina, bird has fine, pale streaking on the crown, an intermediate character, but otherwise is streaked as group A on the upperparts. Three birds from Casino, Rio Grande do Sul, are like the Corrientes specimen, but two from Candiota, only 180 km west, lack streaking on the rump, having it barred like the coverts. A single unsexed specimen from Rio Grande do Sul (no specific locality) has the finely streaked crown, but an unmarked rump and lower back. It is clear that all South American *Cistothorus*, except for *meridae* and *apolinari*, must be included in a single species.

To summarize, South American *Cistothorus platensis* and the allied species *apolinari* and *meridae* are the result of two separate invasions from the north. The earliest invader was apparently characterized by large size; long, barred tail; short tarsi; and uniformly colored crown, lower back, and rump. It extended its range south through the high Andes from (eventually) the Páramo de Mérida south through northern Argentina, and then through the temperate lowlands east to Buenos Aires and south to central Chile and Tierra del Fuego. During subsequent periods of range restriction and extension, it first evolved two distinct plumage phases in the northern and southern parts of its range, respectively, and later a long-tarsused group of populations from western Bolivia north and, independently, two short-tailed populations from Ecuador north and from central Chile south. The final evolutionary event was the isolation of two populations in the Eastern Andes and the Páramo de Mérida, where they speciated into *apolinari* and *meridae*, respectively. Also at a recent date, the southernmost population extended its range to the Falkland Islands. These evolutionary events are summarized in Figure 16. The more recent invasion was by a form similar in plumage pattern and proportions to the earlier one, but smaller and with the inner webs of the rectrices black. It spread east to mid-elevations in the Sierra Nevada de Santa Marta and the mountains of Venezuela and south through the lowlands to southeastern Brazil, eastern Colombia, southeastern Peru, and northern Bolivia. Despite the isolated nature of both montane and lowland populations of this second invasion, there is little difference among them. Where representatives of the two invasions approach each other in northern Colombia, they differ greatly in form and show no signs of intergradation; however, where the respective representatives meet in southern Brazil and northeastern Argentina, they intergrade completely.

Present Distribution

Attention has been drawn to several changes of mensural or plumage characters between adjacent populations of group A *platensis* in the Andes and south-temperate Argentina and Chile. Some of the changes were abrupt, suggesting that there is at present no genetic interchange, and others showed intergradation, presumably the result of such interchange. However, there was no discussion of the possible ecogeographical barriers (Vuillieumier, 1977) that might prevent genetic interchange among the group A populations, or of the barriers that cause such extreme isolation of three of the populations of group B.

South American *C. platensis* is a paradox. At present it is apparently completely sedentary. Chapman (1931) stated, "The presence of a form of this sedentary species on Roraima is one of the most interesting facts connected with the geographic origins of the Roraiman avifauna," and Humphrey et al. (1970) say, "It is surely a year round resident on Isla Grande [Tierra del Fuego]." Olrog (1978) states that *C. p. hornensis* from Rio Negro south (my groups 11–12) is migratory and winters in central Argentina. However, of the 26 specimens examined from central Argentina (groups 8–9), none shows any overlap in relative tail length with 44 specimens of *hornensis*, and the specimen evidence does not support migration. On the other hand, *C. platensis* has not always been a sedentary species, because it has twice spread the length of South America, once south through the Andes to Tierra del Fuego and a second time through the mountains of Venezuela and the eastern lowlands to northeastern Argentina. It is one of the nine passerine species to colonize the Falkland Islands, an overwater distance of more than 200 km. Even today, *platensis* is very catholic in its habitat selection, as it must be to inhabit most of the continent. When collecting localities are posted on Hueck and Seibert's (1972) vegetation map, they are found in a great variety of vegetation formations that support grasslands. In the mountains they occur in the unclassified, high-moun-

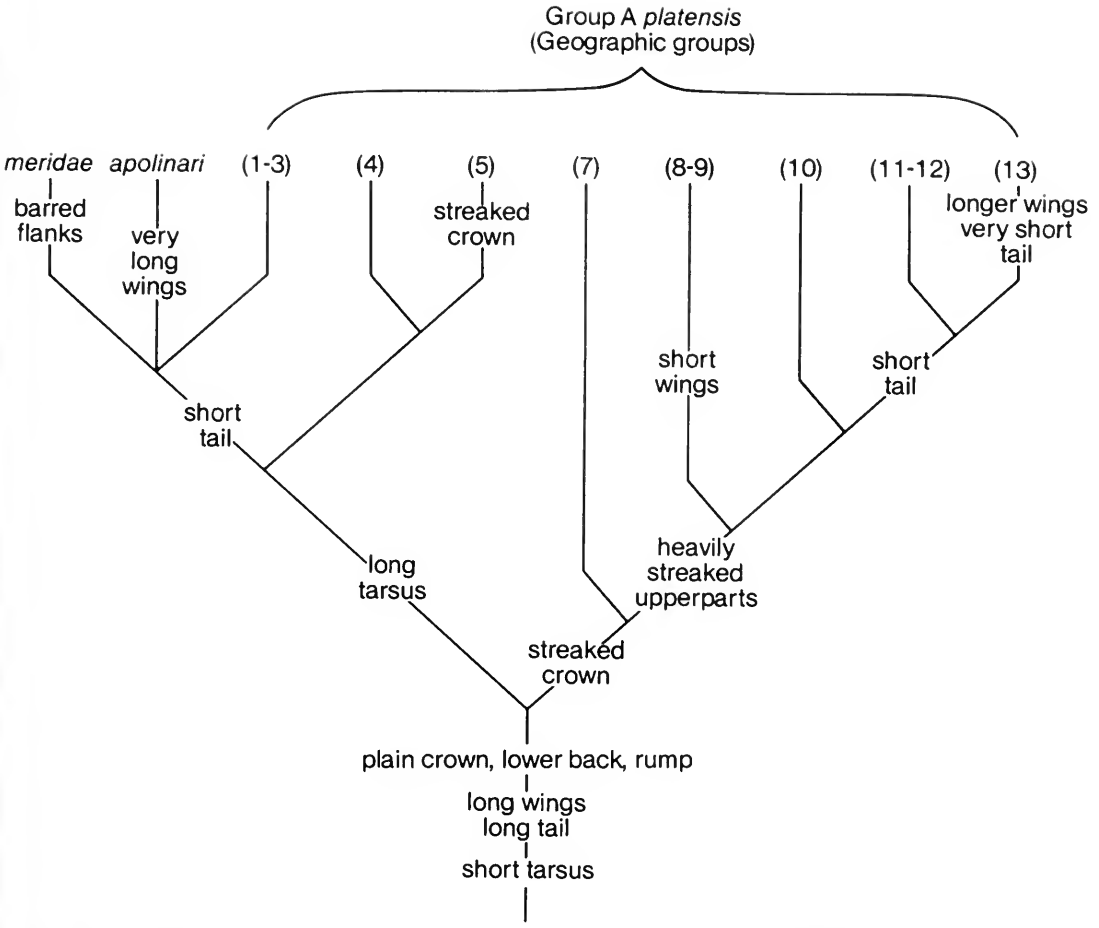

FIG. 16. Postulated evolution of group A *Cistothorus platensis*. The two localized species, *apolinari* and *meridae*, do not appear to be sister groups of group A *platensis* as a whole, but only of the short-tailed *platensis* (groups 1–3).

tain, nonforest vegetation from Venezuela to Tierra del Fuego and in the páramo from Colombia to northern Peru; they are not found, however, in puna (Vuilleumier & Simberloff, 1980). In the lowlands they occur in the llanos of eastern Colombia, in the palm savanna of northern Bolivia, in the deciduous woodland of southeastern Brazil and Paraguay, in the bush steppe of western Argentina, in the level pampas of Buenos Aires Province, and in the Patagonian steppe. Considering the variety of formations in which they do occur, one wonders why they are not found in every formation that supports grassland.

There is a major increase in relative tail length between northern and central Ecuador (group 3) and southern Ecuador and northern Peru (group 4). Ordinarily, character changes in montane species of northern Peru can be traced to the arid valley of the Marañón River and the north Peruvian depression (Vuilleumier, 1977) as a barrier to genetic exchange. That is not the case here. Of the 17 male specimens in group 4, five are from north and west of the Marañón on the left bank drainage on the side bordering Ecuador, and 12 are from south and east of the river on the right bank drainage. However, the mean proportional tail length for the five left bank birds is .924 compared to .873 for birds from northern Ecuador (group 3) and .937 for the entire group of birds from northern Peru (group 4). The difference between the five left bank birds and those of northern Ecuador is strongly significant ($P = .02$), even though there is no evident geographical barrier between them. On the other hand, the five are virtually identical in tail length with those of the same group on the other side of the Marañón.

There is an apparent gap of 150 km between the southernmost short-tailed birds of group 3 in the mountains above Puente de Chimbo (02°10'S) and the northernmost long-tailed birds of group 4 at Taraguacocha (03°40'S) and the Loja hills (ca. 04°05'S), but there is no evident geographic barrier. There may, however, be a vegetational change. Vuilleumier and Simberloff (1980) show páramo extending south to northern Peru, within the range of the long-tailed group 4 birds, but Hueck and Seibert (1972) show the most southerly páramo to be in Ecuador at about the latitude of Puente de Chimbo; south from there is found the unclassified, high-mountain vegetation which is the preferred habitat of group A *platensis* in the Andes from Peru to Tierra del Fuego.

Of the other geographical barriers in the northern Andes discussed by Vuilleumier (1977)—the Táchira depression in Venezuela between páramos of Tamá and Zumbador (between groups 1 and 17); the César River Valley in Colombia between Santa Marta and Perijá (groups 15 and 16); the upper Magdalena Valley in Colombia (groups 1 and 2); and the Cauca and Patía river valleys in Cauca and Nariño, Colombia (groups 2 and 3)—only the first has any genetic significance for *C. platensis*. The Táchira depression is the northern limit of group A *platensis* in the Andes, separating it from *C. meridae*. The other barriers cause gaps in the range of *platensis*, but there are no evident phenotypic or genetic differences across the gaps.

A similar area of abrupt character change occurs in the far south of the species range, between the birds of central Argentina (groups 8–9) and those of southern Chile and adjoining Argentina south of 38°S (groups 11–12). The former two groups have exceptionally long tails proportionately, and the latter two groups, exceptionally short ones; there is no overlap in tail/wing ratios between the two series. Both types occur in a number of vegetation formations: the long-tailed ones in the pampas, bush steppe, and transition between bush steppe and Chaco; the short-tailed ones in Patagonian steppe, deciduous temperate woods, predominantly evergreen woods (*Nothophagus*), and subantarctic tundra. Although birds of differing tail lengths do not occur in the same vegetation types, as mapped by Hueck and Seibert (1972), there could hardly be much difference in the respective grasslands. The gap between the long- and short-tailed populations is about 600 km, mostly of "busch steppe," a habitat in which the species occurs to the north. There are no geographical barriers and no evident reason why the two populations do not occupy the intervening area and interbreed. One can hypothesize that the two populations were separated by the Somuncurá glacier during the last glaciation (Fjeldså, 1985) and have failed to move back during the past few thousand years, but that would not be a very convincing explanation for such an otherwise adaptable species.

Within group B a different type of problem is raised by the two isolated lowland populations in Meta, Colombia (group 21), and El Beni, Bolivia (group 22). These two populations differ only slightly in color from those at Roraima (group 18) and southeastern Brazil (group 19), respectively, even though they are isolated from them by some 1,000 km or more. Haffer (1974) has postulated that, during the latest glacial period, the climate of Amazonia was distinctly drier, the rain forest area was reduced and fragmented, and savanna conditions became more widespread. It was during this period that *C. platensis* spread throughout the eastern lowlands. With the return of more humid conditions, the forest spread again, leaving the group 21 and 22 populations isolated in the west. While this chronology is probably correct, it does not explain why the species disappeared in the intervening lowlands. The llanos, the habitat in which the Meta birds are found, occurs continuously from eastern Colombia through central Venezuela between the mountains and the Orinoco River, a distance of about 1,300 km. There is similar extensive lowland savanna around Roraima and the neighboring highlands, but here *platensis* only occurs above 900 m in the mountains themselves. In the south the population of El Beni occurs in palm savanna, and the more extensive population of southeastern Brazil, in Campo Cerrado and mesophytic woods. Between them occur extensive areas of apparently suitable habitat, pantanal, Campo Cerrado, and the Campo Limpo of southern Mato Grosso, but *platensis* does not occur.

Why has *C. platensis* apparently disappeared so completely from such vast areas of lowlands? If it were not for the two remaining populations (groups 21–22) in the west, one would not suspect that this species had ever occurred in the lowlands west of Roraima or São Paulo. Possibly, the disappearance is only apparent, and more extensive collecting will show that there are scattered populations in the intervening areas. The llanos of Colombia and Venezuela have only been sparsely collected (Paynter & Traylor, 1981; Paynter, 1982), and southwestern Brazil and northern Bolivia,

probably even less so. This, combined with the fact that the *C. platensis* is always an elusive bird, makes it quite possible that its presence has been overlooked.

Subspecies

I have carefully avoided the use of subspecific names during the present discussion of *Cistothorus platensis*, because they would be more confusing than helpful. Even the two oldest and best-known names, *platensis* and *polyglottus*, turn out to be based on populations that are to a degree intermediate between the large, streaked-back, bar-tailed populations of southern Chile and Argentina, and the small, least-streaked, black-tailed populations of southeastern Brazil. On the whole, however, the Andean and temperate southern populations (my group A) can properly use the name *platensis*, type locality Buenos Aires; whereas my group B populations can be called *polyglottus*, type locality Paraguay.

Within *C. platensis* and *C. polyglottus* as defined above, there are groups and subgroups that can be defined on one or more characters and that may be recognized as subspecies. The *platensis* group is particularly fragmented because of the changes in proportions overlying the different plumage patterns. In gross appearance, the first division within the *platensis* group is between the heavily streaked upperparts of southern populations (geographic groups 8–13) and the much less streaked northern populations (groups 1–5, 7). The streaked group is *C. platensis*, and the oldest name for the plainer group is *C. aequatorialis*, type locality Pichincha, Ecuador. The sharp distinction between the southern and northern populations is marred by the fact that, from central Peru to Tucumán, Argentina, the crown is streaked even though the dorsal streaking is reduced and the lower back and rump are plain. A more realistic breakdown might be between the long-tarsused northern populations (groups 1–5) and the short-tarsused southern ones (groups 7–13). The same two names would apply—*aequatorialis* for the long-tarsused groups and *platensis* for the short-tarsused ones—but the populations from eastern Bolivia/Tucumán (group 7) would be shifted to *platensis* with which they do intergrade. This division would still leave one *aequatorialis* group (group 5) from southern Peru and La Paz, Bolivia, with a character otherwise confined to *platensis*; that is, a streaked crown.

Both *C. p. aequatorialis* and *C. p. platensis*, as defined above, can be further broken down. Within *aequatorialis* the northern populations from Colombia and Ecuador (groups 1–3) have a distinctly shorter tail; these populations include topotypical *aequatorialis*. Within this restricted *aequatorialis*, there is an irregular cline in color for segments of which the names *tolimae* and *tamae* have been proposed, but they are not worth recognizing. For the southern populations with streaked crown (group 5), the name *graminicola* is available, leaving the plain-crowned, long-tailed populations of northern Peru (group 4) the only entity without a name. For the moment I would leave it in *graminicola*, apparently its nearest relative, despite the difference in crown pattern. As is noted below, it is questionable whether the streaked crown developed as an independent character in *graminicola*.

Within the streaked *C. p. platensis*, various entities can also be discerned. The east Bolivia/Tucumán populations (group 7) are, for the most part, plain-rumped with reduced dorsal streaking; the name *tucumanus* is available, with *boliviae* as a synonym. In the southern part of its range, some specimens of *C. p. tucumanus* have streaking on the rump, intergrading with the fully streaked *C. p. platensis*. The latter, including groups 8–13, can be broken down into three fairly distinct forms. The populations from western Argentina and Buenos Aires (groups 8–9) have distinctly shorter wings; they are "true" *platensis*. Those from southern Chile and adjoining Argentina to Tierra del Fuego and from the Falkland Islands (groups 11–13) all have short tails, and the Falkland birds are further distinguished by longer wings and even proportionately shorter tails. The name *hornensis* is available for birds of southern Chile (groups 11–12), and *falklandicus*, for those of the Falkland Islands (group 13). The population of north-central Chile (group 10) is like *hornensis* in wing length, but with an intermediate length tail; I would keep it in *hornensis*.

When an attempt is made (fig. 16) to diagram the relationships of the various populations or subspecies of group A, the character of "streaked crown" appears to have evolved twice independently. While it may have done so, since it also occurs in several Central and North American subspecies, its presence in *graminicola* may also be a result of earlier intergradation with the more southern *tucumanus*; the fact that streaked crowns are continuous from Junín southward suggests that this may be so.

The *C. polyglottus* groups of populations (groups 6, 15–19, 21–22) are much more uniform than the *C. platensis* group. The three isolated populations—Carimagua, Colombia (group 21); El Consuelo, Bolivia (group 22), and Oconeque, Peru (group 6)—are known, respectively, only from short series taken over a brief period of time at a single locality. Even though each can be defined by certain color or pattern characters, more should be learned about possible variation within each one before they are named. The Oconeque population, with streaked crown, does have the name *minimus*. Within the more extensive populations of Santa Marta, the Venezuelan highlands, and southeastern Brazil, there is little variation. There is a slight cline of decreasing wing size from Santa Marta (44.8 mm) and the coast range (45.2 mm) through Roraima (43.8 mm) to southeastern Brazil (42.9 mm), and the tails of Roraima and Meta, Colombia, birds are proportionately shorter than those in any other population. The name *alticola* is available for the short-tailed Roraima birds, leaving *C. p. polyglottus* with a disjunct range in southeastern Brazil and in northern Venezuela and Santa Marta. A checklist of South American *C. p. platensis* appears in Appendix B.

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Appendix A

Measurements (in millimeters) of *Cistothorus platensis*

Group	Wing			Tail			Culmen		
	N	Range (and mean)	SD	N	Range (and mean)	SD	N	Range (and mean)	SD
MALES									
1	10	48–51 (49.5)	.88	9	41–44 (42.7)	1.00	10	15–15.5 (15.2)	.24
2	19	47–52 (50.1)	1.58	19	39–47.5 (43.1)	2.33	21	13.5–16 (14.7)	.62
3	23	47–53 (49.7)	1.64	21	40–49 (43.3)	2.51	23	13.5–16 (14.7)	.65
4	17	46–55 (49.5)	2.12	17	39–51.5 (46.4)	2.76	17	14–16 (15.2)	.66
5	8	47–50 (48.6)	1.19	4	43–47 (45.3)	2.06	10	13.5–15.5 (14.5)	.69
7	9	47–50 (48.2)	1.09	9	44–50 (47.9)	1.88	8	13–15 (13.7)	.70
8	8	43–48 (45.3)	1.49	4	43.5–48 (45.1)	1.97	7	12.5–14 (13.4)	.61
9	6	43–46 (44.0)	1.10	5	41–46 (42.6)	2.30	5	12.5–13 (12.8)	.27
10	4	47–50 (48.0)	1.41	4	40–49 (43.8)	3.86	4	all 14 (14.0)	.00
11	10	46–49 (47.3)	1.06	7	37–42.5 (40.2)	1.95	9	13–15 (13.5)	.50
12	20	47–50 (48.2)	0.83	15	39–44.5 (41.0)	1.99	17	12–14 (13.4)	.55
13	8	49–53 (50.9)	1.36	8	40–43 (40.9)	1.13	7	13.5–14.5 (14.0)	.29
15	26	44–47 (44.8)	.76	23	37–46 (41.7)	2.03	22	12.5–15 (13.4)	.56
16	5	43–45 (44.2)	.84	5	40–42 (40.6)	.89	4	14–14.5 (14.1)	.25
17	13	44–47 (45.2)	.99	11	40–47 (42.8)	2.11	11	12–14 (13.2)	.79
18	19	41–46 (43.8)	1.17	15	37–42 (39.4)	1.52	19	13–14 (13.0)	.50
21	4	42–43 (42.8)	.50	3	36–39 (37.7)	1.53	4	12–13 (12.6)	.48
19	12	40–44 (42.9)	1.24	8	39–44 (41.0)	2.00	11	12–13.5 (12.6)	.38
22	8	43–45 (43.0)	.99	8	40–44 (42.9)	1.33	4	12.5–13 (12.9)	.25

Appendix A. *Continued.*

Group	Wing			Tail			Culmen		
	N	Range (and mean)	SD	N	Range (and mean)	SD	N	Range (and mean)	SD
FEMALES									
1	11	47–49 (48.1)	.70	11	37–43 (41.7)	2.00	11	13.5–15 (14.5)	.52
2	21	47–52 (48.9)	1.45	20	37–46 (41.9)	1.87	22	13.5–16 (14.7)	.63
3	5	47–50 (48.4)	1.14	4	41–44 (42.8)	1.50	5	14–15.5 (14.9)	.55
4	9	45–50 (47.4)	1.33	8	40–47 (43.6)	2.39	9	14.5–16 (15.3)	.57
5	11	47–53 (49.1)	1.76	9	39–51 (44.2)	3.53	11	13.5–15.5 (14.6)	.55
7	3	46–47 (46.7)	.58	3	45–46 (45.3)	.58	2	12.5, 14.5 (13.5)	1.41
8	9	43–46 (44.7)	1.00	5	44.5–47 (45.3)	.97	9	13–14 (13.7)	.43
9	3	43–44 (43.7)	.58	3	41–45 (42.7)	2.08	3	12.5–13 (12.7)	.29
10	3	45–48 (46.3)	1.53	3	38–44 (40.2)	3.33	3	13–14 (13.5)	.50
11	9	44–47 (45.7)	1.12	6	36–40 (37.7)	1.86	8	12–14 (12.9)	.73
12	5	46–50 (47.6)	1.52	4	38–42 (39.3)	1.89	5	13–14 (13.6)	.42
13	2	49, 50 (49.5)	.71	2	40, 40 (40.0)	...	2	13, 14 (13.5)	.71
15	13	42–46 (43.5)	1.51	10	38–43 (40.2)	1.81	11	12.5–15 (13.5)	.76
16	4	43–44 (43.3)	.50	3	37–40 (39.0)	1.73	4	13.5–14 (13.8)	.29
17	4	42–45 (43.5)	1.29	4	41–44 (42.3)	1.26	4	11.5–14 (12.9)	1.03
18	5	40–45 (42.6)	1.82	4	38–40 (38.8)	.96	5	13–14 (13.4)	.55
21	0	...	...	...	...	...	...	...	...
19	4	39–44 (42.0)	2.16	4	37–43 (39.5)	2.65	4	12–13 (12.4)	.48
22	1	43	...	1	40	...	1	12.5	...
6	1	44	...	1	39	...	1	13.5	...

Appendix A. *Continued.*

Group	Tarsus			Tail/wing ratio			Culmen/wing ratio			Tarsus/wing ratio		
	N	Range (and mean)	SD	N	Range (and mean)	SD	N	Range (and mean)	SD	N	Range (and mean)	SD
MALES												
1	10	19–20.5 (19.9)	.67	9	.837–.917 (.865)	.028	10	.294–.316 (.306)	.007	10	.380–.427 (.401)	.017
2	21	18.5–21.5 (20.0)	.76	17	.796–.957 (.867)	.046	18	.260–.330 (.294)	.017	18	.363–.457 (.402)	.024
3	23	18–21.5 (19.8)	1.04	21	.804–.980 (.873)	.040	23	.265–.333 (.297)	.019	23	.353–.436 (.400)	.023
4	16	18.5–21 (19.6)	.65	17	.848–1.00 (.937)	.033	17	.282–.333 (.308)	.013	16	.364–.429 (.395)	.018
5	9	17–21 (19.9)	1.45	4	.915–.940 (.933)	.012	9	.280–.316 (.301)	.012	8	.362–.438 (.414)	.023
7	9	16–18 (17.2)	.79	9	.936–1.043 (.994)	.039	8	.265–.300 (.283)	.013	9	.333–.372 (.357)	.018
8	9	16–18 (16.7)	.71	4	.967–1.043 (1.003)	.042	6	.278–.311 (.293)	.012	8	.354–.391 (.367)	.012
9	6	15–17 (16.0)	.63	5	.932–1.000 (.968)	.031	5	.272–.302 (.290)	.012	6	.341–.372 (.364)	.012
10	2	17.5, 18.5 (18.0)	.71	4	.851–.980 (.911)	.059	4	.280–.298 (.292)	.009	2	.365–.370 (.368)	.004
11	9	16–19 (17.7)	1.20	7	.787–.894 (.845)	.037	9	.265–.309 (.285)	.014	9	.333–.404 (.373)	.027
12	19	16–17.5 (16.7)	.45	15	.796–.917 (.854)	.038	17	.256–.298 (.277)	.012	19	.330–.362 (.346)	.009
13	5	17.5–18.5 (17.9)	.42	8	.769–.860 (.804)	.032	7	.260–.286 (.276)	.008	5	.343–.360 (.350)	.006
15	26	15–17.5 (16.6)	.66	23	.841–1.022 (.931)	.043	22	.284–.333 (.301)	.014	26	.333–.398 (.371)	.016
16	5	16.5–17 (16.7)	.27	5	.889–.953 (.919)	.025	4	.311–.322 (.317)	.005	5	.367–.386 (.378)	.008
17	12	15.5–17.5 (16.7)	.58	11	.889–1.022 (.949)	.039	11	.266–.318 (.293)	.019	12	.351–.389 (.371)	.015
18	18	15.5–17 (16.1)	.44	15	.837–.955 (.893)	.036	19	.289–.337 (.308)	.012	18	.348–.390 (.367)	.013
21	4	16–17 (16.3)	.50	3	.837–.910 (.877)	.037	4	.279–.310 (.296)	.013	4	.372–.405 (.380)	.017
19	12	14.5–17 (15.8)	.72	8	.907–1.000 (.954)	.035	11	.284–.313 (.293)	.009	12	.337–.405 (.369)	.020
22	8	16–17 (16.5)	.46	8	.930–1.023 (.978)	.029	4	.278–.302 (.291)	.010	8	.356–.395 (.376)	.016

Appendix A. *Continued.*

	Tarsus			Tail/wing ratio			Culmen/wing ratio			Tarsus/wing ratio		
Group	N	Range (and mean)	SD	N	Range (and mean)	SD	N	Range (and mean)	SD	N	Range (and mean)	SD
FEMALES												
1	10	18.5–20.5 (19.6)	.55	11	.771–.915 (.867)	.040	11	.286–.319 (.301)	.014	10	.378–.418 (.407)	.013
2	21	19–21.5 (19.7)	.70	18	.816–.885 (.856)	.020	20	.276–.320 (.300)	.013	19	.375–.427 (.404)	.014
3	5	19–20 (19.8)	.45	4	.854–.917 (.877)	.029	5	.298–.323 (.308)	.010	5	.396–.426 (.409)	.012
4	9	18.5–20 (19.1)	.65	8	.851–.979 (.918)	.043	9	.309–.333 (.322)	.009	9	.380–.422 (.403)	.015
5	10	18.5–21 (19.7)	.86	9	.813–.980 (.896)	.054	11	.255–.330 (.299)	.021	10	.363–.429 (.402)	.023
7	2	17.5, 18 (17.8)	.35	3	.957–.979 (.971)	.012	2	.266, .309 (.288)	.030	2	.372, .391 (.382)	.013
8	10	15.5–17 (16.6)	.55	5	.978–1.044 (.998)	.027	8	.289–.318 (.309)	.009	9	.353–.386 (.370)	.013
9	2	16, 16 (16.0)	0	3	.953–1.022 (.977)	.039	3	.284–.295 (.290)	.006	2	.364, .364 (.364)	0
10	3	16.5–18 (17.2)	.76	3	.826–.917 (.866)	.046	3	.281–.311 (.292)	.017	3	.354–.400 (.377)	.025
11	9	16.5–18 (17.2)	.44	6	.766–.867 (.825)	.042	8	.267–.311 (.283)	.015	9	.362–.389 (.377)	.010
12	4	16.5–17.5 (17.0)	.41	4	.780–.894 (.819)	.052	5	.277–.293 (.286)	.007	4	.330–.372 (.355)	.018
13	2	16, 17 (16.5)	.71	2	.800, .816 (.808)	.011	2	.265, .280 (.273)	.011	2	.327, .340 (.334)	.009
15	13	15.5–17 (16.3)	.55	10	.867–.956 (.920)	.030	11	.278–.341 (.314)	.017	13	.348–.405 (.376)	.016
16	5	all 16 (16.0)	0	3	.860–.930 (.899)	.036	3	.314–.318 (.315)	.002	4	.364–.372 (.370)	.004
17	4	15–17 (16.0)	.82	4	.911–1.000 (.972)	.040	4	.267–.318 (.296)	.023	4	.356–.386 (.368)	.014
18	3	15.5–16 (15.8)	.29	4	.844–.930 (.896)	.041	5	.302–.326 (.315)	.010	3	.369–.372 (.371)	.002
21	...	...	...	...	...	...	...	...	...	...	...	...
19	3	14.5–15.5 (15.0)	.50	4	.905–.977 (.940)	.030	4	.284–.308 (.295)	.012	3	.349–.372 (.358)	.013
22	1	17	...	1	.930	...	1	.291	...	1	.395	...
6	1	16.5	...	1	.886	...	1	.307	...	1	.375	...

Appendix B

Checklist of South American *Cistothorus platensis platensis*

GROUP A

Cistothorus platensis aequatorialis Lawrence

Cistothorus aequatorialis Lawrence, 1871, Ann. Lyceum Nat. Hist. New York, 10: 3—Pichincha, Ecuador.

Cistothorus platensis tamae Cory, 1916, Publ. Field Columbian Mus., Ornithol. Ser., 1: 344—El Páramo de Tamá, Táchira, Venezuela.

Cistothorus platensis tolimae Meyer de Schauensee, 1946, Not. Nat. (Phila.), no. 161: 2—Nevado del Tolima, Tolima, Colombia.

Diagnosis: crown, lower back and rump plain, unstreaked; tail barred throughout. Belongs with *graminicola*, to the long-tarsused form of the northern and Central Andes; differs from *graminicola* in having a distinctly shorter tail, tail/wing ratio of .865–.873 compared to .933–.937.

Range: páramos of the Eastern and Central Andes, from Páramo de Tamá and Caldas south to central Ecuador (groups 1–3).

Cistothorus platensis graminicola Taczanowski

Cistothorus graminicola Taczanowski, 1874, Proc. Zool. Soc. Lond., p. 130—Maraynioc, Junín, Peru.

Diagnosis: like *aequatorialis* in having a proportionately long tarsus; differs from *aequatorialis* in having a relatively longer tail, and from Junín south in having a streaked crown.

Range: páramos and temperate grasslands from southern Ecuador south to Cuzco and Puno, Peru, and La Paz, Bolivia (groups 4–5).

Cistothorus platensis tucumanus Hartert and Venturi

Cistothorus platensis tucumanus Hartert and Venturi, 1909, Novit. Zool., 16: 163—Tucumán, Argentina.

Cistothorus platensis boliviae Bond and de Schauensee, 1941, Not. Nat. (Phila.), no. 93: 6—Samaipata (5500 ft), Santa Cruz, Bolivia.

Diagnosis: like *graminicola* of southern Peru and La Paz, but with a proportionately much shorter tarsus, tarsus/wing ratio of .357 compared to .414; differs from *platensis* to the south in having a plain lower back and rump, but some birds from Tucumán show intergradation.

Range: locally in temperate grasslands of the Andes and adjacent foothills from Santa Cruz, Bolivia, south to Tucumán, Argentina (group 7).

Cistothorus platensis platensis (Latham)

Sylvia platensis Latham, 1790, Index Ornithol., 2: 548—Buenos Aires, Argentina.

Diagnosis: heavily and completely streaked above; shorter-winged and longer-tailed than *hornensis* to the west and south, average wing length of males 44.0–45.3 compared to 47.3–48.2, and average tail/wing ratio of males .968–1.003 compared to .845–.911. At least half the birds from Buenos Aires show some black on the inner webs of the rectrices, a sign of intergradation with *polyglottus* of group B.

Range: central Argentina: northern Mendoza east to central western Córdoba; Buenos Aires Province (groups 8–9); intergrades extensively with *polyglottus* of group B in southern Paraguay, northeastern Argentina, and Rio Grande do Sul, Brazil (group 20).

Cistothorus platensis hornensis (Lesson)

Troglodytes hornensis Lesson, 1834, L'Institut (Paris), 2, no. 72: 316—"at sea twenty leagues southeast of Cape Horn."

Diagnosis: upperparts as in *platensis*, but wings longer and tail proportionately much shorter (see *platensis*).

Range: locally in Chile and adjoining Argentina from Coquimbo to Tierra del Fuego (groups 10–12).

Cistothorus platensis falklandicus Chapman

Cistothorus platensis falklandicus Chapman, 1934, Am. Mus. Novit., no. 672: 7—Sea Lion Island, Falkland Islands.

Diagnosis: like *hornensis*, but with longer wings and proportionately shorter tail.

Range: Falkland Islands (group 13).

GROUP B

Cistothorus platensis polyglottus (Vieillot)

Thryothorus polyglottus Vieillot, 1819, Nouv. Dict. Hist. Nat., nouv. éd., 34: 59—Paraguay.

Diagnosis: plain crown, lower back and rump, and restricted dorsal streaking as in *aequatorialis*, but with shorter wing, proportionately shorter tarsus and longer tail, and with black instead of barred inner webs on rectrices 2–5.

Range: a divided range; northern part, locally in the highlands of the Sierra Nevada de Santa Marta (group 15), Colombia, the Sierra de Perijá (group 16), and the coastal mountains of Venezuela from Lara to Miranda (group 17), and once in the Páramo de Escorial, Merída; southern part in southeastern Brazil, from southern Goiás to Paraná (group 19), and an isolated population on the lower Río Beni, El Beni, Bolivia (group 22). Intergrades extensively with *platensis* in southern Paraguay, northeastern Argentina, and Rio Grande do Sul, Brazil (group 20).

Cistothorus platensis alticola Salvin and Godman

Cistothorus alticola Salvin and Godman, 1883, Ibis, p. 204—Cerro Roraima, Venezuela.

Diagnosis: similar to *polyglottus*, but with a shorter tail.

Range: moderate elevations on the tepuis of the southeastern corner of Bolívar, Venezuela (group 18); in the lowlands of eastern Meta near the Río Meta, Colombia (group 21).

Cistothorus platensis minimus Carriker

Cistothorus platensis minimus Carriker, 1934, Proc. Acad. Nat. Sci. (Phila.), 87: 354—Oconeque (9000 ft), Puno, Peru.

Diagnosis: similar to *polyglottus* in the lowlands of El Beni, Bolivia, but with a streaked crown; similar in dorsal plumage pattern to *graminicola* of the rest of Puno, but much smaller in all dimensions, and with black on the inner webs of some rectrices.

Range: known only from the type locality (group 6) where it is found within 55 km of the group A *graminicola* at Valcón (group 5).

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