

SYSTEMATICS OF THE "GREEN-THROATED SUNANGELS" (AVES: TROCHILIDAE): VALID TAXA OR HYBRIDS?

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Abstract.—Four species of hummingbirds, *Heliangelus squamigularis* Gould, 1871, *Heliangelus barrali* Mulsant & Verreaux, 1872, *Heliotrypha speciosa* Salvin, 1891, and *Heliotrypha simoni* Boucard, 1892, were described from 19th century commercial "Bogotá" collections. The systematic status of these taxa, which I collectively refer to as "green-throated sunangels" (GTS), is unresolved, but they have been variously treated as one or more valid species or as hybrids. I examined three systematic hypotheses—that GTS specimens represent (1) one or more valid species; (2) genetic variants of other species; or (3) hybrids. Plumage and mensural characters of GTS ($n = 14$) suggest they represent hybrids of *Heliangelus amethysticollis* × *Eriocnemis cupreiventris* from the Eastern Cordillera of the Colombian Andes. Alternate hypotheses of hybridity are discussed. Discrimination of hybrids and identifying their parental species depends upon an efficient "hybrid diagnosis." The current method of diagnosing hybridity is often insufficient in that the materials, methods, and results are not properly documented. I address these problems and suggest guidelines for hybrid diagnoses.

Untold thousands of hummingbird skins were exported from northwestern South America in the 19th century for the millinery trade and collectors of natural history specimens. Systematists sorted through some of the massive shipments of "Bogotá" trade skins and described dozens of new species, a few from unique specimens (e.g., Boucard 1892). Most were subsequently verified by the discovery of populations; others were determined to be of hybrid origin (Berlioz & Jouanin 1944). However, the validity of more than a dozen taxa remains indeterminate (Morony et al. 1975). These represent some of the most challenging problems in avian taxonomy. Resolving their systematic status depends on the mechanics of discriminating avian hybrids from valid biological species.

This paper has two aims that are addressed concurrently. I evaluate the systematic status of an enigmatic group of hummingbird taxa known only from a handful

of 19th century specimens. Of more general interest, I examine the assumptions, materials, and methods of the hybrid diagnosis in avian taxonomy.

Taxonomy of the "Green-throated Sunangels"

Four species of hummingbirds, that I collectively refer to as "green-throated sunangels" (hereafter abbreviated as GTS), were described from 19th century "Bogotá" collections: *Heliangelus squamigularis* Gould, 1871; *Heliotrypha barrali* Mulsant & Verreaux, 1872; *Heliotrypha speciosa* Salvin, 1891; and *Heliangelus simoni* Boucard, 1892. *Heliotrypha* Gould, 1853 is now considered a junior synonym of *Heliangelus* Gould, 1848.

Taxonomic uncertainty within the group began with Gould (1871), who was initially inclined to consider the type specimen of *H. squamigularis* a sport or variant of some

other *Heliangelus* species, but who after further investigation characterized it as a new species related to *Heliangelus exortis* and *H. amethysticollis*. *H. barrali* and *H. squamigularis* were not compared with one another before being described. Salvin (1892) considered these taxa as identical, but distinct from his newly described *H. speciosa*. In the first review of all four taxa, Boucard (1895) followed Salvin's synonymy of *H. barrali* and *H. squamigularis*, but treated *H. simoni* (Boucard 1892) and *H. speciosa* as valid species, while noting the possibility that both were varieties of *H. squamigularis*. Cory (1918) lumped *H. speciosa* and *H. simoni* and initiated the two-species taxonomy for the group adopted by Simon (1921), Peters (1945), and provisionally by Morony et al. (1975). Hartert (1922), perhaps eued by Boucard (1895), proposed that *H. simoni* and *H. speciosa* were aberrations of a single valid GTS species (= *H. squamigularis*). The possible hybrid origin of GTS was first raised by Berlioz (1936), who suggested that a specimen in Paris, which had previously been identified as *H. simoni* (discussed later), represented a hybrid of *Heliangelus exortis* × *Haplophaedia aureliae*. This opinion was endorsed by Jouanin (1950) and Greenway (1978), but Berlioz & Jouanin (1944) were less conclusive, stating simply that GTS were hybrids between either *H. exortis* or *H. amethysticollis* and some species of *Eriocnemis* (including the closely related genus *Haplophaedia*). Meyer de Schauensee (1949) at first doubted the notion of hybridity but later agreed with Berlioz & Jouanin (1944) and supposed that GTS were hybrids of *Eriocnemis* sp. × *Heliangelus* sp. (Meyer de Schauensee 1966). Hilty & Brown (1986) listed *H. speciosa* and *H. squamigularis* as presumed hybrids without mentioning parental species.

Syntypes of *Heliotrypha simoni*

Boucard's (1892) use of the plural "specimens" in his description of *H. simoni* im-

plied that the description was based on two or more syntypes. Cory (1918) and Lord Rothschild (Hartert 1922) each obtained a syntype of *H. simoni*, presumably from Boucard before his death in 1905. The labels of both specimens (FMNH 46294, AMNH 483683) are marked, "*Heliotrypha simoni*, ♂, Typical specimen, Colombia," in what appears to be Boucard's handwriting (fide Greenway 1978). Simon (1921) stated in a footnote that he could not find the type of *H. simoni* in Boucard's collection, which suggests that only two syntypes existed, both of which were sold or exchanged by Boucard to other museums. Berlioz (1936), however, argued that a specimen in the Boucard Collection labeled "*Heliotrypha speciosa*, ♂, Colombia" (now deposited in MNHN, Paris), was in fact the type and only existing specimen of *H. simoni* (see Berlioz & Jouanin 1944, Jouanin 1950). He apparently based his conclusion on the close resemblance of the specimen to Boucard's description of *H. simoni*, and on the fact that Boucard (1895) did not mention possessing a specimen of *H. speciosa*.

Several explanations are possible for this discrepancy. Assuming that there were originally three examples of *H. simoni*, Boucard may have attached a new label to the remaining syntype after disposing of the other two. Other possibilities are that Boucard (1895) obtained the specimen of *H. speciosa* after the publication of his monograph or that the specimen was labeled by Boucard as *H. speciosa* before he described *H. simoni* and never relabeled afterwards. In any event, only specimens designated by Boucard Museum labels as "*H. simoni*" should be regarded as syntypes.

Materials and Methods

The type specimens of GTS are deposited in three different museums and are not available for loan. This prevented me from comparing all type specimens simultaneously. I examined three type specimens: (1) the type of *Heliotrypha barrali* (AMNH

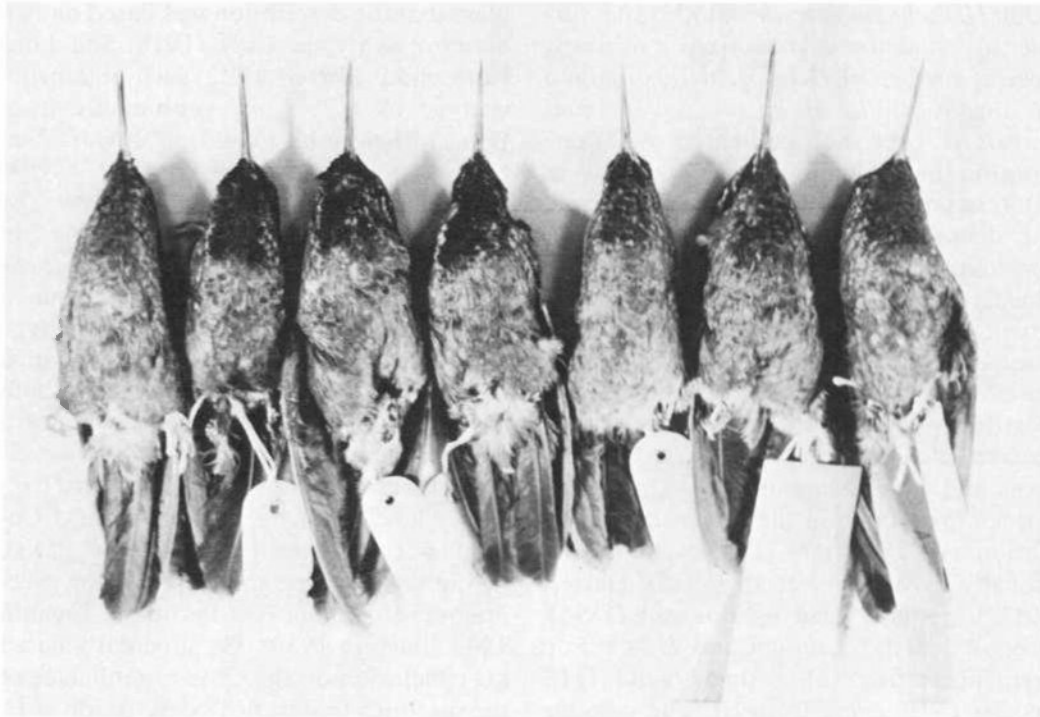


Fig. 1. Ventral view of "green-throated sunangels" deposited in the American Museum of Natural History (from left to right: 483680, 483681, 483678, 483684, 483682, syntype of "*Heliotrypha simoni*" [483683], type of "*Heliotrypha barrali*" [37655]).

37655) and (2) a syntype of *Heliotrypha simoni* (AMNH 483683) in the American Museum of Natural History (see Hartert 1922, Greenway 1978); and (3) a syntype of *Heliotrypha simoni* (FMNH 46294) in the Field Museum of Natural History. The AMNH types were compared directly with five additional specimens (AMNH 483678, 483680, 483681, 483682, 483684) that have been variously identified as one or more of the GTS taxa (Fig. 1). The FMNH type was compared directly with FMNH 46286 (identified as *H. barrali* on its Boucard Museum label). I examined one additional GTS specimen (ANSP 160344 [formerly AMNH 483679]). These specimens were compared with mensural data and color transparencies of the following specimens: one labeled *H. speciosa* (considered by Berlioz [1936] as a syntype of *H. simoni*) in the Museum Na-

tional D'Histoire Naturelle (MNHN), Paris; the types of *H. squamigularis* (BM 88.7.25.178) and *H. speciosa* (BM 87.3.22.889), and an unnumbered specimen of *H. barrali* (photographs only) in the British Museum of Natural History (see Appendix). GTS specimens and color transparencies were compared with series of all hummingbird species in the National Museum of Natural History (USNM) and the American Museum of Natural History. In addition to the GTS specimens examined in this study, at least one other specimen exists (Berlioz 1964). Color comparisons of specimens were made under Examolites® (Macbeth Corp.).

Measurements (wing chord, tail from insertion of central rectrices to tip of the outer and innermost rectrices, and culmen from anterior extension of feathers) were taken

Table 1.—Measurements (mm) of "green-throated sunangels."

	Age ^a	Wing chord	Outermost rectrix	Central rectrix	Culmen
Type specimens					
(1) <i>squamigularis</i> (BM)	adult	63.5 ^b	43.2 ^b	33.0 ^b	16.6 ^c
(2) <i>barrali</i> (AMNH)	immature	63.1	42.8	34.5	17.3
(3) <i>speciosa</i> (BM)	adult	63.5 ^b	40.6 ^b	36.8 ^b	19.4 ^c
(4) <i>simoni</i> (AMNH)	immature	60.4	43.4	33.6	18.5
(5) <i>simoni</i> (FMNH)	adult	64.5	43.3	34.7	16.9
Other specimens					
(6) " <i>speciosa</i> " (MNHN)	adult	64.0 ^d	42.5 ^d	32.0 ^d	19.0 ^d
(7) FMNH 46286	immature	64.5	43.9	35.7	16.8
(8) AMNH 483678	adult	64.6	43.9	35.9	17.1
(9) AMNH 483680	immature	64.5	43.8	35.6	15.7
(10) AMNH 483681	adult	63.7	41.4	33.6	16.3
(11) AMNH 483682	adult	56.5	—	—	—
(12) AMNH 483684	adult	62.3	40.8	—	16.8
(13) ANSP 160344	immature	60.5	39.8	33.6	16.8

^a Immatures have corrugations on the ramphothecum of the upper jaw.

^b Measurement from Salvin 1892.

^c Measurement courtesy of J. Becker.

^d Measurement courtesy of C. Jouanin.

with digital calipers and rounded to the nearest 0.1 mm (Table 1).

I used principal components analysis (PCA) on untransformed variables to reduce the dimensionality of data and to facilitate the analysis of morphology in two dimensions. Unrotated principal components were extracted from correlation matrices (SYSTAT).

Systematic Status of Green-throated Sunangels

Investigations of GTS have engendered a remarkable variety of systematic opinions. If nothing else, this strongly suggests that multiple hypotheses of origin must be addressed. Accordingly, I considered three possibilities. GTS may represent one or more of the following entities: (1) rare genetic variants of other *Heliangelus* species (Gould 1871); (2) hybrids (Berlioz 1936; Berlioz & Jouanin 1944; Meyer de Schauensee 1949, 1966; Jouanin 1950; Greenway 1978; Hilty & Brown 1986), or (3) population samples of one or more valid biological species (Gould 1871, Salvin 1892, Bou-

card 1895, Cory 1918, Peters 1945, Morony et al. 1975).

Do green-throated sunangels represent rare genetic variants of other species?—Several examples of intra-population variation in plumage are known in *Heliangelus* species. Polymorphism in the number of iridescent gorget feathers in females has been well documented, particularly in *Heliangelus exortis* (Chapman 1917; Zimmer 1951; Bleiweiss 1985a, b), and melanism involving part or the entire plumage is known in a number of Andean genera (Hartert 1922, Greenway 1978, Graves, pers. obs.). Intrasexual color polymorphism, however, does not appear to be significantly correlated with size. GTS closely resemble some species of *Heliangelus* (e.g., *H. exortis*), but differ in body proportions from all species and by having lengthened tibial plumes and a green or silvery-green gorget in combination with brilliantly reflective plumage on the posterior part of the body. These qualitative characters indicate that GTS are not plumage variants of any other species of hummingbird.

Hybrids or species?—As demonstrated by a century of equivocal taxonomy, it is difficult to determine whether GTS are hybrids or valid species. This is due primarily to two factors. GTS specimens were collected in the 19th century and are unaccompanied by ecological, sexual, or locality data. They are believed to have originated from the Andean region of northwestern South America, an area of high species diversity where new species of hummingbirds are still being discovered (e.g., *Eriocnemis mirabilis*). The large number of GTS specimens ($n = 15$), presumably collected in a biotically diverse but poorly-known region, favors the valid species hypothesis. On the other hand, the plumage color and morphology of GTS are variable and intermediate between sunangels (*Heliangelus*) and pufflegs (*Eriocnemis* and *Haplophaedia*). This suggests that hybridization is involved. As hybrids have no standing in zoological nomenclature, the burden of proof is on taxonomists to reject the hybrid origin of GTS conclusively before conferring species status on them.

The process of discriminating avian hybrids and their parental species can be termed the "hybrid diagnosis." Most taxonomists consider the pathways of hybrid diagnosis to be self-evident and the documentation of methods and diagnostic assumptions to be unnecessary. However, omissions of these crucial data obscure the diagnoses of all but the most obvious cases of hybridity. Beyond calling attention to an "unusual" specimen, a hybrid report based on an incomplete diagnosis is of little value to taxonomists and evolutionary biologists. As a minimum, the following points (not mutually exclusive), should be explicitly addressed in hybrid diagnoses.

1. Potential parental species: What species were considered as possible parental species and why?

2. Diagnostic assumptions of character analysis: What operational assumptions were made concerning the inheritance of plumage and morphological characters of

hybrids? How were characters defined and apomorphies identified?

3. Documentation of results: Can the hypothesis of hybridity be rejected? If not, how were the parental species identified to the exclusion of all others? How were alternate hypotheses (e.g., valid taxon; genetic or developmental variant) rejected?

Hybrid Diagnosis

Potential parental species.—For any hybrid of unknown parentage, the pool of potential parental species (species hypothetically or actually available for hybridization) can be defined taxonomically and geographically. Interordinal hybridization is unknown in birds (Gray 1958); interfamilial hybridization has been reported in captivity (e.g., turkey \times guinea fowl) but is unknown in nature. Thus, the taxonomic pool can be narrowed considerably if the hybrid can be identified to a particular family-level group (e.g., hummingbird or duck), which is always the case. The taxonomic pool may be further restricted to a subfamily, genus, or a single pair of species when the rationale for doing so can be vigorously supported. For example, Parkes (1984) properly restricted the pool of potential species of a hybrid cuckoo collected in Pennsylvania to the only pair of *Coccyzus* species that occur sympatrically in North America north of the Gulf coast. In the interest of comprehensiveness, however, he could have also addressed the six other species of *Coccyzus* in a few sentences in much the same way a taxonomist would mention other species in the differential diagnosis of a new species.

As suggested by the cuckoo example, the pool of potential parental species can be limited geographically. The degree of limitation depends on knowledge of the migratory habits of the potential parental species and the geographic origin of the hybrid. For instance, the taxonomic pool of potential parental species of a hybrid hummingbird is defined by the family Trochilidae (345+

species). A hybrid hummingbird originating from Arizona could have no more than 20 potential parental species (190 species combinations). On the other hand, a hybrid from an unspecified area of northwestern South America could have 150+ potential parental species (10,440 species combinations). Clearly, the difficulty of hybrid diagnosis is directly proportional to taxonomic species diversity and geographic scope.

Diagnostic assumptions of character analysis.—In diagnosing putative hybrids, I assumed that mensural characters, such as wing and bill length, were polygenic and additive and that the morphology of hybrids does not exceed that of the parental species (Falconer 1981). Plumage characters in hybrids may resemble a mosaic of the parental species or be inherited intact from one parent, depending on the number of encoding genes and their interaction (Hutt 1949, Buckley 1982). Hypothetically, hybrids may exhibit a wide range of plumage phenotypes. The major pigments in bird plumage, melanins, carotenoids, and porphyrins, appear to be under separate genetic control and mutually independent between feather tracts. The inheritance of structural colors, which dominate the plumage of hummingbirds, is poorly understood (Fox & Vevers 1960, Lucas & Stettenheim 1972), but the complexity of color-producing structures suggests a polygenic mode of inheritance.

What little is known about inheritance in hybrid hummingbirds is summarized by Banks & Johnson (1961) and Short & Phillips (1966). Strongly contrasting patterns of non-structural color (e.g., rufous and black rectrices of *Selasphorus* sp.) are expressed in some fashion in all crosses. There is reason to doubt that the same is always true, however, for plumage characters exhibiting brilliant structural color. For example, the coronal iridescence found in species of *Calypte* is evident in five examples of *C. anna* × *Selasphorus sasin* and one specimen of *C. anna* × *Stellula calliope* (although it is never as extensive on the hybrids as it is on

C. anna), but is lacking in the single known *C. anna* × *Archilochus alexandri* hybrid (Banks & Johnson 1961). This suggests either that few genes control the color of coronal plumage or that phenotypic expression is controlled by a modifier in these species. The shape of gorget feathers, rectrices, and remiges of hybrids is generally intermediate between those of the parental species, reflecting a polygenic mode of inheritance.

Banks & Johnson (1961) assumed that hybridization in hummingbirds does not produce traits of species or genera other than those involved in the particular cross. This assumption rules out the possibility of atavistic characteristics—those not found in either parental species but which reflect a pattern postulated to be ancestral or the result of mixed alleles encoding polygenic traits. Although atavism is well known in certain anseriform hybrids (e.g., Harrison & Harrison 1963), it has not been documented in hybrid hummingbirds.

This study was geared toward the identification of apomorphic character states in putative hybrids. The mosaic expression of parental autapomorphies in a number of characters is the best indicator of hybridity of a unique specimen and provides the only direct evidence of parentage. However, because many plumage characters are polygenic, the expression of parental apomorphies may be obscured in hybrids. When parental apomorphies are not identifiable, the parentage of a hybrid may be indicated, although less conclusively, by the expression of a combination of plesiomorphic characters unique to a single pair of parental species.

Results

The original labels of GTS specimens are marked "Columbia" (sic), "Colombia," "New Grenada," or "Bogotá Collection." Thus, the geographic pool can only be defined in general terms. Berlioz & Jouanin (1944) showed that the vast majority of skins

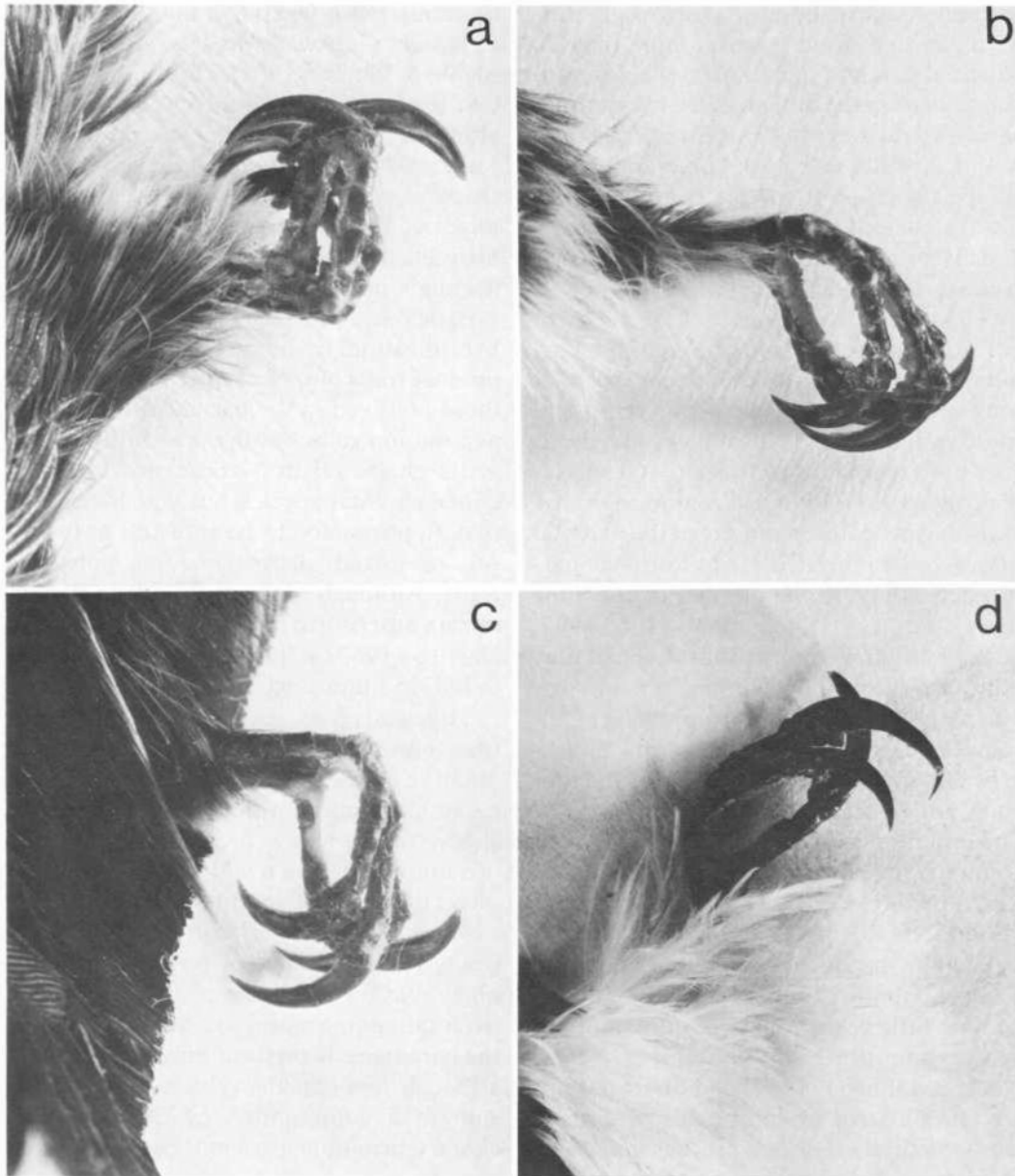
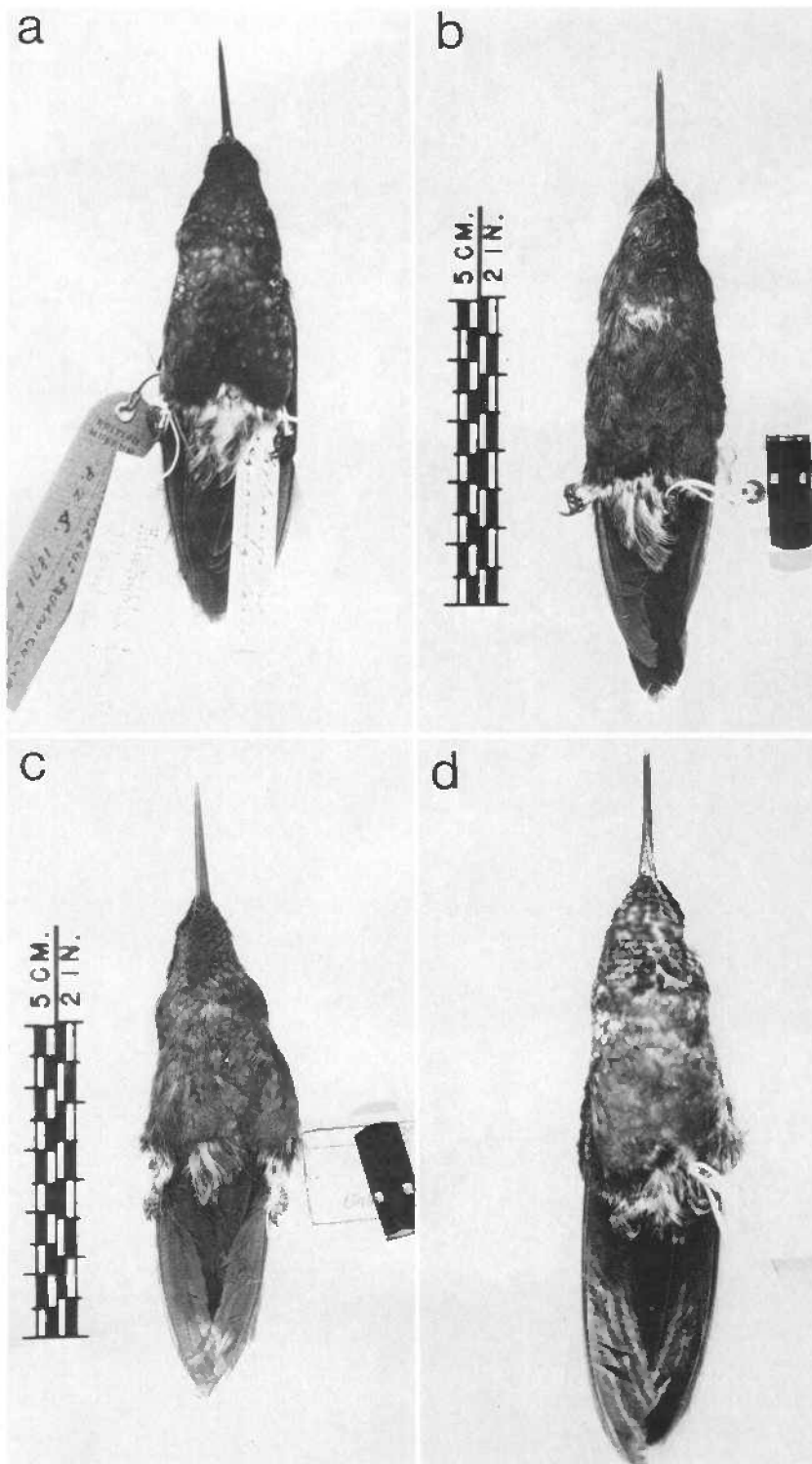
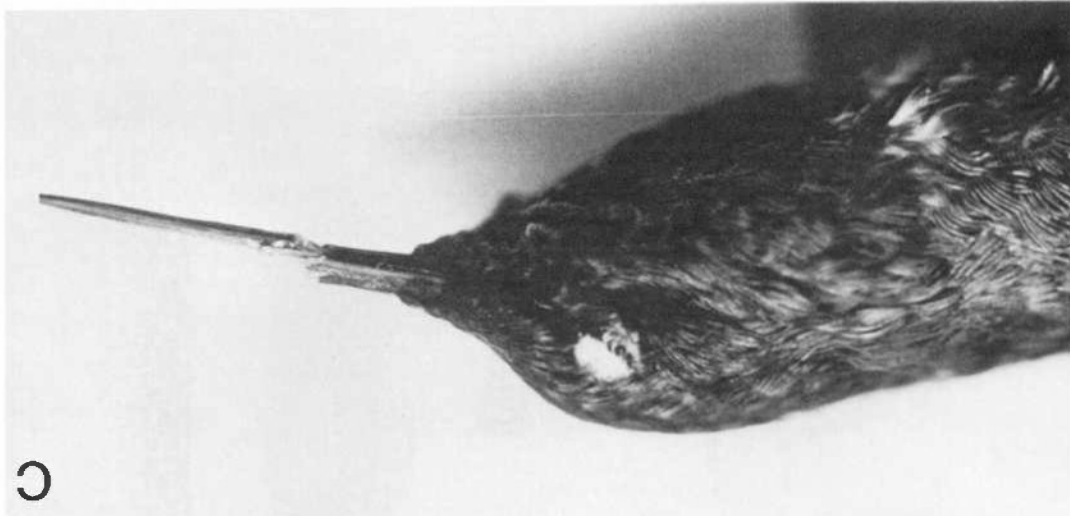


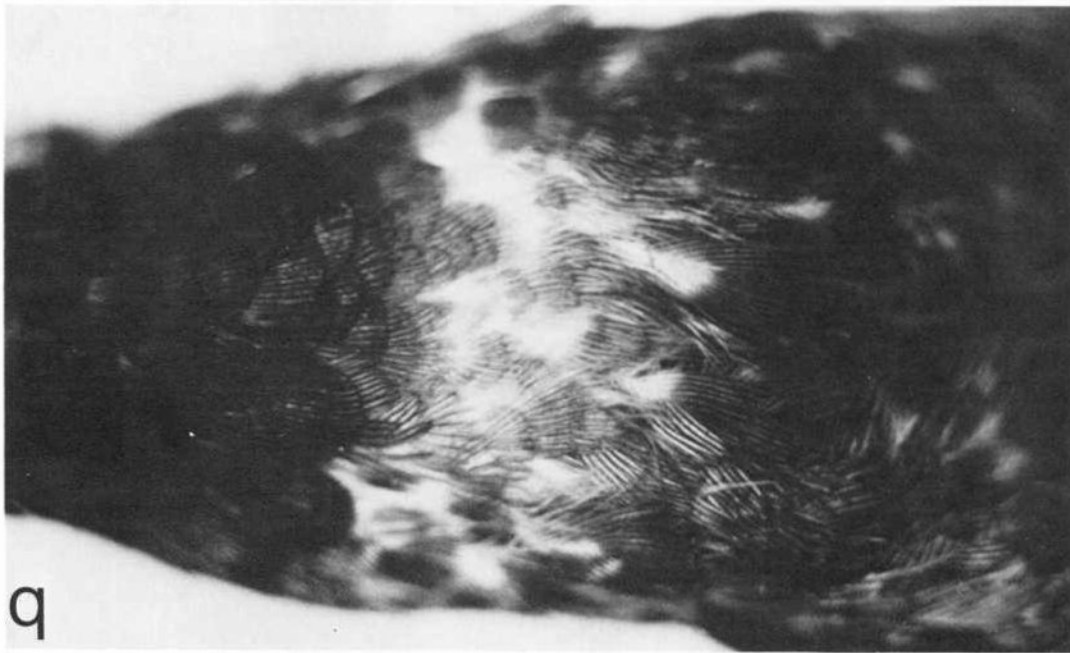
Fig. 2. Feet and tarsi of "green-throated sunangels" (a = FMNH 46286; b = FMNH 46294), *Heliangelus amethysticollis* (c, male), and *Eriocnemis cupreiventris* (d, male). Note downy leg puffs on tibias of a, b, and d.

Fig. 3. Ventral view of "green-throated sunangels": (a) type of "*Heliangelus squamigularis*"; (b) FMNH 46286; (c) syntype of "*Heliotrypha simoni*" (FMNH 46294); (d) "*Heliotrypha speciosa*" (MNHN).

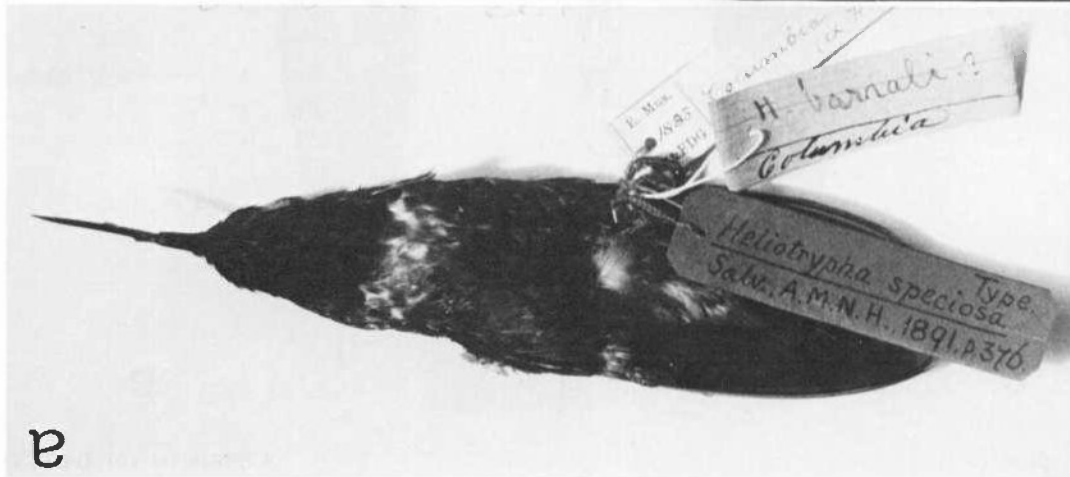




c



b



a

prepared in the "Bogotá" method were collected in the northern Andes and adjacent lowlands, a region roughly encompassed by the present boundaries of Colombia. In the absence of unequivocal locality data for any of the "green-throated sunangels," the geographic pool of potential parental species must initially include all hummingbirds recorded from Colombia, a total of 143 species in 61 genera (Hilty & Brown 1986).

There are two major lineages of hummingbirds, the Phaethornithinae and Trochilinae. As *Heliangelus* and related genera belong to the Trochilinae, I treat the subfamily Phaethornithinae as an outgroup. I identified all species of hummingbirds that occur in Colombia that shared with GTS one or both of the following characters that are apomorphic with respect to species in the outgroup: (1) lengthened downy tibial plumes (leg puffs) (Fig. 2); and (2) a brilliant gorget that contrasts with adjacent plumage and extends from the chin posteriorly to the upper breast (Figs. 3, 4). With the exception of GTS, no taxon exhibits both of these characters. It follows that if GTS are hybrids, then one parental species contributed leg puffs and the other the brilliant gorget.

Species representing four genera of hummingbirds, *Boissonneaua*, *Eriocnemis*, *Haplophaidia*, and *Ocreatus*, have downy tibial plumes that exceed those of GTS in length. Narrowing the pool of potential parental contributors of the brilliant gorget is more difficult. Including taxa with brilliantly reflective throats that do not contrast with adjacent plumage, species representing most of genera of the subfamily Trochilinae could be the gorgeted parent. However, only species of *Heliangelus* have gorgets that are similar in structure, shape, and size to those of GTS. Thus, a first review based on two apomorphic characters limits the potential

parental species to five of the 61 genera of Colombian hummingbirds.

Reduction of the species pool is supported by comparison of general morphology. The remiges, rectrices, body plumage, and bill of GTS are unspecialized and lack many of the elaborations that are common within trochiline hummingbirds. Assuming polygenic inheritance of these structures, if GTS are hybrids, then their parental species must be morphologically unspecialized. Sexual dichromatism within the series of GTS specimens, if any, is minor (Fig. 1). Collections of sexually dichromatic species of hummingbirds from Bogotá collections are often sexually skewed in favor of brightly colored adult males (Graves, in prep.). Plumage of immature males of these species may resemble that of females. Because immature GTS specimens do not differ significantly in appearance from adults (which suggests that the sexes are similar), sexual bias in collecting due to appearance of GTS specimens is unlikely. Assuming a 1:1 sex ratio the probability of finding only males or females in a random sample of 13 (number examined) individuals is $P < 0.0002$ (Binomial test). However, as pointed out by Haldane (1922), the heterogametic sex (♀ in birds) may be rare or absent in F_1 hybrids. Therefore, for diagnostic purposes I entertained the possibility that the sample of GTS specimens was exclusively male.

By structural criteria alone, 106 species (47 genera including *Ocreatus* and *Boissonneaua*) may be eliminated from the pool of potential parental species. These include species with specialized bills (e.g., *Ensifera ensifera*, *Schistes geoffroyi*), remiges (e.g., *Campylopterus falcatus*, *Aglaeactis cupripennis*), rectrices (e.g., *Ocreatus underwoodii*, *Acestrura mulsant*), and body plumage (e.g., *Colibri coruscans*, *Lophornis stictolo-*

←

Fig. 4. Type of "*Heliotrypha speciosa*": (a) ventral view; (b) enlargement of upper breast showing white pectoral band; (c) side view of head showing sloping profile forehead and thick bill.

pha). External morphology of the remaining 37 species representing 14 genera (*Klais*, *Chlorestes*, *Lepidopyga*, *Chrysuronia*, *Goldmania*, *Goethalsia*, *Amazilia*, *Adelomyia*, *Anthocephala*, *Urosticte*, *Phlogophilus*, *Heliangelus*, *Eriocnemis*, *Haplophaedia*) is relatively unspecialized. These bear further scrutiny as potential parental species of GTS.

GTS have unpatterned rectrices and uniformly dark bills. This suggests that species with spotted or patterned rectrices (e.g., *Amazilia* sp., *Anthocephala floriceps*, *Adelomyia melanogenys*, *Phlogophilus hemileucurus*) or markedly bicolor lower rhamphotheca (e.g., *Amazilia* spp.) can be eliminated, leaving species from three genera (*Heliangelus*, *Eriocnemis*, *Haplophaedia*) as potential parental species of GTS. Excepting these, all other species may be rejected from the species pool by two or more criteria (available from the author). In sum, rejection of species whose distinctive characters (some of which are apomorphic) are not found in GTS, reduces the species pool to nearly the same subset of species that share apomorphic characters with GTS.

Berlioz (1936) noted the downy tibial plumes of the MNHN specimen, *Heliotrypha speciosa*, and suggested that some species of Colombian puffleg (*Eriocnemis* spp., *Haplophaedia* spp.) was one of its parents. He concluded that the entirely green body plumage and non-brilliant undertail coverts of this specimen seemed to preclude the possibility of a cross with a species of *Eriocnemis* (with brilliant violet or blue undertail coverts) and that only one hybrid combination was possible, *Haplophaedia aureliae* × *Heliangelus exortis*. Berlioz's statement on undertail coverts may be extended to other GTS specimens—none of the specimens I examined exhibit the struc-

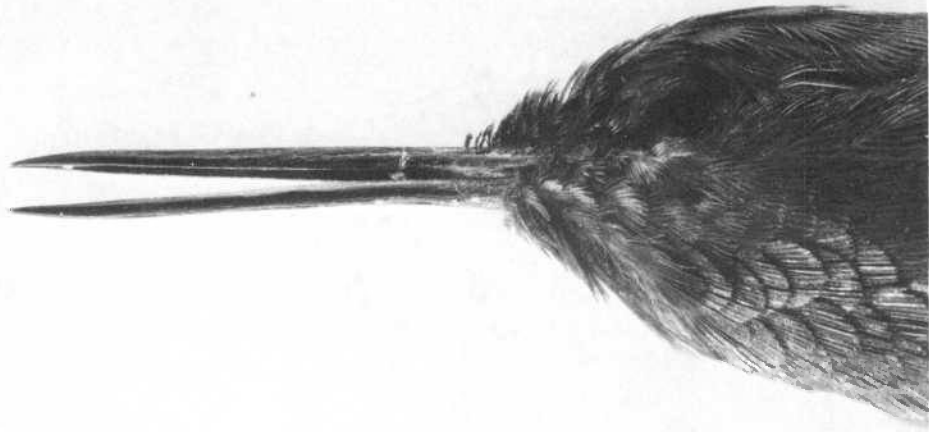
tural brilliance found in many species of puffleg (e.g., *Eriocnemis vestitus*, *E. luciani*, *E. cupreiventris*, *E. mirabilis*, *E. alinae*, *E. derbyi*). Undertail coverts of the potential *Heliangelus* parental species vary from pure white to gray with white margins. Contrary to Berlioz's reasoning, the hybrid progeny of *Eriocnemis* sp. × *Heliangelus* sp. might be expected to have green undertail coverts with white or grayish-white margins, similar to those of GTS.

One character of GTS that has not received mention by previous investigators is the extensive distribution of brilliant green reflections from the body plumage. These reflections extend posteriorly to the vent and upper tail coverts and are particularly apparent when specimens are viewed head-on in direct light. Barbule modifications of this type are well-developed in several species of *Eriocnemis* (e.g., *E. vestitus*, *E. cupreiventris*) but are weakly developed or lacking in both species of *Haplophaedia*. Several species of *Heliangelus* (e.g., *H. exortis*, *H. amethysticollis*, *H. viola*) exhibit brilliant reflections on the upper breast but lack them posteriorly when viewed head-on in direct light. The presence of brilliantly reflective plumage (similar to that of GTS specimens) on the flanks and abdomen of hypothetical *Haplophaedia* spp. × *Heliangelus* spp. hybrids would represent a clear case of "ata-vism," a phenomenon that has not been demonstrated in trochiline hybrids.

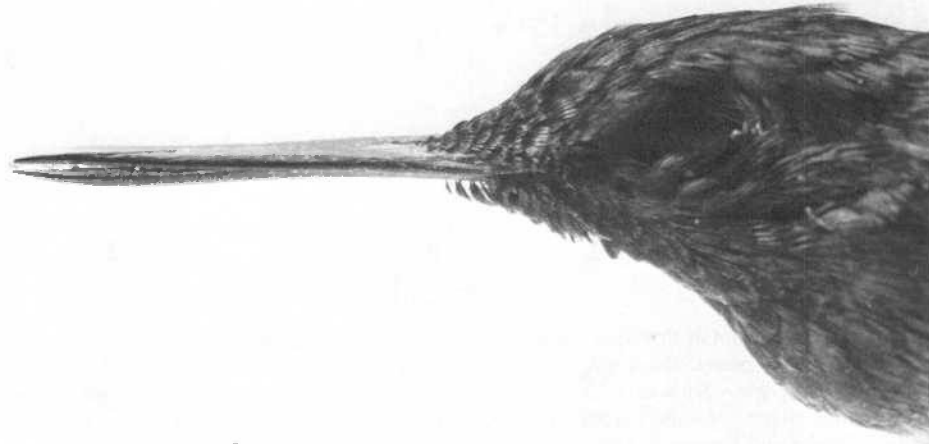
Several other characters contradict Berlioz's hypothesis that *Haplophaedia aureliae* is involved in the parentage of GTS. Both sexes of *H. aureliae* have bronze crowns and uppertail coverts that contrast with the green back and rump. The dorsum of GTS specimens lacks such contrast, and, in fact, some specimens are brightest on the

Fig. 5. Head profiles of "green-throated sunangels" (a = FMNH 46286, b = FMNH 46294) and *Haplophaedia aureliae* (c). Nasal operculum of *H. aureliae* is more inflated and exposed than in "green-throated sunangels" and *Heliangelus* spp.

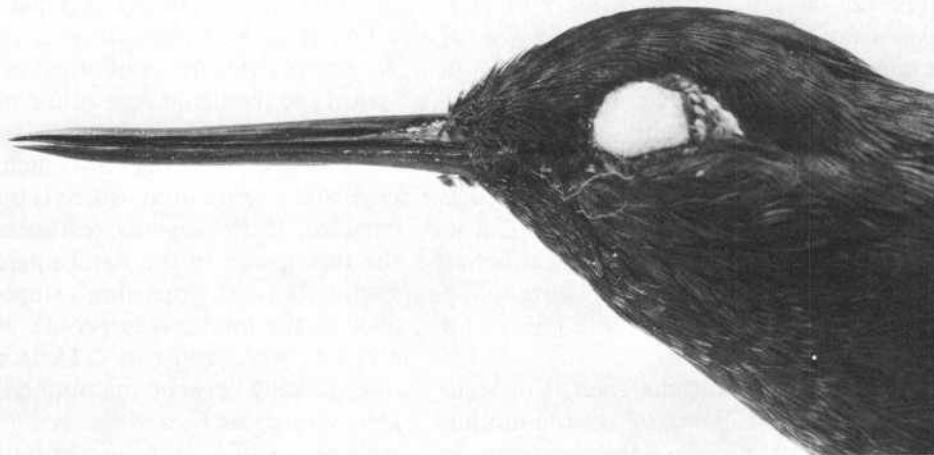
a



b



c



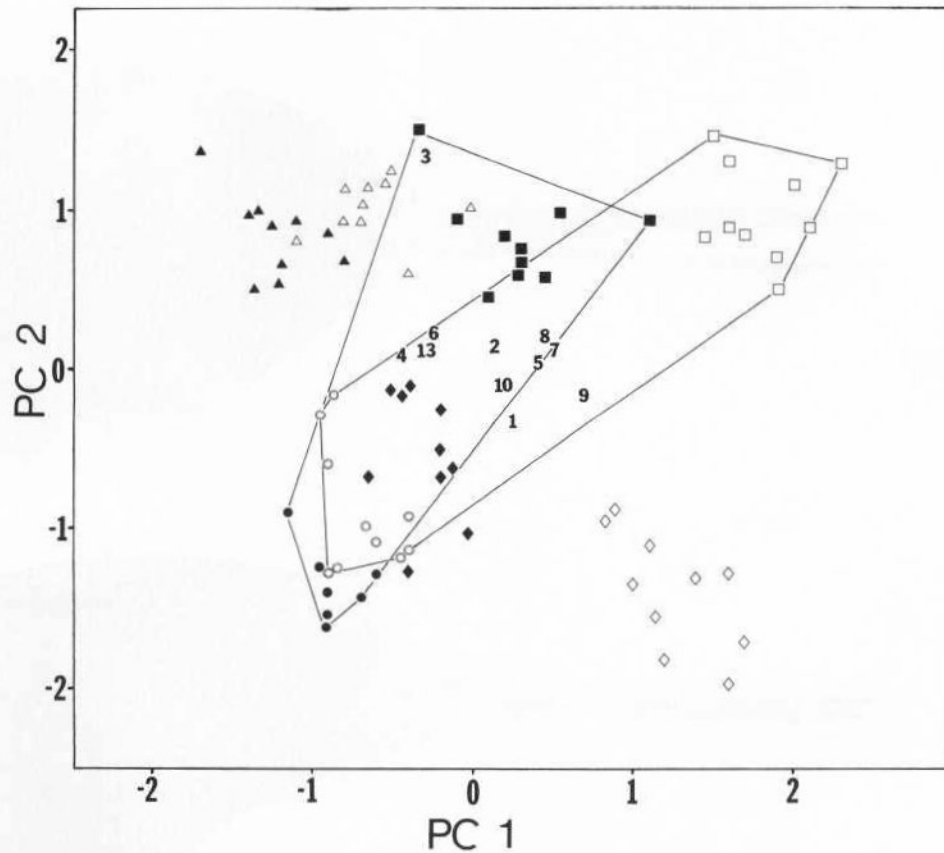


Fig. 6 Bivariate plot of Principal Component factor scores of "green-throated sunangels" and some of their potential parental species. Diamonds = *Heliangelus exortis*. Circles = *Eriocnemis cupreiventris*. Triangles = *Haplophaedia aureliae*. Squares = *Heliangelus amethysticollis*. Hollow and solid symbols represent males and females, respectively. Numbers represent "green-throated sunangel" specimens from Table 1. Lines envelop groups of males and females of *Heliangelus amethysticollis* × *Eriocnemis cupreiventris*.

uppertail coverts. Northern races of *Haplophaedia aureliae* (e.g., *H. a. aureliae*, *H. a. caucensis*), especially females, have white or grayish white abdomens and lower breasts speckled peripherally with green. Feathers of the ventral midlines of females and immature males of Colombian species of *Heliangelus* have wide buffy margins. Consequently, the venters of hypothetical female hybrids of *H. aureliae* × *Heliangelus* spp. would be extensively buffy, not green as in GTS.

Another important character is the relationship between the nasal operculum and the anterior extension of feathering on the

bill of GTS specimens (Fitzpatrick et al. 1979) (Fig. 5). In *Heliangelus exortis* and *H. amethysticollis*, feathering extends anteriorly to the distal edge of the nasal operculum but does not cover it. Feathering in *Haplophaedia* spp. does not reach the distal edge of the operculum, which is inflated and exposed. In *Eriocnemis*, feathers extend to the distal edge of the nasal operculum, or slightly beyond, imparting a sloped appearance to the forehead in profile. Feathering and forehead profile of GTS is somewhat intermediate between that found in *Heliangelus exortis* or *H. amethysticollis* and several species of *Eriocnemis*, but differs from

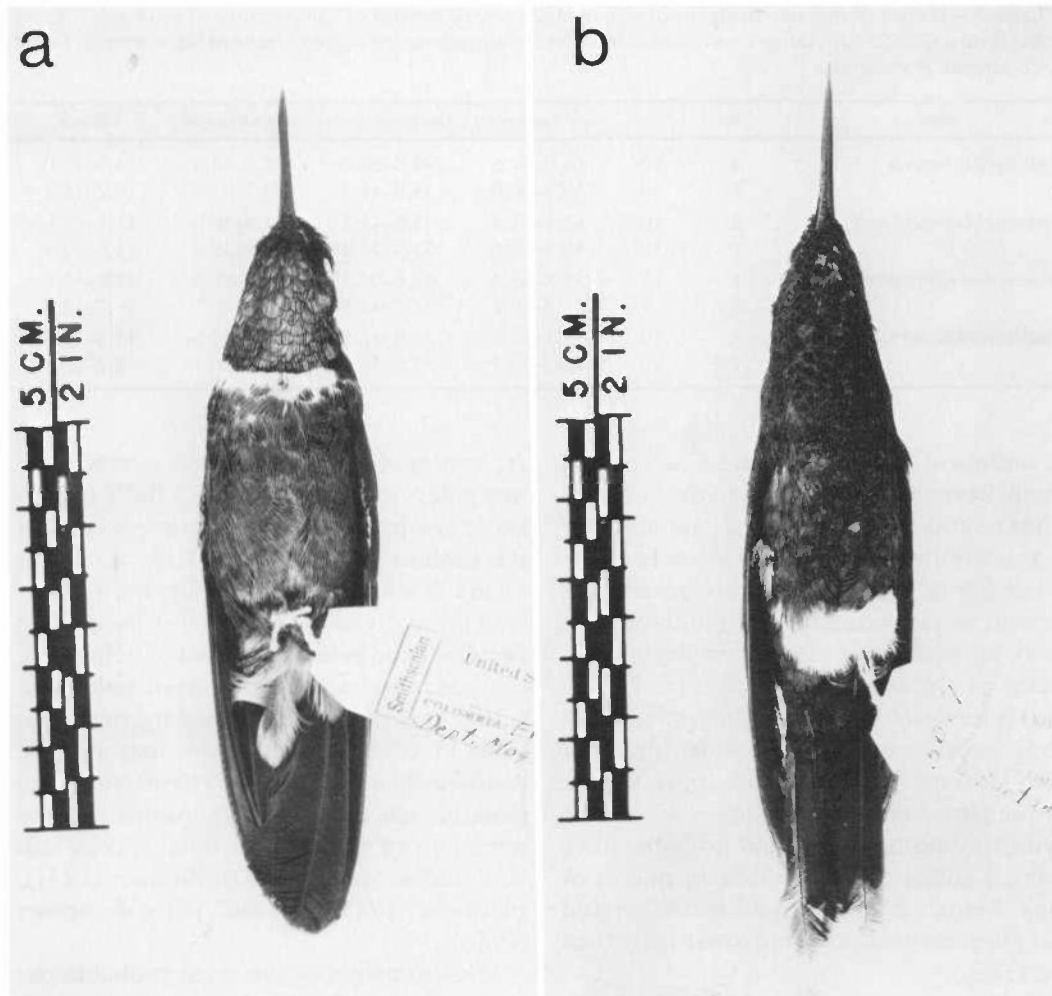


Fig. 7. Males of the two most probable parental species of "green-throated sunangels" examined in this study: (a) *Heliangelus amethysticollis*; (b) *Eriocnemis cupreovertris*.

that of *H. aureliae* or *H. lugens*. This and the other characters mentioned above indicate that both species of *Haplophaedia* may be rejected as potential parental species of GTS and support the hypothesis that the puffleg parent is some species of *Eriocnemis*.

Of the seven species of *Eriocnemis* (excluding *E. godini*, which is of uncertain status) that occur north of Ecuador, all but *E. cupreovertris* can be rejected as a parental species of GTS. Both sexes of *E. mosquera*

(see Bleiweiss [1988] for measurements) and *E. luciani* have deeply forked tails and are significantly larger than GTS specimens or any of its possible *Heliangelus* parents. Neither of these puffleg species occur in the Eastern Cordillera in sympatry with *Heliangelus amethysticollis* and hypothetical hybrids between these species and *H. exortis* would have tails more deeply forked than in any GTS specimen. In addition, GTS lack white bases to throat feathers found in those species and the greenish outer rectrices of

Table 2.—Ranges of measurements (mm) of potential parental species of "green-throated sunangels." Specimens from a number of localities were chosen in order to incorporate the range of intraspecific variation found in Colombian populations.

Species	Sex	n	Wing chord	Outermost rectrix	Innermost rectrix	Culmen
<i>Heliangelus exortis</i>	♂	10	64.0–67.6	44.8–50.0	32.1–34.5	13.3–15.0
	♀	10	56.9–60.9	38.9–41.3	29.7–33.9	14.2–16.8
<i>Heliangelus amethysticollis</i>	♂	10	65.1–71.8	43.6–48.8	41.4–46.0	14.8–16.0
	♀	10	60.5–65.6	35.9–42.4	36.9–39.6	15.5–17.1
<i>Eriocnemis cupreovertris</i>	♂	15	58.8–65.2	40.6–45.3	24.3–28.4	17.8–19.6
	♀	7	58.2–60.6	38.7–42.6	23.2–26.3	16.7–17.9
<i>Haplophaedia aureliae</i>	♂	10	59.1–62.8	35.4–41.3	32.6–37.6	17.3–19.6
	♀	10	55.3–58.9	32.8–37.8	32.3–36.1	16.2–20.1

E. mosquera, *E. mirabilis* and *E. alinae* are small, have restricted ranges in the northern Andes, and possess several apomorphic characters that are not expressed in GTS. *E. derbyi* is sexually dichromatic and divergent in tail structure and plumage (e.g., black leg puffs) and can be conclusively rejected as a possible parent of GTS. *E. vestitus* is moderately sexually dichromatic but both sexes possess a small violet (male) or blue (female) gorget on the upper throat. Hypothetical *Heliangelus* spp. × *E. vestitus* hybrids of both sexes would probably have a small gorget of some shade of purple or pink. Female hybrids would be buffier and less green on the breast and lower belly than are GTS.

E. cupreovertris exhibits weak sexual dichromatism, lacks a contrasting gorget, and is similar in size to both GTS and possible *Heliangelus* parents. The nasal operculum is partially covered with feathers in both sexes. When viewed head-on in direct light, the body plumage of adult males reflect a brilliant golden-green anteriorly changing to bluish-green on the upper tail coverts and to coppery-gold on the breast and belly. Females are slightly duller below. These characters make *E. cupreovertris* the most probable parental puffleg species of GTS.

The probable sunangel parent can be limited to the only two species with extensive distributions in the Colombian Andes, *H. exortis* and *H. amethysticollis*. (*H. mavors*,

H. strophianus, and *H. spencei* possess apomorphies not found in GTS.) Both species occur sympatrically with *E. cupreovertris* in the Eastern Cordillera (see Hilty & Brown 1986). *H. amethysticollis* differs from *H. exortis* primarily in having a well-defined white pectoral band below the throat of both sexes, a larger, more extensive gorget in males, and a less deeply forked tail. Intergeneric hybrids involving these species may best be distinguished by mensural characters of the parental species (Table 2). Additional descriptions of potential parental species can be found in Salvin (1892), Zimmer (1951), Bleiweiss (1985a, b), and Hilty & Brown (1986).

Measurements of the most probable parental species of GTS (*H. exortis*, *H. amethysticollis*, *E. cupreovertris*; *H. aureliae* included for comparison) overlap extensively (Table 2). I compared the measurements of these species and GTS specimens. Under the diagnostic assumptions used in this study, a GTS specimen could not be the hybrid progeny of a pair of species if the measurements of the specimen occurred outside the cumulative range (± 0.5 mm for wing and tail; ± 0.2 mm for culmen) of their measurements. Statistics were not performed because the reference samples were chosen to maximize ranges of measurements. This procedure is conservative because it assumes that the inheritance of quantitative characters is mutually inde-

Table 3.—Comparison of "green-throated sunangel" (GTS) measurements with the cumulative range of measurements for combinations of potential parental species (*Heliangelus amethysticollis*, *H. exortis*, *Eriocnemis cupreovertris*, *Haplophaedia aureliae*). A male or female symbol indicates that all measurements of a particular "green-throated sunangel" specimen fall within the range of measurements (by sex) for that combination of species. Numbers in parentheses refer to specimens listed in Table 1 for which all measurements were available. Ratios at the bottom of each column denote the minimum number of males and maximum number of females possible assuming that all "green-throated sunangels" represented hybrids of those species. Binomial *P*-values are given, assuming a 1:1 sex ratio.

GTS	<i>H. amethy.</i> × <i>E. cupreo.</i>	<i>H. amethy.</i> × <i>H. aureliae</i>	<i>H. exortis</i> × <i>E. cupreo.</i>	<i>H. exortis</i> × <i>H. aureliae</i>
(1)	♂	♂	♂	♂
(2)	♂♀	♂♀	♂	♂
(3)	♂	♂♀	—	♂
(4)	♂	♂	♂	♂
(5)	♂	♂	♂	♂
(6)	♂	♀	♂	♂
(7)	♂	♂	—	♂
(8)	♂	♂	—	♂
(9)	♂	♂	—	♂
(10)	♂♀	♂♀	♂	♂
(13)	♀	♂♀	♂♀	♂♀
♂:♀	8:3	6:5	6:1	10:1
	<i>P</i> ≤ 0.08	<i>P</i> ≥ 0.20	<i>P</i> ≤ 0.05	<i>P</i> ≤ 0.005

pendent. Unfortunately, this procedure rules out few hybrid possibilities (Table 3). None of the possible pairs of parental species can be rejected for 7 of 11 of the GTS specimens.

Multivariate morphological relationships (Table 4) of potential parental species and GTS specimens are illustrated by the first two axes of a Principal Components Analysis in Fig. 6. Inspection of factor scores revealed that most GTS specimens are clustered near the center of the bivariate plot. Only one specimen (type of *H. speciosa*) falls within the envelope outlining the factor scores for *H. aureliae* and *H. amethysticollis* and none occurs in the *H. exortis* × *E. cupreovertris* envelope. Assuming that the inheritance of polygenic size and shape characters is reflected in the spread of factor scores, these pairs of species are not involved in the parentage of GTS, with the possible exception of the type of *H. speciosa*. All GTS specimens fall within the factor score envelope of *H. amethysticollis* × *E. cupreovertris*, and ten of eleven specimens fall within the *H. exortis* × *H. aureliae* en-

velope. However, as noted previously with univariate comparisons, if GTS are the progeny of *H. exortis* × *H. aureliae*, they would be predominately male. This fact, and a variety of plumage characters previously discussed suggest that GTS are not hybrids of the latter two species. The scatter of GTS factor scores within the *H. amethysticollis* × *E. cupreovertris* envelope shows that an even sex ratio is possible. With the exception of *H. speciosa*, plumage characters and measurements of GTS specimens are con-

Table 4.—Factor loadings for the first two principal components from analysis of "green-throated sunangels" and potential parental species (see Fig. 6).

	I	II
Variable		
Wing chord	0.91	0.10
Outermost rectrix	0.85	-0.39
Central rectrix	0.67	0.72
Culmen	-0.72	0.32
Variance explained		
Percent	62.5	19.6
Cumulative	62.5	82.1

sistent with the hypothesis that they represent hybrids of *H. amethysticollis* and *E. cupreovertris* (Fig. 7). Note, however, that the wing chord of AMNH 483682 (Table 1), which is probably a female, is significantly shorter than any specimen in the sample of these two species.

The position of *H. speciosa* on the bivariate plot is well removed from the other GTS specimens. *H. speciosa* differs from other GTS specimens in having a broad white pectoral band (Fig. 4) instead of a few semi-concealed spots, a shallowly-forked tail, and a slightly longer bill. The presence of a white pectoral band and the conformation of the gorget of *H. speciosa* indicates that a white-banded species of *Heliangelus* (e.g., *H. amethysticollis*) is one of the parental species. The well-developed leg puffs of *H. speciosa* (fide M. P. Walters) indicate that the other parental species is a puffleg. The anterior extension of feathering over the nasal operculum of *H. speciosa*, however, indicates that the other parent could not be *H. aureliae* which is similar to it in size and shape. *H. speciosa* lies within the PCA envelope for *H. cupreovertris* × *H. amethysticollis*. Despite the difference in appearance of *H. speciosa* from other GTS specimens, it seems probable that they represent the same hybrid cross. Additional study of the specimen may be required to verify this fact. If true, then *H. speciosa* represents an extreme hybrid phenotype that resembles its sunangel parent much more than its puffleg parent.

Conclusions

With the possible exception of *H. speciosa*, GTS specimens examined in this study, for which measurements were available, are probably hybrids of *Heliangelus amethysticollis* × *E. cupreovertris*. Berlioz's (1936) hypothesis that the MNHN specimen and perhaps others were hybrids of *Haplophaedia aureliae* and *Heliangelus exortis* is not supported by the data. Because the hypothesis of hybridity cannot be re-

jected, GTS cannot be considered as valid taxa. Additionally, the data (especially the variability and inconsistency of plumage characters) do not support the hypothesis that GTS, taken as a whole, represent population samples of one or more valid species.

Geographic origin.—*H. amethysticollis* and *E. cupreovertris* are sympatric in Andean forests and shrublands (2000–3000 m elevation) in the northern half of the Eastern Cordillera. Thus, GTS specimens could actually have been collected in the environs of "Bogotá." Mulsant & Verreaux (1872) reported that the type of *Heliotrypha barrali* was collected on the Río Saldana, Department of Tolima, in the Central Cordillera of the Colombian Andes. However, as previously mentioned, the original labels of *H. barrali* and other specimens lack specific locality data and in the absence of corroborating evidence, the possible Central Cordilleran origin of the type of *H. barrali* can be dismissed.

Nomenclature.—Hybrids are individuals and not taxa. Thus, the names *Heliangelus squamigularis* Gould, 1871, *Heliotrypha barrali* Mulsant & Verreaux, 1872, *Heliotrypha speciosa* Salvin, 1891, and *Heliotrypha simoni* Boucard, 1892, are available only for the purposes of homonymy in taxonomy and should not be used in the popular literature. For the purposes of field guides, these hybrids may be referred to collectively as "green-throated sunangels."

Discussion

Hybrid diagnoses can be simple or extremely complex depending on circumstances. Factors that affect the success of hybrid diagnoses include: (1) the number of hybrid individuals and their age, sex, and hybrid composition (e.g., F₁, backcross); (2) the number of distinctive plumage and morphological characters on the hybrid; (3) the number of species in the putative hybrid's taxonomic group; (4) and knowledge of the hybrid's taxonomic group and of the regional avifauna where the hybrid originat-

cd. (The most challenging diagnoses are of hybrids represented by a unique, unsexed, possibly immature specimen without specific locality data, which belongs to a speciose, dull-plumaged, and poorly known taxonomic group from a poorly collected region of high species diversity!)

Ideally, parental species are identified with certainty, but failing this, what result justifies the considerable effort expended in the average hybrid diagnosis? In terms of value to future researchers, it is far better to have a short list of species that includes the correct pair of parents, than an exact determination of parental species that may be wrong (errors of this sort are frequently perpetuated in the literature; see Graves 1988). Rejection of any species from the pool of potential parental species must be based on the unequivocal violation of diagnostic assumptions, and there is no logical reason for reducing the species pool beyond the limits suggested by the data. Conclusive knowledge of what species or species combinations are *not* parents, as well as those that might be parents of a hybrid is far more valuable than perhaps recognized by most taxonomists, especially when the majority of species fall into the former category. Species in the latter category constitute the nucleus for future analyses.

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Appendix

Comparative Description of "Green-throated Sunangels"

Descriptions of structural colors are unusually subjective and actual color varies with the angle of inspection and direction of light. For this reason I use general color descriptions. Numbers in parentheses refer to specimens in Table 1.

The crown, nape, back, and rump are medium green. Uppertail coverts are medium green to bluish-green. There is no contrast between crown and back. When viewed head-on in direct light, scattered feathers on crown (5), back, wings, and upper tail coverts show brilliant golden-green to green reflections. A brilliant green frontlet, variable in intensity and definition, is found in most adults (absent in 10), but is faint or lacking in immatures. When present, the frontlet is small (1, 2, 4, 6, 8, 11, 12), similar in size to that found in *H. exortis* or *H. amethysticollis*. Prominence of the frontlet is affected by variations in skin preparation. Lores, auriculars, and neck at the sides of the throat are medium green, but appear much darker when viewed head-on. A small white postocular spot is present. A brilliant gorget is found in all specimens but is variable in size, color, and degree of contrast with adjacent plumage. Gorget margins are somewhat irregular and indistinct in all adult specimens. Gorget color is vari-

able and can be characterized (viewed head-on) as bluish-green (4) and silvery-green (2, 9, 13) to silvery bluish-green (7) in immatures, and from bluish-green (5) and pale green (12) to silvery-green (1, 3, 6, 8, 10, 11) in adults. In indirect light, gorgets of some specimens emit faint coppery or pinkish reflections. Color variation appears to be fairly continuous and color characterizations are arbitrary. For example, "silvery-green" includes various shades of pale metallic green (= "leaden" of Salvin 1892). Gorgets of immatures are oval in shape, wider posteriorly and may be surrounded by dull, lax plumage (7). Gorgets of adults are larger, contrast less with adjacent plumage, and may have irregular margins (5). Brilliant gorget feathers are rounded and about the size of those in male *Helianigelus* sp. (e.g., *H. exortis*), but become progressively smaller toward the chin and malar regions in adults. The upper and lower breast, abdomen, and flanks (except 2) are medium green. Feathers along the midline of immatures may have narrow buffy margins. Brilliant golden-green or green reflections (or faint coppery in 5) are scattered over the breast, abdomen, and flanks when viewed head-on. Plumage of immatures is duller than in adults. The type of *H. speciosa* (3) differs from other GTS specimens in having a large white pectoral patch spotted with green discs and darker underparts with few brilliant reflections. White or buffy spots,

mostly subterminal, are present on two to ten feathers of the upper pectoral area on most specimens (1, 2, 7, 8, 9, 10, 11, 13). Undertail coverts are variable in length (not exceeding half the length of the tail) and are medium green or bluish-green with narrow to broad white or grayish white margins; basal barbs in some specimens are long and downy. Central rectrices are dark green to bronzy green; outer rectrices are bluish-black. Depth of tail fork varies from 3.8 to 10.5 mm. Outer web of outermost rectrix is well-developed ($> \frac{1}{2}$ width of inner web). The outermost rectrix ranges from 8.0 to 9.5 mm in width and is more acuminate in shape than in *H. exortis* or *H. amethysticollis*. Tibial feathers (leg puffs) are white or buffy (2), variable in length (2.5 to 8 mm), and more or less downy in texture. [The presence of leg puffs on (1) cannot be determined from photographs of specimens or published descriptions]. The remiges are unmodified (e.g., not emarginate) and dull dark brown in color. Outer webs of primaries of some specimens have a faint bronzy-green sheen. Bills are unmodified and straight and dark blackish-brown. The upper mandible of (3) is broken (Fig. 4). Feathering extends anteriorly on the bill to the distal edge of the nasal flange (not inflated), somewhat obscuring it. Feet are dark brown or dark blackish brown.

Additional notes on plumage can be found in Berlioz (1936).