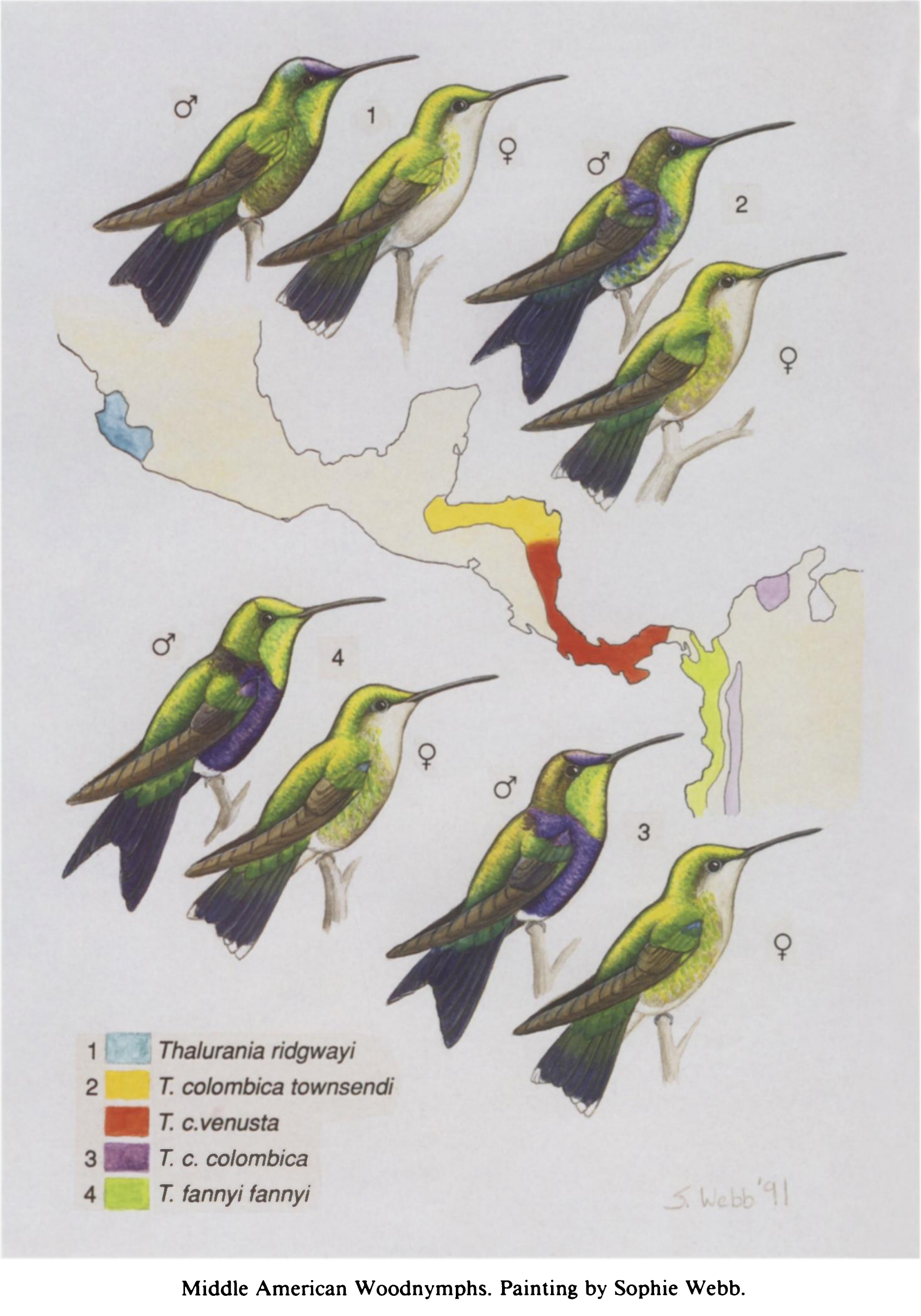

Middle American Woodnymphs. Painting by Sophie Webb.

THE WILSON BULLETIN
A QUARTERLY MAGAZINE OF ORNITHOLOGY
Published by the Wilson Ornithological Society

Wilson Bull., 104(2), 1992, pp. 205–219

GEOGRAPHIC VARIATION AND SPECIES LIMITS IN MIDDLE AMERICAN WOODNYMPHS (*THALURANIA*)

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Abstract.—We analyzed geographic variation in morphology and plumage coloration in male woodnymphs of the genus *Thalurania* in Middle America and northwestern South America. Morphometric characters distinguish the disjunct western Mexican populations from populations to the south. Three groups are distinguished by discrete plumage coloration characters. We propose that these groups be recognized as separate species: *T. ridgwayi* of western Mexico; *T. colombica* of Central America south to western Panama and disjunctly in interior northwestern South America; and *T. fannyi* of eastern Panama, western Colombia, and northern Ecuador. *Received 11 July 1991, accepted 20 Sept. 1991.*

Resumen.—En este trabajo analizamos la variación geográfica en morfología y en patrones de coloración en el plumaje de los machos de las "ninfas de bosque" del género *Thalurania* de Mesoamérica y noroeste de Sudamérica. Los caracteres morfométricos distinguen las poblaciones del oeste de México de todas las poblaciones del sur. Con base en la coloración del plumaje, caracteres discretos separan tres grupos. Proponemos que estos grupos sean reconocidos como especies distintas: *T. ridgwayi* del oeste de México; *T. colombica* desde Centroamérica hacia el sur al oeste de Panamá y continuando después en el noroeste de Sudamérica; y *T. fannyi* del este de Panamá, oeste de Colombia y extremo norte del Ecuador.

In spite of more than a century of study, patterns of geographic variation and speciation in Middle American birds remain poorly understood. Studies employing modern, quantitative approaches are rare (e.g., Johnson 1980). The purpose of the present study is to analyze morphometric and plumage variation in Middle American populations of woodnymphs, hummingbirds of the genus *Thalurania*. Although of limited geographic

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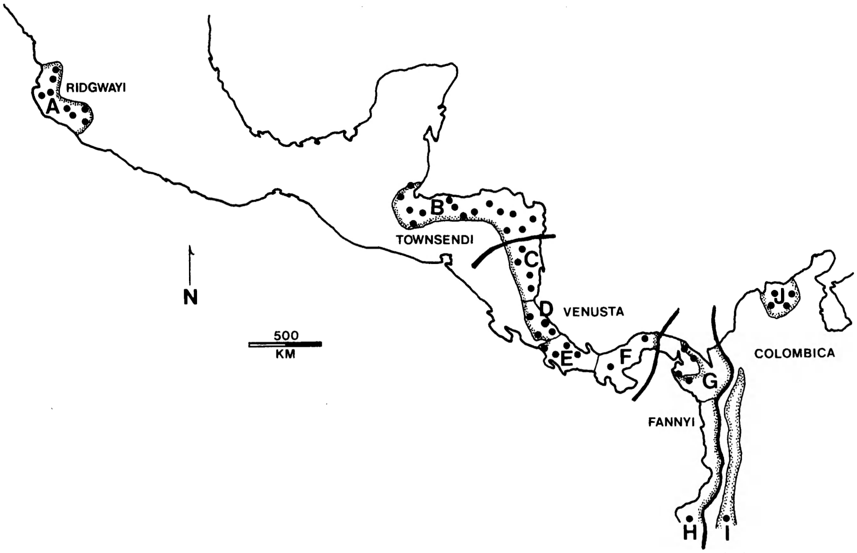


FIG. 1. Geographic range of woodnymphs in Middle America and northwestern South America. Regions for statistical analysis are defined by solid lines; subspecies limits reflecting taxonomy of Peters (1945) are divided by thick lines.

scope (Middle America), we hope that this effort will stimulate other studies of the group as a whole.

As currently recognized, the polytypic Crowned Woodnymph (*T. colombica*) ranges in lowland tropical forest from eastern Guatemala south to northern South America (Fig. 1; A.O.U. 1983), where it is replaced by a congeneric allospecies, the Fork-tailed Woodnymph (*T. furcata*). Poorly known disjunct populations are found in humid canyons and foothills of western Mexico in the states of Nayarit, Jalisco, and Colima. Field surveys in suitable habitat in the intervening area of central and southern Mexico have not provided records of woodnymphs (e.g., Blake 1950, Binford 1989, Navarro et al., in press). Because woodnymphs are usually fairly common where present (Wetmore 1968, Stiles et al. 1989; pers. obs.), the gap between the ranges seems real and not simply a result of incomplete knowledge.

The western Mexican population of woodnymphs was described by Nelson (1900) as a distinct species (*T. ridgwayi*), based on a single male specimen. The form was known only from the type until the 1950s (Phillips 1961), and was eventually merged with the South American species (*T. furcata* by Peters [1945]) and maintained as a subspecies. The availability of new material from Nayarit (Escalante 1988) and Jalisco (recent collections by the Field Museum of Natural History, the Laboratorio Natural Las Joyas de la Sierra de Manantlán, and others) prompted us to review the Middle American populations to document patterns of geographic variation and re-evaluate their taxonomic status.

The distribution of *Thalurania* in Mexico is somewhat unusual. Most Neotropical species ranging into the lowlands of western Mexico (e.g., Olivaceous Woodcreeper [*Sittasomus griseicapillus*], and Golden-crowned Warbler [*Basileuterus culicivorus*]) also are present in the east from Tamaulipas southward and have rather continuous ranges (Friedmann et al. 1957, Miller et al. 1957, Escalante et al., in press). However, several other western Mexican bird species show interrupted distributions similar to *Thalurania,* with closely related populations in Central America or northern South America (e.g., White-fronted Swift [*Cypseloides storeri* sp. nov.]-White-chinned Swift [*C. cryptus*] [Navarro et al., in press], Tufted Jay [*Cyanocorax dickeyi*]-White-tailed Jay [*C. mystacalis*], White-throated Jay [*Cyanolyca mirabilis*]-Silvery-throated Jay [*C. argentigula*], Red-breasted Chat [*Granatellus venustus*]-Rose-breasted Chat [*G. pelzeni*]; A.O.U. 1983).

Plumages of male woodnymphs vary dramatically among populations, forming a mosaic of forms characterized by different combinations of plumage characters that make the genus difficult to interpret taxonomically. Some taxonomists lump populations with glittering forecrowns (*colombica* group; Central America and northwestern South America) and those with dull-forecrowns (*furcata* group; interior South America) into one species (*T. furcata,* Peters 1945, Meyer de Schauensee 1970). Other authors recognize the various differentiated forms as constituting two or more species (e.g., Eisenmann 1955, A.O.U. 1983, Hilty and Brown 1986). The remaining two species in the genus, *T. glaucopis* and *T. watertonii* (as in the original description of Bourcier 1847 and not "*watertoni*" as Salvin 1892 or Cory 1918), of eastern Brazil also have glittering forecrowns. Other diagnostic characters of these two species, such as a green belly, deeply forked tail, and either a violet back (*watertonii*) or no violet on the back (*glaucopis*) are also present in Middle American woodnymphs, although not as pronounced. Clearly, a revision of the entire genus is in order; this paper, however, is restricted to Middle America and extreme northwestern South America, owing to the paucity of specimens and our own lack of experience in other critical areas.

METHODS

We examined a total of 171 specimens of adult male woodnymphs (Appendix I) in 12 museum collections: Academy of Natural Sciences of Philadelphia; American Museum of Natural History; Delaware Museum of Natural History; Field Museum of Natural History;

Instituto de Biología, Univ. Nacional Autónoma de México (UNAM); Los Angeles County Museum of Natural History; Louisiana State Univ. Museum of Natural Science; Museo de Zoología, Facultad de Ciencias, UNAM; Museum of Comparative Zoology; National Museum of Natural History; Peabody Museum of Natural History; and Univ. of California at Los Angeles. A common problem in studies of geographic variation is that females are underrepresented, as was true in the present case. However, variation in females appeared more or less parallel to that of males, although not accompanied by discrete differences in plumage characters in Middle American populations.

We recorded four measurements and three color characters from each study skin. The measurements were: BILL length from the anterior edge of the nostril to the tip, WING chord, TAIL length, and tail NOTCH (difference in length between the long outer rectrices and short central rectrices). Plumage characters included the following: percent of belly colored black, violet, or green; extent of the violet band on back (scored from 0 = absent to 3 = complete); and percent of forecrown violet vs green.

Because sample sizes at particular localities were small, we partitioned individual samples into ten regions (Fig. 1). Regions were established so that localities within each held more or less continuous habitat and so as to coincide with the distribution of named forms. Division among regions were somewhat arbitrary in northern Central America where habitat is continuous. To check the magnitude of geographic variation within regions, we compared measurements from three relatively large individual locality samples within region D (Appendix I).

To locate zones of significant morphological change, we conducted analyses of variance on each morphometric character, using Gabriel's test (sum of squares—simultaneous test procedure, SS-STP, Gabriel and Sokal 1969) on latitudinal sequences (Power 1970). We used two principal component analyses (PCA) to investigate multivariate patterns of variation among regions. First, we extracted principal components from the variance-covariance matrix of log-transformed regional means of measurements; the coefficients obtained were used to calculate individual scores and project them in multivariate space. This procedure projects variation on axes that maximize variance among regional samples (Gibson et al. 1984). A second PCA included two plumage characters (crown and belly), with the measurement data, and was based on the correlation matrix of untransformed regional means. Because within-sample distributions of back-band extent shows strong departures from normal distributions, this character is excluded from the multivariate analyses.

RESULTS

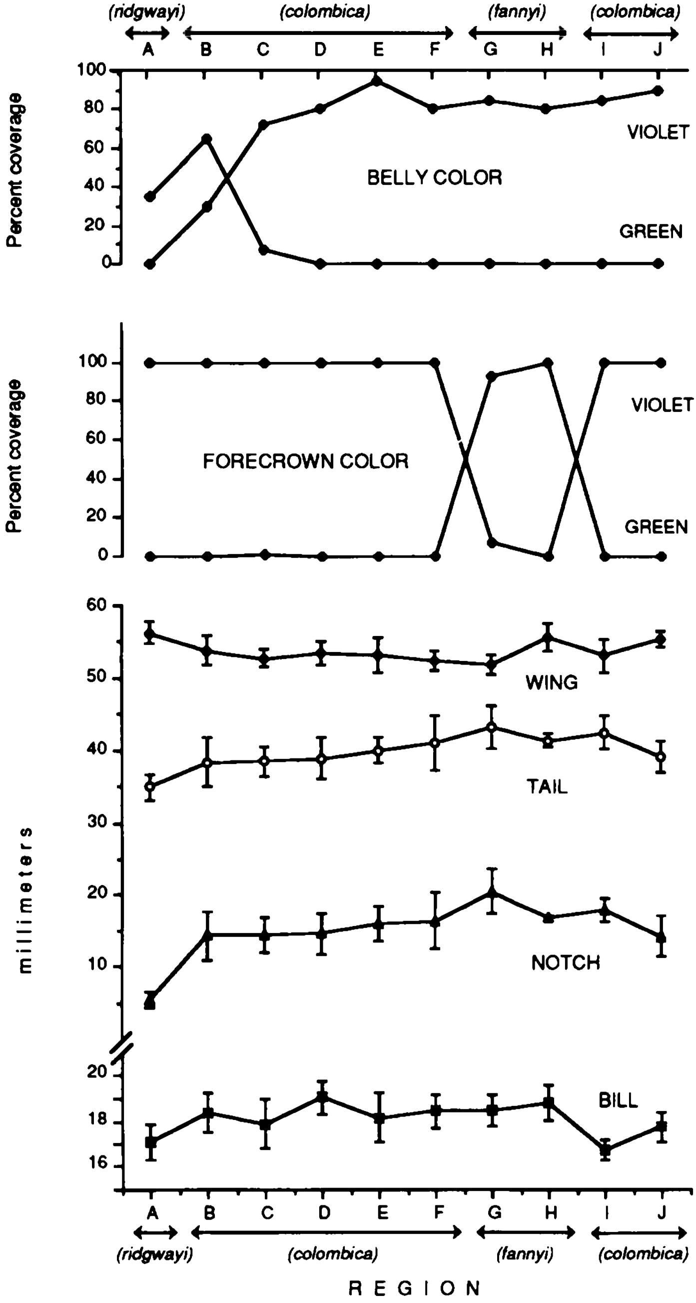
Plumage coloration.—Color patterns show striking differences between regions (Table 1, Fig. 2). Individuals of the western Mexican populations (region A) have predominantly green or black bellies; Guatemalan and Honduran populations (B) are intermediate in belly color, having both green and violet on the belly; Nicaraguan populations (C) have largely violet bellies but still retain some green. Populations farther south have completely violet bellies. Geographic patterns in the second color character, extent of the violet band on the back, are simpler: western Mexican populations have the back completely green with no band, but individuals of all remaining populations have either a complete band or two separate violet scapular patches.

A different geographic pattern is found in forecrown color (Fig. 2). The

TABLE 1

DESCRIPTIVE STATISTICS FOR COLOR PATTERN AND CONTINUOUS VARIABLES OF MIDDLE AMERICAN AND COLOMBIAN WOODNYMPHS. MEDIANS FOR COLOR CHARACTERS, AND MEAN AND STANDARD ERROR FOR MEASUREMENTS ARE PRESENTED. REGION LABELS FOLLOW FIG. 1.

	Region									
Character	A	B	C	D	E	F	G	H	I	J
N	19	32	18	26	13	15	19	5	8	15
Belly										
Violet %	0.0	30.0	72.5	80.0	95.0	80.0	85.0	80.0	85.0	90.0
Green %	35.0	65.0	7.5	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Black %	65.0	15.0	20.0	20.0	5.0	20.0	15.0	20.0	15.0	10.0
Back band										
Median	0.0	2.0	3.0	2.0	3.0	3.0	2.0	1.0	2.0	1.0
Forecrown										
Violet %	100.0	100.0	100.0	100.0	100.0	100.0	7.5	0.0	100.0	100.0
Green %	0.0	0.0	0.0	0.0	0.0	0.0	92.5	100.0	0.0	0.0
Bill										
Mean	17.11	18.39	17.91	19.06	18.16	18.45	18.49	18.82	16.74	17.75
SD	0.18	0.16	0.25	0.16	0.31	0.20	0.16	0.39	0.14	0.17
Wing										
Mean	56.27	53.87	52.78	53.44	53.25	52.34	51.87	55.67	53.10	55.37
SD	0.36	0.38	0.30	0.32	0.68	0.34	0.31	0.81	0.92	0.29


(ridgwayi)
(colombica)
(fannyi)
(colombica)
A B C D E F G H I J
Percent coverage
100
80
60
40
20
0
BELLY COLOR
VIOLET
GREEN
FORECROWN COLOR
VIOLET
GREEN
millimeters
60
50
40
30
20
10
WING
TAIL
NOTCH
20
18
16
BILL
REGION

six northernmost and two southernmost populations have violet forecrowns; two intermediate populations (the Darién region of Panama [G], and Choco, Columbia [H]), have green forecrowns. One to several violet feathers at the rear edge of the forecrown are observed in most Panamanian specimens (region G). The last color character, extent of forecrown, shows no detectable geographic differentiation.

Body dimensions.—Only three of 40 within-region character distributions depart significantly from normality, a level expected with a 5% significance criterion. TAIL and NOTCH are positively correlated (overall $r = 0.87$), but this correlation across samples varies greatly (e.g., region H, $r = 0.45$; region F, $r = 0.92$), indicating that both characters provide some independent information. Hence, all morphometric characters are retained for further analysis, and no transformations are employed except for multivariate analyses. Analyses of microgeographic variation among the three localities within region D indicate significant differences in three of the four characters (bill $P < 0.01$, notch $P < 0.04$, tail $P < 0.001$), suggesting the existence of microgeographic differentiation. However, the scale of these differences is considerably smaller than the among-region differences, so, owing to generally low sample sizes, we combine sites within regions.

SS-STP shows that western Mexican populations (A) differ significantly from southern populations in all dimensional characters and have a nonoverlapping distribution of NOTCH (Figs. 2 and 3). For the remaining regions (B to J), several patterns are evident. In BILL, regions B and C form a subset different from the remaining southern populations in which bill length increases gradually southward to region H and then decreases in I and J. In WING, southern populations show a gradual decrease in wing length south to Panama (region F) and then an increase in Colombian populations. In both TAIL and NOTCH, populations show a gradual increase from north to south, peaking in region G and decreasing in H–J.

Multivariate analyses.—For measurement data alone, the first principal component reflects mainly variation in NOTCH (Table 2). The western Mexican populations separate completely in multidimensional space along the first component (Fig. 4A). The rest of the populations overlap broadly, roughly arrayed in a north-to-south sequence. Specimens from eastern

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FIG. 2. Geographic variation in belly and forecrown colors, and measurement data in male woodnymphs of Middle America and northwestern Colombia. *Y* error bars indicate standard deviations.

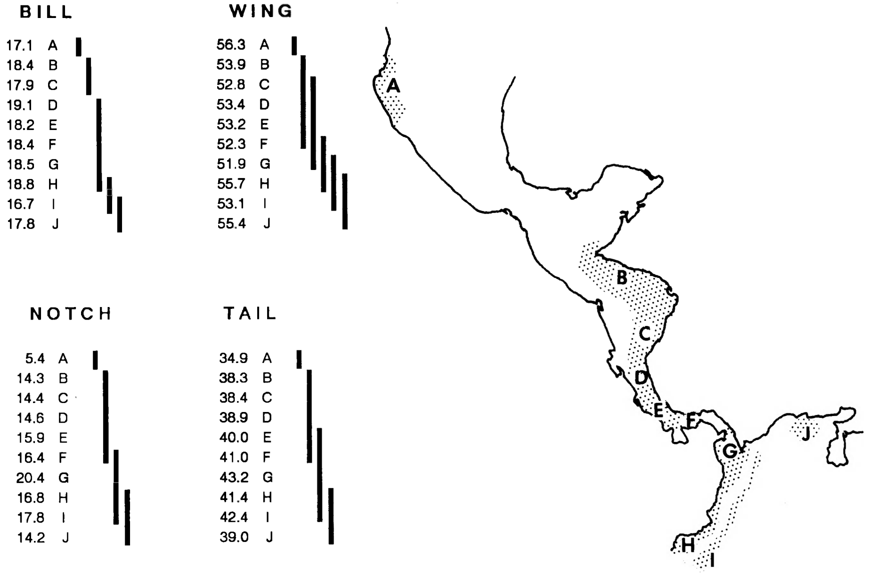

FIG. 3. SS-STP's of bill, wing, tail, and notch of populations of woodnymphs from Middle America and northwestern Colombia. Vertical bars indicate homogeneous subsets of populations.

Panama (region G) cluster tightly at the edge of the cloud but do not separate completely.

In the PCA of six measurements and plumage characters, a clearer pattern is found (Fig. 4B). The first and fourth principal components show the greatest separation between regions, together explaining 58% of the total variation (Table 2). Again, western Mexican populations separate along the first component, followed by a rough north-to-south sequence of the remaining populations. The eastern Panamanian (G) and Chocoan (H) populations separate on the fourth component.

DISCUSSION

The overall pattern of geographic variation in Middle American woodnymphs suggests the existence of three distinct groups. The disjunct western Mexican populations (*ridgwayi*) differ significantly in seven of eight characters, with a nonoverlapping distribution of NOTCH. The second group (*colombica*) is formed by the populations of Central America from Belize and Guatemala south to western Panama and continuing disjunctly in the upper Magdalena Valley (Huila) and Santa Marta region of Colom-

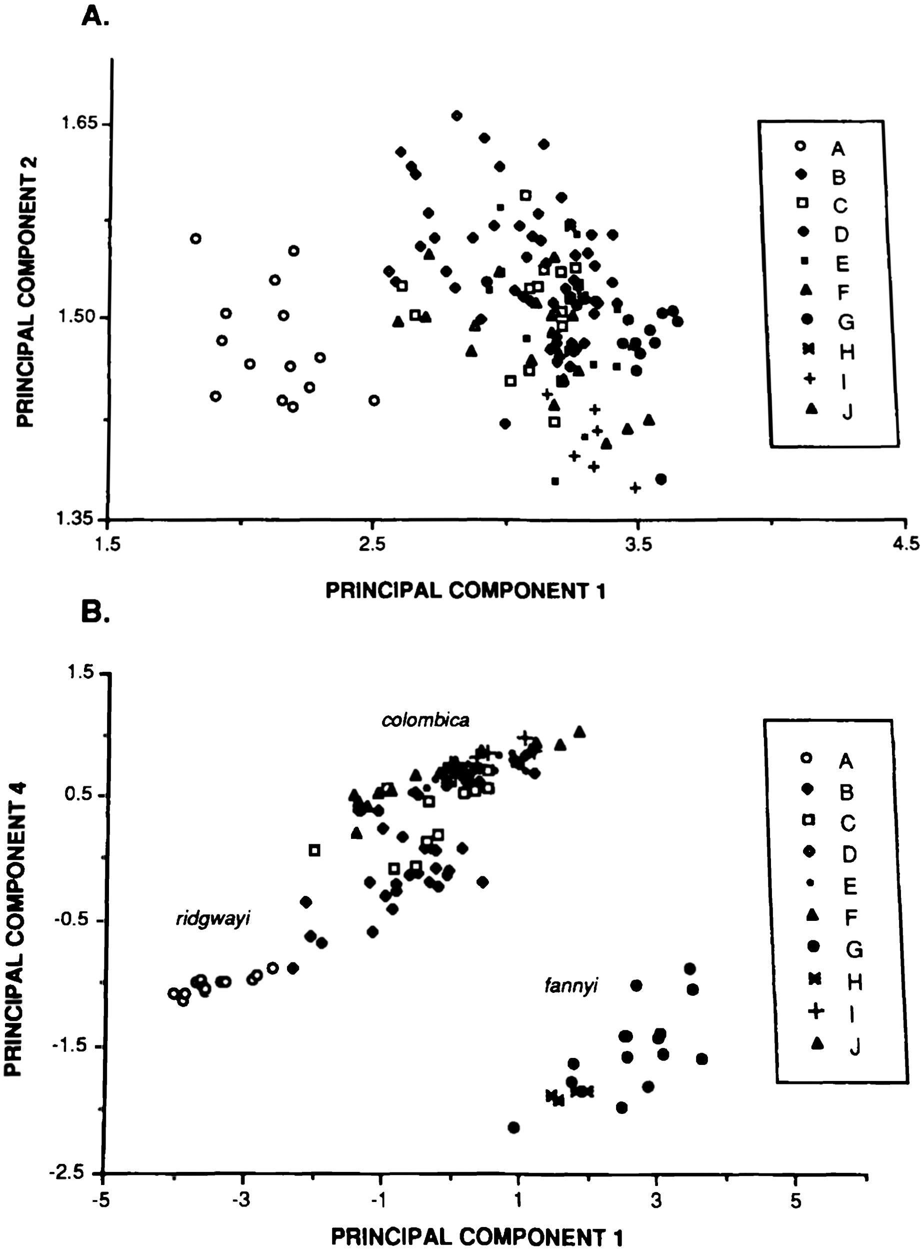

FIG. 4. Principal component scores based on (A) population means of morphometric characters, and (B) population means of morphometric and plumage characters of male woodnymphs of Middle America and northwestern Colombia. Labels correspond to regions in Fig. 1.

Table 2

Principal Component Coefficients for (a) Log-transformed Regional Means of Measurements, Based on the Variance-covariance Matrix, and (b) Untransformed Data, Based on the Correlation Matrix of Color Characters and Measurements Combined for Male Woodnymphs from Middle America and Northwestern Colombia

	Character	Factor				
		PRIN1	PRIN2	PRIN3	PRIN4	PRIN5
(a)	Bill	0.045	0.925	0.315	−0.207	—
	Wing	−0.049	0.040	0.467	0.882	—
	Notch	0.986	0.018	−0.118	0.117	—
	Tail	0.152	−0.377	0.818	−0.407	—
	Eigenvalue	0.14	0.001	0.00	0.00	—
	Proportion	0.98	0.01	0.00	0.00	—
(b)	Belly	0.433	−0.202	−0.156	0.480	0.710
	Forecrown	−0.367	0.086	0.009	0.863	−0.335
	Bill	0.184	0.596	−0.770	−0.017	−0.111
	Wing	−0.282	0.712	0.402	−0.005	0.486
	Notch	0.559	0.139	0.202	0.139	−0.233
	Tail	0.501	0.264	0.424	0.066	−0.284
	Eigenvalue	2.72	1.02	0.91	0.76	0.49
	Proportion	0.45	0.17	0.15	0.13	0.08

bia. *T. colombica* shows pronounced geographic variation in belly color, changing gradually from green to violet on the belly between Guatemala and Costa Rica. The third group (*fannyi*) is formed by the eastern Panamanian, Caucan and Chocoan populations, based on differences in forecrown color.

Taxonomic implications.—A lively debate has centered around species concepts in ornithology (Cracraft 1983, McKitrick and Zink 1988); issues under discussion include the importance of gene flow, monophyly of species, and operational difficulties in applying species concepts. Although reproductive isolation has traditionally been used for defining species limits (biological species concept), we concur with Cracraft (1983) and McKitrick and Zink (1988) that the ability to reproduce is a shared ancestral trait that can be differentially retained, potentially confusing the reconstruction of the evolutionary histories of taxa. Furthermore, because of its dependence on the reproductive isolation criterion, the biological species concept is not directly applicable to allopatric taxa such as several of the forms treated in the present study.

The extreme application of the biological species concept to woodnymphs led to combining populations from Middle America to southern Brazil, Paraguay, and Bolivia into a single highly polytypic species, *T. furcata,* with 21 subspecies (Peters 1945). Differentiated allopatric forms and discrete segments of stepclines are treated as subspecies. Based on results presented above, for Middle American and northern South American woodnymphs, a putative biological species, *T. colombica,* could be recognized (including the five subspecies *ridgwayi, townsendi, venusta, fannyi,* and *colombica*) or a superspecies with three allopatric or parapatric species, the monotypic *ridgwayi* and the polytypic *fannyi* and *colombica.* The latter treatment, which separates the green-crowned *fannyi* populations, is supported by the fact that forecrown color is the character differing most dramatically in one of the few tests of sympatry in the genus (*T. furcata* and *T. glaucopis*).

Under the phylogenetic species concept, the three discrete sets of woodnymph populations in our study (*ridgwayi, colombica,* and *fannyi*) could be recognized as species. *T. ridgwayi* is differentiated in all measurements, is completely separable on the basis of NOTCH, and has no violet on the scapulars or back. Other diagnostic characteristics, such as the violet forecrown and green belly are perhaps primitive within the genus because potentially homologous character states occur in other members of the genus.

T. colombica is diagnosable only on the basis of a combination of violet back-band and forecrown, because both characters occur independently in other forms of the genus. If the presence of these characters in other taxa were confirmed as homologous, it would imply that perhaps *T. colombica* does not fit the monophyly requirement of the phylogenetic species concept. This question can be resolved only through a cladistic analysis of all members of this complex. Although further subdivision of *T. colombica* to the level of the described subspecies might be possible based on belly color, we prefer not to divide this form further because of the intermediate nature of most individuals in populations B and C in this character (Fig. 2).

The third lineage, *T. fannyi* is separable by its green forecrown. Although a green forecrown also occurs in *T. watertonii* and some forms of *T. furcata* of southcentral Brazil and Bolivia (*baeri*), it is neither as well defined nor as glittering as in *fannyi,* and so the glittering green forecrown in *T. fannyi* may represent a unique character.

A phylogenetic analysis based on biochemical characters is clearly necessary for resolution of these questions for the entire genus. In the meantime, we propose the following taxonomy for the northern representatives of *Thalurania,* based on criteria from biological and phylogenetic species concepts: (1) *Thalurania ridgwayi* Nelson, Ridgway's Woodnymph, western Mexico; (2) *Thalurania colombica* (Bourcier), Violet-crowned Woodnymph, including subspecies *townsendi, venusta* and *colombica* recognized by Peters (1945), Guatemala and Belize south to western Panama, and disjunctly in northwestern interior Colombia (Magdalena Valley and Sierra de Santa Marta area) and adjacent northwestern Venezuela, exclusive of the range of the next form, and (3) *Thalurania fannyi* (De Lattre and Bourcier), Green-crowned Woodnymph, including subspecies *subtropicalis, fannyi, verticeps* and *hypochlora,* from eastern Panama (both slopes of Darién) southward continuously in Cauca Valley, in western Colombia (Choco) to northernmost Ecuador (Pichincha), and in western Ecuador (Provincia del Oro). In need of further study is the taxonomic status of the subspecies *hypochlora* of western Ecuador, as well as populations in the *furcata* complex.

Evolutionary implications.—The *Thalurania* woodnymphs present a fascinating mosaic of plumage characters. Relative stasis alternates with abrupt change as one moves through the range of the genus (Fig. 2). Because male plumages of hummingbirds are probably targets of sexual selection (West-Eberhard 1983), the extreme variation in plumage characters in this group may be a consequence of interactions between sexual selection and genetic drift (e.g., Lande 1980). Studies of female preferences and male characters in abrupt and gradual transition zones in woodnymphs might provide an interesting test case for this body of theory.

Studies of geographic variation in Neotropical birds have documented a recurrent pattern of "leapfrog" geographic variation in which populations at the extremes of a species range are more similar to each other than to intermediate populations (Remsen 1984, Fjeldså 1985). This pattern suggests that peripheral populations have retained ancestral characters, whereas intermediate populations have evolved derived states. In *Thalurania,* much of the geographic variation in plumage coloration can be interpreted as a series of leapfrog patterns. However, further exploration of patterns of plumage evolution in this genus in South America based on phylogenetic analysis would be most rewarding.

The richness and high endemicity of the Chocó area of Colombia and eastern Panama have been noted (e.g., Chapman 1917, Haffer 1974). In other vertebrate groups, the pattern of differentiation between Chocoan humid tropical groups and the adjacent populations from arid tropical western Panama and northern Colombia is usually described as a "broken X," in which the similarity between these latter populations is interrupted with differentiated Chocoan forms (e.g., Dunn 1940, Myers 1972). Woodnymphs fit this pattern perfectly, although only few other avian examples have been described in detail (Chapman 1917, Griscom 1932, Cracraft and Prum 1988).

Conservation status.—To our knowledge, the conservation status of woodnymphs in Middle America is of moderate concern. The Mexican populations are restricted in distribution. The area of their habitat has been reduced in recent decades, but their habitat is still fairly extensive and the woodnymphs are common within the proper forest types. Central American woodnymphs are found only in lowland forest which is increasingly endangered throughout; hence, woodnymph populations, like those of many other species, are endangered along with their habitat.

ACKNOWLEDGMENTS

We received valuable comments and criticism on drafts of the manuscript from G. Barrowclough, J. Bates, D. Willard, S. Hackett, A. Navarro S., T. Parker, III, R. Prum, J. Remsen, T. Sillett, and an anonymous reviewer. G. Barrowclough made his computer program SS-STP available to us. The staff of the Laboratorio Natural de Las Joyas de la Sierra de Manantlán, especially Eduardo Santana, provided valuable advice and collaboration during ATP's field studies in Jalisco. Thanks to our many field companions, especially J. Fitzpatrick, H. Benítez D., S. Baker, and N. Vargas B. for invaluable assistance and enthusiasm. Many thanks to the curators and collections managers of the museums mentioned above for allowing us access to collections under their care.

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APPENDIX I.

A: 1: Mexico, Nayarit, Palapita, 18 km S Jalcocotán (2 specimens). 2: Mexico, Nayarit, 10 km Ejido Las Mesillas (1). 3: Mexico, Jalisco, Pto. Vallarta, 1.6 mi. NE, 1 mi E

Guapinole (1). 4: Mexico, Jalisco, San Sebastian (1). 5: Mexico, Jalisco, El Refugio, Zuchitlán, 1 mi N Chimo Rd. (2). 6: Mexico, Jalisco, La Cumbre, 9 mi SSW Autlán (4). 7: Mexico, Jalisco, Puerto Los Mazos, Sierra de Manantlán (3). 8: Mexico, Colima, Puerto Juárez, La Media Luna; and La Zacatosa (4). *B:* 9: Belize, Toledo District, 7 mi NW San Pedro Columbia (1). 10: Guatemala, Gualán (1). 11: Guatemala, Izabal, Escobas; and Río Zarco (2). 12: Honduras, La Leona, Copán (1). 13: Honduras, Lombardía (1). 14: Honduras, Atlántida, San Alejo, 10 mi W Tela (3). 15: Honduras, Lancetilla (2). 16: Honduras, Las Peñitas (3). 17: Honduras, Yaruca (1). 18: Honduras, Olancho, 5 mi S San Esteban (1). 19: Honduras, Catacombas (6). 20: Honduras, Segovia River (1). 22: Nicaragua, Comarca del Cabo, 20 km SSW Waspam (4). 23: Nicaragua, Eden Mine Hill (6). *C:* 21: Nicaragua, Rió Coco/Wanks River (3). 24: Nicaragua, Zelaya, Cum, 45 km WSW Siuna (1). 25: Nicaragua, Los Sábalos, San Juan River (2). 26: Nicaragua, Savala Mata (5). 27: Nicaragua, Zelaya, El Recreo, 16 km W Rama (8). *D:* 28: Costa Rica, Aquinares (2). 29: Costa Rica, Carrillo (10). 30: Costa Rica, Bonilla (5). 31: Costa Rica, Guayabo (9). *E:* 32: Costa Rica, Barranco Boruca (5). 33: Costa Rica, El General (4). 34: Costa Rica, Jiménez (2). 35: Panama, Prov. Bocas del Toro, Zegla, Terebe River (1). 36: Panama, Almirante (1). *F:* 37: Panama, Veraguas, Rió Calovevora; and Chitra (10). 38: Panama, Gatún (5). *G:* 39: Panama, San Blas, Puerto Obaldia (11). 40: Panama, Perme (4). 41: Panama, Piñas Bay (2). 42: Panama, Mt. Sapo (2). *H:* 43: Colombia, Nariño, Buenavista (5). *I:* 44: Colombia, Huila, San Agustín (8). *J:* 45: Colombia, La Concepción (4). 46: Colombia, San Francisco (4). 47: Colombia, San Miguel (3). 48: Colombia, Santa Marta (4).

COLOR PLATE

The frontispiece painting by Sophie Webb has been made possible by an endowment established by George Miksch Sutton.