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SYSTEMATICS OF THE GORGETED WOODSTARS (AVES: TROCHILIDAE: *ACESTRURA*)

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Abstract.—*Acestrura heliodor* (sensu Peters 1945) forms a superspecies composed of two allospecies: *A. astreans* Bangs of the Sierra Nevada de Santa Marta; and *A. heliodor* (Bourcier) of the Andes of Venezuela, Colombia, and northeastern Ecuador. *Acestrura h. meridae* Zimmer and Phelps is synonymized with *A. h. heliodor*. *Acestrura h. cleavesi* Moore of northeastern Ecuador is a valid subspecies. Wing and tail lengths are positively correlated with latitude in the *heliodor* superspecies. Gorget color in males is subject to postmortem change.

The diminutive woodstars of the genus *Acestrura* of the Andean region in western South America are poorly known, underrepresented in museum collections, and are frequently misidentified. *Acestrura berlepschi, A. bombus,* and *A. mulsant* are currently considered to be monotypic. A fourth species, *A. heliodor,* exhibits considerable geographic variation that is recognized at the subspecific level (Peters 1945, Zimmer 1953): *A. astreans* of the Sierra Nevada de Santa Marta, Colombia; *A. h. heliodor* of the Eastern, Central and Western Cordilleras of the Colombian Andes; *A. h. meridae* of the Venezuelan Andes; and *A. h. cleavesi* of northeastern Ecuador.

The purpose of this paper is to re-evaluate the taxonomy of woodstars in the *A. heliodor* complex, incorporating data from previously unreported series of specimens collected from 1946–1952 in Colombia by M. A. Carriker, Jr. and deposited in the National Museum of Natural History, Smithsonian Institution (USNM). Differences among populations in plumage color in both sexes and tail configuration in males suggest that the *Acestrura heliodor* (Fig. 1) is actually composed of two allospecies: *A. astreans* (Santa Marta Woodstar) of the Sierra Nevada de Santa Marta, and *A. heliodor* (Gorgeted Woodstar) (*A. h. heliodor* and *A. h. cleavesi*) of the main Andes.

Acestrura heliodor heliodor (Bourcier)

Ornismya heliodor Bourcier, 1840:275. "Bogota."

Acestrura heliodor meridae Zimmer and Phelps, 1950:1. Paramo Conejos (4000 m), Mérida, Venezuela.

Characters.—Male: Upperparts and flanks are green and the gorget purple. The formula of rectrix length in closed tail is: 3 > 4 > 5 > 2 > 1 (retrices numbered from the inside outward). The width of rectrix 4 is greater than ½ the width of rectrix 3 and nearly intermediate in width between rectrices 3 and 5 (Fig. 2). Females: The chin, throat, breast, and flanks are rich buffy cinnamon. In adult females, the tail is rufous with a broad black band across the center. A trace of green occurs just proximal to the band on the central rectrices. The lower rump and upper tail coverts are rufous; a few feathers have a green central spot.

Distribution.—Scattered localities in the Andes of Venezuela, and the Eastern, Central, and Western Cordilleras of the Colombian Andes (Fig. 1). The reported occurrence of *A. heliodor* at Cana, Cerro Pirre, Panama (Wetmore 1968, Ridgely 1976) is based on a misidentified specimen of *Calliphlox mitchelli* (Robbins et al. 1985).

Specimens examined.—VENEZUELA: Pinos (USNM 1 ♂); "Merida" (USNM 1 ♂,

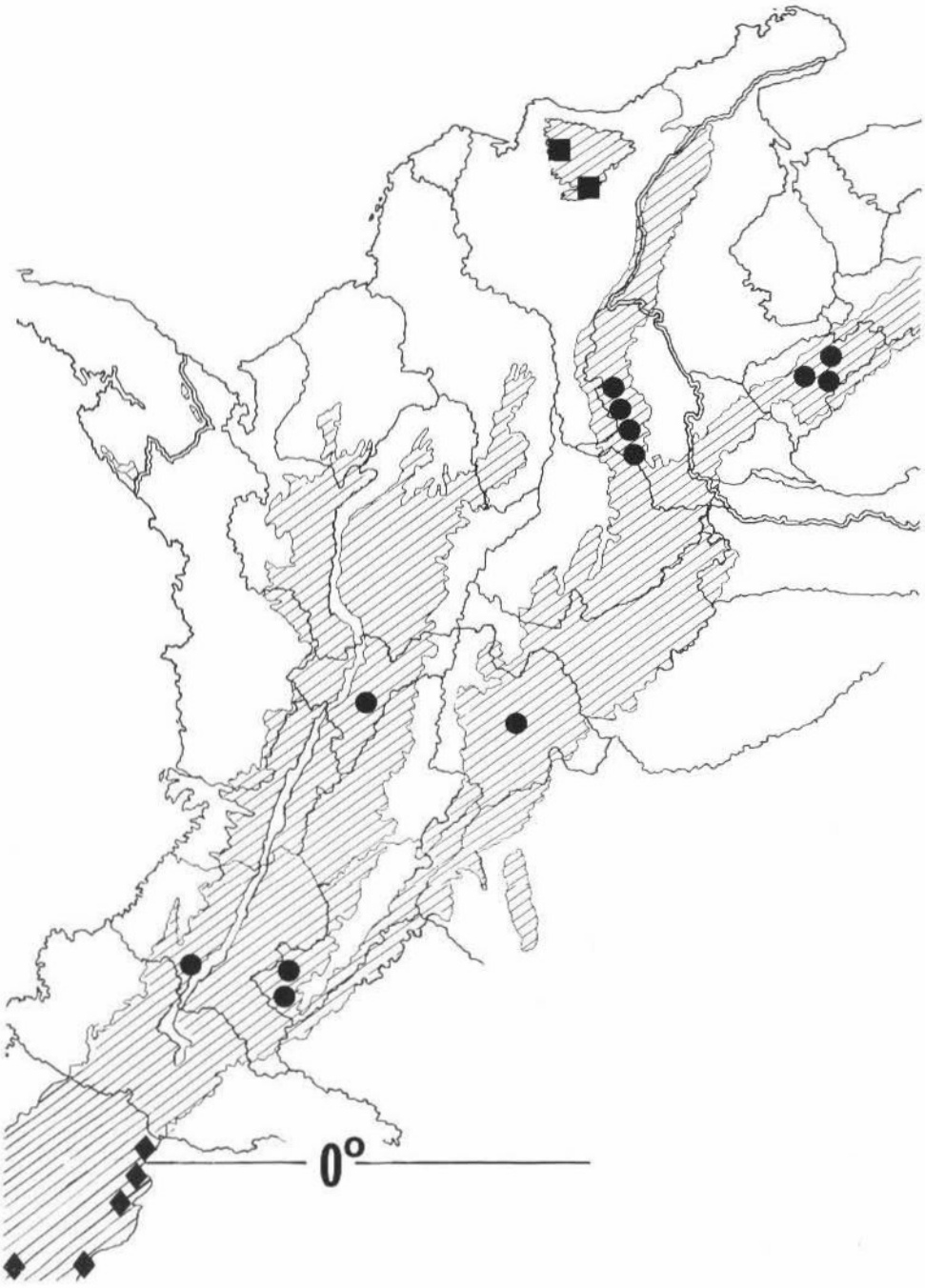

Fig. 1. Distribution of the *Acestrura heliodor* superspecies based on specimens examined in this study. Some symbols represent two closely spaced localities. Squares = *Acestrura astreans*; circles = *A. h. heliodor*; diamonds = *A. h. cleavesi*. Hatching indicates areas above 1000 feet elevation.

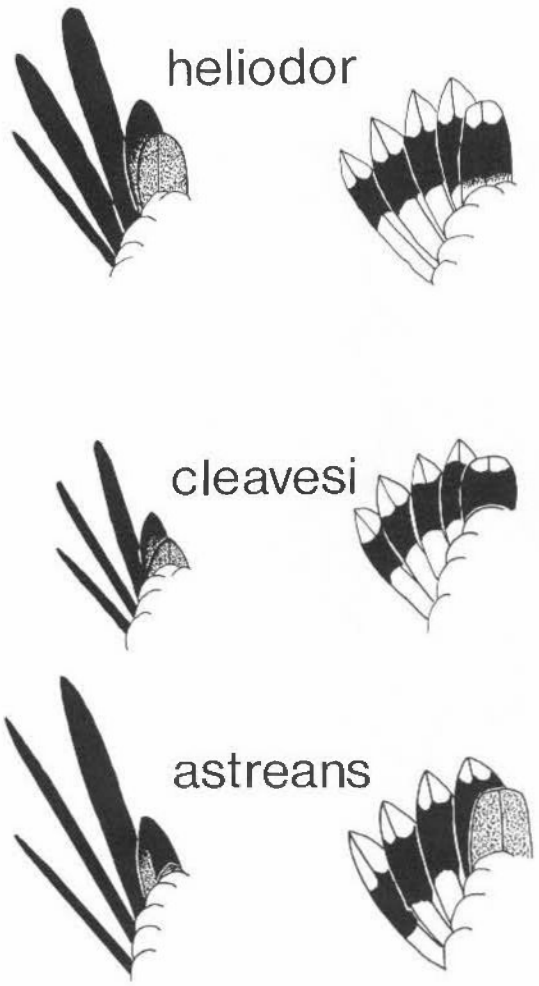

Fig. 2. Tail patterns of *Acestrura h. heliodor, A. h. cleavesi* and *A. astreans*. Males on the left, females on the right. Color of rectrices: stippling = green; unmarked = rufous or rich buff; shaded = black. 1.8× natural size.

2 ♀♀; AMNH 19 ♂♂, 9 ♀♀).—Conejos (USNM 1 ♀; AMNH 1 ♂ type "*meridae*," 1 ♀).—Tambor (USNM 1 ♂, 4 ♀♀; AMNH 9 ♂♂, 2 ♀♀).—Escorial (AMNH 4 ♂♂).—Tierra (USNM 1 ♂). COLOMBIA: (unspecified localities) "Bogotá" (USNM 4 ♂♂, 2 ♀♀; AMNH 24 ♂♂ including type of *A. h. heliodor*, 9 ♀♀).—"Lower Magdalena" (USNM 1 ♂, 1 ♀).—"Colombia" (MLOC 3 ♂♂; USNM 4 ♂♂, 2 ♀♀; AMNH 2 ♂♂).—"Santiago" near Pasto? (FMNH 1 ♀).—"New Grenada" (USNM 1 ♂, 1 ♀; AMNH 2 ♂♂, 2 ♀♀). Norte de Santander: Buenos Aires (USNM 7 ♂♂, 3 ♀♀).—Ocaña (USNM 1 ♂).—Ramírez (CM 3 ♂♂, 1 ♀; ANSP 1 ♀).—Cachirí (CM 1 ♀).—Las Ventanas (CM 2 ♀♀). Caldas: Laguneta (ANSP 1 ♂, 3 ♀♀). Huila: San Agustín (USNM 4 ♂♂, 2 ♀♀; AMNH 1 ♂; ANSP 3 ♂♂, 2 ♀♀).—Belén (USNM 1 ♂). Cauca: El Tambo (FMNH 1 ♂; WFVZ 1 ♂).—Tijeras (FMNH 1 ♂).—Moscopán (USNM 1 ♀).

Acestrura heliodor cleavesi (Moore)

Chaetocercus cleavesi Moore, 1934:1. Cuyuja, Ecuador.

Characters.—Male: The formula for the length of rectrices in *A. h. cleavesi* is: 3 > 4 > 2 > 5 > 1, instead of: 3 > 4 > 5 > 2 > 1, as in *A. h. heliodor* and *A. astreans*. Rectrices 4 and 5 are similar in width, and much narrower than rectrix 3. Female: Similar to *A. h. heliodor* but more richly colored on chin and throat and with rump more extensively rufous.

Distribution.—Known only from the Amazonian slope of the Andes in northeastern Ecuador.

Specimens examined.—ECUADOR: Baeza (MLOC 3 ♂♂, 6 ♀♀; USNM 1 ♂, 1 ♀; AMNH 1 ♂).—Cuyuja (MLOC 1 ♂, 1 ♀).—Pallatanga (MLOC 1 ♀).—Río Hollín (MLOC 1 ♀).—Río Oyacachi Abajo (AMNH 1 ♂, 3 ♀♀).—Río Tigre (MLOC 1 ♂, 3 ♀♀).—Tumbaco (MLOC 1 ♀).

Acestrura astreans Bangs

Acestrura astreans Bangs, 1899:76. San Sebastian (6600 feet), Sierra Nevada de Santa Marta, Colombia.

Characters.—Male: In adults, the back, rump, upper tail coverts, and flanks are metallic bluish-green, instead of green as in *A. h. heliodor* and *A. h. cleavesi*. The gorget is red or reddish-purple, depending on the angle of reflection, not purple as in *A. h. heliodor*. The formula of rectrix length is the

same as in *heliodor*. Rectrices 4 and 5 are very narrow, less than ½ the width of rectrix 3. Female: Adult females differ from those of *A. heliodor* in having the upper tail coverts green instead of rufous. The central rectrices of *A. astreans* are green, instead of rufous with a black band like the other rectrices, as in *A. heliodor* (Fig. 2). The venter of *A. astreans* is lighter, not as richly colored as in *A. heliodor*.

Distribution.—Restricted to the Sierra Nevada de Santa Marta. Specimens have been taken on the western, eastern, and southern slopes at elevations between 2700 and 6600 feet (ca. 825–2010 m).

Specimens examined.—Sierra Nevada de Santa Marta: San Sebastian (USNM 2 ♀♀).—Chinchicuá (USNM 4 ♀♀).—Vista Nieve (USNM 1 ♂, 2 ♀♀).—Cincinati (ANSP 1 ♂, 1 ♀).—El Mamon (AMNH 1 ♂).—No further locality data (USNM 2 ♂♂; AMNH 1 unsexed).

Variation in Male Gorget Color

Gorget color in the *Acestrura heliodor* superspecies exhibits significant geographic variation. In contemporaneously collected specimens from the main Andes, gorget color varies clinally from pinkish-purple in northeastern Ecuador to purple in the Eastern Cordillera of Colombia and the Venezuelan Andes; specimens from the Western and Central Cordilleras are intermediate. The Santa Marta population is characterized by a dark red gorget.

Zimmer and Phelps (1950) separated the Venezuelan (*A. h. meridae*) populations from those of Colombia on the basis of "a darker, more purplish, less reddish throat" in males. Unfortunately, assessment of this character is hampered by previously unrecognized postmortem change in gorget color. They compared their Venezuelan series, collected mostly between 1903 and 1921, with a large series of pre-1900 "Bogotá" specimens, most of which were probably obtained from the Eastern Cordillera. These have consistently pinker, less purplish gorgets than more recently collected specimens from the Eastern Cordillera. For example, specimens from Buenos Aires, Norte de Santander, taken in 1946, have slightly more purplish, less pinkish gorgets than specimens collected in 1916 at Ramirez, Norte de Santander. In turn, the "1916" specimens have gorgets that are more purplish, less pinkish, than those of pre-1900 "Bogota" specimens. Specimens collected at approximately the same time in the Eastern Cordillera and the Venezuelan Andes are indistinguishable in gorget coloration. *Acestrura h. meridae* Zimmer and Phelps, 1950, should thus be considered a synonym of *A. h. heliodor* Boucier, 1840. In another apparent example of postmortem change from shorter to longer wave lengths, the gorgets of specimens (USNM 333521; MLOC 7015, 7016, 7023, 10367, 10377) included in the type series of *A. h. cleavesi*) are presently matched closely by Rose Color (capitalized names from Ridgway 1912), instead of Rhodamine Purple (Moore 1934).

The magnitude of postmortem change observed in specimens collected from a single locality equals that of the contemporaneous geographic variation found among the Colombian populations of *A. h. heliodor*. The gorgets of birds from the Central (Belén, Tijeras, Laguneta) and Western Cordilleras (El Tambo) are pinker, less purplish than those of contemporaneously collected (1942–1957) specimens from the Eastern Cordillera, but match those of older specimens from the same region.

These observations suggest that there are some discrete differences among *heliodor* populations. The lack of contemporaneously collected series from key populations, however, prevents the subspecific partition of *A. heliodor* on the basis of gorget color alone.

Size and Shape Variation

Wing length is positively correlated with latitude in males (Fig. 3; $n = 31$, $r^2 = 0.586$, $P < 0.0001$) and females ($n = 39$, $r^2 =$

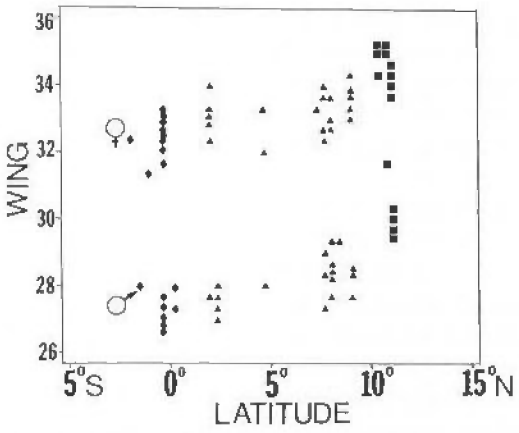

Fig. 3. Relationship of wing length with latitude in the *Acestrura heliodor* superspecies. Squares = *A. astreans*; triangles = *A. h. heliodor*; diamonds = *A. h. cleavesi*.

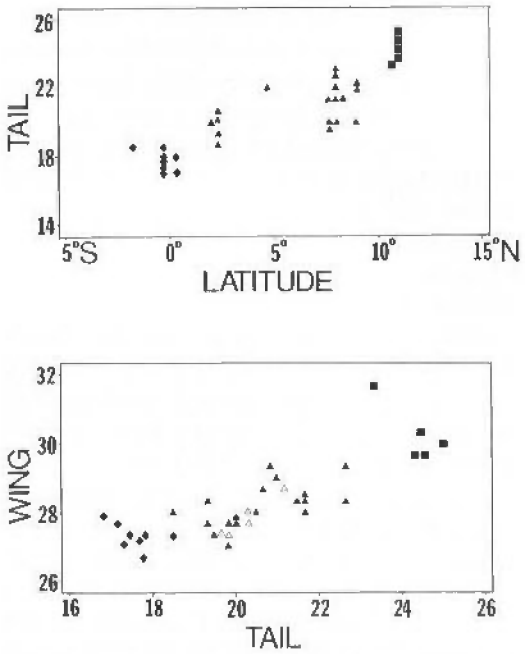

Fig. 4. Relationships of tail length with latitude and wing length in males of the *Acestrura heliodor* superspecies. Squares = *A. astreans*; solid triangles = *A. h. heliodor*; empty triangles = pre-1900 "Bogota" specimen identified as *A. h. heliodor* on basis of plumage but lacking definite locality data; diamonds = *A. h. cleavesi*.

0.522, $P < 0.0001$). Tail length in males, an important taxonomic character (Moore 1934), is also positively correlated with latitude (Fig. 4; $r^2 = 0.761$, $P < 0.0001$) and wing length ($r^2 = 0.658$, $P < 0.0001$). These correlations conform to Bergmann's Rule (cf. Handford 1983, Remsen 1984) and suggest that tail length is more closely linked with allometry and aerodynamic function, than to sexual display. Culmen length is uncorrelated with either latitude or wing length ($P > 0.05$) in either sex. Tail and wing length in males of *A. astreans* and *A. heliodor* do not overlap. I performed a Principal Components Analysis of culmen, wing, and tail lengths of males. Not surprisingly, all three taxa (*A. astreans, A. h. heliodor, A. h. cleavesi*) had nonoverlapping distributions along the axis of the first principal component (which explained 60.8% of the variance).

These taxa are also readily identified by the proportional width of the outermost rectrices (numbers 3–5) in males. The proportional width of rectrices is not clinal. Populations of *A. h. heliodor* from the Western, Central, and Eastern Cordilleras of Colombia and the Venezuelan Andes are not distinguishable from one another on the basis of tail shape, but are easily distinguished from *A. h. cleavesi* and *A. astreans*. As expected, "Bogotá" specimens have wing/tail ratios similar to specimens from known localities in the Eastern Cordillera (Fig. 4).

Taxonomic Conclusions

Acestrura astreans differs from *A. heliodor* in several important characteristics that are not the terminal states of observed clinal variation, and that support the recognition of *A. astreans* as a full species. The most important of these are: (1) the distinctive shape of the rectrices in the males; (2) the coloration of body plumage in both sexes; (3) pattern and color of the central rectrices of females; (4) the gorget color in males. Because of their allopatric distributions, the existence of reproductive isolating mecha-

nisms between *astreans* and *heliodor* can only be surmised. However, the morphological differences between these taxa are of the same scale as those observed among the other species of *Acestrura* and *Chaetocercus jourdanii*. The high degree of endemism in the Santa Martas has long been recognized (Chapman 1917, Todd and Carriker 1922). At least 12 other avian taxa endemic to the Santa Marta massif, with affinities in the northern Andes, are recognized as specifically distinct from their most closely related congeners (*Pyrrhura viridicata, Campylopterus phainopeplus, Coeligena phalerata, Ramphomicron dorsale, Synallaxis fuscorufa, Cranioleuca hellmayri, Grallaria bangsi, Myiotheretes pernix, Myioborus flavivertex, Basileuterus basilicus, Anisognathus melanogenys, Atlapetes melanocephalus*).

The systematic status of *Acestrura h. cleavesi* is uncertain. Except for rectrix shape in males, plumage differences between *A. h. cleavesi* and *A. h. heliodor* appear to be primarily quantitative and clinal. The report of *A. h. heliodor* in Ecuador (Moore 1934) is based on three specimens with definite locality data: Two adult females (MLOC 3083, Pallatanga, 1°59'S; MLOC 3084, Tumbaco, 0°13'S); and an immature male (MLOC 3086, Pallatanga). Both localities are on the Pacific slope of the Andes. Because the plumage of the immature male of *A. h. cleavesi* is unknown, the male specimen cannot be identified to subspecies. The females resemble the more heavily pigmented individuals of the nominate race from Colombia but also match the palest examples of *A. h. cleavesi* from Baeza, near the type locality. Adult male specimens will be needed to determine the racial affinity of the Pacific slope population in Ecuador. On geographical grounds alone, I tentatively consider these specimens as *A. h. cleavesi*.

A female (FMNH 45429, received from the "Museum Boucard") was collected by Delattre before 1850 at "Santiago, Colombia." If correctly located (de Schauensee 1949, Paynter and Traylor 1981), Santiago (1°08'N) is ESE of Pasto, midway between populations of *A. h. cleavesi* at Cuyuja (0°24'N) on the Amazonian slope of the Ecuadorian Andes and those of *A. h. heliodor* at San Agustín (1°53'N) in the Upper Magdalena Valley. Apparently, no specimens of *Acestrura heliodor* have been collected between Cuyuja and San Agustín during the past century. The Santiago specimen is indistinguishable from typical females of *A. h. heliodor*, and differs from all specimens of *A. h. cleavesi* in the intensity and distribution of rufous and cinnamon buff on the underparts and rump.

Appropriate habitat is available in the distributional hiatus, and the two taxa almost certainly intergrade or come into contact somewhere between Santiago and Cuyuja. I recommend that *cleavesi* should best be regarded as a subspecies, rather than a full species, until specimens from the appropriate regions are obtained.

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