

Biogeography, geographical variation, and taxonomy of the hummingbird genera *Eugenes* Gould, 1856, *Sternoclyta* Gould, 1858, and *Hylonomympha* Gould, 1873 (Aves: Trochilidae)

Swen C. Renner and Karl-L. Schuchmann

Biogeografie, geografische Variation und Taxonomie der Kolibrigattungen *Eugenes* Gould, 1856, *Sternoclyta* Gould, 1858, und *Hylonomympha* Gould, 1873 (Aves: Trochilidae)

Nach unseren biogeografischen und morphologischen Daten ist die vormals monotypische Kolibrigattung *Eugenes* als polytypisch, mit zwei distinkten Arten, anzusehen: *Eugenes fulgens* und *Eugenes spectabilis*. Weiterhin begründen wir eine enge Verwandtschaft zwischen *Eugenes* und den monotypischen Gattungen *Sternoclyta* und *Hylonomympha*. Als taxonomische Konsequenz dieser stammesgeschichtlichen Beziehung vereinen wir die beiden letzteren Taxa unter dem älteren Gattungsnamen *Eugenes*. Die polytypische Gattung *Eugenes* umfaßt demnach die Arten *Eugenes fulgens*, *Eugenes spectabilis*, *Eugenes cyanopectus* und *Eugenes macrocerca*. Als Schwestertaxon von *Eugenes* sehen wir *Heliodoxa* an, mit *H. schreibersii* als möglichem Bindeglied zwischen beiden Gattungen.

Key words: Hummingbirds, Trochilinae, *Eugenes*, *Sternoclyta*, *Hylonomympha*, taxonomy, systematics, biogeography, distribution, speciation.

Dr. Swen C. Renner and Prof. Dr. Karl-L. Schuchmann, Alexander Koenig Research Institute and Museum of Zoology, Leibniz Institute for Terrestrial Biodiversity, Research Group: Biology and Phylogeny of Tropical Birds, Adenauerallee 160, D-53113 Bonn, Germany;
e-mail: kl.schuchmann.zfmk@uni-bonn.de

Introduction

Currently the North and Central American hummingbird genus *Eugenes*, Gould 1856 is considered monotypic, comprising two distinct geographical forms *E. fulgens fulgens* Swainson, 1827, southeastern USA to Nicaragua, and *E. fulgens spectabilis* Lawrence, 1867, Costa Rica, Panama. The formerly designated taxa *E. fulgens aureoventris* Van Rossem, 1939, USA southward to the Isthmus of Tehuantepec, Mexico, and *E. fulgens viridiceps* Boucard, 1878, Chiapas, extreme southern Mexico to Nicaragua, are without basis since the suggested phenetic differences are within the geographical variation patterns of the nominate form (Phillips et al. 1964, Schuchmann 1999, this study).

The Venezuelan endemic genera *Sternoclyta* (Gould 1858) and *Hylonomympha* (Gould 1873) are clearly monotypic, no subspecific differentiation is known.

Members of these three medium to large-sized trochilid genera are found in montane humid and dry forests at elevations mainly above 1000 m (Ridgley & Gwynne 1976, Meyer de Schauensee & Phelps 1978, Stiles & Skutch 1989, Howell & Webb 1995, Powers 1996).

The phylogenetic affinities of these taxa, as well as the subspecific status of *Eugenes f. spectabilis*, are still controversially discussed. Based on external morphological characters, Zimmer (1951) presumed a close relationship between *Eugenes* and *Heliodoxa*, while Bleiweiss (1998), based on

DNA hybridization studies, linked *Eugenes* with *Lophornis*, and *Acestura* (now placed in *Chaetocercus*, Schuchmann 1999). A striking similar pattern of the peculiar hind neck cross-over structure of the *Musculus splenius capitis* made Fritsch & Schuchmann (1988) conclude that *Eugenes* is close to the North American genus *Archilochus*. In a more recent systematic treatment (Schuchmann 1999) *Eugenes* was considered a close relative of *Sternoclyta* and *Hylonomympha*, placed next to the South American genus *Heliodoxa*.

The subspecific status of *Eugenes fulgens spectabilis* has occasionally been questioned (e.g., Powers 1996) but maintained in all subsequent systematic treatments.

In this paper, we will examine the phylogenetic relationship of *Eugenes*, *Sternoclyta*, and *Hylonomympha* based on external morphology and biogeographical data, and suggest a new taxonomic status for *E. f. spectabilis*.

Material and Methods

A sample size of 129 museum skins of the three taxa was examined morphologically and morphometrically (*Eugenes fulgens* 50 ♂, 46 ♀, 1 immature; *Sternoclyta cyanopectus* 19 ♂, 6 ♀, 4 immature, 13 unmeasured; *Hylonomympha macrocerca* 3 ♂, 72 unmeasured. Unmeasured specimens were either partially damaged or without geographical information.

For the biogeographical analysis, the coordinates and altitudes (see Appendix, Tab. 1) for each specimen were obtained from maps (Times atlas of the world 1957; ITMB 1999a,b; Instituto Geografico de Mexico) and ornithological gazetteers (Paynter 1982, 1997). Specimens were pooled based on morphological similarities (Vuilleumier 1968). Pools were determined by potential dispersal barriers, such as wide rivers or high mountain ridges (for further methodological details see Heindl & Schuchmann, 1998, Schuchmann et al. 2001). The sampled pools are the basis for Figs. 1, 2, and 3.

Bill length (BL, from tip to proximal end of operculum) and bill width (BW, proximal end of operculum), wing length (W, flattened), and the length of the innermost (R1) and outermost (R5) rectrices of each specimen were measured with a caliper to the nearest 0.1 mm. For pools with more than four adult individuals of one sex, we used the parametric t-test, and for a taxon

comprising more than two pools we used a MANOVA and the Tukeys HSD for unequal n as a post-hoc test (Sachs 1993, Köhler et al. 1996). Significance levels: $p < 0.05$. The statistical analyses were performed with the software programs Statistix 2.0 and Statistica 5.0.

Plumage patterns were compared intra- and inter-specifically according to color differences following Vuilleumier (1968). The non-iridescent and iridescent colors were standardized (capitalized numbers in brackets refer to the Color Guide numbers of Smithe 1975). Iridescent colors were described on a subjective basis. The results were analyzed with PAUP 4.0 (Swafford 1998). The terminology of body and feather areas follows Johnsgard (1997).

Results

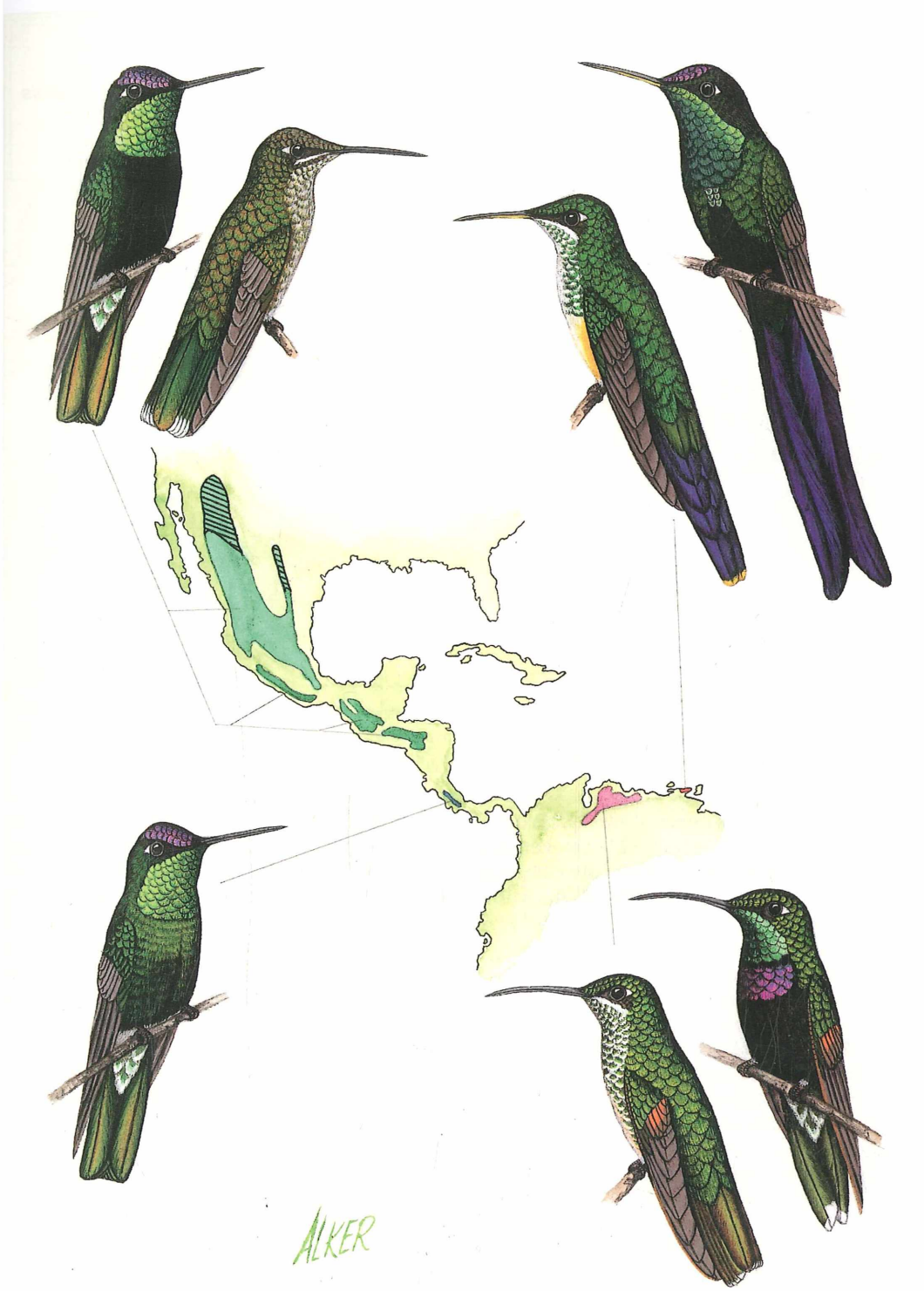
The genera *Eugenes*, *Sternoclyta*, and *Hylonomympha* have several external features in common: blackish underparts, Emerald Green [163] iridescent throat, blue or green iridescent crown in males, and Dark Green [160] upper side. Sexual dimorphism is large. Females exhibit, in addition to Dark Green dorsal parts, a white or gray throat with Lime Green [159] colored disks on each feather's center. They lack iridescent colors on the crown and have only a few disks on their ventral plumage of metallic sheen. Further, females show a characteristic white moustache stripe. Both sexes exhibit a whitish triangular post-ocular spot (for further details see Plate). In all three genera the tips of all rectrices are roundish and widest near the distal end.

The bill of *Eugenes* and *Hylonomympha* is long and straight, whereas in *Sternoclyta cyanopectus* it is slightly curved.

Eugenes fulgens Swainson, 1827

Differing from the general plumage features described above, *E. f. fulgens* exhibits Olive-Green [48] rectrices and Parrot Green [160] undertail coverts with white margins. The male's crown is Ultramarine [270], and feathers on the bill are Jet Black [89]. The abdomen, belly, and lower throat are Jet Black. Females differ in forehead plumage coloration which is Light Drab [119C] with green

Plate. Geographic ranges of *Eugenes fulgens fulgens* (top left: male left, female right), *E. f. spectabilis* (bottom left: male; female not shown, similar to female of *E. f. fulgens*), striped areas indicates breeding range, green areas indicate year-round distribution; *Hylonomympha macrocerca* (right top: female left, male right), distribution range is shown in red; and *Sternoclyta cyanopectus* (bottom right: female left, male right), distribution range shown in lilac. Plate by David Alker.



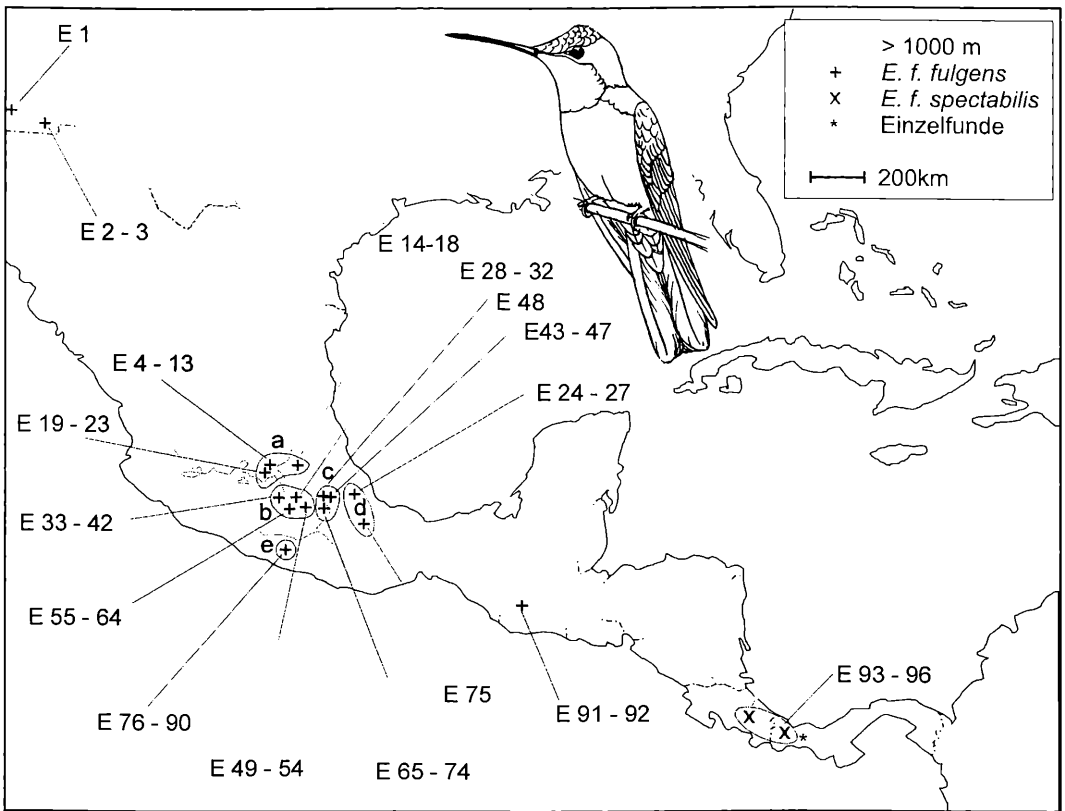


Fig. 1. Geographical distribution of *Eugenes fulgens fulgens* (pools E1-E92) and *Eugenes fulgens spectabilis* (pools E93-96). All data obtained from skins, * indicates a single specimen.

parts on each feather's center. Ventral parts of the female are Smoke Gray [45] with Smoke Gray [46] disks on throat and chin. The nominate form is somewhat smaller than *E. f. spectabilis*, with a body mass of 5.1-9.0 g and a total length of 11.0-12.0 cm in female and 12.0-14.0 cm in male (Howell & Webb 1995, Ridgely & Gwynne 1976, Stiles & Skutch 1989).

Males of *E. f. spectabilis* appear ventrally completely Lime Green [159] because the black parts of the feathers are fringed Lime Green. Females *E. f. spectabilis* exhibit Lime Green instead of Smoke Gray [46] disks on throat, belly, and abdomen.

E. f. fulgens is found from the southwestern United States south to western Nicaragua (see Plate and Fig. 1), at elevations mainly between 1500 and 3300 m, with records as low as 600 m. *E. f. fulgens* occurs in pine-oak forests, and is most abundant at forest edges and clearings. Subpopulations from eastern and western Sierra Madre

of northern Mexico are migratory and only abundant in this region during the breeding season (Powers 1996). During migration they are also found at the periphery of deserts and around farmland (Howell & Webb 1995). The non-migratory (Powers 1996) subspecies *E. f. spectabilis* is confined to the Central Cordillera of Costa Rica and to western Panama. It rarely occurs below 1500 m (see Fig. 1 and Appendix).

E. f. spectabilis covers a body mass range from 8.0-10.0 g and a total length from 12.0-14.0 cm.

The subspecific differences are obvious, with the trend that *E. f. spectabilis* is larger in most characteristics, e.g., bill, tail fork deeper (see Table 1). The wings of *fulgens* and *spectabilis* are similar in length for females, but male wings average significantly longer in the latter subspecies.

Variation in plumage characters. The general features of plumage coloration are shown in the

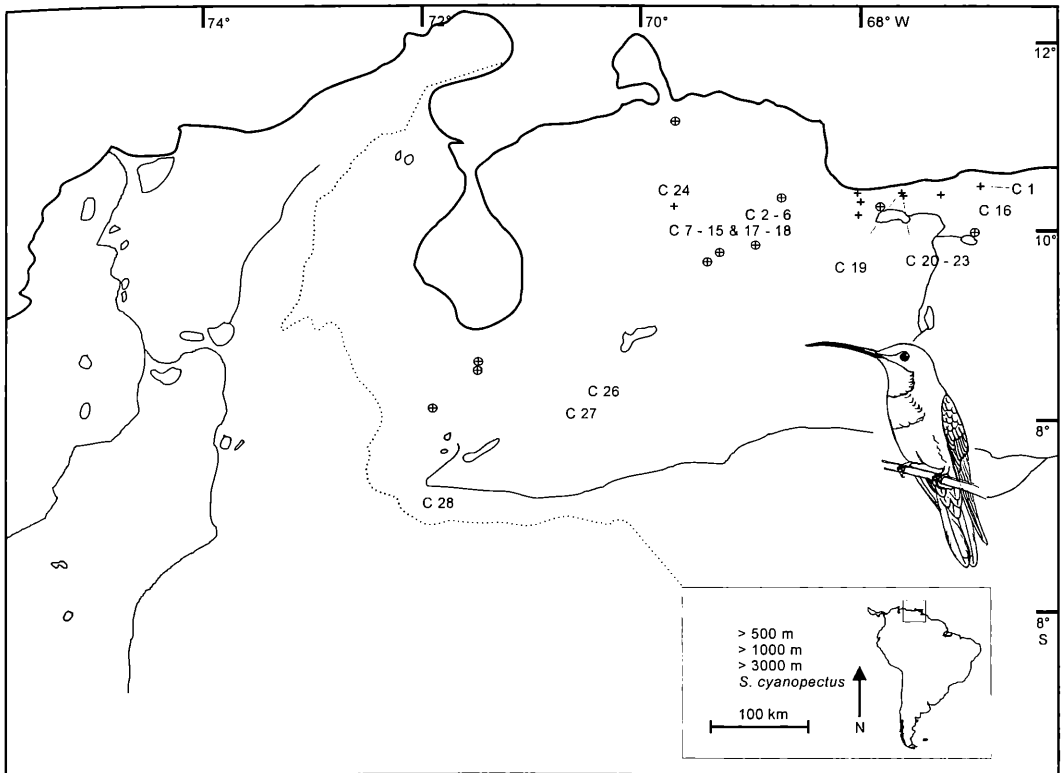


Fig. 2. Geographical distribution of *Sternoclyta cyanopectus* (pools C1-C28). Data obtained from skins and literature (⊕) (Sánchez-Osés 1995).

Plate. Within the subpopulations of *E. f. fulgens* and *E. f. spectabilis* there are no visible differences due to geographical variation. Marked phenetic differences occur only between the two taxa: for example, the feathers of chest, breast and abdomen of male *E. f. fulgens* are completely black in contrast to those of *E. f. spectabilis*, which appear green. In fact the feathers of the latter subspecies are black at the proximal end with visible green glimmer at the fringes of each feather. Female *E. f. spectabilis* are in general appearance more yellow-green than female *E. f. fulgens* with rectrices tipped less white.

The two male specimens from Guatemala (F 91 and F 92, Fig. 1) show no plumage variation in comparison to the individuals from the northern taxon *E. f. fulgens*.

Variation in mensural characters. The mean and standard deviation, sample size, and range of all morphometric parameters for both subspecies are given in Table 1.

We observed no geographical variation in mensural characters within both *Eugenes* subspecies, except for pool A of *E. f. fulgens*. Males of this pool differ significantly from those in pool C and E (Fig. 1). Male bills are longer while wings are shorter and the tail fork is deeper for males in pool A as opposed to other pools of *E. f. fulgens*. The differences between *E. f. fulgens* and *E. f. spectabilis* are much more prominent. Bill and wing length of *E. f. fulgens* are significantly shorter in pools B, C, D, and E, than those of *E. f. spectabilis*, i.e., pool F ($p=0.01$). The bill width is significantly smaller in *E. f. fulgens* ($p=0.01$).

The two male specimens from Guatemala (F 91 and F 92, Fig. 1) are within the range of the individuals from *E. f. fulgens*, and hence are different from the sister taxon *E. f. spectabilis*.

Sternoclyta cyanopectus Gould, 1846

This species is different from both *Eugenes* and *Hylonomympha* in the crown and throat patch of males: the crown is Parrot Green [160] in *Sterno-*

clyta while it is Ultramarine [270] in *Eugenes* and *Hylonompha*. Furthermore *Sternoclyta* is Parrot Green [160] on its chin and throat and also Ultramarine [270] on its breast and chest, while *Eugenes* and *Hylonompha* are iridescent Emerald Green [163] respectively. Its belly and abdomen are Jet Black [89]. Upper tail coverts and rectrices are Olive-Green [48], the outermost two, or sometimes three, with a white tip; the innermost with Tawny [38] tips. Female ventral parts are white with Parrot Green [260] iridescent disks, the abdomen is Cinnamon [39].

First described by John Gould as *Trochilus cyanopectus* in 1846, this species averages 11.5 cm in length varies in body mass from 8.4-10.3 g (Dunning 1993, Meyer de Schauensee & Phelps 1978). It is abundant in the montane forests of the Cordillera de Mérida and the Coastal Cordillera of Venezuela (Sánchez-Osés 1995, Stattersfield *et al.* 1998). For distributional details see Plate and Fig. 2.

The bill of *S. cyanopectus* is elongated, somewhat bulky, and slightly downward bent. Immature males are similar to adult males, but are more gray-green on their belly. Females lack the black ventral colors (see Plate).

Plumage patterns. There is only slight evidence for geographical variation in plumage patterns: males from the southern parts of the Cordillera de Mérida exhibit more white on the tips of the rectrices than those in the Coastal Cordillera.

Mensural characteristics. Most specimens examined were from the coastal mountains of northern Venezuela except for three males from the southern part of their range in the Cordillera de Mérida. There is no basis for statistical evaluation of the mensural data to test the plumage differences found for the southern population ($n=3$, required for t-test: $n>4$). Nevertheless, the values found for these specimens provide no evidence of mensural differences, because they fall within the range of the sample of 14 males from the Coastal Cordillera. These 14 specimens are separated into two pools (α and β , Fig. 1), which show no significant differences for all examined mensural characters.

Hylonompha macrocerca Gould 1873

This species, endemic to the Paría-Peninsula of northeastern Venezuela at elevations of 900-

Tab. 1. Morphometric measurements of *Sternoclyta*, *Eugenes*, and *Hylonompha*, showing mean, SD, sample size (in brackets), and range. All morphometric data in mm, body mass in g.

Taxon	Sex	Bill length	Bill width	Wing length	Rectrix 1	Rectrix 5	Body mass
<i>Eugenes fulgens fulgens</i>	♂	31.4±1.56 (44)	4.4±0.30 (44)	72.5±2.67 (43)	38.1±1.17 (41)	44.4±2.45 (41)	5.9-8.5
		27.4-34.8	3.9-5.7	66.5-77.0	36.3-40.4	38.9-47.7	
	♀	32.9±1.50 (46)	4.5±0.31 (46)	70.7±2.49 (46)	38.1±1.40 (46)	41.5±2.14 (46)	5.1-9.0
		28.9-35.3	3.6-5.2	63.0-75.5	35.5-41.6	38.1-47.1	
<i>Eugenes fulgens spectabilis</i>	♂	35.5±1.15 (5)	4.9±0.27 (5)	78.2±1.79 (5)	39.8±1.78 (3)	47.2±1.47 (4)	10.0
		33.9-36.8	4.6-5.2	75.5-80.5	38.4-41.8	45.2-48.3	
	♀	-	-	-	-	-	
<i>Sternoclyta cyanopectus</i>	♂	33.7±1.06 (18)	5.3±0.29 (18)	67.9±1.39 (19)	34.9±1.22 (16)	42.2±1.27 (17)	
		31.7-36.2	4.7-5.8	65.0-70.0	33.3-38.4	40.0-44.7	
	♀	35.6±1.12 (4)	5.5±0.17 (4)	64.8±1.44 (5)	34.7±1.25 (5)	36.6±0.62 (5)	-
		34.1-36.8	5.3-5.7	62.5-66.5	33.4-36.8	35.8-37.2	
<i>Hylonompha macrocerca</i>	♂	26.9±0.69 (3)	4.9±0.07 (2)	66.1±1.34 (3)	23.4 (1)	99.5 (1)	-
	♀	26.5-27.7	4.8-4.9	65.1-72.0	-	-	-

1200 m, varies from 11.5-19.0 cm in body length (Meyer de Schauensee & Phelps 1978) depending on age and sex. Adult males exhibit a deeply-forked tail that increases overall body length considerably.

In males, the belly, under tail coverts, and rectrices are Jet Black [89] and the throat patch is Emerald Green [163]. The chin is spotted with white. The crown is Ultramarine [270], while the occiput is Jet Black. The dorsal parts are Parrot Green [260]. The female chin is white with green disks, the throat white, and the belly cinnamon.

Variation in mensural and plumage patterns. There is no indication of geographical variation in plumage or mensural characteristics.

Interspecific comparison. Compared with *Eugenes* and *Hylonomympha*, *Sternoclyta* has a broader and, in males, a longer bill. This is obvious when looking frontally at the bill with its bulky proximate appearance. Furthermore, the wing is shorter on average in *S. cyanopectus* than in the other two genera. The mean difference between the wing length of *H. macrocerca* and *S. cyanopectus* is negligible (1.5 mm). Compared to *E. f. spectabilis* and *E. f. fulgens* the differences in *Sternoclyta* amounts to 10 mm and 4 mm respectively. In *Eugenes* and *Sternoclyta* the depth of the tail fork is similar (6.4-7.5 mm), as opposed to *Hylonomympha* which shows a depth of more than 75.0 mm in males.

Discussion

***Eugenes* Gould, 1856.** The range of *E. f. fulgens* covers much of Central America, but its actual distribution is non-homogenous and rather patchy (see Plate and Fig. 1). Both taxa of *Eugenes* have a disjunct allopatric distribution, and there is no evidence of genetic exchange between the populations (Powers 1995, Schuchmann 1999).

Since described by Swainson in 1827 as *Trochilus fulgens*, four subspecies have been listed. Lawrence (1867) described the characters for the taxon *spectabilis*. Boucard (1878) named a third subspecies, *viridiceps*, distinguished by “more violaceous crowns and less blackish underparts of the males”. Most authors doubt the validity of this taxon (e.g., Zimmer 1951, Schuchmann 1999), and we found no characters supporting the given features. Van Rossem (1939) described

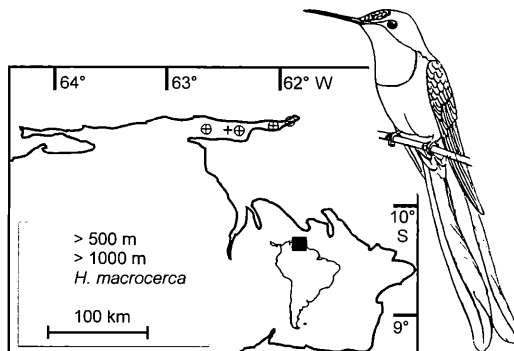


Fig. 3. Geographical distribution of *Hylonomympha macrocerca*, endemic to Paría Peninsula, Venezuela. + represents specimen based data, ⊕ indicates information obtained from the literature (Sánchez-Oses 1995) and pers. communication (M. Lentino, Phelps Collection, Caracas, Venezuela).

a fourth subspecies, *aureoviridis*, based on “yellowish green instead of bluish green or emerald green” which is a very uncertain characterization and by no means visible if considering the iridescent character of the plumage. We conclude that available data support recognition of only two taxa within the group: *fulgens* and *spectabilis*.

***Sternoclyta cyanopectus* Gould, 1846.** The 29 specimens in our sample for this taxon show a considerable variation in tail coloration: the three southernmost specimens show much more white on the tail tips than the northern representatives. This could indicate existence of a barrier for gene flow somewhere in the northern parts of the Cordillera de Mérida. Coastal representatives show white tail tips barely 5 % of rectrix’s surface, while the three southern males show as much as 10 %. Additionally, the latter specimens are all found at altitudes much higher (> 1700 m, montane) than those in the Costal Cordillera (< 1040 m, submontane). Again there is no evidence for a linkage of the two subpopulations between the Costal Cordillera and the Cordillera de Mérida (Meyer de Schauensee & Phelps 1978, Sánchez-Oses 1995). The different habitats of the subpopulations indicate the possibility of an ecological vicariance event, with subpopulations adapted to montane and submontane habitats respectively.

Schuchmann (1999) does not mention or discuss the distribution of *S. cyanopectus* in the provinces of Lara and Falcón, Venezuela, but presumes a distribution in the Cordillera de Trujillo.

However, Meyer de Schauensee & Phelps (1978) and Sánchez-Osés (1995) provide information that there are several localities for the species in the above-mentioned provinces. There are no specimens from the Cordillera de Trujillo north of Mérida in scientific collections. A revised map of the distribution of this species, based on all available data, is presented in the Plate.

The amount of geographical variation and evident gap in the distribution within the population of *S. cyanopectus* do not provide sufficient information at present to propose a recognition of subspecies. Based on the available information and the little geographical distance involved between the separate ranges, the existence of a gene-flow barrier seems doubtful in this "restricted-range species" (Stattersfield et al. 1998). The relatively low numbers of specimens available world-wide in scientific collections may indicate that this species has a low abundance, particularly in the southern range of the population. In contrast, the density of the collecting localities is one of the highest in Venezuela (cf. Paynter 1982). If current rates of deforestation and agricultural expansion within the Venezuelan Andes continue, the threat to *Sternoclyta cyanopectus* will likely become severe (compare Stattersfield et al. 1998).

***Hylonompha macrocerca* Gould 1873.** The distribution of *H. macrocerca* is restricted to a small area (c. 100 km at its longest), and no barriers to gene flow are likely. The three measured males, and additionally all specimens from the Colección Ornitológica Phelps, Caracas, show no visible differences in plumage coloration (Sánchez-Osés, pers. com.).

The small known range of this species within the cloud forests of the Paría-Peninsula is a major reason for its recognition as a "critically threatened species" (Collar et al. 1992, Stattersfield et al. 1998). The principal threat is posed by deforestation and resulting agricultural encroachment by humans visiting and colonizing the Paría-Peninsular National Park (Collar et al. 1992).

Interspecific comparison and related taxa. Differences in interspecific plumage patterns are obvious between all species. Several features are shared by all four taxa. For instance, the males' throats are glittering dark green; all exhibit black portions on the ventral parts; and all show an iridescent forehead, mostly violet-blue. The females of all members of this group have green

and white disk-patterns on their ventral body parts. These patterns are very similar to the presumably next-most closely-related taxon *Heliodoxa*. *Heliodoxa schreibersii*, an Amazonian lowland species in eastern Ecuador, Peru, and western Brazil, shows the same plumage coloration patterns: black ventral parts with dark green iridescent lower throat, green glittering forehead, green iridescent forehead, and violet-blue upper throat. The latter two body parts are of the same color and shape as in males of *S. cyanopectus*. These two species are also similar in body mass and shape.

In fact, *H. schreibersii* is sexually monomorphic, which could indicate a common ancestor between *Heliodoxa* and the *Eugenes-Sternoclyta-Hylonompha*-complex with *Heliodoxa schreibersii* evolving during the early radiation process of the genus *Heliodoxa*.

Speciation process. Based on our analysis of the external morphology and geographical distribution of these taxa, we present the following hypothesis of speciation in the *Eugenes-Hylonompha-Sternoclyta*-complex: The common ancestor, a proto-*Heliodoxa*, was isolated in a refuge (sensu Haffer 1974, Mayr & O'Hara 1986, Oren 1982; cf. disagreement about refuge theories by Endler 1982, Nores 1999, and others) in the western parts of the Amazon basin, most likely in eastern Ecuador. The ancestor gave rise to *Heliodoxa schreibersii* and to a founder population of the *Eugenes-Sternoclyta-Hylonompha*-complex. While *H. schreibersii* remained in the Amazonian lowlands of eastern Ecuador and Peru, the latter entered the higher elevations above 1000 m of the Andes (see Liu & Colinvaux 1985). During the elevational shifts in habitat distribution caused by Pleistocene climatic changes (Haffer 1974) a founder population of the *Eugenes-Sternoclyta-Hylonompha*-complex spread out across the northern parts of South America, covering the Andes between Ecuador and Venezuela. Initial climatic shifts caused the population to break into subpopulations, one in the northern Andes, and one in the southern and western Cordillera of Ecuador and Colombia. *S. cyanopectus* evolved from the population in Venezuela while the second population developed into the ancestor of *Eugenes* and *Hylonompha*.

The ancestor of *Eugenes* and *Hylonompha* could have invaded the Paría-Peninsula during pluvial periods. At the beginning of the interpluvial period, one part of the population stayed at the

Venezuelian Paría-Peninsula. Some individuals adapted to the specific habitat there, tracking the up-and-down shifts of montane forests during periods of climatic change, while a second population stayed in the Andes, ultimately losing contact with the peninsular population during a warming period.

Due to adaptative evolutionary changes and to geographical distance, there was no possibility for the individuals of the separated populations to exchange genes.

Further climatic cycles gave rise to *E. fulgens* in Central America and North America. Based on our speciation hypothesis of the *Eugenes-Sternoclyta-Hylonomympha*-complex three pluvial and interpluvial periods may have been involved.

Fig. 4 shows a phylogenetic tree determined by PAUP. The distant matrix is provided in Table 3 using the trochiline taxon *Coeligena* as an outgroup. The cladogram is based on the analysis of plumage characters (see Table 2 for details).

We derived this configuration using *Coeligena coeligena* and *C. iris* as outgroup taxa, which had in fact no influence on the tree. Following Forey et al. (1992) we selected the outgroup taxa according to their resemblance to our taxon group in only one of the involved characters. *Heliodoxa* species were too similar to use them as an outgroup. *H. schreibersii* was tested as a possible sister taxon of the *Eugenes-Sternoclyta-Hylonomympha*-complex (see Fig. 4). The configuration within the *Eugenes-Sternoclyta-Hylonomympha*-complex was constant, independent of the outgroup, and whether *Heliodoxa schreibersii* was included or not. The probability that *Eugenes fulgens fulgens*

and *Eugenes fulgens spectabilis* are sister taxa is 90.44 %; the probability, that *Hylonomympha* is the sister group of *Eugenes* is 86.00 %; and the probability that both taxa are the sister group of *Sternoclyta* is 76.45 %.

Taxonomy. Both taxa of *Eugenes fulgens* show distinct plumage patterns and no evidence of intergradation, indicating that there is no genetic exchange between the population patches of *E. f. fulgens* and *E. f. spectabilis*. Therefore, the taxa should be treated as species, because of their clear disjunct distribution: *Eugenes fulgens* for the northern subpopulations and *Eugenes spectabilis* for the southern population in Costa Rica and Panama. Both Ridgley & Gwynne (1976) and Powers (1996) presume the species status of these taxa, but do not provide data or references supporting this argument.

The current distribution pattern and similarities in plumage coloration and habitat support placement of the related monotypic genera, *Hylonomympha macrocerca* and *Sternoclyta cyanopectus* within *Eugenes* as *E. macrocerca* and *E. cyanopectus* respectively. *Eugenes* has priority over *Hylonomympha* and *Sternoclyta*, because of the earlier description of this genus.

Systematics. Anatomically *Eugenes fulgens* shows affinities to the North American genus *Archilochus* (Fritsch & Schuchmann 1988), but in terms of ethology, plumage patterns, and body size, *Eugenes* is much closer to *Heliodoxa* (Zimmer 1951, Schuchmann 1999, present paper). Fritsch & Schuchmann (1988) did not describe the *Muscus-*

Tab. 2. Character states and matrix of the morphological data used for PAUP. A: ventral plumage with black parts (0: no, 1: yes, partly), B: crown violet-blue (0: no, 1: yes), C: ♂ exhibit disks on ventral parts (0: no, 1: yes, 2: fringes covering disks), D: ♀ with disks on ventral plumage (0: green disks on white, 1: gray disks on white, 2: ♀ like ♂, i.e., unicolor), E: shape of throat patch (0: circular, 1: kidney shaped, 2: intergrated in throat), F: brown plumage parts on ventral side (0: no, 1: yes), G: brown plumage parts on dorsal side (0: no, 1: yes), H: multi-color iridescent crown (0: yes, 1: no, single color), I: throat patch violet and kidney shaped (0: no, 1: yes), J: females disks pattern (0: no discs, 1: disks with white basic color, 2: disks without white basic color).

	A	B	C	D	E	F	G	H	I	J
<i>Coeligena iris</i>	0	0	0	2	1	1	1	0	1	0
<i>Heliodoxa s. schreibersii</i>	1	0	0	3	1	0	0	1	1	1
<i>Heliodoxa s. whitelyana</i>	1	0	0	3	1	0	0	1	1	1
<i>Hylonomympha macrocerca</i>	1	1	0	0	2	0	0	1	0	0
<i>Sternoclyta cyanopectus</i>	1	0	0	0	1	0	0	1	0	0
<i>Eugenes fulgens fulgens</i>	1	1	1	1	2	0	0	1	0	2
<i>Eugenes fulgens spectabilis</i>	1	1	2	1	2	0	0	1	0	2

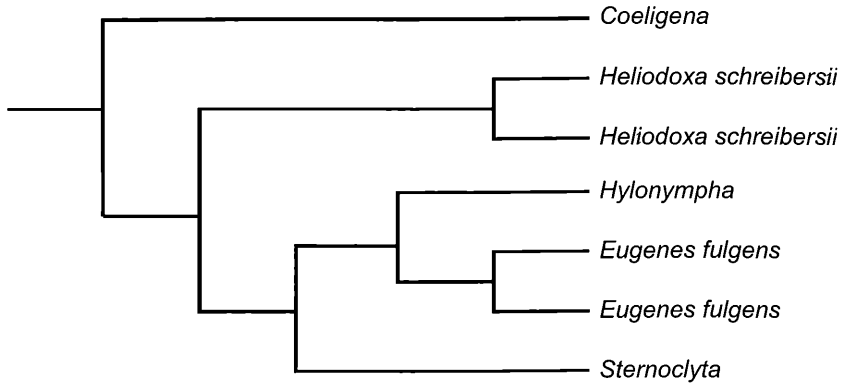


Fig. 4. Cladogram resulted from PAUP analysis (Swafford 1998), showing phylogenetical relationships of *Heliodoxa*, *Hylonympha*, *Eugenes*, and *Sternoclyta* as reconstructed from plumage color characteristics. Outgroup: *Coeligena iris*. For distance matrix see Table 3.

lus splenius capitis for any *Heliodoxa* species, due to lack of material from this genus. So further research is necessary to establish the relative state of this important phylogenetic character in these groups.

Bleiweiss (1998) proposed *Eugenes* as a sister group of *Lophornis* and *Acestura*, while adding *Heliodoxa* to *Coeligena*. However, there are significant morphological and ecological dissimilarities between *Eugenes*, *Lophornis*, and *Acestura*. For instance the overall shape, body size, the lancet shape of the two outermost rectrices of *Acestura*, and the lateral elongated feathers of the crown and throat in *Lophornis* are strikingly different from those of *Eugenes*. Based on similarities of plumage patterns, feather shapes and habitat type, it is much more likely that *Eugenes* belongs close to *Heliodoxa*, as proposed by Zimmer (1951). Zimmer (1951) suggested, that *Eugenes* was related to or even constituted a member of the South American genus *Heliodoxa*, which has species occurring in the Andes and Amazonian lowlands. Some species, like *Heliodoxa schreibersii* as out-

lined above, show comparable morphometric plumage patterns, e.g., the black ventral parts, iridescent green throat, and bulging feathers covering the operculum.

Bleiweiss' studies (in litt.) were based exclusively on molecular data (DNA-hybridisation), which can be misleading in the absence of morphological, ecological, and biogeographical data (compare Lee 2000, Schuchmann 2000). As shown above the molecular data in this case provides information that is completely contrary to other available data.

A large number of genetic changes are required to account for the considerable difference between *Eugenes*, *Acestura*, and *Lophornis*, e.g., (1) smaller body size, (2) change from rounded into lancet shaped outer most rectrices, and (3) lateral feather puffs. These genetic changes require many more genetic modifications than the obvious similarities between *Eugenes* and *Heliodoxa* indicate. Applying the principle of parsimony, our proposed model of speciation is much more likely. Additionally the biogeographic relation-

Tab. 3. Distance matrix. For further explanations see text.

	1	2	3	4	5	6	7
Outgroup	–	0.46154	0.46154	0.61538	0.46154	0.76923	0.76923
<i>Heliodoxa s. schreibersii</i>	6		0.00000	0.38462	0.23077	0.46154	0.46154
<i>Heliodoxa s. whitelyana</i>	6	0	–	0.38462	0.23077	0.46154	0.46154
<i>Hylonympha macrocerca</i>	8	5	5		0.15385	0.23077	0.23077
<i>Sternoclyta cyanopectus</i>	6	3	3	2		0.38462	0.38462
<i>Eugenes fulgens fulgens</i>	10	6	6	3	5	–	0.07692
<i>Eugenes fulgens spectabilis</i>	10	6	6	3	5	1	

ship is much simpler for *Eugenes* and *Heliodoxa*, i.e., an intrusion from the northern South American Andes is much more likely than differentiation without allopatry in Central America, which would be the case if *Eugenes* were a sister group of *Acestura* and *Lophornis*.

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Summary

We conclude that the two currently recognized subspecies of *Eugenes fulgens*, should be recognized as full species within that genus: *E. fulgens* and *E. spectabilis*. Biogeography and morphology further support merge of the monotypic genera *Sternoclyta* and *Hylonympha* into the genus *Eugenes*, whose closest sister taxon is most likely the genus *Heliodoxa* of which *H. schreibersii* is the closest relative.

Resumen

Concluimos que las dos sub-especies de *Eugenes fulgens* actualmente reconocidas, deberían ser consideradas como especies completas dentro del género: *E. fulgens* and *E. spectabilis*. Los estudios biogeográficos y morfológicos también apoyan la unión de los géneros monotípicos *Hylonympha* y *Sternoclyta* al género *Eugenes*, cuyo taxón hermano es probablemente el género *Heliodoxa*, del cual *H. schreibersii* es el grupo mas cercano.

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Appendix

Localities of study specimens and additional records from literature, listed from north to south (see Figs 1, 2, and 3).

Eugenes fulgens fulgens: Tucson, USA, 600 m, 32°15'N, 110°57'W; Portal, USA, 1500 m, 31°55'N, 109°09'W; Landa de Matamoros, Mexico, 1000 m, 21°10'N, 99°25'W; Tlanchinol, Mexico, 1550 m, 21°00'N, 98°40'W; El Deramadero, Mexico, 1200 m, 20°55'N, 99°55'W; Teocelo, Mexico, 19°20'N, 97°05'W; Mexico D. F., Mexico, 2720 m (labels indicate an elevation of 2200 m), 19°20'N, 97°05'W; Toluca, Mexico, 2500 m, 19°20'N, 99°40'W; Volcano Malintec, Mexico, 2760 m (labels indicate an elevation of 3270 m), 19°15'N, 98°00'W; Tlaxcata, Mexico, 2760 m, 19°15'N, 98°10'W; Boca del Monte, 1000 m, 19°10'N, 98°50'W; Morelos, Mexico, 2430 m, 19°15'N, 99°15'W; Puebla, Mexico, 2500 m, 19°13'N, 98°10'W; Teotetlan, Mexico, 1770 m, 18°06'N, 96°58'W; Chilpancingo, Mexico, 2200 m (labels indicate an elevation between 2200 m and 2500 m), 17°30'N, 99°30'W; Quetzaltenango, Guatemala, 1450 m, 14°50'N, 91°30'W.

Eugenes fulgens spectabilis: Cerro de la Muerta, Costa Rica, 3100 m, 09°33'N, 83°40'W; Chiriqui, Panama, 2500 m, 08°49'N, 82°38'W.

Sternoclyta cyanopectus: Caracas, Venezuela, 917 m, 10°30'N, 66°55'W; Puerto Cabello, Venezuela, 0 m, 10°28'N, 68°01'W; San Esteban, Venezuela, 200 m, 10°26'N, 68°01'W; Las Auguas, Venezuela, 200 m, 10°26'N, 68°01'W; Colima Tovar, Venezuela, 1900 m, 10°25'N, 67°17'W; Chiquita, Venezuela, 300 m, 10°24'W, 68°00'W; Las Quiguas, Venezuela, 650 m, 10°24'W, 68°00'W; Rancho Grande, Venezuela, 1040 m, 10°22'N, 67°41'W; Valencia, Venezuela, 1700 m, 10°20'N, 68°00'W; Monte Bacarito, Venezuela, 500 m, 10°20'N, 69°41'W; Cerro Golfo Triste, Venezuela, 1000 m, 10°00'N, 67°01'W; Macachies, Venezuela, 2977 m, 08°45'N, 70°55'W; Mérida, Venezuela, 1641 m, 08°36'N, 72°14'W; Tochiro, Venezuela, 1700 m, 07°46'N, 72°14'W.

Hylonompha macrocerca: Paría-Peninsula, Venezuela, 900 m, 10°40'N, 62°30'W (Sánchez-Osés (1995): Cerro Azul, Venezuela, 920 m, 10°40'N, 61°56'W; Cerro Terón de Azucar, Venezuela, 10°40'N, 62°30'W; Cerro Humo, 10°40'N, 62°30'W).

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