

THE TAXONOMIC STATUS OF THE HUMMINGBIRDS  
*CHALYBURA MELANORRHOA* AND *CHALYBURA UROCHRYSIA*

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The genus *Chalybura* is a small group of tropical hummingbirds notable for modification of the under tail coverts into little downy plumes, hence the vernacular name "Plumeleteer" given them by Gould. The Bronze-tailed Plumeleteer, *Chalybura urochrysia*, is a polytypic species, whose undoubted subspecies range from western Ecuador and Colombia northward to the Caribbean slope of extreme western Panamá. On the Costa Rican border and northward into Caribbean Nicaragua it is replaced by the Dusky Plumeleteer, *C. melanorrhoa*, which differs from all other forms of the genus by having black rather than white under tail coverts. The question whether it is a distinct species or merely a subspecies of *C. urochrysia* has been unresolved. Griscom (1933: 301), on the basis of two examples that seemed "obvious intergrades" between *melanorrhoa* and *C. urochrysia isaurae* of western Panamá, proposed treating them as conspecific. Peters (1945:79) indicated some doubt by listing the northern form as *Chalybura (urochrysia?) melanorrhoa*. Howell (1957:84) expressed the view that *melanorrhoa* was a distinct species, in the belief that in *C. urochrysia*, unlike *melanorrhoa*, females look like males. This view was based on a mis-sexed or masculoid Colombian specimen. In fact females of the *urochrysia* group differ from males in the same manner as do those of *melanorrhoa*, that is, they are drab gray below.

In an effort to solve the problem we examined a total of over 170 examples (see Appendix) of the various forms. We tried to see all available specimens of the rare *isaurae* and of birds from the presumed zone of contact between that race and *melanorrhoa*. While in Europe, Eisenmann was able to examine a number of specimens, including those types of *Chalybura* not held in the United States.

ACKNOWLEDGMENTS

Examination of so many specimens of a small group of hummingbirds with restricted range was possible only because of the cooperation of the curators of many museums and the owners of two private collections. While the majority of the specimens examined are in the collection of the American Museum of Natural History, we are indebted to E. R. Blake of the Chicago Natural History Museum, to H. Friedmann, then of the United States National Museum, to J. C. Greenway, Jr. of the Museum of Comparative Zoology, to H. O. Havemeyer of Mahwah, New Jersey, and to K. C. Parkes of the Carnegie Museum, each of whom lent specimens for comparison. Professor J. Berlioz of the Muséum d'Histoire Naturelle of Paris facilitated the examination not only of examples in that museum but also in his private collection, and, as a hummingbird specialist, afforded us the benefit of his opinion. The authorities of the British Museum (Natural History) made available their examples of this group, including types. Dr. A. Wetmore arranged the loan of several unrecorded specimens in the United States National Museum collected by him, and he generously gave us his views on several matters.

CHARACTERS AND DISTRIBUTION OF THE  
*CHALYBURA UROCHRYSIA* COMPLEX

Before discussing our conclusions, it is necessary to review briefly the characteristics of the different forms and their ranges as presently known. The group as a whole occurs in humid lowland forest from sea level to about 3000 feet and, except for a gap

in central Panamá, has a continuous range from western Ecuador northward to Caribbean Nicaragua.

*Chalybura urochrysia urochrysia* (Gould)

*Hypuroptila urochrysia* Gould, Monog. Trochil., pt. 22, pl. and text, July, 1861. "The neighborhood of Panama" = western Colombia (Peters, 1945:80).

*Range*.—Humid lowlands of western Colombia (Pacific and northwestern Caribbean slopes) to western Ecuador and extreme eastern Panamá (southeastern Darién). The presence of this form in Panamá has not been reported previously. We are indebted to Dr. A. Wetmore for calling our attention to three males in the United States National Museum from Cana, 1800 ft. (coll. Goldman), and Río Jaqué (coll. Wetmore and Perrygo). These examples, although close to *urochrysia* of Colombia, show some characters tending toward *incognita*.

*Type locality*.—Gould attributed the type, obtained from the botanist Warszewicz, to "the neighborhood of Panama." Although now labelled "Panama," the type is undoubtedly a specimen of the race found in Colombia, and Peters (1945:80), unaware of the occurrence of this form in eastern Panamá, substituted "western Colombia" as the type locality. Nevertheless, Peters was probably correct, for (*vide* A. Wetmore *in litt.*) Warszewicz collected in western Colombia, and his sojourn in Panamá was limited to the central and western parts where nominate *urochrysia* does not occur.

*Nomenclature*.—The spelling "*urochrysia*" here adopted is that accepted by Peters (1945:80) as having priority. Earlier authors employed *urochrysa*. Gould, the describer, used three versions, *urochrysia*, *urochrysa*, and *urochrysea*, in publications issued the same year (1861a:2, 1861b:198, 1861c:72). Although Gould used *urochrysa* in the paper read to the Zoological Society of London in May of 1861 (1861b), intended as the original description, that paper was not actually issued until September of 1861 (Duncan, 1937:72), by which time Gould had already published the portion of his monograph of the Trochilidae (1861a) describing this hummingbird under the emended name *urochrysia*, which thus gained technical priority.

*Characters*.—This is the greenest form. Adult males are green above and below, with some bronzy tone on rump and upper tail coverts; the tail is golden-bronze with a strong green gloss; under tail coverts and femoral tufts are white. Adult females resemble the males above but have gray tipping to the outer rectrices; gray underparts, except for dull white under tail coverts and femoral tufts, with a very little green gloss on the sides.

*Comments*.—A specimen from Colombia in the American Museum marked "♀?" and collected by W. B. Richardson, looks like a typical adult male. Richardson-collected birds are often mis-sexed, but it is possible that this specimen may be a masculoid-female—a condition not too rare in some hummingbirds. The emerald green throat and breast color of Colombian and Ecuadorian males resembles that of the distant *melanorrhoea*. Birds from Ecuador tend to be a little greener on the rump and upper tail coverts than those from northern Colombia. The three examples from southeastern Darién are a little more bronzy on the upper tail coverts and tail than most Colombian birds, and one of the three shows a very slight bluish tinge to the green throat, all features suggesting intergradation toward *incognita*.

*Chalybura urochrysia incognita* Griscom

*Chalybura urochrysa incognita* Griscom, Amer. Mus. Novit., no. 293:3, 1928. Tacarcuna, eastern Panamá.

*Range*.—Extreme eastern Panamá, both slopes, San Blas coast of Colón province and most of Darién province except southeastern part. Doubtless intergrades with nominate *urochrysia* in southern Darién and in extreme northwestern Colombia.

*Characters*.—Intermediate in color between *urochrysia* and *isaurae* of western Panamá. Adult males with throat and breast bluish green (usually not so blue as in *isaurae*); rump and upper tail coverts more coppery and tail more bronzy green than in *urochrysia* but distinctly less coppery or bronzy than in *isaurae*. Females show distinctly wider tail tipping (7 to 9 mm. on outer web of outermost rectrices) than the other forms, the tipping being much wider (often by 3 to 4 mm.) on the outer web than on the inner web. In *isaurae* and *urochrysia* the tail tipping runs from 4 to 6.5 mm., and the difference between the two webs of same rectrix is usually slight (1 to 2 mm.).

*Comments.*—Although the number of females examined was small and probably not indicative of the full range of variation, the tail difference suggests that *incognita* may be more than merely an intergrading population between *urochrysis* and *isaurae* of western Panamá. Examples from the Caribbean slope of eastern Panamá (Obaldía and Permé) seem more bluish below and thus are closer to *isaurae* than are those from Tacarcuna, Darién. There appears to be a gap between the known ranges of *incognita* and *isaurae*. No member of this species has been taken in central Panamá, including the Canal Zone. Perhaps the Caribbean forest in this area is not sufficiently humid or too much of it has been cleared. There may thus be competition from the larger White-vented Plumeteer (*Chalybura buffonii*) which favors more open woods. The two species, however, are geographically sympatric in Darién and northwestern South America.

*Chalybura urochrysis isaurae* (Gould)

*Hypuroptila isaurae* Gould, Proc. Zool. Soc. London, 1861:199. "The Bocca del Toro in Costa Rica" = Bocas del Toro, Panamá.

*Range.*—Caribbean slope of western Panamá, provinces of Bocas del Toro, Veraguas and western Colón (Chilar on Río Indio [coll. Wetmore]), in eastern part of range crossing over to humid Pacific foothill forest of eastern Veraguas (Santa Fé).

*Characters.*—Adult male with throat and breast greenish blue to bluish green; mainly bronze green above, sometimes with strong coppery tones, rump usually coppery bronze, the upper tail coverts more coppery (often reddish or purplish coppery); tail bronze, usually with a slight green gloss, sometimes more violaceous; under tail coverts and femoral tufts white. Adult female similar above, but with gray tips to outer rectrices; underparts drab gray, slightly glossed with green on sides; under tail coverts and femoral tufts dull whitish.

*Comments.*—This form, which is very rare in collections, shows considerable variability, especially the population from Bocas del Toro, which presumably is, or has been, in contact with *melanorrhoea* of adjacent Costa Rica. The characters given are those found in examples that differ most from *melanorrhoea*. The bluish throat and breast and the white under tail coverts, sometimes showing a little dusky near the shaft or tip, are the most consistent features; reddish coppery upper tail coverts and bronzy tail are also usually present. The apparent interbreeding with *melanorrhoea* will be discussed beyond.

*Chalybura urochrysis melanorrhoea* Salvin

*Chalybura melanorrhoea* Salvin, Proc. Zool. Soc. London, 1864:585. Tukurriqui, Costa Rica.

*Range.*—Caribbean lowlands of Nicaragua and Costa Rica to the Panamá border region (Río Sixaola).

*Characters.*—Adult male bronzy green above, upper tail coverts dusky violaceous (darker than tail), tail dark violaceous bronze; throat and breast emerald green, abdomen dusky, glossed with green or bronze; under tail coverts black; femoral tufts dark gray. Adult female similar, but tail usually with greenish gloss, the rectrices narrowly tipped with gray (usually 1.5 to 4 mm., occasionally more); underparts drab gray, somewhat darker than in the southern forms, usually with more green gloss, especially on middle of breast; under tail coverts and femoral tufts drab gray. Many specimens from Costa Rica are more green or bronzy on the tail and show other characters suggesting interbreeding with *isaurae*.

*Comments.*—Our reason for treating this form as a race of *C. urochrysis* will be discussed beyond.

In an area of virgin, very humid forest in northeastern Costa Rica, Slud (1960:95, 118, 124) reports *melanorrhoea* "common to abundant," although individuals were usually observed alone; he found it characteristic of the higher stratum of the forest understory, between near eye-level to about five meters, but noted it also in the shady second growth and sometimes in semi-open tree-plantations.

RELATIONSHIP BETWEEN *MELANORRHOA* AND *ISAURAE*

The specific status of *melanorrhoea* depends on whether it is reproductively isolated from *C. urochrysis isaurae*, which it replaces in the Costa Rica-Panamá border region and northward. As we have little behavioral information regarding the members of this

complex beyond the fact that they all occur in humid lowland forest and forest borders, our conclusions are necessarily based on inferences from specimens.

#### COMPARISON OF COLOR CHARACTERS

Comparing specimens of *melanorrhoa* from Nicaragua and northern Costa Rica (farthest away from genic contact with *isaurae*) with the most dissimilar *isaurae* from Veraguas in western Panamá, we find the following differences to distinguish the adult males of each form.

Characters	<i>melanorrhoa</i>	<i>isaurae</i>
Rump	Greenish bronze to violaceous bronze	Coppery bronze
Upper tail coverts	Dusky violaceous	Reddish coppery
Tail	Dark violaceous bronze	Bronze glossed with greenish
Throat and breast	Emerald green	Greenish blue
Abdomen	Blackish glossed with green or bronze	Gray glossed with green or bronze
Under tail coverts	Black glossed with violet	White
Femoral tufts	Dark gray	White

The most uniform and easily determined distinguishing characters are the color of the under tail coverts, throat and breast, and upper tail coverts and tail. In *isaurae* there is a strong tendency to produce individuals with very brassy to coppery pileum and back surface; but a brassy color sometimes occurs in *melanorrhoa* (even in Nicaragua) and in the other populations.

Females of *melanorrhoa* and *isaurae* differ essentially as do adult males, but in lesser degree. Both are predominantly drab gray below, have gray tipping on the lateral rectrices and show little contrast above. In both, the tail usually has some greenish gloss. Females of *melanorrhoa* have the sides of the breast extensively glossed with green, often extending over the center of the breast, the tail tipping is usually narrower, generally from 1 to 4 mm. (rarely 5 to 6.5), and the under tail coverts and femoral tufts are distinctly gray. Females of *isaurae* show very little green on the sides, the tail-tipping runs wider, 4 to 6.5 mm., and the under tail coverts and femoral tufts are paler (dull white).

#### DISTRIBUTIONAL STATUS

The older authors (Ridgway, 1911; Cory, 1918) treated *melanorrhoa* and *isaurae* as sympatric, with a reported range overlap from southeastern Costa Rica (Talamanca) to western Panamá (Veraguas). Ridgway (1911:392) lists a specimen of *melanorrhoa* from western Panamá ("Verágua") and Cory (1918:219) one from "Panama." Ridgway (1911:391) gives Costa Rican localities for *isaurae* as "Talamanca; Puerto Limón." Peters (1945:79) does not include Costa Rica within the range of *isaurae* and states that the Talamanca records are erroneous. The curators of ornithology of the United States National Museum and of the Chicago Natural History Museum advised us (*in litt.*) that they could not find in their collections any examples of *melanorrhoa* from Panamá or any examples of *isaurae* from Costa Rica. Apparent intermediates, presumably the specimens referred to by Ridgway and Cory, are discussed beyond.

The available data fail to indicate sympatry. Birds from Costa Rica are either *melanorrhoea* or closest to that form; birds from western Panamá are either *isaurae* or closest to *isaurae*, except in the immediate vicinity of the Costa Rican border where examples intermediate between the two and some nearer to *melanorrhoea* have been taken. Carriker collected five examples identified as *melanorrhoea*, on "Rio Sicsola, Costa Rica" (Carnegie Museum); he has advised (*in litt.*) that most specimens so labelled by him were taken on the southeast side of the Sixaola River, which now by treaty is Panamanian territory.

The Sixaola River, which forms the international boundary, is certainly no faunal barrier, but in this area the mountains reach close to the Caribbean Sea and thus restrict the lowland forest zone to a narrow strip between the highlands and the coastal mangrove swamps. Suitable habitat has been further reduced, over the past half century or more, by extensive clearing on both sides of the border for the vast banana plantations of the United Fruit Company. As a result the zone of contact for these forest dwelling forms must be narrow, and, at least on the Panamanian side of the border, hummingbirds of this complex are rare. Dr. A. Wetmore (*in litt.*) spent February to March of 1958 in western Bocas del Toro and Eisenmann (1957) was there almost a week in June and July, 1956, without observing a hummingbird of this group.

#### EVIDENCE OF INTERBREEDING

*Specimens from the border area.*—Of the five males taken by Carriker at "Rio Sicsola, Costa Rica" (probably in Panamá) one seems intermediate in all characters except tail color between *melanorrhoea* and *isaurae*; it shows an obvious mixture of black and white on the under tail coverts and some bluish tinge below. Although the other four have solid black under tail coverts, and, in general, seem nearer to *melanorrhoea*, they all deviate from *melanorrhoea* and approach *isaurae* in color of the upper tail coverts and tail. Two show also a perceptible bluish tinge below, and one seems intermediate in the shade of the abdomen and femoral tufts. Two males taken by Carriker at Cuabre, on the Costa Rican side of the Sixaola River, have black under tail coverts but show intermediacy in color of upper tail coverts and tail and in the presence of bluish tinge below; one has femoral tufts somewhat lighter than normal for *melanorrhoea*.

Five males taken by Austin Smith (H. O. Havemeyer collection, now at Yale) come from other localities in the border region. Of three taken at Zegla, Terebé River, Bocas del Toro, Panamá, two have obviously mixed under tail coverts and seem intermediate between *melanorrhoea* and *isaurae* in every character. The third has largely white under tail coverts with narrow dusky marks near the shafts, and, although closer to *isaurae* in bluish throat and other characters, it is by no means typical, having a rather violaceous tail and darker femoral tufts and abdomen. Griscom (1933) designated the two with mixed under tail coverts as intergrades, labelling them "*isaurae* ± *melanorrhoea*," and the third *isaurae*. In the same collection are two birds from the Costa Rican side (Daytonia Farm, Talamanca) that also appear to be of mixed ancestry. Both deviate from *melanorrhoea* in having some bluish tinge below and rather coppery upper tail coverts and rump; one also shows a little whitish at the edges of some under tail coverts, more bluish breast, paler femoral tufts and a bronzy tail that lacks violaceous tone.

In the United States National Museum are a male and female from Puerto Limón, Costa Rica—about 45 kilometers from the Panamá border—which Ridgway (1911) identified and labelled as *isaurae*. The label identifications have since been changed: in the male to *melanorrhoea* x *isaurae*; in the female to *melanorrhoea*. The male shows

obvious intermediate characters. It has mainly white under tail coverts with dusky tips and shaft streaks, bronzy tail with greenish gloss, grayish abdomen and femoral tufts, green throat and breast (without bluish tone), and dark violet upper tail coverts. The female (not in very good condition) looks like *melanorrhoa*, except that the underparts seem less glossed with green and the tail tipping is rather broad (5 mm.), a feature of doubtful significance. Two males from Atalanta, Estrella Valley, about 20 kilometers from the Río Sixaola, seem indistinguishable from Nicaraguan birds, except that one has the tail distinctly greenish and with a very faint bluish tone below. Our notes on a male from Old Harbor [Puerto Viejo], Talamanca (Chicago Nat. Hist. Mus.), indicate no deviation from *melanorrhoa*. A male from Santa Rosa Farm, Limón, deviates from the typical in greenish bronze tail and coppery upper tail coverts. Similar deviations appear in other Costa Rican specimens taken away from the border zone.

From the Panamá side of the border the indications of introgression seem more evident, because, when carefully examined, many examples of *isaurae* show some dusky markings on the under tail coverts. More obviously "intermediate" is an example from Almirante, Bocas del Toro, about 35 kilometers from the border, which has conspicuously mixed under tail coverts, violaceous upper tail coverts, and a rather dusky abdomen. Two others from the same locality show only a trace of dusky on the under tail coverts and are less deeply violaceous on the upper tail coverts. The type specimen of *isaurae*, which probably came from near the town of Bocas del Toro ("the Bocca del Toro"), about 40 kilometers from the border, has the abdomen darker and the throat and breast less blue than normal—probably explicable by immaturity, as the gorget is edged with grayish.

Ridgway's attribution of *melanorrhoa* to "western Panamá (Verágua)" appears to be on the basis of an old specimen from the George Lawrence collection, now in the American Museum of Natural History, which bears on its label the pencilled locality "Veragua" but no date or collector's name. This example resembles *melanorrhoa* in emerald green throat and breast and violaceous tail and upper tail coverts, but it is like *isaurae* in that the remnants of under tail coverts and femoral tufts (feet are missing) seem unmarked white (although discolored), and the dorsal color is more bronzy than usual in *melanorrhoa*. "Veragua" in former times was much more extensive than the modern province of Veraguas; at one period it included what is now Bocas del Toro.

It is plain that in the border zone between Costa Rica and Panamá, using this term in the arbitrary sense of 50 kilometers in each direction from the boundary, almost all males show some mixture of characters of *melanorrhoa* and *isaurae* and many are seemingly intermediate, even to the color of the under tail coverts. Certainly we find no evidence of sympatry. No examples of *isaurae* from Costa Rica could be discovered and no "pure" or typical *melanorrhoa* from Panamá, although intermediates occur in both countries. Indications of introgression tend to decrease with the distance from the zone of contact. Certain characters of each form seem more stable than others.

#### EVIDENCE OF POSSIBLE INTROGRESSION IN INDIVIDUAL CHARACTERS

*Under tail coverts.*—This is the most conspicuous, and in *melanorrhoa* apparently the most stable, distinguishing character. Yet of 20 males from the border zone, almost half (9) showed indications of mixture in this character, and five of these, coming from both sides of the border, had the under tail coverts conspicuously (almost equally) mixed black and white. The tendency was not limited to the border zone. Moreover, mixture in color of under tail coverts was almost invariably associated with some other character that suggested introgression.

Of 64 males from the range of *melanorrhoea*, two (Puerto Limón and Sixaola) showed an obvious mixture, three (Daytonia Farm, Angostura, Parismina) showed a slight amount of white; the rest were solid black. Angostura is over 100 kilometers from the Panamanian border and Parismina is somewhat farther. Both birds from these localities showed a slight bluish tinge below, and the individual from Angostura had greenish tail gloss and rather pale femoral tufts.

Of 25 males from the range of *isaurae*, three (Zegla, Almirante) showed an obvious mixture, eight had at least a trace of dusky near the shaft or at the tip or one or more coverts, and 14 were pure white. Of nine males from Bocas del Toro (all within the border zone), only two had pure white under tail coverts—the type and one from the hills farther east (Boquete trail, 1800 ft.). Of 15 examples from the provinces of Veraguas and Colón, only four have dusky near the shaft, although one Colón bird has a tiny brown spot on one covert. While the broad geographic trend is evident, there is considerable local variation; for example, of three examples from Almirante one is heavily marked with dusky and two are only slightly marked; and of two from Sante Fé, Veraguas, one is pure white and the other very slightly marked.

*Throat and breast.*—With the single exception of the one old "Veragua" example in the American Museum (mentioned previously), all individuals from Panamá show on the throat and breast a distinct bluish tone, which varies from greenish blue to bluish green. The bluest examples seen, one from Almirante, Bocas del Toro, and one from Chilar, Colón, were at almost opposite ends of the range of *isaurae*. Professor Berlioz, in conversation with us, has suggested that extreme blueness is a product of age. So far as we can determine, the variation in blueness does not noticeably differ in Veraguas and Bocas del Toro if we except the few birds from near the Costa Rican border which run greener than the others. In the range of *melanorrhoea* the seven males from Nicaragua are solid green, but of 52 Costa Rican examples, 19 show some (usually slight) tinge of blue. Although the occurrence and strength of a bluish tinge varies even locally, it seems absent in birds from northern Costa Rica and is most frequently noted as one approaches the range of *isaurae*. Specimens with bluish below seem always to show some other character tending toward *isaurae*. On the other hand, two of the five birds taken by Carriker at Río Sixaola (possibly on the Panamá side) are as green below as Nicaraguan birds, although intermediacy is strongly suggested in other features.

*Upper tail coverts.*—Dusky violaceous upper tail coverts are almost as uniform a feature in males of *melanorrhoea* as black under tail coverts. All our Nicaraguan males show it, and likewise 43 out of 52 Costa Rican birds (excluding Carriker's five from Río Sixaola, all of which evidence an approach to *isaurae* in this character). Of the few birds from Costa Rica that tend toward the color of *isaurae* (two from Cuabre near the Panamá border, several from southern Limón province, and one each from El Hogar and Guápiles) all but one show also some other tendency toward the southern form. Panamanian birds, *isaurae*, are much more variable in the color of the upper tail coverts; these range from bronze and reddish copper, to distinctly violaceous bronze. We have seen no Panamanian birds with the upper tail coverts quite as dusky violaceous as in most *melanorrhoea*, although violaceous bronze crops up in specimens from Veraguas as well as in those from Bocas del Toro.

*Tail.*—Tail color is a variable feature in *melanorrhoea*. Intergradation seems apparent. The seven adult male Nicaraguan examples have dark violaceous bronze tails without greenish gloss. This is likewise true of 27 out of 57 Costa Rican specimens. The other 30 show a varying amount of green gloss, and a few lack any violaceous tone. The number of individuals showing some green tail gloss increases southward, but birds from the same locality may be as greenish bronze as *isaurae* from Veraguas or as dark

violaceous as *melanorrhoa* from Nicaragua. It is possible that younger male *melanorrhoa* may have a tendency toward greenish tails; this is certainly true of females, few of which lack some green gloss. From Panamá we have noted only one example (the previously mentioned specimen marked "Veragua") with a tail as dark violaceous as typical *melanorrhoa*; eight out of 21 others show tones varying between bronze and violaceous bronze although always with a green gloss, similar to many Costa Rican individuals. The violaceous tendency, although occurring in more specimens from Bocas del Toro, is also found in some examples from Veraguas and Colón.

*Other characters.*—Rump color is extremely variable. Even Nicaraguan males, usually so uniform, have rumps that may be greenish bronze, coppery bronze, or violaceous bronze. Examples from Costa Rica are matched by those from Panamá, except that the reddish copper extreme of *isaurae* has not been noted in Costa Rica and the dark violaceous extreme of *melanorrhoa* has not been noted in Panamá. The tendency toward a greenish bronze as well as violaceous bronze rump is commoner in Costa Rican birds than in specimens from western Panamá.

The color of the abdomen and femoral tufts seems generally to parallel that of the under tail coverts. Differences and intermediacy between the two forms are much harder to detect, because in both the abdomen usually is heavily glossed with green or bronze, and because the femoral tufts are often missing or soiled in specimens. In a few examples from both Costa Rica and Panamá, intermediacy in one or both of these characters could be detected.

*Females.*—Evidence of introgression in females is more difficult to produce, for in this sex the differences between the two forms are less striking and relatively few specimens (none from the presumed zone of contact) were available. One female from Hacienda La Ibéria, Limón, Costa Rica, has the greenish glossed underparts and the dorsal color of *melanorrhoa* but distinctly suggests *isaurae* in exceptionally wide tail-tipping (6 mm.), strongly green glossed tail, almost whitish femoral tufts, and light gray under tail coverts. Three males from this locality also show two to three characters tending toward *isaurae*, including paler than normal femoral tufts.

#### DISCUSSION AND CONCLUSIONS

In most characters the differences between the various forms of the *C. urochrysis* complex are clinal, involving progressive intensification of color northward. The upper tail coverts and tail gradually become darker, less greenish, and more bronzy and coppery to purplish, from the South American *urochrysis*, through the Panamanian *incognita* and *isaurae*, to the Central American *melanorrhoa*. The cline is different for throat and breast color, as both the terminal forms are emerald green whereas the two isthmian populations are greenish blue or bluish green. In all other characters *melanorrhoa* is closest to its nearest neighbor *isaurae*, and even in throat and breast color, intergradation, or perhaps introgression, is evident in a number of individuals. Except for the contrast between black and white under tail coverts, the differences between *melanorrhoa* and the white-vented members of the *urochrysis* group are not such as to suggest distinct species of hummingbirds.

To be sure, *melanorrhoa* differs more sharply from "typical" examples of the geographically adjacent *isaurae* than does *isaurae* from *incognita*, or *incognita* from *urochrysis*. *Melanorrhoa* may well have developed in Central America in isolation, while the other populations of the group remained in genic contact. The contact between *melanorrhoa* and *isaurae* on the Costa Rica-Panamá border may be relatively recent, although the specimens suggest that it already existed about a century ago.

In a group like the genus *Chalybura*, with under tail coverts peculiarly developed



into plumelets, the supposition is reasonable that this feature is used in display as a sexual signal character. Neither of us has observed, or found described in the literature, the display of any *Chalybura*. It is probable, however, that like certain other hummingbirds, the male gyrates or moves up and down, with body vertical, in a manner exposing the plume-like under tail coverts. Compared with the white coverts of the southern forms, the black coverts of *melanorrhoea* must provide little contrast with the dusky abdomen. *A priori* one would suppose that this might serve as a reproductive isolating mechanism. Yet we have no evidence that such is the case. It may be significant that compared with the other species of the genus *Chalybura*, *C. urochrysia* has less well-developed plumelets, and that within this species the northern races, *incognita*, *isaurae* and *melanorrhoea*, have narrower and shorter plumelets than the nominate South American race.

*Melanorrhoea* and *isaurae* evidently interbreed, forming a mixed population in the zone of contact. Especially in hummingbirds that presumably form no pair bond, the existence of first generation hybrids would not be proof of conspecific relationship. Occasional interspecific mistakes between sympatric forms might be expected (see Banks and Johnson, 1961; Sibley, 1957). But here, although their ranges meet, the parental forms do not seem to be sympatric. We find a zone with a population of variable "hybrid" characters, indicative of considerable genic interchange resulting from back-crossing. The breakdown of biological barriers to reproduction can result from the rarity of one or both of two allied populations in the contact zone, with consequent difficulty of finding suitable mates (Miller, 1955; Bauer, 1957). But when allied contiguous forms known to interbreed in the wild are good species, in the sense of being biologically isolated, the existence of barriers to free genic interchange is usually indicated by the persistence of some sympatry in the parental stocks.

"Smooth" intergradation is not to be expected even between subspecies, where a number of visible differences exist and the contact is secondary. Interbreeding is almost certain to produce a variety of character combinations (*cf.* Banks and Johnson, 1961). That in the range of *melanorrhoea* few birds show admixture of white in the under tail coverts—in contrast with the opposite situation in the range of *isaurae*—may indicate that black is genetically dominant or that there is greater infiltration of the more numerous *melanorrhoea* into the range of *isaurae* than the reverse. It is noticeable, however, that such characters of *isaurae* as the tendency toward blue tone below and green tail gloss occur extensively in the *melanorrhoea* population of Costa Rica, particularly in the region nearest to Panamá.

As *melanorrhoea* appears not to be reproductively isolated from *C. urochrysia isaurae*, we believe it should be treated as conspecific.

#### SUMMARY

The races of the neotropical hummingbird, *Chalybura urochrysia*, are reviewed and their characters and ranges are indicated.

*Chalybura melanorrhoea* from Central America, whose status has been considered doubtful, appears to interbreed with the adjacent form of western Panamá, *C. urochrysia isaurae*, and should be treated as a race of *C. urochrysia*.

#### APPENDIX

##### SPECIMENS OF *CHALYBURA UROCHRYSIA* EXAMINED

Letters in parentheses indicate location of specimens as follows: (A), American Museum of Natural History, New York, N.Y.; (B), British Museum (Natural History), London, England; (C), Carnegie Museum, Pittsburgh, Pa.; (CN), Chicago Natural History Museum, Chicago, Ill.; (CZ), Museum of Comparative Zoology, Cambridge, Mass.;

(H), H. O. Havemeyer Collection (now at Yale Peabody Museum, New Haven, Conn.); (JB), Collection of Professor Jean Berlioz, Paris, France; (P), Muséum d'Histoire Naturelle, Paris, France; (US), United States National Museum, Washington, D.C.; (UC), University of California, Los Angeles, Calif.

All Costa Rican specimens are listed under *melanorrhoea* and all western Panamanian specimens are listed under *isaurae*, although some are evident intermediates, as indicated in the text.

***incognita* (♂♂ 24, ♀♀ 9)**

PANAMA ♂♂ 24: Tacarcuna, Darién 10 (A, incl. type); Permé, Colón 6 (CZ); Ranchón, Colón 2 (B); Puerto Obaldía, Colón 3 (CZ), 3 (JB). ♀♀ 9: Tacarcuna, Darién 5 (A); Permé, Colón 3 (CZ); Puerto Obaldía, Colón 1 (JB).

***urochrysis* (♂♂ 21, ♀♀ 4, sex uncertain 1)**

PANAMA ♂♂ 3: Cana, Darién 1 (US); mouth of Río Imamadó, Río Jaqué, Darién 2 (US); (tending toward *incognita*).

COLOMBIA ♂♂ 10: "Panama" [= western Colombia (?)] 1 (B, type); Buenaventura, Cauca 2 (A); Alto Bonito 1500 ft., Cauca 1 (A); Buenavista 1200 ft., Nariño 1 (A); Río Sipí, Chocó 1 (JB); Río San Juan, Chocó 1 (JB); Medellín, Antioquia 2 (B); Remedios, Antioquia 1 (B). ♀♀ 2: Bahía de Málaga 1 (A); Río San Juan, Chocó 1 (JB). Sex ? : Barbacoas, Nariño 1 (A, sexed "♀ ?" = ad. ♂ ?).

ECUADOR ♂♂ 8: Cachabi, N. Ecuador 5 (A); Río Sapayo, N. Ecuador 2 (A), 1 (JB). ♀♀ 2: Río Goyatá 1 (A); Río Sapayo, N. Ecuador 1 (A).

***melanorrhoea* (♂♂ 64, ♀♀ 22)**

NICARAGUA ♂♂ 7: Peña Blanca 2 (A); Saval Mata [= Savala, Matagalpa] 1 (A); Río Grande 2 (B); Chontales 1 (B); Los Sábalo 1 (US). ♀♀ 4: Río Grande 1 (A); Chontales 1 (B); El Recreo 2 (UC).

COSTA RICA ♂♂ 57: Tucurriqui 4 (B, incl. type); Bonilla 3 (A), 5 (US); Guápiles 4 (C); Parismina 1 (A); Jiménez 1 (A); El Hogar 8 (C); Guácimo 1 (A); Turrialba 1 (B); Angostura 1 (A), 1 (B); Reventazón 2 (A); Guayabal 1 (A); Hacienda La Ibérica, Vol. Turrialba 450-500 ft., Limón 3 (A), 2 (CN); Puerto Limón 1 (US); Atalanta 2 (A); Old Harbor [Puerto Viejo] 1 (CN); Santa Rosa Farm, Limón 1 (A); Cuabre 2 (C); Daytonia Farm, Talamanca 2 (H); Río Sicsola [= Río Sixaola, probably Panamá] 5 (C); "Costa Rica" 1 (A), 2 (B), 1 (JB). ♀♀ 20: Bonilla 2 (A), 5 (US); Guápiles 1 (A), 1 (C), 1 (H); El Hogar 3 (C); Hacienda La Ibérica, Limón 1 (A); Puerto Limón 1 (US); "Costa Rica" 1 (A), 2 (B), 1 (JB); [Costa Rica] coll. by Endres, no loc. 1 (B).

***isaurae* (♂♂ 25, ♀♀ 4)**

PANAMA ♂♂ 25: "The Bocca del Toro in Costa Rica" [= Bocas del Toro, Panamá] 1 (B, type); Zegla, Terebé River, Bocas del Toro 3 (H); Almirante, Bocas del Toro 3 (A); Boquete trail, 1400-1500 ft., Bocas del Toro 2 (CZ); Santa Fé, Veraguas 1 (A), 1 (B); "Santiago de Veraguas" 1 (B); "Veragua" 2 (A), 2 (US), 1 (CN), 3 (P), 2 (JB); Quebrada Torno Rompío, Chilar, Colón 2 (US); "Panama" 1 (JB). ♀♀ 4: Guaval, Río Calovévora, Caribbean coast, Veraguas 1 (A); Santa Fé, Veraguas 2 (B); one with additional label "Santiago de Veraguas"; "Veragua" 1 (CN).

**ADDITIONAL LOCALITIES OF SPECIMENS REPORTED IN LITERATURE**

***melanorrhoea***

COSTA RICA: La Junta and Siquirres (Carriker, 1910); Pacuare (Ridgway, 1911).

PANAMA: "Veragua" (Ridgway, 1911; not in U.S. Nat. Mus.); "Panama" (Cory, 1918; not in Chicago Nat. Hist. Mus.). [Probably these records relate to the probable hybrids mentioned in text or to similar specimens.]

***isaurae***

COSTA RICA: Talamanca; Puerto Limón (Ridgway, 1911; Puerto Limón specimens are the probable hybrids mentioned in the text; no Talamanca spec. of *isaurae* in U.S. Nat. Mus.; see Peters, 1945).

## urochrysia

COLOMBIA: La Guayacana, Córdoba, Malaguita, Sipí, Río Cajón, Potedó, Nóvita, Condoto, El Tambo (Chocó), Quibdó, Río Baudó, Nuquí, Alto del Buey (900 m.), Río Jampavadó, Río Salaquí, Río Juradó, Santa Elena (all from de Schauensee, 1949); Río Tulapa, near Gulf of Urabá (Haffer, 1959).

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