ORNITOLOGIA NEOTROPICAL 22: 25–38, 2011
© The Neotropical Ornithological Society

TAXONOMIC REVIEW AND PHYLOGENY OF THE HUMMINGBIRD GENUS *TOPAZA* GRAY, 1840 USING PLUMAGE COLOR SPECTRAL INFORMATION

Angela Schmitz-Ornés[1,2] & Karl-L. Schuchmann[1]

[1]Alexander Koenig Research Institute and Museum of Zoology, Leibniz Institute for Biodiversity of Animals, Adenauerallee 160, D-53113 Bonn, Germany.
E-mail: kl.schuchmann.zfmk@uni-bonn.de

[2]Current address: Vogelwarte Hiddensee, Zoological Institute and Museum, University of Greifswald, Soldmannstraße 23, D-17489 Greifswald, Germany.
E-Mail: angela.schmitz@uni-greifswald.de

Resumen. – **Revisión taxonómica y filogenética del género *Topaza* GRAY, 1840 utilizando información espectral de la coloración del plumaje.** – Utilizamos la información espectral del color para determinar la variación geográfica en la coloración del plumaje en colibríes del género *Topaza* GRAY, 1840. Realizamos una revisión de su situación taxonómica actual utilizando análisis de componentes principales y análisis de función discriminante. Luego de la aplicación del método de codificación generalizada de frecuencias para convertir información espectral contínua en caracteres discretos, realizamos un análisis filogenético del género para aclarar controversias taxonómicas e identificaciones erradas. También discutimos la situación específica de la subespecie *Topaza pella pamprepta*. Los resultados del presente estudio indican que la variación contínua dentro de *Topaza* parece ser insuficiente para separar el grupo en dos especies. De esta manera, se considera al género *Topaza* como monotípico, conteniendo cuatro subespecies: *T. pella pella*, *T. pella microrhyncha*, *T. pella amaruni* y *T. pella pyra*.

Abstract. – We used color spectral data to determine the geographical variation of the plumage coloration in the hummingbird genus *Topaza* GRAY, 1840. We made a revision of its current taxonomy using principal component analysis and discriminant function analysis. After applying the generalized frequency coding approach to convert continuous spectral information to discrete characters, we conducted a phylogenetic analysis to clarify taxonomic controversies and misidentifications within the genus. We also discussed the specific situation of the subspecies *Topaza pella pamprepta*. The results of the present study indicate that the continuous variation within *Topaza* seems to be insufficient to warrant a split into two species. The genus *Topaza* is therefore considered monotypic with four subspecies: *T. pella pella*, *T. pella microrhyncha*, *T. pella amaruni*, and *T. pella pyra*. *Accepted 21 January 2011*.

Key words: *Topaza*, Trochilidae, taxonomy, phylogeny, color spectra, spectrophotometry.

INTRODUCTION

The hummingbird genus *Topaza* has long been considered among the most brilliant hummingbirds due to its conspicuous coloration (Greenewalt 1960). They are large hummingbirds (c. 10 g) and occur in lowland forests of northern South America, where they are frequently found in the canopy and along gallery forests near river banks and creeks (Schuchmann 1999). The oldest species today allocated to *Topaza* was described by Linnaeus in 1758 as *Trochilus pella* based on an individual that was collected in Suriname.

In 1840, the name *Topaza* was introduced by G. R. Gray (1840) and then adopted by Simon (1921). The taxonomy of the genus *Topaza* is currently under controversial discussion and needs to be elucidated and clarified (see Peters 1945, Schuchmann 1999, Hu *et al.* 2000, Dickinson 2003). Based, among other characters, on plumage color variation, some authors recognize two species within this genus (Peters 1945, Hu *et al.* 2000), the Crimson Topaz *Topaza pella* and the Fiery Topaz *T. pyra* Gould, 1846. The latter has been separated on the basis of the extended blackish violet on the neck, glittering orange-red on the underparts, and bronze-green on the central rectrices of males. Females also show minor color differences, mainly on the blackish violet tail with outer tail feathers having cinnamon outer webs (see Hu *et al.* 2000 for a table with color-based diagnostic characters of both groups). However, Schuchmann (1999) pointed out that these differences only indicate geographical variation at subspecies level, and that some members of the nominate race also show the glittering orange belly. *Topaza pella* has been divided into three subspecies: *T. pella pella* Linnaeus, 1758, *T. pella smaragdula* Bosc, 1872, and *T. pella microrhyncha* Butler, 1926, the latter being the smallest of all taxa with a smaller bill and a reddish tinge on the throat. Similarly, two subspecies have been recognized in *Topaza pyra*, *T. p. pyra* and *T. p. amaruni*, plus an undetermined subspecies suggested by Hu *et al.* (2000, and see Dickinson 2003). According to Hu *et al.* (2000), *T. p. amaruni* differs from the nominate subspecies in having more black in the tibial feathering.

To the contrary, Schuchmann (1999) considered *Topaza* as a monotypic genus. He found that although there are some distinctions in habits, the color difference is only a clinal variation that would neither allow nor warrant a taxonomic differentiation at the species level.

In this study we made a revision of the current taxonomy of the genus, taking into account an integral and more objective view of plumage coloration based on the color reflections of each body part. We then conducted a phylogenetic analysis employing color spectral data in parsimony phylogenetic analyses (Schmitz-Ornés & Haase 2009).

METHODS

We analyzed the geographical variation of plumage coloration following the methodologies introduced by Schmitz-Ornés (2006). Plumage color data from voucher specimens of two hummingbird genera, *Topaza* (n = 177) and *Florisuga* (n = 21) were obtained from several bird collections in Europe and the Americas (see Acknowledgments). We also collected standard morphological data of *Topaza* (bill length, wing length, and rectrices 1, 2, and 5). The genus *Florisuga* was used as an outgroup in the phylogenetic analysis due to its identification as sister taxon of *Topaza* (McGuire *et al.* 2007). We preliminarily classified individuals of *Topaza* according to geographical location following three of the published taxonomies (Peters 1945, Schuchmann 1999, Hu *et al.* 2000) (Fig. 1):

1. Peters (1945) included two species in the genus *Topaza*: *T. pyra* in eastern Ecuador and the Rio Negro region of Brazil, and *T. pella* with four subspecies, *T. p. pella* in Guyana and Suriname; *T. p. smaragdula* in French Guiana; *T. p. microrhyncha* from the south bank of the lower Amazon near Belem; and *T. p. pamprepta* found only in the region of Suno, Rio Napo in Ecuador. Regarding *T. p. smaragdula*, he includes a question mark in its description expressing doubts of its validity.

2. Schuchmann merged Peters's *T. pyra* as a subspecies in *Topaza pella* (*T. pella pyra*) and recognized the other three subspecies: *T. pella pella*, *T. p. microrhyncha*, and *T. p. pamprepta*. However, his *T. pella pella* includes

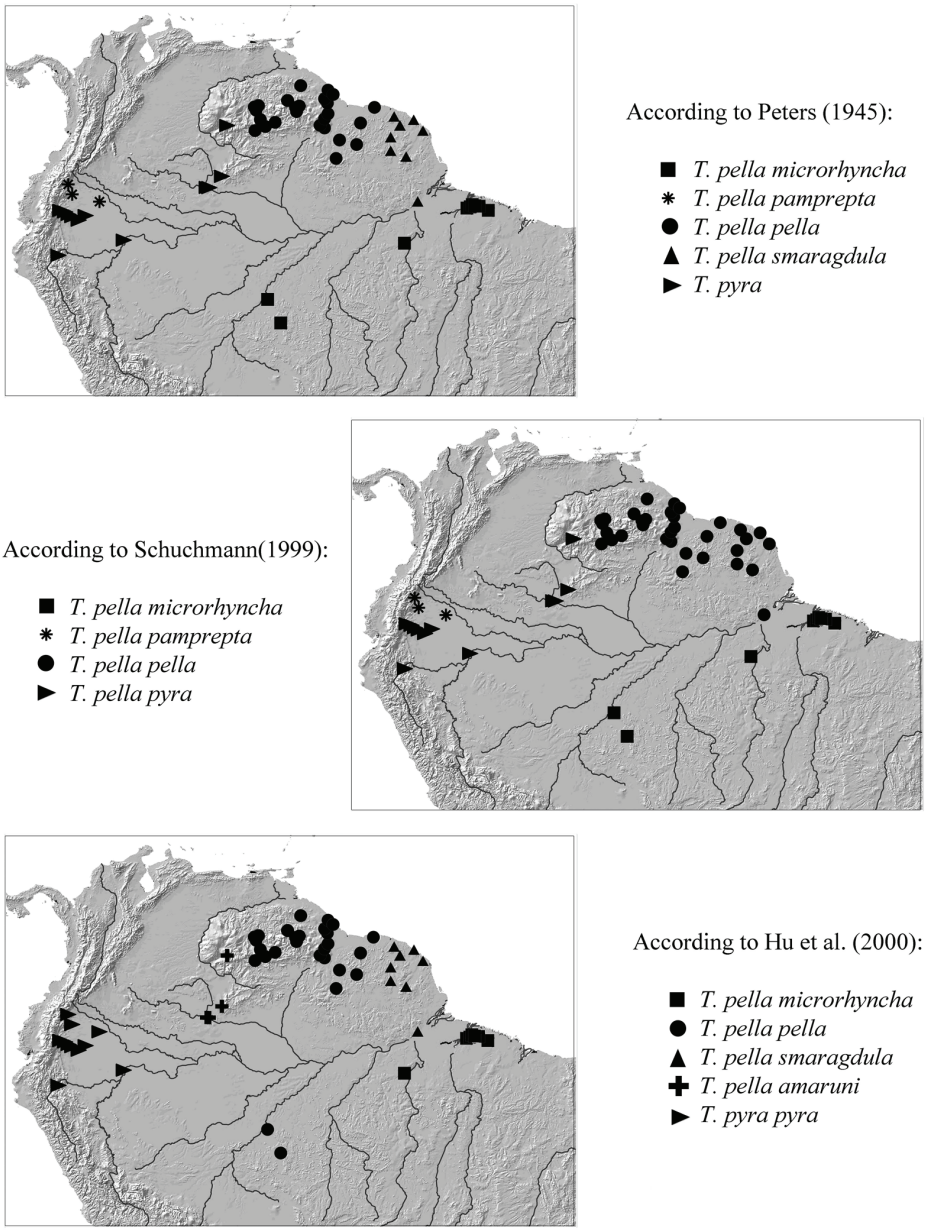

FIG. 1. The genus *Topaza* and the geographical distributions of species and subspecies according to three authors.

populations in the range of former *T. pella smaragdula*, to which he allocated no distinct status.

3. Hu *et al.* (2000) recognized two species of *Topaza* (*T. pyra* and *T. pella*). They separate *T. pyra* into the nominotypical form in south-

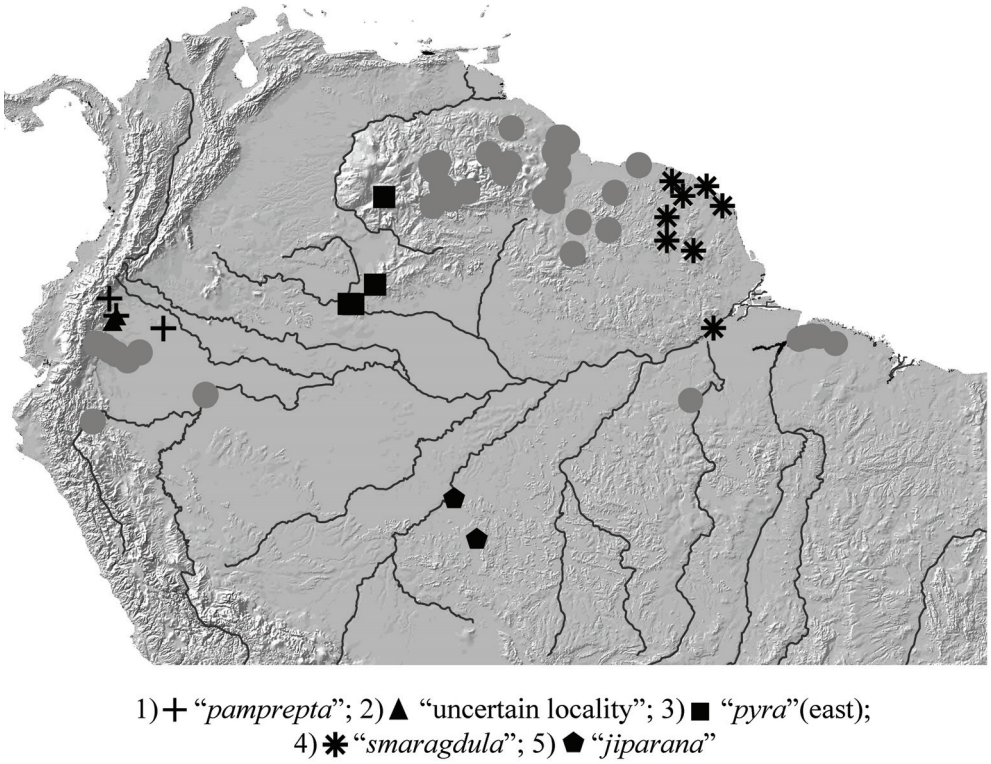

FIG. 2. Taxonomically "unclear" (black symbols) and "unproblematic" (grey dots) populations of *Topaza*.

ern Venezuela (Amazonas) and *T. pyra amaruni* in Amazonian Ecuador, along the Rio Napo and Rio Corrientes, and in western Amazonian Peru. They included "*pamprepta*" in *T. pyra pyra* and accepted the three other subspecies previously recognized by Peters: *T. pella pella*, *T. smaragdula*, and *T. p. microrhyncha*. The only difference is the population in the vicinity of Rio Jiparana in Brazil, which is included in *T. pella pella* (or another potential subspecies), and not in *T. p. microrhyncha* as by Peters (1945).

We compared these published taxonomies on the assumption that they are good preliminary hypotheses. Those populations on which the authors show disagreement we called "unclear." They are specifically (Fig. 2): 1) "*pamprepta*," which includes the Suno, Rio Napo population; 2) "uncertain locality," the ambiguities surrounding the status of these three specimens coming from uncertain localities will be discussed; 3) "*pyra*" (east), which comprises the populations of the southernmost tip of Venezuela and adjacent areas of Colombia and Brazil (*T. pyra pyra* according to Hu *et al.* 2000); 4) "*smaragdula*," which includes the populations of the Guianas and Amapa in Brazil and which, according to Hu *et al.* (2000) and Peters (1945), should be part of a separate subspecies, but this is not accepted by Schuchmann (1999); and 5) "*jiparana*," populations around the Ji-Parana River in Brazil, which according to Peters (1945) and Schuchmann (1999) are part of *T.*

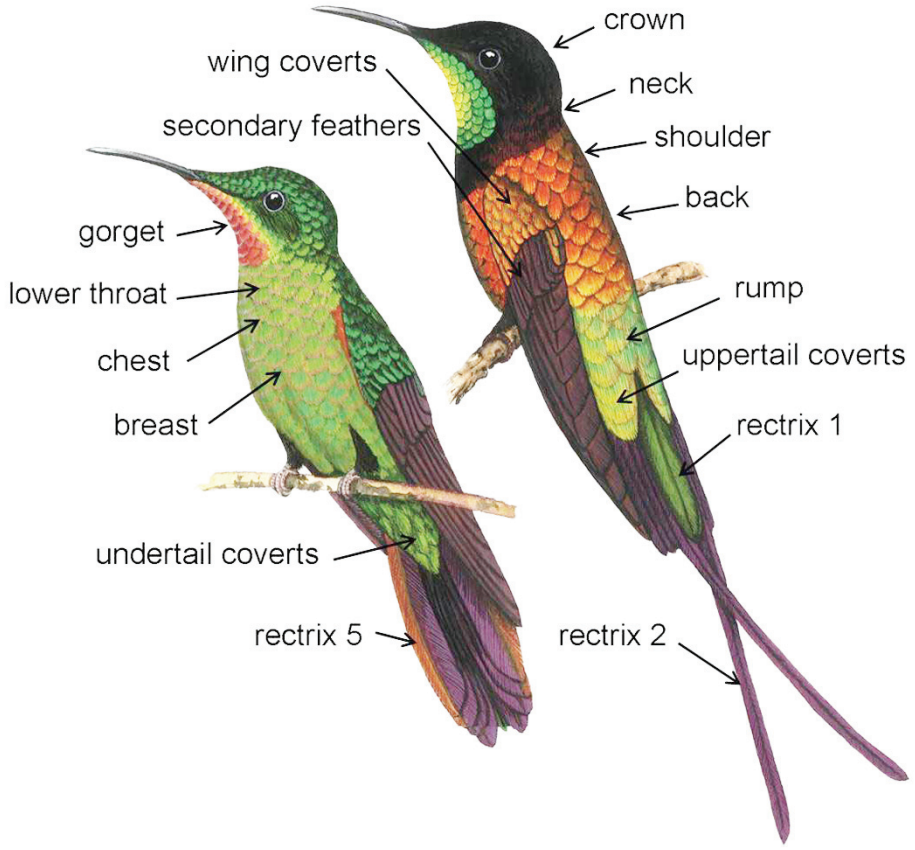

FIG. 3. Body areas where color determination was conducted. Drawings modified from David Alker's original artwork (from Schmitz-Ornés & Haase 2009).

pella microrhyncha and following Hu *et al.* (2000) are either part of *T. pella pella* or possibly represent a new subspecies. These names are used subsequently for discussion purposes.

Color measurements were taken and analyzed following Schmitz-Ornés (2006) using a spectrometer with a black plastic piece at the tip of the optic fiber to prevent ambient light entering the system, and connected to a PX2 pulsed xenon light source. Two different spectrometers were available during our study: a USB2000 fiber optic spectrometer (Ocean Optics Inc.) for the first set of specimens (measurements taken between 2003 and 2006) and an AvaSpec-2048 (Avantes) for the second set (2007–2009). In order to follow an integral approach to color analysis we divided the body of each specimen into a total of 20 parts (Fig. 3): dorsal area: crown, neck, shoulder, back, rump, and uppertail coverts; ventral area (includes not only the central measurement of each body section but also the lateral measurements of each): gorget, lower throat, chest, breast, under tail coverts; wing: coverts, secondary feathers; rectrices: r1, r2, and r5. The probe of the spectrometer, cut at a 45° angle and with a 3-mm-diameter aperture, was always located in the same direction relative to

the body of the specimen and directly on the feathers. Each color measurement represented the percentage of reflectance in a complete 300–730 nm spectrum of each body part. The reflectance along the wavelength range was reduced to the medians of 10-nm bandwidths, and these spectral segments were used as working variables.

The statistic analyses were conducted using the software package PASW Statistics 18 (formerly SPSS). In order to use plumage coloration data to discriminate between subspecies and determine the membership of "unclear" populations, a principal component analysis (PCA) was conducted on each data set (all working variables taken on each body region) to reduce the spectral data and obtain "summarized" color information (see Schmitz-Ornés 2006). We then took the first three principal components (PCs) of each body part to conduct discriminant function analyses (DFA). They were performed to determine the membership of "unclear" populations and to define which variables contribute most to the separation of *Topaza* groups or, in practical terms, what differences in body color are most important to discriminate groups within this genus. Given the sexual dimorphism of *Topaza* hummingbirds, and the almost 100% discrimination of sexes obtained after a previous DFA, all taxonomic analyses were performed separately for males and females.

The same "unclear" populations were used as taxonomic units to conduct the phylogenetic analysis of the genus *Topaza* using the monotypic taxon *Florisuga* as outgroup. This analysis was conducted following the methodology described in Schmitz-Ornés & Haase (2009), in which generalized frequency coding (GFC) (Smith & Gutberlet 2001) was applied to morphological spectral data. GFC is a procedure that allows the coding of any type of quantitative polymorphic character. It translates frequency distributions, such as color spectral data, into discrete states that can be used in phylogenetic analyses. Original working variables are divided into subcharacters and the variation within each subcharacter is coded using frequency bins. The controversial issue of using continuous characters to conduct phylogenetic analyses is addressed in Schmitz-Ornés & Haase (2009)

The morphological (continuous) variables in this case were the three first PCs from the color information from each body part. The 120 color variables (20 body parts for males and 20 for females multiplied by three PC scores) were codified using FastMorphologyGFC Version 1.0. (Chang & Smith 2001). The resulting matrix containing 9 taxonomic units (8 as ingroup) and 7071 weighted characters was entered in the phylogenetic computer program PAUP* 4.0b.10 (Swofford 2003). The ingroup taxonomic units were: "*pyra*" (west), "*amprepta*," "*pyra*" (east), "uncertain locality," "*smaragdula*," "*pella*," "*microrhyncha*," and "*jiparana*."

To reconstruct the phylogenetic relationships between the groups, a maximum parsimony analysis was performed, starting with an exhaustive search for all possible trees. After excluding 5505 constant characters, the remaining final matrix had 1566 informative and ordered characters. They all had weights other than "1" defined by using unequal subcharacter weighting (USW) (Smith & Gutberlet 2001). A bootstrap analysis was carried out with 10,000 replicates.

We conducted a correlation analysis between five standard body measurements (bill length, wing length, and rectrices 1, 2, and 5) and geographical latitude and longitude, to test for clinal variation of morphology.

RESULTS

The results of the first DFA included three individuals with "uncertain locality" ("unclear

TABLE 1. Discrimination (classification) of controversial populations of *Topaza* after DFA conducted on the color data of males (including three individuals with "uncertain locality" supposed to belong to "*pamprepta*").

	Predicted group % (number of individuals)						
	"*pyra*" (west)	"*smaragdula*"	"*microrhyncha*"	"*pella*"	"*pamprepta*"	"*pyra*" (east)	"*jiparana*"
"*pyra*" (west)	100.0	0.0	0.0	0.0	0.0	0.0	0.0
	(6)	(0)	(0)	(0)	(0)	(0)	(0)
"*smaragdula*"	0.0	96.4	0.0	3.6	0.0	0.0	0.0
	(0)	(27)	(0)	(1)	(0)	(0)	(0)
"*microrhyncha*"	0.0	0.0	100.0	0.0	0.0	0.0	0.0
	(0)	(0)	(3)	(0)	(0)	(0)	(0)
"*pella*"	0.0	2.6	0.0	97.4	0.0	0.0	0.0
	(0)	(1)	(0)	(37)	(0)	(0)	(0)
"*pamprepta*"	0.0	0.0	0.0	0.0	100.0	0.0	0.0
	(0)	(0)	(0)	(0)	(4)	(0)	(0)
"*pyra*" (east)	0.0	0.0	0.0	0.0	0.0	100.0	0.0
	(0)	(0)	(0)	(0)	(0)	(2)	(0)
"*jiparana*"	0.0	0.0	0.0	0.0	0.0	0.0	100.0
	(0)	(0)	(0)	(0)	(0)	(0)	(2)
"uncertain locality"	0.0	0.0	0.0	0.0	33.3	66.7	0.0
	(0)	(0)	(0)	(0)	(1)	(2)	(0)

group" number 2). All the groups showed 100% discrimination except for "*pella*" and "*smaragdula*" in males, which presented incomplete but mutual discrimination between the two groups (Table 1). Two specimens with "uncertain locality" were discriminated as "*pyra*" (east) and one as "*pamprepta*." Due to the ambiguity of these three specimens, we excluded them from the remaining taxonomic analyses and their relevance will be discussed in the section on the validity of *T. pella pamprepta*.

The second set of DFAs indicated that the first two discriminant functions (DFs) explain 83.0% of the variation in males (Fig. 4) and 87.4% in females. The standardized canonical discriminant function coefficients are shown in Table 2. The results were complemented with correlations between standard morphological body measurements and geographical variables (Table 3). In males, there was a significant correlation in all measurements with longitude, positive with regard to bill length and negative for the other four mensural traits. In females, the significant negative correlation was found in all measurements except for bill length, which showed no correlation. In all cases, the correlation was slight but significant, indicating a potential longitudinal clinal trend of these characters within the species.

The phylogenetic analysis resulted in a single most parsimonious tree (Fig. 5), with a length of 3783538, consistency index of 0.682, and retention index of 0.355. The bootstrap consensus tree was also fully resolved and corresponded to the most parsimonious tree. This tree showed four main clades, with the sister taxa "*microrhyncha*" and "*jiparana*" being only weakly differentiated and branching off at the base. "*Smaragdula*" and "*pella*" formed the sister clade to the

TABLE 2. Standardized canonical discriminant function coefficients resulting from DFA conducted on the color data of *Topaza* males (only first two functions).

Factor (body part)	Function		Factor (body part)	Function		Factor (body part)	Function	
	1	2		1	2		1	2
1 (crown)	1.021	-2.485	1 (gorget)	0.233	-1.260	1 (wing coverts)	-0.151	0.166
2 (crown)	1.493	-0.226	2 (gorget)	0.52	-0.087	2 (wing coverts)	-1.433	-1.322
3 (crown)	0.206	-0.304	3 (gorget)	0.132	0.671	3 (wing coverts)	-0.315	1.714
1 (neck)	-0.969	2.204	1 (lower throat)	-3.783	-5.542	1 (sec. feathers)	0.219	-1.132
2 (neck)	-1.906	0.671	2 (lower throat)	13.772	6.810	2 (sec. feathers)	0.001	-2.422
3 (neck)	-4.706	1.963	3 (lower throat)	0.958	-1.246	3 (sec. feathers)	1.048	-0.124
1 (shoulder)	-0.208	0.882	1 (chest)	-0.841	-0.655	1 (prim. feathers)	-1.807	-0.571
2 (shoulder)	-1.841	0.707	2 (chest)	0.160	0.514	2 (prim. feathers)	-2.134	1.234
3 (shoulder)	-0.887	0.817	3 (chest)	0.408	1.276	3 (primary feathers)	-0.137	-0.567
1 (back)	-0.746	-0.324	1 (breast)	-0.052	-0.420	1 (rectrix1)	-0.568	0.555
2 (back)	-1.352	1.190	2 (breast)	0.080	0.099	2 (rectrix1)	-0.532	0.560
3 (back)	0.715	0.109	3 (breast)	0.323	-1.517	3 (rectrix1)	-0.177	1.275
1 (rump)	0.179	1.355	1 (abdomen)	0.405	-0.849	1 (rectrix2)	-0.072	0.174
2 (rump)	0.276	0.775	2 (abdomen)	0.093	-0.443	2 (rectrix2)	0.062	0.771
3 (rump)	-0.648	0.752	3 (abdomen)	0.294	0.417	3 (rectrix2)	-0.345	-0.353
1 (uppertail coverts)	-0.850	-0.072	1 (undertail coverts)	-0.849	-0.586	1 (rectrix5)	1.861	-0.071
2 (uppertail coverts)	-0.206	0.141	2 (undertail coverts)	-0.541	-1.463	2 (rectrix5)	-1.803	-0.363
3 (uppertail coverts)	-1.365	0.738	3 (undertail coverts)	0.254	0.997	3 (rectrix5)	0.708	-2.079

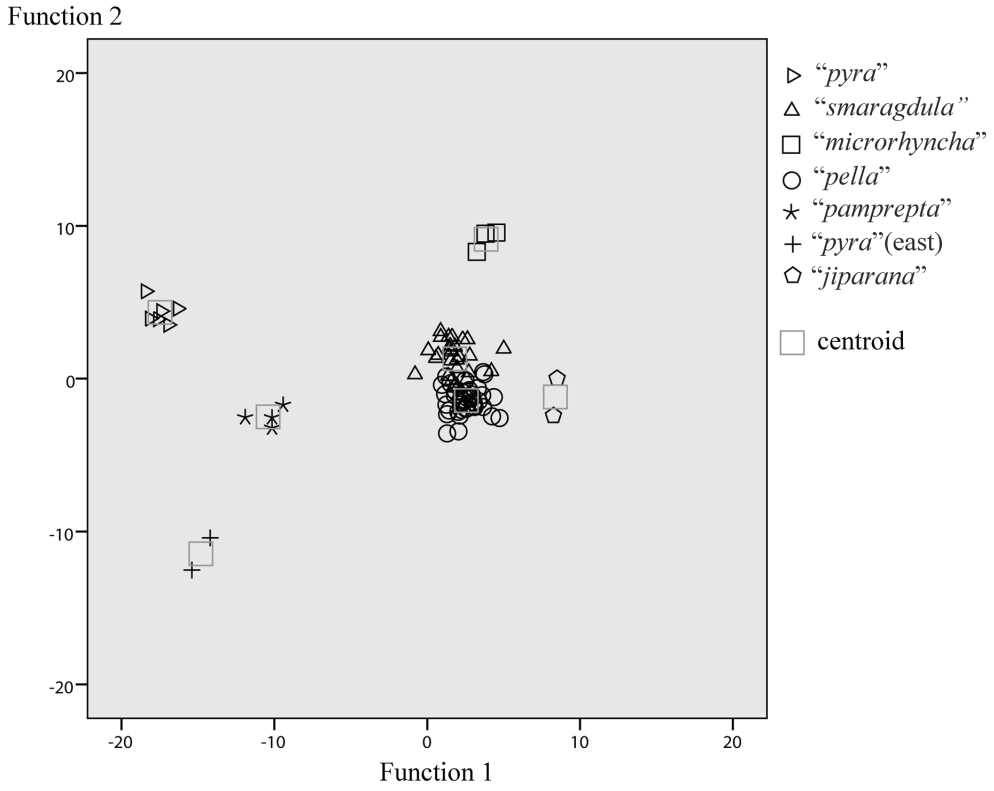

FIG. 4. Results of the DFA conducted on the color data of *Topaza* males (a) to discriminate groups. Note: All female groups classified 100% in their respective groups.

remaining taxonomic units, among which "*pyra*" (east) and "uncertain locality" were separated by short branches in contrast to "*pyra*" (west) and "*pamprepta*." However, the relationships between the clades were only weakly supported.

DISCUSSION

Considerations on the validity of Topaza pella pamprepta. *Topaza pella pamprepta* was first described by Oberholser (1902) from an adult male (174294 USNM) collected on the Rio Napo at the mouth of the Rio Suno by Goodfellow and Hamilton in May 1899. Hu *et al.* (2000) suggest that the subspecies *Topaza pella pamprepta* should not be recognized at all, so this point should be discussed here before continuing. Among other reasons, Hu *et al.* (2000) argue that this subspecies is only known from three specimens taken by the same collectors, Hamilton and Goodfellows, that may have been incorrectly labeled (these individuals were included in the results shown on Table 1 and Fig. 5). Additionally, Zimmer (1951) pointed out that a specimen collected by Hamilton and Goodfellow and marked as "Coca, Rio Napo, E. Ecuador, June 1899" is of uncertain origin since it was also labeled by dealers in London. Moreover, evidence exists of other specimens of *Topaza* with incorrect labeling (when compared with

TABLE 3. Pearson correlation of the morphological measurements of *Topaza* males in relation to latitude and longitude. * p (2-tailed) < 0.05, ** p (2-tailed) < 0.01.

	Bill length	Wing length	Rectrix 1 length	Rectrix 2 length	Rectrix 5 length
Latitude					
Pearson C.	0.565**/0.610**	-0.009/0.272*	-0.254**/0.094	-0.144/-0.221	0.023/0.170
N	119/76	122/76	118/71	114/70	115/68
Longitude					
Pearson C.	0.336**/0.217	-0.304**/-0.271*	-0.546**/-0.386**	-0.218*/-0.530**	-0.267**/-0.265*
N	119/76	122/76	118/71	114/70	115/68

field notes) obtained by the same collectors (Zimmer 1951). In our study, more specimens from the Napo area in Ecuador are included ("*pamprepta*") and the validity of this argument is discussed in detail.

Hu *et al.* (2000) had access to only two of the specimens of *T. p. pamprepta* housed in the USNM collection, including the holotype and another one labeled as "locality wrong, Cayenne skin." A third specimen was sent to Germany and is currently deposited at ZFMK. We had the opportunity to examine all of them. We included these three male specimens as a different group in our analyses to determine which taxa they actually belong to. To the human eye, these three specimens show specific characteristics in plumage coloration that are similar to *T. pella pella* distributed through the Guianas. This includes secondary feathers and rectrices 5 with rufous-brown color, contrary to the dark brown secondaries and violet rectrices 5 of the "*pyra*" group from the western extremity of the distribution. However, the integral and more objective approach taken here (including 20 body parts) places two of the specimens in "*pyra*" (east) and one together with "*pamprepta*" (Table 1). For the phylogenetic analysis we included these three individuals as a separate taxonomic unit, and the results (Fig. 5 and see below for discussion) reveal that they are most referable to "*pyra*" (east).

These results indicate that a re-evaluation of the subspecies "*T. pella pamprepta*" is highly needed. Hu *et al.* (2000) also examined other specimens from the Napo river area (USNM 174293, AMNH 46072) and its vicinity (ANSP 186789). We inspected these and three more specimens found in the SMF collection originating from Coca, Napo area. The latter were misidentified as *T. pella microrhyncha*, perhaps due to the ambiguity of the locality written on the label: "Rio Coca, Amazonas." To the naked eye, they showed the characteristics of the "*pyra*" group from close to the Andes, which include dark brown secondaries and a dark violet rectrix 5, contrary to the rufous-brown secondaries and rectrix 5 of the "*pella*" group from the eastern end of the distribution. The results of the DFAs (see Fig. 4 for males and the discussion below) show "*pamprepta*" as a differentiated group when looking at the centroid distances, although there was only one female available from this population. Phylogenetic analyses are necessary (see below) to make final conclusions about this group.

Taxonomic analysis of the genus Topaza. In order to solve taxonomic conflicts using the plumage coloration data, we focused our analysis and discussion on the "unclear" populations. According to the DFAs for males (Fig. 4) and females, two main groups could be distinguished along the first function correspond-

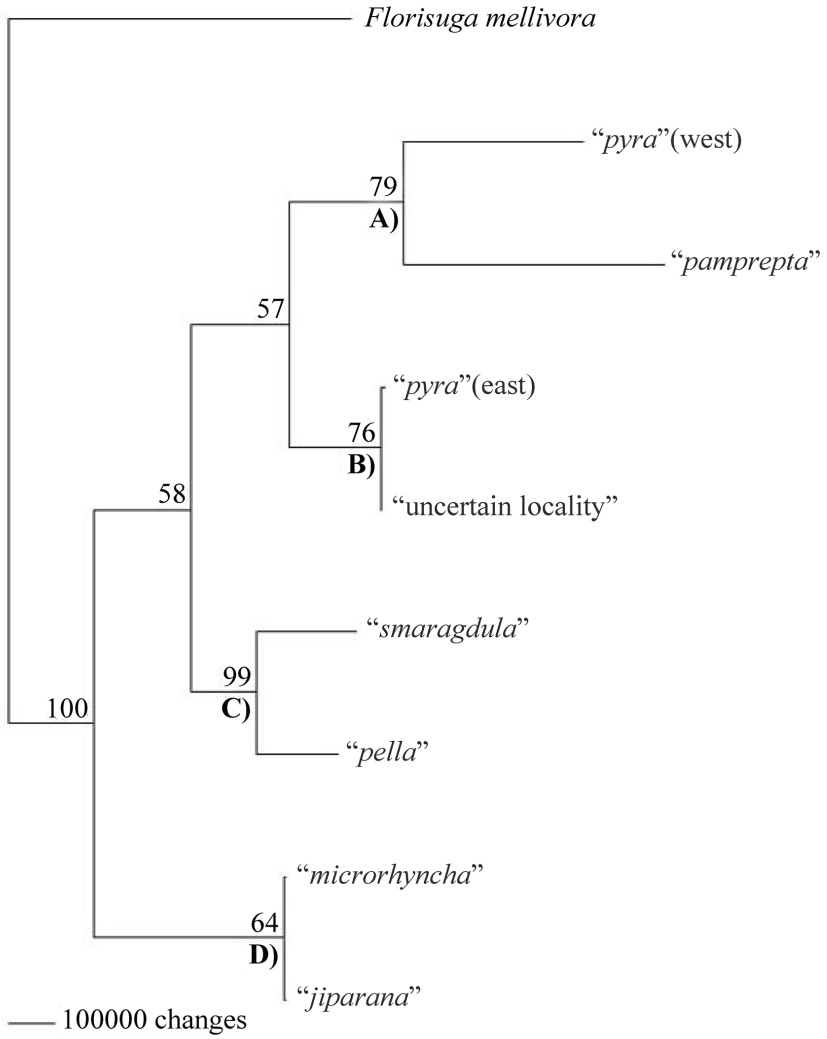

FIG. 5. Single most parsimonious tree with bootstrap support values, using *Florisuga mellivora* as outgroup. (A) *T. pella amaruni*; (B) *T. pella pyra*; (C) *T. pella pella*; (D) *T. pella microrhyncha*.

ing to "*pella*" and "*pyra*". However, we did not evaluate whether this difference is large enough to separate the genus into two different species. All "unclear" populations could be clearly discriminated and the same conclusion is reached in both males and females even when independently analyzed. The only exception occurred with "*pella*" and "*smaragdula*" (see also Table 1), which would be expected if accurate separation of the two groups cannot be made. Additionally, the centroids from "*pella*" and "*smaragdula*" (males and females) are very close together and even overlap, indicating that *T. pella smaragdula* should not be considered as a separate subspecies.

For both males and females, the centroids of "*pyra*" (west), from Ecuador and Peru, and *T. pella microrhyncha* are well separated, and in these groups the working hypotheses or taxonomies (Peters 1945, Schuchmann 1999, Hu *et al.* 2000) show no controversy. They are very well differentiated from the rest, as would be expected when no doubts exist as to their validity as subspecies. "*Pamprepta*" shows a separation from other *T. pella* populations and appears closer to the "*pyra*" (west) populations (Function 1, Fig. 4). Also, if *Topaza* had in fact two species, this group seems to be more similar to *T. pyra* than to *T. pella* as considered by Peters (1945). With regard to "*pyra*" (east), it seems that a different subspecies of "*pyra*" appears in southern Venezuela and adjacent areas, since the group does not overlap with the "*pyra*" (west) populations. The two males from "*jiparana*" both appear closer to "*pella-smaragdula*" than to *T. pella microrhyncha*.

The standardized canonical discriminant function coefficients (following Schmitz-Ornés 2006) indicate that in males the lower throat with the most to discriminate the groups according to the first two DFs (see Table 2). Although the discrimination for females gives the same results as for males, the discriminating variables are not the same. Basically, the dorsal region explains a high portion of the variation. Additionally, the differences in coloration of the wing coverts and rectrix 2 also seem to be important for the separation of *Topaza* female groups. Although the methodology used in this study may seem too abstract given our human visual orientation (Schmitz-Ornés 2006), many of these differences can also be appreciated by the naked eye (see section on "*pamprepta*"). However, a positive aspect of the methodology is that taxonomists do not have to concentrate on the color difference of a few body parts, but on the overall color difference along the body of the analyzed specimens.

The general results of the spectral color data suggest that the main source of variation comes from the separation between "*T. pella*" and "*T. pyra*." The first group would include populations of *T. pella pella* and *T. pella microrhyncha* occurring in the eastern part of the distribution, and seem to be more similar to each other than to the other three groups, possibly *T. pyra pyra*, *T. pyra amaruni*, and "*T. pyra pamprepta*." The phylogenetic analysis will confirm or reject (in the case of "*T. pyra pamprepta*") this separation.

The characters on which Hu *et al.* (2000) base their differentiation of the two species of *Topaza* are the color of the puffy tibial feathering and the prominence of the nasal fossa at the base of the bill. Although we did not make any of these measurements, at this point our analysis is concordant with these results in indicating a separation of *Topaza* between western and eastern populations. However, to which degree these two groups are "good" species or not will be discussed after the phylogenetic analysis.

Phylogenetic analysis of the genus Topaza. The phylogenetic analysis was conducted including the "unclear" populations that do not correspond to real taxa. However, the key problem here was to define whether or not *Topaza* should be divided into two species. The phylogenetic reconstruction (Fig. 5) shows low differentiation for the four main branches, indicating no real separation of the two species used for the working hypothesis ("*T. pella*" and "*T. pyra*"). Additionally, the four clades could each be considered as one taxon. These final taxa also corroborate some indications derived from the DFA: A) the population from "*pyra*" (west) clusters with "*pamprepta*" which definitively cannot be considered as a separate subspecies; B) the three "uncertain locality" specimens are indicated as sister group of "*pyra*" (east); C) "*smaragdula*" and "*pella*"

should also be considered as one taxon; D) "*jiparana*" seems to be part of *T. p. microrhyncha*.

According to our study, *Topaza* seems to be a monotypic genus divided into four distinct subspecies: *T. pella microrhyncha* at the base of the tree, followed by *T. p. pella*, *T. p. pyra*, and *T. p. amaruni*. This sequence corresponds also to the geographical distribution, from *T. pella microrhyncha* at the eastern end to *T. pella pyra* and *T. pella amaruni* at the western end of the distribution.

The major separation seems to be between the subspecies closer to the Andes and *T. pella microrhyncha*, which is not only farther away to the east but is also separated from *T. pella pella* by the Amazon River. *T. pella pella* occurs in the centre of the distribution and supports the existence of an east-west clinal trend of characters among *Topaza* populations, in agreement with the ideas of Schuchmann (1999).

We believe that setting a taxonomic limit at the species level would be a highly subjective conclusion at this point. Unfortunately, the scarcity or lack of specimens from northern and central Brazil (in the centre of the genus' geographical distribution) does not allow final conclusions about a clinal variation. Researchers could be misled into the identification of populations from opposite ends of the species' geographical distribution as two separate species.

The correlation between all the standard body measures (except for bill length of females) and longitude confirm a possible east-west clinal trend of characters (Table 3). The results of the correlation with latitude (Table 3) might reflect regional tendencies in the data, mainly within the populations of *T. pella pella* and *T. pella microrhyncha* that are more dispersed along a latitudinal range. This correlation may explain the difficulty in finding a clear separation of groups in this area, as well as the previously suggested validity of *T. pella smaragdula* by some authors (Peters 1945, Hu *et al.* 2000). The results of the present study indicate that the genus *Topaza* seems to be monotypic and includes only four subspecies, *T. pella amaruni*, *T. pella pyra*, *T. pella pella*, and *T. pella microrhyncha*.

ACKNOWLEDGMENTS

We are very grateful to the following institutions for financial support: DAAD, the Brehm Foundation, German Science Foundation (Schu 766/5-4, 760/5-5), the Alexander Koenig Foundation (AKS), Bonn; The National Museum of Natural History (NMNH), Smithsonian Institution, Washington, D.C.; The American Museum of Natural History (AMNH), New York; The Academy of Natural Sciences (ANSP), Philadelphia; and the European Union Project Synthesys (ES-TAF-4482, ASO; PL-TAF, KLS). We thank the curatorial staff of NMNH, ANSP, Colección Ornitológica Phelps (Caracas), the Muséum National d'Histoire Naturelle (Paris), Naturmuseum Senckenberg (SMF, Frankfurt), The Natural History Museum (Tring), The Field Museum of Natural History (Chicago), Museum of Vertebrates - Cornell University (Ithaca), Denver Museum of Natural History, Carnegie Museum of Natural History (Pittsburgh), Museum of Natural Science - Louisiana State University (Baton Rouge), Western Foundation of Vertebrate Zoology (Camarillo), Peabody Museum of Natural History (New Haven), and Museo Nacional de Ciencias Naturales (Madrid). In particular, we are grateful to the people of the Ornithology Section of Alexander Koenig Research Institute and Museum of Zoology, Bonn. ASO thanks Martin Haase for his support and discussions on the methodology. KLS thanks the Alexander Koenig Gesellschaft for a travel grant to the ornithological dept. of the National Natural History Museum in Rio de Janeiro. Walter

Bock, Marinez I. Marques, John Rappole, and André-A. Weller kindly commented earlier drafts of the manuscript. Special thanks to David Alker for allowing us to include his original artwork in our publication.

REFERENCES

Chang, V., & E. N. Smith. 2001. FastMorphologyGFC Version 1.0. [Online.] Available at www3.uta.edu/faculty/ensmith.

Cuthill, I. C., A. T. Bennett, J. C. Partridge, & E. J. Maier. 1999. Plumage reflectance and the objective assessment of avian sexual dichromatism. Am. Nat. 160: 183–200.

Dickinson, E. C. 2003. The Howard and Moore complete checklist of the birds of the world, 3rd ed. Christopher Helm, London, UK.

Gray, G. R. 1840. A list of the genera of birds, with an indication of the typical species of each genus. R. & J. E. Taylor, London, UK.

Greenewalt, C. H. 1960. Hummingbirds. The American Museum of Natural History, Garden City, New York, USA.

Hu, D. S., L. Joseph, & D. Agro. 2000. Distribution, variation, and taxonomy of *Topaza* hummingbirds (Aves: Trochilidae). Ornitol. Neotrop. 11: 123–142.

McGuire, J. A., C. C. Witt, D. L. Altshuler, & J. V. Remsen. 2007. Phylogenetic systematics and biogeography of hummingbirds: Bayesian and Maximum Likelihood analyses of partitioned data and selection of an appropriate partitioning strategy. Syst. Biol. 56: 837–856.

Oberholser, H. C. 1902. Catalogue of a collection of hummingbirds from Ecuador and Colombia. Proc. U.S. Natl. Mus. 24: 300–342.

Peters, J. L. 1945. Check-list of birds of the world. Museum of Comparative Zoology, Harvard Univ. Press, Cambridge, Massachusetts, USA.

Schmitz-Ornés, A. 2006. Using colour spectral data in studies of geographic variation and taxonomy of birds: Examples with two hummingbird genera: *Anthracothorax* and *Eulampis*. J. Ornithol. 147: 495–503.

Schmitz-Ornés, A., & M. Haase 2009. Adapting generalised frequency coding to use colour spectra in the determination of phylogenetic relationships: an example with hummingbirds. J. Zool. Syst. Evol. Res. 47: 385–390.

Schuchmann, K.-L. 1999. Family Trochilidae (hummingbirds). Pp. 468–680 *in* del Hoyo, J., A. Elliott, & J. Sargatal (eds). Handbook of the birds of the world. Volume 5: Barn-owls to hummingbirds. Lynx Edicions, Barcelona, Spain.

Simon, E. 1921. Histoire naturelle des trochilidés (synopsis et catalogue). L. Mulo, Paris, France.

Smith, E. N., & J. Gutberlet. 2001. Generalized Frequency Coding: a method of preparing polymorphic multistate characters for phylogenetic analysis. Syst. Biol. 50: 156–169.

Swofford, D. L. 2003. PAUP, Phylogenetic Analysis Using Parsimony. Version 4.0b10. Sinauer Associates, Sunderland, Massachusetts, USA.

Zimmer, J. T. 1951. Studies of Peruvian birds No. 60. The genera *Heliodoxa*, *Phlogophilus*, *Urosticte*, *Polyplancta*, *Adelomyia*, *Coeligena*, *Ensifera*, *Oreotrochilus*, and *Topaza*. Am. Mus. Novit. 1513: 1–45.