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GEOGRAPHIC VARIATION, ZOOGEOGRAPHY, AND POSSIBLE RAPID EVOLUTION IN SOME *CRANIOLEUCA* SPINETAILS (FURNARIIDAE) OF THE ANDES

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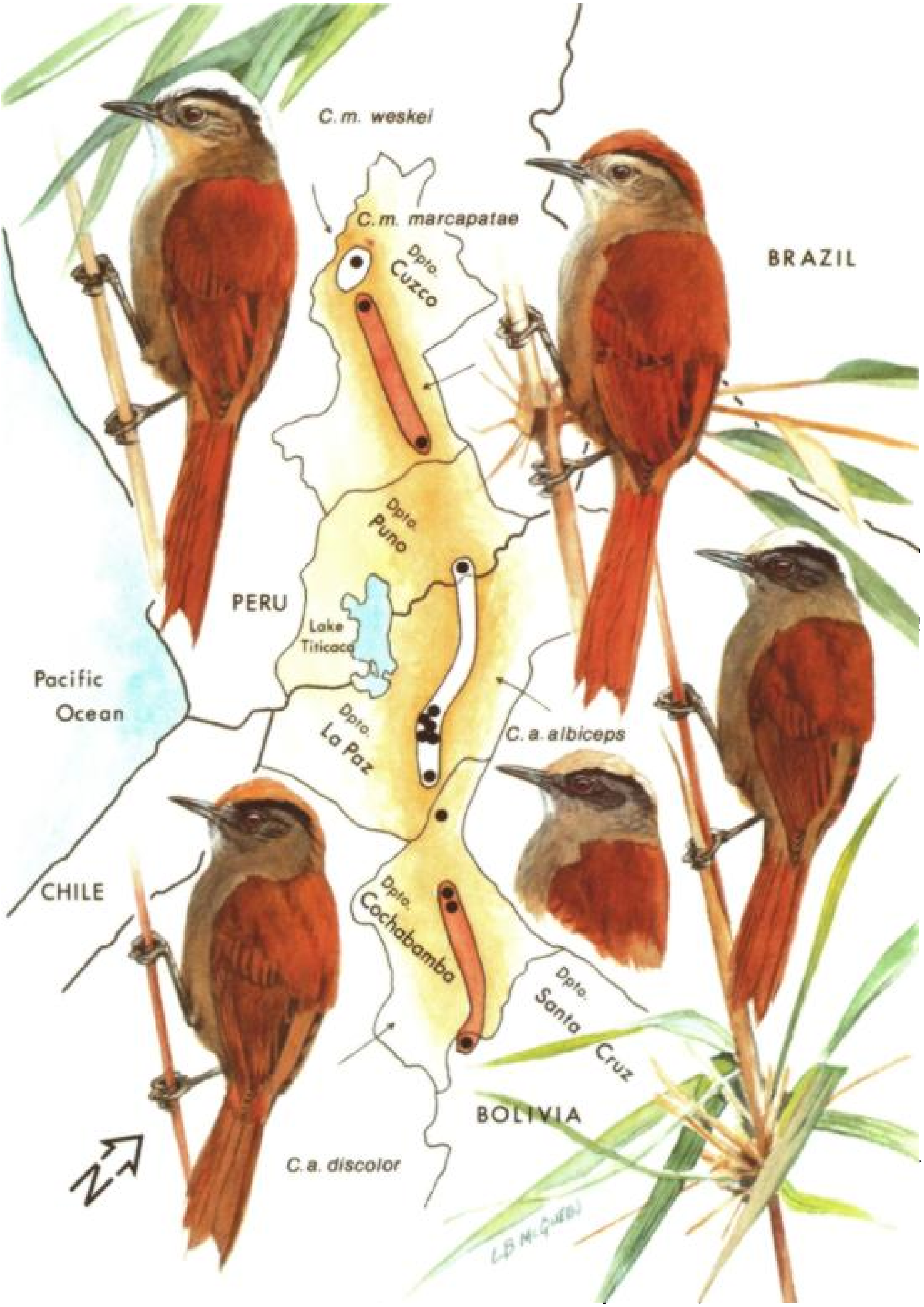
The humid slopes of the Andes Mountains of South America provide one of the world's greatest natural laboratories for the study of evolution and zoogeography. Although the "population structure," nature of geographic variation, and location of zoogeographic boundaries have been described for numerous taxa of the puna and paramo zones of the Andes (Vuilleumier 1980), relatively little has been published concerning birds of the humid, forested eastern slopes. In this paper, I analyze the geographic variation and distribution of the *Cranioleuca albiceps* superspecies (Furnariidae), here considered to consist of Light-crowned Spinetail (*C. albiceps*) (with two subspecies), Marcapata Spinetail (*C. marcapatae*), and a previously undescribed form, here considered a subspecies of *C. marcapatae*, to be called:

Cranioleuca marcapatae weskei subsp. nov.

HOLOTYPE.—American Museum of Natural History No. 820557; male from Cordillera Vilcabamba, elev. 3250 m, Dpto. Cuzco, Peru (12°36′S, 73°30′W), 22 July 1968; John S. Weske, original number 1825.

DIAGNOSIS.—Ventrally very similar to *Cranioleuca m. marcapatae,* but malar region more strongly washed buff; dorsally, virtually identical to white-crowned individuals of *Cranioleuca a. albiceps.*

DESCRIPTION OF HOLOTYPE.—Crown dull white, tinged buff on anteriormost forecrown; white of crown bordered laterally by black stripe that increases in width posteriorly; lores blackish mixed buffy white; eyebrow dull whitish above eye blending to Buffy Brown; faint, dull, blackish postocular line indistinctly delimits eyebrow; auriculars Olive-Brown with pale shaft streaks on some feathers; crown and black border blend raggedly into Saccardo's Umber neck and upper back; rest of back and upper wing coverts Chestnut; rump



Cranioleuca albiceps and *C. marcapatae*, showing
the development of rusty and white-crowned forms in each species and
illustrating *C.m. weskei*, a new subspecies
from the Cordillera Vilcabamba of south central Peru.
From a watercolor painting by Lawrence B. McQueen.

and uppertail coverts Saccardo's Umber mixed with Chestnut; primaries Sooty Black except for outer web mainly Sanford's Brown; most secondaries Sooty Black except for Chestnut edge to outer webs and small Sanford's Brown apical spot; underwing coverts Olive-Brown mixed Cinnamon; rectrices Chestnut; outermost rectrices shortest and innermost longest and very pointed (typical *Cranioleuca* shape); chin and upper throat white, bordered laterally by poorly defined Warm Buff malar area; both throat and malar area blend gradually into darker lower throat, sides and chest, and belly, which are Light Grayish Olive to Light Drab; flanks, thighs, and undertail coverts Drab to Tawny. Bases of some feathers in vent area dull white. Soft parts in life: iris medium reddish-brown, maxilla black, mandible medium gray, tarsi and feet medium greenish-gray (black in dried specimen).

DISTRIBUTION.—Presently known only from cloud forest in the Cordillera Vilcabamba, Dpto. Cuzco, Peru, between 2620 and 3250 m.

SPECIMENS EXAMINED.—*C. m. weskei:* (AMNH) 3 ♂♂, 5 ♀♀, Cordillera Vilcabamba, Dpto. Cuzco, Peru, 12°36–37'S, 73°30–33'W, 2620–2640 m (3), 2830 m (1), 3250 m (3) and 3300 m (1). *C. m. marcapatae* (all Dpto. Cuzco, Peru): (LSUMZ) ♂, 14 km NE Abra Málaga on Ollantaitambo-Quillabamba road, 10,700 ft. (3210 m); (LSUMZ) ♂, ca 20 km NE Abra Málaga on Ollantaitambo-Quillabamba road, 9800 ft. (2940 m); (LSUMZ) ♂, ♀, San Luis on Ollantaitambo-Quillabamba road, 9000 ft. (2700 m); (LSUMZ) ♂, ♀, along Río Marcapata just below Marcapata on road to Quincemil, 9000 ft. (2700 m) (topotypes); (AMNH) ♀, Marcapata (topotype), *C. a. albiceps:* (LSUMZ) 2 ♂♂, 3 ♀♀, Valcón, 5 km NNW Quiaca, 3000 m, Dpto. Puno, Peru (first records for Peru); (LSUMZ) 8 ♂♂, 3 ♀♀, 1 sex ?, ca 1 km S Chuspipata, 3050 m, Dpto. La Paz, Bolivia; (LSUMZ) 5 ♂♂, 3 ♀♀, Cotapata, 4.5 km WNW Chuspipata, 3300 m, Dpto. La Paz; (ANSP) 3 ♂♂, 3 ♀♀, Hichuloma, 10,700 ft. (3210 m), Dpto. La Paz; (AMNH) 1 ♂, Rio Aceromarca, 10,800 ft. (3240 m), Dpto. La Paz. *C. a. albiceps* × *discolor:* (FMNH) 3 ♂♂, 1 ♀ (LSUMZ) 1 ♂, Choro, Prov. Ayopaya, Dpto. Cochabamba, Bolivia. *C. a. discolor:* (LSUMZ) 4 ♂♂, 1 ♀, 2 sex ?, (AMNH) 1 sex ?, km 104, 3100–3200 m, Prov. Chapare, Dpto. Cochabamba; (FMNH) 4 ♂♂, 4 ♀♀, (ANSP) 3 ♂♂, 2 ♀♀, (AMNH) 3 ♂♂, 1 ♀, (LSUMZ) 1 ♀, Incachaca 2400–2500 m, Prov. Chapare, Dpto. Cochabamba (topotype); (ANSP) 2 ♂♂, San Cristobal, 8500 ft. (2550 m), Dpto. Cochabamba; (FMNH) 2 ♂♂, 1 ♀, 28 km W Comarapa, Dpto. Santa Cruz, Bolivia (first records for Dpto. Santa Cruz).

REMARKS.—No differences in plumage pattern were detected between the sexes. Some slight variation among the eight specimens of *weskei* is apparent in grayness of the underparts and paleness of the superciliary; otherwise the series is very homogeneous in plumage and soft part colors. Vaurie (1980) previously identified the Vilcabamba specimens as *Cranioleuca albiceps* and published them as the first record for Peru.

ETYMOLOGY.—It is a pleasure to name this form for John S. Weske, preparator of the entire series from the Vilcabamba and co-leader of the several rigorous and highly productive expeditions to the area.

NATURAL HISTORY NOTES

All eight specimens of *C. m. weskei* were netted in elfin cloud forest along ridges. None of the specimens had the skull more than 20% pneumatized; as in numerous other synallaxines (pers. obs.), it seems likely that the skull never reaches complete pneumatization. Two of the three males had enlarged testes, but none of the five females was in reproductive condition; all were collected between 5 July and 8 August. None of the specimens had more than "little" fat, as is typical for funariids of the eastern slope of the Andes (pers. obs.).

Weske (1972) did not include information on *C. m. weskei* among the natural history data that he compiled for many Vilcabamba birds. It is likely that the natural history of this form is very similar to two relatives, *C. m. marcapatae* and *C. a. albiceps,* for which information is available. Parker and O'Neill (1980) found that *C. m. marcapatae* foraged in two's and three's in mixed-species flocks in bamboo thickets and mossy forest as did Remsen (in press) for *C. a. albiceps.* Both forms "hitch" along limbs to probe moss, bromeliads, dead leaf clusters, and bark; quantitative data on foraging behavior of *C. a. albiceps* are presented by Remsen and Parker (1984) and Remsen (in press). Contrary to Vaurie's (1980) implications from Niethammer's (1956) account, *C. albiceps* is very similar in foraging behavior to other *Cranioleuca* sensu strictu (see also F. Vuilleumier's note in Vaurie 1980:338).

Parker and O'Neill (1980) described the first known nest of *C. m. marcapatae.* On 1 August 1981, I found the first known nest of *C. albiceps*; it was under construction on a steep slope with dense undergrowth and patches of short trees at 3050 m near Chuspipata, Dpto. La Paz. The nest was an oval clump of moss, about 0.3 m in length, wrapped around the distal tip of a living bamboo (*Chusquea*) branch about 6 m above ground. The nest appeared virtually complete. The entrance was on the side about two-thirds of the way from the proximal to distal end (relative to the branch) of the nest; one bird was carrying moss into the nest chamber. Thus, this species' nest is very similar to that of *C. m. marcapatae.* Presumably the nest of *C. m. weskei* is similar.

RELATIONSHIPS AMONG THE TAXA

Should each of the four spinetail taxa in question be considered allospecies of a superspecies complex, subspecies of a single biological species, or some intermediate combination? In the absence of comparative data on vocalizations and other potential reproductive isolating mechanisms or on degree of genetic differentiation, any taxonomic decisions at this point for these primarily allopatric populations are tentative at best.

Current information indicates that crown color differences do not necessarily result in reproductive isolation. Specimens from an area (Choro, Prov. Ayopaya, Dpto. Cochabamba) geographically intermediate between populations of *C. a. albiceps* and *C. a. discolor* are intermediate in crown color between the white-crowned nominate subspecies and tawny-crowned *discolor.* Furthermore, the high frequency of buff-crowned individuals in the Dpto. La Paz population (see below) may indicate gene flow from the southern populations. Thus it seems best to disregard crown color, the character that varies most dramatically among populations, as a potential isolating mechanism (although this conclusion is based on the assumption

TABLE 1
PLUMAGE CHARACTERS IN THE *CRANIOLEUCA ALBICEPS* SUPERSPECIES

Taxon[1]	Plumage characters				
	Crown	Eyebrow	Auriculars	Throat	Breast
C. m. weskei	white	buffy-white	buffy-brown	white bordered buffy	gray-brown
C. m. marcapatae	chestnut	gray-white	gray-brown	white	gray-brown
C. a. albiceps	white or buffy	dark gray	dark gray	mostly gray-olive	olive-brown
C. a. discolor	tawny	dark gray	dark gray	mostly gray-olive	olive-brown

[1] Taxa are listed in geographic order from north to south.

that the populations in question are in secondary contact). Therefore, that *marcapatae* has a chestnut crown, in contrast to neighboring *weskei* and *albiceps,* in itself provides no evidence for reproductive isolation.

Except for crown color, *weskei* and *marcapatae* are much more similar to one another than either is to *albiceps* and *discolor.* Likewise, these latter two are virtually identical to each other except for crown color. Thus, on plumage characters other than crown color, the four taxa can be placed in two groups, the two paler northern forms, *weskei* and *marcapatae,* and the two southern forms, *albiceps* and *discolor* (Table 1).

To avoid changing currently recognized species limits in the absence of critical data, I recommend recognizing two species, *C. albiceps* (with two subspecies, the nominate form and *discolor*) and *C. marcapatae* (with two subspecies, the nominate form and *weskei*). Each of the two subspecies within each species is extremely similar in most plumage characters and differs from each other to about the same degree in crown color. This arrangement may seem unsatisfactory to some, because *C. m. weskei* and *C. a. albiceps* are virtually identical from the dorsal view. This resemblance, however, can be regarded as retention of a shared, primitive character, as proposed below.

Although reconstructions of historical zoogeographic events often contain more speculation than warranted by available data, such historical hypotheses are a necessary part of a zoogeographic and taxonomic analysis. Within the *Cranioleuca albiceps* superspecies, I assume that the white crown is a primitive character, because it seems unlikely that two isolated populations would have independently evolved an identical crown color that is unique in *Craniolecua* (and in the Furnariidae in general). Given this assumption, the following sequence of historical events is plausible.

Originally, a white-crowned population was distributed along the eastern slope of the Andes from the Cordillera Vilcabamba of Peru to Dpto. Cochabamba, Bolivia. Geological and climatological events isolated two populations from one another, proto-*marcapatae-weskei* north of and proto-*albiceps-discolor* south of some unknown barrier in southern Peru, perhaps the canyon of the Río Sangaban in northern Dpto. Puno. In isolation, the two populations differentiated in terms of plumage characters, mainly coloration of the underparts and face. Subsequently, the southern population was further fragmented by the dry canyon of the Río La Paz, and the population to the south of this barrier became tawny-crowned. Also, the northern population was divided in two by the dry canyon of the Río Urubamba, and the population to the south of the Urubamba became chestnut-crowned. These events would have led to the current pattern of distribution of the four forms, with *weskei* and nominate *albiceps* retaining the white crown, a shared primitive character (but a shared derived character for this species group as a whole). Study of other taxa from these regions are required to corroborate this pattern and document its validity (Nelson and Platnick 1981).

PATTERNS OF GEOGRAPHIC VARIATION IN COLOR AND SIZE

Geographic variation in body size in the *Cranioleuca albiceps* group shows the trend counter to Bergmann's "rule" but typical for birds of the humid southern Andes (Remsen 1981, 1982, unpubl.): decreasing size with increasing distance from the equator. Using wing length to index body size, there is a highly significant negative correlation between wing length and latitude: N (♂♂) = 31, $r = -.656$, $P < 0.001$; N (♀♀) = 24, $r = -.677$, $P < 0.001$. The trend is not a "perfect" one, however, because southernmost *discolor* averages slightly larger than nominate *albiceps* to the north.

At first glance, the *C. albiceps* superspecies seems to provide an example of a "leapfrog" pattern of geographic variation in color (Remsen 1984)—the two white-crowned populations are geographically separated from each other by a chestnut-crowned form. This example was not included in my list of taxa that show the leapfrog pattern because crown color is the only phenotypic character to show the pattern; the two northern forms, *weskei* and *marcapatae,* are much more similar to each other in all other plumage characters than either is to the two southern forms (Table 1). Those taxa included in the list showing the leapfrog pattern were those in which the majority of characters that showed geographic variation did so in a leapfrog manner.

Can an adaptive explanation be proposed for the different plumage types? I have previously suggested (Remsen 1984) that the leapfrog pattern is best explained by invoking random change that is not environmentally induced. On the other hand, I have also observed (unpubl.) that in species in which degree of buffy, chestnut, or tawny (="rusty") coloration varies geographically, the "rustiest" form tends to occur at the southern end of the Andes, especially Dpto. Cochabamba, or to a more limited degree at the northern end of the Andes in extreme northern Colombia and Venezuela. Could this increased rustiness be an adaptation for better camouflage because longer dry seasons at the extremes of the Andes make the forest there have a "rustier" appearance? The rainfall data necessary for testing this hypothesis are not available.

POSSIBLE RAPID EVOLUTION IN CROWN COLOR

In 1980 and 1981, LSUMZ field parties collected 28 specimens of *C. a. albiceps* in Dpto. La Paz and 5 in Dpto. Puno. Variation in crown color in these recent specimens contrasts markedly with earlier descriptions, none of which indicated that crown color was anything but white. In contrast, the crowns of only four recent specimens were pure white; the rest were faintly to strongly washed with buffy. Because it seemed highly unlikely that earlier workers such as J. T. Zimmer and C. E. Hellmayr would have overlooked such variation, I began to investigate the possibility that a change in phenotype had occurred between 1936 and 1980.

First, I determined whether the crowns of the earlier specimens were indeed all white. As noted by Zimmer (1935), none of the earlier published descriptions of Dpto. La Paz birds (e.g., type description and Sclater 1980) indicated that the crown was any color other than white. I attempted to examine, or have others examine for me, all specimens of *Cranioleuca a. albiceps* available in museums. Four specimens collected before 1930, including the type specimen at the British Museum, have white crowns, with perhaps only some buffy tinge on forecrown. Five adults collected in 1934–35 also have white crowns, but two obvious juveniles have the crown noticeably tinged buff.

In contrast, specimens collected in 1980–81 show marked variation in crown color with over half of the specimens having their crowns strongly buffy or buffy mixed with white. This variation is not related to sex ($\chi^2 = 0.14$, df = 1, $P > 0.05$); 5 of 12 (42%) adult males and three of nine (33%) of adult females are buffy-crowned. Nor is the variation due to age. Because most individuals may never acquire a completely pneumatized skull (only 1 of 28 LSUMZ specimens with skull data is 100% pneumatized; most are labeled 5–25% ossified), analysis of the effect of age is difficult. Nevertheless, of the four specimens with traces of juvenile plumage, two are buffy-crowned and two are white.

TABLE 2
FREQUENCY OF CROWN COLOR TYPES IN OLD VS NEW SPECIMENS OF *CRANIOLEUCA A. ALBICEPS*

	Number of specimens[1] in each crown color category	
Specimen age	White	Buffy
1936	9	0
1977	9	15

[1] Only adults were included in the table; inclusion of birds in juvenal plumage would add two individuals to the "buffy" category for pre-1936 specimens, and two to the "white" category and two to the "buffy" category for post-1977 specimens.

That the difference in crown color frequencies in the pre-1936 specimens and the recent specimens could be due to geographic variation or anomalies in sampling appears improbable. The older collecting sites are located between the modern sites in Dpto. La Paz and Dpto. Puno, and Carriker's 1934–35 locality, Hichuloma, is only 2 km from, and on the same ridge as, the 1980–81 La Paz localities.

The proportion of individuals in the two crown color categories in old vs recent samples (Table 2) is significantly different ($\chi^2 = 5.9$, df $= 1$, $P < 0.05$) if juveniles are included and highly significantly different ($\chi^2 = 23.3$, df $= 1$, $P < 0.0001$) if only birds in adult plumage are analyzed. Two interpretations are possible. Conservatively, if the juveniles are included, one could argue that a combination of differences in sampling technique (guns for old specimens, mostly mist-nets for recent) and collecting localities produced a difference in proportions of borderline significance. On the other hand, especially if juveniles are excluded, one could argue, almost heretically, that a new phenotype is in the process of spreading through the population over a 40-year period. This possibility has also been suggested by Fitzpatrick (1980) for another Andean bird population—that of the White-winged Brush-Finch (*Atlapetes leucopterus*). In birds, such rapid evolutionary change has been reported so far only in species introduced into novel environments (Johnston and Selander 1964, Aldrich and Weske 1978, Baker and Moeed 1979, Barlow 1980), although Zink (1983) found minor changes in skeletal morphometrics in samples of a non-introduced bird population over a 50-year time span. In the case of *C. albiceps,* such change could be the result of: (1) introgression of *discolor* genes into the nominate *albiceps* population; (2) evolutionary change independent of secondary contact with *discolor* populations; or (3) change in frequency of a polymorphic character state. Available data do not allow evaluation of these alternatives.

SUMMARY

A distinct new form of *Cranioleuca* from the Cordillera Vilcabamba, Dpto. Cuzco, Peru, is described as a subspecies (*weskei*) of *Cranioleuca marcapatae.* Natural history notes concerning *weskei* and its close relative *C. a. albiceps* are presented, including a description of the first known nest of the latter. Relationships among the members of the *C. albiceps* superspecies are discussed, as are the patterns of geographic variation that this group exhibits in color and body size. Samples of *C. a. albiceps* taken approximately 50 years apart show strong differences in crown color frequencies that can be interpreted tentatively as a case of rapid evolution in a phenotypic character.

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COLOR PLATE

Inclusion of the frontispiece of *Cranioleuca* spp. has been made possible through an endowment established by George Miksch Sutton (1896–1982). Painting by Lawrence B. McQueen.