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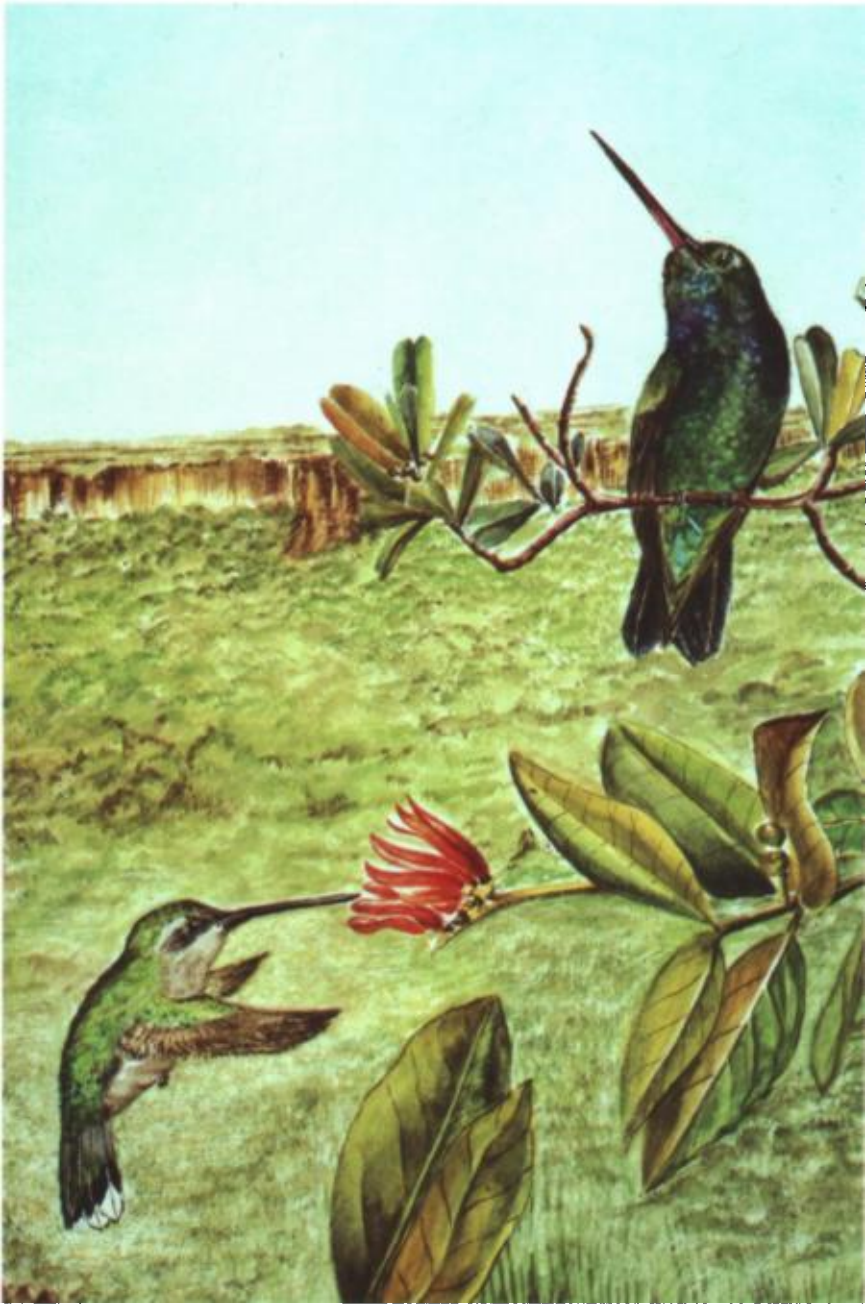
A NEW SPECIES OF EMERALD HUMMINGBIRD (TROCHILIDAE, *CHLOROSTILBON*) FROM THE SIERRA DE CHIRIBIQUETE, SOUTHEASTERN COLOMBIA, WITH A REVIEW OF THE *C. MELLISUGUS* COMPLEX

F. GARY STILES¹

ABSTRACT.—The Chiribiquete Emerald (*Chlorostilbon olivaresi* sp. nov.) is described from the Sierra de Chiribiquete, an isolated range of table-top mountains rising from the flat Amazonian lowlands of the Departments of Guaviare and Caquetá, SE Colombia. This hummingbird is a common inhabitant of the edaphic scrub and adjacent forests of the middle and upper levels of the Sierra, but evidently does not occur in the surrounding lowlands. In its morphology, the new species shows closer affinities with *C. gibsoni* of the Magdalena Valley than with the adjacent cis-Andean populations of *C. mellisugus*, but it is much larger than all related forms. The Chiribiquete Emerald probably originated through the dispersal of *gibsoni*-type birds to the Sierra during a dry period of the Pliocene or early Pleistocene, perhaps in conjunction with hybridization with the local form of *mellisugus*; large body size probably evolved subsequently in the population as a response to its peculiar, insular habitat. Variation in the *Chlorostilbon mellisugus* complex in NW South America is described and analyzed, and I conclude that the various forms are best treated as comprising a single superspecies; *melanorhynchus* (including *pumilus*) of western Colombia and western Ecuador is sufficiently distinct from the adjacent *assimilis* and *gibsoni*, as well as from the eastern forms of *C. mellisugus* to deserve (allo)species rank, and I suggest for it the English name of West Andean Emerald. I recommend recognition of the following allospecies (from north to south): *auriceps*, *forficatus*, *canivetii*, *assimilis*, *melanorhynchus*, *gibsoni*, *olivaresi*, and *mellisugus*. Received 16 Feb. 1995, accepted 10 June 1995.

ABSTRACTO.—Se describe *Chlorostilbon olivaresi* sp. nov. de la Sierra de Chiribiquete, una serie aislada de mesetas en la planicie amazónica de los Departamentos del Guaviare y del Caquetá, SE Colombia. Este colibrí es común en las sabanas casmófitas y los bosques aledaños de la parte media y superior de la Sierra, pero evidentemente no ocurre en los bosques basales circundantes. Por sus caracteres morfológicos, *C. olivaresi* probablemente tiene más afinidad con *C. gibsoni* del Valle del Magdalena, que con las formas cisandinas

¹ Instituto de Ciencias Naturales, Universidad Nacional de Colombia, Apartado 7495, Bogotá, Colombia.



Frontispiece. The Chiribiquete Emerald, *Chlorostilbon olivaresi*. Male (above right) perched on branch of *Tepuianthus savannarum*; female (below left) feeding from flowers of *Decagonocarpus cornutum*, on a mesa of the Sierra de Chiribiquete, southeastern Colombia.

vecinas de *C. mellisugus*, pero es un ave mucho más grande que cualquier forma de estas especies. La población de *C. olivaresi* posiblemente originó a través de la dispersión de un(os) individuo(s) del tipo *gibsoni* a la Sierra durante un período seco del Plioceno o Pleistoceno temprano, tal vez incluyendo hibridización con la forma local de *mellisugus*; subsecuentemente, el tamaño corporal grande evolucionó en esta población en respuesta a su hábitat peculiar y aislado. Se describen y se analizan los patrones de variación en el complejo de *Chlorostilbon mellisugus* en el NO de Suramérica, y se concluye que *melanorhynchus* (incluyendo a *pumilus*) del O de Colombia y Ecuador es suficientemente distinta de *gibsoni* y *assimilis*, las formas adyacentes, como para ser considerado como una (alo)especie. Recomiendo que el complejo de *C. mellisugus* se considere como una sola superespecie, constituida por las aloespecies (de norte a sur) *auriceps*, *forficatus*, *canivetii*, *assimilis*, *melanorhynchus*, *olivaresi*, y *mellisugus*.

The small hummingbirds of the genus *Chlorostilbon* are widespread in the Neotropics from central México to northern Argentina and the West Indies. The genus is quite uniform in coloration: males of all species have flashing green underparts, while females are pale gray below, nearly always with a distinctive facial pattern and dusky malar auricular area bordered above by a white postocular stripe. Several species are easily distinguished by the distinctive form and color of the rectrices of the males (e.g., *poortmanni*, *alice*, *stenura*), very bronzy or coppery coloration (*rusatus*), or extensively red bills (*aureoventris*). However, a number of mostly or entirely allopatric forms in which the males have blue, more or less forked tails, have long been a source of taxonomic confusion. These forms, which collectively might be called the “*mellisugus* complex”, cover most of the range of the genus from México to Bolivia and eastern Brazil. Variation among them involves bill color and, in males, the presence or absence of a glittering crown, the depth of the tail fork, the shape of the outer rectrices, and the color of the underparts and, in females, the shape of the rectrices and the amount of gray in the outer rectrices (cf Zimmer 1950). Geographic variation in these characters presents something of a mosaic pattern, with similar forms often separated by others of rather different appearance, making the determination of species limits controversial. The discovery of a new form in the *C. mellisugus* complex, here described as a new (allo)species, makes it desirable to review the patterns of geographic variation in this complex in northwestern South America, and to reevaluate the relationships among the various members of the complex as a whole in the light of recent studies.

The avifauna of Colombia has received at least as much attention from ornithologists, both native and foreign, as has that of any large South American country. The birds of Colombia have been comprehensively monographed no less than three times (Chapman 1917, Meyer de Schauensee 1948–1952, Hilty and Brown 1986). Nevertheless, many parts of Colombia

have been visited only briefly or sporadically by ornithologists, and a number of areas remain ornithologically unexplored. Until very recently, one such area was the Sierra de Chiribiquete, a small, isolated mountain range in the Departments of Guaviare and Caquetá. Because of its topographic uniqueness and pristine character, this area had been set aside as the Parque Nacional Natural Chiribiquete in September 1989, but aside from a visit by botanist Richard E. Schultes in 1943–1944, the Sierra remained biologically unexplored until the present decade. The only previous ornithological collections from this entire region of Colombia were made by H. Romero for the Instituto de Ciencias Naturales of the Universidad Nacional de Colombia at Aracuaara, over 100 km S of the Sierra de Chiribiquete on the Río Caquetá, in August–September 1977.

Between December 1990 and December 1992, three expeditions to the Sierra de Chiribiquete were organized by the Agencia Española de Cooperación Internacional, the Instituto de Ciencias Naturales, and the Instituto de Recursos Naturales Renovables (INDERENA) of the Colombian government. The first two expeditions, in December 1990 and August 1991, were devoted to botanical, archaeological, and geological studies. During the first expedition, the Colombian botanists P. Palacios and P. Franco obtained a specimen of an unusual hummingbird (the only bird specimen taken) that I was unable to identify: it appeared to be the male of an undescribed form of *Chlorostilbon*, notable for its very large size, but its rather rough preparation made precise comparisons with other material difficult.

I obtained additional material of this hummingbird during the third expedition (18 November–2 December 1992). With J. L. Tellería and M. Díaz of the Universidad Complutense of Madrid, I observed and collected birds in the vicinity of the expedition's base camp in the northern part of the Sierra at 0°56'N, 72°42'W at the site called "el Valle de los Menhires" (Valley of the Monoliths) by Estrada and Fuertes (1993). Seven specimens (3 males, 4 females) of the *Chlorostilbon* were collected and eight others measured and released; all specimens are housed in the collection of the Instituto de Ciencias Naturales. On the basis of this sample, I here describe this hummingbird as

Chlorostilbon olivaresi, sp. nov.

CHIRIBIQUETE EMERALD

HOLOTYPE.—Adult male, no. 31266 of the ornithological collection of the Instituto de Ciencias Naturales (original number FGS 2941), collected on 24 November 1992 in the Valle de los Menhires, elev. 570m, Sierra de Chiribiquete, Depto. del Caqueta, Colombia (0°56'N, 72°42'W) by F. G. Stiles, J. L. Tellería, and M. Díaz.

PARATYPES.—One adult male (ICN 31252, orig. no. FGS 2927) and one sub-adult male (ICN 31253, orig. no. FGS 2928) taken on 21 Nov. 1992 and three adult females (ICN

31244, 31245, and 31254, orig. nos. FGS 2915, 2916, 2929) and one subadult female (ICN 31243, orig. no. FGS 2914), taken on 19 and 24 Nov. 1992, all at the type locality.

DIAGNOSIS.—Clearly a member of the genus *Chlorostilbon* because of the entirely steel-blue, forked tail of the males, and the distinct dusky face and cheeks and white post-ocular stripe and uniform gray underparts of the females. Size significantly larger than any other South American form of *Chlorostilbon* (exposed culmen always >18 mm, vs 17 mm or less in all other forms); total culmen >21 mm vs <19.5 mm; wing chord >48 mm in males, >47 mm in females, vs <47.5 mm and <46.5 mm respectively, except for the isolated *C. mellisugus duidae*, which may reach 49.5 mm in both sexes; and weight usually >3.5 g, vs <3 g). Differs from all forms of *C. mellisugus* in having the basal half of the mandible red in males, or with a trace of red in females; in the dull, non-iridescent crown (males) and extensively grey bases of the lateral rectrices (females). In these characters resembles *C. gibsoni* from north and west of the Andes, but differs from all forms of *gibsoni* in having the tail much more shallowly forked, with the lateral rectrices more truncate (males) to rounded (females) at the tip, and the breast and throat much more strongly bluish in color (males). In the latter feature is most like *C. aureoventris* of southeastern South America, but always lacks red on the upper mandible (which is extensively red in the latter); females of *aureoventris* also lack gray on the lateral rectrices.

ETYMOLOGY.—I take pleasure in naming this species for Fr. Antonio Olivares in honor of his many pioneering contributions to Colombian ornithology and his indefatigable labor in building the bird collection of the Instituto de Ciencias Naturales. The English name refers to the isolated mountain range which includes the type locality and evidently encompasses the entire distribution of the species.

DESCRIPTION OF HOLOTYPE.—(Color nomenclature follows Smithe 1975, 1981). Crown, nape, back, and rump metallic green, near 162, Shamrock Green; a few feathers of the nasal area of the anterior forehead more brilliant golden green (near 158, Chartreuse); a small grayish-white postocular spot. Upper tail-coverts more bluish green (163, Emerald green); tail dark steely blue, nearest 90, Blue-black. Facial area and sides of neck brilliant Emerald Green, with Chartreuse reflections, passing abruptly to brilliant blue-green (between 164, Cyan, and 65, Turquoise Blue, depending on viewing angle) over the entire throat and upper breast, this passing to brilliant green (near 62, Spectrum Green) on the lower breast and belly; lower tail coverts more bluish, near Emerald Green; a small tuft of downy white feathers on the thigh. Remiges blackish with faint bluish gloss (near 73, Indigo). Basal 3/4 or more of lower mandible red (between 13, Geranium Pink, and 10, Ruby); rest of bill, legs, and feet black. Exposed culmen 19.5 mm, total culmen 21.8 mm, wing chord 49.6 mm, tail length 25.6 mm, tarsus 4.4 mm, weight 3.4 g. Adult male, left testis 2.4 × 2.3 mm, no fat; tiny diptera in stomach.

DESCRIPTION OF ADULT FEMALE (based on ICN 31244).—Upperparts somewhat more bronzy-green than in the adult male, nearer 60 (Parrot Green), somewhat duller on the crown; the more worn feathers of the back with more bluish tips (near Emerald Green), producing a slightly scaly effect; longest upper tail coverts and most of central rectrices more bluish (between Emerald Green and Cyan but darker); the second and third pairs of rectrices similar, but shading to dark blue (near 173, Indigo Blue) at the tips. The outer two rectrices are extensively pale gray basally (near 86, Light Neutral Gray), with the medial portion Indigo Blue; the outermost rectrix is tipped broadly, the fourth and third progressively more narrowly, with Light Neutral Gray. The malar and auricular areas are dark sooty gray, tinged with dull bronze; a white stripe extends from the eye back over the auriculars. The underparts are pale gray, slightly tinged brownish (near 79, Glaucous, but paler), averaging palest on the throat and darkest on the upper breast. The basal 1/4 of the lower mandible is tinged with dark red, the rest of the bill and feet are black.

PLUMAGE VARIATION IN THE TYPE SERIES.—Variation among the adults of the type series is slight in both sexes, reflecting chiefly feather wear (the degree of 'scaliness' in the dorsal plumage, the degree to which the crown is dull and soiled in females); one female (ICN 31245) has the tip of the first rectrix tinged with blue. The subadult male (ICN 31253) is approaching adult plumage, with the brilliant feathers below colored as in the adults but more scattered over a dull, dusky green juvenal plumage; traces of a dusky mask and whitish postocular and malar stripes remain; the tail is less forked than in the adult males, and the outer rectrix is very narrowly tipped with dull gray. The subadult female (ICN 31243) is a more uniform, bronzy green dorsally with no bluish tinge to the upper tail coverts or central rectrices, and a darker, duller gray below.

ADDITIONAL SPECIMENS EXAMINED.—Between May and August 1993, Diego Silva and Tomas Walschburger of the Fundación Puerto Rastrojo, conducted studies of birds in the area of the Río Mesay, just south of the border of the National Park (0°4'N, 72°26'W), some 85 km SSE of our study area. They observed and collected birds along a transect from the river (ca 230 m elevation) to the top of a low mesa (ca 360 m), an isolated southern outlier of the main Sierra. Four specimens of *C. olivaresi* were taken in the scrub atop the mesa in July 1993 and were available for examination. These specimens agree perfectly in measurements and coloration with the type series, allowing for differences in plumage wear: in particular, the golden-green reflections of the facial area and sides of the neck of the males are stronger, increasing the contrast with the bluish green of the throat. The adult male specimen from the 1990 expedition does not differ from the males of the type series. Thus, the characters of *C. olivaresi* appear to be uniform over most or all of the Sierra de Chiribiquete.

THE SIERRA DE CHIRIBIQUETE AND THE ECOLOGY OF *C. OLIVARESII*

The Sierra de Chiribiquete consists of a series of sandstone mesas and buttes some 125 km long and 30 km wide, extending in an arc that curves from NW–SE in the north to NE–SW in the south, between the latitudes of 1°20'N and 0°20'N, centered along the line of 73°W longitude (Fig. 1). The mesas rise abruptly from the surrounding flat lowlands to heights of 800–900 m in the north and 600 m in the south, often presenting several levels or terraces separated by vertical cliffs. Many of the larger mesas are riven by spectacular chasms or cracks; the flat upper surfaces are drained by streams flowing through vertical cracks that emerge as waterfalls at the edges of the mesas. The thin, sandy soil of the table-tops supports a scrubby vegetation interspersed with areas of naked rock: the stature of the vegetation reflects the depth of the soil (or the absence thereof) at any given point. Further details of the topography, vegetation, and geology of the Sierra de Chiribiquete are given by Estrada and Fuertes (1993). Extending south of the main part of the Sierra are a series of progressively lower mesas (ca 300–350 m) which reach the Río Caquetá at Araracuara (ca 0°30'S).

The base camp of our expedition was situated on the flat middle level of a large (ca 3 km long) mesa at an elevation of 570 m. To the north and east, a line of cliffs rises abruptly to the top level of the mesa (ca 700 m); to the west, the mesa is bounded by a steep-sided canyon some

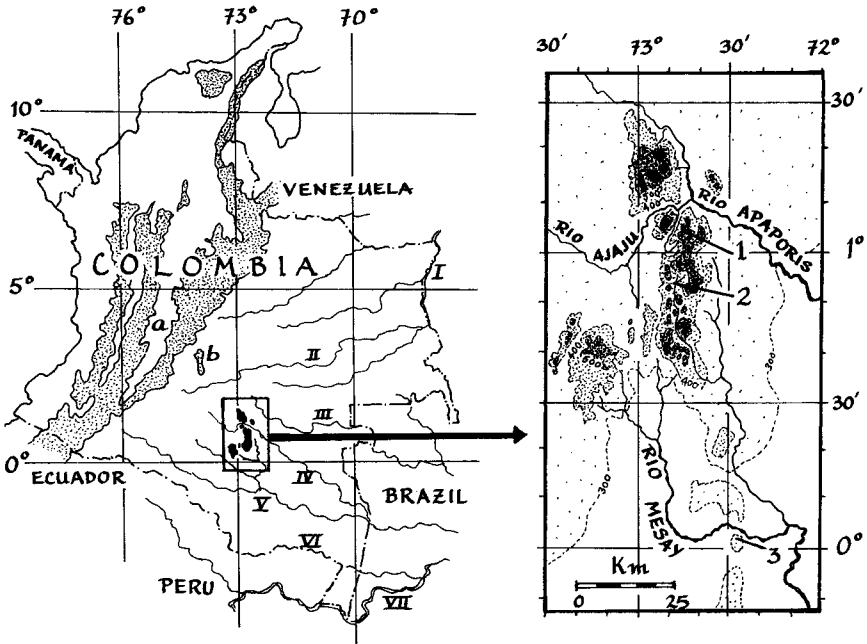
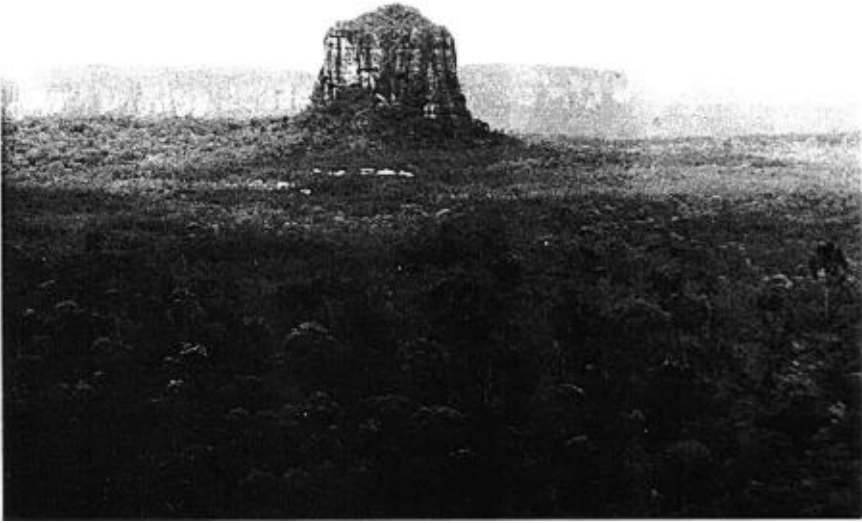


FIG. 1. *Left*: location of the Sierra de Chiribiquete (inset) in relation to the major mountain ranges (stippled) of Colombia, and the major rivers of SE Colombia and adjacent areas (Roman numerals). The rivers are I. Orinoco; II. Guaviare; III. Vaupés; IV. Apaporis; V. Caquetá; VI. Putumayo; and VII. Amazon. Other localities indicated are a. Magdalena Valley and b. Sierra de la Macarena. *Right*: The Sierra de Chiribiquete and adjacent areas showing major rivers and the collecting localities for *Chlorostilbon olivaresi*. The 300, 400, 500, and 600 m contour lines are indicated. Localities: 1. Type locality (Valle de los Menhires); 2. Collecting site of December 1990 specimen (Valle de las Abejas); 3. Río Mesay site. Redrawn from Estrada and Fuertes 1993, in part.

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FIG. 2. Landforms and vegetation at the type locality. A. General topography, showing the butte and our campsite, with adjacent stunted forest and surrounding *Bonnetia* scrub of the middle level of the mesa; taller forest at the base of the fringing cliffs in foreground and other mesas just visible in the background. B. Aspect of *Bonnetia* scrub, the most important habitat of *C. olivaresi*. Note areas of naked rock and patches of low vegetation (mainly *Navia garcia-barrigae*) in foreground, the stiff, coriaceous-succulent leaves of many shrubs (*Graffenriedia* sp. in foreground, *Clusia chiribiquetensis* at center). The low shrub L of center is *Decagonocarpus cornutus*, the most important nectar source of *C. olivaresi*; taller shrubby in background (with large white flowers) is *Bonnetia martiana*.



100–150 m deep that slopes steeply down towards the surrounding lowlands. The base camp was located some 100 m SE of the base of an isolated butte that rises precipitously to a height of ca 75 m.

The vegetation around the base camp consisted of open scrub dominated by the shrub *Bonnetia martiana* (Theaceae); patches of dense scrub, in which the taller shrubs attained a height of 2–3 m, alternated with patches of low, savannalike vegetation and areas of naked rock (Fig. 2). The principal shrubs of the area had thick, coriaceous leaves and twigs suggesting adaptation to resist drought, doubtless reflecting the shallow, sandy soil with low nutrients and minimal water retention capacity. The most common shrub species included, besides *Bonnetia*, *Clusia chiribiquetensis* (Guttiferae), *Tepuianthus savannensis* (Tepuianthaceae), *Graf-fenriedia* sp. (Melastomataceae), and *Decagonocarpus cornutus* (Rutaceae). Between the shrubs, and in slight depressions where a thin layer of sandy soil accumulated, occurred a low herbaceous vegetation dominated by Xyridaceae, Eriocaulaceae, Burmanniaceae, Cyperaceae, and *Vellozia phantasmagorica* (Velloziaceae) with only occasional grasses (Gramineae); where drainage was impeded, pools formed after every rain in which *Utricularia* spp. (Lentibulariaceae) were abundant. Areas of bare rock were colonized by a terrestrial bromeliad, *Navia garcia-barrigae*. A low, dense, tangled forest (canopy height 3–5 m) dominated by *Clusia* spp. and *Licania* sp. grew around the base of the butte.

The level of the mesa sloped very gently towards the fringing cliffs to the north and east, at the bases of which grew a much taller forest (canopy height 20–25 m) with numerous palms and a relatively well-developed understory; in the canyon bottom grew a forest of similar canopy height but with few palms and notably low tree species diversity and a few large-leaved monocots (*Heliconia*, *Calathea*, *Costus*, *Phenakospermum*) in the understory. The northern part of the mesa was drained by a stream along which grew an extremely dense, tall (canopy ca 5 m) stand of *Bonnetia* whose tangled aspect suggested that of a young mangrove swamp. A general inventory of the avifauna and its biogeographical affinities (Stiles et al. 1995), and a detailed analysis of mist-net captures in relation to vegetation characteristics (Díaz et al. 1996) will appear elsewhere.

In the study area, *Chlorostilbon olivaresi* was fairly common in the open *Bonnetia* scrub of the mesa, where 12 of the 15 individuals were captured; in fact, it was the bird most frequently captured in mist-nets in the open areas of the mesa. In this habitat, both sexes were observed visiting only the red-orange flowers of *Decagonocarpus cornutus* (see Frontispiece) and were frequently noted gleaning small arthropods from the foliage and flowers of *Bonnetia* and other shrubs and flycatching at breaks in the vegetation, especially in late afternoon. Pollen samples taken

from the beaks of eight mist-netted birds with transparent Scotch tape contained only pollen of *Decagonocarpus*, usually <10 grains (5 cases), three grains of pollen of *Decagonocarpus* and one of *Bonnetia* (one bird), or no pollen at all (2 birds). The visit to *Bonnetia* was almost certainly to obtain insects such as thrips which were often present on the large, open, and fragrant camellialike flowers of this species (which do not produce nectar). Stomach contents of collected individuals contained tiny insects, mainly flies, but a few thrips and/or microhymenopterans were present in at least two stomachs. The only other hummingbirds to occur regularly in the *Bonnetia* scrub were the Versicolored Emerald (*Amazilia versicolor*), which also visited *Decagonocarpus* but was much scarcer; and the Black-throated Mango (*Anthracothorax nigricollis*), which appeared to be more insectivorous and was seen to visit only the flowers of a small tree of the Bombacaceae in the low forest at the base of the butte. We never saw any interactions between any of these species.

The only other habitat in which we regularly recorded *C. olivaresi* was the forest at the base of the fringing cliffs at the north end of the mesa. Here, small numbers occurred in the understory and at gaps; three birds were captured, and on several occasions a female was observed visiting the flowers of a small understory tree of the Violaceae. In several days of observation and netting, we never encountered *C. olivaresi* in the forest of the canyon bottom. In visits to other areas at the base of the Sierra, including mist-netting, other members of the expedition (A. Repizzo, B. Ortiz) never encountered *C. olivaresi* in the forests at lower elevations. During their work at the Río Mesay site, Silva and Walschburger only recorded *C. olivaresi* in the *Bonnetia* scrub on the top of the mesa or in the adjacent low forest (340–360 m), never lower or closer to the river. The 4–6 months difference between the dates of our observations and those of Silva and Walschburger would appear to preclude the possibility of extensive seasonal movements (e.g., into the surrounding lowland forests) by this hummingbird. Thus, *C. olivaresi* may be restricted to the scrubby vegetation and adjacent forests on the mesas of the Sierra, and it is quite probably absent from the surrounding forested lowlands. It evidently occurs widely in the Sierra de Chiribiquete, given the distance between the Río Mesay site and the type locality; the 1990 specimen was taken some 20 km south of the type locality, also in *Bonnetia* scrub at a slightly lower elevation (ca 420 m). The southern limit of *olivaresi* remains to be determined but is evidently somewhere between the Río Mesay and the Río Caquetá, since it was not taken during intensive collecting by H. Romero at Araracuara in similar *Bonnetia* scrub.

Of the specimens of *C. olivaresi* we collected, one adult male and two females (as well as both of the subadults) had the gonads small and

undeveloped; one male and one female had moderately enlarged gonads. Among the birds measured and released, one female had a developing brood patch. The two subadult specimens were at least several months old, as they had lost their bill corrugations. Taken together, these data indicate that *C. olivaresi* was at the start of its breeding season during our observations, although courtship displays were not observed, and we found no active nests. None of the individuals captured were molting, and most were in slightly to moderately worn plumage, consistent with the inference that the breeding season was beginning (cf Stiles 1985b). Although meteorological data for the Sierra de Chiribiquete do not exist, extrapolation from the data for other sites in Colombian Amazonia suggest that our expedition took place at the very beginning of the dry season (Estrada and Fuertes 1993). Flowering of at least *Decagonocarpus*, evidently the most important nectar source at this time for *C. olivaresi*, was definitely increasing during our observations (many flower buds, few developing fruits). Fruiting of several species was also increasing or about to begin in late November 1992, and a number of other bird species were evidently just starting gonadal maturation, suggesting that the dry season might include the main breeding period for a considerable segment of the Chiribiquete avifauna (Stiles et al. 1995).

The four Río Mesay specimens, taken in July 1993, were for the most part in very fresh plumage, and one female was in heavy molt; neither of the two with gonad data were in breeding condition. If the seasonality of the two sites is similar, this suggests that the breeding season of *C. olivaresi* falls between late November or December and perhaps May. Molt in the population extends from perhaps May through at least July, as both males and one female of the Río Mesay specimens had completed molt by July; in hummingbirds it is not unusual for males to molt a month or so ahead of females (cf Stiles 1985b).

Like other members of its genus, *C. olivaresi* is a rather quiet hummingbird under most circumstances. The only vocalization heard was a sharp, dry, scratchy "cht", similar to the calls of other *Chlorostilbon* but somewhat louder, and given by birds foraging at flowers. We never heard it sing. Compared to others of the genus I have observed, *C. olivaresi* is less nervous and flighty at flowers and shows much less of the incessant rapid flicking or pumping of the tail while foraging (cf Stiles and Skutch 1989).

PATTERNS OF VARIATION IN THE *C. MELLISUGUS* COMPLEX IN
NORTHWESTERN SOUTH AMERICA

No fewer than 10 forms in this complex are recognized by most authors from Colombia and adjacent areas of northwestern South America (see Table 1, Fig. 3). Because *C. olivaresi* appears to be a member of this

TABLE 1
CURRENTLY ACCEPTED SUBSPECIES OF THE *CHLOROSTILBON MELLISUGUS* COMPLEX IN
NORTHWESTERN SOUTH AMERICA, WITH THEIR DISTRIBUTIONS AND DIAGNOSTIC CHARACTERS^a

Subspecies	Distribution	Characters ^f
<i>pumilus</i>	W Colombia from Pacific slope of W Andes E to W edge of Magdalena Valley	Bill black. M: tail moderately forked; glittering crown; breast with little or no blue. F: trace of grey in outer rectrices, extensive green in central rectrices.
<i>melanorhynchus</i> ^b	Extreme SW Colombia (Nariño) and W Ecuador	Like <i>pumilus</i> but averaging larger.
<i>gibsoni</i>	Upper and middle Magdalena Valley Colombia	Lower mandible largely red. M: tail very deeply forked, outer rectrices attenuate; breast green; crown dull. F: outer rectrices with extensive grey bases, broad whitish tips.
<i>chrysogaster</i>	N lowlands of Colombia E to Santa Marta; W of Lago de Maracaibo, Venezuela–Colombia	Like <i>gibsoni</i> but M: tail even more deeply forked, forehead glittering, throat and breast tinged blue; F: grey of outer rectrices darker, less extensive.
<i>nitens</i> ^c	Arid N coast of extreme NE Colombia and NW Venezuela	Like <i>chrysogaster</i> but tail of M slightly less deeply forked.
<i>caribaeus</i> ^d	Most N coastal region of Venezuela, S to Orinoco region and Llanos of Colombia	Bill black. M: glittering crown; breast with trace of blue; tail shallowly forked. F: at most a trace of dusky on lateral rectrices, otherwise blue.
<i>napensis</i> ^e	SE Colombia S of Llanos; E Ecuador; adjacent NE Perú	Like <i>caribaeus</i> but averaging larger. M: tail very shallowly forked, nearly truncate, breast strongly tinged blue. F: extensive green flecking on sides.
<i>phaeopygos</i>	E Perú to NE Bolivia, incl. adjacent Brazil	Like <i>napensis</i> but M: belly duller, darker, less contrast with blue of breast; F: much less green flecking below. Also averages larger, especially tail.
<i>subfurcatus</i>	S+SE Venezuela E to Guayana, and adjacent NW Brazil	Like <i>caribeus</i> but M: tail less forked, breast more bluish. Averages slightly larger.
<i>duidae</i>	Mt. Duida, SE Venezuela	Like <i>subfurcatus</i> but decidedly larger; M: tail longer, more forked; breast less bluish.

^a Characters and distributions from Meyer de Schauensee (1964, 1966); Meyer de Schauensee and Phelps (1978); Zimmer (1950), and Zimmer and Phelps (1952).

^b May not be distinct from *pumilus*.

^c May not be distinct from *chrysogaster*.

^d Includes *nanus* from the Orinoco region.

^e Often lumped with *phaeopygos*.

^f M = male, F = female.

complex, I decided that to evaluate properly its status and affinities a broader analysis of the patterns of variation in the complex over northwestern South America would be required.

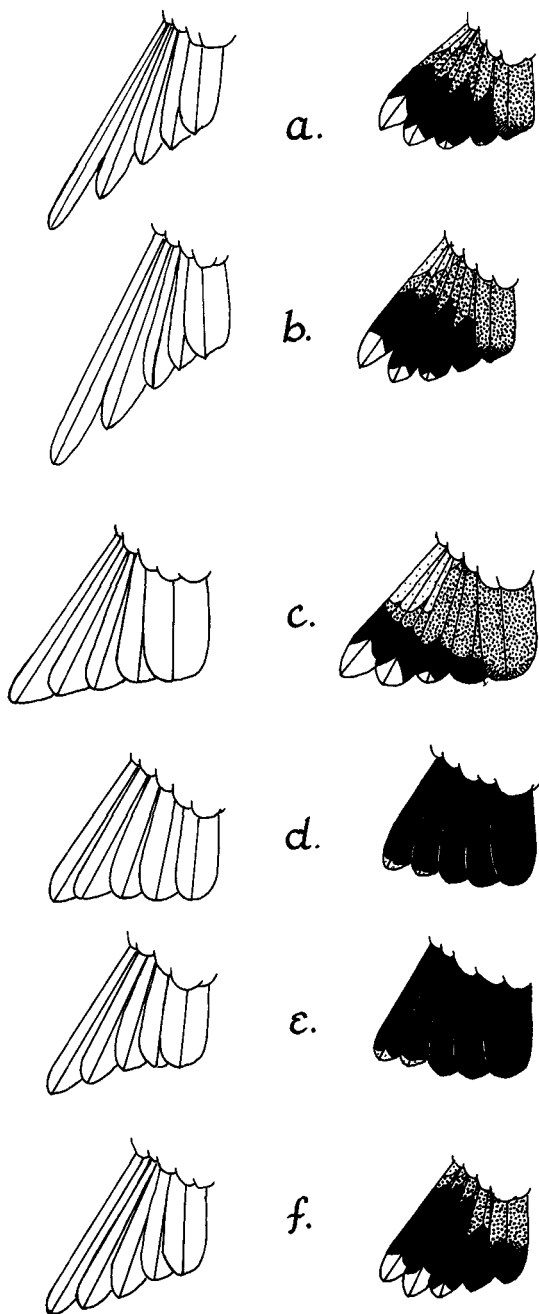
Previous studies.—The first comprehensive study of the *mellisugus* complex was that of Zimmer (1950) who concluded that the mosaic nature of the patterns of geographic variation, plus the allopatric distributions of most forms, justified considering all forms of the complex as subspecies of a single, variable species *mellisugus*. However, several points of confusion exist in his analysis. Evidently, Zimmer started by considering two forms from northern South America, *nitens* and *chrysogaster*, as members of different subspecies groups and later concluded that they might not be separable at all, thus favoring lumping the “eastern” and “western” groups.

In his initial study of the birds of Colombia, Meyer de Schauensee (1948–1952) had considered all Colombian forms of the complex as subspecies of *gibsoni*, but he later (1960, 1966) noted that two groups of races could be distinguished on the basis of bill color: those with the lower mandible largely red (*gibsoni*, *chrysogaster*, and *nitens*) and those with all-black bills (all other forms). He noted that the red-billed forms were also those with the most deeply forked tails and attenuated outer rectrices in the males, and with the most gray in the rectrices of the females. He noted apparent sympatry of a red-billed (*gibsoni*) and black-billed (*pumilus*) form without evident intergradation at two localities on the western edge of the Magdalena Valley in Colombia and concluded that two species should be recognized in Colombia: the red-billed *gibsoni* (including *chrysogaster* and *nitens*) and the black-billed *mellisugus* (including *pumilus*, *melanorhynchus*, *caribaeus*, and *phaeopygus* (= *napensis*)).

Wetmore (1968) adopted Meyer de Schauensee’s character of bill color as a criterion for distinguishing species in the complex when he separated the black-billed *assimilis* of southwestern Costa Rica and W Panamá from the red-billed *canivetii* of farther north. The arrangement of Meyer de Schauensee (1960, 1966) has been followed by recent authors for the South American forms of the complex (Meyer de Schauensee and Phelps

→

FIG. 3. Tails of members of the *C. mellisugus* complex from Colombia, drawn to the same scale. Left: tails of adult males, showing form of rectrices; in all, rectrices are uniform steely blue-black. Right: tails of adult females, showing form, pattern, and colors of the rectrices. Solid: steely blue-black; heavy stipple: green; light stipple: grey; open: white. The forms illustrated are: a. *chrysogaster*; b. *gibsoni*; c. *olivaresi*; d. *napensis*; e. *caribaeus*; f. *pumilus*.



1978, Hilty and Brown 1986, Sibley and Monroe 1990). However, because the characters of *olivaresi*, as detailed above, appear to be in part a mosaic of features of *gibsoni* and *mellisugus* as currently recognized, this arrangement requires a detailed reevaluation. For this analysis, I consulted specimens of the *mellisugus* complex available in the following museums (numbers of specimens in parentheses): the Instituto de Ciencias Naturales, Universidad Nacional de Colombia (69); the Universidad de La Salle, Bogotá (12); the Unidad de Investigación "Federico Medem" (UNIFEM), INDERENA (6), Bogotá; and the Colegio de San José, Medellín (8). For each specimen, I measured the exposed culmen, total culmen, wing chord, and tail length to the nearest 0.1 mm with dial calipers. For males only, I measured the depth of the tail fork as the difference between the lengths of the first and fifth rectrices. In addition, I took detailed notes on color characters of each form and made detailed drawings of the rectrices of representative individuals of both sexes of all forms (Fig. 4). Field work in various parts of Colombia has also given me the opportunity to capture and measure an additional 18 individuals of various forms of the *mellisugus* complex. For these birds, I made the preceding measurements except depth of tail fork, also with dial calipers, and to the same level of accuracy; I also weighed all birds to the nearest 0.1 g with a 10 g Pesola spring balance. Because in previous studies I had found that my field measurements did not differ from those taken in the museum and that my measurements of birds in the field agree closely with remeasurements of the same birds prepared as museum specimens (Stiles 1985a, 1995), I have included both types of measurements in the quantitative analyses below. In addition, M. Marín kindly measured 10 specimens of *napensis* and *pheaopygus* in the collection of the Museum of Natural Science, Louisiana State Univ. Having worked with and measured birds previously with Marín, I am confident that his measurements are comparable with mine and have incorporated them into the analyses.

In all, measurements from 111 specimens of the following forms were used in the analyses: *olivaresi*, *pumilus*, *gibsoni*, *chrysogaster*, *caribaeus*, and *napensis* (Table 2). Of the remaining forms in Table 1, none occurs in areas adjacent to *olivaresi* and is likely to bear upon its status; I was able to examine only two specimens of *nitens*, and none of *melanorhynchus*, *subfurcatus*, *duidae*, or *phaeopygus*. For the characters of these forms (Table 1), I have relied upon the descriptions of Zimmer (1950) and Zimmer and Phelps (1952). For the six forms mentioned above, measurements were analyzed by one-way analysis of variance (ANOVA) for each sex separately. Where a significant result was obtained in the ANOVA, Tukey a posteriori tests were performed to determine which forms differed significantly with respect to the measurement in question (Zar

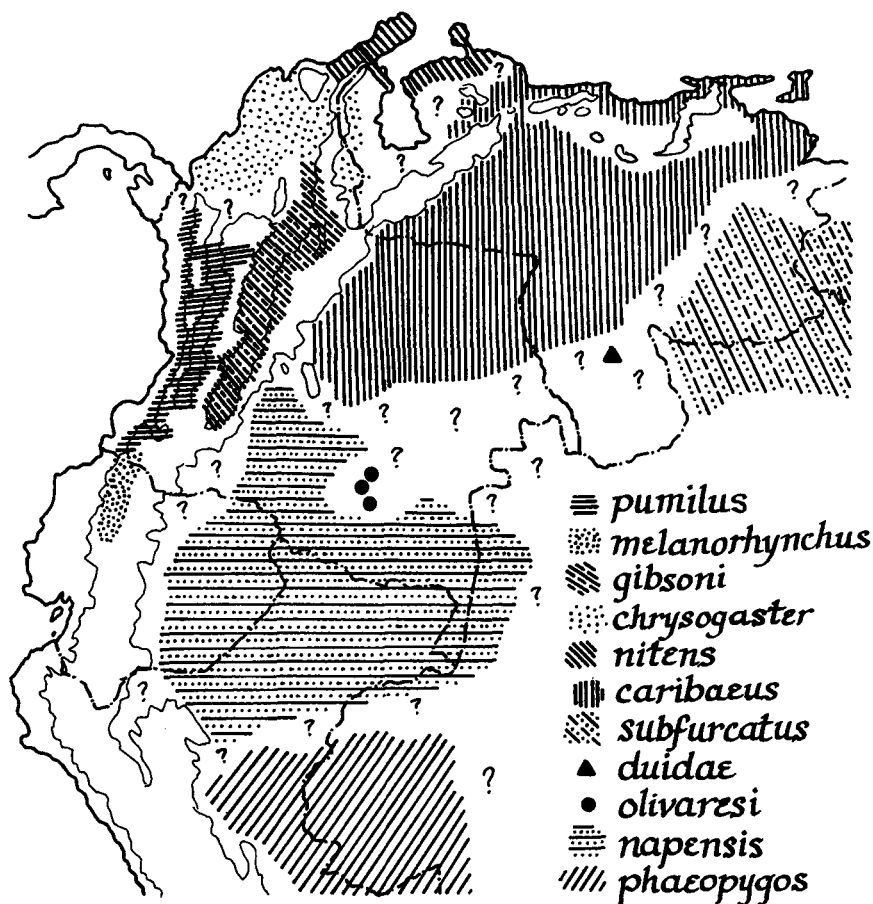


FIG. 4. Distributions of the members of the *C. mellisugus* complex in northwestern South America. Note that limits of some forms are imperfectly known, as are possible zones of contact; especially east of the Andes, distributions are probably more continuous than shown, but collecting localities are often widely scattered.

1988). For the measurement of depth of tail fork, I derived a measure of "relative tail fork" by dividing the difference $r5-r1$ by the tail length for each specimen, to control for differences in absolute size between the various forms.

The most striking result of the analyses of variance of the measurements (Table 3) is the clear-cut separation of *olivaresi* (at a significance level of $P < 0.001$) from all other forms of the *Chlorostilbon mellisugus* complex, with respect to bill length (both exposed and total culmen), wing

TABLE 2
MEASUREMENTS^a OF VARIOUS FORMS OF THE *CHLOROSTILBON MELLISUGUS* COMPLEX FROM COLOMBIA AND ADJACENT AREAS

Form	Sex	N	Exposed culmen	Total culmen	Wing chord	Tail length	Relative tail fork	Body mass (N)
<i>pumilus</i>	M	12	14.09 ± 0.63	16.09 ± 0.92	46.02 ± 1.01	24.71 ± 1.02	0.252 ± 0.039	2.63 ± 0.18 (4)
	F	10	14.73 ± 0.78	16.41 ± 0.88	44.91 ± 0.91	23.64 ± 1.12		2.57 ± 0.21 (6)
<i>gibsoni</i>	M	12	15.38 ± 0.53	17.98 ± 0.66	46.48 ± 0.76	26.30 ± 1.06	0.411 ± 0.041	2.79 ± 0.17 (4)
	F	9	15.80 ± 0.51	18.36 ± 0.68	45.14 ± 0.71	23.88 ± 1.25		2.65 ± 0.20 (4)
<i>chrysoaster</i> (N. coast)	M	9	15.10 ± 0.42	17.38 ± 0.59	42.90 ± 1.09	27.43 ± 1.43	0.462 ± 0.046	
	F	4	15.90 ± 0.56	18.55 ± 0.66	43.05 ± 0.69	23.88 ± 1.05		
<i>chrysoaster</i> (Nrt. Sant.)	M	5	15.23 ± 0.25	17.65 ± 0.54	45.86 ± 0.36	27.70 ± 0.67	0.419 ± 0.021	
	F	5	16.38 ± 0.41	18.58 ± 0.31	44.88 ± 0.92	25.62 ± 0.60		
<i>caribaeus</i>	M	10	14.80 ± 0.59	16.93 ± 0.91	43.69 ± 1.03	21.25 ± 0.89	0.203 ± 0.20	2.68 ± 0.18 (6)
	F	6	15.47 ± 0.72	18.08 ± 0.91	42.58 ± 1.14	21.47 ± 0.93		2.54 ± 0.23 (4)
<i>napensis</i>	M	8	15.89 ± 0.59	17.91 ± 0.83	44.81 ± 1.34	21.36 ± 1.08	0.094 ± 0.031	2.73 ± 0.25 (4)
	F	6	15.90 ± 0.64	17.73 ± 1.28	42.47 ± 0.48	21.05 ± 0.70		2.37 ± 0.32 (3)
<i>olivaresi</i>	M	7	20.29 ± 0.45	22.44 ± 0.68	49.77 ± 0.63	25.71 ± 0.59	0.184 ± 0.019	3.78 ± 0.26 (6)
	F	12	20.91 ± 0.85	22.91 ± 0.61	48.60 ± 0.60	24.63 ± 0.87		3.60 ± 0.22 (11)

^a Mean and standard deviation. Masses are in g; culmen, wing chord, and tail length are in mm.

TABLE 3
 RESULT OF ANALYSES OF VARIANCE COMPARING MEASUREMENTS OF MEMBERS OF
CHLOROSTILBON MELLISUGUS COMPLEX FROM NORTHWESTERN SOUTH AMERICA

Measurement	Sex	F	P	Result of Tukey tests ^a						
Exposed culmen	M	109.19	<0.001	PU	CA	CC	CN	GI	NA	OL
	F	94.75	<0.001	PU	CA	GI	NA	CC	CN	OL
Total culmen	M	53.90	<0.001	PU	CA	CC	CN	NA	GI	OL
	F	71.83	<0.001	PU	NA	CA	GI	CC	CN	OL
Wing chord	M	48.81	<0.001	CC	CA	NA	CN	PU	GI	OL
	F	65.53	<0.001	NA	CA	CC	CN	PU	GI	OL
Tail length	M	53.08	<0.001	CA	NA	PU	OL	GI	CC	CN
	F	17.57	<0.005	NA	CA	PU	GI	CC	OL	CN
Body mass	M	29.64	<0.001	PU	CA	NA	GI	OL		
	F	42.47	<0.001	NA	CA	PU	GI	OL		
Relative tail fork	M	103.89	<0.001	NA	OL	CA	PU	GI	CN	CC

^a Abbreviations: CA = *caribaeus*; CC = *chrysogaster*—N coast of Colombia; CN = *chrysogaster*—Norte de Santander; NA = *napensis*; GI = *gibsoni*; OL = *olivaresi*; PU = *pumilus*.

Forms not significantly different ($P < .05$) in a given measurement are connected by solid lines. Breaks in the lines indicate significant differences, and the number of slashes indicates the degree of significance: one slash = $P < 0.05$; two slashes = $P < 0.01$; three slashes = $P < 0.001$.

chord, and mass. The larger size of *olivaresi* is most dramatically shown by the data on body mass, perhaps the best indicator of overall size: this form is fully 35–40% heavier than all the other forms, which do not differ among themselves. In fact, *olivaresi* is apparently the largest form in the

entire genus *Chlorostilbon*, exceeding in size even the Cuban Emerald C. *ricordii* (cf Ridgway 1911, Howell 1993). Regarding measurements of the tail, the separation of *olivaresi* is more equivocal, chiefly because this form, because of its overall large size, has a tail length more similar to those of the *gibsoni* group with their relatively long, deeply forked tails, but in its shallowly forked tail, *olivaresi* resembles closely various members of the *mellisugus* group.

Although some of the remaining forms differed significantly from others in one or another dimension, similar clean-cut separations between groups were the exception. Males of the *gibsoni* group differed from those of the *mellisugus* group significantly in tail length and highly significantly in relative depth of tail fork; however, in most other dimensions the pattern was less clear: often differences significant in one sex were not so in the other, and the rank order of the forms often varied from one measurement to another and/or between the sexes for a given measurement (Tables 2, 3). This is undoubtedly at least in part a reflection of the mostly small sample sizes (Table 2). One interesting result was the significant difference in wing length between the northern and cis-Andean populations of *chrysogaster*; however, these populations were similar in other dimensions. Aside from *olivaresi*, the most distinctive form, in terms of measurements, was *pumilus*, with its unique combination of a very short bill and a relatively long wing (Table 3; see below).

Patterns of plumage variation.—In eastern Colombia, specimens of *caribaeus* showed no obvious variation between Arauca and Meta (in particular, those from Arauca showed no tendency to approach *chrysogaster*). To the south, *napensis* differed in having a shorter, less forked tail and more strongly bluish throat in the males, more lateral green flecking below and less pale tipping on the outer rectrices in the females, and a somewhat longer bill in both sexes. I could detect no consistent differences in size or color between specimens of *napensis* from extreme southern Meta, northwestern Caquetá, eastern Vaupés, or southern and eastern Amazonas in Colombia, or (in size at least) eastern Ecuador or extreme northeastern Peru. The largest male measured was from eastern Peru, where the range of this form approaches that of the possibly indistinguishable *phaeopygos*. I have not seen specimens of *phaeopygos* from Peru, so cannot comment on the validity of separating *napensis*; however, female specimens of the latter I have seen do show the extensive green flecking below used by Zimmer (1950) to distinguish this race from *phaeopygos* and *caribaeus*. Although *napensis* and *caribaeus* differed significantly in relative tail fork in this analysis (Table 3), it is worth noting that this difference is apparently bridged by the adjacent *subfurcatus* and *duidae*, to judge from the measurements of these forms given by Zimmer

and Phelps (1952). I should note in passing that my measurements are in reasonably close agreement with those of Zimmer for those forms which we both measured.

The range of *olivaresi* appears to be nearly completely nested within that of *napensis*. Although I have seen no specimens of the latter from localities adjacent to the Sierra de Chiribiquete, those from northwest, south, and east of this range show no approach to the characters of *olivaresi*; in fact, *napensis* differs from *olivaresi* in most characters at least as much as does any other cis-Andean form of the *mellisugus* complex. This indicates that gene flow between *olivaresi* and *napensis* does not occur; given the great difference in size, it is highly questionable whether interbreeding could occur at all.

Within the *gibsoni* group, *chrysogaster* males have a glittering fore-crown and usually, at least, a faint bluish tinge to the throat (more than either *pumilus* or *gibsoni*). The tail is even more deeply forked than in *gibsoni*; in females, the pattern of the tail is similar, although the gray area at the bases of the outer rectrices tends to be darker and less extensive. The difference in wing length between the populations of this form east and west of the Serranía de Perijá is interesting: at the very least, it appears that the former shows no approach to the geographically adjacent form of *mellisugus caribaeus*. In color, pattern, and tail shape, the cis-Andean population of *chrysogaster* also appears as different from *caribaeus* as does the trans-Andean population, suggesting that gene flow between these populations is not occurring. The little information I have on *nitens* suggests that this form is very similar to the trans-Andean *chrysogaster*. Although data are required on possible zones of contact between *nitens* and *caribaeus*, the information currently available again favors maintaining separate species status for the *gibsoni* group (including *chrysogaster* and *nitens*) and *mellisugus*.

The case of C. pumilus.—This form of western Colombia agrees with members of the *mellisugus* group in having an all-black bill, in the glittering crown of the males, and in the virtual absence of grey in the outer rectrices of the females. However, the males have significantly longer, more deeply forked tails and less bluish breasts than do any of the eastern forms of this group. Females of *pumilus* differ from those of the eastern races in their slightly forked to double-rounded tails, with extensive green in most rectrices, and in the more extensive pale tips to the outer rectrices, as well as in showing some dark gray at the bases of these rectrices. In overall proportions, *pumilus* has a shorter bill and longer wing and tail than do the eastern races, sex for sex.

In several of these characters, *pumilus* rather resembles the adjacent *gibsoni* of the Magdalena Valley; however, it differs strongly from *gibsoni*

in bill color, tail shape, bill length, crown color (males), and the color of the outer rectrices (females). Moreover, these differences appear to be as great in specimens from areas where the two forms approach each other (western Tolima, western Antioquia), as in areas far from the possible contact areas. Hence, the evidence presently available favors continuing to separate *pumilus* and *gibsoni* at the species level.

Considering the next form to the north, *assimilis*, *pumilus* also shows a number of clear-cut differences based upon the measurements, weights, and descriptions of the latter in Wetmore (1968). In males, the crown of *pumilus* is highly iridescent, while in *assimilis* it is plain; the gray of the outer rectrices of the females is much more extensive in *pumilus*. In measurements, *pumilus* has a much shorter bill, longer wing, and shorter tail and also weighs considerably less in both sexes. The ranges of the two forms are separated by a wide gap in eastern Panamá (cf Wetmore 1968) but from my observations of both forms in the field, I suspect that they differ in ecology, with *pumilus* preferring significantly wetter areas than does *assimilis*. I conclude from this analysis that *pumilus* is best considered an allospecies in the *mellisugus* superspecies rather than as a subspecies of *mellisugus* (sensu stricto); this also eliminates the disjunct distribution of the latter (with *pumilus* separated by *gibsoni* from the other forms of *mellisugus*).

Although I was unable to examine specimens of *melanorhynchus*, there seems little reason to doubt that this form is conspecific with *pumilus*; Zimmer (1950) noted that the two differ little, if at all, in coloration and overlap in measurements and, in fact, might not be separable. The two forms were supposed to differ in their preferred elevations, with *melanorhynchus* occurring mostly above 2000 m, and *pumilus* at lower elevations; however, this difference also tended to break down in the series of specimens available to Zimmer (1950). If *pumilus* and *melanorhynchus* are considered to comprise a separate allospecies in the *mellisugus* complex, as I feel the evidence indicates, this species will have to be called *C. melanorhynchus* (since *melanorhynchus* Gould 1860 has priority over *pumilus* Gould 1872). Without having seen specimens of *melanorhynchus* itself, I cannot comment on the advisability of synonymizing *pumilus* and recommend further study.

On the basis of a phylogenetic species concept (Cracraft 1983, McKittrick and Zink 1988), *melanorhynchus* (with *pumilus*) would also clearly be entitled to species status; it possibly differentiated from other forms of the *mellisugus* complex in the Chocó humid forest refugium during one of the dry epochs of the Pleistocene (cf Haffer 1974). I suggest the English name West Andean Emerald for this form in view of its basically

Andean distribution, which lies to the west of all other members of the *mellisugus* complex in South America.

Origin of the Chiribiquete Emerald.—*C. olivaresi* represents an anomaly among the cis-Andean populations of the *mellisugus* complex: its characters are sharply discordant with the general trends of variation over this broad area. Although large size is a character shared by another isolated mountain endemic, *duidae* of Venezuela, the differences in color and morphology of the latter relative to the forms occurring elsewhere in southern and southeastern Venezuela, *caribaeus* and particularly *subfuscatus*, are differences of degree only: there seems little reason to doubt that *duidae* is but a derivative of one or the other (apparently neither has been recorded from the adjacent lowlands), and there is little reason to suspect that it is reproductively isolated from them (Zimmer and Phelps 1952). In fact, *duidae* was not considered by Mayr and Phelps (1967), although it was recognized as distinct by Meyer de Schauensee and Phelps (1978). The case of *olivaresi* is clearly not comparable to that of *duidae*: it is certainly not an isolated derivative of *napensis* (or any other cis-Andean form). The many points of resemblance to *gibsoni* (bill color, the dull crown of the males, and the rectrix color of the females) suggest that the origins of *olivaresi* might lie with that form, at least in part. At the present time, the ranges of *olivaresi* and *gibsoni* are separated by at least 300 km of forested lowlands and foothills, which constitute unsuitable habitat for both forms which are evidently adapted to dry or edaphically scrubby habitats (and which are inhabited, at least at present, by *napensis*). It is likely that the eastern foothills of the Andes in southeastern Colombia represented a humid enclave or "forest refugium" through Pliocene-Pleistocene times (Haffer 1974, 1985), such that the range of *gibsoni* has probably never included or approached the Sierra de Chiribiquete. A more likely scenario is for one or a few individuals of the ancestral population of *gibsoni* to have dispersed across the forested lowlands to Chiribiquete, perhaps during a dry period in the Pliocene or early Pleistocene. During such a period, the low passes south and west of the Sierra de la Macarena might well have supported a more xeric, scrubby, vegetation suitable for *gibsoni*, facilitating its arrival on the eastern slope of the Andes. Consisting of sandstones of Permian age or earlier, the Sierra de Chiribiquete antedates at least the final uplift of the Andes (cf Galvis, in Estrada and Fuertes 1993), and would have been available for colonization by forms adapted to xeric or open habitats throughout the latter part of the Cenozoic. The final population of *Chlorostilbon* to colonize the Sierra de Chiribiquete might even have been the result of hybridization of the newly arrived *gibsoni*-type birds with the form of *mellisugus* already present in the adjoining areas. At least, this would provide

a tentative explanation for the *mellisugus*-like characters of *olivaresi* (very shallowly forked tail and blue breast of the males). Once established, this population of possibly hybrid origin might well have developed large size in the process of adapting to its peculiar insular habitat. Large size is a feature of some island populations (cf Grant 1965) including those of *Chlorostilbon* (cf Ridgway 1911, Howell 1993), and the large size of *duidae* may represent a result of the same processes, albeit at an earlier and more incomplete stage. A possibly analogous case of presumptive hybrid origin of a currently stable and well-differentiated form among the white-eyes of Reunion Island has been discussed by Gill (1973). Genetic studies in the *mellisugus* complex would assuredly shed light on the origins of *olivaresi*, and might help to resolve several other questions regarding geographical variation and species limits in the complex. In any case, by both biological and phylogenetic criteria, *olivaresi* appears as entitled to separate (allo)species status as does any other form within the entire *mellisugus* complex.

Among the avifauna of the Sierra de Chiribiquete, *C. olivaresi* is also an anomaly. Virtually all of the species of the upper levels of the Sierra whose subspecific allocations could be determined, belong to forms whose distributions include the Llanos, the Orinoco region, and/or the savannas of eastern Vaupés and adjacent Brazil, rather than the Amazonian lowlands and Andean foothills to the west and south (Stiles et al. 1995). The lack of differentiation of these forms suggests a vicariance pattern, probably a relict of more a continuous distribution of savanna or scrub-adapted birds during the dry periods of the Pleistocene. The present isolation of these birds from their relatives to the north and east probably dates back no more than 15,000–20,000 years, much too short a time to have permitted significant differentiation among birds of the Amazon drainage (Capparella 1988).

Interestingly, one other species of Chiribiquete appears to have dispersed from the xeric upper Magdalena Valley rather than having its affinities with forms to the north and east. This species, *Hemitriccus margaritaceiventer*, also appears to have differentiated in Chiribiquete from its putative ancestral population in the Magdalena Valley, although to a much lesser extent. This population clearly represents a distinct subspecies of *margaritaceiventer* (Stiles, unpubl. data), probably of more recent origin than *C. olivaresi*. In general terms, the Chiribiquete avifauna is basically a relict of a formerly more continuous Orinoquian avifauna upon which is superimposed a small number of forms that have dispersed from similar habitats to the west, at different periods of the geological past (cf Mayr and Phelps 1967). The most distinctive, and probably the oldest, of

these forms is undoubtedly the Chiribiquete Emerald, *Chlorostilbon olivaresi*.

AN OVERVIEW OF THE *C. MELLISUGUS* COMPLEX

The most recent treatment of this complex as a whole is that by Sibley and Monroe (1990). These authors consider as allospecies of the *mellisugus* superspecies *canivetii* of México and northern Central America, *assimilis* of southern Costa Rica and western Panama, and *mellisugus* (including *pumilus* and *melanorhynchus*) of northern South America, while excluding *gibsoni* (including *chrysogaster* and *nitens*). This represents the opposite extreme from the broad treatment of Zimmer (1950) who considered all these forms as subspecies of *mellisugus*. Especially in view of the characters of *olivaresi*, which combines certain features of both *gibsoni* and the *mellisugus* group, I would agree with Zimmer that all of these forms are representatives of a common stock. In particular, I see no justification for including the *canivetii* group while excluding *gibsoni* from this complex: they share characters, such as the red lower mandible and deeply forked tail of the males, and extensive gray bases and broad white tips to the lateral rectrices of females (Zimmer 1950). These features could well represent parallel adaptations to more open, seasonal habitats than are occupied by neighboring forms.

In general, I feel that too little attention has been paid to the ecology of these hummingbirds—in particular, the range of elevations and humidity conditions occupied by each form. Although all members of the group prefer open, brushy habitats, so far as known, there are a number of differences that could have bearing on their status. For instance, *pumilus* appears to be primarily a bird of humid foothills, entering well into the subtropical zone where it has been recorded to elevations of 2000 m or more (Hilty and Brown 1986; pers. obs.); the same evidently is true of *melanorhynchus* (Zimmer 1950). The preferred habitat of *gibsoni* appears to be in hotter, drier areas; it occupies the floor of the middle and upper Magdalena Valley, up to ca 2000 m or more in dry valleys, mainly on the western side; *chrysogaster* and *nitens* are mainly or exclusively lowland forms, with the latter occupying the driest areas along the northern coast (Meyer de Schauensee 1948–1952). Also occurring primarily in the lowlands east of the Andes are *caribaeus* (probably throughout the Llanos) and *napensis* in more humid areas farther south, apparently largely in areas of riverine scrub. *Subfurcatus*, by contrast, occurs mostly above 1000 m in the Gran Sabana and tepuis of eastern and southeastern Venezuela and adjacent Brazil and Guyana (Meyer de Schauensee and Phelps 1978); *duidae* is evidently isolated at similar elevations on Cerro Duida (Zimmer and Phelps 1952). Different habitat preferences may help to

promote or reinforce reproductive isolation of different forms where they meet, as perhaps is the case between *pumilus* and *gibsoni* on the western side of the Magdalena Valley. This would likely be the case for *napensis* and *olivaresi*, which appear restricted to the upper elevation *Bonnetia* scrub of the Sierra de Chiribiquete. A detailed study of the displays of these hummingbirds (cf Stiles 1983) might also help to clarify species limits.

On present evidence, I recommend that the relationships of these forms are best expressed by considering the *mellisugus* complex to comprise a single (*mellisugus*) superspecies. In South America, the forms *melanorhynchus* (including *pumilus*), *gibsoni* (including *chrysogaster* and *nitens*), *olivaresi*, and *mellisugus* (including *caribaeus*, *napensis*, *phaeopygos*, *subfurcatus*, *duidae*, and one or more races in eastern South America beyond the scope of this study; see Zimmer 1950) should be considered allospecies within this superspecies.

In this connection, an interesting analysis of the northern forms of the *mellisugus* complex has recently appeared (Howell 1993). Using arguments similar to those employed here, Howell has presented strong evidence for recognizing *auriceps* of western Mexico and *forficatus* of Cozumel Island, as distinct species. He also advocates recognizing *salvini* of northern Central America as distinct from *canivetii* of southeastern Mexico and extreme western Guatemala (considering the two to comprise a superspecies). In the latter case, however, depth of tail fork (in both sexes) appears to be the only reasonably clear-cut difference. This difference is on the same order of magnitude as that between *caribaeus* and *napensis* (in fact, the mean ratio of the relative tail forks of males of the latter two forms is ca 2.19, whereas the corresponding mean ratio for *canivetii* and *salvini* is only 1.30). The differences in patterns of the rectrices cited by Howell between the two forms (cf his fig. 1) are of a magnitude that, in my experience, could be subsumed by individual variation. In the absence of a more detailed analysis of geographic variation within each form, I am hesitant to follow Howell (1993) in separating these forms at the species level. For the present, I prefer to adopt a more conservative species criterion and consider *canivetii* and *osberti* (the form of *salvini* in question) as only subspecifically distinct, particularly as there does not appear to be any significant ecological difference between them; this is also more consistent with species criteria in the *mellisugus* complex as a whole (contra Howell 1993). This problem clearly merits further study. Also, in keeping with the mosaic pattern of variation in this complex as discussed here, I consider *auriceps* and *forficatus* as allospecies of the *mellisugus* superspecies, rather than as species apart.

I should note here that I had previously (Stiles and Skutch 1989) ques-

tioned the distinctness of *assimilis* from *canivetii*, based upon apparently intermediate birds that I had observed and trapped (but in most cases not collected) along the Pacific coast of southcentral Costa Rica. While widespread hybridization and introgression does occur between Hoffmann's Woodpeckers *Melanerpes hoffmanni* of northwestern Costa Rica and Red-crowned Woodpeckers (*M. rubrucapillus*) of the southern Pacific area following deforestation (cf Stiles and Skutch 1989; various specimens), I now feel that the evidence for the same in *Chlorostilbon* is still too weak to justify lumping *assimilis* and *canivetii* and recommend further study of this problem. For the present, it seems best to follow current practice (A.O.U. 1983, Sibley and Monroe 1990) in considering these forms to be allospecies; indeed, a limited zone of hybridization would not be inconsistent with this interpretation.

In conclusion, I recommend that the "mellisugus complex" be recognized as a single superspecies rather than being divided into a mixture of separate species and superspecies, some with disjunct distributions. From Mexico to northern South America, I recommend recognition of the following allospecies: *auriceps*, *forficatus*, *canivetii*, *assimilis*, *melanorhynchus*, *gibsoni*, *olivaresi*, and *mellisugus*. Together, the members of the *mellisugus* superspecies show a fascinating pattern of allopatric distributions and mosaic geographical variation that bespeaks a complex evolutionary history fully in keeping with the complicated geological history of Central America and northern South America during the latter part of the Cenozoic. These hummingbirds would seem to comprise a most fruitful group for further genetic, phylogenetic, and biogeographical studies.

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