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A new taxon in the *Amazilia viridifrons* (Chordata: Aves: Trochilidae) complex of southern Mexico

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Abstract.—We examined variation among populations of the complex assemblage of hummingbirds presently considered to constitute *Amazilia viridifrons* (Elliott, 1871), of Guerrero, Oaxaca, and Chiapas. A previous author had correctly suggested recognition of most Oaxaca populations as a full species, *A. wagneri* Phillips, 1964. We found that the Chiapas populations are also recognizable as a distinct taxon; because no name had previously been applied to these populations, we name it as a new subspecies, *A. viridifrons villadai*. Populations recently described as *A. viridifrons rowleyi* are actually referable to *A. wagneri*; moreover, that subspecies is not valid as an entity distinct from the remainder of *A. wagneri*.

Resumen.—Se examinó la variación entre las poblaciones del complexo de colibries que actualmente constituyen *Amazilia viridifrons* (Elliott, 1871), habitando a partes de Guerrero, Oaxaca y Chiapas. Otro autor había sugerido correctamente la separación de muchas de las poblaciones de Oaxaca como *A. wagneri* Phillips, 1964. Nosotros encontramos que las poblaciones también son reconocibles a nivel de especie, y proponemos el nombre de *A. viridifrons villadai*. Argumentamos también que las poblaciones recientemente descritas como *A. viridifrons rowleyi* Howell, 1993 pertenecen más bien a *A. wagneri*, y que la subespecie no se debe de considerar válida.

The taxonomic history of the *Amazilia violiceps* (Gould 1859) and *A. viridifrons* (Elliott 1871) species groups has been complex. A brief historical summary of the taxonomic treatment of the group follows. *Amazilia violiceps* was described in 1860 by Gould, and eleven years later Elliott (1871) described *A. viridifrons* based on a specimen from Putla de Guerrero, in western Oaxaca. Salvin (1892) treated the two forms as separate species, as did Ridgway (1911). Salvin & Godman (1892) described an additional violet-crowned species, *A. guerrerensis*, now in the synonymy of *A. violiceps*.

In general, early treatments recognized violet- (*violiceps*) and green-crowned (*viridifrons*) forms as full species. Peters (1945), however, not only did not recognize the two forms as full species, but also included both violet- and green-crowned forms within the nominate subspecies of *Amazilia violiceps* (see also Wetmore 1947). Although Friedmann et al. (1950) recognized the green-crowned forms as a full species, Phillips (1964) reduced them again to the rank of subspecies within *A. violiceps* on the basis of the absence of a clear zone of sympatry between the two forms. Most subsequent authors (e.g., AOU 1983, 1998; Binford 1989) have treated the violet- and green-crowned forms as full species.

In the only recent treatment of the group, Howell (1993) also recognized *Amazilia viridifrons* as a species separate from *A.*

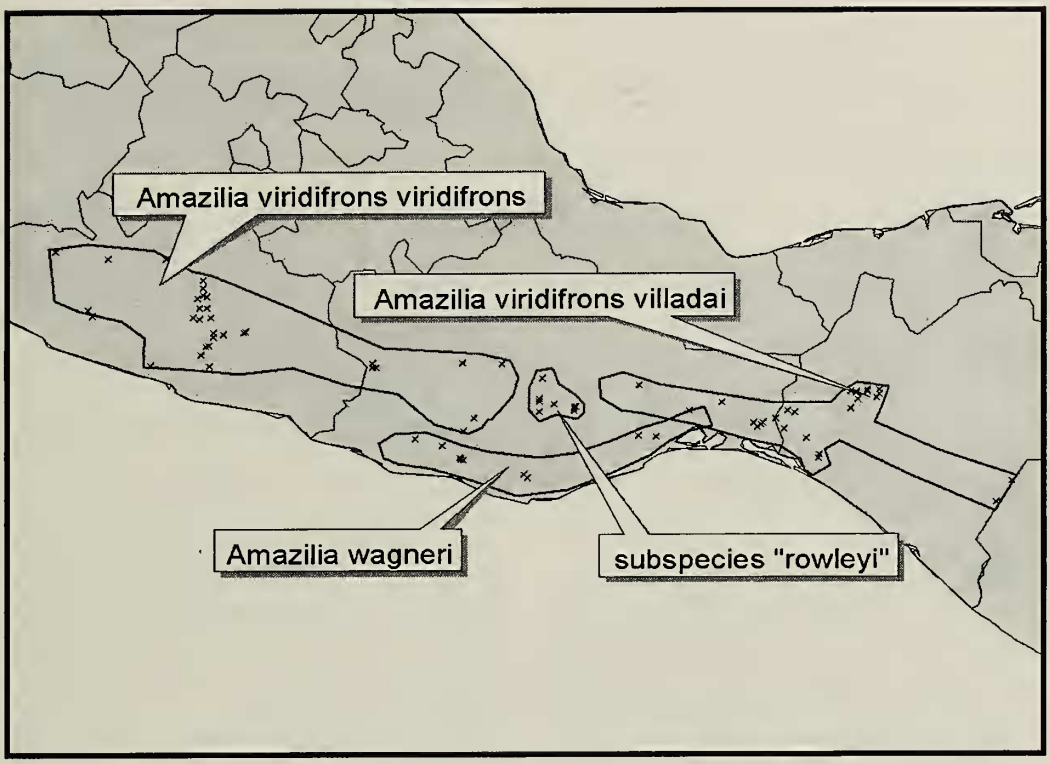

Fig. 1. Map showing geographic distributions of the *Amazilia viridifrons* complex in southern Mexico.

violiceps. He further suggested elevation of the cinnamon-sided populations of southern Oaxaca to species status (*A. wagneri*, Cinnamon-sided Hummingbird), and pointed out the odd geographic situation that resulted, with two green-sided populations separated by cinnamon-sided populations in Oaxaca. Finally, he described a new subspecies (*rowleyi*) from central Oaxaca, which he placed within *A. viridifrons*.

The AOU (1998) did not follow Howell's (1993) recommendation regarding the species status of the cinnamon-sided populations, instead treating them as a "group" within *Amazilia viridifrons*. Our own review indicates that Howell's *rowleyi* is not valid, and in fact that the populations Howell so named should be placed with *A. wagneri*, and not with *A. viridifrons*. Finally, because Howell (1993) ignored characters of size and shape among green-sided forms, he failed to note the marked differentiation of the western populations (Guerrero and western Oaxaca) from the eastern green-fronted populations (eastern Oaxaca and Chiapas) (Fig. 1), which we herein describe as a subspecies of the biological species *A. viridifrons*.

Materials and Methods

Specimens were assembled for study from numerous scientific collections: Academy of Natural Sciences of Philadelphia (ANSP), Field Museum of Natural History (FMNH), Moore Laboratory of Zoology (MLZ), Southwestern College (Winfield, Kansas, SWC), University of Michigan Museum of Zoology (UMMZ), U.S. National Museum of Natural History (USNM), Delaware Museum of Natural History (DMNH), Louisiana State University Museum of Natural Science (LSUMZ), Western Foundation of Vertebrate Zoology

Table 1.—Summary of measurements (mean ± standard deviation in mm, *n*) for *Amazilia viridifrons viridifrons*, *A. v. villadai*, and *A. wagneri*.

Character	*viridifrons*	*wagneri*	*villadai*
Bill length–males	20.3 ± 0.86, 22	21.1 ± 0.5, 6	21.3 ± 0.6, 21
Bill length–females	20.5 ± 0.7, 13	20.9 ± 1.8, 7	22.6 ± 1.1, 22
Wing chord–males	57.5 ± 1.7, 20	58.5 ± 0.9, 5	60.3 ± 1.6, 19
Wing chord–females	56.5 ± 1.2, 14	56.1 ± 1.7, 7	58.2 ± 1.2, 19
Tail length–males	32.4 ± 1.0, 17	33.9 ± 1.6, 3	34.5 ± 1.2, 19
Tail length–females	32.1 ± 1.1, 12	32.4 ± 1.2, 6	33.7 ± 1.3, 21

(WFVZ), University of Kansas Natural History Museum (KUNHM), and Museum of Vertebrate Zoology (MVZ). Sample sizes are presented in Specimens Examined below. Preliminary examinations of interpopulation variation were based on named taxa and geography.

Comparisons of plumage coloration were made under natural light conditions. Measurements on each specimen included bill length from anterior edge of nostril, wing chord, and tail length from base of central rectrices. Measurement data were $\log_{10}$-transformed; MINITAB (version 11.12, MINITAB 1996) was used for multivariate analyses. Principal components (PC) analyses were based on covariance matrices of $\log_{10}$-transformed data; percent diagnosability was taken from classification errors for samples available to us in a discriminant function analysis of $\log_{10}$-transformed data. *T*-tests were used in univariate comparisons of PC scores and raw measurements of sexes within each species to evaluate sexual size dimorphism; *t*-tests were then used to compare populations based on PC scores and raw measurements, with sexes analyzed separately.

Amazilia viridifrons villadai, new subspecies

Holotype.—University of Michigan Museum of Zoology (UMMZ), 102297, adult male from Mexico, Chiapas, Arriaga, 100 m, collected 25 May 1939 by Pierce Brodkorb.

Diagnosis.—Distinguishable from most *Amazilia* hummingbirds by the combination of green-and-white-only plumage with relatively large size (Table 1, Fig. 2). Within the species group discussed above, differs from *A. violiceps* in lacking the violet crown, and from *A. wagneri* in lacking cinnamon edging on sides and flanks.

Closely similar to the disjunct *Amazilia viridifrons viridifrons* in coloration, although green flecking and edging on the sides and flanks is less frequent, making the underparts appear whiter overall. Larger in size, with measurements of wing and tail contrasting strikingly (*t*-tests, all three measurements in both sexes, $10^{-5} > P > 10^{-9}$) (Fig. 2). Also differs in having marked sexual dimorphism in size (*t*-tests, $P < 0.001$ for all three PC scores, bill, and wing; $P = 0.051$ for tail), whereas *A. viridifrons* has no detectable sexual size dimorphism (*t*-tests, all $0.86 > P > 0.14$). Based on the limited measurement data (Table 1) available ($n = 74$), discriminant function analysis indicated 86% (30 of 35 individuals) correct classification (diagnosability) of males, and 83% (24 of 29 individuals) correct classification of females.

Distribution.—Known from a restricted zone extending from eastern Oaxaca (vicinity of Tapanatepec), east in the coastal lowlands to western Chiapas (vicinity of Arriaga), and in the interior of Chiapas from north of Arriaga east to the Guatemalan border near Ciudad Cuauhtémoc (Delaware Museum of Natural History, DMNH 24527, 24528, 24530, 24533, 24548). Probably occurs in adjacent areas of western Guatemala as well.

Description of holotype.—Color desig-

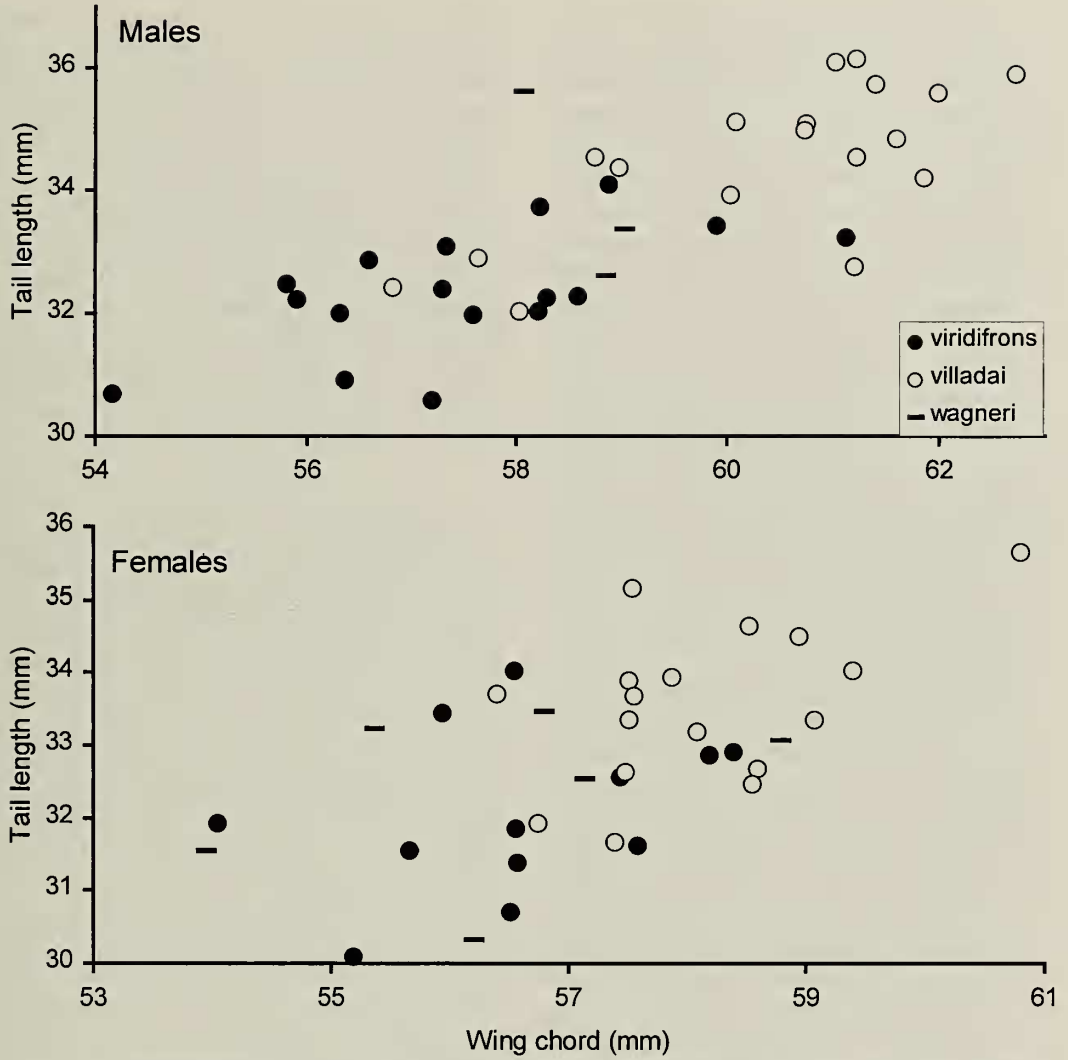

Fig. 2 Bivariate scattergrams of wing chord versus tail length in males and females of the *Amazilia viridifrons* complex in southern Mexico.

nations given as capitalized names are from Smithe (1975); noncapitalized colors are descriptors only. Forecrown very dark green, approaching dusky blackish. Hindcrown and back glossy Parrot Green, tending towards more olivaceous on the rump and upper tail coverts; the latter narrowly fringed white. Dorsal surface of tail glossy Parrot Green strongly tinged with bronzy.

Underparts clean white, with a slight indication of a collar or chest band made up of feathers that are Parrot Green. Sides and flanks lightly tinged with medium buffy gray. Undertail coverts white. Undersurface of rectrices glossy Parrot Green tinged with bronzy. Bill on dried specimen is light yellow, with tip black. Tarsi and feet on dried specimen are dusky, approaching black.

Measurements of holotype.—Wing chord, 59 mm; tail length, 35 mm; bill from anterior edge of nares, 20.6 mm; total exposed culmen, 22.5 mm; bill depth at anterior edge nares, 2.6 mm; bill width at anterior edge nares, 2.6 mm; body mass not recorded.

Description of female.—Adult female, Louisiana State University Museum of Natural Science, LSUMZ, No. 87570. Closely similar to holotype. Upper tail coverts and rectrices glossy Parrot Green, but with notably more pronounced bronzy tinge. Comparisons of series of males and females indicate little consistent sexual dichromatism in this or any character, nor do they indicate a tendency towards differentiation of eastern and western populations in this regard, contra Howell (1993).

Description of juvenile.—Juvenile male, Western Foundation of Vertebrate Zoology, WFVZ, No. 15610. Similar to holotype. Entire back Olive-Green, with buffy edgings on each feather, giving an overall scaly appearance to the back. Upper tail coverts and rump with whitish edgings. Rectrices glossy Parrot Green, with strong bronzy tinge as in adult female.

Specimens examined.—Adult-plumaged individuals examined are listed here. *Amazilia viridifrons villadai*, western Chiapas: 14 males, 17 females (ANSP 167843, DMNH 24547, 53194-96, FMNH 153210, 208726-28, LSUMZ 40191-93, 44607, 85547, 87570, MLZ 27362, 27364, SWC 8069, UMMZ 102294-99, 109145, USNM 155273-74, WFVZ 15610-12, 19725); eastern Chiapas: 3 males, 2 females (DMNH 24527-28, 24530, 24533, 24548); eastern Oaxaca: 7 males, 4 females (DMNH 24543, LSUMZ uncat., 24350, 40190, 44609, 85657, USNM 57772, 57774, WFVZ 15607-08, 16861); eastcentral Oaxaca near Rancho Las Animas: 13 males, 2 females (DMNH 24544, 45125, 45129, LSUMZ 40188, MLZ 45117, 45120, 45126, 45131, 49538–39, 49543, 54427, 54432, WFVZ 15600-01). *Amazilia wagneri*, Oaxaca, vicinity of Tehuantepec and Juchitán: 3 males (LSUMZ 40189, MLZ 59715, UMMZ 137649); Oaxaca, vicinity of Santiago Matatlán: 5 males, 4 females, 1 unsexed (LSUMZ 24352-53, WFVZ 19598, 19620, 49356-60, 49362); Oaxaca, Sierra de Miahuatlán: 6 males, 10 females (DMNH 24534, 24536-41, 24546, LSUMZ 24352, 27432, WFVZ 21492-94, 21538-39, 21542). *Amazilia v. viridifrons*, Oaxaca, Putla de Guerrero, 1 male (LSUMZ 33092); Guerrero, central: 23 males, 19 females (DMNH 24487, 24490–97, 24499–511, 24513–26, 24550–51, KUNHM 45823, MLZ 10172, MVZ 109971, 113452)

Etymology.—We are pleased to name this species in honor of Manuel M. Villada, influential Mexican naturalist and scientist of the nineteenth century, who produced important works on the hummingbirds of the Valley of Mexico (e.g., Villada 1875).

Discussion

For the *Amazilia viridifrons* complex, errors and misinterpretations began with the super-inclusive "*Amazilia violiceps violiceps*" of Peters (1945). Unfortunately, problems have continued up to the most recent treatment of the group (Howell 1993). The above description of *A. viridifrons villadai* represents one step in setting the situation straight and arriving at a taxonomy for the group in which all distinct biological entities are recognized; several additional considerations follow.

Amazilia wagneri.—Most Oaxaca populations of this complex are easily distinguishable by their warm cinnamon sides of the white underparts. Given their clear differentiation in plumage over very small geographic distances (possible parapatry), we concur with Howell (1993) that they are best treated as a separate species, *A. wagneri*. Variation does exist, however, in the degree to which the species' characters are expressed, deserving some comment.

Examining in detail specimens available, those from the coastal slopes of the Sierra de Miahuatlán uniformly show the cinnamon sides and other characters attributed to *Amazilia wagneri* (Howell 1993). The only four specimens (DMNH 24541, WFVZ 21492, 21538, 21542) available to us from the *interior* slopes of the Sierra de Miahuatlán, near San Miguel Sola de Vega, however, show no trace of cinnamon on the

sides and flanks, and thus we concur with Howell (1993) that they represent *A. v. viridifrons*. Under our view, however, they represent the eastern extreme of that subspecies' geographic distribution (contra Howell 1993, see below). *A. wagneri*, then, has an extremely restricted geographic distribution in southern Oaxaca, found only along the southern fringes of the Sierra de Miahuatlán and intruding narrowly into the Oaxaca Valley near Santiago Matatlán (see below).

Subspecies Amazilia viridifrons rowleyi *Howell.*—Among the specimens we examined were 12 individuals (8 adults, 4 immatures) from the series that Rowley collected at a point 13 miles south of Santiago Matatlán, as well as two specimens from 18 miles southeast of Santiago Matatlán from other collectors. Matatlán is located about midway between the Guerrero and Chiapas green-and-white forms, and on the opposite (interior) side of the Sierra de Miahuatlán from the Oaxaca populations. Although, as noted by Howell (1993), specimens collected from the region by other collectors are clear examples of *wagneri*, the plumages of the entire series available to us (11 individuals) from the Rowley collection are worn, and colors seriously faded for unknown reasons (perhaps exposure to sunlight?).

Given the poor condition of the Rowley series, we were concerned about the validity of the subspecies *rowleyi*, which was based principally on that material (Howell 1993). Our inspection, which did not include the type, lead us to conclude that the subspecies is not valid, with diagnostic characters ("Readily distinguished from *wagneri* by duller and less extensive cinnamon on flanks and axillars, lack of rufous or dull cinnamon on wings except as concealed patch in adult ♂, and bronzy to purplish-copper tail"; Howell 1993) based on seriously worn specimen material. All material at hand for *rowleyi*–which according to Howell (1993) agrees well with the type specimen–is so extremely heavily worn that color comparisons would not be reliable.

Moreover, our inspection of Rowley's Matatlán series leads us to question Howell's (1993) placement of these populations within *Amazilia viridifrons*. *All* individuals in the series available to us show some degree of cinnamon or buffy on sides and flanks, fall within the range of variation in the series of coastal-slope *wagneri* that we examined, and do not coincide with the green-and-white plumage of *A. viridifrons*. Howell's (1993) confusion is perhaps understandable given the heavy wear and probable fading of the Rowley series, but less so given that specimens *not* collected by Rowley from a nearby locality represent clear examples of *A. wagneri*, unless this were to be a zone of near-sympatry.

Interestingly, about 50 km farther south and east in Oaxaca, in the vicinity of Rancho Las Animas, extensive series have been collected. These individuals are clearly referable to *Amazilia viridifrons villadai*, characterized by large size, no cinnamon edgings, and clear white breasts. Given close proximity to *A. wagneri* populations, and in fact spatial overlap with *wagneri* populations (e.g., at 12 miles E Juchitan, LSUMZ 40189), potential sympatry (or at least interdigitating distributions) exists, yet we see no evidence of intergradation, suggesting that the populations are reproductively isolated.

Systematic characters and species concepts.—This study illustrates clearly the importance of consideration of all available information–geographic and phenotypic–in systematic studies. In the taxonomic history of the group, early workers unfamiliar with the geography of southern Mexico, presented with small and incomplete series of specimens, and using a very inclusive version of the Biological Species Concept, created artificially inclusive taxa in this group. Later, Howell (1993) considered only characters of coloration, ignoring size and shape, and for that reason missed the marked differentiation of the Chiapas pop-

ulations. Although these populations are herein treated as a subspecies of *A. viridifrons*, they are a clearly diagnosable form (size differences, presence of sexual dimorphism), likely monophyletic, and so probably recognizable as a valid evolutionary (Wiley 1978, Wiley & Mayden 2000) or phylogenetic (Zink & McKitrick 1995) species, particularly if additional character suites can be marshaled to the question.

Acknowledgments

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