PROCEEDINGS OF THE BIOLOGICAL SOCIETY OF WASHINGTON
109(4):764–769. 1996
23 December 1996

Diagnoses of hybrid hummingbirds (Aves: Trochilidae). 2. Hybrid origin of *Eriocnemis soderstromi* Butler

Gary R. Graves

Department of Vertebrate Zoology, National Museum of Natural History, Smithsonian Institution, Washington, D.C. 20560, U.S.A.

Abstract.—*Eriocnemis soderstromi* (Butler 1926) is shown to be a hybrid between *E. nigrivestis*, an endemic of the Volcán Pichincha region in Ecuador, and *E. luciani*, an inhabitant of timberline Andean forest from southern Colombia to Bolivia. This is the first report of intrageneric hybridization among the nine species of *Eriocnemis*. Plumage characters of the hybrid appear to be a blended intermediate of those of the parental species. External measurements of the hybrid are intermediate of those of parental species.

Butler (1926) described *Eriocnemis soderstromi* from a unique specimen [The Natural History Museum, formerly British Museum (Natural History) (BM(NH)) 97.11.12.98] collected by Ludovico Söderström at Nono, on the western slope of Volcán Pichincha, Ecuador, in January 1890. This taxon was the last in a series of enigmatic or questionable Trochiline species discovered in the environs of Quito. Opinions on the taxonomic status of *E. soderstromi* have varied. Peters (1945) listed *E. soderstromi* with a question mark, whereas Meyer de Schauensee (1966) suggested that it might represent an aberration of *E. godini*. Morony et al. (1975) considered it a valid species without elaboration. Sibley and Monroe (1990) listed three possibilities—that it might be an aberrant specimen of *E. godini*, a valid race of *E. godini*, or a distinct species. Fjeldså & Krabbe (1990: 275) regarded *E. soderstromi* as a possible hybrid or "at least not a valid taxon," and Collar et al. (1992) omitted it from their compilation of threatened birds of the Americas. Here I report that *E. soderstromi* represents an intrageneric hybrid between *Eriocnemis nigrivestis* and *E. luciani*.

Methods

I employed the analytical methods of hybrid diagnosis outlined in Graves (1990). Because of the specimen's size and shape and general configuration of plumage elements, *Eriocnemis soderstromi* cannot be attributed to mutation or a rare genetic variant of any known taxon. Assuming its hybrid origin, the geographical source pool of potential parental species may be drawn from the list of hummingbird species (n = 47, see Appendix 1) that inhabit the Andes of northern Ecuador above 2000 m elevation (see Fjeldså & Krabbe 1990). The type specimen of *E. soderstromi* appears to be fully adult by plumage characters and lacks striations on the rhamphotheca at 10× magnification. Söderström sexed the bird as male and there is no evidence to suggest otherwise. The type was compared to large series of all source pool species in The Natural History Museum. Plumage colors were compared under natural light. Wing chord, bill length (from anterior extension of nasal feathering), and rectrix length (from the point of insertion of the central rectrices) of males of several species were measured with digital calipers and rounded to the nearest 0.1 mm (Table 1).

I used principal components analysis (PCA) on $\log_{10}$ transformed rectrix length to reduce the dimensionality of tail data to a single value. Unrotated principal compo-

Table 1.—Ranges and means (± one standard deviation) of measurements (mm) of adult male *Eriocnemis nigrivestis*, *E. luciani*, *E. vestitus* from Ecuador, and the hybrid, *E. nigrivestis* x *E. luciani* (= *E. soderstromi* Butler).

Character	*nigrivestis* (*n* = 15)	*luciani* (*n* = 15)	*vestitus*[a] (*n* = 15)	Hybrid BM(NH) 97.11.12.98
Wing chord	57.6–60.5	69.1–72.5	57.8–61.3	65.6
	58.9 ± 0.9	70.7 ± 1.1	59.4 ± 1.1	
Bill length	14.4–15.8	19.2–20.8	15.9–18.8	19.2
	15.1 ± 0.5	20.1 ± 0.5	17.5 ± 0.8	
Rectrix 1	25.7–28.5	25.5–29.0	26.2–29.7	27.4
	26.8 ± 1.0	27.8 ± 0.9	28.4 ± 1.1	
Rectrix 2	26.8–29.8	29.1–33.6	28.0–31.5	29.8
	28.1 ± 1.1	32.0 ± 1.3	29.9 ± 1.0	
Rectrix 3	28.8–33.1	38.5–44.1	31.1–35.3	33.5
	31.0 ± 1.5	41.5 ± 1.7	33.1 ± 1.4	
Rectrix 4	32.0–37.1	49.4–53.1	35.3–39.7	41.0
	34.2 ± 1.9	51.8 ± 1.3	37.9 ± 1.5	
Rectrix 5	34.9–39.3	55.4–60.2	40.6–45.3	46.6
	37.1 ± 1.3	58.0 ± 1.3	42.7 ± 1.4	

[a] Includes 10 specimens from the Eastern Cordillera of the Colombian Andes.

nents were extracted from covariance matrices (Wilkinson 1989).

The hybrid diagnosis followed a two-step procedure. The presumed parental species of *Eriocnemis soderstromi* were hypothesized through the comparative analysis of plumage pattern and color, as well as the shape of external keratinized structures (bill and feathers). Then, the restrictive hypothesis was further examined with quantitative analyses of size and shape. As pointed out in a series of hybrid diagnoses (e.g., Graves 1990, 1993, 1996; Graves & Zusi 1990), I consider the concordance of results as strong support for the hypothesis of presumed parentage. Atavism or hybrid luxuriance has not been demonstrated in hybrid hummingbirds Banks & Johnson 1961, Graves 1990.

Results

Butler's (1926:62) description of the type of *Eriocnemis soderstromi* was brief but generally accurate:

> "Forehead greenish-blue, crown darker and more bronze than the back, turning to velvet-black when viewed from in front, whereas in *E. godini* the forehead and crown are of the same colour as the back, remaining green when viewed from in front; back of a darker shade; lower rump and upper-tail coverts dark steel-blue, only margined with green (in *E. godini* they are entirely shining grass-green); blue throat-patch much larger, and lower surface darker without the strong golden gloss of *E. godini*."

Unfortunately, Butler's description compared the type of *E. soderstromi* with that of *E. godini* (also in The Natural History Museum) rather than the six species of *Eriocnemis* that occur in northern Ecuador. Recent examination of the type of *E. godini* suggests that it too is a hybrid (Graves, in prep.).

Key plumage characteristics of *E. soderstromi* (Fig. 1) that permit its parental species to be identified include: elongated, silky tibial plumes (commonly referred to as "leg puffs"); small poorly-defined gorget; unmarked and forked tail (depth = 19.2 mm); steel-blue upper-tail coverts margined with green; brilliant purplish-blue under-tail coverts; and bluish-green forecrown (Fig. 1).

Well-developed, silky leg puffs are the

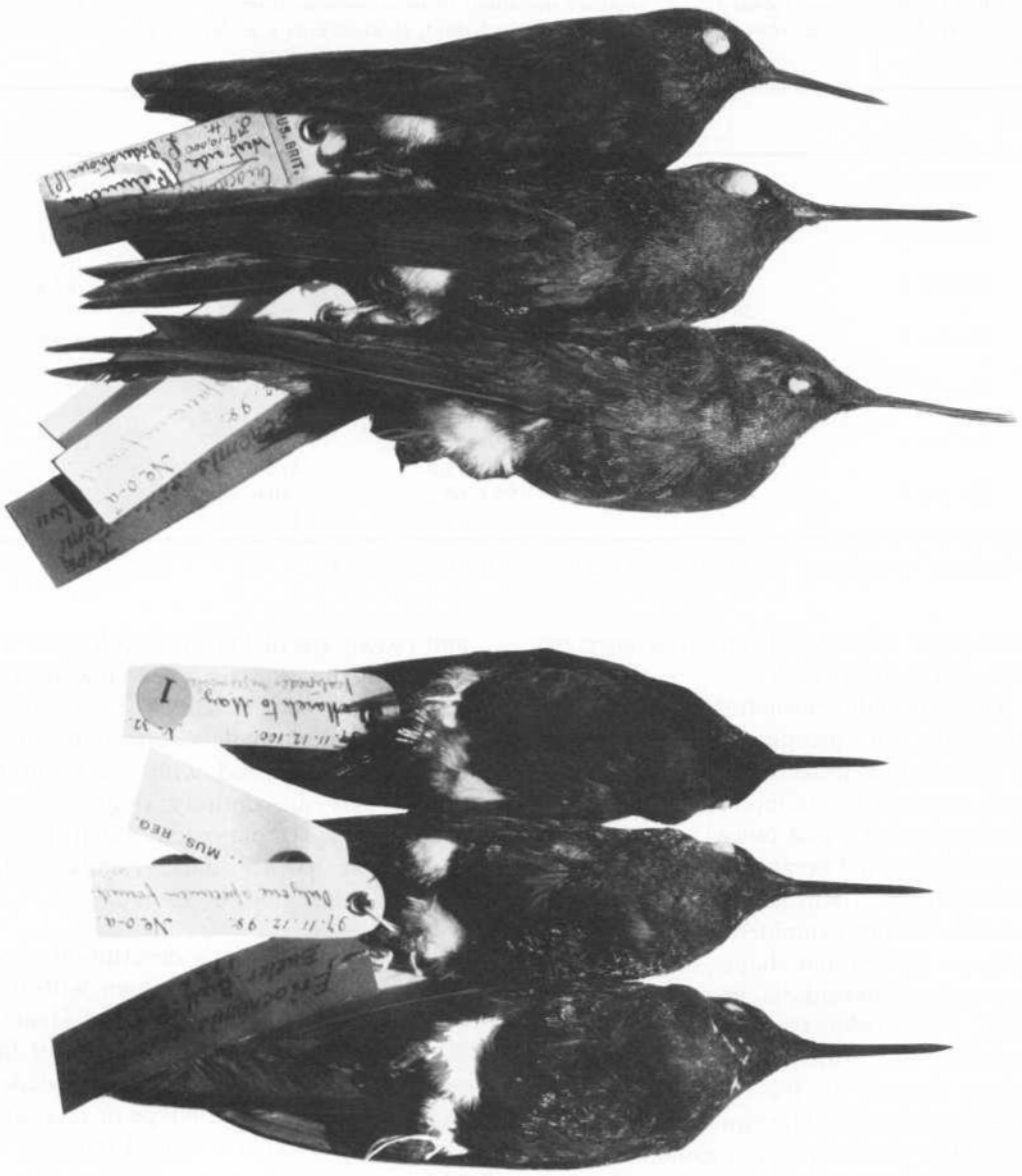

Fig. 1. Lateral and ventral views of male *Eriocnemis nigrivestis* (top), *E. luciani* (bottom), and their hybrid (= *E. soderstromi* Butler, BM(NH) 97.11.12.98).

most distinctive character of *E. soderstromi*. Species in three genera from the Ecuadorian Andes (*Eriocnemis, Haplophaedia, Ocreatus*) possess leg puffs (see Appendix 1). *Ocreatus* can be eliminated from consideration because the hybrid lacks evidence (even as traces) of racket-tipped rectrices. Both species of *Haplophaedia* may be excluded from the pool of potential parental species because the breast, belly and flanks of *E. soderstromi* lack grayish-white or buffy margins, its leg puffs are pure white, and its nostrils are obscured by adpressed feathers. Based on this evidence, both of the parental species of *E. soderstromi* can be drawn from the assemblage

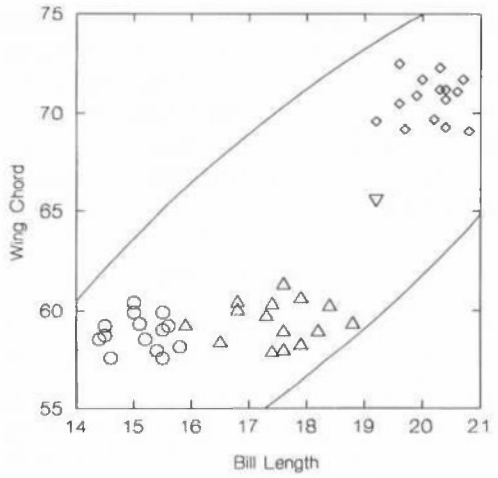

Fig. 2. Bivariate relationship of wing chord and bill length (mm) in males of *Eriocnemis nigrivestis* (circles), *E. vestitus* (triangles), *E. luciani* (diamonds), and the hybrid, *E. nigrivestis* × *E. luciani* (BM(NH) 97.11.12.98) (inverted triangle). Curved lines represent the boundaries of the 95% confidence ellipse.

of five Ecuadorian species of *Eriocnemis* with white leg puffs (*nigrivestis, vestitus, luciani, mosquera, alinae*). The uniformly steel-blue tail and brilliant, blue under-tail coverts of *E. soderstromi* nullifies the inclusion of *E. mosquera* and *E. alinae* in the pool of potential parental species.

Only two of the remaining triad of species could have contributed the unique combination of characters exhibited by *E. soderstromi*. The bluish-green forehead of *E. soderstromi* is found only in *E. luciani*, while the steel-blue upper-tail coverts are found in *E. nigrivestis* but not in *E. luciani* or *E. vestitus*. I conclude from plumage characters, that *E. soderstromi* represents a hybrid between *E. nigrivestis* and *E. luciani* (see Appendix 2). Hybridization between other combinations of species could not have produced the characters present in the type of *E. soderstromi*.

External measurements.—Measurements of *Eriocnemis soderstromi* fell within the character means of the hypothesized parental species (Table 1). However, *E. nigrivestis* and *E. vestitus* are so similar in size and shape, that *E. nigrivestis* × *E. luciani* and *E. vestitus* × *E. luciani* hybrids may not be distinguished by mensural characters alone (Table 1, Figs. 2, 3).

Table 2.—Factor loadings from a principal components analysis (PCA) of rectrix length in male specimens (see Table 1) of *Eriocnemis luciani, E. nigrivestis*, and their hybrid (= *E. soderstromi* Butler, BM(NH) 97.11.12.98).

Variables	PCA 1
Rectrix 1 (innermost)	0.006
Rectrix 2	0.024
Rectrix 3	0.056
Rectrix 4	0.078
Rectrix 5	0.081
Percent variance explained	95.4%

Remarks

Eriocnemis nigrivestis has one of the most restricted geographic ranges of any avian species in South America and valid records are limited to Volcán Pichincha and Volcán Atacazo, Pichincha Province, in northwestern Ecuador (Collar et al. 1992). This taxon was locally abundant in the late 19th century as judged by the number of specimens in museums (e.g., Oberholser 1902, Lonnberg & Rendahl 1922, Chapman 1926), but populations are currently threatened by grazing, agriculture, and wood cutting (Bleiweiss & Olalla 1983, Collar et al. 1992).

Notwithstanding the plumage and morphological evidence, the possibility that *E. soderstromi* represents the only known specimen of a valid species is diminished by the fact that the avifauna of Volcán Pichincha is well known, and that no additional specimens or sight records have been obtained in that region (Chapman 1926, Meyer de Schauensee 1966, Bleiweiss & Olalla 1983, Fjeldså & Krabbe 1990). The specimen of *Eriocnemis nigrivestis* × *E. luciani* is the first intrageneric hybrid reported for the genus, although a number of presumed intergeneric hybrids between *Heliangelus amethysticollis* and *E. cupreov-*

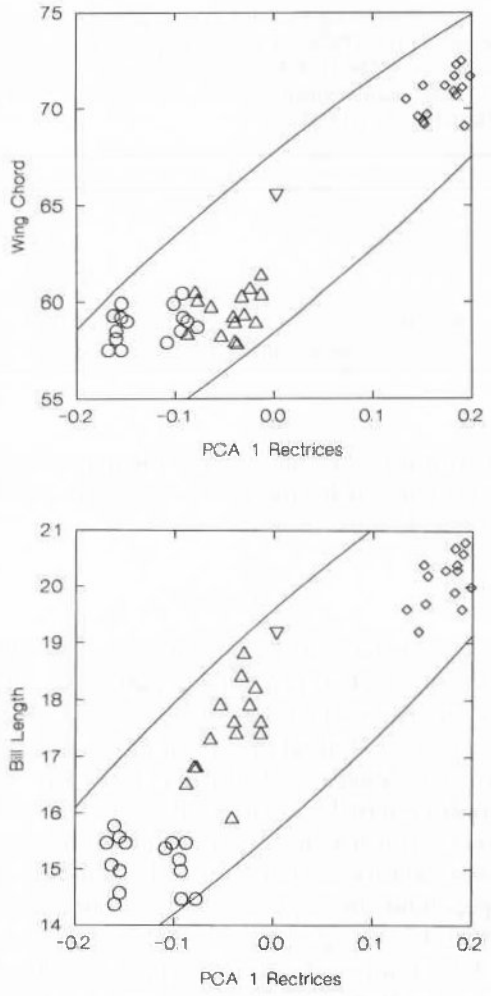

Fig. 3. Bivariate relationship of wing chord (top) and bill length (bottom) with factor scores from the first principal component (PCA 1) of an analysis of rectrix length in males of *Eriocnemis nigrivestis* (circles), *E. vestitus* (triangles), *Eriocnemis luciani* (diamonds), and the hybrid, *E. nigrivestis* × *E. luciani* × (BM(NH) 97.11.12.98) (inverted triangle) (see Table 2). Curved lines represent the boundaries of the 95% confidence ellipse.

entris have been documented (Graves 1990).

Acknowledgments

I thank Robert Prŷs-Jones and Michael Walters for permitting me to examine and photograph the type of *E. soderstromi* in The Natural History Museum, and Smithsonian photographic services for making usable prints from my poor negatives. Ralph Browning, Robert Prŷs-Jones, Michael Walters, and Richard Zusi made helpful comments on the manuscript. Travel was supported by the Smithsonian Research Opportunities Fund.

Literature Cited

Banks, R. C., & N. K. Johnson. 1961. A review of North American hybrid hummingbirds.—Condor 63:3–28.

Bleiweiss, R., & P. M. Olalla. 1983. Notes on the ecology of the Black-breasted Puffleg on Volcan Pichincha, Ecuador.—Wilson Bulletin 95: 656–661.

Butler, A. L. 1926. [Humming-bird from W. Ecuador.]—Bulletin of the British Ornithologists Club 47:62.

Chapman, F. M. 1926. The distribution of bird-life in Ecuador.—Bulletin of the American Museum of Natural History 55:1–784.

Collar, N. J., L. P. Gonzaga, N. Krabbe, A. Madrono Nieto, L. G. Naranjo, T. A. Parker, III, and D. C. Wege. 1992. Threatened birds of the Americas: The ICBP/IUCN Red Data Book, 3rd edition, part 2. International Council for Bird Preservation, Cambridge, U.K., 1150 pp.

Fjeldså, J., & N. Krabbe. 1990. Birds of the high Andes. Zoological Museum, University of Copenhagen, Denmark.

Graves, G. R. 1990. Systematics of the "green-throated sunangels (Aves: Trochilidae): valid taxa or hybrids?—Proceedings of the Biological Society of Washington 103:6–25.

———. 1993. A new hybrid manakin (*Dixiphia pipra* × *Pipra filicauda*) (Aves: Pipridae) from the Andean foothills of eastern Ecuador.—Proceedings of the Biological Society of Washington 106:436–441.

———. 1996. Hybrid wood warblers, *Dendroica striata* × *Dendroica castanea* (Aves: Fringillidae) and the diagnostic predictability of avian hybrid phenotypes.—Proceedings of the Biological Society of Washington 109:371–388.

———, & R. L. Zusi. 1990. An intergeneric hybrid hummingbird (*Heliodoxa leadbeateri* × *Heliangelus amethysticollis*) from northern Colombia.—Condor 92:754–760.

Lönnberg, E., & H. Rendahl. 1922. A contribution to the ornithology of Ecuador.—Arkiv for Zoologi 14:1–87.

Meyer de Schauensee, R. 1966. The species of birds of South America. Livingstone Press, Narberth, Pennsylvania, 577 pp.

Morony, J. J., Jr., W. J. Bock, & J. Farrand, Jr. 1975.

Reference list of the birds of the world. American Museum of Natural History, New York. 207 pp.

Oberholser, H. C. 1902. Catalogue of a collection of hummingbirds from Ecuador and Colombia.—Proceedings of the United States National Museum 24:309–342.

Peters, J. 1945. Check-list of birds of the world. Vol. 5 Museum of Comparative Zoology, Cambridge, Massachusettes. 306 pp.

Sibley, C. G., & B. L. Monroe, Jr. 1990. Distribution and taxonomy of birds of the world. Yale University Press, New Haven, Connecticut, 1111 pp.

Wilkinson, L. 1989. SYSTAT: the system for statisties. SYSTAT, Inc., Evanston, Illinois, 822 pp.

Appendix 1

Species of hummingbirds that occur regularly above 2000 m in the northern Ecuadorian Andes: *Phaethornis syrmatophorus, Doryfera ludoviciae, Colibri thalassinus, C. coruscans, Chlorostilbon mellisugus, Adelomyia melanogenys, Heliodoxa rubinoides, H. leadbeateri, Urochroa bougueri, Oreotrochilus chimborazo, Patagona gigas, Aglaeactis cupripennis, Lafresnaya lafresnayi, Pterophanes cyanopterus, Coeligena coeligena, C. torquata, C. lutetiae, Ensifera ensifera, Boissonneaua flavescens, B. matthewsii, Heliangelus strophianus, H. exortis, H. viola?, Eriocnemis nigrivestis, E. vestitus, E. luciani, E. muxquera, E. alinae, E. derbyi, Haplophaedia aureliae, Ocreatus underwoodii, Lesbia victoriae, L. nuna, Ramphomicron microrhynchum, Metallura williami, M. tyrianthina, Chalcostigma ruficeps?, C. stanleyi, C. herrani, Opisthoprora euryptera, Aglaiocercus kingi, Schistes geoffroyi, Philodice mitchellii, Myrtis fanny, Acestrura mulsant, A. bombus, A. heliodor.*

Appendix 2

Comparative description of plumages of adult male *Eriocnemis luciani* and *E. nigrivestis* from Volcán Pichincha, Ecuador, and their hybrid, BM(NH) 97.11.12.98 (= "*Eriocnemis soderstromi*" Butler 1926). 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 I use general color descriptions.

Nasal feathering and forecrown of *luciani* are shining blue, shading to bluish-green on the lores when viewed head-on in direct light. These plumage regions in *nigrivestis* are black with very faint green reflections. The forecrown of the hybrid exhibits pronounced bluish-green reflections, surrounded by matte black when viewed from in front. The frontal profile of the hybrid is intermediate between that of *nigrivestis* and the more sloping profile of *luciani* (see Fig. 1).

The crown, back, wing coverts, and upper-tail coverts are green in *luciani*. In *nigrivestis* the crown, back, and wing coverts are black with faint greenish-blue reflections; the upper-tail coverts are shining steel blue (brilliant pale green in *vestitus*). The crown and back of the hybrid are green, but of a darker shade than in *luciani*; a few feathers on the lower back are shaded with steel-blue, whereas the upper tail coverts are steel-blue with green margins. The rectrices of *luciani* are black with faint blue reflections in strong light, whereas the more angular rectrices of *nigrivestis* are somewhat more glossy and bluer. Rectrices of the hybrid are intermediate in color and shape.

The chin, throat, breast and belly are green in *luciani*; white feather bases are exposed on the throat. In *nigrivestis*, these plumage regions are black with green reflections on the sides of the throat, and with narrow green feather margins on the sides and flanks; a small, brilliant, purplish-blue gorget is present on the center of the throat. The throat, breast and belly of the hybrid are darker than in *luciani* and exhibit fewer and less intense reflections when viewed head-on. A shining (but diffusely defined) turquoise gorget (ca. 12 feathers) occurs on the throat of the hybrid. A coppery-gold sheen on some feathers adjacent to the gorget can be observed at certain angles. The bases of the brightest, most differentiated, gorget feathers are gray with huffy-white margins separated from the broad turquois tip by a narrow transitional band of greenish gray.

Tibial plumes (leg puffs) of *luciani, nigrivestis*, and the hybrid are well developed and silky white. Undertail coverts of *luciani, nigrivestis*, and the hybrid are brilliant purplish-blue.