A primer on the hybrid zone of Jamaican streamertail hummingbirds (Trochilidae: *Trochilus*)

Author(s): Gary R. Graves
Source: Proceedings of the Biological Society of Washington, 128(1):111-124.
Published By: Biological Society of Washington
DOI: http://dx.doi.org/10.2988/0006-324X-128.1.111
URL: http://www.bioone.org/doi/full/10.2988/0006-324X-128.1.111

PROCEEDINGS OF THE BIOLOGICAL SOCIETY OF WASHINGTON
128(1):111–124. 2015.

A primer on the hybrid zone of Jamaican streamertail hummingbirds (Trochilidae: *Trochilus*)

Gary R. Graves

Department of Vertebrate Zoology, MRC-116, National Museum of Natural History, Smithsonian Institution, P.O. Box 37012, Washington, DC 20013-7012, USA; Center for Macroecology, Evolution and Climate, Natural History Museum of Denmark, University of Copenhagen, DK-2100, Copenhagen Ø, Denmark.

Abstract.—The endemic hummingbirds *Trochilus polytmus* and *T. scitulus* hybridize in a narrow zone of secondary contact in eastern Jamaica. The cline in bill width across the hybrid zone represents the steepest morphological gradient documented thus far in avian biology. Hindlimb size and skeletal proxies for core body size, however, exhibit incongruent patterns of variation across the same transect. Significant correlation between bill width and skull width indicates that genetic loci that affect bill width have pleiotropic effects on cranial morphology posterior of the craniofacial hinge. This study is the first direct examination of skeletal size variation across an avian hybrid zone.

Keywords: hummingbird, hybrid zone, Jamaica, James Bond, streamertail, *Trochilus*

Perhaps the most enigmatic avian hybrid zone discovered to date occurs in eastern Jamaica (10,991 km^2), where the geographic ranges of the Red-billed Streamertail (*Trochilus polytmus*) and Black-billed Streamertail (*T. scitulus*) meet in Portland and St. Thomas parishes (Bond 1956, Gill et al. 1973). This endemic pair of taxa represents the only known avian example of *in situ* speciation on an island smaller than New Guinea (786,000 km^2) and Madagascar (588,000 km^2) (Bond 1956, Diamond 1977). Bill color is the principal morphological character differentiating the two sexually dimorphic taxa (Brewster & Bangs 1901, Gill et al. 1973, Schuchmann 1978). *Trochilus scitulus*, which has an entirely black bill in both sexes, is restricted to the extreme eastern tip of the island. The better known *T. polytmus,* which possesses a coral red bill in males, occurs widely in the remainder of Jamaica except in deforested landscapes and in the most arid areas along the southern coast (Fig. 1). Females of both taxa lack the extravagant tail streamers of males that gave rise to their common English names. The approximate location of the narrow hybrid zone was documented by Gill et al. (1973), but the circumstances under which the differentiation arose and the factors that maintain the hybrid zone and prevent the coalescence of red-billed and black-billed populations are unknown. Summary size metrics for samples of *T. polytmus* and *T. scitulus* were reported by Brewster & Bangs (1901), Gill et al. (1973), Schuchmann (1978), and MacColl & Lewis (2000); however, the nature of size variation across the hybrid zone remains unexplored.

The aims of this paper are twofold. First, I briefly review the taxonomic history of streamertails and discovery of the hybrid zone. Second, I present an exploratory analysis of morphological

DOI: 10.2988/0006-324X-128.1.111

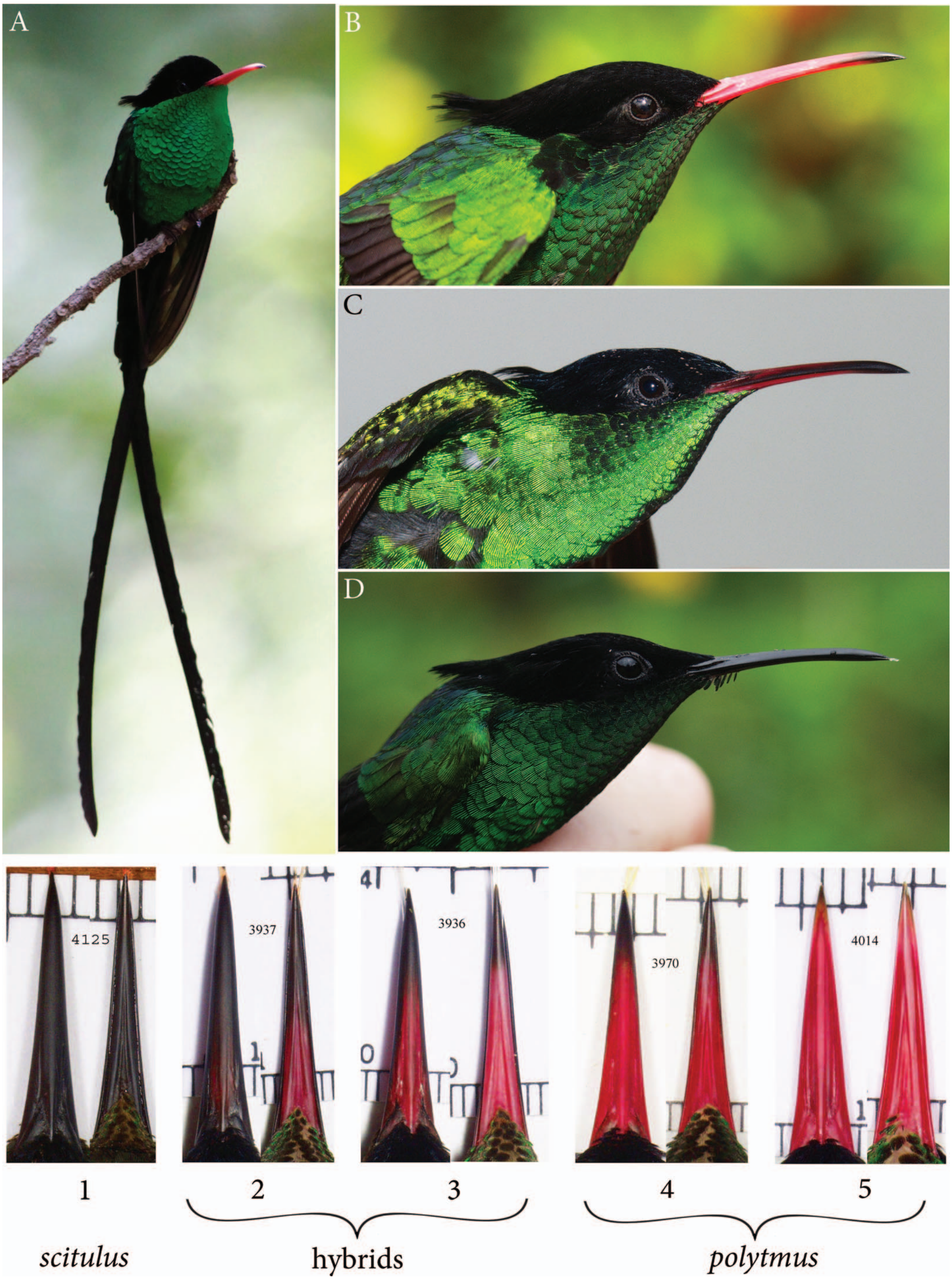

Fig. 1. Male *Trochilus* in definitive basic plumage: (A) *T. polytmus* from Trelawny Parish; (B) *T. polytmus* from Ginger House, Portland Parish; (C) hybrid (*T. polytmus* × *T. scitulus*; USNM 635675; bill color category = 3) from Tom's Hope, Portland Parish (see locality 6, Fig. 2); (D) *T. scitulus* from Millbank, Portland Parish. Apparent differences in body color result from varying light exposures during photography. Lower panel illustrates bill color categories of males in definitive basic plumage: dorsal (left) and ventral (right) views in each pair of images.

variation in male streamertails derived from a recently collected series of specimens from a longitudinal transect across the hybrid zone. These data constitute the background material and baseline documentation for a comprehensive genetic and morphological analysis of the streamertail hybrid zone that will be published in the future.

Historical overview of streamertails and the hybrid zone

Trochilus polytmus was known to English naturalists as early as 1688 (Sloane 1725) and was one of the original 13 species of hummingbirds described by Linnaeus in the 10th edition of *Systema Naturae* (Linnaeus 1758). The coral-red bill, long tail streamers, brilliant emerald breast plumage, and elongated black crest feathers of adult males (Fig. 1) create one of the most visually arresting displays in the avian world. Its spectacular appearance and ubiquity in forested habitats are undoubtedly responsible for the penetrance of the "doctor bird" in rural Jamaican folklore and made it an enduring national symbol of Jamaica. *Trochilus polytmus* was long believed to be the sole species of streamertail (Sloane 1725, Browne 1756, Gosse 1847) until two other species were described in the mid-to late 19th century. These taxa—*T. maria* Gosse, 1849 and *T. taylori* Rothschild, 1894—were ultimately determined to be juvenile or aberrant specimens of *T. polytmus* (Brewster & Bangs 1901, Graves & Prys-Jones 2011).

A second valid streamertail species was discovered in the Priestmans River watershed of Portland Parish in 1891 (Scott 1892, 1904). *Trochilus scitulus* (Brewster & Bangs, 1901), the last of the extant avian endemic species to be discovered in Jamaica, differs from the widespread *T. polytmus* in having a wholly black bill in both sexes as mentioned in the introduction. The geographic range of *T. scitulus* is currently thought to be restricted to the eastern tip of Jamaica, centered on the John Crow Mountains in Portland and St. Thomas parishes. However, its description in 1901 sowed confusion about the ranges of the two *Trochilus* species that took more than three-quarters of a century to clarify (Bangs & Kennard 1920, Danforth 1928, Bond 1936, 1940, 1956, Gill et al. 1973).

Knowledge that *T. polytmus* was the common streamertail in Bluefields near the southern coast and in Kingston (Gosse 1847, Scott 1892), and *T. scitulus* was common near the northern coast in Portland Parish (Scott 1892, Brewster & Bangs 1901, Scott 1904), gave rise to the notion that the geographic ranges of the two streamertails were separated by the long axis of the island (Cory 1918). Ridgway (1911) listed Moneague, St. Ann Parish, as a locality for *T. polytmus*, but failed to realize that this site lies on the north slope of the island. In the first checklist of Jamaican birds to appear after the description of *T. scitulus,* Bangs & Kennard (1920:12) defined the distribution of *T. polytmus* as "very common all over the southern slope of the island," and that of *T. scitulus* as "found on the northern slope of the island … it appears to be quite as abundant in its country as is *A.* [*T.*] *polytmus* on the south slope." This hypothesis was questioned by Danforth (1928:486–487) after he conducted six weeks of fieldwork in central and western Jamaica.

> "All the male *Aithurus* [*Trochilus*] collected or seen, whether on the north or south side of the island, were of the red-billed variety, and Miss Perkins, who has lived most of her life in various localities in the northern part of the island, tells me that she cannot definitely remember ever seeing a black-billed individual. These facts led me to doubt the validity of *A. scitulus* even before a talk I had with Mr. Panton in which he stated that he did not believe *scitulus* to be distinct. If it is distinct, it certainly does not occur at all commonly along the north coast in St. Ann's and

> Trelawney, where I found *polytmus* to be very common."

Bond (1936:213) noted that *T. polytmus* occurred throughout Jamaica, except in Portland Parish: "The red-billed species is found on the main ridge of the Blue Mountains, being common on Blue Mountain Peak. I am unable to say whether the ranges of the two forms of this genus overlap." Bond (1936:214) added that *T. scitulus* was confined to Portland Parish in northeastern Jamaica and was best regarded as a subspecies of *T. polytmus*. Bond did not reference the source of field data that was used to refine the geographic ranges of the two species. A few years later, Bond (1940:79) amended the range of *T. scitulus*, "Extreme eastern Jamaica, replacing the nominate race [*T. polytmus*] in this section of the island. Common. Found at Port Antonio, Priestman's River, in the Cuna Cuna Pass, and at Bath. Accidental in 'Kingston' (Scott)."

The first evidence that the geographic ranges of *T. polytmus* and *T. scitulus* were parapatric was provided by James Bond who collected specimens in January 1951 in the vicinity of Port Antonio on the north coast (Bond 1956, Gill et al. 1973). Bond (1956:94) described the range of *T. polytmus*: "Abundant and widespread, but not found in extreme eastern Jamaica; occurs along the northern coast as far east as the vicinity of Hope Bay, in the Blue Mountains to Sugar-Loaf Peak, along the southern coast to extreme western St. Thomas." Bond (1956:94–95) amended the range account of *T. scitulus*: "Extreme eastern Jamaica (chiefly John Crow Mountains region), replacing the nominate race in this section of the island. Common. Found at Priestman's River, in the Cuna Cuna Pass, Cornpuss Gap, and at Bath. Inhabits a humid area with heavy rainfall . . . The population of this species [streamertails] at Port Antonio is intermediate (*scitulus* × *polytmus*), and even in the vicinity of Priestman's River an occasional individual shows some reddish at the base of the mandible."

Additional evidence of hybridization was noted in April 1951 on the southern slope at the base of the divide between the John Crow Mountains and the Blue Mountains in St. Thomas Parish (Jeffrey-Smith 1956). Jeffrey-Smith observed typical examples of *T. polytmus* and *T. scitulus* at the fountain in Bath, as well as an adult in "full plumage" with a red bill that exhibited more black than she was accustomed to seeing in the streamertails of Trelawny Parish.

A fuller resolution of the contact zone between the red-billed and black-billed forms was offered by Gill et al. (1973), who examined *Trochilus* specimens in museum collections, including the type series of *T. scitulus,* and made field surveys of streamertail populations on 13 field days in January 1971. Gill created a hybrid index of male bill color based on nine ranked categories that ranged from pure black to solidly red. Bills of *T. scitulus* were invariably black (index score = 1), whereas typical adult male *T. polytmus* had bills narrowly tipped with black (index score = 7–8) or had solidly red bills (index score = 9). Index scores from the Kingston reference sample of *T. polytmus* males ranged from 6–9 in adults to 4–8 in subadults. Noting the difficulty of classifying subtle differences in male bill color in free-living birds under field conditions, Gill et al. (1973) binned observed birds in four broader categories: "black" (index score = 1), black intermediate (index scores = 2–3), "red intermediate" (index scores = 4–6), and "red" (index scores 7–9). Specimens and free-living birds with index scores of 2–5 (adults) and 2–3 (subadults) were classified as hybrids.

Gill et al. (1973) concluded that *T. polytmus* and *T. scitulus* exhibited a limited amount of hybridization in the zone of contact that roughly paralleled the eastern slope of the Rio Grande Valley south of Port Antonio on the northern slope of island. The contact zone on the southern slope was more difficult to resolve but hybridization appeared to be limited to a relatively narrow sector east of the Morant River. Gill's portrait of the contact zones was remarkably accurate given the brief amount of time his field team devoted to site surveys (Graves, *personal observation*). MacColl & Lewis (2000) made binocular surveys of streamertail bill color and conducted limited mist netting at many of the same localities in Portland and St. Thomas parishes. They concluded that the position of the hybrid zone had not changed appreciably in the 29 years since Gill's survey (MacColl & Lewis 2000). Schuchmann (1978), however, questioned the evidence for hybridization, arguing that the extent of red coloration in bill tissues increased with age in *T. polytmus,* which rendered bill color an unreliable measure of hybridization. Neither Gill et al. (1973) or Schuchmann (1978) decisively determined at what age bill color becomes a legitimate indicator of hybridization. Graves (2009a) later demonstrated that *T. polytmus* attains adult bill color at the completion of the first prebasic molt, whereas bill color in *T. scitulus* is black in all fledged individuals. Bill color thus provides an authentic marker of hybridization in male streamertails in first basic and definitive basic plumages.

The systematic status of *Trochilus polytmus* and *T. scitulus* remains unsettled. Bond (1936) considered the two forms to be distinctive species, but later changed his mind and treated *T. scitulus* as a subspecies of *T. polytmus* (Bond 1956). Gill et al. (1973) followed suit. Schuchmann (1978, 1980) noted differences in courtship displays and song between *polytmus* and *scitulus* and treated them as reproductively isolated species. The current *Check-list of North American Birds, 7th edition* (American Ornithologists' Union 1998) considers *scitulus* as a subspecies of *T. polytmus*. Preliminary analysis of microsatellite loci from small population samples of *T. scitulus* and *T. polytmus* collected near the hybrid zone in Portland Parish and from a geographically allopatric sample of *T. polytmus* from western Jamaica (Trelawny Parish) failed to reveal spatially structured genetic variation (Lance et al. 2009). A second exploratory study of single nucleotide polymorphisms (SNPs) detected subtle population differences between geographically distant population samples of *T. polytmus* and *T. scitulus* (McCormack et al. 2011). Neither study identified a molecular marker that was diagnostic for bill color.

Materials and Methods

Specimens and measurements.—Male *Trochilus* specimens were collected at 12 sites located along a longitudinal transect in the vicinity of Port Antonio, Portland Parish, from November 2003 to March 2006 (Table 1, Fig. 2). Collection sites were strategically located to span the contact zone between *Trochilus polytmus* and *T. scitulus* near the northern coast. Altitude (above sea level) of collection sites varied from 10 to 390 m ($\bar{x}$ = 131 m ± 124.2). Distances along the transect (Table 1) begin at Somerset Falls (0.0 km) and terminate at Ecclesdown (24.8 km). Voucher specimens (round skins, partial skeletons, tissues) collected under licenses issued by the National Environment and Planning Agency (NEPA), Kingston, are deposited in the research collection of the National Museum of Natural History (USNM), Smithsonian Institution (see Appendix).

Body weight measurements of living hummingbirds are biased by gut contents, reproductive condition, and fat deposits (Calder et al. 1990). Fluids pass rapidly through the gut of active individuals and are excreted within 30 minutes of ingestion (Karasov et al. 1986, Tiebout 1989). Gut passage times for insects and spiders, the principal sources of proteins and fats in

Table 1.—Collecting localities (west to east) for male streamertails (*Trochilus polytmus* and *T. scitulus*) in Portland Parish, Jamaica ordered by longitude. A reference population of *T. polytmus* from western Jamaica (Windsor, Trelawny Parish) is provided for comparison. Population means (mm ± standard deviation) are presented for selected morphological characters.

Collecting locations	Taxon	Distance (km)[a]	Sample size[b]	Latitude (N)[c]	Longitude (W)[c]	Bill width	Ectethmoidale width	Bill length
Trelawny Parish[d]	*polytmus*		9	18.36	77.66	4.94 ± 0.17	6.89 ± 0.15	22.6 ± 0.7
Somerset Falls	*polytmus*	0	5	18.20	76.55	4.53 ± 0.27	7.06 ± 0.22	22.8 ± 0.7
Burlington	*polytmus*	6.1	10	18.18	76.50	4.46 ± 0.12	7.01 ± 0.18	22.7 ± 0.8
Springbank	*polytmus*	8.7	7	18.18	76.47	4.33 ± 0.08	6.97 ± 0.23	22.3 ± 0.9
Fellowship	*polytmus*	11.8	5	18.14	76.46	4.33 ± 0.21	7.15 ± 0.20	22.3 ± 0.3
Windsor	hybrids	14.5	3	18.11	76.45	4.37 ± 0.05	6.87 ± 0.19	22.7 ± 1.4
Tom's Hope	*polytmus,* hybrids	13.9	3	18.13	76.44	4.31 ± 0.08	6.97 ± 0.28	22.5 ± 0.8
Trowel Hill	*scitulus*	14.7	8	18.14	76.43	4.08 ± 0.24	6.88 ± 0.37	22.5 ± 0.7
Mt. Lebanus	*scitulus*	16.0	2	18.13	76.42	4.00 ± 0.56	6.77 ± 0.35	22.1 ± 1.8
Nonsuch	*scitulus*	14.8	7	18.15	76.42	4.01 ± 0.11	6.88 ± 0.24	22.2 ± 0.4
San San	*scitulus*	16.2	7	18.17	76.40	3.88 ± 0.09	6.72 ± 0.28	21.9 ± 0.7
Cambridge	*scitulus*	19.6	3	18.12	76.38	4.01 ± 0.29	6.85 ± 0.14	21.4 ± 0.3
Ecclesdown	*scitulus*	24.8	7	18.09	76.35	3.88 ± 0.21	6.92 ± 0.34	21.7 ± 0.7

[a] Distance from Somerset Falls along axis from Somerset Falls to Ecclesdown

[b] Males in basic plumage

[c] Rounded to the nearest hundredth of a decimal degree

[d] Reference population from western Jamaica (118 km west of Somerset Falls)

[e] Adult males in definitive basic plumage (sample sizes for wing and rectrix length in parentheses): Trelawny Parish (3, 0), Somerset Falls (3, 3), Burlington (4, 4), Springbank (4, 4), Fellowship (2, 2), Windsor (2, 1), Tom's Hope (3, 2), Trowel Hill (3, 2), Mt. Lebanus (1, 1), Nonsuch (2, 2), San San (3, 3), Cambridge (0, 0), Ecclesdown (3, 3).

hummingbird diets (Remsen et al. 1986), are unknown. In any event, the time of capture, the duration between capture and weighing, and the precision of weighing scales, can have a significant effect on the estimation of lean body mass (Graves 2009b). To circumvent these problems, I used skeletal proxies for body size of streamertails. Selected skeletal elements were measured with digital calipers to the nearest 0.01 millimeters (mm) under a 10× stereo microscope: (*i*) sternum length, (*ii*) keel depth, (*iii*) keel length, (*iv*) femur length, (*v*) tibiotarsus length, (*vi*) tarsometatarsus length, (*vii*) humerus length, (*viii*) coracoid length, and (*ix*) skull width across the ectethmoidale prominences immediately caudal of the craniofacial hinge. There are no differences in skeletal size between males in first basic plumage and those in definitive basic plumage (Graves 2009b).

The outer primaries of adult male streamertails produce a distinctive whirring sound in flight (Clark 2008). Many earlier observers noted that subadult males that lacked elongated streamers and females were unable to produce whirring sounds. What this suggests and what examination of museum specimens proves is that the morphology of both primaries and rectrices changes progressively as males mature (Graves, *personal observation*). Males in definitive basic plumage have longer wings than males in first basic plumage. For this reason, I limited the presentation of data on wing chord and tail measurements to males in definitive basic plumage. The length of rectrix 1 (shortest) and rectrix 4 (streamer) was measured from the point of insertion of the central rectrices to the tip of the longest feather in each pair.

Brewster & Bangs (1901) observed that *Trochilus polytmus* from Kingston had

Table 1.—Extended.

Collecting locations	Sternum length	Keel depth	Keel length	Femur length	Tibiotarsus length
Trelawny Parish[d]	16.38 ± 0.44	11.15 ± 0.24	18.05 ± 0.52	8.60 ± 0.18	13.79 ± 0.37
Somerset Falls	16.57 ± 0.36	11.17 ± 0.64	18.37 ± 0.55	8.73 ± 0.16	13.93 ± 0.43
Burlington	16.71 ± 0.35	11.34 ± 0.24	18.53 ± 0.46	8.80 ± 0.21	14.03 ± 0.35
Springbank	16.60 ± 0.48	11.43 ± 0.26	18.16 ± 0.48	8.73 ± 0.16	14.02 ± 0.31
Fellowship	16.89 ± 0.61	11.36 ± 0.31	18.38 ± 0.70	8.86 ± 0.22	14.09 ± 0.41
Windsor	16.98 ± 0.51	11.49 ± 0.28	18.69 ± 0.74	8.75 ± 0.22	13.94 ± 0.26
Tom's Hope	16.71 ± 0.47	11.25 ± 0.49	18.32 ± 0.95	8.85 ± 0.30	14.00 ± 0.41
Trowel Hill	17.07 ± 0.44	11.47 ± 0.29	18.77 ± 0.74	8.81 ± 0.16	14.08 ± 0.19
Mt. Lebanus	17.11 ± 0.32	11.58 ± 0.52	19.02 ± 0.85	8.73 ± 0.23	14.51 ± 0.01
Nonsuch	16.54 ± 0.36	11.39 ± 0.21	19.19 ± 0.42	8.72 ± 0.20	13.93 ± 0.48
San San	16.58 ± 0.41	11.38 ± 0.24	18.31 ± 0.56	8.64 ± 0.16	14.00 ± 0.45
Cambridge	16.57 ± 0.29	11.22 ± 0.38	18.36 ± 0.17	8.54 ± 0.14	13.63 ± 0.41
Ecclesdown	16.89 ± 0.36	11.36 ± 0.19	18.85 ± 0.53	8.83 ± 0.18	14.10 ± 0.45

Fig. 2. Schematic map of northeastern Jamaica depicting the collecting localities (meters above sea level): (1) Somerset Falls (30 m); (2) Burlington (10–15 m); (3) Springfield (85–110 m); (4) Fellowship (40–75 m); (5) Windsor (75 m); (6) Tom's Hope (35 m); (7) Trowel Hill (390 m); (8) Mt. Lebanus (340–355 m); (9) Nonsuch (160–165 m); (10) San San (45–50 m); (11) Cambridge (135–140 m); and (12) Ecclesdown (205–225 m). Symbols: red circles (*Trochilus polytmus* only), black circles (*T. scitulus* only), black and red circle (vertical, hybrid and *T. polytmus*), and black and red circle (horizontal, hybrids only). Line represents the long axis between Somerset Falls and Ecclesdown. Distances in Table 1 were calculated along the long axis from Somerset Falls to the intersection of perpendicular lines drawn from the long axis to each collecting locality. Areas shaded in dark gray represent montane landscapes above 500 m.

Table 1.—Extended.

Collecting locations	Tarsometatarsus length	Humerus length	Coracoid length	Wing chord[e]	Rectrix 4 length[e]	Rectrix 1 length[e]
Trelawny Parish[d]	5.73 ± 0.22	5.86 ± 0.09	7.54 ± 0.17	63.7 ± 3.33	—	30.2 ± 0.9
Somerset Falls	5.80 ± 0.12	5.93 ± 0.14	7.59 ± 0.19	63.9 ± 0.6	145.3 ± 1.5	29.7 ± 1.0
Burlington	5.83 ± 0.13	5.98 ± 0.10	7.57 ± 0.09	63.1 ± 0.8	161.3 ± 13.3	29.9 ± 0.7
Springbank	5.83 ± 0.15	5.94 ± 0.16	7.54 ± 0.17	62.0 ± 3.1	157.5 ± 11.5	29.5 ± 0.2
Fellowship	5.81 ± 0.19	5.90 ± 0.17	7.67 ± 0.17	62.5 ± 0.4	160.5 ± 20.5	28.1 ± 1.1
Windsor	5.74 ± 0.17	5.96 ± 0.04	7.67 ± 0.06	62.1 ± 1.0	147	28.8 ± 1.0
Tom's Hope	5.84 ± 0.24	5.95 ± 0.19	7.69 ± 0.17	62.4 ± 1.2	166.5 ± 2.1	27.6 ± 0.5
Trowel Hill	5.79 ± 0.15	5.93 ± 0.14	7.60 ± 0.22	60.7 ± 1.5	144.0 ± 11.3	29.1 ± 1.2
Mt. Lebanus	6.03 ± 0.07	5.99 ± 0.18	7.75 ± 0.19	63.8	172	28.8
Nonsuch	5.73 ± 0.12	5.88 ± 0.07	7.56 ± 0.10	62.1 ± 2.0	169.1 ± 14.0	28.1 ± 0.5
San San	5.74 ± 0.19	5.86 ± 0.08	7.49 ± 0.16	62.7 ± 0.8	150.3 ± 11.1	28.5 ± 1.4
Cambridge	5.74 ± 0.14	5.92 ± 0.13	7.48 ± 0.28	—	—	—
Ecclesdown	5.89 ± 0.18	5.88 ± 0.12	7.55 ± 0.13	61.5 ± 1.0	183.7 ± 32.7	28.3 ± 1.3

broader bills than *T. scitulus* from the Priestmans River. This was confirmed quantitatively by Gill et al. (1973) from measurements of the original specimen series collected by Scott (Scott 1892, Brewster & Bangs 1901). However, bill width in hummingbirds is often distorted during specimen preparation (Gill et al. 1973) because the fragile ventral bar of the maxilla (Zusi 2013) is easily flexed when the bill is tied shut. Preparation artifacts and shrinkage during drying introduce error that is impossible to factor out in comparative analyses of hummingbird bill width derived from museum specimens. These problems were circumvented by photographing bills of freshly euthanized *Trochilus* specimens in dorsal aspect next to a millimeter scale (Fig. 2). Two independent photos were made for each specimen (camera was moved and then repositioned at a fixed focal distance for the second photograph). I measured bill width to the nearest 0.01 mm at the anterior extension of feathers on dorsal surface of the mandible from enlarged images (30×). I present the average value of bill width measured from the two photographs. Bill length (to the nearest 0.1 mm) was measured in dried specimens from the bill tip to the posterior edge of the nasal flange.

Bill color in *Trochilus* is genetically determined, develops rapidly in nestlings, and attains a definitive color pattern in first basic plumage (Graves 2009a). Red bill color in *T. polytmus* fades within a few minutes after death and turns pinkish-gray within weeks in museum specimens. The rapid changes indicate that the red color is produced by blood-suffused tissues rather than carotenoid pigments (Graves 2009a). Descriptions of bill color in this paper are therefore based on digital photographs of living or very recently euthanized males.

As mentioned in the introduction, Gill et al. (1973) devised a complicated index of bill color for *Trochilus* with nine categories ranging from wholly black (category 1) to solidly red (9), which he collapsed to four categories for field classification of bill color. After a lengthy evaluation, the application of the "Gill" index (nine categories) to the current series of freshly collected specimens was deemed to be unfeasible. Although categorization of wholly black or red bills is unequivocal, bills that exhibit varying amounts of black pigmentation are difficult to place in a 9-category index. I thus used a simpler 5-category index that yielded repeatable classification of bill color from photographs (Fig. 1).

Statistical analysis.—Previous analyses of skeletal correlates of body mass in *T. scitulus* showed that both sternum length and multivariate measures of the sternum provide good and reproducible estimates of lean body weight (Graves 2009b). This is not surprising because the sternum supports the principal flight muscles (pectoralis and supracoracoideus), which compose as much as 33% of the lean body weight in hummingbirds (Hartman 1961). In the present study, I used principal components analysis (PCA) of correlation matrices extracted from untransformed measurements of sternum length, keel depth, and keel length to reduce the dimensionality of skeletal data and to generate an index of core body size. I conducted a second PCA on the untransformed lengths of femur, tibiotarsus, and tarsometatarsus to provide an overall index of hindlimb size. In each case, indices were based on variable loadings from the first axis (PCA 1).

I ran a battery of regression models and constructed scatterplots to examine the spatial variation of morphological variables and bill color as a function of longitude and distance from Somerset Falls (see Table 1, Fig. 2). Scatterplots and residual plots revealed that cline shape across the longitudinal gradient for most morphological characters was nonlinear, or non-sigmoidal, and could not be accurately described by simple equations. For this reason, I do not present estimates of slopes, intercepts, or measures of goodness-of-fit (r^2) for morphological variation across the transect. Instead, I present scatter plots of variables and smoothing curves derived from distance-weighted least squares regression (Fig. 4). In this procedure, a polynomial (second-order) regression is calculated for each value of X to determine the corresponding Y value such that the influence of individual data points on the regression decreases according to their distance from the particular X value. All statistical tests were performed with SYSTAT (version 12). A comprehensive analysis of cline shape in morphological and molecular characters will be presented in a future paper.

Results

Bill color exhibits a steep sigmoidal cline across the zone of contact (Fig. 3). Unequivocal hybrids (bill color categories = 2 and 3) were collected at only two sites near the center of the contact zone, Tom's Hope (1 of 3 specimens) and Windsor (3 of 3 specimens). The minimum distance between sampled populations with wholly red bills (Fellowship, 5 of 5 specimens classified as *Trochilus polytmus*) and wholly black bills (Trowel Hill, 8 of 8 specimens classified as *T. scitulus*) was 3.2 km.

Bill width varied 16.8% across the transect (24.8 km), ranging from $\bar{x} = 3.88$ mm at Ecclesdown to $\bar{x} = 4.53$ mm at Somerset Falls (Table 1, Fig. 3). The gradient in bill width between Trowel Hill ($\bar{x} = 4.08$ mm) and Fellowship ($\bar{x} = 4.33$ mm) was significantly steeper (0.078 mm/km) than the overall gradient (0.026 mm/km). Bill width ($n = 67$) was uncorrelated with altitude ($p = 0.30$) when longitude ($p < 0.0001$) was included as an independent variable in linear regression. Skull width measured across the ectethmoidale prominences showed no obvious coherent pattern across the hybrid zone (Fig. 3). Bill width was significantly correlated with ectethmoidale width in individuals ($n = 63$; $r^2 = 0.16$, $p < 0.001$). By comparison, variation in bill length was far less pronounced across the transect (5.1%), ranging from $\bar{x} = 21.7$ mm at Ecclesdown to $\bar{x} = 22.8$ mm at Somerset Falls. Bill length in the red-billed population at Fellowship ($\bar{x} = 22.3$ mm) was virtually

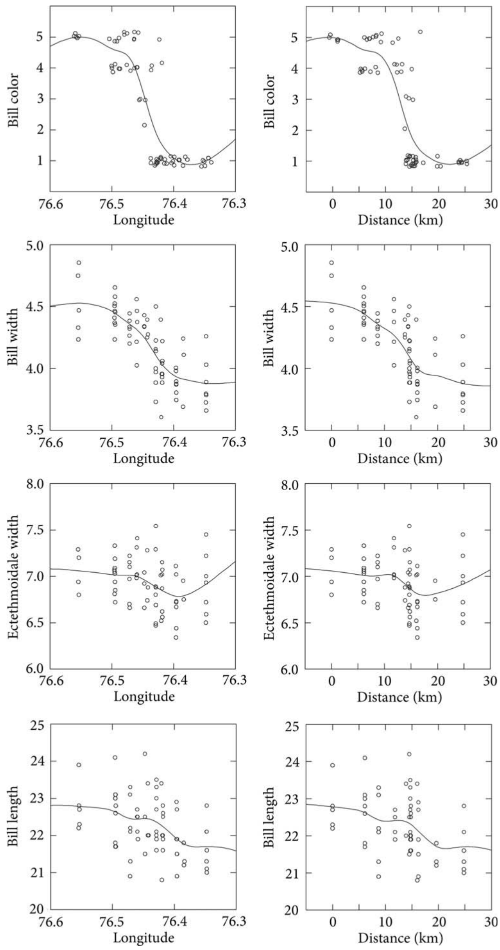

Fig. 3. Variation of bill color (see Fig. 1 for bill color index) and skull measurements (mm) of *Trochilus polytmus* and *T. scitulus* along a longitudinal transect across the hybrid zone in Portland Parish, Jamaica. Data points for bill color are jittered slightly to show sample size. The distance from Somerset Falls (see Fig. 2) is depicted in the x-axis of plots on the right hand side of this and successive figures.

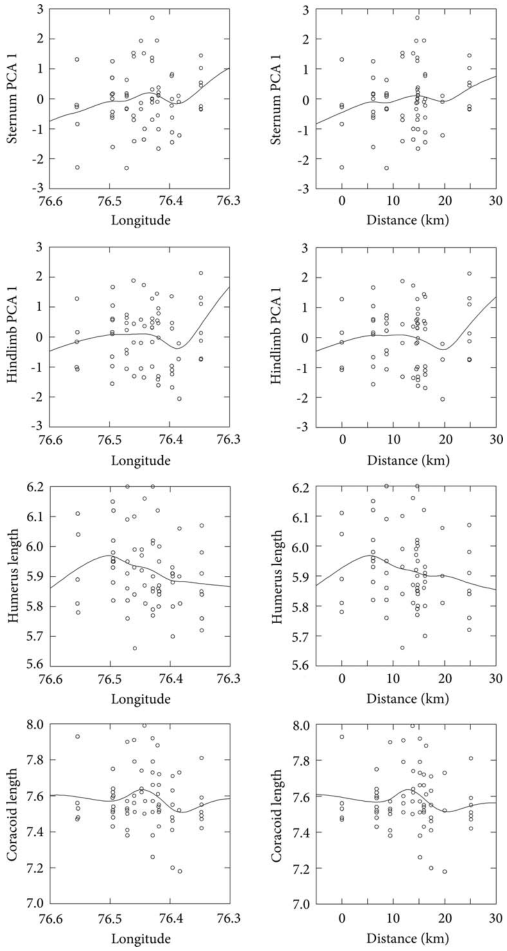

Fig. 4. Variation in sternum size (PCA 1), hindlimb size (PCA 1), humerus length (mm), and coracoid length (mm) across the hybrid zone between *Trochilus polytmus* and *T. scitulus* in Portland Parish, Jamaica.

identical to the black-billed population at Trowel Hill ($\bar{x} = 22.5$ mm).

PCA 1 explained 79.7% of the total variance in sternum measurements (core body size; $n = 67$) with high positive loadings for sternum length (0.92), keel depth (0.83), and keel length (0.92). Core body size (PCA 1 sternum measurements) increased slightly with altitude ($p = 0.04$), even when longitude ($p = 0.92$) was included as an independent variable in linear regression. For the analysis of hindlimb elements ($n = 64$), PCA 1 explained 76.2% of the total variance with high positive loadings for femur length (0.89), tibiotarsus depth (0.92), and tarsometatarsus length (0.81). Hind limb size (PCA 1 hindlimb elements) was uncorrelated with altitude ($p = 0.17$) when longitude ($p = 0.54$) was included as an independent variable in linear regression. Neither measure of body size exhibited smooth clinal patterns across the zone of contact (Fig. 4). Two additional measures of skeletal size, coracoid length and humerus length, showed incongruent patterns across the zone of contact (Fig. 4). Bill width was uncorrelated ($p > 0.05$) with all four skeletal measures of body size (PCA 1 sternum, PCA 1 hindlimb, coracoid length, humerus length).

Wing chord ($n = 38$) of adult males in definitive basic plumage increased from east (Ecclesdown, $\bar{x} = 61.5$ mm) to west (Somerset Falls, $\bar{x} = 63.9$ mm) across the hybrid zone (Fig. 5). Wing chord was uncorrelated with altitude ($p = 0.14$) when longitude ($p = 0.37$) was included as an independent variable in linear regression. Streamer length (rectrix 4; $n = 27$), which increased from west (Somerset Falls, $\bar{x} = 145.3$ mm) to east (Ecclesdown, $\bar{x} = 183.7$ mm), was uncorrelated with altitude ($p = 0.64$) when longitude ($p = 0.04$) was included as an independent variable in linear regression. In sum, *Trochilus scitulus* has a narrower and shorter bill, shorter wings, and a longer more deeply forked tail than *T. polytmus*.

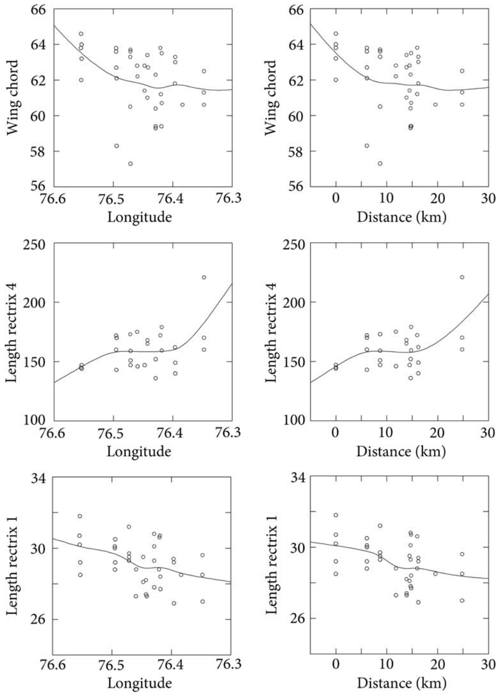

Fig. 5. Spatial variation of wing chord (mm) and rectrix length (mm) across the hybrid zone between *Trochilus polytmus* and *T. scitulus* in Portland Parish, Jamaica.

Conclusions

Hybridizing species often exhibit precipitous clines in morphological and genetic characters across zones of secondary contact (Meise 1928, Mayr 1963, Barton & Hewitt 1985). Variance in cline width has been used to infer selection coefficients associated with particular characters (Barton & Hewitt 1985). The majority of avian hybrid zones studied thus far exhibit cline widths of 100–1000 km (Barrowclough 1980, Rohwer et al. 2001, Irwin et al. 2009, Mettler & Spellman 2009). Case examples of narrow avian hybrid zones with cline widths of 10–100 km have been documented in manakins (Brumfield et al. 2001), wrens (Selander 1965), crows (Meise 1928), titmice (Curry & Patten 2014), warblers (Toews et al. 2011), and grackles (Yang & Selander 1968). Narrow hybrid zones are particularly intriguing because they suggest that high coefficients of sexual or natural selection are impeding gene flow between hybridizing populations.

The sigmoidal clines associated with the *Trochilus* contact zone constitute the steepest morphological character gradients documented thus far in avian biology. Of particular note, bill width increased a remarkable 2% per kilometer between Trowel Hill (wholly *T. scitulus*) and Fellowship (wholly *T. polytmus*). The environmental component of size and shape variation in streamertail bills is unknown. However, it is unlikely that the steep gradient observed in bill width is caused by variation in climatic variables thought to influence size variation in birds (James 1970, Graves 1991). Sampling localities were closely spaced in a high rainfall area where annual precipitation exceeds 3000 mm (Jamaica Meterologic Service 1963). Moreover, bill width variation was uncorrelated with the altitude of sampling locality. Significant correlation between bill width and skull width indicates that the genetic loci affecting bill shape have pleiotropic effects on cranial morphology posterior of the craniofacial hinge, or vice versa.

Acknowledgments

I thank Brian Schmidt and Errol Frances (1950–2011) for field assistance. Permits and permissions were issued by the National Environment and Planning Agency (NEPA), the Jamaica Conservation and Development Trust (JCDT), and private land owners. Logistical assistance was kindly offered by Catherine Levy (Kingston), Susan Koenig and Mike Schwartz (Windsor Research Centre) and Carla Gullotta (Drapers San). Insightful comments by Mike Carleton and two anonymous reviewers improved the manuscript. Field research was funded by the James Bond and Alexander Wetmore funds of the Smithsonian Institution. I thank the Smoketree Trust for continued support.

Literature Cited

American Ornithologists' Union. 1998. Check-list of North American Birds, 7th edition. American Ornithologists' Union, Washington, D.C., 829 pp.

Bangs, O. & F. H. Kennard. 1920. A list of the birds of Jamaica. Government Printing Office, Kingston, Jamaica, 18 pp.

Barrowclough, G. F. 1980. Genetic and phenotypic differentiation in a wood warbler (genus *Dendroica*) hybrid zone. Auk 97:655–668.

Barton, N. H. & G. M. Hewitt. 1985. Analysis of hybrid zones. Annual Review of Ecology and Systematics 113–148.

Bond, J. 1936. Birds of the West Indies. Academy of Natural Sciences, Philadelphia, 456 pp.

Bond, J. 1940. Check-list of birds of the West Indies. Academy of Natural Sciences of Philadelphia, Philadelphia, 184 pp.

Bond, J. 1956. Check-list of birds of the West Indies. Academy of Natural Sciences of Philadelphia, Philadelphia, 214 pp.

Brewster, W. & O. Bangs. 1901. On an overlooked species of *Aithurus*. Proceedings of the New England Zoological Club 2:47–50.

Browne, P. 1756. The civil and natural history of Jamaica. Printed for the author, and sold by T. Osborne and J. Shipton, London, 503 pp.

Brumfield, R. T., R. W. Jernigan, D. B. McDonald & M. J. Braun. 2001. Evolutionary implications of divergent clines in an avian (*Manacus*: Aves) hybrid zone. Evolution 55:2070–2087.

Calder, W. A., L. L. Calder & T. D. Fraizer. 1990. The hummingbird's restraint: A natural model for weight control. Cellular and Molecular Life Sciences 46:999–1002.

Clark, C. J. 2008. Fluttering wing feathers produce the flight sounds of male streamertail hummingbirds. Biology Letters 4:341–344.

Cory, C. B. 1918. Catalogue of birds of the Americas. Part 2, No.1. Field Museum of Natural History Zoological Series 13:1–315.

Curry, C. M. & M. A. Patten. 2014. Current and historical extent of phenotypic variation in the Tufted and Black-crested Titmouse (Paridae) hybrid zone in the southern Great Plains. American Midland Naturalist 171:271–300.

Danforth, S. T. 1928. Birds observed in Jamaica during the summer of 1926. Auk 45:480–491.

Diamond, J. M. 1977. Continental and insular speciation in Pacific land birds. Systematic Zoology 26:263–268.

Gill, F. B., F. J. Stokes & C. Stokes. 1973. Contact zones and hybridization in the Jamaican hummingbird, *Trochilus polytmus* (L.). Condor 75:170–176.

Gosse, P. H. 1847. The birds of Jamaica. Bentley, Wilson and Fley, London, 447 pp.

Graves, G. R. 1991. Bergmann's rule near the equator: Latitudinal clines in body size of an Andean passerine bird. Proceedings of the National Academy of Sciences USA 88:2322–2325.

Graves, G. R. 2009a. Ontogeny of bill color in streamertail hummingbirds. Journal of Caribbean Ornithology 22:44–47.

Graves, G. R. 2009b. Skeletal correlates of body weight in the Black-billed Streamertail (*Trochilus scitulus*) of Jamaica. Caribbean Journal of Science 45:1–4.

Graves, G. R. & R. P. Prys-Jones. 2011. Rediscovery of the holotype of *Trochilus maria* Gosse, 1849 (Aves: Apodiformes: Trochilidae). Zootaxa 2929:59–63.

Hartman, F. A. 1961. Locomotor mechanisms of birds. Smithsonian Miscellaneous Collections 143:1–91.

Irwin, D. E., A. Brelsford, D. P. L. Toews, C. MacDonald & M. Phinney. 2009. Extensive hybridization in a contact zone between MacGillivray's warblers *Oporornis tolmiei* and mourning warblers *O. philadelphia* detected using molecular and morphological analysis. Journal of Avian Biology 40:539–552.

Jamaica Meteorological Service. 1963. The rainfall of Jamaica. Scientific Research Council, Jamaica, 18 pp.

James, F. C. 1970. Geographic size variation in birds and its relationship to climate. Ecology 51:365–390.

Jeffrey-Smith, M. 1956. Bird-watching in Jamaica. Pioneer Press, Kingston, Jamaica, 159 pp.

Karasov, W. H., D. Phan, J. M. Diamond & F. L. Carpenter. 1986. Food passage and intestinal nutrient absorption in hummingbirds. Auk 103:453–464.

Lance, S. L., C. Hagen, T. C. Glenn, R. T. Brumfield, K. F. Stryjewski & G. R. Graves. 2009. Fifteen polymorphic microsatellite loci from Jamaican streamertail hummingbirds (*Trochilus*). Conservation Genetics 10:1195–1198.

Linnaeus, C. 1758. Systema naturae. 10th edition. Holmiae : Impensis direct. Laurentii Salvii., 823 pp.

MacColl, A. D. C. & S. Lewis. 2000. Hybridisation and ecology of Jamaican streamertail hummingbirds. BirdLife Jamaica Broadsheet 75:4–10.

Mayr, E. 1963. Animal species and evolution. Harvard University Press, Cambridge, Massachusetts, 797 pp.

McCormack, J. E., J. M. Maley, S. M. Hird, E. P. Derryberry, G. R. Graves & R. T. Brumfield. 2011. Next-generation sequencing reveals phylogeographic structure and a species tree for recent bird divergences. Molecular Phylogenetics and Evolution 62:397–406.

Meise, W. 1928. Die Verbreitung der Aaskrähe (Formenkreis *Corvus corone* L.). Journal für Ornithologie 76:1–203.

Mettler, R. D. & G. M. Spellman. 2009. A hybrid zone revisited: molecular and morphological analysis of the maintenance, movement, and evolution of a Great Plains avian (Cardinalidae: *Pheucticus*) hybrid zone. Molecular Ecology 18:3256–3267.

Remsen, J. V., F. G. Stiles & P. E. Scott. 1986. Frequency of arthropods in stomachs of tropical hummingbirds. Auk 103:436–441.

Rohwer, S., E. Bermingham & C. Wood. 2001. Plumage and mitochondrial DNA haplotype variation across a moving hybrid zone. Evolution 55:405–422.

Schuchmann, K.-L. 1978. Allopatrische Artbildung bei der Kolibrigattung *Trochilus*. Ardea 66:156–172.

Schuchmann, K.-L. 1980. Die Jamaika Kolibris *Trochilus polytmus* und *Trochilus scitulus*. Biotropic-Verlag, Frankfurt and Baden-Baden, 55 pp.

Scott, W. E. D. 1892. Observations on the birds of Jamaica, West Indies. II. A list of the birds recorded from the island, with annotations. Auk 9:273–277.

Scott, W. E. D. 1904. The story of a bird lover. MacMillan, New York, 372 pp.

Selander, R. K. 1965. Hybridization of rufous-naped wrens in Chiapis, Mexico. Auk 82:206–214.

Sloane, H. 1725. A voyage to the islands of Madera, Barbadoes, Nieves, St. Christophers, and Jamaica; with the natural history of the herbs and trees, four-footed beasts, fishes, birds, insects, reptiles, &c. of the last of those islands. Vol. 2. Printed by B. M. for the author, London, 499 pp.

Tiebout, H. M. 1989. Tests of a model of food passage rates in hummingbirds. Auk 106:203–208.

Toews, D. P. L., A. Brelsford & D. E. Irwin. 2011. Hybridization between Townsend's *Dendroica townsendi* and black-throated green warblers *D. virens* in an avian suture zone. Journal of Avian Biology 42:434–446.

Yang, S. Y. & R. K. Selander. 1968. Hybridization in the grackle *Quiscalus quiscula* in Louisiana. Systematic Zoology 17:107–143.

Zusi, R. L. 2013. Introduction to the skeleton of hummingbirds (Aves: Apodiformes, Trochilidae) in functional and phylogenetic contexts. Ornithological Monographs 77:1–94.

Associate Editor: Michael D. Carleton

Appendix

Specimen numbers (USNM) and localities for streamertails (*Trochilus polytmus, T. scitulus,* hybrids) examined in this study (see Table 1).

Trochilus polytmus.—**Trelawny Parish**: Windsor (636169, 636170, 636172–636178); **Portland Parish**:

Somerset Falls (633621, 633624–633626, 633628), Burlington (636142–63651), Springbank (636154, 636156–636161), Fellowship (635678–635680, 635683, 635686), Tom's Hope (633584, 635674).

Trochilus hybrids.—**Portland Parish**: Windsor (633550, 633551, 633555), Tom's Hope (635675).

Trochilus scitulus.—**Portland Parish**: Trowel Hill (633591–633594, 635676, 635677, 636167, 636168), Mt. Lebanus (636165, 636166), Nonsuch (635687, 635690–635692, 636162–636164), San San (633610–633613, 633615, 633617, 633618), Cambridge (633600, 633602, 633609), Ecclesdown (636134, 636135, 636137–636141).