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Diagnoses of hybrid hummingbirds (Aves: Trochilidae). 17. Documentation of the intrageneric hybrid (*Archilochus colubris* × *Archilochus alexandri*)

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Abstract.—Although the breeding ranges of *Archilochus alexandri* (Black-chinned Hummingbird) and *Archilochus colubris* (Ruby-throated Hummingbird) are narrowly parapatric in central Texas and central and southern Oklahoma, there have been few reports of hybridization in the literature and no well-documented hybrid specimens. Here we provide a comprehensive assessment of two male hybrids collected, respectively, in Grayson County, Texas, and East Baton Rouge Parish, Louisiana. As has been the pattern in other hummingbird hybrids, both specimens exhibit a blended mosaic of plumage characters of the parental species. Sequence for mitochondrial cytochrome c oxidase subunit 1 (CO1) for the hybrid specimen from East Baton Rouge Parish (LSU 182,831) confirms *A. colubris* as the female parent.

Keywords: *Archilochus alexandri; Archilochus colubris;* Black-chinned Hummingbird, hybridization; Ruby-throated Hummingbird

A majority of hummingbirds that breed north of the Mexican border of the United States belong to the Mellisugini, a clade generally known as the "bee" hummingbirds (Bleiweiss et al. 1997, McGuire et al. 2014). Intrageneric hybridization in this group is well documented (Banks & Johnson 1961, Short & Phillips 1966, Wells et al. 1978, Newfield 1983, Stiles 1983, Graves & Newfield 1996, Graves 1997, 2003, 2006, van Dongen et al. 2012). Indeed, the earliest described examples of hybridization in the family Trochilidae involved bee hummingbirds (Fisher 1893, Hartert 1900, Thayer & Bangs 1907). Breeding ranges of bee hummingbirds exhibit varying degrees of geographic overlap, but only a single pair of sister species (sensu McGuire et al. 2014) that breed in North America north of the Mexican border with the United States are distributed parapatrically in a way that suggests secondary contact following allopatric speciation. An extensive zone of breeding parapatry occurs between the Black-chinned Hummingbird (*Archilochus alexandri*) and the Ruby-throated Hummingbird (*Archilochus colubris*) from southcentral Oklahoma southward to the Gulf coast of Texas, roughly bracketed between 97° and 98°W longitude (Oberholser 1974, Pulich 1988, Judd et al. 2011). Surprisingly little evidence of hybridization has been reported in the literature during the past century (Vacin 1969, Pulich 1988), given the large area of parapatry (>50,000 km^2) and the moderate degree of genetic divergence observed

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between the species (McGuire et al. 2014). In central Oklahoma, Vacin (1969) banded a male that exhibited a purple gorget with a reddish glint that was thought to be a hybrid. However, no photographs were taken and only the culmen was measured (18 mm) before the bird escaped. Recently, Judd et al. (2011) reported a cluster of 11 suspected hybrid males captured and released at banding stations in Comanche and Grady counties, Oklahoma. No measurements were published and the paper does not indicate whether any were taken before the males were banded and released. However, a photograph of a handheld male showed gorget iridescence intermediate in color between that of *A. alexandri* and *A. colubris,* supporting the hybrid hypothesis (Judd et al. 2011).

The only suspected specimen of *Archilochus colubris* × *A. alexandri* on record was reported by Pulich (1988:32), who noted, "An adult male hummingbird found dead at Austin College [in Sherman], Grayson County [Texas], on 2 May 1975 (KH) was said to be a hybrid between a Ruby-throated Hummingbird and a Black-chinned Hummingbird (confirmed by Lester L. Short)." Although neither Pulich nor Short published photographs or a description of the specimen, the record has been uncritically cited in the secondary literature (Panov 1989, McCarthy 2006). A second probable male hybrid was salvaged as a window-kill in Baton Rouge, Louisiana on 26 March 2010. Here we provide a comprehensive assessment of both specimens employing the methods and assumptions outlined in Graves (1990) as modified by subsequent papers (Graves & Zusi 1990, Graves 1998, 1999).

Methods

The Grayson County hybrid (Fig. 1) was transferred from Austin College to the Texas Cooperative Wildlife Collection, Texas A&M University, where it was cataloged (TAMU 12,453). The specimen was salvaged in Sherman, Grayson County, Texas (675 ft) by Joe Whitson on 2 May 1975 and prepared by Karl W. Haller (KWH 3183). Inked data on label: weight 2.7 g; fat; TSE [= testes slightly enlarged]; SFO [= skull fully ossified]; slipping when skinned; hit glass doors. Penciled data on label: cul. 16.5 mm; *Archilochus colubris* × *alexandri* LLS '75. When received for examination in October 2013, the distal half of the upper bill was missing and substantial portions of the posterior ventral plumage was missing.

The Baton Rouge specimen was salvaged by Jessica R. Eberhard on the campus of Louisiana State University, Baton Rouge, East Baton Rouge Parish, Louisiana, on 26 March 2010, prepared by Donna L. Dittmann (DLD 9925), and deposited in the Museum of Natural Science, Louisiana State University (LSUMNS 182,831). Data on label: 2.9 g; light fat, stomach—tiny spiders, flies (saved); skull 0% oss; no bursa; no body, wing, or tail molt; wingspan 9.7 cm; left testis 3 × 2 mm; iris very dark brown; black tarsi; feet blackish gray; found dead, hit window.

Both specimens are adult males in definitive plumage based on smooth maxillary ramphotheca and large iridescent gorgets. Consequently, all descriptions in this paper refer to definitive male plumage. We subjected the specimens to a hybrid diagnosis (Graves 1990), which focuses on the identification of apomorphic character states in putative hybrids. Complete dominance and polygenic inheritance of plumage characters may obscure the expression of parental apomorphies in hybrids. When parental apomorphies cannot be identified, the parentage of a hybrid may be indicated, although less conclusively, by the presence or absence of a suite of plesio-

Fig. 1. Ventral view of adult males: (in columns from left to right) *Archilochus alexandri* (LSU 160,022); *A. colubris* × *A. alexandri* (TAMU 12,453); *A. colubris* × *A. alexandri* (LSU 182,831); and *A. colubris* (LSU 127,366).

Table 1.—Measurements (mm; range and mean ± one standard deviation) of adult males of *Archilochus colubris,* two hybrids *A. colubris* × *A. alexandri* (TAMU 12,453; LSU 182,831); and *A. alexandri.*

Characters	*Archilochus colubris* $n = 16$	*A. colubris* × *A. alexandri* (TAMU 12,453) $n = 1$	*A. colubris* × *A. alexandri* (LSU 182,831) $n = 1$	*Archilochus alexandri* $n = 5–6$
Wing chord	37.3–40.2 (x = 38.7 ± 0.7)	40.8	37.8	40.4–42.3 (x = 41.07 ± 0.7)
Bill length	14.2–16.6 (15.0 ± 0.6)	[16.5][a]	16.7	15.4–17.5 (16.6 ± 0.7)
Rectrix 1	19.4–21.4 (20.3 ± 0.6)	22.0	20.4	20.5–22.2 (21.4 ± 0.6)
Rectrix 2	21.9–23.7 (23.0 ± 0.6)	24.2	22.8	22.8–23.7 (23.2 ± 0.3)
Rectrix 3	24.2–27.1 (25.9 ± 0.7)	26.9	25.0	24.1–25.6 (25.0 ± 0.7)
Rectrix 4	25.7–29.6 (28.3 ± 1.0)	28.7	27.3	23.7–25.5 (24.6 ± 0.7)
Rectrix 5	24.9–29.6 (28.1 ± 1.1)	28.7	26.3	22.4–24.5 (23.4 ± 0.9)

[a] "culmen = 16.5 mm" penciled on specimen label by Lester L. Short in 1975

morphic characters (Graves 1990, Graves & Zusi 1990, Graves 1998, 1999).

Given the migratory behavior of North American hummingbirds, both specimens could have been hatched nearly anywhere in the continental United States. We compared the specimens with large series (100+ adult males) of *Archilochus colubris* and *A. alexandri* and with all other hummingbirds that regularly breed north of the Mexican border—*Eugenes fulgens* (Magnificent Hummingbird), *Lampornis clemenciae* (Blue-throated Hummingbird), *Calothorax lucifer* (Lucifer Hummingbird), *Calypte anna* (Anna's Hummingbird), *C. costae* (Costa's Hummingbird), *Selasphorus platycercus* (Broad-tailed Hummingbird), *S. rufus* (Rufous Hummingbird), *S. sasin* (Allen's Hummingbird), *S. calliope* (Calliope Hummingbird), *Cynanthus latirostris* (Broad-billed Hummingbird), *Amazilia beryllina* (Beryline Hummingbird), *A. yucatanensis* (Buff-bellied Hummingbird), *A. violiceps* (Violet-crowned Hummingbird), and *Hylocharis leucotis* (White-eared Hummingbird). Wing chord, bill length (from anterior extension of feathers), and rectrix length (from point of insertion of the central rectrices to the tip of each rectrix) were measured with digital calipers and rounded to the nearest 0.1 mm. Rectrices (R1–R5) and primaries (P1–P10) are numbered from the innermost to the outermost. Scatterplots of measurements were used to illustrate size differences among specimens (Fig. 1). General color descriptions presented in Appendix 1 were made under natural light.

In order to determine the female parent of the Baton Rouge specimen, we subjected a frozen tissue sample to the standard DNA barcoding protocol in the Smithsonian Feather Identification Lab in Washington, D.C. (Kerr et al. 2007). A 660 base-pair section of the mitochondrial cytochrome c oxidase subunit 1 (CO1) was sequenced for comparison with vouchered sequences deposited in the BOLD database (http://www.boldsystems.org/index.php/IDS_OpenIdEngine). We did not seek to sample tissue from the fragile Grayson County specimen.

Results and Discussion

We considered two hypotheses—the specimens in question represent (*i*) a color morph of *Archilochus alexandri* or *A. colubris*, or (*ii*) a hybrid. The first hypothesis can be rejected because the external measurements and proportions of the specimens are substantially different from those of all age classes of male *A. alexandri* and *A. colubris* (Table 1). Evidence presented below suggests that the specimens

represent an intrageneric hybrid, *Archilochus colubris* × *A. alexandri*. In the remainder of the paper we refer to the specimens individually as the Grayson County and Baton Rouge hybrids and collectively as hybrids.

Plumage characters of the hybrids that facilitated the identification of their parental species include (a) black chin bordered posteriorly by a brilliant gorget, (b) forked tail, (c) relatively narrow inner primaries, and (d) relatively straight bill. The hybrids also lack an extended list of traits that are present in other North American hummingbirds (a) elongated lateral gorget feathers (*Calothorax lucifer, Calypte anna, C. costae, Selasphorus calliope*), (b) iridescent coronal patch (*Eugenes fulgens, Calypte anna, C. costae*), (c) white tail spots (*Lampornis clemenciae*), (d) strongly emarginated outermost primary (*Selasphorus platycercus, S rufus, S. sasin*), (e) rufous pigmentation on dorsal feather tracts (*Selasphorus rufus, S. sasin*), (f) rufous or buff pigmentation on rectrices (*Selasphorus platycercus, S. rufus, S. sasin, S. calliope, Amazilia beryllina, A. yucatanensis*), (g) rufous or buff pigmentation on primaries and secondaries (*Amazilia beryllina*), (h) thick white postocular stripe (*Lampornis clemenciae, Hylocharis leucotis*), (i) black lower breast and belly (*Eugenes fulgens*), and (j) red or orange ramphotheca (*Cynanthus latirostris, Amazila yucatanensis, A. violiceps, Hylocharis leucotis*).

Only two of the potential parental species possess the aforementioned characters expressed in the hybrids and lack the corresponding list of traits found in other potential parental species. Detailed examination reveals that the hybrids exhibit a blended combination of the plumage characters of *Archilochus colubris* and *A. alexandri* (Fig. 1, comparative notes in Appendix 1). Inheritance of iridescence in intergeneric hybrid hummingbirds is poorly understood and not easily predicted from the colors exhibited in parental species (Graves 1990, Graves & Zusi 1990, Graves 1998, 1999, Graves 2007). So far as is known, intra- and intergeneric hybridization within the bee hummingbird clade (sensu McGuire et al. 2014) results in gorget iridescence in offspring that is intermediate between the dominant wavelengths exhibited by the parental species (Jeffries 1888, Fisher 1893, Banks & Johnson 1961, Short & Phillips 1966, Wells et al. 1978, Stiles 1983, Graves & Newfield 1996, Graves 1997, 2003, 2006, Clark et al. 2013). In this case, although the gorget color of the Grayson County and Baton Rouge hybrids were distinctly different from one another, both exhibit dominant wavelengths that are bracketed by those of *Archilochus colubris* (red) and *A. alexandri* (violet).

We tested this parental hypothesis, *Archilochus colubris* × *A. alexandri,* with an examination of size and external proportions (Table 1). External measurements of trochiline hybrids generally fall within the mensural ranges exhibited by their parental species as a consequence of a polygenic mode of inheritance (Banks & Johnson 1961, Buckley 1982, Graves 1990, Graves & Zusi 1990, Graves 1996), although there is at least one known trivial exception to this rule in rectricial measurements (Clark et al. 2013). Wing length and presumably body size in *Archilochus alexandri* display geographic variation with smaller birds found in southern breeding populations (Baltosser 1987). For this reason, we restricted comparisons with male *A. alexandri* collected in central and southern Texas (Table 1). Measurements of the hybrids fall within the cumulative range of measurements observed in *Archilochus colubris* and the relatively small sample of *A. alexandri* (Fig. 2) with exception of rectrix 2 length in the Grayson County specimen which was 0.5 mm longer than those of the presumed parental species. Because

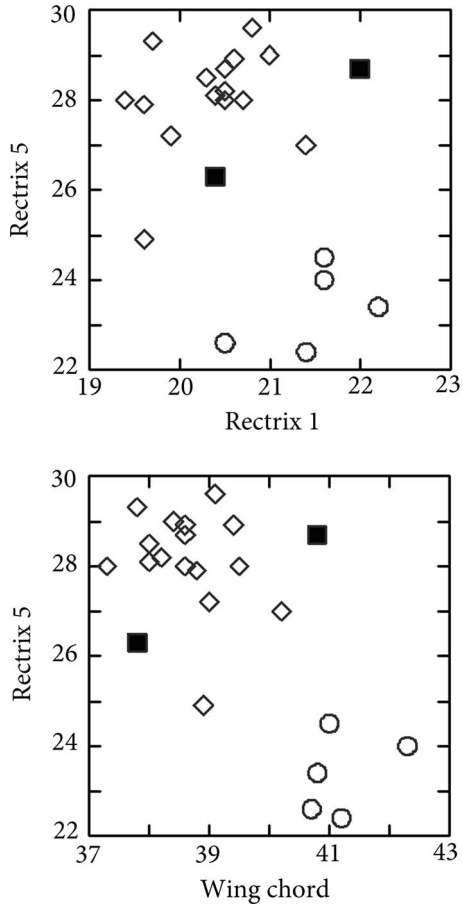

Fig. 2. Bivariate relationships of wing chord and selected tail measurements (mm) of adult males: *Archilochus colubris* (◇); hybrids (■) *A. colubris* × *A. alexandri* (TAMU 12,453, LSU 182,831); and *A. alexandri* (○).

the presumed parental species are relatively similar in size, the observation of size intermediacy provides a robust confirmation of the conclusions drawn from plumage color. In summary, evidence obtained from overall size, tail proportions, and plumage pattern and color are consistent with the hypothesis that both the Grayson County and Baton Rouge specimens represent hybrids between *Archilochus colubris* and *A. alexandri*.

Genetic analysis. Sequence for mitochondrial cytochrome c oxidase subunit 1 (CO1) for the hybrid specimen from Baton Rouge (LSU 182,831) was identical (100% similar) to vouchered CO1 sequences for *Archilochus colubris* deposited in the BOLD database (Appendix 2). This confirms *A. colubris* as the female parent of the hybrid.

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Appendix 1

Comparative notes on males of *Archilochus colubris, A. alexandri,* and two probable hybrids, *Archilochus colubris* × *Archilochus alexandri* (TAMU 12,453 = GC [Grayson County, TX]; LSU 182,831 = BR [East Baton Rouge Parish, LA]). Descriptions of structural colors are unusually subjective, as color seen by the observer varies according to the angle of inspection and direction of light. For this reason we use general color descriptions.

The dorsal plumage of *A. colubris,* including wing coverts, ranges from green to golden green. Bluish highlights are present on some specimens and the crown is often shaded with bronze green. In *A. alexandri,* the dorsal plumage including wing coverts is dull bronze green becoming darker and less reflective on the crown. The GC hybrid is closer in color to *alexandri* but exhibits more bronze highlights on the lower back and rump (a patch of mantle plumage is missing). The BR hybrid is roughly intermediate in hue between *A. colibris* and *A. alexandri.*

The chin, loral and suborbital regions, and auriculars are velvety black in *colubris.* The brilliant gorget (metallic ruby-red to orange-red when viewed head-on) extends posteriorly to the lower throat and laterally to the rear of the auriculars. The gorget is bordered posteriorly by a thin somewhat irregular grayish-white pectoral band. The lower breast and flanks are grayish brown, the feathers on the flanks and sides glossed with bronze green. Feathers near the midline lack green highlights. Undertail coverts are pale bronze gray, broadly margined with pale grayish white.

In *A. alexandri,* the chin and upper throat as well as the loral, suborbital, and auricular regions are dull to velvety black. A vertically compressed brilliant gorget (metallic violet to violet-purple) extends across the lower throat to the rear of the auriculars. The remainder of the ventral plumage is similar to that of *A. colubris* in pattern but overall appearance is lighter.

In the GC hybrid, the chin, loral and subocular regions, and the auriculars are dusky black. The brilliant gorget is rosy purple with a few black discs in the upper throat and scattered violet-tinted discs on the lower throat. Gorget shape is nearer to that of *A. colubris* but the color is roughly intermediate between that of the parental species. Gorget margins of the GC hybrid extend posteriorly at the sides of the throat but this appearance may be accentuated by the understuffed skin preparation. Substantial portions of the ventral plumage are missing but what remains appears more similar to that of *A. colubris* than *A. alexandri.*

In the BR hybrid, the chin, loral and subocular regions, and the auriculars are dusky black with greenish iridescence along the lower gape. The size and shape of the gorget are similar to that of *A. colubris.* The gorget emits a dim rose iridescence with purplish overtones that are most intense on the sides of the throat. For comparative purposes, gorget color is intermediate between that of *A. colubris* and *A. alexandri.* The remainder of the underparts is intermediate in appearance between typical *A. colubris* and *A. alexandri.*

Both parental species and the hybrids have slate-colored primaries faintly glossed with brownish purple. Inner primaries of *A. colubris* and *A. alexandri* are narrow and characterized by a subtle projection (or notch) on the inner web at the base of the terminal taper (Baltosser 1987). Both hybrids have narrow and notched inner primaries. However, the inner web projection is prominent in the BR hybrid but barely visible in the GC hybrid. The outer primary (P10) of the hybrids are tapered and narrow and thus more closely resemble those of *A. colubris* rather than the relatively wide and bluntly tipped P10 of *A. alexandri.*

The central rectrices (RI) of *A. colubris* are metallic green or golden green. The other rectrices are dusky black with purplish-brown highlights. In *A. alexandri*, the central rectrices (RI) are bronze green. The outer rectrices (R2–R5) are dull black with purplish-brown highlights. Rectrices are paler distally and often highlighted with green or grayish-green, especially R2. Tail fork in *A. alexandri* is significantly shallower than in *A. colubris.* Tail fork depth, rectrix shape, and rectrix color in the hybrids are roughly intermediate between those of the parental species. Rectrices (especially R4–R5) of the GC hybrid are more narrowly attenuated than those of the BR hybrid and thus more similar in shape to those of *A. alexandri* (see Fig. 2 in Banks and Johnson 1961).

The maxillary ramphotheca of *A. colubris,* A. *alexandri,* and the hybrids are black.

Appendix 2

660 bp (position 11-670) of the mitochondrial cytochrome c oxidase subunit 1 (CO1) from a hybrid specimen (LSU 182,831), *Archilochus colubris* × *Archilochus alexandri*, collected in East Baton Rouge Parish, Louisiana.

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            cttcggagcatgggctggaatagttggaacctctctaagcctactaatcc          60

gagcagaactcggccagccaggcaccctcctaggggacgaccaaatttataatgtgatcg          120

tcactgcccatgccttcgtaataatcttcttcatagttataccaattataatcggaggct          180

ttggaaactgattagtcccactcataattggagcccccgacatagcattcccacgtataa          240

ataacataagcttctgactcctaccaccatcgttcctcttactccttgcttcctctaccg          300

tcgaagcaggcgcaggcacgggatgaactgtatacccccctctggccggcaacttagccc          360

acgcaggagcatcagtagacctagccatcttctccttacacctatcaggcatctcatcaa          420

tcctaggagcaattaacttcattaccaccgcaatcaatataaaaccacccgccctatctc          480

aataccaaaccccctatttgtttgatccgtcctcattactgccgtcctactccttcttt          540

cactcccagtacttgctgccggaattaccatgctactcacagaccgaaacctaaacacca          600

cattttcgaccccgctggaggaggagaccccatcctctatcagcacttattctgattct          660

ttggcccccc
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