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Systematics and Evolution in *Diglossa* (Aves, Coerebidae)

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INTRODUCTION

During studies on the mechanisms of speciation in birds living in open, non-forested habitats of the high Andes of South America I analyzed, for purposes of comparison, patterns of species formation in some genera of montane forests and brushlands, among them *Diglossa*. My investigation of *Diglossa* showed it to be interesting to the evolutionist because it presents a wide range of easily detected speciation phenomena. In order to understand these phenomena I found it necessary to re-evaluate species limits and species relationships within the genus. This work led to a classification of *Diglossa* differing from earlier schemes in some taxonomic details, especially in the use of superspecies and species-groups. The study of speciation patterns is based on the analysis of discontinuities in the range of species and superspecies, and of the (presumably) concomitant differentiation in the birds initiated after the gap has appeared. The present paper, therefore, consists of two parts, a taxonomic revision of *Diglossa* at the species level, and a discussion of the factors responsible for the isolation of populations and species formation in that genus. The study has revealed that *Diglossa* is in a state of dynamic evolutionary change, and that much work remains to be done before a complete understanding of the mechanics of this change is obtained.

The information on distribution, geographical variation, species limits,

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and interspecific relationships comes from three sources: an examination of about 900 skins; a study of the pertinent literature; and a field study of the genus during trips to the Andes of Ecuador (1964), Peru (1965), and Bolivia (1967–1968).

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The present paper is the second in a series of speciation studies on Andean birds (see Vuilleumier, 1968).

THE GENUS *DIGLOSSA*

DIAGNOSIS

A genus of nine-primaried oscines comprising 10 or 11 to 17 species depending on the taxonomic treatment of allopatric taxa on the border-

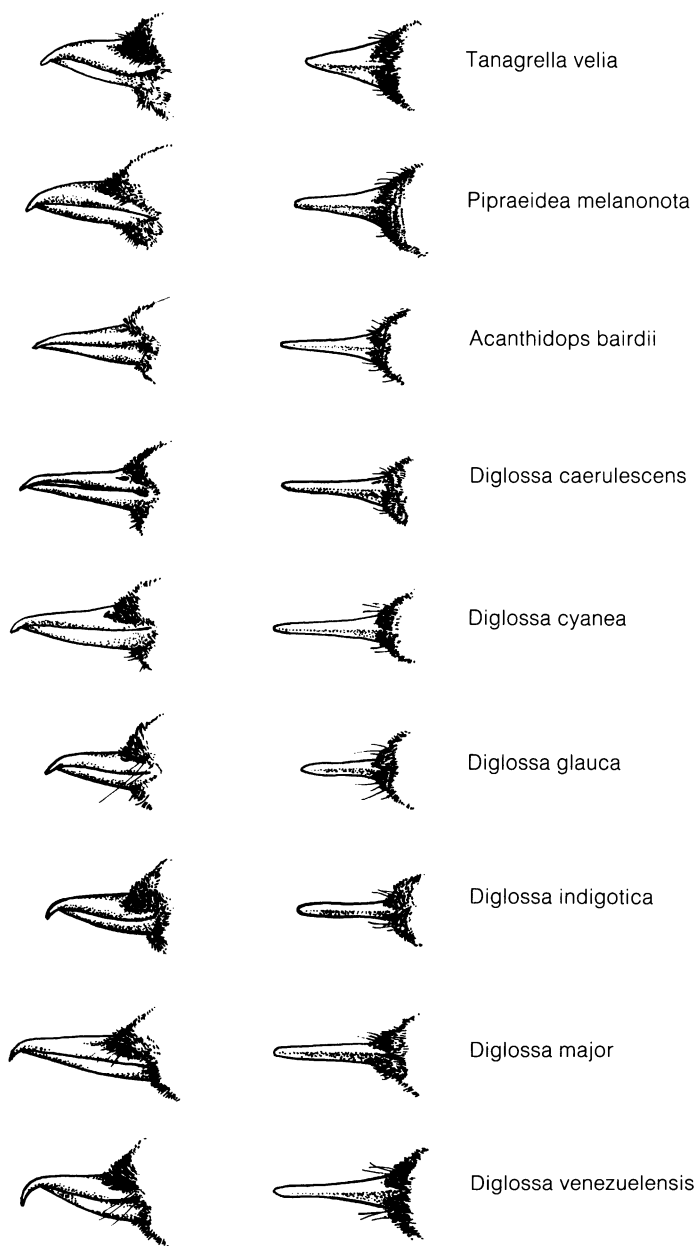


FIG. 1. Bill structure of *Pipraeidea*, *Tanagrella*, *Acanthidops*, and *Diglossa*. Note the variation in hook curvature, the “upturning” of the mandibles, and the bill width.

line between species and subspecies. All forms of *Diglossa* have a narrow, straight or slightly upturned, vertically compressed, and hooked bill. The curvature of the tip of the hooked bill is less marked in *D. caerulescens*, *D. cyanea*, and *D. glauca* (least in *D. caerulescens*) than in the other species. Some tanagers (e.g., *Pipraeidea melanonota*, *Tanagrella* sp.) have a hook a little like that of *D. caerulescens* but have a much wider bill. The bill of the "finch" *Acanthidops bairdii* is long, narrow, and compressed like that of *Diglossa caerulescens* but, unlike it, has no terminal hook. Figure 1 illustrates the bill morphology of several species of *Diglossa*, of the tanagers *Pipraeidea* and *Tanagrella*, and of the "finch" *Acanthidops*.

Both a rather dull bluish gray to black plumage (with or without ruddy or chestnut) and a brilliant, glossy blue plumage are found in *Diglossa*. Some of the dull-colored species resemble other Coerebidae.¹ *Diglossa gloriosissima* resembles *Conirostrum sitticolor* in pattern and in some color characteristics, and *D. sittoides* is somewhat similar to *Conirostrum ferrugineiventris* in color and pattern, yet some of the blue-colored species of *Diglossa* resemble tanagers (Thraupidae). The general color and pattern of *D. cyanea* and *Tangara vassorii* are roughly similar, and the glossy blue of *D. indigotica* is found in some other tanagers (e.g., some species of *Tangara* and *Iridosornis*), as well as in some honeycreepers (e.g., *Cyanerpes*). The peculiar compressed and hooked bill, however, readily distinguishes *Diglossa* from genera of the Coerebidae and Thraupidae. Furthermore, *Diglossa* differs "from all other Coerebidae in having the gonydeal angle decidedly posterior to the nostril" (Ridgway, 1902, p. 337).

Most members of *Diglossa* have relatively long and conspicuous rectal bristles, which are relatively conspicuous in some tanager genera, but are absent from, or short and inconspicuous in, coerebid genera other than *Diglossa*.

ADAPTATIONS FOR NECTAR FEEDING

Nectar is the major food of *Diglossa* but several (possibly all) species consume insects, feed them to their nestlings, and eat fruit (see Skutch, 1954, p. 437; Moynihan, 1963, p. 328; and Niethammer, 1956, p. 129). Generic specializations for nectar feeding are briefly reviewed below.

The tongue of *Diglossa* (personal observation) is a long, thin, U-shaped canal that divides into two smaller U-shaped canals toward the distal end. Hairlike projections at the tip of these two canals give them a

¹ I use the term Coerebidae for convenience. I shall not discuss the question whether the Coerebidae are a monophyletic or polyphyletic assemblage (cf. Beecher, 1951; Skutch, 1962; de Schauensee, 1966).

brushy aspect. The U-shaped tongue fits facing downward into the U-shaped lower mandible, so that the two together form a hollow tube. In other nectar-eating birds (other coerebid genera, Trochilidae, Nectariniidae, Meliphagidae, parrots of the genus *Trichoglossus*), the U-shaped tongue faces upward, and when it rests in the lower mandible it forms an open canal. The possible functional significance of this morphological difference is not known.

Gadow (1883) postulated that if a vacuum were created in the mouth of a bird when the tongue is protruded, nectar would be sucked in through the capillary tube formed by the tongue. This explanation presents a difficulty because the bird opens its bill in order to protrude the tongue when it feeds, and consequently the vacuum effect is lost (Bock, personal communication).

Skutch (1954, pp. 422–423; and Moynihan, 1963) described individuals of *Diglossa* that held the base of tubular flowers with the hook of the upper mandible, as they slit the corolla with the lower mandible in order to produce an opening for the tongue. In this regard, it is noteworthy that species with a very conspicuous hook (as, for example, *D. major* and *D. venezuelensis* depicted in fig. 1) also have two to four small notches and “teeth” along the sides of the upper mandible just beyond the hook (at the point where the tip of the lower mandible fits into the upper mandible). These “teeth” might, together with the hook, provide a grip on the flower as the bird extracts nectar from it.

Although I carefully observed several species of *Diglossa*, I could not see the details of the nectar-eating operation as Skutch (1954) did, because the birds spent too little time at any given flower. In one instance, however, I saw two different individuals of *D. mystacalis* (a large and relatively slow-moving species) in Bolivia feeding at the purple flowers of *Brachyotum microdon* (Naud.) Triana (Melastomataceae). These birds inserted their lower mandible into the opening of the tubelike corolla and pressed their upper, hooked mandible against the outside of the corolla. This method is slightly different from that described by Skutch (1954), because the birds did not make a slit in the corolla through which the tongue could be inserted. Flower pollination would only take place if the birds feed in the manner observed by me.

Other apparent adaptations to nectar feeding in *Diglossa* convergent toward those of hummingbirds are the regurgitation movements of the parent birds, the esophageal sac of nestlings, the synchronization of the breeding season with the flowering period (see Skutch, 1954), and the kind and degree of interspecific aggressiveness shown by at least some taxa (see Moynihan, 1963, 1968).

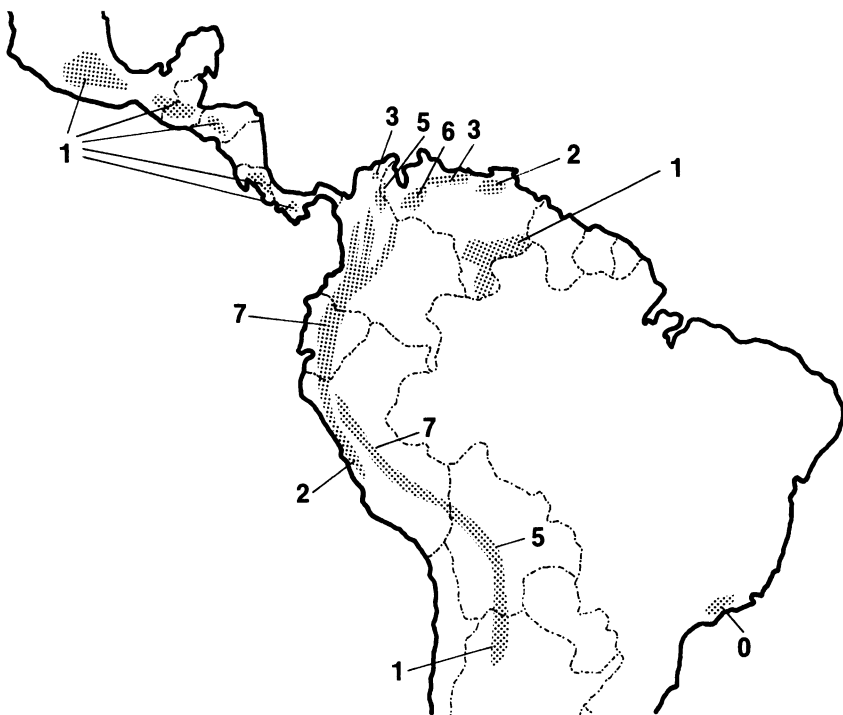


FIG. 2. Distribution of *Diglossa*. 1–7 represent the number of sympatric species; 0 signifies absence from mountains of southeastern Brazil.

ECOLOGY AND DISTRIBUTION

All members of *Diglossa* inhabit montane forests and brushlands up to timberline in the mountains of southern Mexico and Central America, in the Andes from Venezuela and Colombia to northern Argentina, in the coastal mountains of Venezuela, and on the mesas of southeastern Venezuela and adjacent Brazil (fig. 2). The northern Andes constitute the present distribution center of the genus, with as many as seven species sympatric there. In contrast, only a single species is found on any one mountain range in Central America, in the southern Venezuelan highlands, or in the Andes of Argentina (fig. 2).

Because several genera of Andean birds are also present in the mountains of southeastern Brazil (or are replaced by close relatives), it is worth noting that *Diglossa* is not found there. Its absence could be explained by the lack of some ecologically essential factor (i.e., lack of tubular flowers). Such an explanation is unlikely, because Brade (1956)

listed various genera on Mt. Itatiaia, e.g., several Melastomataceae, *Fuchsia* (Onagraceae), *Salvia* (Labiatae), and *Lobelia* (Campanulaceae), visited by individuals of *Diglossa* in the Andes (personal observation) or in Central America (Skutch, 1954).

It seems more likely that *Diglossa* failed to colonize southeastern Brazil. The nearest Andean localities in which *Diglossa* lives are about 1200 kilometers away in northwestern Argentina and southern Bolivia (fig. 2). The two allopatric species of *Diglossa* that live in the south Venezuelan highlands are probably colonists from the Andes. In this case, the shortest distance is about 500 kilometers from the Andes to Cerro Paraque, where *D. duidae* occurs. Colonization might have been achieved by long-distance dispersal, as Mayr and Phelps (1967) suggested, or by dispersal during periods when a climatic depression permitted suitable habitat to be much closer than 500 kilometers, as Eisenmann believes (personal communication). In any case, successful colonization in *Diglossa* appears to be possible for distances of about 500 kilometers, but seems less likely for increasing distances, and impossible for 1200 kilometers.

RELATIONSHIPS

The evidence adduced so far is insufficient to permit an assessment of the position of *Diglossa* within the tanager-honeycreeper-emberizine finch complex. The jaw musculature suggested to Beecher (1951) that *Diglossa* is an offshoot from tanager stock, but his view has not yet gained wide acceptance. Other lines of evidence are ambiguous (breeding biology; Skutch, 1954, 1962) or remain to be studied (e.g., functional morphology of the tongue-hyoid apparatus).

Eisenmann (*in de Schauensee*, 1966, p. 456, and personal communication) is of the opinion that *Diglossa* is related to *Conirostrum* and "finches" such as *Haplospiza*, *Spodiornis*, and *Acanthidops*, partly because the latter genus has a bill much like the one of *Diglossa*, but without a terminal hook (fig. 1). An alternative possibility is that *Acanthidops* evolved from a "finch" stock (perhaps toward nectar eating?) in a way that paralleled the differentiation of *Diglossa* from tanagers.

ANALYSIS OF SOME CHARACTERS OF *DIGLOSSA*

The species limits of *D. caerulea*, *D. cyanea*, *D. glauca*, *D. indigotica*, *D. duidae*, and *D. major* are unequivocal. In the other taxa of the genus, however, the worker must decide whether allopatric and morphologically differentiated populations should be given specific rank or not. Several characters of these birds are analyzed below to assess their value as

species specific characters or as group characters.

SEXUAL DIMORPHISM

Only five taxa (*D. baritula*, *D. plumbea*, *D. sittoides*, *D. albilatera*, and *D. venezuelensis*) show sexual dimorphism that involves major color differences between the sexes. Males of these taxa are dark slate gray above and ruddy below, or entirely dark slate gray, or black, and females are greenish olive or pale grayish above, and pale buffy brown below. The females of the first four species are quite similar to one another, whereas the female of *venezuelensis* differs in having a yellowish green wash on the head. In the other taxa of *Diglossa*, females are more similar to males, being slightly duller in color or smaller in size.

There is no apparent correlation between geographical variation and sexual dimorphism, because there are isolated species such as *D. duidae* and *D. major* (southern Venezuelan highlands) with no sexual dimorphism, isolated species such as *D. baritula* and *D. plumbea* (Central America) with no geographical variation in sexual dimorphism, and widespread species such as *D. sittoides* and *D. albilatera* (Andes) with no geographical variation in sexual dimorphism. *Diglossa venezuelensis*, also sexually dimorphic, has too restricted a range to show geographical variation.

The question arises: Are the five sexually dimorphic species closely related to one another, and, if so, are they, as a group, closely related to the non-dimorphic or less-dimorphic species?

The three taxa *baritula*, *plumbea*, and *sittoides* are certainly closely related (treated as the *baritula* superspecies in this paper, and as *D. baritula* by Hellmayr, 1935, pp. 219–225, and Zimmer, 1942). They are similar to one another in female and immature plumages and show resemblances in size, proportions, and in male plumage pattern.

The two taxa *albilatera* and *venezuelensis* are also closely related (considered as the *albilatera* superspecies here; see Hellmayr, 1935, footnote, p. 233).

Members of the *baritula* superspecies differ, however, from those of the *albilatera* superspecies in details of coloration and in proportions. Furthermore, the adult male of *venezuelensis* is similar in color and proportions to the black member of a third superspecies (*D. humeralis* of the *carbonaria* superspecies; see below).

In spite of these differences, the *baritula* and *albilatera* superspecies do seem more similar to each other than either is to other species of *Diglossa*. One might thus argue that they are related, but how close this

relationship is still open to question.

SIZE AND PROPORTIONS

Interspecific differences in size or proportions within *Diglossa* are not well marked. Furthermore, both size and proportions vary geographically in every wide-ranging species and thus should be used only in connection with other taxonomic characters. For example, *D. indigotica* has a short tail (between 58% and 64% of wing length), whereas the tail of *D. glauca* is proportionally longer (between 72% and 81% of wing length), yet generally shorter than the tail of other species of *Diglossa*. This character, plus the plumage color and pattern, and the ecology and distribution suggest that *D. glauca* and *D. indigotica* are more closely related to each other than either is to other species.

Diglossa major has the largest tail/wing ratio within the genus, but in some specimens of the *lafresnayii* superspecies, this ratio is as large as, or larger than, that of some specimens of *D. major*. In proportions, and in the mystacal stripe and rufescent crissum, *D. major* appears close to such species as *D. mystacalis*, although in other characters (facial mask, bluish upper parts) it seems closer to such species as *D. caerulescens* and *D. cyanea*.

SHAPE AND STRUCTURE OF FOREHEAD FEATHERS

In *D. gloriosissima*, *D. lafresnayii*, *D. mystacalis* (three taxa forming the *lafresnayii* superspecies), *D. carbonaria*, *D. humeralis* (*carbonaria* superspecies), and *D. duidae* the feathers of the forehead are compact (i.e., have many barbs) and have rather pointed tips. These feathers lend the forehead a somewhat scaly aspect, most noticeable in *gloriosissima*, *lafresnayii*, and *mystacalis* (*lafresnayii* superspecies).

In the other species (including *D. major*) the forehead feathers are less compact (fewer barbs) and have more rounded tips; consequently the forehead appears non-scaly.

COLOR AND PATTERN

Allopatric taxa of three superspecies of *Diglossa*, the *baritula* superspecies (*baritula*, *plumbea*, *sittoides*), the *lafresnayii* superspecies (*lafresnayii*, *gloriosissima*, *mystacalis*), and the *carbonaria* superspecies (*gloriosa*, *humeralis*, *carbonaria*) differ conspicuously in color and pattern. With minor differences, all three superspecies have populations of black or dark gray, unpatterned birds, which are abruptly replaced geographically by ruddy-bellied or chestnut-bellied birds, as shown in detail in table 1 and figures 3-6. Other characters, such as details of coloration (e.g., color of

TABLE 1
DISCONTINUOUS GEOGRAPHICAL VARIATION IN PLUMAGE PATTERN AND COLOR IN THREE SUPERSPECIES OF *Diglossa*

Taxa and Their Distribution	Color and Pattern Characters	
	Plumage Unpatterned	Plumage Patterned
<i>baritula</i> superspecies		
<i>baritula</i> (Mexico, Guatemala, Honduras)		Gray above, ruddy below
<i>plumbea</i> (Costa Rica, Panama)	Entirely slate gray	Gray above, ruddy below
<i>sittoides</i> (Andes of South America)		Black above, chestnut below
<i>lafresnayii</i> superspecies		
<i>gloriosissima</i> (Andes of western Colombia)		Black with white or brown mystacial stripe, chestnut crissum, white or brown pectoral band
<i>lafresnayii</i> (Andes of Venezuela, Colombia, Ecuador, and Peru)	Black with gray humeral patch	Black above, chestnut below
<i>mystacalis</i> (Andes of Peru and Bolivia)		Black with white or brown mystacial stripe, chestnut crissum, white or brown pectoral band
<i>carbonaria</i> superspecies		
<i>gloriosa</i> (Andes of western Venezuela)		Black above, chestnut below
<i>humeralis</i> (Andes of Colombia, Ecuador, and northwestern Peru)	Either all black or black with gray humeral patch	
<i>carbonaria</i> (Andes of Peru and Bolivia)		Black above, below either chestnut or gray

rump and axillary feathers) and size, clearly show that within each of the three superspecies the differentiated populations are closely related.

If all these discontinuously variable populations were completely allopatric it would be impossible to know whether the degree of morphological differentiation reflects reproductive isolation, and hence specific status. Fortunately, there are two cases in the *carbonaria* superspecies (in Peru and Bolivia), in which previously existing barriers have broken down and formerly allopatric populations now have come together. These two instances are summarized in table 2 and discussed in more detail under the *carbonaria* superspecies. It can be pointed out here that some differences in color pattern, such as black and chestnut versus black and gray, are probably not correlated with reproductive isolation, whereas others, such as all black versus black and chestnut, are.

Because similar kinds of discontinuous variation occur in the *baritula* and *lafresnayii* superspecies (table 1) and in other members of the *carbonaria* superspecies across geographical barriers, it is not possible to make unequivocal taxonomic decisions. The taxonomic solution adopted in the present paper is discussed in the section on Classification below.

CLASSIFICATION OF *DIGLOSSA*

Two general synopses of *Diglossa* (Cassin, 1864; Sclater, 1875) have been published since an earlier list by Lafresnaye (1846) and prior to the more modern classification of Hellmayr (1935, pp. 218-242). Both Cassin and Sclater placed the various species in two genera: *Diglossopsis* Sclater, 1856, with only the species *caerulescens*, because of its slightly hooked bill, and *Diglossa* Wagler, 1832, with all the others; but *D. cyanea* and *D. glauca* bridge the gap in hook curvature between *D. caerulescens* and the other species of the genus (see fig. 1). Berlepsch (1884) merged *Diglossopsis* with *Diglossa*, a practice followed by most ornithologists (see also Zimmer, 1930, pp. 420-421, who was apparently unaware of Berlepsch's suggestion).

Cassin (1864) divided *Diglossa* on the basis of color and pattern into five subgenera which resulted in the relegation to different subgenera of closely related but differently patterned species such as *D. baritula* and *D. plumbea*. Although Sclater (1875) criticized Cassin's subgenera, he also based his classification on color and circumscribed two sections of *Diglossa*: "*Diglossae rufo-pictae*" with rufescent in the plumage, and "*Diglossae homochroae*" with unpatterned plumage. Again, closely related taxa were placed in different sections (e.g., *D. baritula* in one section, and *D. plumbea* in the other).

Hellmayr (1935) improved the taxonomy by grouping together closely

TABLE 2
CORRELATION OF MORPHOLOGICAL DIFFERENTIATION WITH REPRODUCTIVE ISOLATION BETWEEN CLOSELY RELATED MEMBERS
OF THE *carbonaria* SUPERSPECIES

Taxa in Contact and Region of Contact	Morphological Differentiation	Degree of Reproductive Isolation between Taxa
<i>brunneiventris</i> and <i>carbonaria</i> (western Bolivia)	<i>brunneiventris</i> : black upper parts, chestnut under parts, chestnut mustache <i>carbonaria</i> : black upper parts, gray under parts, no mustache, chestnut crissum	Reproductive isolation incomplete: <i>brunnei-</i> <i>ventris</i> and <i>carbonaria</i> produce hybrids in the wild
<i>brunneiventris</i> and <i>aterrima</i> (northwestern Peru)	<i>brunneiventris</i> : same as above <i>aterrima</i> : black with grayish rump	Reproductive isolation complete or nearly so: no hybridization between <i>brunneiventris</i> and <i>aterrima</i>

related, geographically replacing taxa and by reducing the number of species to 11. His treatment of *D. lafresnayii* and *D. carbonaria* followed Zimmer (1929). Hellmayr's scheme has been generally accepted by ornithologists, and was followed with only a minor modification by de Schauensee (1966, pp. 456-458).

The classification suggested here differs from Hellmayr's in two ways. First, there are several instances in *Diglossa* in which allopatric taxa are on the borderline between species and subspecies. In these cases, the best course, it seems to me, is to keep as separate species discontinuous, morphologically differentiated, and isolated taxa but to indicate their evolutionary interrelationships by including them in superspecies. The changes from Hellmayr's classification are the following: *Diglossa baritula* (polytypic species in Hellmayr, 1935, and in Zimmer, 1942) is considered a superspecies with three component semispecies ("borderline cases between species and subspecies," Mayr, 1963, p. 671), nomenclaturally treated as species: *D. baritula*, *D. plumbea*, and *D. sittoides*. *Diglossa lafresnayii* (polytypic species in Zimmer, 1929, and Hellmayr, 1935) is a superspecies with three semispecies, nomenclaturally treated as species: *D. lafresnayii*, *D. gloriosissima*, and *D. mystacalis*. Finally, *D. carbonaria* (polytypic species in Zimmer, 1929, and Hellmayr, 1935) is considered a superspecies with two semispecies, nomenclaturally treated as species: *D. humeralis* and *D. carbonaria*.

The second change from Hellmayr's classification consists of a different linear sequence of species, and in the use of species-groups to define units below the rank of the genus and above that of the superspecies. These groups, and the species within each, are arranged in the classification outlined below in sequence from least to most specialized. The species-groups have been named after the species thought to be the least specialized within the group. This practice endorses Cain's view (1954, p. 270) that "As the species-group is burdened by no formal rules [of nomenclature] there is no necessity to use the oldest valid name within a group as the name of that group."

On the basis of the character analysis I would divide *Diglossa* into four species-groups.

1. The *caerulescens* species-group includes four species with blue plumage, a poorly marked to well-marked facial mask, "non-scaly" forehead, and poorly marked sexual dimorphism. Three of these four species (*D. caerulescens*, *D. cyanea*, and *D. glauca*) have the least-specialized bills (least hooked) in the genus. These species and the fourth (*D. indigotica*) are extensively sympatric, a fact that suggests a relatively old evolutionary history. This group is placed first in the sequence on the tentative assump-

tion that blue plumage or less-specialized bill, or both, represent an ancestral condition also found in modern tanagers, a stock from which *Diglossa* might have originated.

2. The *major* species-group contains only *D. major*. This species, the largest of the genus, exhibits characters both of the *caerulescens* species-group (dull blue upper parts, black mask, "non-scaly" forehead) and of the *lafresnayii* species-group (mystacial stripe, rufous crissum, tail/wing ratio, absolute size). Yet *D. major* also shows a unique character of blue shaft streaks of the dorsum feathers.

3. The *lafresnayii* species-group comprises two superspecies (*lafresnayii* and *carbonaria*) and a "good" species (*D. duidae*), with poorly marked sexual dimorphism, a dull gray or black, or a patterned (black and chestnut) plumage, and a "scaly" forehead. *Diglossa duidae* is an isolated species in this group, although it is closer in size to the *carbonaria* superspecies than to the *lafresnayii* superspecies. There is active speciation in the two superspecies *lafresnayii* and *carbonaria*.

4. The *albilatera* species-group consists of sexually dimorphic species with a "non-scaly" forehead. The males are dull gray or black, or patterned gray and ruddy, whereas the females are clad in pale grayish, brownish, or greenish tones. The two superspecies comprising this species-group (*albilatera* superspecies and *baritula* superspecies) are actively speciating. Marked sexual dimorphism might be a relatively recent development in the genus, because it is found only in the above two superspecies, which have colonized away from the Andean distributional center perhaps in the recent past.

In the following specific check list, the semispecies considered to be members of superspecies are included in braces. The superspecies are named after the oldest name of any taxon within each. References to original descriptions and detailed synonymies are omitted, because they can be found in Hellmayr (1935). For the sake of completeness, however, subspecies described since Hellmayr's work are listed in brackets under their respective species. The general range of each recognized species is given for convenience.

Genus *Diglossa* Wagler, 1832

1. *caerulescens* species-group

D. caerulescens Sclater, 1856. Along the Andes from Venezuela and Colombia to Bolivia. [Subspecies described since 1935: *intermedia* Carriker, 1935 = *media* Bond, 1955; *mentalis* Zimmer, 1942; *ginesi* Phelps and Phelps, 1952.]

D. cyanea Lafresnaye, 1840. Along the Andes from Venezuela and Colombia to Bolivia. [Subspecies described since 1935: *dispar* Zimmer, 1942; *tovarensis* Zimmer and Phelps, 1952; *obscura* Phelps and Phelps, 1952.]

- D. glauca* Sclater and Salvin, 1876. Along the Eastern Andes from southern Colombia to Bolivia.
- D. indigotica* Sclater, 1856. Along the Western Andes of Colombia and Ecuador.
2. *major* species-group
- D. major* Cabanis, 1849. Tablelands of southeastern Venezuela in Bolivar and of northern Brazil. [Subspecies described since 1935: *gilliardi* Chapman, 1939; *disjuncta* Zimmer and Phelps, 1944; *chimantae* Phelps and Phelps, 1947b.]
3. *lafresnayii* species-group
- lafresnayii* superspecies
- D. gloriosissima* Chapman, 1912. Western Andes of Colombia.
 - D. lafresnayii* Boissonneau, 1840. Andes of western Venezuela, of Colombia except the Western Andes, of Ecuador and extreme northwestern Peru.
 - D. mystacalis* Lafresnaye, 1846. Along the eastern Andes of Peru and Bolivia.
- carbonaria* superspecies
- D. humeralis* Fraser, 1840. Santa Marta Mountains in northern Colombia, Perijá Mountains, extreme western Andes of Venezuela, Eastern Andes of Colombia, southern end of central and Western Andes of Colombia, Andes of Ecuador and of extreme northwestern Peru.
 - D. carbonaria* Lafresnaye and d'Orbigny, 1838. Andes of northwestern Venezuela; northern end of Western and central Andes of Colombia, Andes of Peru (except northwestern corner) and Bolivia.
 - D. duidae* Chapman, 1929. Tablelands of southeastern Venezuela in Amazonas. [Subspecies described since 1935: *hitchcocki* Phelps and Phelps, 1947a; *parui* Phelps and Phelps, 1950.]
4. *albilatera* species-group
- albilatera* superspecies
- D. albilatera* Lafresnaye, 1843. Along the coastal range of northern Venezuela, and the Andes from Venezuela and Colombia to Peru. [New subspecies described since 1935: *affinis* Zimmer, 1942.]
 - D. venezuelensis* Chapman, 1925. Coastal ranges of extreme northeastern Venezuela.
- baritula* superspecies
- D. baritula* Wagler, 1832. Mountains of southern Mexico, Guatemala, and Honduras.
 - D. plumbea* Cabanis, 1860. Mountains of Costa Rica and western Panama.
 - D. sittoides* Lafresnaye and d'Orbigny, 1838. Along the coastal ranges of Venezuela, and the Andes from Venezuela and Colombia to northwestern Argentina. [Subspecies described since 1935: *mandeli* Blake, 1940; *coelestis* Phelps and Phelps, 1953.]

VARIATION AND SPECIATION IN *DIGLOSSA*

1. THE *caerulescens* SPECIES-GROUP

Diglossa caerulescens

This species ranges from the coastal cordillera and the Perijá Range

of Venezuela through Colombia, Ecuador, and the eastern Andes of Peru to Bolivia (department of La Paz). It inhabits wet montane forests (cloud forests) in which it is relatively uncommon (at least in Venezuela; see Schäfer and Phelps, 1954, p. 135).

In spite of its vast range, *caerulescens* exhibits little geographical variation, which is summarized as follows. Birds from the coastal mountains of Venezuela form one group of populations characterized by their pale dorsum (subspecies *caerulescens*). Birds from the Andes of western Venezuela, the Sierra de Perijá, and the Andes of Colombia form a second group with dark dorsum (subspecies *saturata* and *ginesi*). Birds from Peru and Bolivia form a third group with pale back (subspecies *media*, *pallida*, and *mentalis*). I have seen only one specimen from Ecuador, where the species has rarely been collected, but Ecuadorian birds are probably close to the third, pale-backed group, because de Schauensee (1951, p. 101) allocated two Ecuadorian specimens to the subspecies "*intermedia*" (= *media*; see Bond, 1955, p. 37).

Diglossa cyanea

This species ranges from the coastal cordillera and the Perijá Mountains of Venezuela through Colombia, Ecuador, and eastern Peru to Bolivia (department of Cochabamba), in upper montane forests and open shrubbery at or below timberline (personal observation; Moynihan, 1963, p. 329).

Diglossa cyanea exhibits minor and apparently discontinuous geographical variation, but I have examined too few specimens to assess this variation properly. The isolated or partly isolated populations living in the coastal cordillera of Venezuela (subspecies *tovarensis*) and the Perijá Mountains (*obscura*) show slight differentiation, as do the birds living, respectively, northwest (*dispar*) and southeast (*melanopsis*) of the dry basin of the upper Marañon of northern Peru.

Diglossa glauca

This species consists of two isolated groups of populations, separated from each other by a broad distribution gap, apparently centered around the dry basin of the upper Marañon of northern Peru. The northern populations (subspecies *thyrianthina*) occur in southeastern Colombia and eastern Ecuador. They are smaller and duller than the southern populations (subspecies *glauca*), which live in the eastern Andes from central Peru to Bolivia (south to the department of Cochabamba).

Diglossa glauca seems to live between 1000 and 2000 meters in altitude in dense mid-montane forests (from data on specimen labels).

Diglossa indigotica

This species occurs along the Western Andes of Colombia and Ecuador. Geographical variation appears nil, although it could be masked by the small number of available specimens. The altitudinal range falls between 700 and 2100 meters and suggests that this species, as does *D. glauca*, lives in mid-montane forests.

SPECIATION IN THE *caerulescens* SPECIES-GROUP

None of the three species *caerulescens*, *cyanea*, and *glauca* shows marked geographical variation, yet study of very large series of specimens would probably show that in each species morphological differentiation, although minor, is positively correlated with geographical isolation. Some differentiation is thus apparent in populations of *caerulescens* and *cyanea* isolated in the coastal range of Venezuela and in the Sierra de Perijá, and in populations of *cyanea* and *glauca* isolated along each side of the basin of the upper Mara  n of northern Peru.

The morphologically rather similar *D. glauca* and *D. indigotica* may be similar also in their ecological preferences, although precise data are lacking. Both occur allopatrically in southern Colombia and Ecuador, but *D. glauca* is found only along the eastern slope of the Eastern Andes, and *D. indigotica* along the western slope of the Western Andes. The non-forested high Andean ridges and the dry inter-Andean uplands separating the Eastern from the Western Andes might thus constitute a barrier to dispersal across the Andes. The allopatry of the two species is not sufficient, however, to authorize the suggestion that they belong in one super-species. Indeed, they are morphologically distinct enough for one to doubt the closeness of their relationship.

Speciation phenomena in the *caerulescens* species-group are therefore relatively insignificant. Three out of four species have isolated populations, but their differentiation is so weak that it seems too bold to speak of incipient speciation. Furthermore, there is much sympatry in the species-group as a whole. *Diglossa caerulescens* and *D. cyanea* are entirely sympatric and possibly share the same habitats, and the ranges of both *D. glauca* and *D. indigotica* fall wholly within those of *D. caerulescens* and *D. cyanea*. It is therefore impossible to make inferences about the speciational history of the *caerulescens* species-group.

2. THE *major* SPECIES-GROUP*Diglossa major*

This species shows a mixture of characters. Some of them are found

in the *caerulescens* species-group, others in the *lafresnayii* species-group, whereas still another is unique. It is therefore difficult to ascertain the relationships of this species, but it does seem clear to me, as it did to Chapman (1939, p. 12) that *D. major* is not closely related to *D. duidae*.

Diglossa major occurs in the eastern part of the Venezuelan highlands and adjacent northern Brazil, but is not sympatric with *D. duidae*. Although the geographical variation in *major* is slight, four subspecies have been described (see Phelps and Phelps, 1963, pp. 306–307).

The morphological characters of *D. major* suggest that its ancestor was derived from an Andean stock, although it is not possible to suggest which. This stock might have invaded the Venezuelan highlands by long-distance colonization (Mayr and Phelps, 1967). The distinctness of *major* within *Diglossa* might be interpreted as evidence that this invasion took place a relatively long time ago, but the very slight subspeciation within the species contradicts this interpretation.

The seemingly conflicting phenomena of morphological distinctness combined with lack of extensive variation and incipient speciation can, I think, be resolved by the following hypothesis. As suggested by the lack of major geographic variation, proto-*major* invaded the Pantepui area in the relatively recent past. The morphological distinctness of the species can be understood as resulting from relaxed selection pressures. In the Andes, where several species of *Diglossa* live sympatrically, there is some evidence (Moynihan, 1963, 1968) that selection due to the presence of other species in the same habitats has modified the morphology (and other characters) of some species. Lack of sympatric *Diglossa* species in the Venezuelan highlands, however, may have produced a situation with relaxed selective forces which tended to favor the evolution, or rather maintenance, of a “generalized” species, retaining characters found in several of the Andean groups that were rapidly diverging (and converging? See section on speciation parallelism below) from one another. Incidentally, the other species living on Pantepui, *D. duidae*, can also be thought of as “generalized” (retaining characters of several groups), although perhaps less so than *D. major*, because the characters of *D. duidae* are found only within the *lafresnayii* species-group.

3. THE *lafresnayii* SPECIES-GROUP THE *lafresnayii* SUPERSPECIES

Members of the *lafresnayii* superspecies range from the Andes of western Venezuela through Colombia, Ecuador, and the eastern Andes of Peru to Bolivia (south to the department of Cochabamba; see fig. 3). They live in the open shrubbery of timberline and in the wet upper mon-

tane forests below. Zimmer (1930, p. 419) and Niethammer (1956, p. 128) found members of the *lafresnayii* superspecies uncommon, but this experience is not supported by my own with these birds in Ecuador, Peru, and Bolivia.

The *lafresnayii* superspecies is made up of several allopatric and morphologically differentiated units, all closely interrelated. Zimmer (1929), who merged all these forms in one species (*D. lafresnayii*), discussed the characters showing this relationship, so that they need not be repeated here. The allopatric units fall into three taxonomic groups: (*gloriosissima*, *lafresnayii*, and *mystacalis*) described below.

Diglossa gloriosissima

These birds have black upper parts and head, a contrasting chestnut belly, and a bluish gray humeral patch (fig. 4). Their range is restricted to two apparently isolated populations along the Western Andes of Colombia (fig. 3).

Diglossa lafresnayii

These birds are black with a bluish gray humeral patch (fig. 4). Their range includes the Andes of western Venezuela, the Eastern and central Andes of Colombia, the Andes of Ecuador and of extreme northwestern Peru. The distribution of populations of *lafresnayii* appears partly continuous and partly disjunct (fig. 3). A trend of increasing size from Venezuela southward is apparent, but I am not satisfied that it is clinal. A study of very large series might reveal a positive correlation between geographical variation and the discontinuities in distribution. In any event, morphological differentiation within *D. lafresnayii* is minor, even between populations isolated by rather clear-cut geographical barriers, such as the Río Magdalena in Colombia (fig. 3).

Diglossa gloriosissima and *D. lafresnayii* are isolated from each other by the dry Río Patía Canyon and the upper Río Patía-upper Río Cauca valleys (fig. 3). Zimmer (1929, p. 30) cited two specimens of *lafresnayii*, one from Venezuela and the other from the Eastern Andes of Colombia, far from the range of *gloriosissima*, which in his opinion showed a morphological approach toward *gloriosissima*. There is, furthermore, one specimen of *gloriosissima* from "Coast Range West of Popayán," Western Andes of Colombia, which is supposed to "vary somewhat in the direction of *D. l. lafresnayii* by the blackish suffusion along the sides of the breast and abdomen" (Hellmayr, 1935, footnote, p. 226), indicating that the barrier just mentioned does not seem to isolate the two forms effectively.

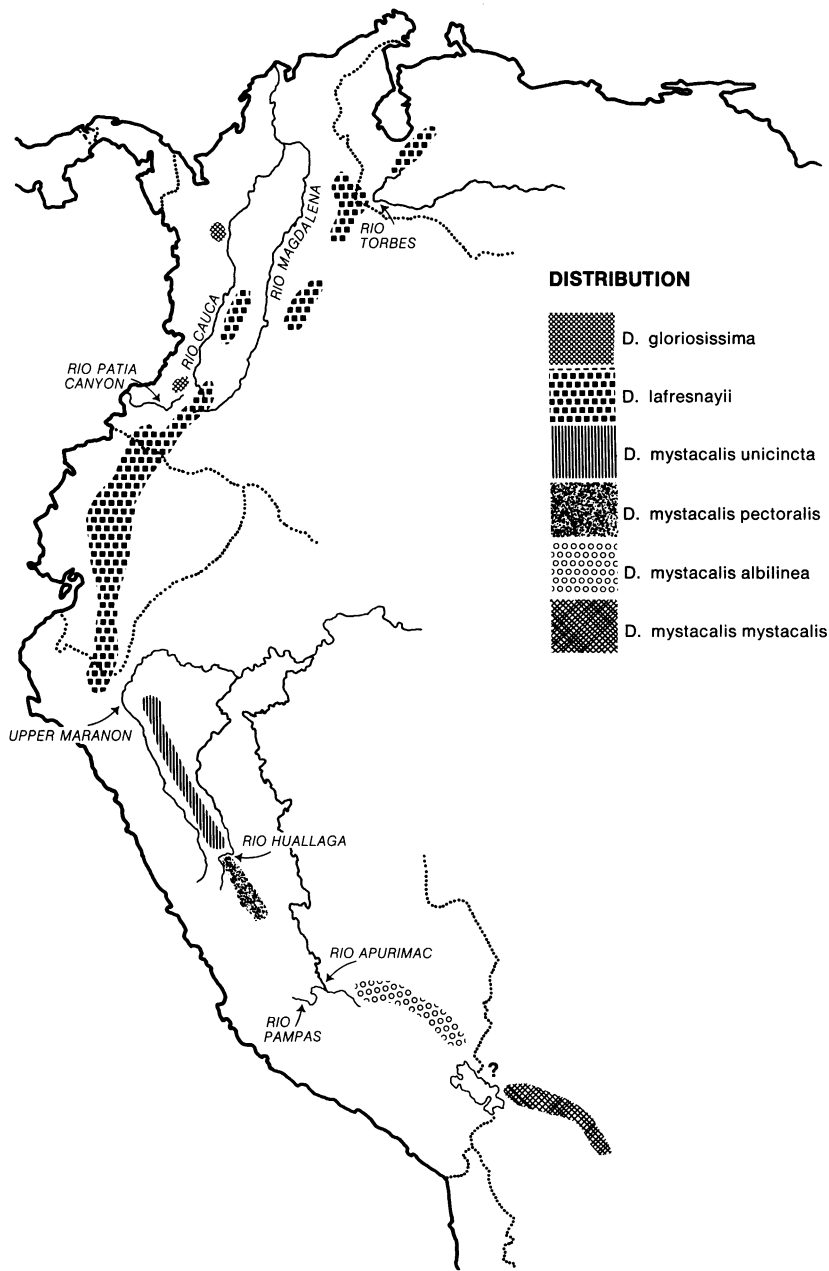


FIG. 3. Distribution of the *lafresnayii* superspecies.

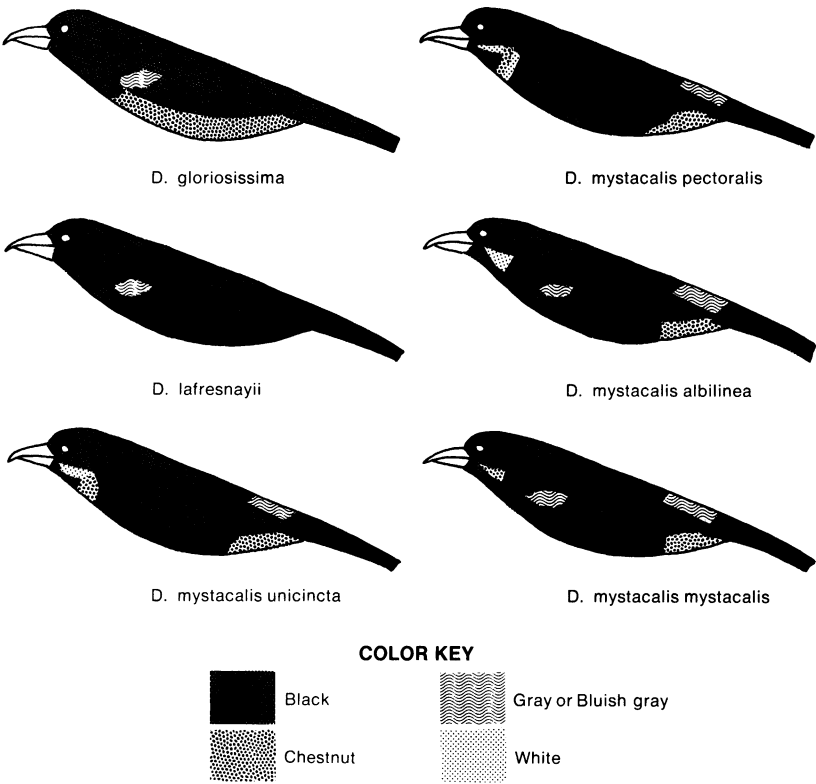


FIG. 4. Geographic variation of the *lafresnayii* superspecies.

Nevertheless, only extensive further collecting at the southern end of the Western Andes of Colombia will establish the precise limits of the ranges of the two forms, and whether or not more extensive hybridization takes place between them. On the ground that their morphological differentiation is analogous to that found in the *carbonaria* superspecies (see discussion below), I tentatively suggest that *gloriosissima* and *lafresnayii* are close to achieving or have only recently achieved reproductive isolation.

Diglossa mystacalis

The birds included in this taxon are black, with a white or buffy mustache, a grayish rump, a rufous crissum, and (in some populations) a bluish gray humeral patch and a brownish or brown and white pectoral band (fig. 4). *Diglossa mystacalis* is found along the eastern slope of the

Andes from northern Peru to western Bolivia (department of Cochabamba). The distribution of *mystacalis* is discontinuous, and its geographical variation is positively correlated with the range disjunctions (figs. 3 and 4).

A brownish pectoral band is seen in birds from northern Peru to north-central Peru near Huánuco north of the Río Huallaga (subspecies *unicincta*). From near Huánuco south of the Río Huallaga to Junín in central Peru, birds have a largely white pectoral band with a brownish anterior margin (subspecies *pectoralis*). When a large series is examined, the color differences in pectoral band just cited do not hold well, however, because within each subspecies there are individuals that fall within the variation of the other. This suggests that the dry basin of the upper Río Huallaga near the city of Huánuco only partially isolates populations living, respectively, north (*unicincta*) and south (*pectoralis*) of it (figs. 3 and 4).

No specimens of *D. mystacalis* have been collected (to my knowledge) between Junín and Cuzco. The gap includes the departments of Huancaavelica, Ayacucho, and Apurímac. The populations from Machu Picchu and Cuzco (subspecies *albilinea*) are rather sharply distinct from both *unicincta* and *pectoralis* because they lack a pectoral band and have a conspicuous bluish gray humeral patch. They resemble most closely the birds from Bolivia (subspecies *mystacalis*), which differ only in having a buffy mustache (fig. 4). The distribution gap between *albilinea* and *mystacalis* seems to correspond not to an ecological barrier, but to the lack of collections in the intermediate areas. It is likely that collecting in the Cordillera of Apolobamba, stretching across the Peruvian-Bolivian boundary, will show birds intermediate between *albilinea* and *mystacalis* ("?" on fig. 3).

In summary, the most obvious discontinuity in geographical variation in *D. mystacalis* is the abrupt transition (as far as now known) from birds with a pectoral band but no humeral patch in central Peru (*pectoralis*) to birds without a pectoral band but with a humeral patch in southern Peru (*albilinea*). The dry valleys of the Río Pampas and the upper Río Apurímac (fig. 3) might present barriers to the dispersal of these birds, but this presumption should be checked in the field.

For the present time, I consider that *unicincta*, *pectoralis*, *albilinea*, and *mystacalis* are best considered as a single species (*D. mystacalis*), with two subspecies-groups (*pectoralis*, with subspecies *unicincta* and *pectoralis*; and *mystacalis*, with subspecies *albilinea* and *mystacalis*). Each subspecies-group is, from the speciation viewpoint, an incipient species.

Diglossa mystacalis occurs only south and east of the arid upper Mar-

añon Basin, whereas *D. lafresnayii* occurs only north and west of it (fig. 3). I do not know of any specimen of either *D. mystacalis* or *D. lafresnayii* from near the area where they come close to each other which indicates hybridization, suggesting that the upper Marañon Basin is an effective barrier to gene flow. Under these circumstances of isolation, it is perhaps just as arbitrary whether one considers *D. mystacalis* and *D. lafresnayii* conspecific or separate species. Because their morphological differentiation is analogous to that seen in the *carbonaria* superspecies (see discussion below), I would consider them semispecies of a superspecies.

SPECIATION IN THE *lafresnayii* SUPERSPECIES

As discussed above, isolated populations have reached various degrees of morphological differentiation (fig. 4) which presumably reflect similar degrees of genetic differentiation. Thus the populations treated as subspecies of *D. mystacalis*, especially the *D. m. pectoralis* and *D. m. mystacalis* subspecies-groups, are not thought to have reached reproductive isolation, whereas this stage in the speciation process appears more nearly (or entirely) complete in the semispecies *D. gloriosissima*, *D. lafresnayii*, and *D. mystacalis*. Isolation positively correlated with morphological differentiation in the *lafresnayii* superspecies is apparently due to dry inter-Andean valleys and basins separating mountain ranges covered with wet montane forest and brushland, habitats favored by members of the *lafresnayii* superspecies.

THE *carbonaria* SUPERSPECIES

The populations of this superspecies live from the Andes of western Venezuela and northern Colombia (Santa Marta Mountains) to Bolivia (south to the department of Chuquisaca; fig. 5). They inhabit brushlands and open woodlands at elevations of 1500 to 3800 meters. There does not seem to be major ecological differences between populations, even between those most morphologically differentiated (personal observation).

The characters indicating close relationships of the taxa of this superspecies have been listed by Zimmer (1929), who believed that all the taxa of this complex should be considered conspecific (*D. carbonaria*). The evidence presented below, however, suggests that species level has been reached in at least two taxa: the black populations of Venezuela, Colombia, Ecuador, and Peru (*D. humeralis*); and the chestnut-bellied birds of Venezuela, Colombia, and Peru, and gray-bellied ones of Bolivia (*D. carbonaria*) (fig. 6).

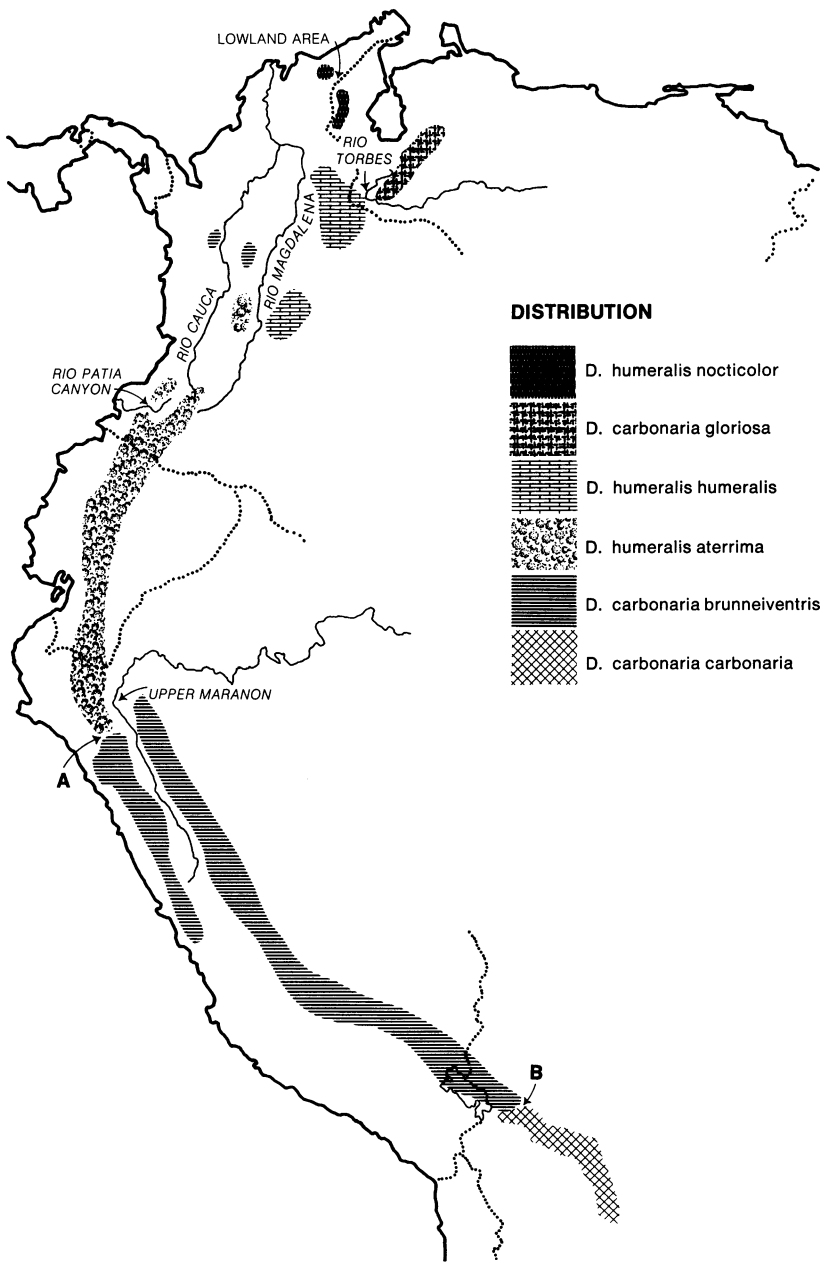


FIG. 5. Distribution of the *carbonaria* superspecies. A, B. Zones of secondary contact (see text).

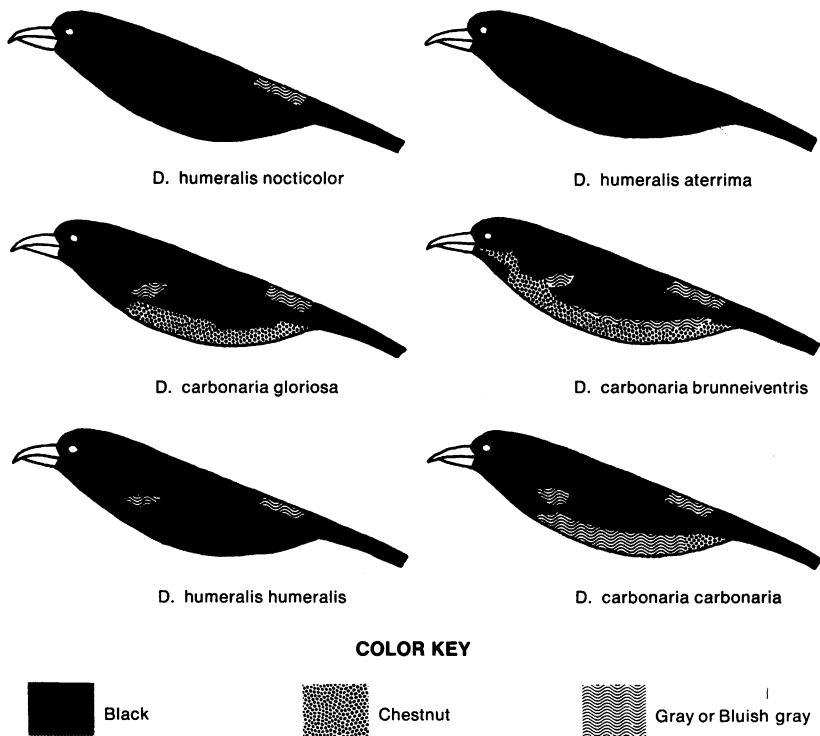


FIG. 6. Geographic variation in the *carbonaria* superspecies.

Diglossa humeralis

This semispecies is made up of discontinuous populations belonging to three subspecies (see figs. 5 and 6): *D. humeralis-nocticolor* (black with a gray rump; Santa Marta and Perijá Mountains), *D. humeralis humeralis* (black with grayish rump and bluish gray humeral patch; extreme western Venezuelan and Eastern Colombian Andes), and *D. humeralis aterrima* (essentially black; southern part of central and Western Andes of Colombia, Ecuador, and northwestern Peru). Range disjunctions occur within each of the above three subspecies, but only the one within *D. humeralis-nocticolor* seems to correspond to a clear-cut geographical barrier, the lowlands separating the Santa Marta Range from the Perijá Mountains (fig. 5).

Zimmer (1929) presented some evidence suggesting that intergradation occurs between the three subspecies, even though they appear isolated geographically. It is noteworthy that the Río Patía Canyon is not a bar-

rier in *D. humeralis*, whereas it acts as such in the *lafresnayii* superspecies. On the other hand, the Río Torbes Valley acts as a barrier between semispecies of the *carbonaria* superspecies, but no comparable differentiation occurs in the *lafresnayii* superspecies (compare figs. 3–4 with figs. 5–6).

Diglossa carbonaria

This semispecies includes birds with a chestnut belly (*gloriosa*), others with an interconnected chestnut belly and mystacial stripe (*brunneiventris*), and still others with a gray belly and no mystacial stripe (*carbonaria*) (fig. 6). The latter two hybridize in the area in which they meet.

Black upper parts, head, and flanks, chestnut belly, gray rump, and bluish gray humeral patch characterize the taxon *gloriosa*. These birds live in the Venezuelan Andes (Trujillo, Mérida, and eastern Tachira), and are isolated from neighboring *D. humeralis* found in the Páramo de Tamá (extension of the Eastern Andes of Colombia into Venezuela) by the valley of the Río Torbes near San Cristobal (fig. 5). This depression seems effective as a barrier. As far as I can determine from specimens examined and from published data, there is no specimen intermediate between *gloriosa* and *humeralis*.

Zimmer (1929, pp. 24–25) and Hellmayr (1935, footnote, p. 228), however, cited several specimens of *gloriosa* that show an “approach” toward the morphologically rather similar, but entirely allopatric *brunneiventris*. This is confirmed by my examination of specimens. This approach consists especially in the presence of chestnut in the mystacial area of some specimens of *gloriosa*, a feature characteristic of *brunneiventris*. These specimens of *gloriosa*, in fact, resemble hybrids between *brunneiventris* and *carbonaria*, to be described in another paper. Even though *gloriosa* and the nearest Colombian population of *brunneiventris* are geographically isolated from each other (and furthermore some of the intervening regions are occupied by *humeralis*), on morphological grounds alone it is difficult not to consider them conspecific (polytopic subspecies; see Mayr, 1963).

Two isolated populations of *brunneiventris* occur at the northern end of the Western and central Andes of Colombia (fig. 5). These birds are almost identical to each other and to birds from much farther south, in Peru (also named *brunneiventris*). Here, even less than in the instance just cited, is there morphological ground for considering all of them anything but conspecific (polytopic subspecies if they had been given different names). Now the two Colombian populations of *brunneiventris* are spatially isolated from the neighboring populations of *D. humeralis* (see fig. 5). I cannot trace any intermediate specimen and would thus con-

clude tentatively that there is no gene exchange between the two taxa.

The situation is different in northwestern Peru. In Cajamarca (letter A on fig. 5) the southernmost populations of *D. humeralis* (subspecies *aterrima*) come in contact with the northwesternmost populations of *brunneiventris*. Specimens of *D. humeralis aterrima* have been collected at Cutervo; and specimens of *brunneiventris*, at Chota, only about 30 kilometers southeast of Cutervo. Furthermore, two specimens of *aterrima* and one of *brunneiventris* were collected after an interval of two days at Chira, near Tambillo (see Bond, 1955, p. 37). These birds do not show evidence of hybridization. The taxa *aterrima* and *brunneiventris* are apparently not separated by an ecological barrier. I would infer that they are reproductively isolated. Nonetheless field work in Cajamarca is desirable to find out whether the two taxa overlap geographically at all, and whether there is really no hybridization. I suspect that the meeting of *aterrima* and *brunneiventris* took place after the latter taxon extended its range from the eastern to the western Peruvian Andes across the upper Marañon Basin. Other groups of birds showing evidence of such east to west dispersal across the Andes of northern Peru include *Cranioleuca antisensis* (Furnariidae), *Scytalopus unicolor* (Rhinocryptidae), and *Cyclarhis gujanensis* (Vireonidae) (Koepcke, 1961, pp. 5-6).

The populations of *brunneiventris* range along the western Andes of Peru southward to about the latitude of Lima, and along the entire length of the eastern Peruvian Andes. Farther south, in the La Paz region of Bolivia (letter B on fig. 5), *brunneiventris* comes in contact with *carbonaria* (black above, gray below, with a chestnut crissum). Several specimens collected near La Paz are intermediate in various characters between *brunneiventris* phenotype and *carbonaria* phenotype (Zimmer, 1929; Niethammer, 1956, pp. 128-129; skins collected personally in 1967-1968). There is clearly gene exchange. The inference is that the two taxa met before they had achieved complete reproductive isolation. Further details of this allopatric hybridization will be given in a separate paper. In anticipation of the results of this study, I tentatively maintain *brunneiventris* and *carbonaria* as conspecific (as did Zimmer, 1929).

SPECIATION IN THE *carbonaria* SUPERSPECIES

The speciation pattern of the *carbonaria* superspecies seems similar to that of the *lafresnayii* superspecies, namely, splitting of an ancestral stock into several isolates separated from one another by dry inter-Andean basins and valleys. As in the *lafresnayii* superspecies, various degrees of morphological differentiation are shown by isolated populations of the *carbonaria* superspecies (Fig. 6). In the latter, however, geographical

TABLE 3
A COMPARISON OF BARRIERS AND THEIR EFFECTS ON POPULATIONS OF THE *lafresnayii* AND *carbonaria* SUPERSPECIES

Barrier	Morphological Differentiation in the Superspecies	
	<i>lafresnayii</i> Superspecies	<i>carbonaria</i> Superspecies
Río Torbes Valley, western Venezuela	None: <i>lafresnayii</i> on both sides of barrier	Marked: barrier separates chestnut-bellied <i>carbonaria gloriosa</i> from black <i>h. humeralis</i>
Magdalena Valley, Colombia	None: <i>lafresnayii</i> on both sides of barrier	Slight: barrier separates gray-shouldered, black <i>h. humeralis</i> from all black <i>humeralis aterritina</i>
Cauca Valley, Colombia	Marked: barrier separates chestnut-bellied <i>gloriosissima</i> from black <i>lafresnayii</i>	Marked: barrier separates chestnut-bellied <i>carbonaria brunneiventris</i> from black <i>humeralis aterritina</i>
Patía Canyon, Colombia	Marked: barrier separates chestnut-bellied <i>gloriosissima</i> from black <i>lafresnayii</i>	None: <i>humeralis aterritina</i> on both sides of barrier
Upper Marañon Valley, northwestern Peru	Marked: barrier separates black <i>lafresnayii</i> from patterned <i>mystacalis</i>	Marked: barrier separates black <i>humeralis aterritina</i> from chestnut-bellied <i>carbonaria brunneiventris</i> (but secondary range extension of latter enables contact)

isolation has broken down in two instances, thus permitting us to correlate morphological differentiation with reproductive isolation.

A comparison of the zones of isolation in the *lafresnayii* and *carbonaria* superspecies shows that the barriers that have affected one are not necessarily the same as those that have played a role in the other (table 3, and compare fig. 3 with fig. 5). These differences are hardly surprising; they illustrate the well-known fact that any two species or superspecies are only rarely alike in their ecological requirements. The situation in Bolivia can be given as a local illustration of this phenomenon. In that country *brunneiventris* (*carbonaria* superspecies) occurs widely in shrubbery far away from the upper montane forest belt, a biotope not visited, as a rule, by *mystacalis* (*lafresnayii* superspecies). On the other hand, *mystacalis* is common in upper montane forests with dense bamboo thickets, areas to which *brunneiventris* ventures rarely (personal observation).

In spite of the differences in isolation potential between the two superspecies, the parallelisms in morphological differentiation of sympatric populations of the two superspecies are so striking that they can hardly be due merely to independent evolution in two different stocks (see table 4 and figs. 4 and 6). These parallelisms were already noticed by Zimmer (1929) and are worthy of further consideration.

SPECIATION PARALLELISM IN THE *lafresnayii* AND *carbonaria* SUPERSPECIES

Table 4 summarizes the morphological resemblances and differences between sympatric populations of the two superspecies. It shows that color resemblance is greatest in populations from the Eastern Andes of Colombia (*D. h. humeralis* and *D. l. lafresnayii*). Table 4 also shows a negative correlation between color resemblance and size difference. For example, in Venezuela, the two sympatric species do not resemble one another in color, but in size they have a wide overlap. In other words, when there is character convergence in color there is character divergence in size, and vice versa. This peculiar situation suggests the possibility that interspecific interactions have played a role in the speciational history of the two superspecies. Is there any evidence that the color pattern and size parallelisms observed between sympatric taxa of the *lafresnayii* and *carbonaria* superspecies are the result of selection pressures favoring convergence rather than divergence?

Moynihan (1963) studied the interspecific relations of four species of the Coerebidae, including the very similar *D. humeralis aterrima* and *D. l. lafresnayii* (see table 4, also figs. 4 and 6) in the Quito region of Ecuador.

TABLE 4
MORPHOLOGICAL DIVERGENCE AND CONVERGENCE IN SYMPATRIC TAXA OF THE *lafresnayii* AND *carbonaria* SUPERSPECIES

Region of Sympatry	Taxon of <i>carbonaria</i> Superspecies	Taxon of <i>lafresnayii</i> Superspecies	Similarities and Differences of Sympatric Taxa Color	Size
Mérida Andes, Venezuela	<i>carbonaria gloriosa</i>	<i>l. lafresnayii</i>	<i>gloriosa</i> rufous-bellied, <i>lafresnayii</i> black (most different)	Broad overlap in dimensions (very similar)
Eastern Andes, Colombia	<i>h. humeralis</i>	<i>l. lafresnayii</i>	Both black with gray humeral patch (most similar)	Slight overlap in dimensions (very different)
Andes of Ecuador	<i>humeralis aterrima</i>	<i>l. lafresnayii</i>	<i>aterrima</i> black, <i>lafresnayii</i> black with gray humeral patch (very similar)	Almost no overlap in dimensions (most different)
Eastern Andes, Peru	<i>carbonaria bruneiventris</i>	<i>mystacalis pectoralis</i>	<i>bruneiventris</i> entirely rufous-bellied, <i>pectoralis</i> partly rufous-bellied (more or less similar)	Broad overlap in dimensions (very similar)

He suggested that these four species have developed specialized avoidance mechanisms which "seem to be adaptations (or the indirect result of adaptations) to keep individuals of different species at least a few feet apart, at any given moment, by some method other than actual fighting or more active expression of hostility" (p. 336). By contrast, intraspecific aggressiveness, he reported, was very strong. Such avoidance behavior between members of the *lafresnayii* and *carbonaria* superspecies was said to be the rule "in most areas of sympatry" (Moynihan, 1968, p. 318).

In two other Andean areas, however, Moynihan (1968, pp. 318-319) noted overt fighting between members of the two superspecies: (a) in the Eastern Andes of Colombia between *D. h. humeralis* and *D. l. lafresnayii* (most similar in color, see table 4 and figs. 4 and 6), and (b) in the Andes of north-central Peru between *D. carbonaria brunneiventris* and *D. mystacalis pectoralis* (more or less similar in color, see table 4 and figs. 4 and 6, but very similar in song according to Moynihan, *loc. cit.*).

Moynihan (1968) believed that both the avoidance behavior and the fighting behavior can be understood as part of behavioral interactions which are correlated with varying degrees of morphological resemblance and which he included under the term of social mimicry.

If such were true, the evolution of similar plumage patterns in the *lafresnayii* and *carbonaria* superspecies in parts of the Andes where they are sympatric could be due to selection pressures arising mainly out of the advantages for sympatric forms to associate when foraging.

The morphological parallelism found in *Diglossa* is reminiscent of the cases described in babblers of the genus *Garrulax* (Ticehurst in Stanford, 1938, cited by Mayr, 1942) and in African bush-shrikes of the genus *Malaconotus* (Hall, Moreau, and Galbraith, 1966).

Diglossa duidae

This species, the only one of the genus in the western part of the Venezuelan highlands, shows only a small amount of geographical variation in the intensity of bluish gray in the scapular region, and in the amount of black coloration in the facial area. The two subspecies described are therefore not well differentiated. They are *duidae* from Cerros de la Neblina, Duida, Huachamacari, and Paru; and *hitchcocki* from Cerros Yavi, Guanay, and Paraque (Phelps and Phelps, 1963). A third subspecies, *parui*, was described by Phelps and Phelps, 1950, but later merged by them with *duidae*.

Chapman (1929, p. 26) first believed *D. duidae* to be related to *D.*

humeralis of the *carbonaria* superspecies; then (1931, p. 124), following a suggestion of Hellmayr, thought its nearest relative to be *D. major*. Nevertheless, the morphological distinctness of *D. duidae* induced Chapman (*loc. cit.*) to remark that *D. duidae* and *D. major* "are too unlike to be considered as even representative forms." (See also Chapman, 1939, p. 12.) In more modern terms, Chapman's opinion was that *duidae* and *major* are closer taxonomically to each other than to other species of the genus, but that they should not be treated as members of the same superspecies.

It seems to me that color, pattern, and proportions indicate that *D. duidae* is not a relative of *D. major*, but, rather, of either the *lafresnayii* or the *carbonaria* superspecies (*lafresnayii* species-group), but I believe *D. duidae* is too distinct morphologically to allow any speculation about whether it is closer to the *lafresnayii* or to the *carbonaria* superspecies.

As with *D. major*, discussed above, the differentiation of *duidae* as a species and its lack of marked subspeciation might indicate that proto-*duidae* invaded the south Venezuelan highlands from the Andes in the recent past, and that once there it has enjoyed relaxed selective pressures favoring the maintenance of a rather generalized plumage.

4. THE *albilatera* SPECIES-GROUP THE *albilatera* SUPERSPECIES

Diglossa albilatera extends from the coastal range of Venezuela and the Perijá Mountains to Colombia (including Santa Marta), Ecuador, and Peru (along the eastern Andes to the department of Huánuco). It exhibits only slight geographic variation in color and in size, which appears to be of a checkerboard nature. In the Santa Marta Mountains, *albilatera* lives "in shrubbery, isolated trees, or along the edge of the forest" (Todd and Carriker, 1922, p. 465). *Diglossa venezuelensis* is found only in the mountains of extreme northeastern Venezuela and does not vary geographically.

The two species resemble each other in having marked sexual dimorphism, white axillary feathers, and similar proportions. They differ in details of coloration and absolute size. These differences indicate that species level has probably been reached (the level termed allo-species by Amadon, 1966).

Diglossa venezuelensis is clearly a differentiated peripheral isolate of proto-*albilatera* stock. One could postulate that the ancestral species extended formerly over the mountains of northern Venezuela, including the Turumiquire region, and that isolation was initiated, or reinforced, by the Pleistocene increase of aridity in northern South America which

broadened the unsuitable belt of dry vegetation between the coastal range and the Turumiquire Range. An alternative possibility is colonization across the gap and rapid genetic reorganization in the founder population.

THE *baritula* SUPERSPECIES

This superspecies includes three allopatric taxa. *Diglossa baritula* has disjunct populations on mountain ranges in southern Mexico, Guatemala, and Honduras. Geographic variation in both color and size is minor. The habitat was described by Skutch (1954, p. 421).

Diglossa plumbea has two disjunct populations on mountains in Costa Rica and western Panama. Skutch (1954, p. 431) and Slud (1964, p. 314) described the habitat. The males of *plumbea* differ from *baritula* by their gray instead of ruddy belly. Hellmayr (1935, footnote, p. 221) mentioned that Guatemalan specimens of *baritula* have more gray on the throat, thus marking "a decided step in the direction of the Costa Rican" specimens of *plumbea*. I have not noticed this tendency in the specimens that I examined, yet I agree with Hellmayr that *baritula* and *plumbea* are closely related.

Diglossa sittoides is the most widespread species of the genus. It occurs from northern Colombia and extreme northeastern Venezuela (Cerro Turumiquire) along the Andes to northwestern Argentina. Interestingly, *D. sittoides* is absent from the western slope of the Western Andes of Colombia, perhaps because of the extreme wetness of the area. At San Antonio, near the crest of the Western Andes, but on the eastern, drier, slope, Miller (1963, p. 55) noted that "this species was scarce." Birds were seen "in the forest edge and large bushes in pastures, always about flowers or fruiting trees." Geographic variation in *D. sittoides* is slight and appears to me entirely or almost completely gradual. Like *baritula*, *sittoides* is gray above and ruddy below, but it lacks gray on the throat.

The three members of the *baritula* superspecies have been considered conspecific by some ornithologists (Hellmayr, 1935; Zimmer, 1942), or as distinct species by others (Eisenmann, 1955; Blake, 1958). In the absence of range overlap or contact of any sort between them, the question cannot be answered objectively, and I believe it is best to consider the three nomenclaturally as species, but evolutionarily as semispecies of a single superspecies. Morphological differentiation in the *baritula* superspecies is approximately similar to that of the *carbonaria* superspecies, in which reproductive isolation has been reached

in at least one case but not in a second. The *baritula* superspecies represents a straightforward case of speciation by isolation of populations on mountaintops. The barriers seem to have been and to be areas of lowland forest, provided that the gap is broad enough. For example, the rather narrow lowland area of Tehuantepec does not seem to constitute a barrier within the semispecies *baritula*.

DISCUSSION

SYMPATRY AND OLDER SPECIATION PATTERNS

The genus *Diglossa* is composed of six distinct species (*caerulescens*, *cyanea*, *glauca*, *indigotica*, *major*, and *duidae*), plus four more superspecies (*lafresnayii* and *carbonaria*, with three semispecies each; *baritula* and *albilatera*, with two). If the superspecies are treated as species for purposes of analysis, it is obvious that sympatry in *Diglossa* is quite extensive.

In the northern Andes (Colombia, Ecuador, and Peru), as many as three of the good species and members of all four superspecies occur sympatrically. Some of the sympatric species and superspecies even live in habitat co-occupancy (*sensu* Hamilton, 1962; Moynihan, 1963; and personal field data). The number of sympatric taxa decreases only in marginal areas of the Andes and in the most peripheral areas of the range of the genus (fig. 2).

The extensive sympatry provides no clues about possible early patterns of species formation in *Diglossa*. It does suggest, however, that this genus has been present in montane forests and brushlands of tropical America, especially along the Andes, for some time, but there is no evidence as to how long. The pattern of distribution of sympatric species in the Andes from Colombia to Peru might be interpreted as evidence that *Diglossa* originated there. Taken at face value, the genus would seem to be Andean, but an earlier extra-Andean or Central American origin cannot, of course, be categorically ruled out. There is no doubt that the Andes have constituted a center of speciation and radiation, even if they are not a center of origin. Speciation phenomena in *Diglossa* today show that there is now opportunity for isolation and species formation in the Andes and suggest ways in which new species are being formed.

Before present speciation patterns are discussed, it should be noted that the extensive sympatry of *Diglossa* spp. in the Andes and the consequent difficulty of detecting early speciation patterns recall the situation described by Moreau (1966, p. 220) for the genus *Nectarinia* (sunbirds, nectar eaters) on East African mountains.

PRESENTLY ACTIVE SPECIATION

Diglossa is one of the most actively speciating genera of Andean birds, being equaled or surpassed by only few others (e.g., *Phrygilus* [emberizine finches] and *Asthenes* [spinetails] among the genera I have personally studied). The following stages of the speciation process can be found in *Diglossa* (table 5): species and semispecies with no geographical variation; species with only slight, mostly gradual, geographical variation; species with discontinuous geographical variation and one or more slightly differentiated isolates; allopatric and isolated taxa at the borderline between species and subspecies, zones of secondary contact, with and without hybridization; and fully formed, broadly sympatric species. What are not found in *Diglossa* are superspecies or species-groups in which two or more members of the group show only slight secondary range overlaps. There is thus no transitional stage between fully allopatric, morphologically differentiated semispecies and extensively sympatric good species.

Evolutionists (cf. Mayr, 1963) have emphasized that a key aspect of speciation and potential speciation is the presence of geographical isolates, because the isolate, being freed from gene flow and swamping, will diverge increasingly from its parental population under its different selection pressures. Of course not all isolates become species, but the presence of a sufficiently large number of isolates contributes to the probability of further speciation in any given group.

The numerous isolates found in *Diglossa* are both well and poorly differentiated morphologically. (Genetic divergence is not necessarily parallel to morphological differentiation, but in *Diglossa* there is little else to rely on.) Some kind of discontinuous geographical variation associated with a distribution gap is found in every species of *Diglossa*, except *indigotica*, which has a relatively restricted range. (Here also superspecies are treated as species for the purposes of the analysis of isolates.)

Almost every mountaintop population of *D. major* and *D. duidae*, which occur on isolated south Venezuelan mountains, could be considered an isolate geographically, but the minimal amount of variation in these two species suggests that there is still enough gene flow to prevent or retard speciation. In contrast, *D. caerulea*, *D. glauca*, and *D. cyanea*, which occur along the Andean cordillera, show weakly discontinuous geographical variation that seems positively correlated with actual range discontinuities (gaps).

The process of isolate formation is clearest, however, in the *lafresnayii*,

TABLE 5
STAGES OF THE SPECIATION PROCESS IN *Diglossa*

Species and Semispecies	Geographical Variation			Discontinuous (Isolates Slightly Differentiated)	Member of a Superspecies	Secondary Hybridization	Closest Relative Broadly Sympatric
	Absent	Gradual					
<i>D. caerulescens</i>	—	—		+	—	—	+
<i>D. cyanea</i>	—	—		+	—	—	+
<i>D. glauca</i>	—	—		+	—	—	—
<i>D. indigotica</i>	+	—		—	—	—	—
<i>D. major</i>	—	—		+	—	—	—
<i>D. gloriosissima</i>	+	—		—	+	—	—
<i>D. lafresnayii</i>	—	+	(?)	—	+	—	—
<i>D. mystacalis</i>	—	—		+	+	—	—
<i>D. humeralis</i>	—	—		+	+	—	—
<i>D. carbonaria</i>	—	—		+	+	+	—
<i>D. duidae</i>	—	—		+	—	—	—
<i>D. albilatera</i>	—	+	(?)	—	+	—	—
<i>D. venezuelensis</i>	+	—		—	+	—	—
<i>D. barthula</i>	—	—		+	+	—	—
<i>D. plumbea</i>	—	—		+	+	—	—
<i>D. sitioides</i>	—	+		—	+	—	—

carbonaria, *albilatera*, and *baritula* superspecies. In these four groups one finds isolates both little differentiated and well differentiated morphologically. The following distributional gaps, listed from north to south, separate isolates that have reached, or are close to reaching, species level.

1. The Nicaraguan lowlands separate the semispecies *baritula* and *plumbea* of the *baritula* superspecies. It should be noted, however, that *Diglossa* is absent from the Cordilleras of Guanacaste and Tilaran in Costa Rica (Slud, 1964, p. 314).

2. The lowlands of central and eastern Panama and northwestern Colombia keep apart the semispecies *plumbea* and *sittoides* of the *baritula* superspecies. No *Diglossa* is known from the highlands of eastern Panama (Darien), and de Schauensee (1966, p. 456) did not list the superspecies from the western slope of the Western Andes of Colombia.

3. The depression between the Turumiquire Range and the Coastal Range in Miranda, northern Venezuela, separates the semispecies *venezuelensis* and *albilatera* in the *albilatera* superspecies.

4. The valley of the Río Torbes near San Cristobal, cutting the Andes of western Venezuela from the eastern spur of the Eastern Andes of Colombia into Venezuela (Páramo de Tamá), isolates the semispecies *D. carbonaria gloriosa* from *D. humeralis* of the *carbonaria* superspecies (fig. 5).

5. The depression of the upper Río Cauca and upper Río Patía valleys and Patía Canyon in southwestern Colombia separates the semispecies *gloriosissima* and *lafresnayii* of the *lafresnayii* superspecies (fig. 3).

6. The valley of the upper Río Marañón in northern Peru provides a barrier between the semispecies *lafresnayii* and *mystacalis* of the *lafresnayii* superspecies (fig. 3). It probably also provided a barrier between the semispecies *humeralis* and *brunneiventris* of the *carbonaria* superspecies prior to the crossing of the gap by the latter taxon (fig. 5).

7. The valleys of the upper Río Apurimac and Río Pampas in south-central Peru divide the *pectoralis* subspecies-group and the *mystacalis* subspecies-group of the *lafresnayii* superspecies (fig. 3).

With the exceptions of the Nicaraguan and Panamanian-Colombian lowlands (gaps 1 and 2) the gaps listed above are dry to arid regions of low or medium altitude, interposed between the mountain ranges covered by the wet montane forest and scrub favored by *Diglossa*.

Species of *Diglossa* are usually active, restless birds, which move about a great deal (often in flocks with other birds). One may assume that their dispersal faculties are relatively good, or at least better than those of birds living a more sedentary existence. Under these circumstances, the width of the barrier is probably more important in pre-

venting dispersal than the ecological severity of the barrier *per se*. Successful colonization across a broad gap should be a rather rare event, but the chances of survival of a founder population should be relatively good, because of the low probability of a second invasion and subsequent swamping. The taxa of *Diglossa* isolated by barriers 1 through 5 above might well have originated as peripheral founder populations. The semispecies *baritula* and *plumbea* occupy relatively small ranges at the periphery of the *baritula* superspecies. The semispecies *venezuelensis* occupies a very small range, peripheral to that of the *albilatera* superspecies. The semispecies *gloriosa* has a small, peripheral range in the distribution of the *carbonaria* superspecies. Finally, the semispecies *gloriosissima* again is a peripheral isolate within the *lafresnayii* superspecies. The remaining taxa, isolated by barriers 6 and 7, cannot be considered either peripheral or small-ranging at the same time, although the *mystacalis* sub-species-group of the *lafresnayii* superspecies has a peripheral range.

Although all the semispecies listed above as being affected by barriers 1 through 7 are fully allopatric, we can infer that they either have just achieved or are close to achieving reproductive isolation by analogy with the secondary contacts described earlier in the *carbonaria* superspecies. It seems reasonable, therefore, to assume that the morphological differentiation (and presumably underlying genetic differentiation) in these semispecies was initiated relatively recently, perhaps during the Pleistocene.

Evidence is accumulating to document events of glacial episodes in the mountains of Central America (see, e.g., Weyl, 1956) and in the Andes of South America (e.g., Wilhelmy, 1957). From the point of view of speciation, the most relevant considerations are that during periods of glacial maximum the climate in the Andes was generally wetter than during interglacials, and the temperature gradient on mountain slopes was depressed. It follows that the vegetation belts, especially the upper ones, were lowered during glacials and raised during interglacials (see, e.g., van der Hammen and Gonzalez, 1960). These vertical fluctuations would have permitted the upper montane forests and the brushlands of timberline (habitats of *Diglossa*) to form a much more continuous band along the mountains of Central America and the Andes during glacial episodes than during interglacials. In other words, the barriers (1 through 7) that prevent or retard gene flow today, a period climatically rather comparable with that of an interglacial, would have been much narrower during glacials so that dispersal across them would have been easier. In *Diglossa*, as we have seen, the formation of new species might take place mostly through the successful establish-

ment of founder populations in peripheral areas. The subsequent geographical isolation of these peripheral populations is essential for the speciation process to continue. I submit that in the *lafresnayii*, *carbonaria*, *albilatera*, and *baritula* superspecies founder populations could reach peripheral areas of the range of the formerly existing species (proto-*lafresnayii* superspecies, proto-*carbonaria* superspecies, and others) during a glacial period, when suitable habitat was both at lower elevations and in broader stretches along the Andes. These peripheral populations would become isolated (first geographically, and later genetically) only during an interglacial, after the habitat continuity or near-continuity would have become much disrupted at barriers (for example, 1 through 7 listed above), as a result of an increase in the altitude of the suitable habitats.

A full discussion of the correlation of speciation phenomena with Pleistocene glacial events in the Andes will be postponed to a forthcoming comprehensive paper, taking into account all the avian genera (including *Diglossa*) that I have analyzed in this regard.

SUMMARY

Diglossa, a genus of nine-primaried oscines that feed on nectar, can be diagnosed from more or less related genera of the families Coerebidae and Thraupidae by its peculiar, compressed, and characteristically hooked bill. It occurs on the mountains of Central and South America, except those of southeastern Brazil. Adaptations to nectar-feeding in *Diglossa* include a U-shaped tongue, a hooked bill, serrations along the anterior edge of the upper mandibular tomia (in some species), regurgitation behavior, an esophageal sac in nestlings, and strong interspecific aggressiveness. *Diglossa* might be a tanager derivative, but the evidence in favor of such relationship is not conclusive, and more work remains to be done before the relationships of the genus are ascertained.

Diglossa consists of six unequivocal species and an additional 10 taxa on the borderline between species and subspecies. The taxonomic solution adopted in this paper is to treat these 10 taxa nomenclaturally as species, but to point out their evolutionary interest by considering them as semispecies, members of superspecies. The six species and four superspecies of *Diglossa* are arranged in four species-groups, which can be diagnosed by a combination of morphological characters.

The *caerulescens* species-group comprises four species: *D. caerulescens*, *D. cyanea*, *D. glauca*, and *D. indigotica*. The *major* species-group contains a single species, the morphologically very distinct *D. major* from the south Venezuelan highlands. The *lafresnayii* species-group contains two

superspecies, the *lafresnayii* and *carbonaria* superspecies, and the isolated species *D. duidae*, from the Venezuelan highlands. The *albilatera* species-group includes the *albilatera* and *baritula* superspecies.

An analysis of geographical variation, species limits, and interspecific relationships in *Diglossa* revealed active species formation in the *lafresnayii* and *albilatera* species-groups. The four superspecies included in these two groups total 10 component semispecies, each of which can be considered as (at least) an incipient species. Secondary contacts have taken place in two instances, both in the *carbonaria* superspecies of the *lafresnayii* species-group. In only one of these contacts, in northwestern Peru, is there a suggestion that differentiation in color pattern is positively correlated with reproductive isolation. In the other case, in Bolivia, the two differentiated populations hybridize in the zone of contact.

In three superspecies (*lafresnayii*, *carbonaria*, and *baritula*) the pattern of color differentiation and geographical isolation present intriguing similarities. The parallelisms are most remarkable in the *lafresnayii* and *carbonaria* superspecies and include the distribution of the superspecies as a whole, some of the barriers that have permitted morphological differentiation of isolates, and especially color and pattern exhibited by members of the two superspecies when sympatric. Thus black members of the *lafresnayii* superspecies occur with black members of the *carbonaria* superspecies and mustached birds of one are sympatric with mustached birds of the other.

These parallelisms appear to be the result of complex social interactions between members of the two superspecies in areas of sympatry, whereby selection has favored morphological convergence rather than divergence (social mimicry).

Extensive sympatry between species within each species-group, permitting up to seven species and semispecies to be sympatric in the northern Andes, suggests that *Diglossa* has been present there for some time and that repeated opportunities for speciation have existed in the past. Although it is difficult to draw inferences about early speciation patterns, present speciation trends suggest that *Diglossa* is in an evolutionarily active phase and that its adaptive radiation is by no means ended.

Most of the geographical isolates that have the earmarks of incipient species in *Diglossa* are peripheral in distribution and occur over relatively small areas. It seems thus likely that the establishment of founder populations is an important mode of species multiplication in this genus. The barriers separating differentiated isolates are usually dry intermontane valleys (more rarely wet lowlands) providing clear-cut

interruptions in the distribution of upper montane forests and brushlands, in which *Diglossa* lives. The temperature depression accompanying Pleistocene glacials would have brought closer together montane types of vegetation, thus narrowing the width of these barriers and favoring dispersal across them.

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