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## Patchy Distribution and Systematics of *Oreomanes fraseri* (Aves, ?Coerebidae) of Andean *Polylepis* Woodlands

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### ABSTRACT

The Giant Conebill, *Oreomanes fraseri* Sclater, 1860, is an endemic, monotypic genus of coerebid or thraupid-like bird distributed in the high Andes of South America from southern Colombia to southwestern Bolivia. This well-marked taxon appears to be restricted ecologically to "islands" of woodland vegetation above timberline that are dominated by trees of the endemic Andean genus *Polylepis* (Rosaceae). The geographical distribution of *Oreomanes fraseri* is quite patchy. *Oreomanes fraseri* shows geographical variation in bill size and plumage color. Geographical variation, however, is very minor, and so it does not seem useful to describe it in terms of subspecies. The pattern of this variation is partly clinal and partly checkerboard, as one would expect from the nature of the discontinuous distribution of the species.

Range disjunctions and geographical isolation of populations do not appear conducive to incipient speciation. The patterns of geographical distribution and variation suggest either: (a) that the origin of the disjunctions is recent (i.e., there has not been enough time for the isolates to become morphologically and presumably also genetically differentiated); (b) the geographical isolation has been insufficient to promote differentiation (i.e., gene flow exists between isolated populations and counters the disrupting effects of geographical isolation); or (c) geographical isolation is effective and is relatively old in origin but the rate of morphological differentiation in the isolates is slow. Data are lacking at present to permit one to check which of these hypotheses is the most likely to explain the observed patterns.

### RESUMEN

El Pájaro de los queñuales, *Oreomanes fraseri* Sclater, 1860, es un género endémico y monotípico de ave relacionado a los Coerebidae o a los Thraupidae, distribuido en los altos Andes de América del Sur, desde el sur de Colombia hasta el

suroeste de Bolivia. Esta especie parece restringida ecológicamente a islas de vegetación leñosa encima del límite superior del bosque andino nublado, dominadas por árboles del género andino endémico *Polylepis* (Rosaceae). La distribución geo-

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gráfica discontinua de *Oreomanes* esta relacionada con la distribución insular de los bosques de *Poly-lepis*. *Oreomanes fraseri* tiene variación geográfica en algunos caracteres morfológicos externos, especialmente el tamaño del pico y el color de su plumaje. Esta variación es irregular, como se hubiera podido predecir según la distribución discontinua de las poblaciones de la especie. Sin embargo, esta variabilidad geográfica es menor y no parece biológicamente significativa describirla con una nomenclatura subespecífica. Aunque distribuida en poblaciones aisladas, el patrón de diferenciación en *Oreomanes fraseri* no parece apropiado a especiación. Tal distribución y variación

geográfica sugieren tres hipótesis explicativas: (a) el origen de las discontinuidades de distribución es muy reciente y el tiempo no ha sido suficiente para una mayor diferenciación morfológica (y genética?) de las poblaciones aisladas; (b) el aislamiento geográfico no es suficiente para resultar en variación marcada, pues el intercambio de genes entre poblaciones aparentemente aisladas se opone a los efectos del aislamiento parcial; (c) la diferenciación morfológica se ha producido muy despacio, aunque podría haber sido muy antiguo el origen de las discontinuidades distribucionales. No tenemos datos todavía para averiguar cual sería la más probable de esas tres hipótesis.

## INTRODUCTION

The Giant Conebill, *Oreomanes fraseri* Sclater, 1860, is a remarkable bird of the high Andes of South America. It is about the size of a large nuthatch *Sitta* (Sittidae), and it also roughly has the color, aspect and branch or tree-climbing behavior (H.-W. Koepcke, 1961, p. 176; George, 1964; Pearson and Pearson Ralph, 1978, p. 29; personal observ.). Bull (personal commun.) was struck by the resemblance in color and general behavior between *Oreomanes* and *Sitta castanea*. *Oreomanes* is dark slate gray above and chestnut brown below, with a conspicuous white cheek patch. Without this white cheek patch, the color pattern of *Oreomanes* resembles that of *Conirostrum ferrugineiventre*, a high Andean coerebid that is occasionally found sympatrically with *Oreomanes* (Parker and O'Neill, 1980; Schulenberg, in press). The family Coerebidae is now considered by some workers to be a polyphyletic assemblage of unrelated genera. Paynter and Storer (1970, p. ix) placed *Xenodacnis*, *Oreomanes*, and *Diglossa* in the subfamily Thraupinae of the family Emberizidae, and kept *Conirostrum* out. Lowery and Monroe (1968, p. 3) considered *Conirostrum* (and *Coereba*) to be genera *incertae sedis*, which they placed "at the end of the family" Parulidae. Paynter and Storer (1970, p. ix) stated that "*Oreomanes* may be close to *Diglossa* or to *Conirostrum* or both." Recently, Bock (in press) argued on anatomical grounds that *Diglossa* may be a polyphyletic genus. Thus the interrelationships of the genera *Xenodacnis*, *Oreomanes*, *Conirostrum*, and *Diglossa*, which are all An-

dean in distribution, are quite uncertain. For convenience I shall retain in this paper the term Coerebidae to include them all.

Two interesting problems are posed by *Oreomanes*. The first is of the taxonomic affinities of this genus. Its describer, Sclater (1860, p. 76), believed *Oreomanes* to be "more nearly allied to *Diglossa* . . . than to any other genus of Coerebidae." A hundred years later, George (1964, p. 26) suggested again "a near relationship" between the two genera. Specifically, George (1964) stated that *Oreomanes fraseri* was perhaps close to *Diglossa carbonaria* (a taxon belonging to a series of allopatric and parapatric semispecies and allospecies. See Vuilleumier, 1969a, in press; Graves, 1982). Storer (1970, p. 38) remarked that "This nuthatch-like genus may be related to *Diglossa* and to the emberizine finches. Its systematic position remains to be determined" (he placed it between *Xenodacnis* and *Diglossa* in the Thraupinae of the Emberizidae). However, bill shape in *Oreomanes* is unlike that in any species of *Diglossa* but more like that in species of *Conirostrum*, whereas the color pattern of *Oreomanes* resembles as much that of some species of *Diglossa* (e.g., *D. sittoides*) as that of some species of *Conirostrum* (e.g., *C. ferrugineiventre*). Clearly, the affinities of *Oreomanes* are in need of further study. Anatomical evidence and biochemical data (from electrophoresis of proteins and from DNA × DNA hybridization) would be especially useful. The recent description of a hybrid specimen *O. fraseri* × *Conirostrum ferrugineiventre*

*entre* (Schulenberg, in press) adds a substantial element strongly supporting the hypothesis of close taxonomic relatedness of these two genera.

The second problem stems from the fact that the geographical distribution of *Oreomanes fraseri* is patchy (figs. 1 and 2), and seems to coincide ecologically with the distribution of its preferred habitat, the rather open woodlands dominated by trees of the genus *Polylepis* (Rosaceae). These woodlands are of exceptional interest in Andean ecology and biogeography because they usually occur as small islands of arboreal vegetation above timberline in the open, scrubby or grassy expanses of the alpine-like páramo or puna vegetation formations (Simpson, 1979, in press). All specimen labels of *Oreomanes* that include an indication of habitat mention either "*Polylepis*" or "queñual" (the Quechua name for these woodlands), and all authors who have written about *Oreomanes* have mentioned this preference (e.g., M. Koepcke, 1970, p. 111; H.-W. Koepcke, 1961, p. 176; George, 1964, p. 26; Vuilleumier, 1969b, p. 606; Parker and O'Neill, 1980, p. 173). Furthermore, H.-W. Koepcke (1961, p. 176) noticed that the color pattern of *Oreomanes* corresponds very closely ("hervorragend übereinstimmend" are his words!) to the gray and reddish color of the flaky bark of *Polylepis* trees. George (1964, p. 26) went so far as to state that "the bird is so well camouflaged that it ranks high among species that provide support for the theory of protective coloration in animals." Whether he is right or not, the striking resemblance between bird and bark color can easily be gauged by looking at Arthur Singer's attractive color plate illustrating George's article.

In the present paper I do not discuss the systematic position of *Oreomanes* within the Coerebidae, the Thraupidae, the Emberizidae, or the nine-primaried oscines, leaving this problem to anatomists or biochemists (see also Schulenberg, in press). Instead, I investigate two interrelated aspects of the second problem mentioned above. First, I will verify whether the patchy distribution of *Oreomanes* corresponds to the patchy distribution of *Polylepis* woodlands. Second, if there is geographical variation in *Oreomanes*, I will check whether it is correlated with the

bird's patchy distribution. If the distribution of *Oreomanes* is island-like, one might expect this species to be made up of geographically and ecologically isolated populations varying from one another either in checkerboard fashion, thus showing a population structure (*sensu* Mayr, 1959, p. 294) conducive to speciation, or in clinal fashion, thus showing the influence of environmental conditions along the Andes, such as moisture gradients.

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TABLE 1  
Localities of *Oreomanes fraseri*  
(see fig. 1)

Locality	Number of Specimens		References or Specimens* [specimens examined in brackets]
	Re-ported	Exam-ined in This Study	
1. "Pasto," Nariño, Colombia (no altitude given)	2	2	Meyer de Schauensee (1951, p. 958) [BM 85.4.1.80; USNM 90465]
2a. Papallacta, Napo, Ecuador (no altitude given)	1	1	[Moore Collection Occidental College Ec-L 320]
2b. Papallacta Road, Napo, about 3700 m.	—	—	John Bull (personal commun.); sight record
3. Cerro Huamani arriba, Pichincha, Ecuador (no altitude given)	2	2	Chapman (1926, p. 641) [MCZ 233512; AMNH 180788]
4. Guamani Pass, Pichincha, Ecuador (16,000 ft. = 4850 m.)	1	1	[BM 1916.8.24.87]
5. Cerro Puntas, Pichincha, Ecuador (no altitude given)	2	2	[PM CG 1931 No. 830, PM CG 1931 No. 831]
6. Chaupi, Cotopaxi/Pichincha, foot of Mts. Iliniza and Corazón, Ecuador (3200 m.)	1	—	Salvadori and Festa (1899, p. 12)
7. Panza, s slope of Mt. Chimborazo, Ecuador (14,000 ft. = 4200 m.) (type locality of <i>fraseri</i> )	2	—	Sclater (1860, p. 75)
8. Mt. Chimborazo, Ecuador (14,000 ft. = 4200 m.)	2	—	Taczanowski and von Berlepsch (1885, p. 76)
9. Sical, eastern Ecuador (no altitude given)	1	1	Sclater (1886, p. 13); locality "not located" (Paynter and Traylor, 1977, p. 117) [BM 85.4.1.79]
10. Mocha Canon, Tungurahua, Ecuador (11,000 ft. = 3300 m.)	2	2	Chapman (1926, p. 641) [AMNH 145898, AMNH 145899]
11. El Parotillo, S. José, Loja, Ecuador (no altitude given)	1	1	[Moore Collection Ec-R 263]
12. Laguna Querecocha, Ancash, Peru (4200 m.)	1	1	[Basel Museum, Markl No. 166]
13. Llanganuco, Yungay, Ancash, Peru (4000 m.)	2	2	[Basel Museum, Markl No. 864; Museo "Javier Prado" Lima No. 4116]
14. Yáñac, Ancash, Peru (13,000–15,000 ft. = 3900–4550 m.); Bosque Quipis Munte, above (south) Yáñac, ca. 13,000 ft. (=3900 m.); Quebrado Tutapac, 13,200 ft. (=4000 m.)	9	7	See Carriker (1933, pp. 9–10 and 28–29 about Yáñac); LSUMZ 82300, LSUMZ 82301 [ANSP 109336, ANSP 109337, ANSP 109338, ANSP 109339, LSUMZ 80873, LSUMZ 80874, MCZ 179385]
15. Above Huariaca, km. 335, Carretera Central, Cerro de Pasco, Peru (no altitude given)	2	2	[LSUMZ 75364, LSUMZ 79125]
16. Cerro Pumaj, upper valley of Rio Santa Eulalia, Lima, Peru (4100 m.)	1	1	[Museo "Javier Prado" Lima No. 3233]
17. Ca. 13 km. W Milloc, Lima, Peru (12,600–13,200 ft. = 3800–4000 m.)	8	4	See M. Koepcke (1970, p. 111) for description of range in Department of Lima; LSUMZ 79987, LSUMZ 97929, LSUMZ 106753, LSUMZ 106940 [LSUMZ 79126, LSUMZ 79127, LSUMZ 79128, LSUMZ 79630]

TABLE 1—(Continued)

Locality	Number of Specimens		References or Specimens <sup>a</sup> [specimens examined in brackets]
	Re- ported	Exam- ined in This Study	
18. Lachocc, Huancavelica, Peru (13,000 ft. = 3900 m.)	3	3	Morrison (1939, p. 486) [BM 1946.49.757, BM 1946.49.758, BM 1946.49.759]
19. Pampa Galeras, Ayacucho, Peru (about 4000 m.)	—	—	Brokaw (1976, p. 29), Venero G. and Brokaw (1980); sight records
20. Cedrobamba Ruins, near Machu Picchu, Cuzco, Peru (12,000 ft. = 3600 m.) (type locality of <i>binghami</i> )	1	1	Chapman (1919, p. 331) [USNM 273004]
21. Anta, Cuzco, Peru (3500 m.)	1	—	von Berlepsch (1900–1901, p. 197)
22. 14 km. NE Abra Malaga on Ollantaitambo-Quillabamba Road, Cuzco, Peru (13,000 ft. = 3900 m.)	2	2	Parker and O'Neill (1980, p. 173) [LSUMZ 79130, LSUMZ 79131]
23. 6 km e Nuñoa, via road to Macusani, Puno, Peru (13,000 ft. = 3900 m.)	2	2	George (1964, p. 26) [W. George No. 1630, AMNH 786678]
24. Ollachea, 20 mi. (=32 km.) W (N?) of Macusani, Carabaya, Puno, Peru (11,500 ft. = 3500 m.)	3	3	Hellmayr (1912, p. 159) [Munich Museum 11.251, Munich Museum 11.252, Munich Museum 11.253]
25. Rochanga (road from Chuquibamba to Pampacolca), Arequipa, Peru (4000 m.)	1	1	[Museo "Javier Prado" No. 4115]
26. 20 km. e Chiguata, Arequipa, Peru (12,800 ft. = 3900 m.)	1	1	[LSUMZ 79129]
27. 20 km. ne Tarata, Tacna, Peru (no altitude given)	1	1	George (1964, p. 26) [W. George No. 1993]
28. 6 km. ne Tarata, Tacna, Peru (3900 m.)	—	—	Pearson and Pearson Ralph (1978, p. 29); sight record
29. 10 mi. (=16 km.) n of Viloca [=Viloco], La Paz, Bolivia (11,500–13,500 ft. = 3500–4100 m.)	1	1	Bond and Meyer de Schauensee (1942, p. 370); altitudes of "Viloco" given as 13,800–17,000 ft. in Paynter, Traylor, and Winter (1975, p. 68) [ANSP 134212]
30. 43 km. from Cochabamba City along road to Morochata, Cordillera Tunari, Prov. Quillacollo, Cochabamba, Bolivia (3630 m.)	1	1	Vuilleumier (1969b, p. 606) [AMNH 793132]
31. Pocona, Cochabamba, Bolivia (2700 m.)	1	1	Vuilleumier (1969b, p. 606) [CM 120242]
32a. Finca Salo, Oploca, Potosí, Bolivia (11,500 ft. = 3500 m.)	2	1	Bond and Meyer de Schauensee (1939, p. 1) [ANSP 134211]
32b. Mina Isca-Isca, above La Torre, about 25 km. NNE Tupiza, Sud Chichas, Potosí, Bolivia (3900 m.)	—	—	Vuilleumier (1969b, p. 606); sight record
Totals	60	47	

<sup>a</sup> Museum abbreviations: AMNH, American Museum of Natural History; ANSP, Academy of Natural Sciences of Philadelphia; BM, British Museum (Natural History); CM, Carnegie Museum of Natural History; LSUMZ, Louisiana State University Museum of Zoology; MCZ, Museum of Comparative Zoology; PM, Muséum National d'Histoire Naturelle, Paris; USNM, United States National Museum, Smithsonian Institution.

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## MATERIALS AND METHODS

The present study is based on 47 of the 60 specimens of the species known to me (table 1), and deposited in various museums in the United States, England, West Germany, France, Switzerland, and Peru. The specimens are cited (table 1) by museum number or collector number, or by references to the literature cited. I have had personal field experience with *Oreomanes* in the Andes of Bolivia (see Vuilleumier, 1969b, p. 606), and I have visited stands of *Polylepis* in Venezuela, Colombia, Ecuador, Peru, Bolivia, and northwestern Argentina.

## THE GENUS *OREOMANES*

*Oreomanes fraseri* was described by Sclater (1860, p. 75) on the basis of two specimens, one prepared as a skin and one in spirits, obtained at 14,000 ft. (=4200 m. locality 7 of table 1) on Mt. Chimborazo, Ecuador. Additional specimens collected in Ecuador and in Peru at the end of the nineteenth century, and during the first years of the twentieth century, were referred to the same species. In 1919 Chapman described a second species, *O. binghami*, on the basis of one specimen from the Cedrobamba ruins near Machu Picchu, Cuzco, southern Peru (locality 20, table 1, fig. 1). In that paper Chapman mentioned that the record of *O. binghami* represented a southward range extension of the genus of approximately a thousand miles (about 1600 km.) but in fact one specimen of *O. fraseri* had already been collected near Cuzco in 1899 at Anta (locality 21, table 1, fig. 1, von Berlepsch, 1900–1901). The third and last taxon to be described in *Oreomanes* was the subspecies *O. fraseri sturninus* (Bond and Meyer de Schauensee, 1939; see also 1942). Ac-

cording to Bond and Meyer de Schauensee the taxon *sturninus* corresponds to the populations from Bolivia, of which they saw several specimens from the Departments of La Paz, Cochabamba, and Potosí.

It appeared at one time that the wide ranging *O. fraseri* was geographically variable (two subspecies, *sturninus* and nominate *fraseri*) and that the localized *O. binghami* occurred in Cuzco, perhaps sympatrically with *fraseri*. The problem of whether one or two species exist in the genus *Oreomanes* was solved by Hellmayr (1919, pp. 11–12) who showed that the type specimen of *O. binghami* is an immature bird referable to *O. fraseri*. Chapman (1921, p. 115) agreed with this view and relegated his own taxon to the synonymy of *O. fraseri*. Zimmer (1942, p. 16), however, thought that "There is reason to believe that Chapman's proposed name should be revived for Peruvian examples of *Oreomanes fraseri*." On the basis of his examination of 10 specimens (three from Ecuador, four from Peru, and three from Bolivia) and his study of the literature (Hellmayr, 1912, 1919; and Hellmayr in Morrison, 1939), Zimmer concluded that *O. fraseri* showed geographical variation in back color, crown color, white line above the rufous superciliary stripe, and bill length. He recognized three subspecies: *O. f. fraseri* (Ecuador; and presumably also southern Colombia), *O. f. binghami* (Peru), and *O. f. sturninus* (Bolivia). Bond and Meyer de Schauensee (1939) also mentioned geographical variation in several color characters and in bill length. Finally, Storer (1970) recognized the three subspecies admitted by Zimmer (1942).

Chapman (1919, 1921) seems to be the only author who had noticed at an early stage in the study of *Oreomanes* the problem of discontinuity in its range. "Such gaps in distribution indicate lack of continuity in the Temperate Zone itself, and when the species formed in these Temperate Zone islands show no appreciable differentiation, it seems evident that they have become isolated at a comparatively recent date" (Chapman, 1921, p. 115). Chapman did not know, apparently, that *O. fraseri* was ecologically specialized and restricted in its distribution to islands of *Polylepis* woodland.

The distributional records of *O. fraseri*

TABLE 2  
The "Populations" of *Oreomanes fraseri*  
(see fig. 2)

Popu- lation	Localities	Region	Altitudes (m.)	No. Specimens ("sample")
A	1	Nariño, Colombia	—	2
B	2a, 2b, 3, 4, 5, 6	Eastern Andes, Ecuador	3200–4850	6
C	7, 8, 10	Mt. Chimborazo, Ecuador	3300–4200	2
D	11	Loja, Ecuador	—	1
E	12, 13, 14	Ancash, Peru	3900–4550	10
F	15, 16, 17	Cerro de Pasco and Lima, Peru	3800–4100	7
G	18	Huancavelica, Peru	3900	3
H	19	Ayacucho, Peru	about 4000	—
I	20, 21, 22	Cuzco, Peru	3500–3900	3
J	23, 24	Puno, Peru	3500–3900	5
K	25, 26	Arequipa, Peru	3900–4000	2
L	27, 28	Tacna, Peru	3900	1
M	29	La Paz, Bolivia	3500–4100	1
N	30, 31	Cochabamba, Bolivia	2700–3630	2
O	32a, 32b	Potosí, Bolivia	3500–3900	1
Total included in sample				46

known to me are set out in table 1 and figure 1, and the "populations" in table 2 and figure 2. These illustrations provide an updated view of the geographical patchiness in the distribution of *O. fraseri*, and of some of the gaps that might be correlated with present-day Andean barriers.

#### GEOGRAPHICAL ECOLOGY OF *OREOMANES*

*Oreomanes fraseri* occurs along the Andes from southern Colombia (Pasto) to Ecuador, Peru, and Bolivia as far south as the Department of Potosí (figs. 1 and 2). All locality records accompanied by a description of the habitat stated that the species was collected in *Polylepis* woodlands or queñual scrub, as already mentioned in the Introduction. One may therefore assume, insofar as *Oreomanes* has not been collected or observed outside these woodlands, that this genus is indeed restricted to them. It is one of the few instances in birds of a well-marked taxon at the genus level found only in a specific kind of vegetation type. Another example in the high

Andes is the monotypic coerebid *Xenodacnis parina*, which interestingly also lives only in *Polylepis* woodlands (often associated with *Gynoxys*, Compositae) in Ecuador (see, e.g., Ridgely, 1980, pp. 247–248) and in Peru (see, e.g., Short and Morony, 1969, p. 115). (All or most other species of birds living in *Polylepis* woodlands seem to inhabit one or more other vegetation types, whether páramo, puna, dry montane woodlands, or cloud forests; Vuilleumier, in press.)

*Polylepis* woodlands are a very distinctive ecological feature of the high Andes. The genus *Polylepis* (family Rosaceae) occurs from Venezuela (Mérida) to northern Chile and northwestern Argentina (Tucumán) (Bitter, 1911; Herzog, 1923; Hueck, 1966; Simpson, 1979, in press). Trees of the genus *Polylepis* form distinct stands or patches above timberline right within the various grassland and scrub associations of the páramo and puna (e.g., Troll, 1959, p. 31).

Because potential habitat for *Oreomanes*, that is, islands of woodland made up mostly of *Polylepis* trees, occurs in all Andean countries from Venezuela to Argentina, it is sur-

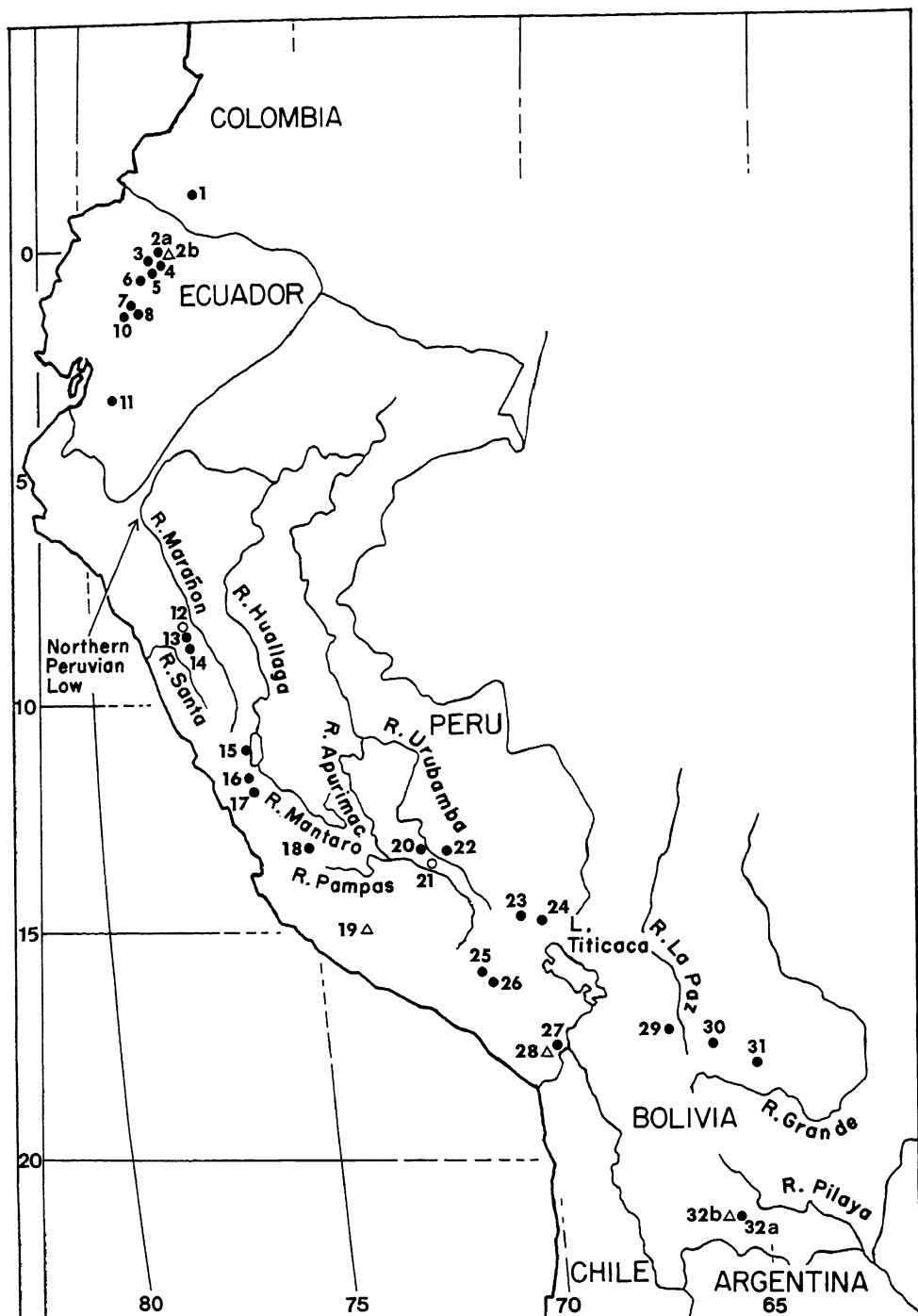


FIG. 1. Localities of *Oreomanes fraseri*. Black dots = localities from which specimens were examined; circles = literature records or unpublished specimens not examined personally; triangles = sight records. See table 1 for description of localities.



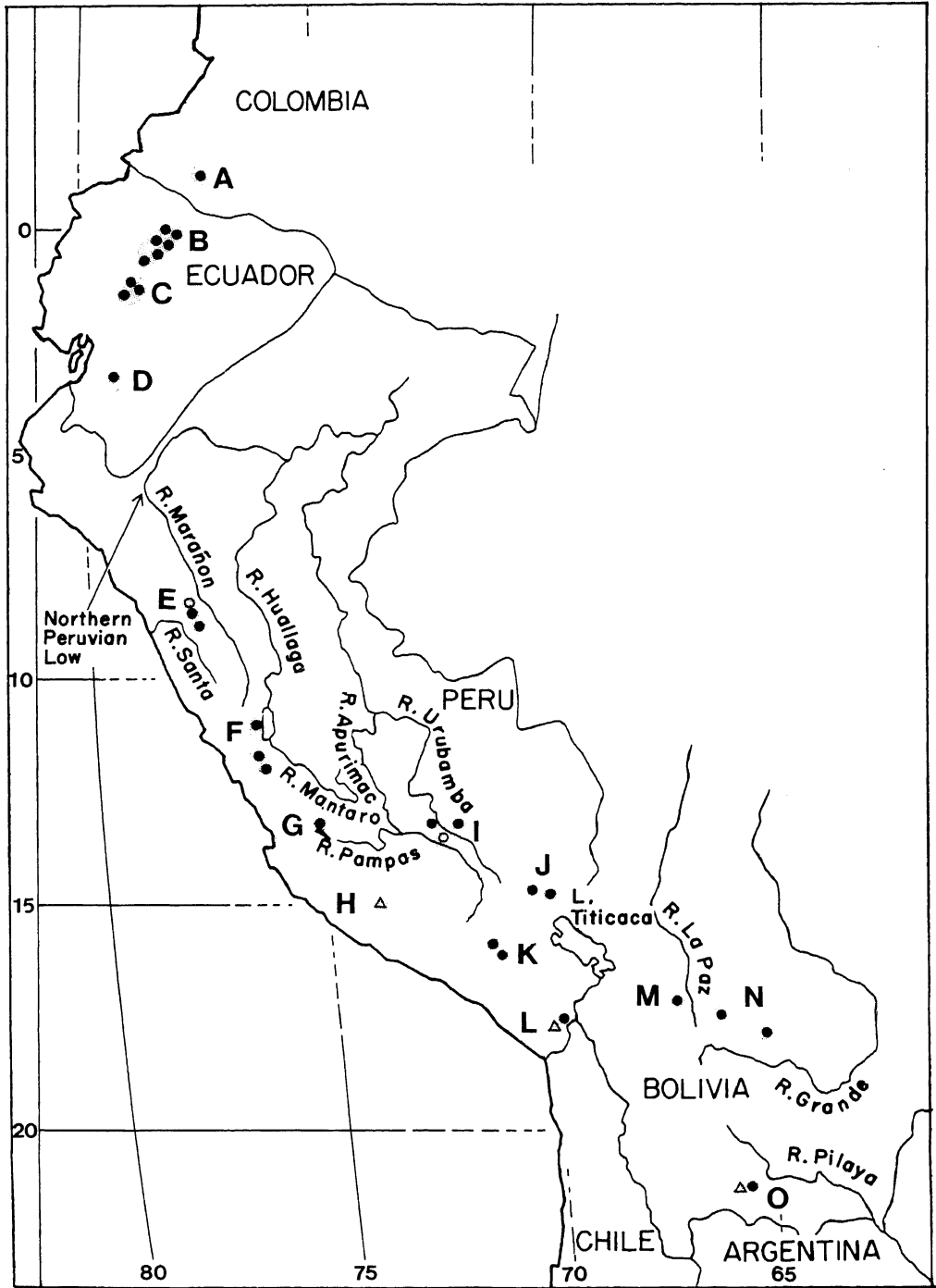


FIG. 2. The "populations" of *Oreomanes fraseri*. The populations are identified in table 2.

TABLE 3  
Sexual Variation in Mensural Characters and Weight in *Oreomanes fraseri*

Population	Sex	Mean Size of Character (n = sample size) <sup>a</sup>					
		Wing Length (mm.)	Tail Length (mm.)	Tarsus Length (mm.)	Culmen Length (mm.)	Bill Depth (mm.)	Weight (g)
B (Eastern Andes, Ecuador)	M	86.5 (1)	62.1 (2)	22.3 (2)	12.1 (2)	6.4 (2)	—
	F	85.5 (2)	59.3 (3)	22.0 (4)	13.1 (4)	6.2 (3)	—
E (Ancash, Peru)	M	89.0 (2)	60.0 (2)	23.0 (1)	13.0 (1)	5.8 (2)	25.1 (2)
	F	88.6 (8)	62.2 (8)	22.9 (7)	13.4 (5)	6.4 (6)	24.5 (1)
F (Pasco and Lima, Peru)	M	92.2 (3)	66.0 (3)	—	—	5.5 (2)	23.75 (3)
	F	89.8 (3)	64.0 (2)	—	—	5.7 (3)	25.0 (2)
All available birds (weights only)	M	—	—	—	—	—	24.8 (9)
	F	—	—	—	—	—	24.7 (4)

<sup>a</sup> Measurements were taken as follows: Wing length = chord; Tail length = from base of innermost two rectrices to tip of tail; Tarsus length = diagonally from articulation to last scute prior to digits; Culmen length = from anterior edge of nostril to tip of bill; Bill depth = at anterior edge of nostril.

prising that *Oreomanes* should not have been discovered farther north than Pasto in southern Colombia or farther south than Potosí in southern Bolivia. As far as is known at present the genus *Oreomanes* is absent from Venezuela, Colombia except the extreme south (Nariño), Chile, and Argentina. In view of the rather thorough ornithological work carried out in the Andes in recent years, it seems unlikely that a bird as striking as *Oreomanes* would have been overlooked there. One may therefore surmise that its absence in Venezuela, most of Colombia, Chile, and Argentina is genuine and not due to the artifact of "collecting gaps," although to be sure many *Polylepis* woodlands remain to be explored ornithologically in all four countries. *Oreomanes* may be absent from some areas with apparently suitable *Polylepis* habitat. For example, I visited extensive stands of *Polylepis* in western Bolivia near Volcán Sajama in 1968 but failed to observe *Oreomanes* there, although I was constantly on the lookout for it. Although few ornithologists have visited the *Polylepis* woodlands in the western Andes of Bolivia, nevertheless it is possible that in the future *Oreomanes* could be discovered there.

The distribution of *Oreomanes* in Colombia is based on two old specimens from "Pasto," both of which I examined (table 1). Hilty (*in litt.*) believes that these two birds were indeed taken in Colombia, and that "Volcan

Chiles and Volcan Cumbal certainly have sufficient elevation and fairly extensive *Polylepis* woodland, and they are remote enough to have escaped extensive habitat alteration. I think this is where the birds likely were taken." According to Hilty (*in litt.*), no recent records exist for Colombia.

In the remainder of the Andes, especially in Ecuador, Peru, and Bolivia, the distribution of *Polylepis* woodlands is patchy, as is the distribution of *Oreomanes*. Large gaps in distribution, illustrated on figure 2, exist between some of the 34 localities and some of the 15 "populations" where *Oreomanes* has been collected or observed. Examples of such gaps are the area between the southernmost Ecuadorian record in Loja (sample D) and the northernmost Peruvian ones in Ancash (E) (Northern Peruvian Low); and the region between populations N (Cochabamba) and O (Potosí) in Bolivia. In both gap areas *Polylepis* occurs (personal observ.) but *Oreomanes* has not been observed or collected so far. At present it is not possible to say whether such distribution gaps are due to lack of collecting efforts and hence are artifacts or not.

#### GEOGRAPHICAL VARIATION

Figure 1 illustrates the geographical range of localities from which specimens of *Oreomanes* have been collected (see table 1). Figure 2 and table 2 group these localities into "populations" in the same way I pooled col-

TABLE 4  
Geographical Variation of Mensural Characters in *Oreomanes fraseri*  
(adult males and females pooled)

Pop- ula- tion <sup>a</sup>	Wing Length (mm.) <sup>b</sup>			Tail Length (mm.) <sup>b</sup>			Tarsus Length (mm.) <sup>b</sup>			Culmen Length (mm.) <sup>b</sup>		
	Range	(Mean)	(n)	Range	(Mean)	(n)	Range	(Mean)	(n)	Range	(Mean)	(n)
A	87.0-91.0	(89.0)	(2)	61.0-62.0	(61.5)	(2)	21.5-23.5	(22.5)	(2)	—	(12.0)	(2)
B	84.0-87.0	(85.5)	(4)	59.0-63.2	(61.0)	(5)	20.5-23.0	(21.9)	(6)	12.4-14.0	(12.8)	(6)
C	—	(88.5)	(2)	62.5-65.0	(63.8)	(2)	22.0-22.5	(22.3)	(2)	12.5-13.0	(12.8)	(2)
D	—	—	—	—	—	—	—	—	—	—	—	—
E	86.0-93.0	(89.3)	(9)	58.5-66.5	(61.8)	(10)	21.5-24.0	(22.9)	(8)	13.0-14.0	(13.3)	(6)
F	86.5-94.0	(91.0)	(6)	60.5-67.5	(65.2)	(5)	—	24.5	(1)	14.0-14.5	(14.3)	(2)
G	92.0-93.0	(92.5)	(2)	62.5-65.0	(63.8)	(2)	24.0-24.5	(24.3)	(2)	14.0-14.5	(14.3)	(2)
H	—	—	—	—	—	—	—	—	—	—	—	—
I	89.0-90.5	(89.8)	(2)	63.0-63.5	(64.0)	(2)	—	22.9	(1)	—	—	—
J	83.5-89.0	(86.8)	(4)	59.0-60.5	(59.5)	(4)	23.0-24.0	(23.5)	(3)	13.0-14.5	(13.8)	(4)
K	—	91.0	(2)	65.0-65.5	(65.3)	(2)	—	—	—	—	—	—
L	—	89.0	(1)	—	61.0	(1)	—	23.5	(1)	—	15.0	(1)
M	—	87.0	(1)	—	63.0	(1)	—	20.5	(1)	—	—	—
N	86.5-89.0	(87.8)	(2)	61.0-63.0	(62.0)	(2)	23.0-23.5	(23.3)	(2)	14.5-16.0	(15.3)	(2)
O	—	86.0	(1)	—	61.5	(1)	—	24.5	(1)	—	15.5	(1)

<sup>a</sup> Populations lettered as in table 2.

<sup>b</sup> Wing, tail, tarsus, and culmen measurements: see footnote to table 3.

lecting localities when studying geographical variation in the *Asthenes flammulata* super-species (Vuilleumier, 1968). The reason for the geographical grouping is that the number of specimens available from any single locality is so small that it is impossible to assess intra-populational variation. I hoped that pooling localities into populations would enable me to obtain samples with a sufficient number of specimens to be able to analyze trends of variation statistically. In fact, as can be seen from table 2, the numbers of specimens in each pooled sample are so small even after such grouping that statistical analysis appears meaningless.

Table 3 summarizes sexual variation for three sample areas for which both males and females were available in small numbers. Males appear on the average to be slightly larger than females in wing, tail, and tarsus length, whereas females may be slightly larger than males in culmen length and bill depth. Because these sexual differences are very small, and because the samples are small, males and females have been pooled in the analysis of geographical variation. Only the immature specimens have been excluded from consideration.

Tables 4 and 5 show that there appears to

be no important geographical variation in wing length, tail length, or tarsus length. However, there is a trend of clinal variation in culmen length (table 4, fig. 3), the southernmost birds from Bolivia being larger than the northernmost ones from Colombia and Ecuador, whereas the geographically intermediate ones from Peru are morphologically intermediate also. But because of the small number of individuals in each sample area one cannot be entirely certain that geographical variation in culmen length is truly clinal, or is in fact slightly discontinuous. So further discussion of what appears to be a discontinuity (marked "—" in table 5) must be postponed until more specimens are available.

Geographical variation in some color characters (e.g., forehead, dorsum) appears to be clinal (table 6). Thus the darkest birds are from the northern part of the range of *O. fraseri* (Ecuador), whereas the palest ones come from the southern part of the range (Bolivia), with intermediate birds in the geographical center (Peru). This decrease in the intensity of pigmentation from north to south along the high Andes is found in a number of other bird species, including *Nothoprocta ornata* (Tinamidae), *Attagus gayi* (Thinocoridae), *Metriopelia melanoptera* (Columbi-

TABLE 5  
Trends of Geographical Variation in Mensural  
Characters in *Oreomanes fraseri*  
(adult males and females pooled)

Popula- tion <sup>a</sup>	Trend of Increase or Decrease Beginning with Northernmost Population <sup>b</sup>			
	Wing Length	Tail Length	Tarsus Length	Culmen Length
A				
B	—	—	—	+
C	+	+	+	=
D	(?)	(?)	(?)	(?)
E	+	—	+	+
F	+	+	(?)	+
G	+	—	+	=
H	...	...	...	...
I	—	=	(?)	(?)
J	—	—	—	—
K	+	+	(?)	(?)
L	(?)	(?)	(?)	(?)
M	(?)	(?)	(?)	(?)
N	—	—	=	+
O	(?)	(?)	(?)	(?)

<sup>a</sup> Populations lettered as in table 2.

<sup>b</sup> Only samples of two or more specimens (see table 4) have been included; the "(?)" indicates that no trend can be detected because of lack of data (no, or too few specimens); a "+" indicates an increase in size; a "—" a decrease; an "=" no change (trend from north to south); and a "..." no specimen.

dae), *Bolborhynchus aurifrons* (Psittacidae), *Phrygilus unicolor* (Emberizidae) (Vuilleumier, unpubl. data), the *Muscisaxicola alpina* superspecies (Tyrannidae) (Vuilleumier, 1971), and *Diglossa caerulescens* (Coerebidae) (Vuilleumier, 1969a). This trend of relatively gradual geographical variation, in *Oreomanes* and in the other species cited above, can be correlated with the amount and seasonality of rainfall along the Andes from Colombia southward to Bolivia. Thus rainfall is both more abundant and less seasonal in Colombia and Ecuador than in Peru and Bolivia, and the Peruvian and Bolivian Andes are progressively drier from east to west (Lauer, 1952). The trends of variation in birds living under such climatic regime can be ascribed to Gloger's Rule. In *Oreomanes*, however, discontinuities in the clines of decreasing color saturation can be found in several characters (supraciliary stripe, under-

parts), so that the overall trend of geographical variation in color and color pattern appears to be more checkerboard than gradual in nature.

In summary, the data presented in tables 4, 5, and 6 and in figure 3 show that geographical variation in mensural and color characters in *Oreomanes fraseri* is minor, partially clinal, and partially checkerboard. It appears to be clinal for some characters taken individually, but checkerboard when all characters are considered together. If this is so, then geographical variation in *Oreomanes fraseri* may reflect both the major ecological influences prevailing from north to south in the high Andes and the geographical disruptions in the range of the species. From a taxonomical point of view, I conclude from this analysis of geographical variation that the formal recognition of subspecies is unwarranted in view of the lack of clearcut differentiation within the species as a whole.

#### GEOGRAPHICAL BARRIERS

In other papers on speciation in Andean birds I was able to correlate patterns of discontinuous geographical variation and distribution in several species with geographical and ecological barriers along the Andes. This was the case, for instance, in the *Asthenes flammulata* superspecies (Vuilleumier, 1968), in several superspecies of the genus *Diglossa* (Vuilleumier, 1969a), in the Andean caracaras (Vuilleumier, 1970), and in several groups of ground tyrants (Vuilleumier, 1971). The geographical distribution of *Oreomanes* is in many ways parallel in its patchiness to that of these taxa, but there is no evidence, either that the patchiness is directly correlated to geographical variation, or that the variation is correlated to obvious ecological or geographical barriers. Hence, unlike several other high Andean taxa, *Oreomanes* does not show incipient speciation correlated with eco-geographical barriers (Vuilleumier, 1977, 1980).

In other words, whereas species such as *Attagis gayi* (Thinocoridae) or *Iridosornis rufivertex* (Thraupidae) have morphologically well-differentiated populations on either side of the Northern Peruvian Low that can be considered isolates of potential speciation

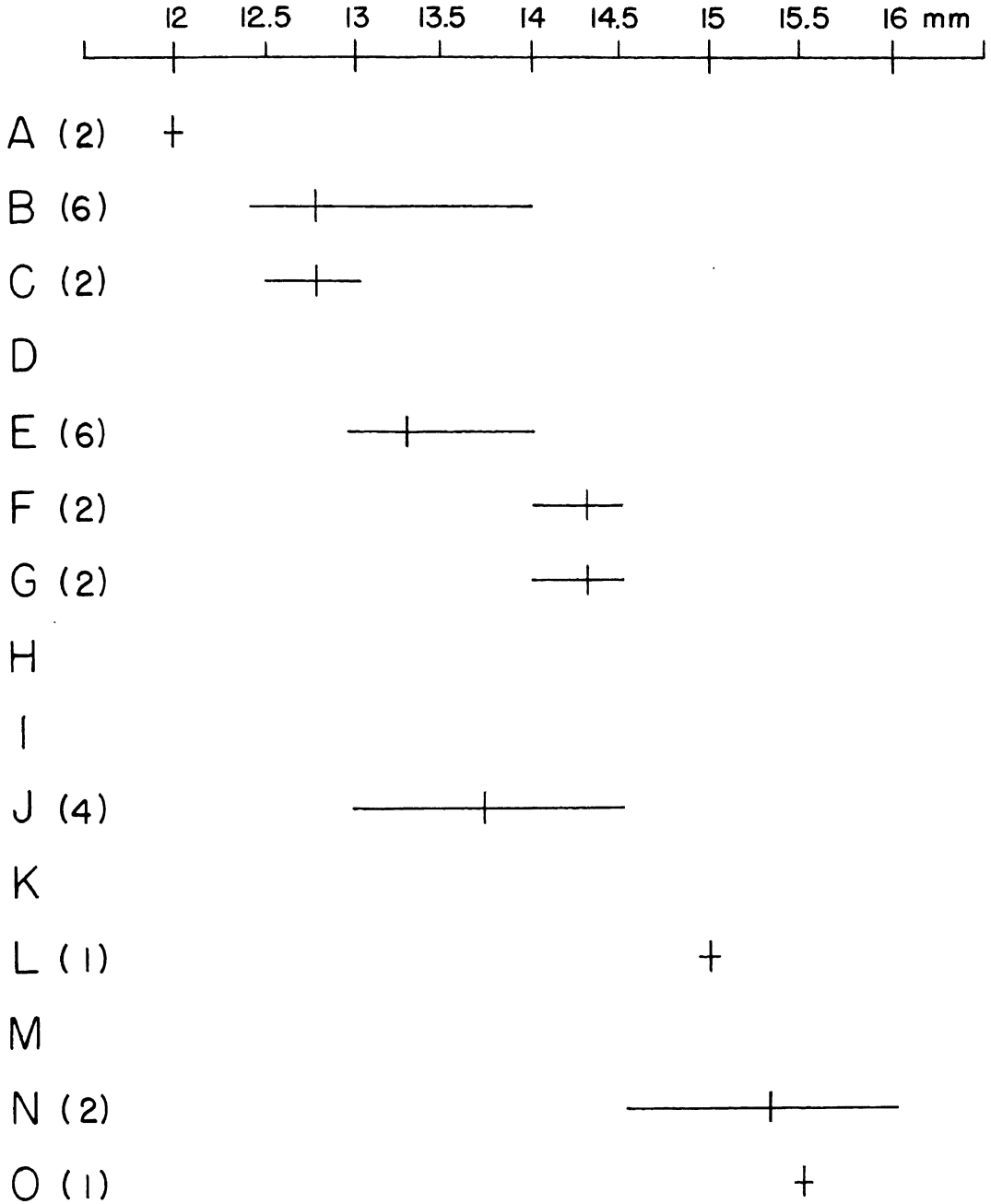


FIG. 3. Geographical variation in culmen length (adults) in *Oreomanes fraseri*. See table 4 for measurements.

significance (Vuilleumier, 1977, p. 37), the populations of *Oreomanes fraseri* living across this gap are poorly differentiated morphologically (table 6; see also fig. 3). Similar lack of marked morphological differentiation across other eco-geographical barriers also

TABLE 6  
Geographical Variation of Color Characters in *Oreomanes fraseri*

Character <sup>b</sup>	Population <sup>a</sup>														
	A	B	C	D	E	F	G	H	I	J	K	L	M	N	O
Supraciliary stripe	I	I	I	D	I-D	I-D	D	-	D-V	D	D	V	V	D	D
Forehead	D	D	D	D	S	S	D-S	-	D-S	D-S	S	S	S	S	S
Crown	St	St	St	St	St-U	St-U	St	-	St	St	St	St	St	U	U
Dorsum	DG	DG	DG	- <sup>c</sup>	DG-G	G	DG	-	G	G	G	DG	G-PG	PG	PG
Underparts	CO	CO	CO	CO	CO-CB	CO-CB	CB	-	CO	CO	CB	CO	PCO	CO-PCO	PCO

<sup>a</sup> Populations lettered as in table 2.

<sup>b</sup> Symbols for characters:

Supraciliary stripe—I = indistinct white supra-loral stripe, very narrow; sometimes extending over eye; D = distinct white supra-loral stripe; sometimes extending a little beyond eye; V = very distinct white supraciliary stripe ("supercilium");

Forehead—D = generally dark gray, with only thin whitish edges to feathers giving the forehead a slightly "scaly" appearance; S = silvery gray, with broad whitish edges to feathers, giving the forehead a distinctly "scaly" aspect (when feathers are fresh), or a pale silvery gray sheen (when feathers are worn);

Crown—St = distinctly streaked with dark gray; U = unstreaked, or indistinct, or obsolescent pale gray streaks only;

Dorsum—DG = dark slate gray with a bluish tinge; G = slate gray with a bluish tinge; PG = pale slate gray, with an indistinct bluish tinge or a brownish tinge;

Underparts—CB = dark, rich chestnut brown; CO = chestnut brown with a slightly orange tone; PCO = pale chestnut brown with orange tone.

<sup>c</sup> The only specimen seen from population D may not be fully adult, and its dorsum color may not be comparable with that of birds of other populations.

exists elsewhere in the range of *Oreomanes fraseri* (e.g., Rio Apurimac and Rio Pampas in Peru, or Rio La Paz in Bolivia). *Oreomanes fraseri* is thus a well-marked genus with a single species having only minor geographical variation. Its patterns of variation and distribution, by themselves, give no clues as to the history of the taxon in the Andes. Hybridization between *Oreomanes* and *Conirostrum* (Schulenberg, in press), however, strongly suggests that *Oreomanes* originated in the Andes from ancestors living in the high, wet, and cool environments of the cloud forest type.

### DISCUSSION

The two problems investigated in this paper can now be addressed.

(1) *Oreomanes* and *Polylepis*: The patchy distribution of *Oreomanes* does indeed correspond to that of *Polylepis* woodlands. So far as I know, *Oreomanes* has not been observed or collected in another habitat, although it might be expected to occur in montane forests at or just below timberline. Observers should look for *Oreomanes* in habitats other than *Polylepis* woodlands. They are also urged to search for this taxon in *Polylepis* woodlands in other areas than those cited in this paper, both within and outside its known range. For example, why does *Oreomanes* not live in *Polylepis* woodlands of most of Colombia or of Chile and Argentina? Are the ecological conditions of the *Polylepis* woodlands found in these countries unsuitable for *Oreomanes fraseri*? Wet *Polylepis* woodlands of Colombia, where *Oreomanes* is absent, do not seem very different from those of Ecuador, where it occurs (personal observ.). Both kinds of woodlands have avifaunas including such typical montane forest species as *Margarornis squamiger* (Furnariidae), *Grallaria quitensis* (Formicariidae), *Myioborus melanocephalus* (Parulidae), *Diglossa carbonaria*, and *D. cyanea* (Coerebidae). A detailed investigation of the ecological requirements of *Oreomanes* should be undertaken at several localities along its range, including both moist and dry *Polylepis* woodlands. Besides its nuthatch-like feeding behavior, very little else is known of the for-

aging behavior of this species, including its precise food preferences. Ornithologists who have the opportunity to study *Oreomanes* in detail will be able to answer some of the questions about the ecology and distribution of this unique bird.

(2) Distributional patchiness and incipient speciation: The patchy distribution of *Oreomanes* can be correlated with geographical variation in color and size, but the minor, clinal and checkerboard nature of this variation does not appear conducive to incipient speciation, unlike what has been found in several other Andean taxa having similar distribution patterns. It is noteworthy that the other *Polylepis* specialist, *Xenodacnis parina*, shows more geographical variation than *Oreomanes fraseri*. The correlation between patchiness and gene flow (or its absence) in *Oreomanes* is thus unclear. George (1964) thought that the resemblance between the color of *Oreomanes* and that of *Polylepis* bark was an example of protective coloration. If this were the case, then some selection pressure arising from predation could be held responsible for the "mimicry" between bird and bark. One could therefore expect that, as a result of such selection, the geographical variation in color of *Oreomanes* would parallel the geographical variation in bark color of the different species of *Polylepis*. I attempted to match the color of pieces of *Polylepis* spp. bark from Peru and Bolivia with bird skins from these areas, but failed to obtain good correlations, perhaps because I had too few bark samples for a precise analysis. A thorough comparison with adequate samples should be undertaken and future investigators should also look for potential predators of *Oreomanes* in order to test the hypothesis of protective coloration.

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