

VARIATION AND DISTRIBUTION IN TWO SPECIES
OF DIGLOSSA.BY JOHN T. ZIMMER.¹

AMONG the birds inhabiting the Andes of northern South America, the various members of the genus *Diglossa* (family Coerebidae) present some of the most interesting problems of distribution and taxonomy. Included in this genus are several species which exhibit certain parallelisms that are most puzzling, and more than one arrangement has been suggested to explain the apparent anomalies. *D. gloriosa* bears a striking general resemblance to *gloriosissima* but the two birds inhabit distinct and distant areas. *D. lafresnayii* resembles *humeralis* but the two are found together over a portion of their ranges. *D. brunneiventris* occurs without apparent variation in two widely separated regions.

In a comparatively recent paper (Ornith. Monatsb., Vol. 34, pt. 3, p. 83, 1926), Stresemann unites *Diglossa gloriosissima*, *gloriosa*, *humeralis* and *carbonaria* in one "formenkreis." Acting on the ideas suggested by this arrangement, I have made an extended study of these and related forms and have reached somewhat different conclusions. Stresemann's arrangement is possible on purely geographic grounds but I believe that it takes advantage of one case of superficial resemblance and ignores several cases of more basic similarity involving a number of forms not included in his survey.

The form known as *gloriosissima* resembles *gloriosa* in its general style of coloration, being black with a rufous crissum, belly and lower breast, a pale gray shoulder and a dark gray rump, but there the resemblance ends. It is a much larger bird than *gloriosa* and has a larger and longer bill which, although its dorsal aspect is not so strikingly distinct, presents a very different appearance when viewed from below and measured along the gonys. The feathers of the forehead and crown have their tips more pointed than in the other species, and more distinctly outlined, giving a noticeably

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scaly appearance; the rump is darker and less grayish; more nearly uniform with the back; the gray of the shoulder is distinctly bluish in tone, not ashy carbon gray; the under wing-coverts are whiter, less grayish; and the black of the flanks is sootier.

In all of these distinctive respects *gloriosissima* finds a counterpart in *lafresnayii* although the latter bird is all black except for the gray shoulder, dark gray rump and pale under wing-coverts. In the opposite respects *gloriosa* is matched by *humeralis* which superficially resembles *lafresnayii*. It is quite possible, therefore, that the resemblances in general color between *gloriosa* and *gloriosissima* and between *humeralis* and *lafresnayii* are accidental or at least not of taxonomic importance since more numerous and varied characters of form, size and details of color suggest a different relationship. In other words, *lafresnayii* may be allied to *gloriosissima*, and *humeralis* to *gloriosa*. With respect to the last two forms, this arrangement is in accord with Stresemann's proposal. Before examining *carbonaria* there are other forms which must be taken into consideration.

In the first place the bird described by Bangs as *nocticolor*, from the Santa Marta region, presents all the distinguishing characteristics of *humeralis* and *gloriosa* as opposed to those of the *lafresnayii* group, and differs from *humeralis* only in the lack of the gray shoulder, having this region black like the remainder of the upper wing-coverts. To bridge this difference, one specimen of *nocticolor* from San Lorenzo, Santa Marta (No. 37799, Carnegie Museum) has most of the lesser upper wing-coverts on both sides rather broadly tipped with the same tone of gray as appears on the shoulder of *humeralis*; another specimen (No. 37891, Carnegie Museum) exhibits faint traces of the same. In *humeralis* the amount of gray on the shoulder is quite variable although the tone is rather constant. The ranges of the two forms are not continuous but individual variation has produced intermediates so that *humeralis* and *nocticolor* are shown to be only subspecifically distinct.

To the southward we know *humeralis* from as far as the Bogotá region although its range may extend farther south along the chain of the eastern Andes where little intensive collecting seems to have been done. Across the Magdalena Valley at Laguneta and thence

southward across central Colombia and Ecuador to north-western Peru, there exists the form known as *aterrima*. This bird is black like *humeralis* and *nocticolor* but without gray on shoulder, rump, or upper wing-coverts, although in the other characteristics of size, shape of bill and form of frontal plumage it agrees with the other two forms. I have found little evidence of intergradation in nineteen specimens of *aterrima* which I have examined, but in three examples from Almaguer and Laguneta (unfortunately not fully adult), there are ill-marked traces of grayish tips on the lesser upper wing-coverts; any suggestions of possible grayish color on the rump are lost in a brownish tinge due to immaturity. However, there is no material at hand from the Andean highlands near La Candela or from the ridge of the eastern Andes south of the Bogotá region where intermediates should occur, since it is there alone that the ranges of *aterrima* and *humeralis* could meet; elsewhere they are separated by the valley of the Magdalena River at an elevation below that of the temperate zone inhabited by these birds.

Geographically there is no valid objection to the specific unity of *aterrima* and *humeralis*. Chapman's record of *aterrima* from Chipaque, Colombia (Bull. Amer. Mus. Nat. Hist., Vol. 36, p. 581, 1917), within the range of *humeralis*, was based on a single specimen which proves, on examination, to be an undoubted *humeralis*. Sclater records one example of *humeralis* from Ecuador (Cat. Birds Brit. Mus., Vol. 11, p. 8, spec. "i," 1886). Dr. Hellmayr has examined this specimen in the British Museum and writes me that it is an undoubted *humeralis* but that its origin is open to question. It is a dealer's skin procured from Dillwyn, without any original label and of preparation by no means Ecuadorean, while skins of various other species, likewise secured from Dillwyn and of similar preparation, are marked either "Colombia" or "Bogota." In view of these facts and without corroborative specimens from Ecuador, this record should be discarded. With regard to Sclater's record of *aterrima* from Santa Marta (Cat. Birds Brit. Mus., Vol. 11, p. 8, specs. "a-c" and "d," 1886), Dr. Hellmayr writes me that the specimens in question are typical *nocticolor* with gray rump and black shoulder. There is thus no definite knowledge of the occurrence of any of these forms within the range of any other.

In Peru, *aterrima* has been found at El Tambo and at Cutervo. At Chota, a short distance south-east of Cutervo, another form, *brunneiventris*, occurs. This bird is like *gloriosa* above; below it is paler rufous with the flanks gray, instead of sooty, and with the black of the breast and throat restricted to a large chin spot, while the rufous of the breast is continued forward in broad malar stripes. Taczanowski (Orn. Per., Vol. I, pp. 420, 421, 1884) has recorded *brunneiventris* also from Cutervo on the authority of Stolzmann, but a perusal of his original reports on Stolzmann's collections (Proc. Zool. Soc. Lond., 1879, p. 225; 1882, p. 8) shows that the species was collected only at Chota and Tamiapampa while the Cutervo record is based solely on field notes. An examination of five males of *aterrima* from El Tambo has shown little evidence of intergradation with *brunneiventris* and it is largely on geographic grounds and group-characteristics that I am assured of the continuity of the series. While *aterrima* cannot, with present material, be shown to intergrade directly with the adjacent forms, it does unquestionably and exactly fit into a gap in the distribution of the group which otherwise would be difficult to explain; and, in a complete survey of all the associated species, its relationship to *brunneiventris* can be seen to better advantage through *nocticolor*, *humeralis* and *gloriosa*.

Throughout the highlands of Peru and extending over the border into Bolivia, *brunneiventris* occurs with a certain amount of individual variation not associated with locality. There are considerable differences in the tone of rufous on the belly, in the amount of gray on the flanks and upper tail-coverts, and in the extent of the rufous malar stripes. Most of the specimens show a distinct line of pale gray above the eye but this is not always present. In extremes of these variations some examples come very close to certain specimens of *gloriosa*. It is true that the ventral rufous color of *gloriosa* is usually deeper, but in one specimen from Mérida, Venezuela (No. 57130, Field Mus. Nat. Hist.) it is paler than in several Peruvian skins of *brunneiventris*. The flanks in the same example are not the usual sooty black but are distinctly gray, the under wing-coverts are unusually pale, and there are a few rufous feathers in the malar region suggesting the malar stripe of the other form. A specimen from Santo Domingo, Venezuela

(No. 190448, U. S. Nat. Mus.), has the lower flanks inclined toward gray, the grayish color of the rump as broad as in some skins of *brunneiventris*, and the rufous feathers of the malar region extended to form a distinct, elongate spot, although the belly is dark rufous as in typical *gloriosa*. Another skin from Santo Domingo (No. 190447, U. S. Nat. Mus.) is like normal *gloriosa* except for a small malar spot of rufous. No. 89220, Carnegie Museum, from Teta de Niquitao, Venezuela, is similar to the last example; No. 89219 has the malar spot a little more pronounced. No. 24286, Field Mus. Nat. Hist., from Mérida, has a small malar spot of rufous on one side only; Nos. 57131 and 57132 are typical *gloriosa* without any mystacial markings.

On the other hand, some of the specimens of *brunneiventris* show the malar stripe separated from the base of the bill by an area of black connecting the chin and the auricular region; in other examples the stripe reaches the bill. No. 256272, U. S. Nat. Mus., from Paramillo, Colombia, has dusky subterminal bars on the lateral feathers of the throat, concealed only by narrow rufous tips and tending to reduce the extent of the malar stripe and sever it from the rufous of the breast. The figure of the type of *brunneiventris* given by Des Murs (Iconog. Ornith., pl. 43, 1847) shows the rufous malar stripe completely separated from the pectoral area of the same color and although this apparent separation may have been due to disarrangement of the plumage it possibly may have been exactly as shown, due to an increase in the amount of black on the sides of the lower throat. However, in all these particulars there is a significant approach of *brunneiventris* and *gloriosa* to each other, while the characters of the group, as compared with those of *lafresnayii*, are the same in both forms.

Curiously enough, *brunneiventris* occurs in north-western Colombia, beyond the range of *aterrima*, with no apparent differences from Peruvian examples. All of the Colombian birds have blackish outer margins on the extreme lateral pectoral feathers, thus extending the black of the neck a little farther ventrally in an approach toward *gloriosa* or *humeralis*; but some of the Peruvian skins show the same condition. The size of the Colombian specimens falls well within the range of variation of my Peruvian series and only one example (that mentioned above) has blackish

subterminal bars on the sides of the throat. I am not able, therefore, to separate the Colombian and Peruvian birds even subspecifically except on the sole ground of geographic isolation, which is not adequate for racial distinction.

If isolation were a sufficient ground for racial separation it would be necessary to subdivide the Colombian *brunneiventris* into two subspecies since it occurs on both sides of the lower Cauca Valley where intercommunication is prohibited. On the eastern side, in the central Andes, the range is contiguous to that of *aterrima* which occupies the mountain chain southward past the only place where the central and western Andes of Colombia are connected by high land, at the headwaters of the Cauca River. The distribution of either form west of the Cauca River is unknown except for the records of *brunneiventris* from Paramillo. In order for this "colony" to have become established in its present divided form, it must have entered the region before the valley was eroded to a prohibitive depth or before the bird became an inhabitant of the temperate zone, or else it must have occupied, at one time, part of the range now inhabited by *aterrima*. I believe the last theory to be most in accordance with other facts which I shall discuss a little later.

Southward, *brunneiventris* ranges into north-western Bolivia. In the British Museum there are three adult birds collected by Buckley at Khapaguaia (Yungas of La Paz?), and one specimen from Sorata; two of the Khapaguaia specimens are recorded in the Catalogue of Birds as from "Simacu." According to a letter from Dr. Hellmayr, all of these are typical *brunneiventris*. However, among various examples of the Bolivian *carbonaria*, recorded and otherwise, there are certain specimens which indicate a close relationship between these two forms. The more southern form, *carbonaria*, has the uniform black throat and breast of *gloriosa* and the gray flanks of *brunneiventris*, while the crissum and upper parts are much the same in all three forms, but the entire belly is gray at variance with the rufous abdomens of the other two birds. Berlepsch, in manuscript notes, cites two males from Iquico and one male from La Paz as hybrids between *carbonaria* and *brunneiventris* but does not describe them. He lists another example as *carbonaria* and describes it as having a rufous feather in the malar region.

Another bird from Iquico is said to have a mixture of rufous in the middle of the abdomen.

The specimen with the rufous malar feather is now in Field Museum of Natural History (No. 56872) and is simply as described. One of the so-called hybrids is in the U. S. National Museum (No. 211680). It has a distinct, broad malar stripe of deep rufous on both sides, about 11 millimeters long, one of the lower pectoral feathers exhibits a rufous spot, and the gray of the rump is quite restricted. A specimen in the Carnegie Museum (No. 85712) from Incachaca, Cochabamba, has the gray of the rump fully as extensive as in *brunneiventris* while the lower mid-belly is pale rufous and the gray shoulder patch is paler than is usual in *carbonaria*. Another example from Incachaca in the Carnegie Museum (No. 81514), has two or three rufous marks in the malar region of one side, the whole mid-belly is pale rufous and the gray of the rump is quite extensive. Dr. Hellmayr, examining the specimens in the British Museum for me, writes that one specimen "ex Bolivia" has the entire malar region and a stripe along the middle of the breast and belly rufous. On the other hand, occasional specimens of *brunneiventris* from Peru show faint grayish tips to the rufous abdominal feathers which may be significant. These examples, intermediate in varying degree, seem to point to intergradation instead of hybridization and to show that *carbonaria* and *brunneiventris* are only subspecifically distinct.

It is interesting to speculate on the probable origin of the various forms of this group. Judging from the relative geographical positions which they now occupy, it appears to me that *brunneiventris* represents the most primitive form of the group. Its original range, whether or not it was coterminous with the range of the entire species today, may have been divided into three parts by the development of a melanic race in the middle which extended its range in all directions and usurped a large portion of the central area occupied by the group. An eastern segregated unit then developed into the somewhat distinct *gloriosa*; the north-western and southern colonies remained alike and less modified, although from the southern division there arose a peripheral variety, *carbonaria*. Thus *gloriosa*, although separated from the range of *brunneiventris*, tends to revert to the more ancestral form by the production of

rufous malar spots and paler rufous belly; similar reversions in the case of *carbonaria* amount to definite intergradation since *brunneiventris* has an immediately contiguous range.

Meanwhile the melanic form which supplanted *brunneiventris* or its ancestor in the center of its range, drove the north-western colony of that form northward, either following its retreat or encroaching on its domains, until it passed the head of the Cauca Valley and was left in two dissociated units on opposite sides of the river. The south-western colony similarly retreated southward. The fact that *aterrima*, although least like *brunneiventris* of all the races, stands exactly in the midst of three morphologically inseparable units of that form, indicates that it probably represents the original melanic variant and that it probably was mutational.

Morphologically, *aterrima* is nearer to the Santa Martan *nocticolor* than to the adjacent *humeralis* while *humeralis* is nearer to *brunneiventris* than is either of the others. It seems probable, therefore, that *humeralis* is a later, atavistic development which appeared in the middle of the range of *aterrima* and divided it, cutting off a northern colony. This developed into *nocticolor* or had already developed into that race before it was permanently separated from the other races by the isolation of the Santa Marta plateau.

This theoretical account of the racial phylogeny of the group may not be the correct one but it is an attempt to account for the peculiar distribution in existence at the present time. The fact that one member of the group, *brunneiventris*, occupies three distinct areas separated by the range of another race suggests that, in this case, an older form was divided and remained constant at the opposite ends rather than that three identical forms developed at the periphery while a fourth, nearly similar, race developed at another peripheral point.

Whatever course was followed in the evolution of the group, I believe that the relationships of the six existing forms are so close, directly and indirectly, as to justify their assemblage into one modern species. This species will have to take the name *carbonaria* as the oldest one in the group. The accompanying map (fig. 1) will show the distribution of the various subspecies.

Returning to *lafresnayii* and *gloriosissima*, we find, as noted

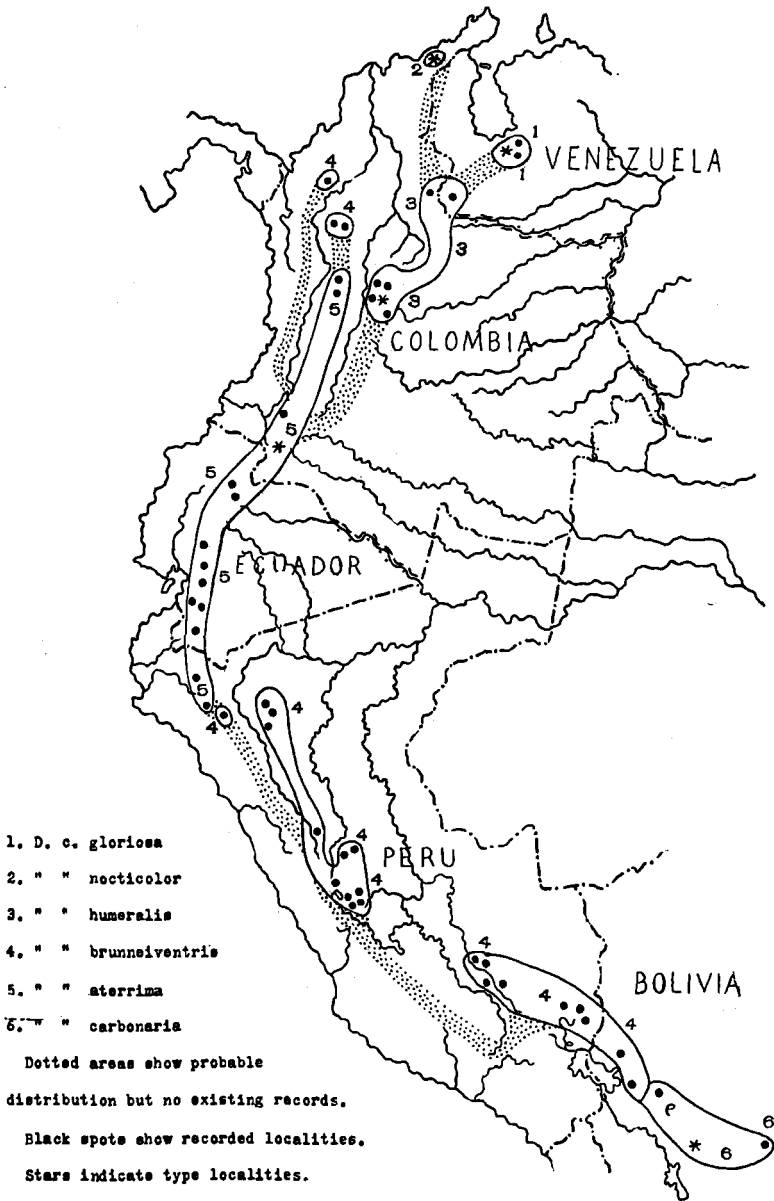


Fig. 1. Distribution of *Diglossa carbonaria*.

earlier in this paper, that they differ from each other in their general coloration but that they resemble each other sufficiently in details of size, form and special color to suggest close relationship between them. Geographically this relationship meets with no opposition, for nowhere does one occur with the other although their respective ranges, as known at present, are almost contiguous. As shown on the accompanying map (fig. 2), their ranges for the most part are separated by the valleys of the Rio Patia and the Rio Cauca, but above the headwaters of these streams, in the neighborhood of the Cerro Munchique, the central and western chains of the Andes come together, and at this point alone *lafresnayii* could meet *gloriosissima*. No material is at hand from this exact region but there is other evidence that intergradation may take place.

Specimens of *gloriosissima* from the western Andes near Popayán show considerable black along the flanks, and in this respect approach closer to *lafresnayii* than do birds from Paramillo and other more distant points. Away from any possible meeting ground, taken at Culata, Mérida, Venezuela, one specimen of *lafresnayii* (No. 24282, Field Mus. Nat. Hist.) has the mid line of the belly tinged with dusky drab or light seal brown—a definite, though slight, approach to the rufous belly of *gloriosissima*. Another specimen from Bogotá (No. 11734, Field Mus. Nat. Hist.) faintly suggests the same condition. With these indications of intergradation at hand, I do not hesitate to unite the two forms under the older specific name *lafresnayii* and to consider them as subspecies.

Southward, *lafresnayii* extends its range into north-western Peru. Chapman (Bull. Am. Mus. Nat. Hist., Vol. 55, p. 638, 1926) records two specimens from Chaupe near Huancabamba. This record carries the known range of *lafresnayii* southward to about the same point reached by the black *aterrima* of the *carbonaria* group, a significant fact in relation to the parallelism exhibited by the two species. In the central Andes of Peru, across the Marañon River from Chaupe, a large *Diglossa* is found which was described by Hellmayr as *D. pectoralis uncinata*. At first glance this bird appears to belong to a totally different group from *lafresnayii* and *gloriosissima*, although it shows certain characteristics in common.

To understand the full relationship it is necessary to examine several other forms whose affinity to *unicincta* is more evident.

The highlands between the Marañon and the Huallaga rivers form the home of *unicincta*, at present known only from the extreme northern portion of this region. Farther east and south, between the Huallaga and Ucayali rivers and near the Junin plateau, occurs a related form, *pectoralis*. Still farther east and south, in the Urubamba River region is found *albilinea*, while in the highlands of Bolivia exists a fourth bird known as *mystacalis*. Between *unicincta* and *mystacalis* there is a graded succession of changes in color, lacking in demonstrably perfect continuity for the reason, I am sure, that all four forms are quite rare in collections and known from but few scattered localities, while the intervening regions where they could come together have not yet been explored sufficiently to bring to light the intermediate specimens.

The Bolivian bird, *mystacalis*, is almost exactly intermediate between *lafresnayii* and *gloriosissima*, having a rufous crissum but a black breast and belly, but it differs from both of the others in the possession of ochraceous-tawny malar stripes. In the glossy, somewhat squamate forehead, large bill, dark gray rump, bluish gray shoulders, white under wing-coverts and general structural features it shows the significant characters which seem to belong to the *lafresnayii* group. The adjacent *albilinea* has the malar stripes paler in front but darker posteriorly, showing a tendency to extend inward toward the center of the breast. In the single adult specimen examined (No. 273384, U. S. Nat. Mus.) there is, furthermore, a rufous feather in the center of the lower margin of the throat, suggesting the development of a rufous pectoral band. The shoulder patches are smaller than in *mystacalis* and the rufous of the crissum has advanced up the lower portion of the belly in a somewhat paler tint. In *pectoralis* the rufous band across the breast has been completed with its posterior border white to a varying extent. The malar stripes have become white anteriorly, the rufous of the belly has ascended farther toward the breast and the gray shoulder patches have been still more reduced in size. In *unicincta*, the pectoral band has become deeper rufous, more like the breast of *gloriosissima*, with its lower border paler but not white. The abdominal stripe is also darker rufous while the

shoulder patches are very small though not obsolete. In some respects *unicincta* is closer to *gloriosissima* than is *mystacalis*. It has the shoulder patches smaller than in *gloriosissima* but the breast and belly are both rufous although disconnectedly. The most striking difference is in the presence of the white mystacal stripes. To suggest the existence of this feature in the more northern birds, one specimen of *lafresnayii* from Páramo de Tamá Venezuela (No. 43672, Field Mus. Nat. Hist.) has several feathers in the left malar region with distinctly whitish subterminal areas. With more material than I have seen, other similarities might be found.

Between *unicincta* and *lafresnayii* directly there is a fairly wide gap but by way of *mystacalis* and *gloriosissima* the hiatus is considerably less. The two forms now could meet only by way of the coastal range of the Peruvian Andes and there are no collections available from that region to show what transition may take place. The occurrence of the malar stripes in the Peruvian races is comparable to the case of *brunneiventris* in the *carbonaria* group, from the same region. Similarly, in the northern portion of the range of the *carbonaria* group a rufous-bellied, non-mustached *gloriosa* exists as a counterpart of *gloriosissima*, although its actual range is different, while in the intervening central region of Colombia, Ecuador and north-western Peru a mostly black *humeralis* and a wholly black *aterrima* duplicate parts of the range of *lafresnayii*.

This similarity in coloration and distribution is, to say the least, remarkable. Whatever the natural causes were which produced, retained or removed the malar stripes or developed black birds in one region and rufous and black ones elsewhere, they seem to have operated with nearly equal effect upon two distinct species of the temperate zone so as to bring into present existence a series of forms in each case which, in a major sense, exhibit the same characters in the same geographic regions.

In the present instance it is possible that *gloriosissima*, perhaps modified by the presence of a malar stripe, may represent the closest approach to the ancestral form. The black *lafresnayii* developed in the central region and separated the Peruvian and Colombian colonies which then were further modified in turn. The Peruvian sector finally broke into several forms segregated by

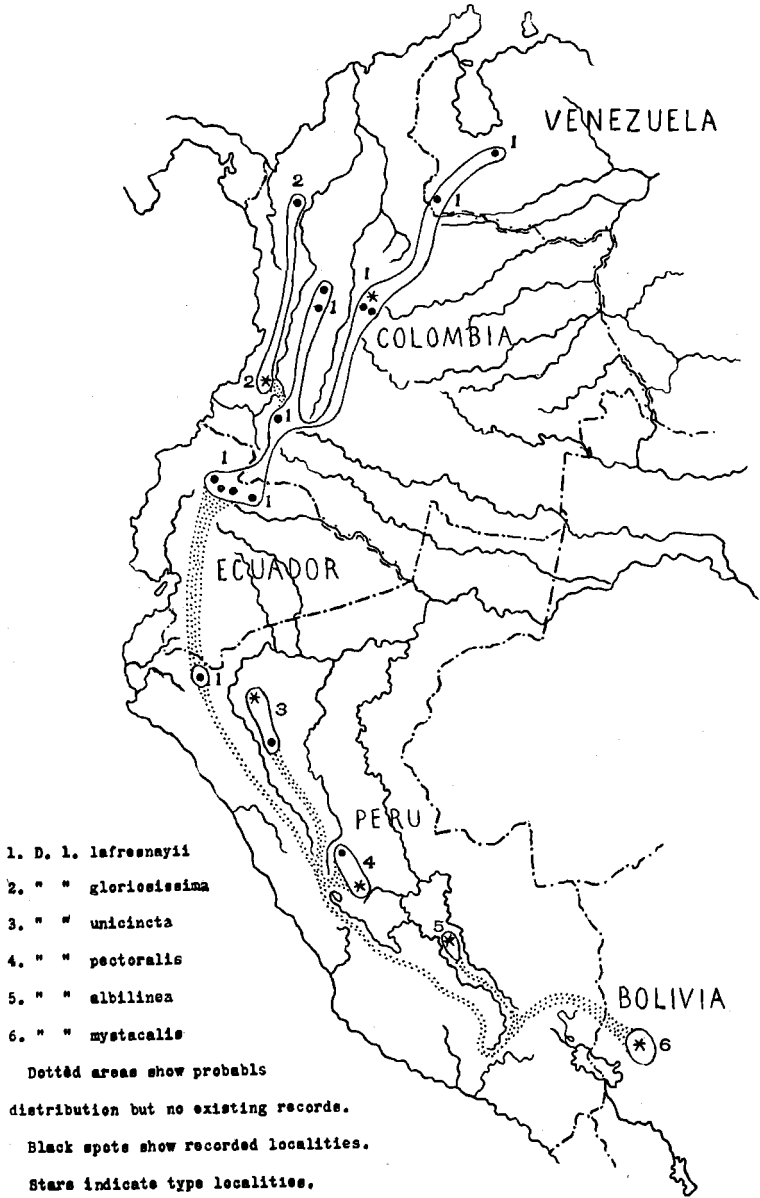


Fig. 2. Distribution of *Diglossa lafresnayii*

the larger river valleys. This subdivision in Peru is interesting in view of the fact that the corresponding form, *brunneiventris*, is not similarly broken up in the same region. Judging from my own observations of *pectoralis* in the field, with which the recorded data on *albilinea* agree, the members of the present group in central and southern Peru are partial to very high elevations and are not found at the lower altitudes in the temperate zone where *brunneiventris* is common; consequently the early formation of deep valleys as distributional barriers would have operated first with the present group and have left it all but isolated on distantly connected highlands while *brunneiventris* would have been, as it still is, able to pass from one mountain to another by considerably wider and more numerous highland bridges. Given this comparative isolation, the formation of distinct races could easily follow in the course of time.

Those who demand a degree of intergradation between subspecies, finer than can be shown here at present, may prefer to recognize a *lafresnayii* group and a *mystacalis* group or to retain all of the forms as distinct species. If so, all of the species must then be placed in the same "formenkreis" or "species-complex"; their intimate relationship is unquestionable and is much closer than that which exists between the members of the group and any species outside of it. It is a fault of our present system of nomenclature (for which I am not prepared to suggest a new remedy) that affinities of this sort can not be expressed in the names applied to each unit of the group unless we regard the related forms as subspecies. It is surely no more of an error to call them subspecies than it is to apply different specific names which connote a greater degree of distinctness than actually exists. The recognition of "formenkreisen" is serviceable only to a limited degree; it permits the association of mutually representative geographical species under a single heading, but neither the binomials of the included species nor the trinomials of their respective subspecies indicate the close relationship that exists among all the members of the group. To be most serviceable, nomenclature must indicate existing relationship as well as distinctness. To call *mystacalis* a species apart from *lafresnayii* indicates its distinctness but does not show that it is more closely related to *lafresnayii* than is *aterrima* or even one of the *sittoides* group; to call it a race of *lafresnayii* indicates both its

affinity and its distinctness. As remarked by Stone (*Auk*, 16, p. 375, 1899), "a trinomial name carries to the average student just twice the information that a binomial would under these circumstances."

The argument against this is, of course, that complete intergradation has not been proved. However, while intergradation is the best proof of specific unity, it should not be made the sole criterion. Insular forms may have no connecting links and still be obviously races of the same species. Similarly two closely related mainland forms may have no perfectly intermediate individuals because of isolation and still be found to represent one species in two different parts of its range. To quote Chapman on the same subject (*Auk*, Vol. XLI, p. 18, 1924), "it seems perfectly logical to insist that if a systematist refuses to rank certain forms as subspecies until their intergradation is proven, he should also refuse to treat them as species until the fact of their nonintergradation is established. . . . Is it not more scientific to treat each case on its merits, basing our conclusions on due consideration of all the available pertinent evidence?"

With this in mind, after an examination of all the forms which come under the present discussion, I have no hesitation in concluding that the species *lafresnayii* embraces six subspecies ranging from *l. lafresnayii* in Venezuela to *l. mystacalis* in Bolivia. Their distribution is shown on the accompanying map (fig. 2).

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SUMMARY.

1. Certain species of the genus *Diglossa* (Coerebidae), living in the highlands of north-western South America, may be arranged in

two distinct groups which show striking parallels of distribution and variation over a wide range.

2. Each group has a black form in the center of its range, a rufous-bellied, non-mustached form at the north and a rufous-bellied, rufous-mustached form at the south with additional variations in some places.

3. One of the mustached birds occurs without racial distinctions in two widely separated regions with all the suitable intervening country occupied by a black form of the same group. One of the isolated regions is divided by a deep valley which segregates two colonies of the mustached form; highlands which might connect the two ranges are occupied by the black form.

4. Within each group there is perfect geographic replacement of forms, no two of which occur together.

5. Intergradation is variously established or indicated among most of the forms of each group. Where it is only indicated there is usually a gap in the known distribution; the intervening region where intergradation probably occurs is not sufficiently explored to demonstrate the actual transition.

6. The relationships are best observed in a survey of the entire group since affinities are sometimes with a distant member of the group rather than with the adjacent form.

7. Throughout each group certain characters remain constant and establish the relationship in spite of superficial differences.

8. The evidence indicates that each of the two groups is a highly variable species of which the various forms are subspecies.

Specimens examined (in Field Museum of Natural History unless otherwise specified):

D. carbonaria carbonaria—Bolivia: Illimani, Iquico 1 ♂; Iquico 2 ♂ ♂¹; Cochabamba 1 ♂²; Incachaca, Cochabamba 4 ♂ ♂².

D. c. brunneiventris—Peru: La Quinoa 1 ♂ 1 ♀; mountains near Huánuco 6 ♂ ♂ 3 ♀ ♀; mountains near Pano 1 ♂; Culleui, Marañon River 1 ♂ 1 ♀; mountains east of Balsas 1 ♂; Limbani, Carabaya 2 ♀ ♀; Ollantaytambo 1 ♀¹; Torontoy 1 ♂¹. Colombia: Paramillo 1 ♂ 2 ♀ ♀¹, 1 ♀.

D. c. aterrima—Peru: El Tambo, Piura 5 ♂ ♂³. Ecuador: "Ecuador"

¹ Specimens in U. S. National Museum, Washington.

² Specimens in Carnegie Museum, Pittsburgh.

³ Specimens in American Museum of Natural History, New York.

- 1 ♂; Chillo 1 ♂¹; Taraguacocha 2 ♂♂³; El Paso, P. de Azuay 1 ♂³; Loja 1 ♂³; Yanacocha 1 ♀³; El Chiral 1 ♀³; Urbina, Mt. Chimborazo 1 ♀³. Colombia: Laguneta 2 ♂♂³; Sta. Isabel 1 ♂³; Almaguer 1 ♂¹ ♀³.
- D. c. humeralis*—Colombia: La Pradera 1 ♂; Palo Hueco 1 ♂; Chipaque 1 ♂³; "Bogotá" 2 ♀♀[?]; Ramirez, Santander 3 ♂♂ 2 ♀♀²; La Pica, Santander 1 ♂². Venezuela: Páramo de Tamá 2 ♂♂ 1 ♀.
- D. c. gloriosa*—Venezuela: Mérida 1 ♂; Hechisera, Mérida 2 ♂♂; Culata 1 ♂; Santo Domingo 2 ♂♂¹; Teta de Niquitao 2 ♂♂².
- D. c. nocticolor*—Colombia: S. Lorenzo, Sta. Marta 2 ♂♂ 2 ♀♀².
- D. lafresnayii lafresnayii*—Colombia: "Bogotá" 3 ♂♂[?]; Almaguer 1 ♂³. Venezuela: Mérida 1 ♂; Páramo de Tamá 1 ♂ 1 ♀.
- D. l. gloriosissima*—Colombia: Coast Range west of Popayán 1 ♂ 1? ³, 1 ♂¹, 1 ♂; Paramillo 2 ♂♂¹, 1 ♂ 1 ♀³.
- D. l. uncinata*—Peru: mountains east of Balsas 1 ♂ 1 ♀.
- D. l. pectoralis*—Peru: mountains near Huánuco 1 ♂ 2 ♀♀.
- D. l. albilinea*—Peru: Machu Picchu 3 ♂♂¹.
- D. l. mystacalis*—Bolivia 1? (Type)⁴.

¹Specimens in U. S. National Museum, Washington.

²Specimens in Carnegie Museum, Pittsburgh.

³Specimens in American Museum of Natural History, New York.

⁴Specimens in Museum of Comparative Zoology, Cambridge.

Field Museum of Natural History,
Chicago, Ill.