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AN INTERGENERIC HYBRID HUMMINGBIRD (*HELIODOXA LEADBEATERI* × *HELIANGELUS AMETHYSTICOLLIS*) FROM NORTHERN COLOMBIA[1]

GARY R. GRAVES AND RICHARD L. ZUSI
Department of Vertebrate Zoology, National Museum of Natural History, Smithsonian Institution, Washington, DC 20560

Abstract. We describe a new intergeneric hybrid hummingbird, *Heliodoxa leadbeateri* × *Heliangelus amethysticollis,* from the Eastern Cordillera of the Colombian Andes based on external characteristics. A hypothesis of parentage based on external characteristics is supported by cranial features.

Key words: Heliodoxa leadbeateri; Heliangelus amethysticollis; *hummingbird; Andes; Colombia; Melbourne A. Carriker, Jr.; intergeneric hybrid.*

INTRODUCTION

On 21 September 1946, Melbourne A. Carriker, Jr. collected an adult male hummingbird that he tentatively identified as "*Heliangelus speciosa*?" at Buenos Aires, 6,050 ft (=1,845 m), 8°01′N, 72°58′W, Santander del Norte, on the eastern slope of the Eastern Cordillera of the Colombian Andes. The specimen (National Museum of Natural History, USNM 392141) was cataloged under this name but was never reported in the literature, despite the fact that *H. speciosa* (Salvin 1892, Graves 1990) was known only from the type specimen in the British Museum.

During a recent analysis of enigmatic hummingbird taxa from the Andes, Graves examined Carriker's specimen and came to the conclusion, on the basis of plumage characters, that it represented a previously unreported intergeneric hybrid between the Violet-fronted Brilliant (*Heliodoxa leadbeateri*) and the Amethyst-throated Sunangel (*Heliangelus amethysticollis*). Because the genus *Heliodoxa* exhibits derived cranial characters that might be used to test this hypothesis, we extracted the skull from the specimen. Zusi's analysis of the skull supported Graves' findings. In this paper, we present the combined analyses of the hybrid.

MATERIALS AND METHODS

Graves compared the plumage and other external features of the hybrid with study skins of all species of hummingbirds in the National Museum of Natural History and the American Museum of Natural History. Color descriptions were made under Examolites (Macbeth Corp.). Measurements (wing chord, culmen from anterior extension of feathers) were taken with digital calipers and rounded to the nearest 0.1 mm. Diagnostic assumptions and methods of hybrid diagnosis based on plumage characters and measurements follow Graves (1990).

The skull of the hybrid was extracted by J. Phillip Angle using techniques outlined by Olson et al. (1987). Zusi compared it with his unpublished data on skulls of species representing 104 hummingbird genera, and directly with all species known to occur in the Eastern Cordillera of the Colombian Andes. The illustrations were drawn using a dissecting microscope and drawing tube.

RESULTS

To our knowledge, Carriker's specimen is the only hybrid hummingbird from northwestern South America that was sexed internally and accompanied by field notes (National Museum of Natural History). Between 2 September and 3 October 1946, Carriker and his assistant collected 496 bird specimens in a mixture of second growth and remnant cloud forest separated by pastures near the settlement of Buenos Aires and on the ridge and mountain rising to the west (Alto de Pozo). This collection (National Museum of Natural History) is composed of species that occur in midelevation (1,700–2,700 m) habitats in the Eastern Cordillera (see Hilty and Brown 1986).

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Once we concluded that the specimen was not a typical example of any described hummingbird taxon, we considered three options: the specimen represented (1) a rare genetic plumage variant of some Andean species; (2) a hybrid; or (3) a new species. Our analyses focussed on the 50+ species of hummingbirds that occur in the northern half of the Eastern Cordillera above 1,000 m elevation, and especially on the 13 species of hummingbirds that Carriker collected near Buenos Aires (*Colibri thalassinus, C. coruscans, Chlorostilbon stenura, Adelomyia melanogenys, Heliodoxa leadbeateri, Coeligena coeligena, C. helianthea, Boissonneaua flavescens, Heliangelus amethysticollis, Ocreatus underwoodii, Metallura tyrianthina, Aglaiocercus kingi,* and *Acestrura heliodor*).

Although the specimen resembles *H. amethysticollis* in its pattern of white pectoral band and glittering gorget, it differs significantly in proportions and color from that species and all others. These characters demonstrate that the specimen is not a plumage variant or an undescribed race of any known species of hummingbird.

Determining whether a unique specimen represents a hybrid or a valid species can be difficult. Nevertheless, a number of Andean species have been described from only one or two specimens (e.g., Graves 1988). In such cases, rejection of alternatives, especially hybridism, has been construed as proof of specific status. Our initial investigations of potential hybridism were based on characters of the male plumage and on an assumption of polygenic inheritance of most plumage characters (Graves 1990).

The specimen exhibits a number of plumage characters, such as a brilliant gorget and frontlet, that are restricted to the subfamily Trochilinae. The body plumage, remiges, rectrices, bill, and feet of the hybrid are relatively unmodified, lacking such elaborations as the tail rackets, tibial plumes, and emarginated primaries found in some trochiline hummingbirds. We assumed that, if the specimen were a hybrid, the parental species would be similarly unmodified, and that they would possess collectively the distinctive plumage characters exhibited by the hybrid: (1) white pectoral band; (2) large brilliant frontlet; and (3) a large, well-defined, brilliant gorget. No potential parental species exhibits all three characters.

Among the Eastern Cordilleran species, only two morphologically unspecialized species, *Coeligena torquata* and *H. amethysticollis,* have white pectoral bands. *Coeligena torquata* may be eliminated as a parental species because it has a strongly patterned tail, whereas the rectrices of the hybrid are unmarked. Thus, *H. amethysticollis* is indicated as one of the parental species. However, this species has only a small green frontlet at the base of the bill, not the large frontlet of the Carriker specimen. Only two species with unpatterned tails could have contributed a large frontlet and greenish gorget to the hybrid: *H. leadbeateri* and *H. jacula. Heliodoxa jacula* can be eliminated tentatively because it occurs at lower elevations (500–1,500 m) and has not been recorded in the Eastern Cordillera north of Cundinamarca (Hilty and Brown 1986). Also, males of *H. jacula* have a violet spot in the center of the throat, and a *H. jacula* × *H. amethysticollis* hybrid would probably have a small throat spot of some shade of purple or pink. All other Eastern Cordilleran species are eliminated by two or more well-defined external characters that are not found in the Carriker specimen (data available from the authors).

Thus, plumage pattern and color indicate that the Carriker specimen is a hybrid between *H. leadbeateri* and *H. amethysticollis* (Fig. 1). The wing chord and culmen measurements (mm) fall within the range of Colombian samples of males of the two parental species but are closer to *H. leadbeateri*: *leadbeateri* (n = 15), wing chord, 67.3–72.2, culmen, 17.3–20.7; *amethysticollis* (n = 15), wing chord, 67.5–71.8, culmen, 14.8–16.1; hybrid, wing chord, 71.8, culmen, 18.2.

A complete description of the external characters of the hybrid and comparisons with its parental species follows. Descriptions of structural colors are unusually subjective and actual color varies with the angle of inspection and direction of light. For these reasons we use general color terms.

CAPITAL TRACT

In *leadbeateri,* an oblong, brilliant violet frontlet extends from the posterior edge of the crown to the base of the bill. The hindcrown and the feathers bordering the frontlet are dark bronzy green. The crown of *amethysticollis* is dark green with a small brilliant green frontlet at the base of the bill. The crown of the hybrid is dark green with bronze highlights; a brilliant golden-green frontlet extends from the center of the crown above the orbits to the base of the bill. Thus, the hybrid's frontlet is intermediate in size between

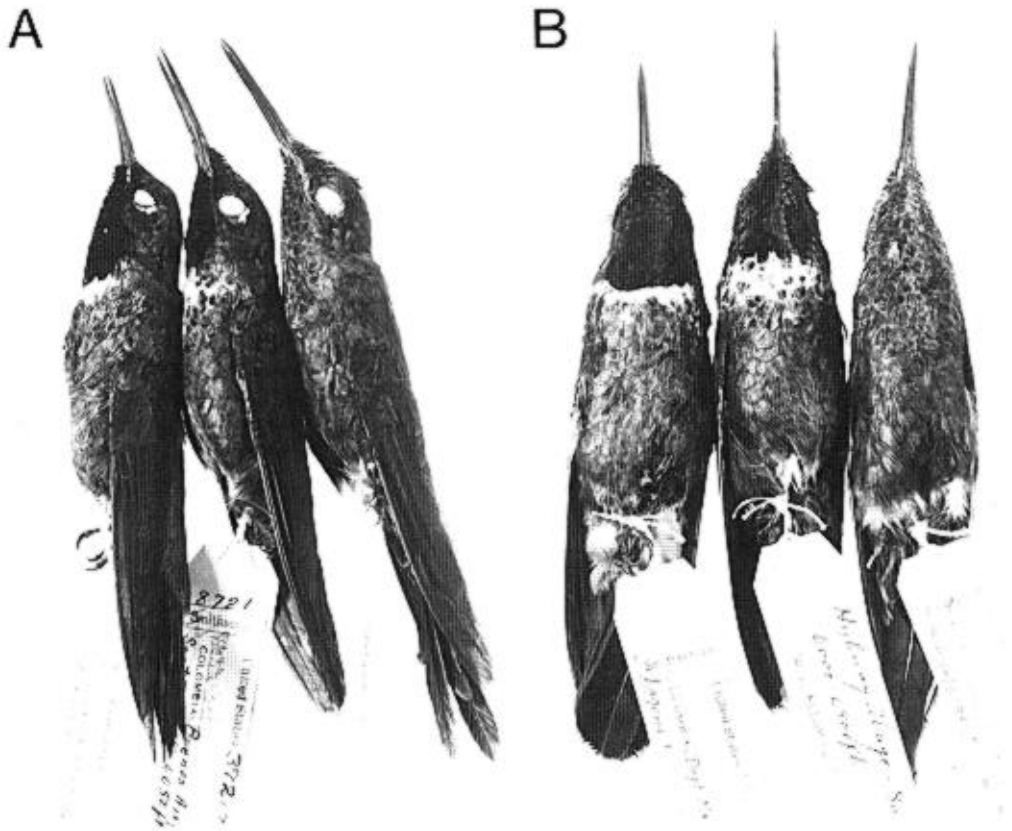

FIGURE 1. Lateral (A) and ventral (B) view of adult male specimens (from left to right) of *Heliangelus amethysticollis, H. leadbeateri* × *H. amethysticollis* hybrid (USNM 392141), and *Heliodoxa leadbeateri.*

leadbeateri and *amethysticollis.* The feathering on the dorsal base of the bill in *amethysticollis* extends rostrally to the level of the anterior limit of the external nares or slightly beyond (0.4 mm); in *leadbeateri* it extends ≥1.5 mm beyond; the hybrid is intermediate (1.1 mm). When viewed head-on in direct light, the lores and the green plumage adjacent to the frontlet of *leadbeateri, amethysticollis,* and the hybrid appear sooty black. Both parental species and the hybrid have a small white postocular spot.

SPINAL TRACT

The back, scapulars, and rump of both parental species and the hybrid are dark green. The dark bronze-green crown and hindneck of *leadbeateri* contrasts with the back, whereas contrast in *amethysticollis* is variable but less pronounced than in *leadbeateri.* The hybrid is intermediate.

VENTRAL TRACT

The auriculars and the side of the neck of *leadbeateri* are dull green and contrast slightly with the brilliant throat in indirect light. In *amethysticollis,* the auriculars are dull blackish-green, becoming greener on the side of the neck, and contrast sharply with the gorget. The auricular region of the hybrid is intermediate in color but resembles *amethysticollis* in contrasting sharply with the gorget. The large brilliant green gorget of *leadbeateri* extends from the gular area between the rami of the bill posteriorly to include the upper breast. Contrast between the gorget and surrounding plumage is indistinct except when the former is seen to glitter (viewed head-on in direct light). The chin of *amethysticollis* is sooty black, bordered posteriorly by a well-defined, brilliant amethyst gorget that extends only to the

lower throat. The gorget of the hybrid resembles *amethysticollis* in general configuration and feather shape, but resembles *leadbeateri* in extending anteriorly to the gular area; the color is golden-green (same as the frontlet) in direct light but exhibits bluish-green reflections at some angles in indirect light, and thus is intermediate but much closer to *leadbeateri.*

The lower breast and belly of *leadbeateri* are green; the undertail coverts are dull green to bronze-green tipped with grayish-white or buffy-white. The gorget of *amethysticollis* is bordered posteriorly by a white band on the upper breast, and then a green band across the breast (brilliant when viewed head-on). In indirect light, the lower breast is dull green and does not contrast greatly with the sides. The feathers along the midline of the lower breast and belly are broadly edged with buff; the undertail coverts are white or pale gray with broad white margins. The hybrid is intermediate; the gorget is bordered posteriorly by a white pectoral band spotted with green feather tips. When viewed head-on, the lower breast is crossed by an indistinct band of golden-green iridescence; in indirect light it is intermediate in color and pattern between the two parental species. The undertail coverts of the hybrid are intermediate—bronzy-gray with white margins. Downy white feathers are present in the vent area of the hybrid and both parental species.

The tibial feathers of all three forms have a tufted appearance caused by long barbs with radiating hairlike barbules. In *amethysticollis* these feathers are gray with short white tips. In *leadbeateri* and the hybrid, they are more extensively white, making the tufts more prominent. The feathers that cover the distal end of the tibiotarsus and proximal end of the tarsometatarsus are short and structurally unmodified. These are brownish-gray in *amethysticollis*; brownish-gray with prominent white tips in *leadbeateri,* and intermediate—brownish-gray with inconspicuous tips—in the hybrid.

ALAR TRACT

The flight feathers of the parental species and hybrid are similar in color. The wing coverts of *leadbeateri* are greener and more iridescent than in *amethysticollis*; those of the hybrid are intermediate. The flight feathers of the parental species are roughly similar in shape, but the inner primaries of *leadbeateri* are slightly more pointed than in *amethysticollis*; those of the hybrid are intermediate in shape.

CAUDAL TRACT

The tail of *leadbeateri* is moderately forked. The central rectrices are green with bronzy highlights; the outer pairs of rectrices are progressively blacker (the outermost is often entirely black). The color is similar in *amethysticollis* but the tail is unforked or slightly forked. The tail of the hybrid is colored like those of the parents. Its shape is uninformative because all rectrices have basal sheaths. The central pair is almost fully developed; the others are about half-grown.

BILL

The bills of *leadbeateri* and *amethysticollis* are essentially straight with a gradually decurving culmen and a correspondingly recurving gonys. In *amethysticollis* the tip is slightly swollen because the ventral outline of the mandibular ramus in lateral view is slightly concave in contrast to the convex gonys; the culmen begins to decurve somewhat distal to the point where the gonys begins to recurve. The tomium of the mandible is also recurved near the tip. The bill tip in *leadbeateri* is more evenly attenuate, without the appearance of a swollen tip. The lateral profile of the hybrid is more like *leadbeateri* in the even attenuation of the bill tip. The tomia of both species and the hybrid are unserrated. In the hybrid the ventral bars of the upper jaw and their rhamphothecae were broken by shot anterior to the nasal cavities, causing the bill to collapse inward and become much narrower in ventral view than it was in life (Fig. 1).

The rhamphotheca of the mandible of *amethysticollis* is two-toned in its proximal one-half to two-thirds, the ventral portion being blackish and sharply demarked from the dorsal yellowish portion. Most *leadbeateri* differ in being uniformly blackish, or dark brown and somewhat paler in the dorsal portion. The hybrid is intermediate, blackish below and whitish and somewhat blotched with pale brownish on the dorsal portion.

The lack of rhamphothecal corrugations on the hybrid indicates that it is an adult.

OSTEOLOGY

In an osteological test of *Heliodoxa* × *Heliangelus* parentage, the hybrid might be expected to

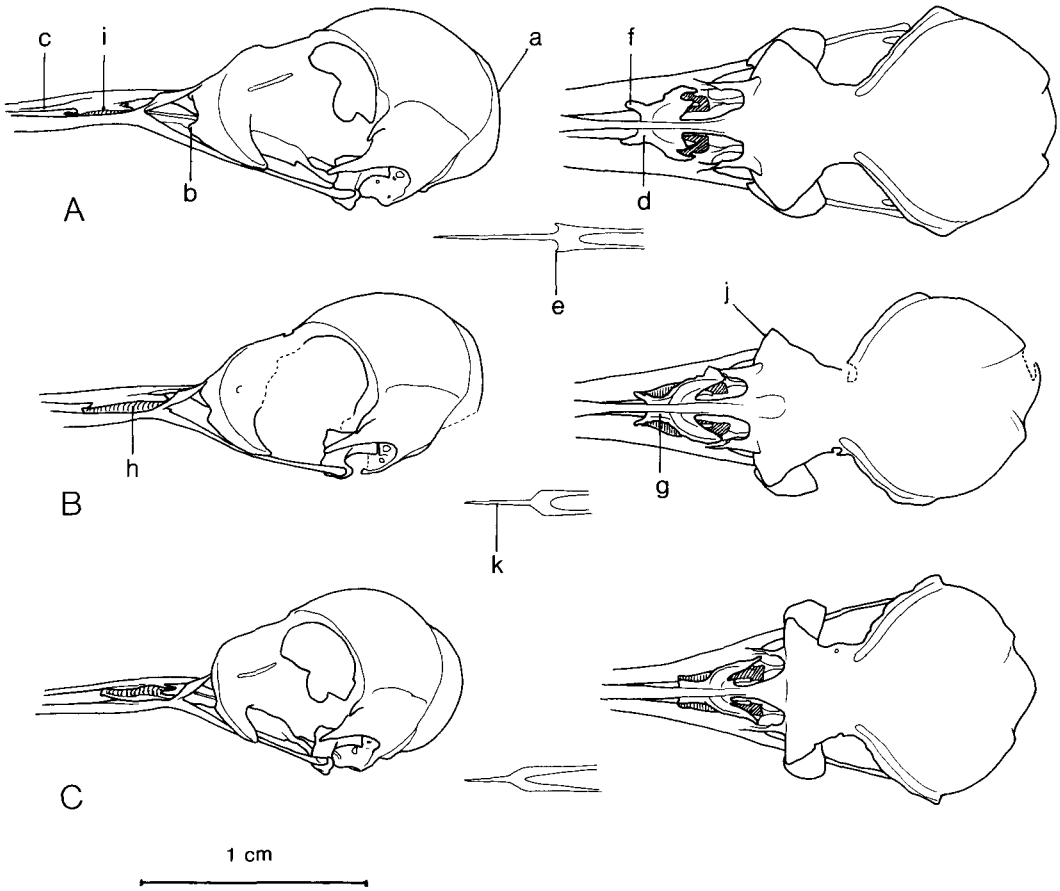

FIGURE 2. Diagnostic features of the skull: (A) *Heliodoxa leadbeateri*; (B) hybrid (USNM 392141); (C) *Heliangelus amethysticollis*. Left, lateral view; right, dorsal view; middle, vomer in dorsal view. See text for explanation. Features a–f are probably derived in *Heliodoxa* (sensu lato). Vomers enlarged 20% relative to skulls.

exhibit a mosaic of the derived characters of its parent genera, intermediacy of characters, and the absence of derived characters of other genera. Several derived characters of the skull distinguish *Heliodoxa* (sensu lato, including *Clytolaema, Sternoclyta, Polyplancta; Hylonympha* not available). No characters of the skull were found to be derived for *Heliangelus*.

A derived feature of *Heliodoxa* is the modified lateral profile of the cerebellar prominence of the braincase—relatively straight as opposed to evenly curved in other hummingbirds (Fig. 2—a). A profile like that of *Heliodoxa* is found also in *Patagona*, whose relationships are unresolved, and in *Schistes*, which is not phylogenetically close to *Heliodoxa*. Both genera can be eliminated as possible parents on other grounds. For example, the nasal cavities and conchae of *Schistes* are largely unossified but those of *Heliangelus, Heliodoxa*, and the hybrid are ossified. The Carriker specimen exhibits a straight lateral profile of the cerebellar prominence. Although the braincase is damaged and somewhat distorted, this feature is not an artifact because its shape is maintained by the unbroken left half of the braincase.

Several other characters are probably derived for *Heliodoxa*. One is a marked anterior projection of the nasal surface of the ectethmoid (Fig. 2—b). A similar feature occurs in the unrelated genus *Eutoxeres* (Phaethornithinae) and is manifested in a less extreme form in many other genera including *Heliangelus*. The size of the anterior projection of the ectethmoid in the hybrid

is intermediate between those of *Heliodoxa* and *Heliangelus*.

Most species of *Heliodoxa* exhibit bilateral asymmetry of the dorsal bar of the upper jaw (Fig. 2—c) and of the adjacent bony roof of the vestibular and respiratory nasal cavities (Fig. 2—d). The asymmetry is associated with elongate hyoid horns that pass on one side (right or left) of the dorsal bar and over the right or left nasal chambers to enter a sheath in the concavity of the upper jaw (Zusi, unpubl.). The hyoids vary in length among species such that asymmetry ranges from none to well marked within the genus. *Heliodoxa leadbeateri* shows marked asymmetry. Asymmetry outside *Heliodoxa* is found in *Eugenes, Topaza, Chalybura, Heliomaster, Ensifera,* and *Coeligena.* Asymmetry of the dorsal bar and nasal roof is pronounced in *leadbeateri* and absent in *Heliangelus.* The hybrid is symmetrical (a slight swelling on the left side of the base of the dorsal bar may or may not represent asymmetry related to displacement of elongate hyoid horns to the right); the tongue and hyoid horns are, of course, missing. The anterior tips of the hyoid horns of *amethysticollis* lie well short of the craniofacial hinge when the tongue is retracted into the bill; those of the hybrid could have extended forward somewhat beyond the hinge without causing asymmetry. Lack of asymmetry is thus not an argument against *leadbeateri* as a parent; it probably reflects intermediacy in length of the hyoid horns.

Probably derived independently in *Heliodoxa* is a truncate form of the body of the vomer from dorsal view in contrast to a smoothly tapered form (Fig. 2—e). A truncate vomer is found also in *Amazilia, Chlorostilbon,* their relatives, and a few other genera. In *Heliodoxa* (and some *Amazilia*) the anterolateral angles of the vomer are accentuated by anteriorly directed spikes. The vomer of the hybrid is intermediate in shape and lacks the anterior spikes of *Heliodoxa.* Another feature of *Heliodoxa* is an anteriorly forked bony roof of the vestibular nasal cavity from dorsal view (Fig. 2—f). A similar feature appears elsewhere in a variety of genera. In the hybrid, the anterior profile of the roof of the vestibular nasal cavity is forked as in *Heliodoxa.* None of the above characters is unique to *Heliodoxa,* but in combination they are diagnostic of the genus.

Among other features, the roof of the vestibular nasal cavity of the hybrid is narrower and longer than in *Heliodoxa,* and similar to *Heliangelus* (Fig. 2—g). The hybrid also resembles *Heliangelus* in that the lateral wall of the rostral nasal concha is broadly concave between a projecting roof and broad floor in lateral view (Fig. 2—h). In *leadbeateri* this lateral concavity is narrower and reduced in length—a derived feature in hummingbirds. The roof of the nasal cavities is depressed below the ridge of the dorsal bar in *Heliodoxa* and lies almost at the level of the ridge in *Heliangelus* (Fig. 2—i); in this the hybrid is intermediate. It is also intermediate in the orientation of the nasal surface of the ectethmoid (swept back in *Heliodoxa* and transverse in *Heliangelus*; Fig. 2—j). The median spine of the vomer is long in *Heliodoxa,* short in *Heliangelus,* and intermediate in the hybrid (Fig. 2—k).

In summary, osteology of the hybrid skull exhibits derived characters of *Heliodoxa,* similarities to *Heliangelus,* and intermediacy between the two genera. It lacks derived characters of other genera. These features support the hypothesis that a species of *Heliodoxa* is one parent of the hybrid, and that a species of *Heliangelus* could be the other.

DISCUSSION

The analysis of independent data sets is a powerful but under-utilized tool in hybrid diagnoses. In this case, the parental hypothesis suggested by plumage characters could have been falsified by skeletal characters. Had this occurred, we would have re-examined the diagnostic assumptions of the analyses and considered alternate parentage or other hypotheses such as atavism (see Buckley 1982, Graves 1990).

Problematic specimens of hummingbirds are relatively common in museum collections, and many of those reported in the literature are regarded as intergeneric hybrids (see examples in Meyer de Schauensee 1966). The high frequency of "intergeneric" hybridization in hummingbirds was interpreted by Sibley (1957) and Short and Phillips (1966) as evidence that the genera are oversplit. Banks and Johnson (1961, p. 26), however, suggested that "lack of intrageneric hybridization in . . . North American hummingbirds may result from the perfection of intrageneric isolating mechanisms without the concurrent development of intergeneric isolating mechanisms." However, the significance of hybridization at different taxonomic levels can be determined only after parentage has been identified critically in each case, and after the phy-

logeny of hummingbirds has been determined accurately. Examples of well-documented hybrid analyses are rare, and investigations of phylogeny are still in the formative stages (e.g., Zusi and Bentz 1982; Zusi, unpubl.). Among carefully analyzed hybrids, we think those described by Banks and Johnson (1961) and Short and Phillips (1966) among the "genera" *Archilochus, Calypte, Stellula,* and *Selasphorus* represent hybridization between very closely related species. By contrast, the hybrids *Eugenes* × *Cynanthus* (Short and Phillips 1966) and *Heliodoxa* × *Heliangelus* involve hybridization between species in distinct genera that are not sister taxa. No hybrids have been reported between species from different subfamilies (Phaethornithinae, Trochilinae). Only one (Ruschi 1944) has been reported between "primitive" and "advanced" trochilines (see Zusi and Bentz 1982), and one (Berlioz 1932, 1938) between the small, gorgeted hummingbirds (last 19 genera of Peters [1945]) and other groups (data from Gray 1958, Meyer de Schauensee 1966). It is premature to estimate the frequency of hybridization at different taxonomic levels or the implications of such patterns.

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