A new methodology to use color spectral data for taxonomic, phylogenetic, and biogeographic studies. An example with three genera of lowland hummingbirds: *Topaza, Anthracothorax,* and *Eulampis.*

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Tag der Promotion:

Dedico este trabajo a mi hija

ANDREA CAROLINA

por ser mi motor de vida y fuente de inspiración ...

Contents

Introduction

Color patterns have long been considered an important component of the evolutionary process in the natural world. This trait can be greatly influenced by predator-prey relationships and sexual selection. Specifically the latter has been frequently studied and assumed to be directly related to speciation (Darwin 1871, Andersson 1994, Townsend Peterson 1996, Moller & Cuervo 1998). Coloration can be highly variable among individuals or groups of individuals and may reflect phylogenetic relationships, mainly at lower-taxa levels, such as species and subspecies. This characteristic has been used to evaluate geographical differences in bird populations, consequently, also being important for identification, taxonomy, systematics, and historical biogeography (e.g., Vuilleumier 1968; Graves 1985, 1997; Marin 2000; Molina *et al.* 2000).

Most taxonomic and evolutionary studies based on coloration have assumed that the human subjective experience of color approximates to that of birds (Bennett *et al.* 1994). However that may not be the case, since birds have probably the most sophisticated color vision system of all vertebrates (Goldsmith 1990). This means that the inability of humans to perceive the color world of animals applies most dramatically to birds, and consequently to the results of many of the current taxonomic, phylogenetic, and evolutionary studies conducted on this group.

Color depends not only on the physical characteristics of the observed object and the sensory system of the receiver, but also on the ambient effect. Endler (1992) has extensively discussed the evolution of coloration, and according to him the evolution of visual signals among animals is a complex process that depends on behavior and microhabitat selection. A specific behavior is required in order to choose the times, seasons, and microhabitats that transmit the signal most efficiently with the minimum degradation and attenuation, the least ambient noise, and the minimum risk of predation. Hence, both breeding behavior and microhabitat selection are likely to coevolve with sensory systems and signals (Endler 1992, Endler & Thery 1996).

These factors and interrelationships may have strong implications for geographical differentiation and speciation, since the evolutionary bias of the sensory drive is unlikely to be geographically uniform (Endler 1992). Because signal transmission conditions and background noise also vary with microhabitats, times, and seasons, divergences among populations and species are very likely. Variation in intraspecific signals may not only maintain but also cause differences among populations. Speciation and further divergence can result if populations and species evolve in different directions (Endler 1992).

Ideally, color researchers would have knowledge of the visual system of their study organism, including detailed information on cone pigments, spectral sensitivities, etc., as well as data describing attenuation patterns, timing and location of peak animal activity, ambient light levels, etc. (Grill & Rush 2000). However, this information for birds (and other animals) is rarely available. If we assume that differences in reflectance spectra translate to differences in the perceived colors, then approximations still provide useful information about the role of color in biology (Grill & Rush 2000). Moreover, since color patterns are the ultimate consequences of this complex evolutionary process discussed by Endler (1992), the direct, objective measurement of plumage color must be useful for phylogenetic, systematic, and taxonomical studies.

A color classification based directly upon the reflectance spectra rather than human perception is a better starting point in studies of animal color patterns (Endler 1990). However, despite its advantages, there are also problems involved with the collection and use of spectral data. Spectrometers generally represent the color of a structure of an organism as the reflectance at a given nanometer value of a large number of arbitrary wavelength points along the electromagnetic spectrum (Thorpe 2002). As color changes, spectra can change in a number of ways, including shifts in curve slopes, amplitude, and number and position of peaks, and these changes are often difficult to quantify. Therefore, a challenge in color research is that of how to condense the enormous quantity of data contained in a color spectrum into one or a few useful units of measure (Grill & Rush 2000).

Phylogenetic, systematic, and taxonomic bird studies

The origin and evolution of biotic diversity remains a central problem within evolutionary biology (Cracraft & Prum 1988). Establishing family trees or phylogenetic relationships among vertebrates, both living and fossil, has been one of the most challenging aspects of the study of organisms since the time of the ancient Greeks, who designed a classificatory system based on their view of overall similarity (Feduccia 1996). To understand processes of faunal assembly within biotas, it is necessary to document the historical patterns of speciation within their components (Cracraft & Prum 1988), and although there have been many attempts to study the patterns of speciation and evolution of diverse groups of animals and plants, the lack of historical information makes this topic very controversial. For the construction of the current models of biotic diversification (Vuilleumier 1971; Haffer 1974a, 1978, 1982; Simpson & Haffer 1978; Haffer & Fitzpatrick 1985), systematic and biogeographic analyses of the Neotropical biota in general and of birds in particular have played a main role. Patterns of endemism and geographical variation have been established for many groups of Neotropical birds. However, considering that only traditional collecting sites have been well surveyed for the overview of geographical distributions (Fjeldså & Krabbe 1986), the phylogenetic patterns of avian differentiation within the Neotropics are still not well understood (Cracraft & Prum 1988).

There are several studies on the geographic population structure of birds (among them: Vuilleumier 1968, Simpson-Vuilleumier 1971, Vuilleumier & Simberloff 1980, Graves 1982). These have added to the understanding of speciation patterns of groups of vertebrates and have generated several hypotheses that try to explain the origin and patterns of avian tropical diversity (Haffer 1969, Vuilleumier 1971, Simpson & Haffer 1978, Endler 1982, Rahbek & Graves 2001). The best-known and most widely accepted mode of evolution in the Neotropical biotas is the Refuge hypothesis (Haffer 1969, Simpson & Haffer 1978, Prance 1982). According to this model, speciation patterns of Neotropical faunal taxa arose as a result of cyclical expansions and contractions of forest and non-forest habitats during Quaternary climatic fluctuations (Haffer 1969, 1974a,b, 1977, 1979, 1982; Vuilleumier 1971;

Simpson & Haffer 1978; Haffer & Fitzpatrick 1985; Mayr & Ohara 1986). However, other possible explanations have also been proposed, and the most important alternative hypothesis regarding a mechanism of vicariance has concerned the origin and development of broad river valleys or epicontinental marine transgressions. Distributions of species of plants and animals within Amazonia are frequently bounded by river systems; however, a number of arguments have been presented against the role of major river systems as agents of vicariance (Haffer 1978, Simpson & Haffer 1978, Cracraft & Prum 1988).

Besides the river hypothesis, there is also the Paleogeography hypothesis, the River-Refuge hypothesis, the Disturbance-Vicariance hypothesis, and the Gradient hypothesis (for more details see Haffer 1997, Nores 1999). In general, several of these hypotheses are probably relevant to different degrees for the speciation process in different faunal groups or during different geological periods (Haffer 1997). Specifically within Amazonia, the large majority of biologists who have attempted to explain diversity have done so using a model of allopatric speciation via vicariance. A few researchers have proposed an alternative hypothesis to explain contiguous areas of endemism. They suggest that such patterns are the result of present-day ecological barriers to gene flow and that diversification within Amazonia is primarily a manifestation of parapatric, not allopatric, processes (Cracraft & Prum 1988).

It has been suggested that the Eocene was an epoch of the greatest importance in the evolution of birds and that by the end of the Miocene all of the non-passerine families were probably established (Brodkorb 1981 *in* Vuilleumier 1984). It has also been postulated (Simpson-Vuilleumier 1971; Haffer 1974a, 1979; Vuilleumier 1980, 1993) that the majority of extant avian species and subspecies of the Neotropical region evolved during the Pliocene and Pleistocene epochs, and that Pleistocene biogeographic events have had a major role in promoting speciation. However, this paradigm has recently come under challenge from a review of interspecific mtDNA genetic distances in birds, in which most sister-species separations date to the Pliocene (Avise & Walker 1998).

Hummingbirds: phylogeny and origin

Among birds, hummingbirds (Trochilidae) are specially known for their magnificent colors. Hence this feature has been used as a taxonomic character in many studies (Bleiweiss 1985; Schuchmann & Duffner 1993; Schuchmann & Heindl 1997; Graves 1998, 1999b, 2000; Heindl & Schuchmann 1998; Weller & Schuchmann 1999; Hu *et al.* 2000; Schuchmann *et al.* 2000; Schuchmann *et al.* 2001; Weller 2000a,b).

Current efforts to understand the diversification of hummingbirds are limited by the lack of a historical framework for the study of evolutionary patterns and processes. In fact, generic limits and species relationships within the trochilines are still poorly understood (Schuchmann 1999) and present a considerable challenge for future systematic and biogeographic research. The study of specific groups within the trochilids (Heindl & Schuchmann 1998, Schuchmann *et al*. 2000, Weller 2000a, Sanchez-Oses 2003, Valdés-Velásquez 2003, Renner & Schuchmann 2004, Weller & Schuchmann 2004), together with the present study, are important for the understanding of general patterns within the group.

The trochilids are, possibly, of mid-Tertiary origin (Feduccia 1996) with a distribution centered in South America. They most likely derive from primitive swifts (Feduccia 1996). In fact traditionally, trochilids are placed in the order Apodiformes together with treeswifts (Hemiprocnidae) and true swifts (Apodidae), and currently it is widely accepted that swifts and hummingbirds constitute a monophyletic group (Bleiweiss *et al.* 1994, Schuchmann 1999). The divergence is probably ancient and may date back to the beginning of the Tertiary or even to the late Cretaceous, when a large tectonic plate broke from Gondwanaland, giving rise to South America (Feduccia 1996, Schuchmann 1999). According to Sibley & Alquist (1990), it seems probable that the swifts and hummingbirds diverged more recently from one another than either diverged from any other lineage, and are the nearest relatives of the Strigiformes (owls, nightjars). However, the construction of a hummingbird phylogeny is handicapped by the scarce amount of fossil records, which date only from the Recent and Pleistocene ages (Cohn 1968 *in* Vuilleumier 1984, Bleiweiss *et al*. 1994) with a recent

addition of two fossil remains from the early Oligocene of Europe (Mayr 2004), which, although they might change all previous conceptions about the origin of hummingbirds, are still too recent and need further verification. For many hummingbird taxa, allopatric speciation in refuges due to Pleistocene events has been proposed to explain extant biogeographic patterns (Schuchmann & Duffner 1993, Schuchmann & Heindl 1997).

Two Subfamilies compose the Family Trochilidae: Phaethornithinae or hermits, and Trochilinae, also called typical hummingbirds. According to molecular studies (Bleiweiss *et al*. 1994, 1997), the rate of molecular evolution in hummingbirds seems to be more rapid than in many other birds, and calibration of divergence times with the earliest known fossil swift suggests possible changes to that classification or divergence times. However, the hummingbird classifications and systematic affinities made by Simon (1921), and adopted by Peters (1945), are still in use today, except for some modifications (Schuchmann 1999). Most of them, including the present work, rely on external morphological and plumage characters such as coloration. Although these characters are misleading indicators of higher-level relationships, as they vary within hummingbird genera, they are good indicators at subspecies and species levels, since they may be greatly influenced by foraging and social behaviors (Feinsinger & Colwell 1978). Additionally, if classificatory studies take into account biogeographic and evolutionary patterns, the sometimes negatively viewed traditional morphological character analysis may still yield valuable information on intraspecific and interspecific phylogenetic relationships, serving as a useful hypothesis to be tested with other methods (Schuchmann 1999). In general, knowledge of biogeographical and morphological affinities among closely related species has proved to be a useful tool for the evaluation of taxonomy and for the reconstruction of the phylogeny of widespread lowland or montane hummingbird clades (Schuchmann & Duffner 1993, Schuchmann & Heindl 1997, Heindl & Schuchmann 1998, Schuchmann *et al*. 2000, Weller 2000a), and I will use this approach in the present proposed research.

Although hummingbirds probably constitute a monophyletic group, they have radiated widely when compared with other bird families, constituting a very heterogeneous group (Bleiweiss

et al. 1994); in fact, in this regard, Greenewalt (1960) said: "it is improbable that any family of related creatures varies so widely in physical equipment as do the hummingbirds." This high variability makes them an interesting group in which to study general patterns of speciation in different types of habitats and topographies, mainly in the Neotropical Region where the highest biodiversity in the world is found.

Characteristics and distribution of the study taxa

Within the trochilines, the patterns of tail feather coloration, display, song structure, and features of the hindneck muscle (Zusi & Bentz 1982) place the "tooth bills" *Androdon* and *Doryfera* at the base of the phylogeny, followed by a more derived grouping containing the "sabrewing and mango" genera *Campylopterus* (including *Phaeochroa*, *Eupetomena*, *Aphantochroa*), *Florisuga* (including *Melanotrochilus*), *Colibri*, *Anthracothorax* (including *Avocettula*), *Topaza*, *Eulampis*, *Chrysolampis*, *Orthorhyncus*, *Klais*, *Stephanoxis*, and *Abeillia* (Schuchmann 1999). DNA analysis (Bleiweiss *et al*. 1997) of the phylogeny of the hummingbirds includes the mangoes at the base of the tree, the emeralds being more derived. Unfortunately the authors only analyzed two of the genera included in the present study (*Eulampis* and *Campylopterus*), and did not investigate any species of *Anthracothorax* or *Topaza*, which would have been precious information for the phylogenetic analyses made in this work.

Hummingbirds (Trochilidae) are one of the largest avian families (in number of species) in the New World (Fjeldså & Krabbe 1990). They include the smallest of all birds, while most species are 6-12 cm in size and have a body mass of around 2.5- 6.5 g (Schuchmann 1999). Trochilids show a characteristic hovering flight and are highly evolved nectarivores, reaching their liquid food with thin elongated bills of various shapes that protect their specialized long, sensitive tongues (Schuchmann 1999). Many species show a marked sexual dimorphism, in which males show iridescent bright colors mainly on the head and throat, and in general in the upper- and underparts, while females are duller in appearance. The appearance of dimorphism may be understood as a specialization to specific ecological conditions (Schuchmann, pers.

comm.). However, the widespread occurrence of dull monomorphic plumage among the trochilinae may suggest, according to Bleiweiss *et al*. (1994), a complicated pattern of convergences.

Trochilids constitute a very important group for the dynamics of tropical forest, pollinating in total more than 30% of the angiosperm plant species in the Neotropics (Schuchmann pers. comm.). Unfortunately, many species in the group show specific habitat requirements or a restricted geographical distribution, making them theoretically vulnerable to extinction. For example, Collar *et al.* (1992) consider *Campylopterus ensipennis* as vulnerable to extinction, and additionally, some members of the Trochilidae family are sensitive to man-made habitat modifications (Collar *et al*. 1992, Sánchez-Osés & Pérez 1999), adding importance to the group from the conservation point of view.

Hummingbirds constitute a widespread group of birds occurring nearly throughout the Americas, but the majority of species inhabit humid forests near the Equator (Fjeldså & Krabbe 1990, Schuchmann 1999). The focus of this research is on the mango clade, a group of hummingbird genera (*Topaza*, *Anthracothorax*, and *Eulampis*) occurring in lowlands ranging from Mexico to Argentina, and including the Caribbean islands.

A few hummingbird species are long-distance migrants (mainly North American), others are altitudinal migrants or need to move at high altitudes through a range of latitudes to forage. The genera selected for this study are not only widely distributed and highly variable but are also considered basically sedentary, although there is scarce information on this biological aspect (Schuchmann 1999). They show only altitudinal or local migration to reach food resources, which make them interesting subjects to speculate on general evolutionary patterns in the lowlands of the Neotropical region. The degree of sedentarism is an important characteristic to help draw conclusions on patterns of speciation because it determines the dispersal capabilities of different groups.

Within the group under study, Schuchmann (1999) places the topaz hummingbirds (*Topaza*) close to the mango hummingbirds (*Anthracothorax*) and the caribs (*Eulampis)* on the basis of form of nest and display. He states that *Eulampis* must be phylogenetically very close to *Anthracothorax* due to some specific similarities in coloration (the white stripes in the abdomen of *Anthracothorax* females that are visible in juveniles of *Eulampis*), and characteristics of the construction of the nest (Schuchmann 1980b). This information from the literature, together with preliminary observations of the geographic variation in the morphological characters shown by the study genera, leads to the following hypothesis: The genera *Topaza* and *Eulampis* are sister taxa and they are closely related to *Anthracothorax*.

Research goals and structure of the study

In this study I propose a methodology that will increase objectivity in the determination and analysis of bird plumage coloration for systematic, taxonomic, phylogenetic, and biogeographic studies. I apply the methodology to obtain information on the geographical variation of the plumage coloration of the study taxa, and combine these data with other standard morphological external measurements of the birds. Then, as examples of the possibilities of the methodology, I review the taxonomy of the mango clade covering the genera *Topaza*, *Anthracothorax* and *Eulampis*. I also present phylogenetic hypotheses for the three genera, using two species of the genus *Campylopterus* (*C. cuvierii*, and *C. largipennis*) as an outgroup. I then use the final phylogenetic result to speculate on the biogeography of the group.

The first step is to justify, describe, and discuss the developed methodology, then to apply it to clarify the controversial *Topaza* taxonomy to the subspecific level. Second, I review the taxonomy of the genus *Anthracothorax*, which shows some controversies that have not been previously analyzed. The genus *Anthracothorax* appears to be homogeneous in mensural characters but shows a wide variability in color patterns, mainly in regard to the gorget iridescence. The genus *Eulampis* is geographically more restricted and apparently less morphologically variable than *Anthracothorax*. Finally, the genus *Campylopterus*, used as

outgroup, appears to be more variable, not only in external morphological characters such as shape and size of the tail, but also in coloration patterns throughout the ranges of its species. However, the two species chosen for the phylogenetic analysis are the dullest in appearance of all the species in the genus.

This research will be based on the following assumptions:

- Plumage coloration plays an important role in avian evolution, and needs to be evaluated independently of human perception.
- Phenotypic variance, such as plumage coloration and morphometrics, is directly related to population genotypic variance. Reproductive isolation will cause emergence of discrete entities that will show less variability within their limits than in comparison with any other such entity.
- Taxonomic structure at the species and subspecies levels identifies relatively isolated populations that can be regarded as discrete entities. Therefore these entities should be separable from others by phenotypic differences.
- Since variations in external morphology reflect genetic variation, the lower the morphological variation the higher the degree of relatedness.
- The speciation process results in patterns of successive branching. The terminal branches are taxa joined by nodes of common ancestors, and for a given group of related taxa there only can exist one history of speciation events and consequently one phylogeny.
- Based on phenotype (in this case plumage coloration and morphometrics), it is possible to reconstruct the phylogeny of a group of taxa. Therefore morphological variables will reflect past speciation history and common ancestry.

The specific goals of this study are:

- To develop an objective methodology to study color variation, using color spectral data, in order to review the taxonomy of bird populations.

- To review the taxonomy of three mango hummingbird genera occurring in southern Central America and the Caribbean islands (*Topaza*, *Anthracothorax*, and *Eulampis*) as an applied example of the methodology.
- To use generalized frequency coding (GFC) as a tool to codify continuous spectral and morphometric data to enable phylogenetic analysis on bird populations to be conducted.
- To perform a phylogenetic analysis of the genera *Topaza*, *Anthracothorax*, and *Eulampis*, using *Campylopterus* as outgroup, by using morphological continuous variables, such as color spectral data from different body parts and some standard morphometric measurements.
- To analyze the geographical distribution of the three taxa and infer its possible causes, based on the phylogenetic reconstruction of these groups. This information would allow conclusions on the biogeography of the area to be made.

The work is structured in nine sections, each containing a different aspect of the study: The first two are very general: "Introduction" and "General methodology", the first including the general theoretical framework and assumptions of the study, as well as the main goals and objectives; the second includes the description of the data collection and a general view of the analyses performed. The next six sections constitute the main body of the study, and each includes its own specific theoretical framework: "Methodology to measure and analyze color spectral data," "Geographical variation and review of the taxonomy and phylogeny of the genus *Topaza*," "Geographical variation and review of the taxonomy and phylogeny of the genus *Anthracothorax*," "Geographical variation and review of taxonomy of the genus *Eulampis*," "Phylogenetic relationships of the three genera, *Topaza*, *Anthracothorax*, and *Eulampis*," and the "Historical biogeographical events in the speciation process of the study group". The first section explains in detail the development of the methodology used to analyze spectral color data, which will be the basis for the rest of the work. The next three sections are dedicated to each of the genera studied. They include a description of current taxonomic status, review of their accepted taxonomies, definition of the taxonomic units (TUs) to be used in the phylogenetic analyses, and resulting phylogenetic relationships. The next section includes the phylogenetic relationships based on external morphology of the three

genera, using two species of the genus *Campylopterus* as outgroup (a short description of this genus is also included). The next section contains the conclusions as to the probable causes of the current geographical distribution of the taxa under study. Concluding remarks are included in the last main section.

General methodology

Specimens included in the study

Mensural and color data from voucher specimens from the four genera were collected from several ornithological collections in Europe and the Americas (Table 1). The following Institutions were visited: Zoologisches Forschungsinstitut und Museum Alexander Koenig, Bonn, Germany (ZFMK, Bonn); Forschungsinstitut und Naturmuseum Senckenberg, Frankfurt, Germany (Senckenberg); Musèum National d´Histoire Naturelle, Paris (MNHN Paris), France; The Natural History Museum, Tring, U.K. (NHMUK); National Museum of Natural History, Washington D.C., USA (USNM); American Museum of Natural History, New York, USA (AMNH); Academy of Natural Sciences, Philadelphia (ANSP); Colección Ornitológica Phelps, Caracas, Venezuela (COP). Additionally, specimens from other ornithological collections were sent to USNM to be available for this study: Field Museum of Natural History, Chicago, USA (FMNH); Cornell University Museum of Vertebrates (CUMV); Denver Museum of Natural History (DMNH); Carnegie Museum of Natural History (CMNH); Museum of Natural Science - Louisiana State University, Baton Rouge, USA (MNS-LSU); Western Foundation of Vertebrate Zoology, Camarillo, USA (WFVZ); Peabody Museum of Natural History, Yale University (PMNH).

In general, only adult birds were considered, and sex was determined by obvious color differences of the specimens when information on the label was not available. Specimens with unknown sex or with juvenile characteristics were excluded from further analysis. Additionally, of the total amount of *Campylopterus* specimens measured, only those of *C. cuvierii* and *C. largipennis* were included in the final analyses. A total of 2147 specimens were selected for analysis (Table 2).

Table 1. Number of specimens from *Topaza*, *Anthracothorax*, *Eulampis*, and *Campylopterus* measured in ornithological collections (for abbreviations see text).

Ornithological Collection	Total number of *Topaza* specimens measured	Total number of *Anthracothorax* specimens measured	Total number of *Eulampis* specimens measured	Total number of *Campylopterus* specimens measured	TOTAL
(ZFMK,Bonn)	27	94	29	153	303
(Senckenberg)	12	112	50	92	266
(MNHN Paris)	26	83	27	124	260
(NHMUK)	36	201	108	241	585
(USNM)	18	254	117	274	663
(AMNH)	29	133	11	234	407
(ANSP)	19	36		55	110
(COP)	21	155		390	566
(FMNH)	14	43		106	163
(CUMV)	2	17		22	41
(DMNH)	1	8		18	27
(CMNH)	10	74		101	185
(MNS-LSU)	2	21	7	72	102
(WFVZ)	1	8		32	41
(PMNH)		11		6	17
TOTALS	**218**	**1250**	**349**	**1920**	**3737**

Table 2. Number of specimens of each species of *Topaza*, *Anthracothorax*, *Eulampis,* and *Campylopterus* included in the analysis.

SPECIES (according to Schuchmann 1999)	**Total number of specimens**	**Males**	**Females**
Topaza pella	204	128	76
Sub-total *Topaza*	**204**	**128**	**76**
Anthracothorax viridigula	107	77	30
Anthracothorax prevostii	257	175	82
Anthracothorax nigricollis	537	349	188
Anthracothorax veraguensis	27	20	7
Anthracothorax dominicus	131	80	51
Anthracothorax viridis	33	22	11
Anthracothorax mango	33	21	12
Anthracothorax recurvirostris	20	13	7
Sub-total *Anthracothorax*	**1145**	**757**	**388**
Eulampis Jugularis	95	58	37
Eulampis holosericeus	149	87	62
Sub-total *Eulampis*	**244**	**145**	**99**
Campylopterus cuvierii	142	95	47
Campylopterus largipennis	412	251	161
Sub-total *Campylopterus*	**554**	**346**	**208**
TOTAL	**2147**	**1376**	**771**

Mappings

Collecting localities (see Appendices 1a-1d) were mapped as dots into a global Digital Elevation Model (DFEM) base map of the Americas (United States Geological Survey- USGS http://edcdaac.usgs.gov/gtopo30/gtopo30.html), using the geographical information system program ArcView GIS 3.2 (ESRI 1999). Coordinates and altitudes of collecting sites were taken from specimen labels, ornithological gazetteers (Paynter & Traylor 1983; Stephens & Traylor 1983; Paynter 1992, 1993, 1997; Sánchez-Osés 19957), electronic gazetteer (Alexandria Digital Library Gazetteer, from the Alexandria Digital Library Project, University of California at Santa Barbara (UCSB): http://fat-albert.alexandria.ucsb.edu:8827/gazetteer), and directly from Atlas and Maps of Central and North America and the Caribbean islands. Specimens with unknown localities were excluded from the analysis.

Morphometric data

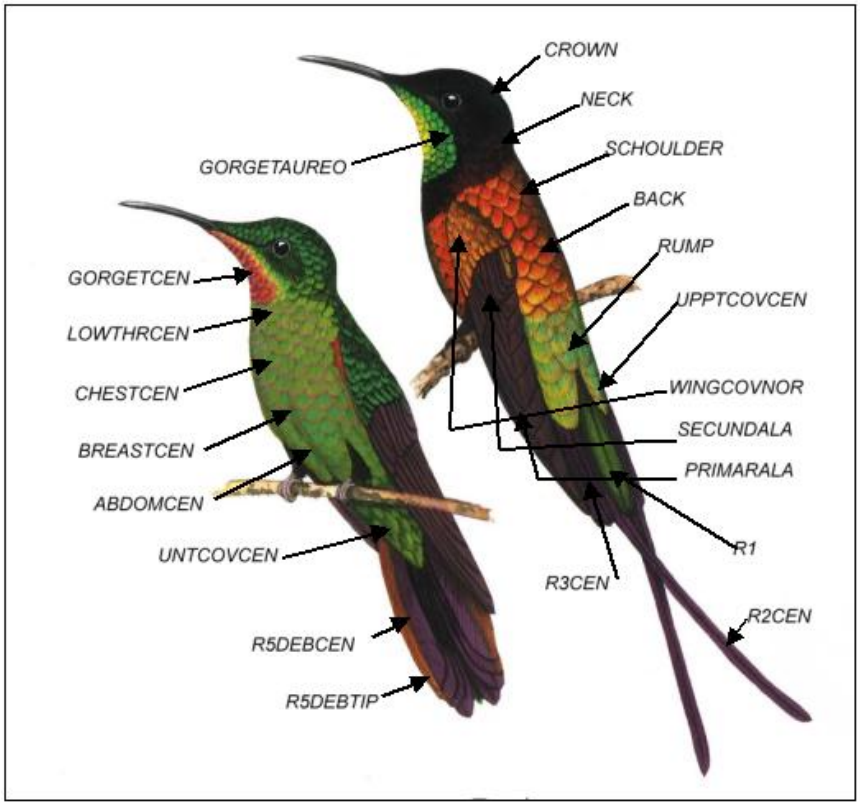
Standard morphometric measurements on the specimens were taken using a digital caliper to the nearest 0.1 mm. These measurements included:

- Bill length: distance from tip to proximal end of operculum.
- Wing length: distance from wrist to wing tip (unflattened)
- Length of the innermost tail feathers (Rectrix 1)
- Length of the second innermost tail feathers (Rectrix 2)
- Length of the outermost tail feathers (Rectrix 5)
- Body length and body mass: are taken only when available from specimen's labels, or from bibliographic references.

Color measurements (spectral data)

Color measurements were conducted using USB2000 fiber optic spectrometer connected to a PX-2 pulsed xenon light source (both from Ocean Optics Inc), and combined to the

OOIBase32 spectrometer operating software. Reflectance was calculated relative to a WS-1 white standard. The measurements were made on the various body areas. Modifying Johnsgard (1997) plumage topography, the body of the specimens was divided in 30 areas with some of the corresponding lateral measurements (Fig. 1). In order to conduct the different analyses, these body parts were codified, and each was assigned a number (Table 3).



Drawings modified from David Alker ´s original artwork

Fig. 1. Body areas where color determination was conducted (for abbreviations see text below).

The body parts considered for this research can be divided into four groups:

- Dorsal area: crown, neck, shoulder, back, rump, and uppertail coverts (upptcover);
- Ventral: This area includes not only the central measurement of each body section but also the lateral measurements of each. Gorget (gorgetmed, gorgetaureo, gorgetlat), lower throat (lowthrcen and lowthrlat), chest (chestcen and chestlat), breast (breastcen and breastlat), abdomen (abdomcen and abdomlat), undertail coverts (untcovcen);
- Wing: coverts (wingcovnor), secondary feathers (secundala), primary feathers (primarala);
- Rectrices: r1 (r1cen, r1tip), r2 (r2cen, r2tip), r3 (r3cen, r3tip), and r5 (r5debcen, r5debtip).

Body parts	Code	Body parts	Code	Body parts	Code
crown	1	chestcen	17	r1	32
neck	2	chestlat	18	r2cen	33
shoulder	3	breastcen	20	r2tip	34
back	4	breastlat	21	r3cen	35
rump	5	abdomcen	23	r3tip	36
upptcovcen	6	abdomlat	24	r5tip	38
gorgetmed	12	untcovcen	26	r5debcen	39
gorgetlat	13	wingcovnor	29	r5debtip	40
lowthrcen	14	secundala	30	gorgetaureo	41
lowthrlat	15	primarala	31	r1tip	43

Table 3. Codes used to identify the body parts of specimens.

Data analyses

The morphometric and spectral data were handled and analyzed using four software packages: (1) The spreadsheet Excel (Microsoft Excel 2000) to enter and handle both morphometric and plumage spectral color data, and to make graphs of the spectral data; (2) the computer statistical package SPSS version 10.0 (SPSS 2000) to conduct all statistical analyses and to construct part of the graphs for the presentation of statistical results; (3) the phylogenetic analyses were performed using the computer software PAUP* 4.0b.10 (Phylogenetic Analysis using Parsimony) (Swafford 2001); (4) the geographical information system program ArcView GIS 3.2 (ESRI 1999) was used to make all the working maps and also to help in the definition of preliminary groups within each species in order to conduct further analyses.

A t-test (significance level of $p<0.05$) was conducted on the morphometric data of each species to determine significant sexual dimorphism (Appendices 2a, b, c and Appendix 3). Since all the species under study showed a certain degree of sexual dimorphism, all the subsequent analyses were performed separately for males and females. Only for the phylogenetic analysis were color and morphometric variables from both males and females pooled together for each analysis. Analysis of variance (ANOVA), and the *post hoc* Tukey test for unequal samples, with a significance level of $p<0.05$, were used to complement the information that allowed the separation of preliminary groups. ANOVA was also used to describe the morphometric differences in the final taxa. A Pearson correlation analysis was performed to find the relationship between morphometric data and geographical variables, such as latitude and longitude.

The analyses of the color spectra data were conducted by principal component analysis (PCA) and discriminant function analysis (DFA) (Sokal & Rohlf 1981, Otto 1999, Malinowski 2002). A PCA was conducted on each body region of males and females of each taxon or group of taxa to reduce the spectral color data. The scores of the first three principal components (PCs) were then used as data sets to perform DFAs to evaluate the separation of natural taxa. These first analyses provided the taxonomic units (TUs) to be used in the phylogenetic analyses.

In order to conduct phylogenetic analyses by PAUP* 4.0b.10 (Swafford 2001) the variables needed to be discrete. Therefore, the generalized frequency coding (GFC) (Smith & Gutberlet 2001) was used to code the morphological continuous data. The color data (three first PCs of each body part) and morphometric data (body mass, total length, bill length, wing length and the length of rectrices 1, 2, and 5) were then coded and further analyzed.

Some practical considerations:

- Due to the great amount of data handled during this study, all subjects (species, sex, ornithological collection, body part) are coded, and the terminology used for the variables in the GFC is also explained (see Appendix 4).
- Due to the amount of PCAs, I include appendices with tables showing only the PC scores used to conduct each analysis.
- After each DFA I include only the final plots using factors 1 and 2 as coordinates, and some of the final statistics (as will be explained in each section).
- In the case of the phylogenetic conclusions, I show the resulting phylogenetic trees with basic statistics and add appendices with the PC scores and morphometric data used, the final matrices introduced in each PAUP analysis, and a list with the variables and their weights.
- To show plumage coloration differences among groups, I include appendices with all the spectral graphs, leaving only those more relevant as figures within the text.

Definition of preliminary pools for analysis

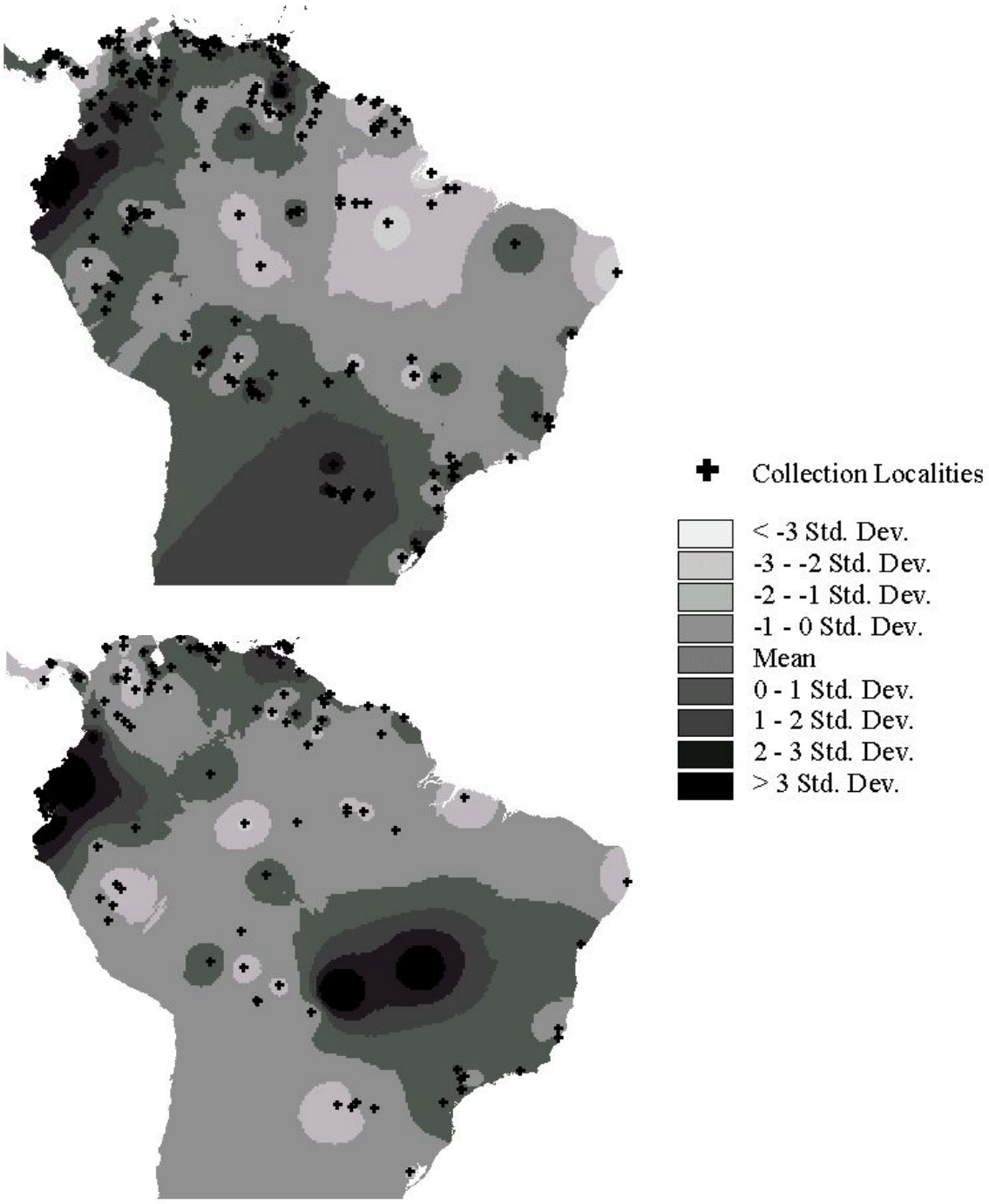
The definition of populations or pools of individuals is essential in order to investigate the geographic variation of a character within a given species. The present study includes taxa occurring on islands or groups of islands, like *Eulampis* and some *Anthracothorax* species that inhabit Caribbean islands. For these cases, each island constitutes a separated natural preliminary pool. However, in the case of the genera *Topaza*, *Campylopterus*, and those *Anthracothorax* species distributed on the mainland, the definition of pools needs another set

of criteria. Usually this separation has been done by using criteria such as distance between pools or the existence of potential geographical barriers (Vuilleumier 1968; Graves 1980, 1985; Bleiweiss 1985; Schuchmann & Heindl 1997; Weller & Schuchmann 1999; Schuchmann *et al*. 2000; Schuchmann *et al.* 2001). However, without adequate knowledge of the natural history of the species, this might be a very arbitrary method. I tried to find more objective criteria that would include the use of the surface tools of ArcView on part of the morphological data to make a preliminary delimitation of groups that would then be corroborated by other statistical analysis (ANOVA). The definition of preliminary pools is made following this sequence (see Fig. 2 as an example of the procedure):

1. I assume every species is a uniform group (in the case of *Topaza*, all specimens within the genus).
2. I conduct a PCA on the morphometric data (bill length, wing length, r1, r2, and r5) of each species and extract the first PC.
3. I use the surface tools of the Geographical Information System, ArcView, to determine a preliminary differentiation of groups within each species according to the first PC. Using the surface menu of the program, I interpolate a grid on the geographical distribution of the species using the IDW method and the value of the first PC from the morphometric analysis as Z-value field, assuming no barriers. The standard deviation is set to classify the output grid.
4. The groups determined by the ArcView are then statistically compared (ANOVA and Tukey test $p<0.05$) and regrouped according to the geographic proximity, and the statistical morphometric differences among them. This process is done independently for both sexes and a consensus conclusion is found for each species.
5. After the first separation of individuals through this graphical procedure, the preliminary pools also need to follow these further criteria:

    - A preliminary pool cannot be part of two or more recognized subspecies (according to Schuchmann (1999) and/or Peters (1945), and/or Hu *et al*. (2000) for *Topaza*).
    - A group cannot be divided by potential geographical barriers.

Fig. 2. Graphs of surface created by ArcView, using the first PC extracted from the morphometric data of *Anthracothorax nigricollis* as an example of the first step in the methodology used to define pools to conduct the statistical analyses of each species.



Practical consideration

Due to the number of graphs and statistical analyses conducted for each species, I only show the surface figures resulting for *Anthracothorax nigricollis* as an example of the method (Fig. 2). The final grouping will be shown for each species in the corresponding section. The idea behind the procedure is to combine the information coming from the data itself with the data on distance between populations and potential geographical barriers, in order to avoid a potential circular argument. This procedure allows a finer subdivision of preliminary pools that would then be used as the basis for the analysis of geographical plumage color variation.

Methodology to measure and analyze color spectral data

Theoretical framework on studies of color variation in animals

Different methodologies have been used to conduct studies related to animal coloration. For a long time human subjective color perception was the rule, but it has been extensively discussed that filtering color data through the human sensory system introduces many problems into the analysis of color (Endler 1990, Cuthill & Bennett 1993, Bennett *et al*. 1994, Hunt *et al.* 1998, Grill & Rush 2000). One problem is that human color judgments are difficult to repeat and almost invariably subjective (Grill & Rush 2000). In order to minimize the subjectivity, several color references, such as the Munsell Color Standards, have been used (Smithe 1975; Schuchmann & Duffner 1993; Schuchmann & Heindl 1997; Heindl & Schuchmann 1998; Weller & Schuchmann 1999; Schuchmann *et al*. 2000; Weller 2000a, b; Schuchmann *et al*. 2001).

Another negative aspect of the human visual system as a reference to study color variation in organims is that in a very real sense all humans are "color blind" when compared with many other vertebrates (Thorpe 2002). Considerable evidence now exists that birds and some fish species probably have at least four dimensions to their color vision, owing to the possession of more than three cone types. Since at least one of these four receptors lies in the UV spectrum, this does not just mean that humans are missing out on a few colors within the UV, but implies that only a few hues seen by birds and fish can be perceived by humans (Burckhardt & Maier 1989, Goldsmith 1990, Burckhardt & Finger 1991, Jacobs 1992, Bennett *et al*. 1994, Finger & Burckhardt 1994, Burkhardt 1996). The "dimensionality" of color vision is determined by the number of interacting receptor types, and if color is produced by the interaction of *n* cone types there are *n* orthogonal dimensions of color vision (Bennett *et al*. 1994). Additionally, different wavelength spectra can produce the same hue if the output from the cones remains identical, and the same wavelength spectra will produce different hues for animals that differ in the absorption spectra of their cone types. Specifically in hummingbirds, this UV visual capacity has been linked to their behavior and social evolution (Bleiweiss 1994).

Contrary to what has been previously thought, humans seem to be the exception rather than the rule in not seeing within the UV spectrum (Bennett *et al*. 1994). An amino acid mutation in the SWS1 visual pigment of primates shifts the cone sensitivity to longer wavelengths and renders cones insensitive to UV light; hence, human color vision is restricted to wavelengths between 400 and 700nm (Yokoyama & Shi 2000). Much has been said of the consequences of this restriction on human vision for behavioral studies of other vertebrates with UV vision, but it is still not known to what extent this is pertinent to comparative evolutionary studies using color (Thorpe 2002), and consequently to systematic, taxonomic or phylogenetic studies based on color characters.

Romney & Indow (2002) stated that there is no difference between human perception and spectrometric measurements of the Munsell color standards; however, they measured human perception directly from the cone receptors, without taking into account all the external factors that play an important role in visual perception. At the same time, other researchers have pointed out that different results are obtained when direct human examination or a spectrometer are used to determine color. They also state that spectroradiometry provides a higher resolution and is more sensitive in detecting variation of color than Munsell color matching techniques (Endler 1990, Zuk & Decruyenaere 1994). Throughout the years several photometric techniques have also been tried, such as the "LAB" system to describe color characters in terms of opponent-color coordinates (e.g., Graves 1997, 1999a, 2000). However, when this and other methods were first introduced, they had the same limitation as the Munsell colors, since most standard cameras and other photometric equipment were optimized to the human visual system (Endler 1990, Zuk & Decruyenaere 1994, Grill & Rush 2000).

Currently there is sophisticated equipment available to increase objectivity when measuring color in specimens. One of these possibilities is the collection of spectral data coming directly from the object under study; such data are superior to observational data in several ways (Grill & Rush 2000). Resolution and range of spectrophotometers can far exceed the capabilities of human vision. This is especially important when infrared or ultraviolet wavelengths play important biological roles (Grill & Rush 2000). Increasingly, studies use reflectance spectra

over the bird-visible range to quantify the colors of avian plumage (Burckhardt & Maier 1989, Burckhardt & Finger 1991, Cuthill *et al.* 1999), and there has been an improvement in the measuring techniques and statistical methods for comparing color spectra. Cuthill *et al* (1999) present an extensive discussion on the history of these different methods.

To find the best technique to analyze color spectral data is still a challenge. Several studies have been conducted by cutting the spectrum in different, mutually exclusive adjacent units of equal nanometer range. They justify their approach on a visual biological context such as segment classification or color space (Endler 1990, 1993; Zuk & Decruyenaere 1994; Endler & Thery 1996). Thorpe (2002) has argued that dividing the spectrum into a few arbitrary units of equal nanometer range may not be optimal for many comparative evolutionary studies. He has proposed a methodology to derive a few relatively independent and informative spectral segments. They are non-overlapping but may be of unequal size with gaps between them. According to the author, his segments are free of biological context and can be used as characters in comparative evolutionary and systematic studies.

Some authors divide the spectrum into equal units, along the wavelength range of the group under study, and treat them as different variables to be subjected to principal component analysis (PCA) (Endler 1990, Endler & Thery 1996, Bennett *et al.* 1997, Hunt *et al*. 1998, Cuthill *et al*. 1999, Grill & Rush 2000). PCA simply describes the variation in the reflection spectra and makes no assumption about the color vision of the animal, in contrast to color-space modeling (Cuthill *et al*. 1999). Additionally, PCA decreases the number of variables to be considered without sacrificing the information provided by the whole spectra. These new variables are the first principal components (PCs), which are independent of each other. Usually the first three are enough to explain almost 100% of the variation of reflectance spectra (Cuthill *et al*. 1999). These PCs obtained from the PCA have also been subsequently used to conduct other analyses, such as discriminant function analysis (DFA) (Cuthill *et al*. 1999). This perspective is superior to selecting only parts of each spectrum, such as "highest peaks" or "mean reflectance," and that is the reason why I take it in order to use all the information of the spectra for statistical analysis.

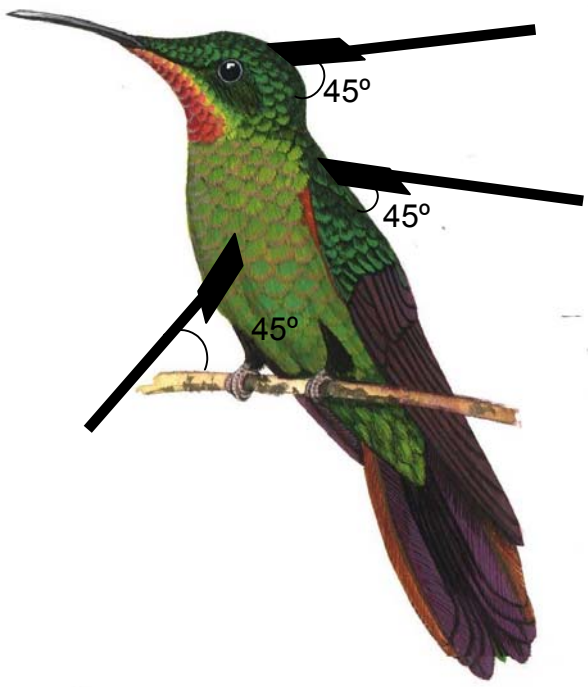
It may be argued that the level of detail provided by spectrometric measurements of color is not needed for taxonomic studies and that human vision is enough to evaluate "biologically meaningful" differences that may be important to identify species, moreover, when the very species concept is a controversial unit created by man. However, if color is an important consequence of the evolutionary process, and groups of organisms are subjected to different adaptive pressures, we have a direct connection to the need to find a more objective way to determine color differences. Additionally, the detection of subtle differences in plumage coloration may reveal more taxonomic diversity, adding a conservation component to the method (Cuthill *et al*. 1999).

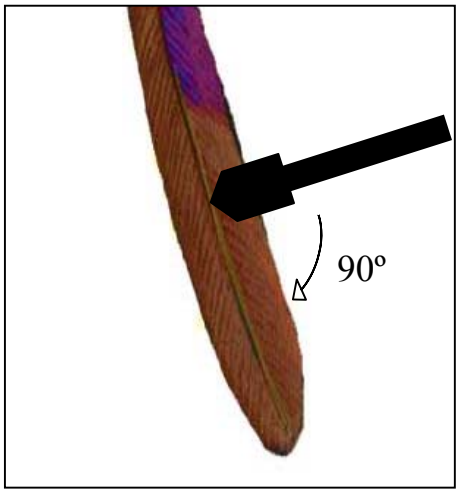
Color determination on the bird specimens

Animal color patterns can consist of structural colors and pigments. Most pigment-based colors and some structural colors reflect roughly evenly in all directions, and their reflectance color does not change with the angle of the reflected light (Endler 1990). Hummingbirds have long been known for having an important structural color component, and these structural colors characteristically change depending on viewing and lightning angles (Endler 1990). However, the means by which many avian structural colors are produced is still contentious (Finger 1995).

Reflectance will be maximized when the angle of incidence and reflection are equal because the layers producing the iridescence act in a mirror-like fashion (Finger 1995). An empirical preliminary analysis was conducted to find the angle that would produce the largest amount of total reflectance. An angle of 45 degrees resulted from this preliminary analysis. It is important to note that the spectral shape did not change with the angle of light incidence, which means that hue remains basically the same and the repeatability of the measurement was high. Previous works have also determined 45 degrees as the most useful angle for characterizing iridescent avian plumage (Church *et al.* 1998, Hunt *et al*. 1998, Cuthill *et al*. 1999).

For the present study (and the preliminary determination of angle) an optic fiber was used to take each measurement. At the tip of this fiber I added a plastic piece cut at a 45-degrees angle to maximize the mean reflectance from the feathers. To prevent ambient light entering the system I wrapped the plastic with black tape and placed a black sheet of paper underneath the bird. The probe was located directly on the skin (Fig. 3 and Fig. 4), so that the light measured is only that comming from the original light source reflected by the feathers.





Drawings modified from David Alker ´s original artwork

Fig. 3. (left). Angle of color measurement. **Fig. 4. (right)**. Color measurement on rectrices.

In birds in general, and especially in hummingbirds that show iridescence, not only the angle of measurement can make a difference, but also the direction of the light in relation to the feather when taking the measurement. For this reason, and in order to be consistent and minimize the variation, determination of plumage color was also made in the same direction relative to the feathers (Fig. 3). Only for rectrices was the highest total reflectance detected

when taking the measurement perpendicular to the main shaft of the feather (Fig. 4). It is important to consider that depending on the level of detail needed for each study and depending on the objective of the research, individual feathers should be measured (see Cuthill *et al*. 1999). The objective of this study, besides testing the methodology, was to use the data to study the geographical variation of color in different hummingbird taxa, in order to conduct taxonomic, phylogenetic and biogeographic studies, so a general measure of each part of the body appeared to be sufficient.

Handling of spectral data

The USB2000 spectrometer, with associated PX-2 pulsed xenon light source and OOIBase32 spectrometer operating software, allowed me to obtain, in each measurement, the complete spectrum from 220 to 750nm, in terms of percentage of reflectance at intervals of approximate 0.28 nanometers. This spectrum is graphically represented by a curve indicating reflectance (%) (Y-axis) *versus* wavelength (X-axis). This curve is then limited to the range between 300 nm and 730 nm for each measurement. Less than 300 nm is not relevant here, since 300 to 400nm constitute the UV part of the spectrum that can be detected by birds with UV receptors. The other extreme (730-750 nm) is excluded to avoid errors made by the instruments (pers. observation). Each color determination used for analysis was already the mean of 30 measurements (made automatically by the instrument when set on the software) from the same body spot with an approximate diameter of 3 mm.

Each color measurement taken on a body area of a specimen produced an output file of approximately 2000 lines. This file gives the percentage of reflectance along the range from 220 to 750 nm. (which is then limited to 300-730 nm as already explained). In order to be able to make further analyses with the spectra, and avoid unnecessary detail, the information on reflectance along the wavelength range is reduced to the medians of 10-nm bandwidths following Cuthill *et al*. (1999). Each 10-nm segment is considered a different variable to be used in further analyses. This rearranged information is then added to unique Excel files, one for each genus under study, using a macro that allows the more rapid import of data. This was

necessary, taking into account that every specimen generates 30 different original color files (30 different body parts). For the 3,737 specimens measured from the four genera studied, I handled a total of 112,110 original files and converted them into only four files (one per genus) with the color information on each body part from each individual to conduct statistical analyses.

Cuthill *et al* (1999) consider that medians have the advantage of being insensitive to the occasional artifactual "spike" in recordings. I agree with this statement, and this method also improves the measurements made by the PX-2 pulsed xenon light source. According to the manufacturers (Ocean Optics, pers. comm.), the PX-2 lamp is not supposed to be an ideal choice for making color measurements due to the "spikiness" of the lamp spectra and its inherent flash-to-flash variation. However, by using the multiple flash mode and averaging multiple scans very repeatable data can be obtained. This light source is more accessible than the deuterium light source that has been used to take the UV range of the spectra in other studies (Andersson & Amundsen 1997, Thorpe 2002). Moreover, after testing the PX-2 light source during my study, and using the mean of 30 scans for each color determination, I do not only find very consistent spectra, but I also corroborate Cuthill´s statement that taking the medians prevents potential problems.

As expected, the color variables (each 10-nm segment), being consecutive "pieces" of the spectra, show a high correlation between them. For this reason PCA is a useful tool, since the variation in spectra is normally described by a small number of principal components that are by definition independent (orthogonal) (Cuthill *et al*. 1999). In PCA, the first PC is the linear combination of the original variables that show the highest variance. PC2 is defined as the axis with the next highest variance, subject to the constraint that it is orthogonal to PC1, and so on (Sokal & Rohlf 1981, Otto 1999, Malinowski 2002).

Interpretation of the first PCs in coloration data

Color has been explained as having three psychophysical dimensions, or three main features: brightness, chroma, and hue. Brightness refers to overall light intensity at all wavelengths, chroma is a measure of saturation of the focal color, and hue is what people usually refer as color (e.g., yellow, red, blue, etc.). Colors with high chroma are very pure, vibrant colors with little or no gray mixed in while low chroma colors appear faded and washed out (Grill & Rush 2000).

PC1, PC2, and PC3 have been interpreted as brightness, chroma, and hue, respectively (Grill & Rush 2000). The researchers have based their interpretation on the loading patterns; when they are strong across the entire range of the wavelengths, PC1 can be interpreted as brightness, or overall light intensity. According to Cuthill *et al*. (1999), in a PCA on raw spectra, PC1 would typically describe variation in mean reflectance, since it often forms the majority of between-spectra variation (typically > 90%). There is now fairly universal agreement that PC1 is best described as brightness but there is considerably less certainty about the nature of PC2 and PC3 (Endler 1990, Hunt *et al*. 1998, Cuthill *et al*. 1999, Grill & Rush 2000).

Subsequent principal components would capture variation in spectral shape. Component loadings for PC2 suggest that this component describes the relationship between levels of short and long wavelengths; largely the slope of the spectral curve determines this relationship. According to several authors (Endler 1990, Grill & Rush 2000), curve shape is indicative of the level of chroma in a color sample. After PC1, much of the subsequent variation between spectra is in the relative amount of long-to-short-wavelength light (objects are either reddish or bluish), then PC2 would have positive coefficients associated with long-wavelength reflections, negative coefficients with short wavelengths, and zero coefficients with medium wavelengths (there is no variation at these wavelengths) (Cuthill *et al*. 1999).

Based on the importance of the middle wavelengths in the loading for the third component, these same authors (Endler 1990, Grill & Rush 2000) have interpret PC3 as hue. Hue is directly related to the regions of a spectrum with the highest slopes. However, slopes of most spectra are not maximized at the extreme ends of the spectrum, rather, maximum slope usually occurs in the "middle" of the spectrum, so accurate interpretation for PC3 for all cases is still the subject of study and controversy.

Some authors (Cuthill *et al*. 1999, Thorpe 2002) have removed the brightness element from the spectra by standardizing the data in different ways. They argue that the variation in brightness is too high among the spectra compared with the shape of the spectrum. Although that may be true, total reflectance is an important component of color in animals and may play a biological role. For this reason I believe that brightness has to be included in these types of analysis.

The derived principal components have a direct relationship to coloration being independent as variables. For this reason, I use them as a way of describing spectral shape in a concise way to be able of applying statistics to compare groups, as was used by Cuthill *et al* (1999).

Using color data to determine differences among populations

In order to compare preliminary pools and make taxonomic conclusions, the spectral data needed to be reduced without sacrificing the information provided by the whole spectra. The data of each spectrum were then entered into a principal component analysis (PCA) (Otto 1999) in which each 10-nm segment of spectrum is a variable and each spectrum an observation. The *eigenvectors* were then used to give scores to each spectrum that maximized the variance among spectra (Endler 1990, Otto 1999, Malinowski 2002). Each principal component (PC) is a weighted linear sum of the original data. Usually the first three PCs of spectra represent more than 95% of the variation. These findings are consistent with previous results where PCA was used to assess color (Endler & Thery 1996, Bennett *et al*. 1997, Cuthill

et al. 1999, Grill & Rush 2000). In this study, the first three PCs are taken in order to conduct two sets of discriminant function analysis (DFA).

PCA essentially generates a new color space for the variables, and differences between data sets must be accounted for if comparisons are made. As a consequence, several authors have discussed whether PCA may not be suitable when direct quantitative comparisons are needed between experiments or between groups (Endler 1990, Bennett *et al*. 1997, Cuthill *et al*. 1999, Grill & Rush 2000). In the analysis of color spectra using PCA, this has to be conducted to all and only the data to be compared (no data can be added afterwars). In order to add more data, the analysis has to be remade from the beginning. This statistical method is simply a way of redescribing variation in an efficient manner, and one must start by deciding what variation one is most interested in describing (Cuthill *et al*. 1999). Here I separated the data of each sex in order to avoid differences between sexes masking the differences between the compared populations. As implied by Cuthill *et al*. (1999), if a PCA is performed on all the plumage regions together, the majority of between-spectra variation in shape comes between the iridescent and non-iridescent regions. PC scores from one body region cannot be compared with PC scores of another, unless only the data from these two regions is included in the analysis from the beginning.

For the DFA I used the PCs from each body region, since I wanted to use as many variables as possible that would allow me to discriminate different groups of individuals and assign membership to the controversial populations. Applying a PCA to the spectral data from each body region only gives a new color space to each set of data. Performing a DFA to the first three PCs resulting from the color data of each body part (30), I obtained a discrimination of almost 100% in both sexes of *Topaza* and a high discrimination for all the other genera.

It may seem abstract to conduct a DFA using the PCs coming from a PCA. The DFA takes these PCs to build other factors (discriminant factors) that will again explain most of the variance in the data. The three first PCs provide “summary information” on the important

components of the color on each specific part of the body. Then the DFA takes this overall information on body color and analyzes distances between bird populations.

There is controversy about the use of PCs as variables to conduct other multivariate analysis. Thorpe (2002) does not recommend using the output from one multivariate analysis (orthogonal PCA scores) where between-group and within-group covariances are compounded to conduct another multivariate analysis, which is specifically designed to separate between-group and within-group covariance. However, according to Cuthill *et al*. (1999), PC scores can be entered into multivariate analyses to determine group differences in plumage. The authors state that a single multivariate test on several PCs together provides a useful summary statistic for whether any aspect of spectral shape differs between groups. Additionally, they used DFA to separate and accurately sex particular individuals of European starling (*Sturnus vulgaris*) on plumage spectra alone. They used the mean reflectance and the first two principal components for the iridescent throat and coverts (the same as using the first three PCs without excluding the overall brightness), and obtained a discriminability between sexes of a 100% on the sexually dichromatic regions most likely to be involved in mate choice.

Phylogenetic analysis based on spectral color data

Conclusions about similarity among pools (groups of individuals) can be made by using DFA. However, this analysis alone does not allow the making of any conclusion on the degree of relationship among these pools. The DFA results give us a phylogenetic working hypothesis that can be tested by conducting a phylogenetic analysis.

The software program PAUP* 4.0b.10 (Swafford 2001) is one of the software packages most often used to conduct parsimony phylogenetic analysis. However, this program can only be applied if the characters under study are discrete. This status applies neither to color spectral data nor to morphometric data.

Generalized Frequency Coding applied to continuous morphological data

The generalized frequency coding (GFC) is a method developed by Smith & Gutberlet (2001) that can be used to code any type of polymorphic multistate character (qualitative or quantitative). This method makes a direct translation of frequency distributions into a suite of discrete states that can be handled by PAUP* 4.0b.10 (Swafford 2001). By using GFC, continuous characters, such as the morphological data used here, are divided into subcharacters so that each observable state is treated as its own character. Variation within each subcharacter is then coded by using frequency bins (Smith & Gutberlet 2001).

In order to apply GFC to my morphological data to be used by PAUP, I prepared the data sets for each analysis. In this section I describe the general methodology applied to each data set, and in each result section the details of each analysis will be specified. For each analysis to be performed I prepared one unique Excel file (spreadsheet software) for males and one for females, each with all the spectral information of all body parts of all the specimens from the groups in analysis. Then a PCA was conducted on the data of each body part. Only the first three PCs were extracted per body part, and the scores saved as new variables for each individual to conduct further analyses. As explained, these three first PCs explain more than 95% of the variation in the data. The PC scores coming from the PCAs were included in a new Excel file and the morphometric data for each individual were also added at this point. Groups are made and tested according to the working hypothesis in each case. The taxonomic units (TUs) (species or subspecies depending on the hypothesis) are identified in this unique Excel file and the GFC is then applied.

To perform GFC, three main matrices have to be created from the morphologic variables (see Smith & Gutberlet 2001). The morphologic (continuous) variables in this case are the three first PCs from each body part plus seven morphometric measurements (body mass, total length, bill length, wing length, and length of rectrices 1, 2, and 5). In the cases where all the 30 body parts were taken, I considered a total of 194 variables (30 body parts for males and 30 for females multiplied by three PCs plus the seven morphometric variables of each sex). The

total number of body parts included in each phylogenetic analysis is variable, and usually less than 30. The data from body parts including many gaps (missing data) are not considered.

To create matrix A (see Smith & Gutberlet 2001) each color character is subdivided into sections of 0.2 units. For morphometric data, body mass is divided into sections of 1 unit (unit = g), total length into sections of 1 unit (unit = mm), and the others into sections of 0.5 units (mm) each. Depending on the total variation within each variable in each analysis, totals of between 85 and 141 subvariables were obtained. For example, if I considered 24 body parts and seven morphometric characters and divided the variables in 100 subvariables (or new variables), then I had a total of 18,000 (180*100) working variables that were then used to conduct further analysis. With these subvariables I created another data set that was then used to obtain the frequencies of specimens that presented a given variation within each new variable from each of the TUs of the working hypothesis.

The information from matrix A was then used to create matrix B (see Smith & Gutberlet 2001) by calculating cumulative frequencies. A cumulative frequency is the sum of all sample frequencies (from matrix A) within a TU to the right of the subcharacter column being filled. A new matrix C of subcharacters by taxa is constructed (see Smith & Gutberlet 2001) to replace the cumulative frequencies in matrix B with letters, according to a coding table (Table 4). This table is modified from the frequency bins of Wiens (1995), to finally obtain the new coded variables to conduct the phylogenetic analysis.

Range	Code
{0-0.04)	a
{0.04-0.08)	b
{0.08-0.12)	c
{0.12-0.16)	d
{0.16-0.2)	e
{0.2-0.24)	f
{0.24-0.28)	g
{0.28-0.32)	h
{0.32-0.36)	i
{0.36-0.4)	j
{0.4-0.44)	k
{0.44-0.48)	l
{0.48-0.52)	m
{0.52-0.56)	n
{0.56-0.6)	o
{0.6-0.64)	p
{0.64-0.68)	q
{0.68-0.72)	r
{0.72-0.76)	s
{0.76-0.8)	t
{0.8-0.84)	u
{0.84-0.88)	v
{0.88-0.92)	w
{0.92-0.96)	x
{0.96-1}	y

Table 4. Codifying table for the generalized frequency coding technique (GFC).

To apply PAUP I had to create the final matrix for the phylogenetic analysis. So I merged states for all characters from each matrix C (each polymorphic multistate character had been transformed into a separate matrix C) into a single final matrix. This matrix included information for both sexes together.

Some characters are non-informative because they present no variation among TUs or are autapomorphic. The non-informative characters are then eliminated from the data set, and in order to avoid extra-weighting due to the number of subcharacters of each original variable, each new variable is weighted following the approach of "unequal subcharacter weighting" (USW) (Smith & Gutberlet 2001). The multiple subcharacters used to represent a single character are not independent, so subcharacter weights needed to be adjusted such that GFC did not artificially inflate the influence of polymorphic multistate characters (Smith & Gutberlet 2001). Weighting is used to make the contribution of the set of subcharacters for a given character equal to that of one non-polymorphic character (Smith & Gutberlet 2001).

The weight of each character must be divided by the total number of informative subcharacters (IS) used to represent the single character of which it is part. Then the weight of every subcharacter should be divided by the number of steps (NS) between the lowest and the highest frequency bins included in it. The maximum number of steps is 24, which, because of the ordered treatment of each subcharacter, occurs if at least one taxon is assigned an "a" and at least one other is assigned a "y" (Wiens 1995, Smith & Gutberlet 2001). Then I used the formula (32.676/NS)/IS to give each subcharacter an adequate weight. The number 32.676 come from the program PAUP, and it represents the maximum weight allowed in PAUP 3.1 and PAUP* as explained by Smith & Gutberlet (2001).

The final matrix containing all the informative weighted variables was entered in the phylogenetic computer program PAUP* 4.0b.10 (Swafford 2001). To reconstruct the phylogenetic relationships among the studied taxa, a maximum parsimony analysis was performed to obtain the final phylogenetic results in each case. The analysis, using PAUP* 4.0b.10, starts with a heuristic search for all possible trees, with the branch-swapping

algorithm set to “tree-bisection-reconnection” (TBR) and a simple addition sequence. The generated trees are rooted with the outgroups and, fortunately, for all cases in this study only one tree was generated. To verify how the frequency of characters in the nodes supported each branch, a Bootstrap analysis was carried out based on a heuristic search with the parameters mentioned above.

Geographical variation and review of the taxonomy and phylogeny of the genus *Topaza* GRAY, 1840

Theoretical background

Within the hummingbirds, members of the genus *Topaza* are among the most distinctive and commonly illustrated trochilids (Plate 1). They have been considered one of the most brilliant hummingbirds due to their conspicuous coloration (Greenewalt 1960). *Topaza* is a large hummingbird of about 10 g that occurs in South America up to the northern hemisphere, and inhabits lowland forests, up to 500 m.a.s.l., mainly inland, and it is frequently found in the forest canopy and along gallery forests near river banks and creeks (Schuchmann 1999). *Topaza* does not show flocking behavior, and individual social contacts are rare, occurring occasionally around superabundant nectar sources (Schuchmann 1999). The Crimson Topaz (*Topaza pella*) is one of the few species that have nest aggregations, within a radius of 20-30 meters (Schuchmann 1999). The genus *Topaza* shows a marked sexual dimorphism in morphometric characters (Appendix 2a) and in plumage coloration, in which males show iridescent bright colors mainly on the head and throat, but also on the upper- and underparts, while females are duller in appearance (see Appendix 5).

The original description of *Topaza* was made by Linnaeus (1758) based on an individual that was captured in Surinam, and was designated as *Trochilus pella*. Only in 1840 was the name *Topaza* recognized by G. R. Gray (1840) and then adopted by Simon (1921). The genus *Topaza* presents a currently controversial taxonomy that needs to be elucidated and clarified (see Peters 1945, Schuchmann 1999, Hu *et al*. 2000, Dickinson 2003).

Some authors recognize two species within this genus (Peters 1945, Hu *et al*. 2000, Dickinson 2003): *Topaza pella* and *Topaza pyra*. *Topaza pella* is divided into three subspecies: *T. pella pella* Linnaeus, 1758, found in eastern Venezuela and the Guianas; *Topaza pella smaragdula* Bosc, 1872 in Surinam and northeastern Brazil (north of the Amazon); *Topaza pella microrhyncha* Butler, 1926 from the south bank of the Amazon river (north-central Brazil).

Topaza pyra is divided into three subspecies: *Topaza pyra pyra* Gould, 1846 found in eastern Colombia, southern Venezuela, northwestern Brazil; *Topaza pyra amaruni* Hu *et al*., 2000 in eastern Ecuador, and northwestern Peru; *Topaza pyra* subs.? from west-central Brazil. Contrary to this description, Schuchmann (1999) considers the genus monotypic, including only the species *Topaza pella.*

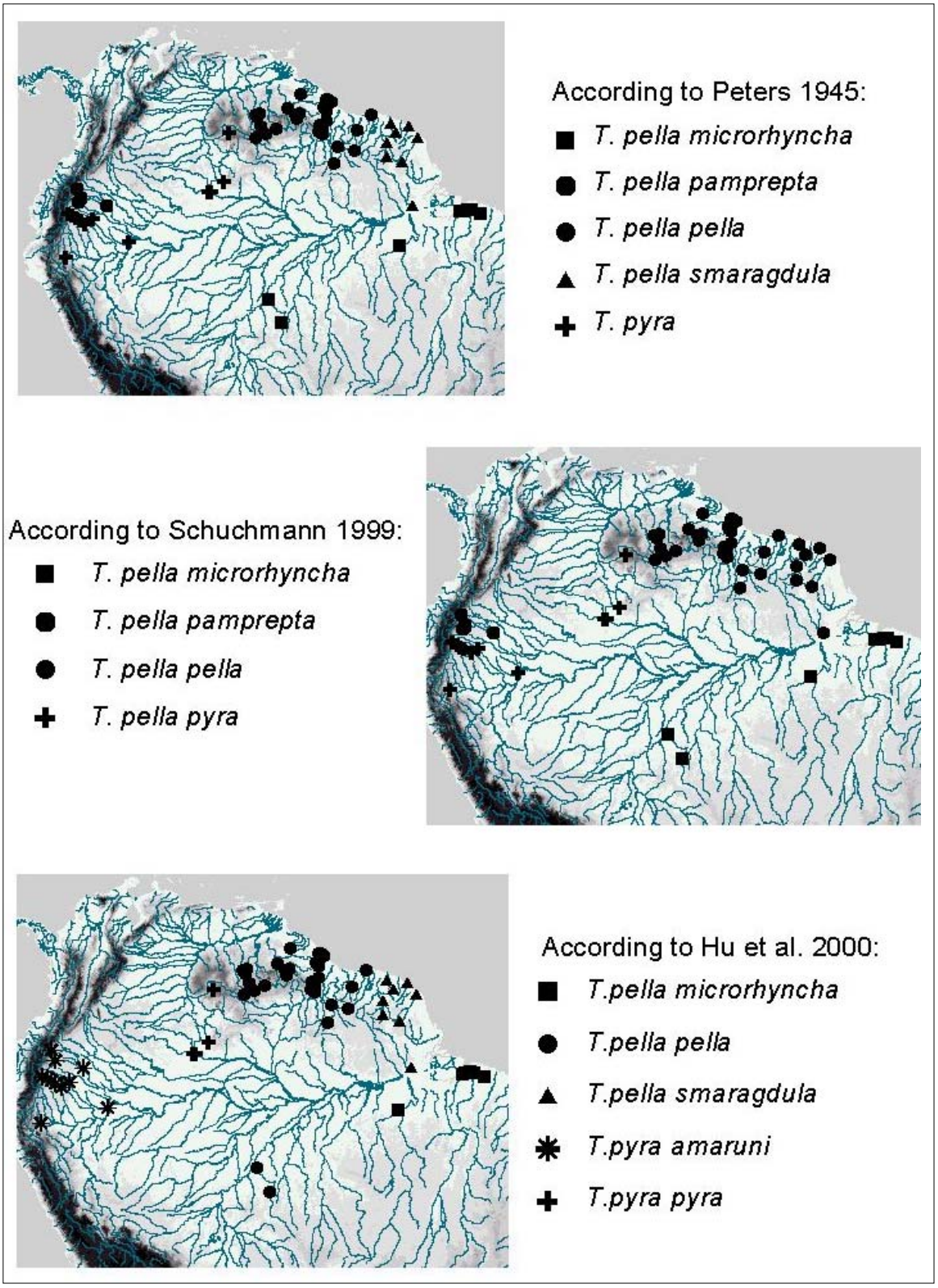
Here I separate recognized subspecies according to geographic location following three of the published taxonomies: Peters (1945) (Fig. 5a), Schuchmann (1999) (Fig. 5b), and Hu *et al.* (2000) (Fig. 5c).

1. Peters (1945) includes 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 Guiana and Surinam; *T. p. smaragdula*, in French Guiana; *T. p. microrhyncha* from in 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 showing doubts on the validity of this subspecies.

2. Schuchmann (1999), conservatively considers *Topaza* as a monotypic genus. He finds that although the two previously accepted species show some differences in habits, the color difference is only a clinal variation that would not warrant a taxonomic differentiation. Schuchmann includes Peters's *T. pyra* as a subspecies of *Topaza pella* (*T. pella pyra*), and recognizes the other three subspecies: *T. pella pella*, *T. pella microrhyncha*, and *T. pella pamprepta*. However, his *T. pella pella* includes populations in the range of former *T. pella smaragdula*, not recognized by him as a different group. The other two are in agreement with Peters's conclusions.

3. Hu *et al.* (2000), on the basis of a new morphology and coloration study, go back to Peters taxonomy, recognizing two species of *Topaza* (*T. pyra* and *T. pella*). They separate *T. pyra* into the subspecies: *T. pyra pyra* in southern Venezuela (Amazonas) and *T. pyra amaruni* in Amazonian Ecuador, along Rio Napo and Rio Corrientes, and

Fig. 5. The genus *Topaza* and the geographical distributions of species and subspecies according to three authors:



western Amazonian Peru. They include the taxon *pamprepta* in *T. pyra pyra* and accept the three other subspecies previously recognized by Peters: *T. pella pella*, *T. pella smaragdula* and *T. pella 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 according to a published map), and not *T. p. microrhyncha* as in Peters (1945).

***Preliminary 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) consider that the subspecies *Topaza pella pamprepta* should not be recognized at all, and I would like to discuss and clear this point before the analyses. Hu *et al.* (2000) have several arguments to support their statement. Among them they argue that this subspecies is only known from three specimens taken by the same collectors (Hamilton & Goodfellows) that may have been incorrectly labeled. Additionally, it has also been discussed by Zimmer (1951) that a specimen collected by Hamilton and Goodfellows, marked as "Coca, Rio Napo, E. Ecuador, June 1899" is of uncertain origin since it was also labeled by dealers in London. Moreover, there exists evidence of other specimens of *Topaza* obtained by the same collectors that had incorrect data when compared to field notes (Zimmer 1951). In this study more specimens from the Napo area in Ecuador are included and the validity of this argument is discussed in detail.

For their study, Hu *et al.* (2000) only had access to two specimens of *T. p. pamprepta* in USNM Washington (including the holotype). One of them has been labeled as "locality wrong, Cayenne skin." The third one was sent to Germany and it is currently at Museum Alexander Koenig in Bonn. I had the opportunity to examine this third specimen (Figs. 6 and 7) and it does not differ from the two in Washington (also examined). The results place these specimens in *T. pella pella*. These three specimens show plumage color of the populations of *T. pella pella* from the extreme tip of the *Topaza* distribution through the Guianas, that include

Fig. 6. Dorsal (left) and ventral (right) view of the specimen with wrong locality found in Museum Alexander Koenig under the code 8305 and collecting number 174295.

Fig. 7. Secondaries (left) and rectrix 5 (right) view of the specimen with wrong locality found in Museum Alexander Koenig under the code 8305 and collecting number 174295.

secondary feathers (Fig. 7 left) and rectrices number 5 (Fig. 7 right) with rufous-brown color (to the naked eye), contrary to the dark brown secondaries and violet rectrices number 5 of the "*pyra*" group from the western extremity of the distribution (Fig. 8). The results of this research (see section "Taxonomic analysis of the genus *Topaza*") and these observations make it highly probable that these three individuals are really Cayenne specimens incorrectly labeled.

Fig. 8. Secondaries (left) and rectrix 5 (right) view of the specimen of *"pyra"* from Ecuador found in Museum Alexander Koenig under the code 8306.

The conclusion that these three specimens were in fact misidentified does not automatically invalidate the subspecies. Hu *et al*. (2000) also checked other specimens from the Napo river area (USNM 174293, AMNH 46072), and around this locality (ANSP 186789). I checked these specimens and three more specimens found in the Senckenberg Museum in Frankfurt that were collected in the Coca, Napo area (Figs. 9a and 9b). These specimens from Frankfurt were misidentified as *T. pella microrhyncha*, perhaps due to the ambiguity of the locality written on the label: "Rio Coca, Amazonas." However, they showed the characteristics of the "*pyra*" group from close to the Andes, that to the naked eye include dark brown secondaries (Fig. 8 left) and dark violet rectrix 5 (Fig. 9b right), contrary to the rufous-brown secondaries and rectrix 5 of the "*pella*" group from the eastern end of the distribution.

Fig. 9a. Dorsal (left) and ventral (right) view of two specimens found in Senckenberg Museum. They were incorrectly labeled as *T. pella microrhyncha*, but belong to the *T. pella pamprepta* population.

Fig. 9b. Secondaries (left) and rectrices number 5 (right) view of two specimen found in Senckenberg Museum. They were incorrectly labeled as *T. pella microrhyncha*, but belong to the *T. pella pamprepta* population.

Taxonomic analysis of the genus Topaza

I focus the analysis on the comparison of the three published taxonomies already presented, on the assumption that these previous taxonomies are good hypotheses to begin with. Those populations on which the authors show disagreement I call "unclear" (Fig. 10). They are specifically: 1) "*pamprepta*", which includes the Suno, Rio Napo population; 2) "uncertain locality", according to Hu *et al*. (2000) the subspecies "*pamprepta"* should not be recognized at all. The status of these three specimens has already been discussed in the previous section but I include them here to corroborate the conclusion; 3) "*pyra*-east," which includes 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) "*T. pella smaragdula*," which includes the populations of the Guianas and Amapa in Brazil, that according to Peters (1945) and Hu *et al.* (2000) should be part of a separate subspecies, but this is not accepted by Schuchmann (1999); and 5) "jiparana," which includes populations around the Jiparana River in Brazil that according to Peters (1945) and Schuchmann (1999) are part of *T. pella microrhyncha* and according to Hu *et al.* (2000) are part of *T. pella pella*, or possibly a new subspecies. These names are given for the purpose of the following discussion.

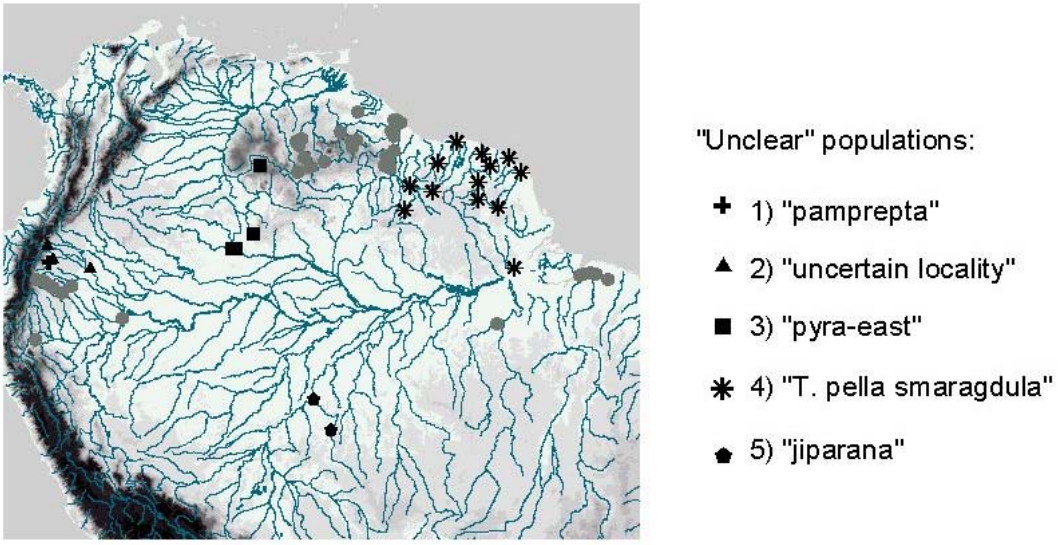


Fig. 10. Controversial populations of *Topaza*, also called "unclear" populations.

In order to solve these taxonomic conflicts, and using the data on coloration obtained here for the genus *Topaza*, I focus my discussion on these "unclear" populations.

In order to use plumage coloration data to discriminate among subspecies from the published taxonomies, and determine the membership of "unclear" populations, a principal component analysis (PCA) was conducted on each data set (body region) to reduce the spectral data (see Appendices 6a and 6b). I conducted two sets of discriminant function analyses (DFA) based on the first three PCs of each body part. The first DFA was performed to determine the membership of "unclear" populations of *Topaza*, and the second to define which variables contribute the most to the separation or discrimination of *Topaza* groups, or in practical terms, what differences in body color are more important to separate groups within this genus.

The general significance of the first scores in terms of color interpretation was extensively explained in previous sections. However, I also include a group of graphs showing the relationship between the three PC scores found for the different body parts of individuals of the genus *Topaza* and each point of the spectral range (Appendix 7a for males and 7b for females). In these graphs it is clear that a very similar relationship between these variables exists for all the body parts measured. The first PC is represented in each case by a very stable line in the positive range that would represent the mean reflectance found in the data that will be very similar across the whole spectral range. The second and third PCs can be interpreted as showing complementary information on the variation between different ranges of the spectrum, which means the differences between short and long frequencies or extreme versus medium frequencies. By looking at these graphs it is clear that these three first PCs give us enough information on the plumage color of each body part to be used for the DFAs that follow.

Discrimination of groups:

For discrimination of groups I conducted two DFAs, for male (Fig. 11) and female data (Fig. 12) respectively. In each case I took the first three PCs corresponding to the color information

Fig. 11. Results of the first DFA conducted on the color data of males of *Topaza* in order to discriminate groups.

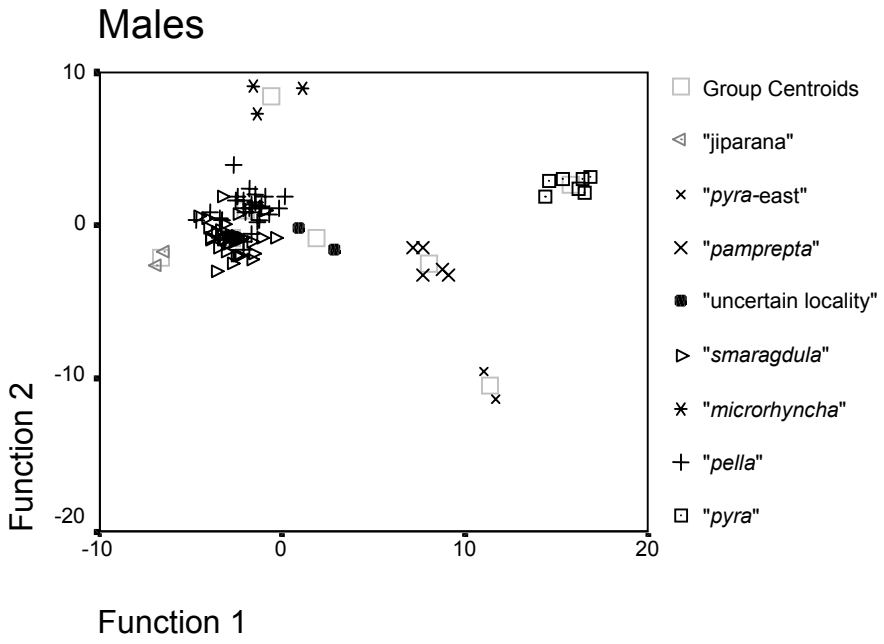
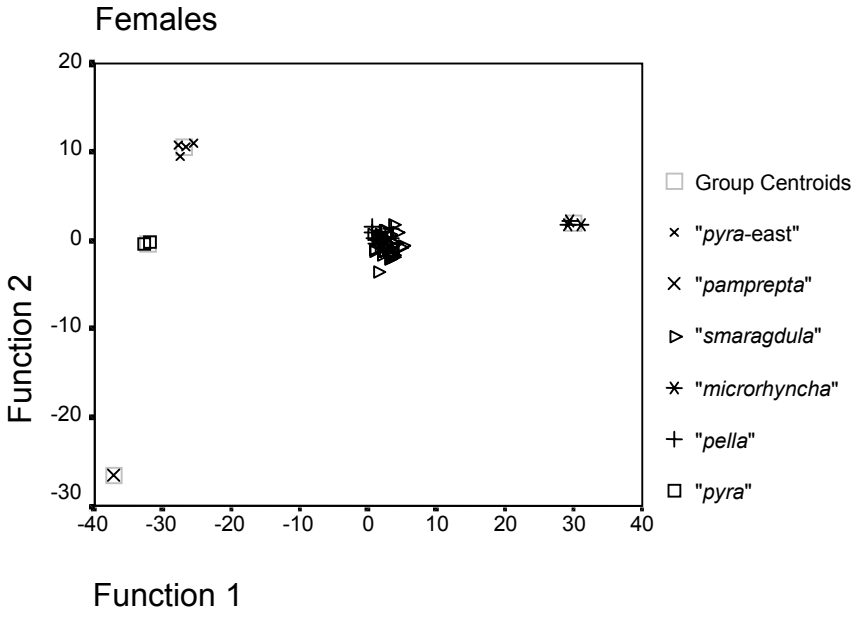


Fig. 12. Results of the first DFA conducted on the color data of females of *Topaza* in order to discriminate groups.



of each part of the body and considered bird coloration as a whole (integral approach). For males, all the groups showed 100% discrimination except for "*pella*" and "*smaragdula*," which showed incomplete discrimination, which would be expected if the two groups cannot be really separated. The rest of the groups showed full discrimination and, furthermore, when looking at the graphs, the same conclusion is reached in both males and females even when independently analyzed. For males the first two discriminant functions explained 74.4% of the variation, and for females 84.7% of the variation.

In general, a discriminant function analysis is used to assign membership to unknown objects (Sokal & Rohlf 1981, Otto 1999). DFA is used in data sets where some of the groups are known and individual "objects" need to be assigned membership in one of these previously known groups. In this case, I gave a name to each group of "unknown objects" or "unclear" populations and they were computed together with the rest. The reason is that I do not have unknown objects, but unknown groups of objects (individuals) that are assumed to belong to the same group and might be assigned to one of the known groups. Since I treat them as groups, they may be differentiated into their own groups, as happens here. However, the important conclusion to draw from this first DFA comes from the relative distances of the centroids of each group to each other. From the separation of centroids in each graph the following conclusions can be extracted: 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 authors 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. With regard to the "unclear" populations:

1) "*pamprepta*" shows a separation from other *T. pella* populations, and appears closer to the "*pyra*" populations, as could be expected taking the geographical distances into account. Also, if *Topaza* had in fact two species, this group should be a subspecies of *T. pyra* and not of *T. pella* as considered by Peters (1945).
2) When I separated the three specimens from "*pamprepta*" called "uncertain locality" (unfortunately males only) the DFA results put them closer to the populations of

"*pella*"-"*smaragdula*," which implies that they could really come from populations of the Guianas (possibly Cayenne as written on one of their labels) and not from Ecuador.

3) 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.
4) The centroids from "*pella*" and *smaragdula*" are very close together and overlap, making me believe that these two groups should not be separated into subspecies. Furthermore, *T. pella smaragdula* should not be recognized.
5) The two males from "jiparana" both appear closer to "*pella-smaragdula*" than to *T. pella microrhyncha*.

Discriminating variables

DFA is a very useful tool for classifying cases into groups with a better than chance accuracy, but also provides the means for detecting the variables that allow the researcher to discriminate between different (naturally occurring) groups. For the first part of the analysis I used the first potentiality of DFA, but here I am interested in determining which body parts (plumage coloration) make possible the discrimination of final groups. In other words, it is necessary to interpret the spectral data results in terms of real plumage coloration differences.

I conducted another DFA, again by sex, using the same PCs from the spectral data (Appendix 6a and 6b), but this time I used the final groups resulting from the first analysis to regroup the data. In this case I am not interested in the level of discrimination (that was already defined), but I used the descriptive power of DFA to determine the source of the color differences between groups. The DFA made for males (Fig. 13) uses only four discriminant functions to differentiate the groups, and the first two functions explain 81% of the variation. From the standardized canonical discriminant function coefficients table (SCDFCT) (Table 5), I can extract those variables (body regions) that contributed the most in the first two functions. These coefficients point to the gorget (Fac2_12), the lower throat (Fac2_14), and rectrix 5 (Fac3_39 and Fac1_39) as the body parts that make the most contribution to the overall

discrimination of two groups (see Function 1 in Fig. 13 and Table 5): "*pella*" ("*pella*" and "*microrhyncha*") and "*pyra*" ("*pyra,*" "*amaruni,*" and "*pamprepta*"), which does not necessarily mean that they should be considered different species. Neck (Fac3_2), back (Fac2_4), secondaries (Fac2_30 and Fac3_30), primaries (Fac2_31), and r1 (Fac3_32) explain the separation of "*pella*" and "*microrhyncha*" on the one hand, and "*pyra,*" "*amaruni,*" and "*pamprepta*" on the other (see Function 2 in Fig. 13 and Table 5).

Although the discrimination of groups for females gave the same results as for males, the variables that made the difference are not the same. The first two discriminant functions explained 85.7 % of the variation among groups. Basically, the dorsal region of the body explains a high portion of the variation (Fac2fe3, Fac3fe3, Fac1fe4, Fac2fe4, Fac3fe4, Fac1fe5, Fac2fe5, and Fac2fe6), while breast (Fac1fe20, Fac2fe20), and wing coverts (Fac3fe29) explain the remainder to separate mainly "*pamprepta*" from the rest (see Function 1 in Fig. 14 and Table 6). For the separation of the other *Topaza* groups (see Function 2 in Fig. 14 and Table 6), not only the dorsal region of the body is important (Fac1fe2, Fac2fe2, Fac2fe3, Fac3fe3, Fac3fe5, and Fac2fe6), but also wing coverts, primaries, and secondaries (Fac1fe29, Fac2fe29, Fac3fe29, Fac2fe30, Fac3fe30, and Fac2fe31).

The DFA indicates where the main differences are found as previously described, but for the interpretation of real color differences among groups we can also rely on more graphical representations of the data. In order to reduce the potential confusion that the presentation of this amount of figures, text, and graphs would bring, the information on color differences by body part for the five groups under analysis in this section will be included in Appendices (Appendix 8a and 8b).

In conclusion, my spectral color data results suggest that the main source of variation comes from the separation between *T. "pella"* and *T. "pyra."* The first group would include populations of *Topaza* occurring in the eastern part of the distribution, and include two groups, possibly *T. pella pella* and *T. pella microrhyncha*, that seem more similar to each other than to

Fig. 13. Results of the second DFA conducted on the color data of *Topaza* males.

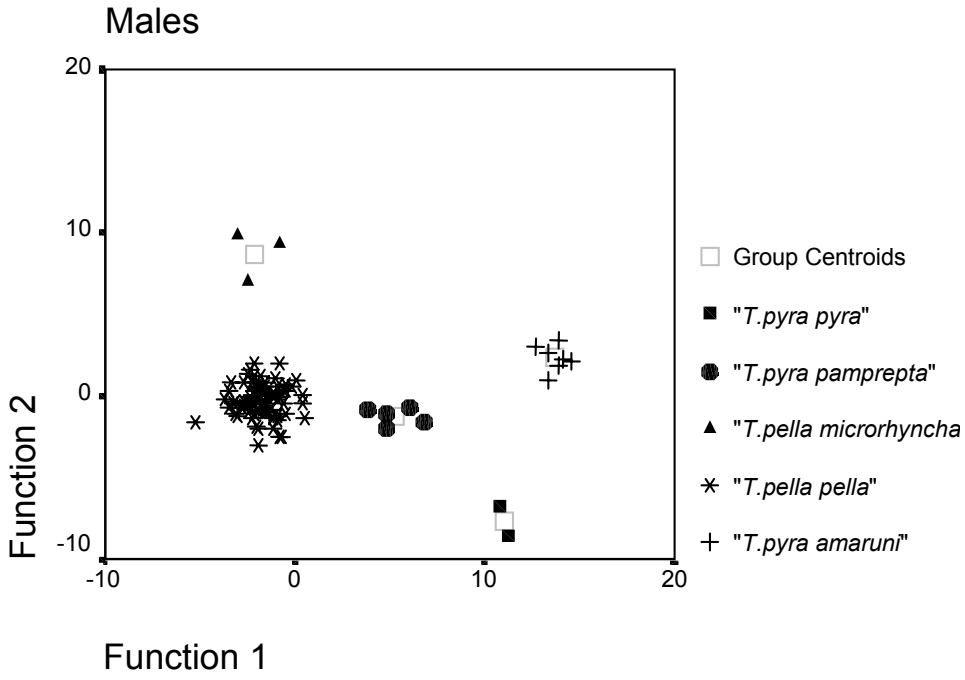


Fig. 14. Results of the second DFA conducted on the color data of *Topaza* females.

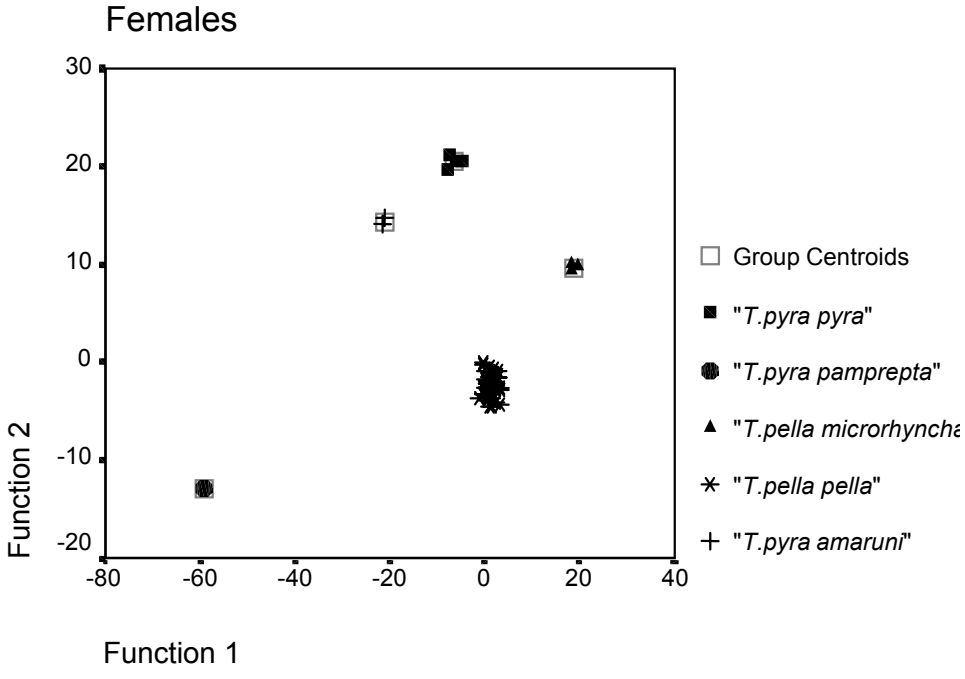


Table 5. Standardized canonical discriminant function coefficients resulting from the second DFA conducted on the color data of *Topaza* males. Note: Appendix 4 shows the codes of factors and body parts used here.

Standardized Canonical Discriminant Function Coefficients for MALES

	Function			
	1	2	3	4
FAC1_1	-,250	-,798	,336	-,485
FAC2_1	,362	-,063	,935	-1,248
FAC3_1	,312	,298	,657	-,543
FAC1_2	-,199	,686	-,312	,216
FAC2_2	,412	-,971	-1,159	1,623
FAC3_2	,586	-1,147	-1,519	3,329
FAC1_3	,310	-,001	1,191	,281
FAC2_3	,762	,000	-,372	,401
FAC3_3	,606	,833	,230	,316
FAC1_4	-,082	-,438	,383	,315
FAC2_4	-,279	1,083	,829	,451
FAC3_4	-,044	-,176	,697	-1,030
FAC1_5	-,319	,957	-,237	,100
FAC2_5	-,193	,309	,132	,008
FAC3_5	,226	,155	-,169	-,617
FAC1_6	,537	,151	-,426	,043
FAC2_6	,476	,600	,038	,409
FAC3_6	,898	,039	1,196	-,278
FAC1_12	-,731	,519	,600	,068
FAC2_12	-1,226	,117	,826	,127
FAC3_12	,373	,466	-,079	-,723
FAC1_14	-,342	-,239	-,894	-,289
FAC2_14	-1,228	-,065	-,647	-,293
FAC3_14	-,316	-,043	-,079	-,218
FAC1_17	,361	-,744	-,717	-,300
FAC2_17	-,265	,853	1,343	,571
FAC3_17	-,004	,391	-,038	,163
FAC1_20	,011	-,104	-,498	,088
FAC2_20	,736	-,027	-,800	,081
FAC3_20	-,448	-,915	,229	-,523
FAC1_23	-,058	,120	,093	-,241
FAC2_23	,061	-,107	,227	,043
FAC3_23	,129	,201	-,238	,299
FAC1_26	,658	,573	,237	,434
FAC2_26	-,594	,868	,917	-,191
FAC3_26	,250	,329	-,180	-,014
FAC1_29	1,028	-,093	-,620	,360
FAC2_29	,587	-,679	-,039	,728
FAC3_29	-,043	-,380	-,610	-,288
FAC1_30	,004	-,092	,290	-,531
FAC2_30	,159	-1,459	,995	-,622
FAC3_30	,358	-1,644	,296	-,655
FAC1_31	-1,027	,267	,155	-,486
FAC2_31	-,813	1,861	,733	-,900
FAC3_31	,079	-,664	-,590	,252
FAC1_32	,339	,754	-,161	-,051
FAC2_32	,024	-,512	,884	,112
FAC3_32	,128	1,510	-1,057	-,274
FAC1_33	-,032	,531	-,035	,270
FAC2_33	-,591	,948	-,153	,649
FAC3_33	,349	,813	,041	,572
FAC1_39	-1,197	-,122	-,012	-,034
FAC2_39	,962	,286	,290	-,349
FAC3_39	-1,390	,152	1,136	,278
FAC1_41	-,295	-,964	-,315	,542
FAC2_41	,316	-,617	-,620	-,208
FAC3_41	-,231	-,579	-,071	,247

Table 6. Standardized canonical discriminant function coefficients resulting from the second DFA conducted on the color data of *Topaza* females. Note: Appendix 4 shows the codes of factors and body parts used here.

Standardized Canonical Discriminant Function Coefficients FEMALES

	Function			
	1	2	3	4
FAC1FE1	-2,821	-,482	,306	1,823
FAC2FE1	1,837	1,482	1,931	,357
FAC3FE1	2,124	-2,310	1,638	1,210
FAC1FE2	3,487	8,242	-,317	,117
FAC2FE2	-4,182	-5,283	1,505	-2,589
FAC3FE2	4,545	,967	-5,917	3,083
FAC1FE3	-1,561	3,106	,831	-1,166
FAC2FE3	-9,605	-6,597	-2,860	,166
FAC3FE3	23,988	15,247	3,461	,950
FAC1FE4	-8,042	-4,505	-3,678	1,528
FAC2FE4	6,600	1,532	-,799	3,151
FAC3FE4	-5,226	-2,265	6,730	-6,773
FAC1FE5	15,468	,931	2,462	1,250
FAC2FE5	7,955	,077	-2,024	1,358
FAC3FE5	-1,339	-5,791	-5,017	1,127
FAC1FE6	2,802	2,189	-2,105	-,935
FAC2FE6	-10,987	6,199	5,991	,741
FAC3FE6	-,970	-3,793	-,036	,631
FAC1FE12	-,843	-1,012	,443	-1,365
FAC2FE12	-,047	4,601	2,124	-2,319
FAC3FE12	-4,948	-2,393	-2,283	-,628
FAC1FE14	-2,583	-3,370	,257	,460
FAC2FE14	2,078	,660	1,119	,438
FAC3FE14	-1,664	-1,366	-3,615	,216
FA1CFE17	1,893	,606	2,111	,659
FAC2FE17	-1,211	5,463	1,146	-,200
FAC3FE17	1,981	2,269	-2,980	-2,159
FAC1FE20	-8,536	-2,949	,852	,035
FAC2FE20	6,803	-1,902	-3,178	,107
FAC3FE20	-3,417	1,264	6,684	4,728
FAC1FE23	1,649	-1,116	-1,447	,576
FAC2FE23	-1,865	1,760	1,643	,190
FAC3FE23	-1,425	-2,215	-1,602	-,117
FAC1FE26	1,956	-,166	-1,214	,250
FAC2FE26	3,494	1,724	1,482	-1,331
FAC3FE26	1,063	3,097	-1,332	-,246
FAC1FE29	1,331	6,699	-1,505	-2,096
FAC2FE29	3,497	12,719	3,781	-1,728
FAC3FE29	5,787	6,630	,435	,323
FAC1FE30	-2,801	1,448	8,403	2,446
FAC2FE30	3,365	7,543	10,752	,768
FAC3FE30	-1,559	-7,554	-4,840	-2,670
FAC1FE31	2,034	-2,087	-11,087	-1,855
FAC2FE31	-2,316	-8,332	-15,517	,900
FAC3FE31	,043	3,598	5,473	1,480
FAC1FE32	-2,229	-1,079	,247	,948
FAC2FE32	-,823	-,391	-1,329	1,891
FAC3FE32	-3,990	-1,909	1,759	-,499
FAC1FE33	-,916	2,152	1,807	-,921
FAC2FE33	-,805	-,044	,119	1,412
FAC3FE33	3,320	5,094	-2,060	,068
FAC1FE39	2,982	1,746	-,667	-,185
FAC2FE39	,640	2,517	3,353	,424
FAC3FE39	2,609	-1,681	4,117	-,769
FAC2FE41	-4,817	-,543	-1,900	-2,041
FAC3FE41	3,639	-1,009	-,484	1,476

the other three groups, possibly *T. pyra pyra*, *T. pyra amaruni*, and *T. pyra pamprepta*, which seem to be included in *Topaza "pyra."*

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 I did not make any of these measurements, at this point my analysis is concordant with these results in the sense that it also indicates a separation of *Topaza* between western and eastern populations. However, to what degree these two groups are separate will be discussed after the phylogenetic analysis.

Phylogenetic analysis of the genus **Topaza**

The results from the preceding section point to some potential changes to the taxonomy of the group. According to the findings, the new working hypotheses for the phylogeny of the genus *Topaza* should be as follows: *T. pella* and *T. pyra* should be considered different species; *T. pella* would only include 2 subspecies: *T. pella pella* and *T. pella microrhyncha*; and *T. pyra* three subspecies: *T. pyra pyra*, *T. pyra amaruni*, and *T. pyra pamprepta*. However, conclusive results can only be given through a phylogenetic analysis.

Of the hummingbird taxa considered in this study there are arguments to choose either *Campylopterus* or *Eulampis* as the outgroup for the *Topaza* analysis. I conducted two PAUP analyses and a discussion of the probable best outgroup to make appropriate phylogenetic conclusions about the genus *Topaza* follows below.

Campylopterus as outgroup

The ingroup (taxonomic units) for the analysis, as defined according to the new working hypothesis is:

- *Topaza* "*pyra amaruni*" (group 1)
- *Topaza* "*pyra pamprepta*" (group 12)

- *Topaza* "*pyra pyra*" (group 13)
- *Topaza* "*pella pella*" (group 2)
- *Topaza* "*pella microrhyncha*" (group 3)

Following the methodology already set out, I selected the whole group (ingroup and outgroup taxa) and proceeded with the following method:

1. I separated the raw spectral color data by sex, and included the data in two Excel files (one for males and another for females).
2. For each data set, I conducted a PCA with the measurements from each body part.
3. I selected the first three PC scores resulting for each body part of the individuals included in each analysis and created new data sets by sex with three variables for each part.
4. Morphometric data were added to the files (see Appendix 9a and 9b).
5. The individuals were identified as belonging to a specific taxonomic unit (TU) to calculate frequencies for the analysis.
6. The generalized frequency coding (GFC) was applied to the cumulative frequency data in order to code them for the phylogenetic (PAUP) analysis.
7. The data for males and females are combined into the final matrix.

At the end of step 4, there was a total of 134 variables (color of 20 body parts for males and 20 for females multiplied by three PC scores, plus seven morphometric variables for each sex) (Appendices 9a and 9b). In order to apply the GFC (step 6) each variable was subdivided into 0.2 % of the variation, giving a total of 141 subvariables for males and 141 for females that were sections of each original variable. At the end there were 9447 ((60*141)+(7*141)) working variables for males and the same for females, which were then used to create matrix A (Appendix 10a and 10b). This matrix contained the frequencies of specimens that presented a variation within each new variable for each of the TUs of the working hypothesis. Then a cumulative frequency matrix (matrix B) was created (Appendix 11a and 11b). The coding was then completed and after eliminating the uninformative characters the final matrix

(Appendix 12) contained seven taxa and 3580 parsimony informative characters that were weighted (Appendix 13) and entered in the phylogenetic computer program PAUP* 4.0b.10.

Results of the PAUP analysis

The maximum parsimony analysis resulted in a single most parsimonious tree (Fig. 15 and Table 7). According to the Bootstrap analysis each node showed a 100% probability, except for nodes 11 with 99% and 10 with 80%, which are still high percentages. This reconstruction shows *Topaza* as a monotypic genus since there is no real differentiation between the two groups in the working hypothesis ("*pella*" and "*pyra*"). Although there is a scaled sequence from *T. pella microrhyncha* (eastern end of the geographical distribution) to "*T. pyra pyra"* (western end of the distribution), there is no clear separation between the five taxonomic units.

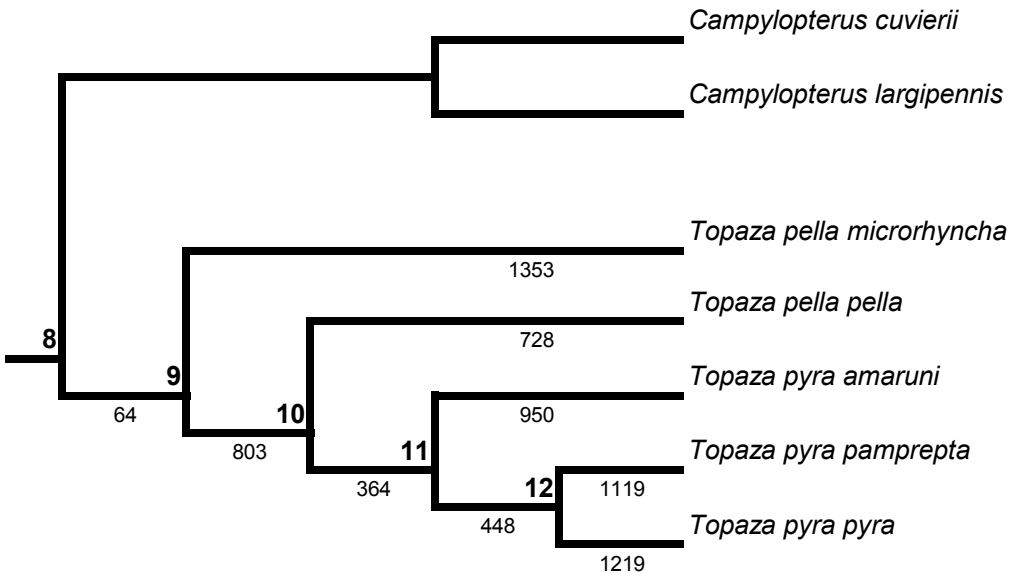


Fig. 15. Phylogenetic tree resulting from the PAUP analysis of *Topaza* using *Campylopterus* as outgroup.

Table 7. Main descriptive parameters of the phylogenetic tree resulting from the PAUP analysis of *Topaza* groups using *Campylopterus* as outgroup.

Tree characteristics	Values
Tree length	5859.64
Consistency Index (CI)	0.6955
Homoplasy Index (HI)	0.3045
Retention Index (RI)	0.4277
Rescaled Consistency Index (RC)	0.2974

Eulampis as outgroup

For this analysis the ingroup is the same as before, and only the outgroup changes: *Eulampis jugularis* and *Eulampis holosericeus*. The steps are also the same as for the previous analysis.

Results of the PAUP analysis

At the end of step 4, there were two files of data containing the three PC scores from each body part and the morphometric data of the specimens considered (Appendices 14a and 14b). Body mass and total length had to be excluded due to the scarcity of data for *Eulampis*. There were a total of 127 variables (color of 19 body parts for males and 20 for females multiplied by three PC scores, plus five morphometric variables by sex). In order to apply the GFC (step 6) each variable was subdivided into 0.2 % of the variation, giving a total of 141 subvariables for males and 141 for females that were sections of each original variable. Each individual was assigned to one of these sections within each variable. Another data set was created with this new information to get obtain the frequencies. The working variables were 8742 ((57*141)+(5*141)) for males and 9165 ((60*141)+(5*141)) for females and were used to create matrix A (Appendix 15a and 15b). This matrix contained the frequencies of specimens

that presented a variation within each new variable for each of the TUs. A cumulative frequency matrix (matrix B) was created (Appendices 16a and 16b). The coding was completed and after deleting the uninformative characters the final matrix with information from both sexes (Appendix 17) contained seven taxa and 2955 parsimony informative weighted characters (Appendix 18). These data were entered in PAUP.

The maximum parsimony analysis resulted in a single most parsimonious tree (Fig. 16 and Table 8). According to the Bootstrap analysis each node has a 100% probability, except for node 8 with 98%. The reconstruction shows the *Topaza* group as two main subgroups: "*pella*" and "*pyra*" and each with its subspecies as predicted by the working hypothesis.

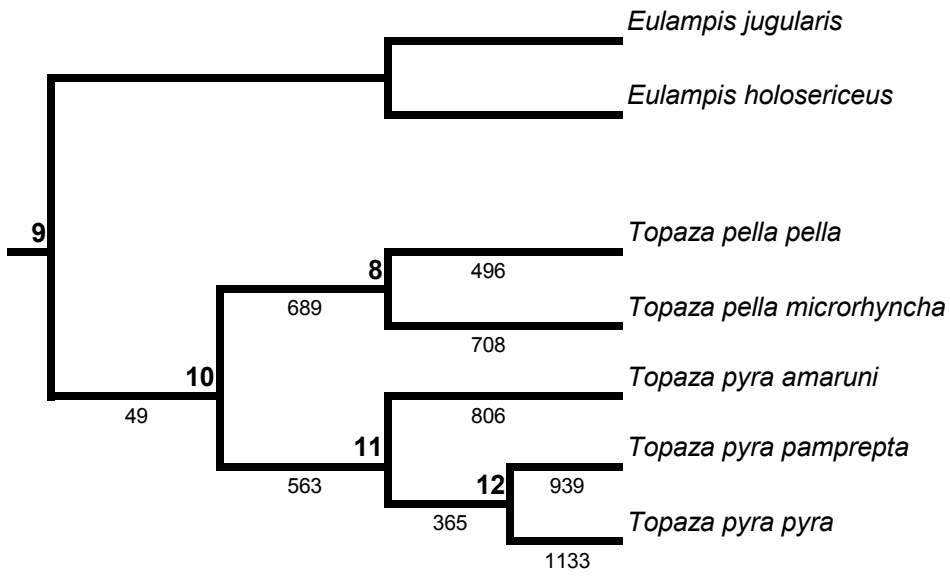


Fig. 16. Phylogenetic tree resulting from the PAUP analysis of *Topaza* using *Eulampis* as outgroup.

Table 8. Main descriptive parameters of the phylogenetic tree resulting from the PAUP analysis of *Topaza* groups using *Eulampis* as outgroup.

Tree characteristics	Values
Tree length	6061.68
Consistency Index (CI)	0.7013
Homoplasy Index (HI)	0.2987
Retention Index (RI)	0.6906
Rescaled Consistency Index (RC)	0.3376

Phylogenetic conclusions for the genus **Topaza**

An appropriate outgroup has to be determined to conduct a phylogenetic analysis. These conflicting results do not help to clear the controversy about the existence of only one species (Schuchmann 1999) or two species (Peters 1945, Hu *et al*. 2000) of *Topaza*. The final decision will be possible after deciding the best outgroup (*Eulampis* or *Campylopterus*). Unfortunately, there is not enough information on the phylogeny of hummingbirds, and especially no published information on the specific phylogenetic relationships within the mango group.

As already mentioned in the Introduction, the genera *Topaza*, *Anthracothorax*, and *Eulampis* are all members of the mango group, and are presumably phylogenetically closer to each other than to any other taxa. The conclusions of Zusi & Bentz (1982) do not provide additional useful information in this case since they consider *Topaza*, *Anthracothorax*, *Eulampis*, and *Campylopterus* only as basal groups, making no conclusions on the relationships between them. The DNA molecular conclusions of Bleiweiss *et al*. (1997) place the mango group at the base of the non-hermits, and within them, *Eulampis* is at the base of the phylogeny, but we

do not have any information about the position of *Topaza* or *Anthracothorax*. The genus *Campylopterus* is included within the emeralds, which are considered more derived than the mangoes. The authors considered only *Campylopterus villaviscensio* for their analyses, and this species might be a derived taxon within the emeralds. However, their results indicate that *Campylopterus* would be phylogenetically farther away from *Topaza* than *Anthracothorax* and *Eulampis* from *Topaza*. This limited information makes *Campylopterus* the best outgroup to determine the phylogeny of *Topaza*, or any other of the mango species, until further information is presented.

This phylogenetic reconstruction (using *Campylopterus* as outgroup) showed *Topaza* as a monotypic genus since there is no real differentiation between the two groups in the working hypothesis ("*pella*" and "*pyra*"). As already mentioned, there is no clear separation among the five taxonomic units. According to these results, the subspecies "*T. pyra pamprepta"* seems to be closer to "*T. pyra amaruni"* and "*T. pyra pyra"*, these three being the subspecies distributed at the western extremity of the geographical distribution of *Topaza*. The other two subspecies, *T. pella pella* and *T. pella microrhyncha*, occur at the eastern end of the range.

At this point we can combine this bibliographic information with the results of the phylogenetic tree obtained using *Eulampis* as outgroup. By similarities of color characters of females and of ecological characteristics, such as nest construction in both genera, Schuchmann (1980c) considers *Eulampis* as the sister group of *Topaza*. If that is the case, *Topaza* and *Eulampis* might be phylogenetically too close to each other and any real difference within *Topaza* might be augmented.

When both resulting phylogenetic trees (Fig. 15 and Fig. 16) are observed and compared it seems clear that a real difference between the groups of "*pella*" (east) and "*pyra*" (west) exists. This difference might be greater at the extremes 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* seems to be at the center of the distribution, which is in

agreement with the ideas of Schuchmann (1999) and supports the existence of an east-west clinal trend of characters within the *Topaza* populations. I also believe that setting a taxonomic limit at the species level would be a very subjective conclusion at this point. Unfortunately, the scarcity or lack of specimens from northern and central Brazil, (in the middle of the *Topaza* geographical distribution) makes it more difficult to reach a decision. Researchers could be confused by differences between the groups found at the extrems of the distribution, leading them to consider two separate species. In any case, it is clear that the subspecies *T. pella pamprepta* should not have been included in *Topaza pella* (*sensu* Peters 1945, Hu *et al*. 2000). If two different species are proposed, then this subspecies should have been part of the "*pyra*" populations close to the Andes.

***Further arguments supporting the clinal trend of* Topaza**

The taxonomic analysis of this taxon is mainly based on plumage coloration differences; however, I have added the morphometric information to the phylogenetic analysis. At this point I want to complement the morphological comparison of the five subspecies of *Topaza* by adding some statistical analysis and comparative figures from the morphometric data (body mass, total length, bill length, wing length, and rectrices 1, 2, and 5). These additional observations will help in the discussion of a possible east-west clinal trend of the morphological characters of *Topaza*. First I present the descriptive statistics and comparisons made on the five final subspecies (Tables 9 and 10). The data on body mass and total length are included as a reference but they are too scarce for definite comparisons. For the other body measurements, in both sexes, significant differences among groups exist, with the only exception of rectrix 5.

After the first comparison, I conducted a correlation analysis between the seven body characters and geographical variables, such as latitude and longitude, to complement the information on potential cline of characters. These results are shown in Tables 11 and 12 for males and females respectively. The results by latitude might reflect regional tendencies in the data, mainly within the populations of *T. pella pella* and *Topaza pella microrhyncha* that

Table 9. Morphometric measurements of males of the five subspecies of *Topaza*, indicating statistically significant differences between them.

Taxon		Body mass (g)	Total length (mm)	Bill length (mm) **	Wing length (mm) *	Rectrix 1 (mm) **	Rectrix 2 (mm) **	Rectrix 5 (mm)
Topaza pella amaruni	x=			**28.57**	**80.76**	**48.38**	**101.47**	**46.49**
	σ=	-	-	1.27	2.35	1.93	24.54	4.50
	n=			15	16	14	14	13
Topaza pella pyra	x=	**12.00**		**29.67**	**78.15**	**47.05**	**116.80**	**42.77**
	σ=	-	-	0.23	2.55	5.48	12.13	4.78
	n=	1		2	3	2	3	3
Topaza pella pamprepta	x=	**14.50**		**29.91**	**82.11**	**50.03**	**112.49**	**46.13**
	σ=	-	-	1.18	2.74	2.55	7.52	4.93
	n=	1		5	5	5	5	5
Topaza pella pella	x=	**13.03**	**175**	**30.75**	**78.88**	**44.73**	**87.00**	**44.15**
	σ=	1.50	18.71	1.21	3.36	2.37	21.72	3.48
	n=	6	9	89	90	89	84	87
Topaza pella microrhyncha	x=			**27.92**	**76.92**	**42.33**	**78.45**	**42.58**
	σ=	-	-	0.97	2.22	2.09	28.11	3.32
	n=			3	3	3	3	3

*Significant difference (t-test; $p<0.05$) among subspecies for this variable.

**Significant difference (t-test; $p<0.01$) among subspecies for this variable.

Table 10. Morphometric measurements of females of the five subspecies of *Topaza*, indicating statistically significant differences between them.

Taxon		Body mass (g)	Total length (mm)	Bill length (mm) **	Wing length (mm) **	Rectrix 1 (mm) *	Rectrix 2 (mm) **	Rectrix 5 (mm)
Topaza pella amaruni	x=			**26.94**	**72.82**	**42.29**	**50.03**	**36.79**
	σ=	-	-	2.02	2.97	1.16	0.40	5.40
	n=			2	2	2	2	2
Topaza pella pyra	x=	**11.00**	**148**	**28.96**	**74.05**	**44.82**	**46.50**	**36.13**
	σ=	-	-	0.98	2.71	2.23	2.89	1.21
	n=	1	1	4	4	4	4	3
Topaza pella pamprepta	x=			**27.77**	**68.89**	**42.66**	**45.79**	**37.31**
	σ=	-	-	-	-	-	-	-
	n=			1	1	1	1	1
Topaza pella pella	x=	**11.61**	**139.67**	**30.05**	**73.01**	**41.58**	**42.87**	**35.93**
	σ=	0.92	5.17	1.19	2.46	1.76	2.72	2.79
	n=	7	9	64	64	59	58	58
Topaza pella microrhyncha	x=			**27.86**	**68.36**	**38.49**	**39.82**	**32.38**
	σ=	-	-	0.28	1.20	.78	1.93	0.67
	n=			3	3	3	3	2

*Significant difference (t-test; $p<0.05$) among subspecies for this variable.

**Significant difference (t-test; $p<0.01$) among subspecies for this variable.

Table 11. Pearson correlation of the morphometric measurements of *Topaza* males in relation to latitude and longitude.
** Sig. (2-tailed) < 0.01, * Sig. (2-tailed) < 0.05

***Topaza* (males)**						
		Bill length (mm)	**Wing length (mm)**	**Rectrix 1 (mm)**	**Rectrix 2 (mm)**	**Rectrix 5 (mm)**
Latitude	Pearson Correlation= n=	.565** 119	-.009 122	-.254** 118	-.144 114	.023 115
Longitude	Pearson Correlation= n=	.336** 119	-.304** 122	-.546** 118	-.218* 114	-.267** 115

Table 12. Pearson correlation of the morphometric measurements of *Topaza* females in relation to latitude and longitude.
** Sig. (2-tailed) < 0.01, * Sig. (2-tailed) < 0.05

***Topaza* (females)**						
		Bill length (mm)	**Wing length (mm)**	**Rectrix 1 (mm)**	**Rectrix 2 (mm)**	**Rectrix 5 (mm)**
Latitude	Pearson Correlation= n=	.610** 76	.272* 76	.094 71	-.221 70	.170 68
Longitude	Pearson Correlation= n=	.217 76	-.271* 76	-.386** 71	-.530** 70	-.265* 68

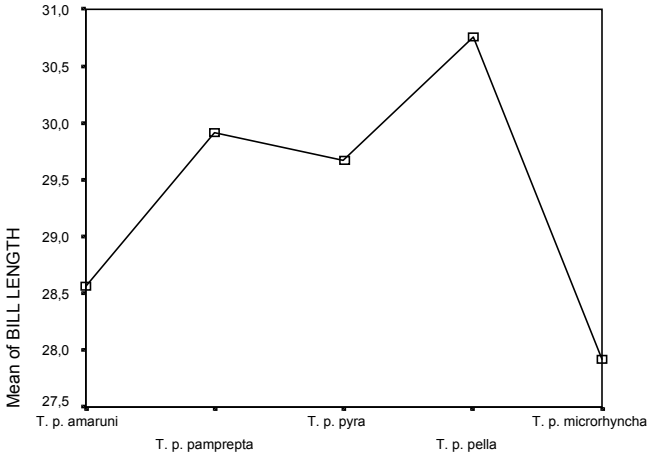
are more dispersed along a latitudinal range. In fact, as additional observation, taking only the specimens in the range of these two subspecies there is a slight positive significant correlation of PC1 for morphological measurements (representing the size) of males ($r2= 0.36$, $p<0.01$) and of females ($r2= 0.57$, $p<0.001$) with latitude. This correlation may explain the difficulty in finding a clear separation of groups in this area, as well as previous consideration of the subspecies *T. pella smaragdula* by some authors (Peters 1945, Hu *et al*. 2000).

I am particularly interested in the correlation with longitude. In males there is a significant correlation in all measurements, positive with regard to bill length and negative for the other four. In females, the significant negative correlation is found in all measurements, except for bill length which shows no correlation. In all cases the correlation is slight but significant which means a potential longitude clinal trend of these characters within the species. These tendencies are shown in Figures 17 and 18.

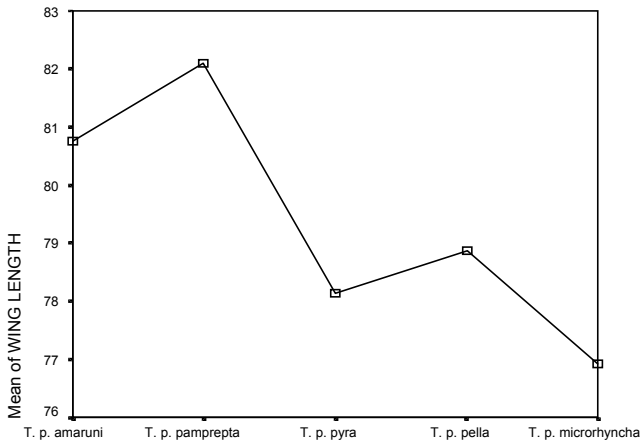
The results of the present study indicate that the variation between the two groups of subspecies within the genus *Topaza* seems to be insufficient to separate it in two species. The genus *Topaza* seems then monotypic, and includes five subspecies: *T. pella amaruni*, *T. pella pyra*, *T. pella pamprepta*, *T. pella pella*, and *T. pella microrhyncha*.

Figures 17a, b, c, d, e. Tendencies of morphometric measurements of *Topaza* males among subspecies ordered by longitude.

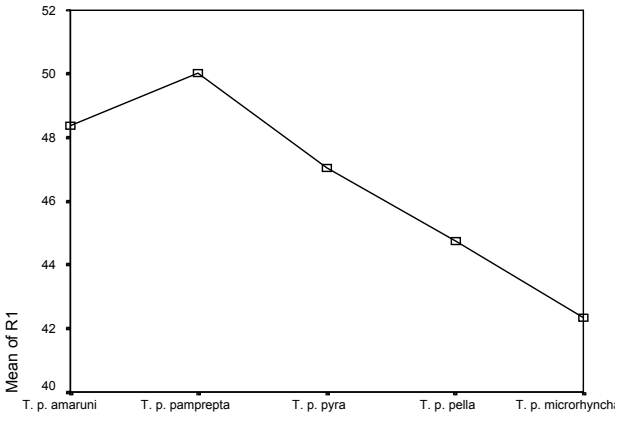
a.



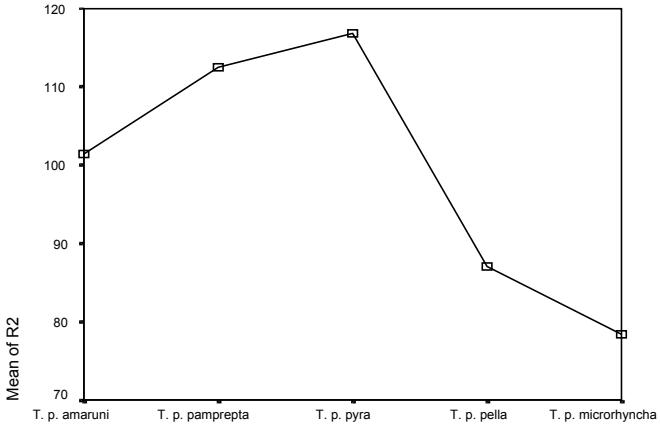
b.



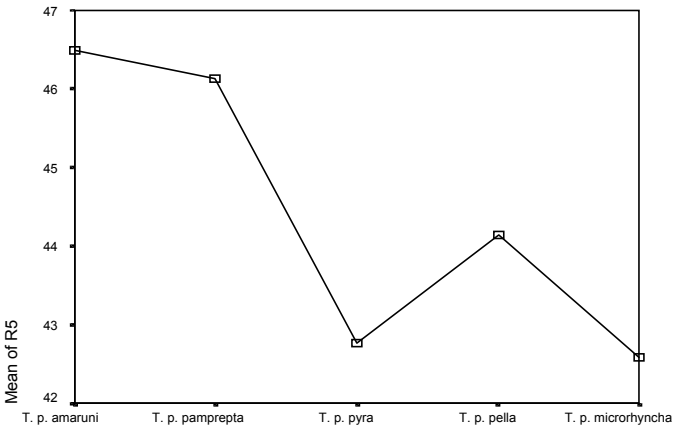
c.



d.

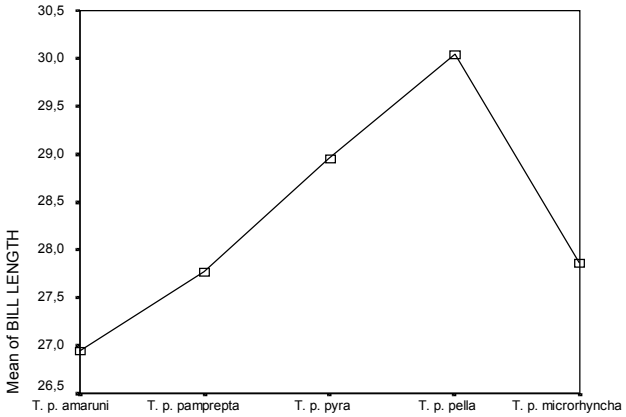


e.

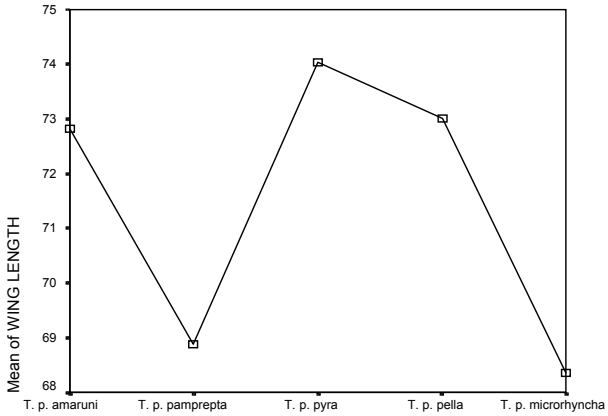


Figures 18a, b, c, d, e. Tendencies of morphometric measurements of *Topaza* females among subspecies ordered by longitude.

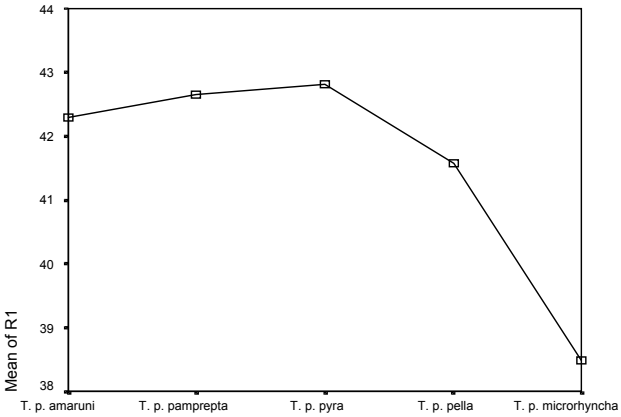
a.



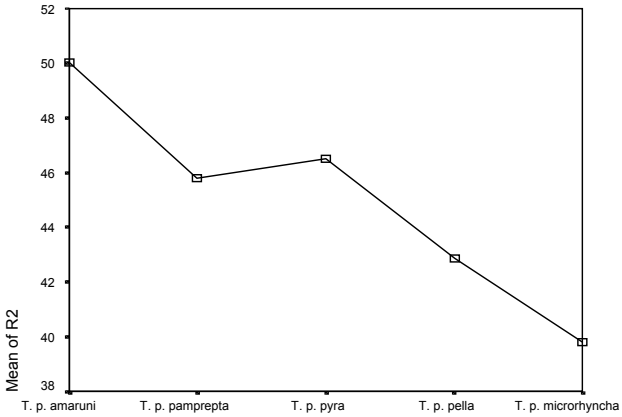
b.



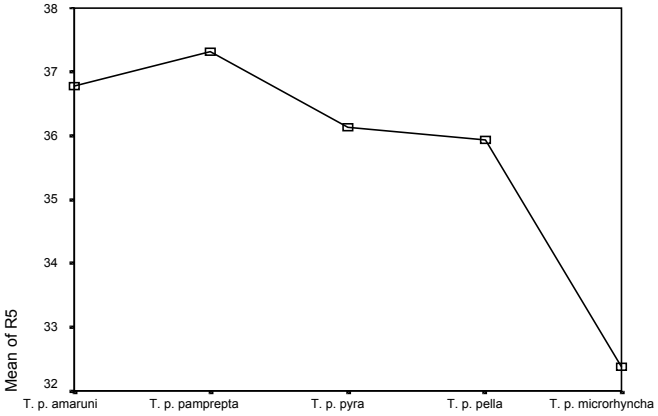
c.



d.



e.



Geographic variation and review of the taxonomy and phylogeny of the genus *Anthracothorax* BOIE, 1831

Theoretical background

The genus *Anthracothorax* is composed of mainly lowland, relatively large hummingbirds of about 7.5 g body mass (Plate 2). They are mostly found in open habitats near water, from mangroves to cultivated areas depending on the species, from Mexico to Argentina. A few species of *Anthracothorax* also occur on the Greater Antilles, where they are mainly found in habitats of primary vegetation from near the coast to the interior mountains (Schuchmann 1980b).

There are only a few distributional notes and descriptive papers on the habits of the group (Chapman 1928; Danforth 1928, 1929; Hellmayr 1929; Wetmore 1930, 1968; Bond 1936, 1939; Street 1946; Wagner 1946; Zimmer 1950; Robertson 1962; Land 1963; Monroe 1968; Ruschi 1973; Munves 1975; Schuchmann 1980a; Wendelken & Martin 1989; Contreras 1992; Quesnel 1995; Pérez *et al.* 1998). A few anatomical and physiological studies have been conducted on members of *Anthracothorax* (Craigie 1932, Hartman 1954, Hartman & Lessler 1963, Prinzinger *et al.* 1981, Krüger *et al.* 1982, Schuchmann *et al.* 1983, Udvardy 1983, Prinzinger & Schuchmann 1985, Prinzinger *et al.* 1986, Schuchmann & Prinzinger 1987, Fritsch & Schuchmann 1988, Schuchmann 1996).

Foraging behavior and sexual selection in a few species have also been investigated in relation to morphology (Kodric *et al.* 1984, Brown & Bowers 1985, Temeles & Roberts 1993, Colwell 2000, Temeles *et al.* 2000). Additionally, a few ecological and evolutionary studies have been made (Snow & Snow 1972; Schuchmann 1980d, c, 1987, 1991; Cotton 1998a, b, c). However, there is not much specific information on the systematics or phylogeny of the genus, making the results of this study the first quantitative analysis conducted on the taxon.

The genus *Anthracothorax* replaces *Lampornis* Swainson, 1827 and is considered polytypic. It includes eight currently recognized species with their respective subspecies (Schuchmann 1999):

- *Anthracothorax viridigula* Boddaert, 1783 (Green-throated Mango) is found in northeastern Venezuela, Trinidad, the Guianas, and northern Brazil.
- *Anthracothorax prevostii,* (Green-breasted Mango) includes five subspecies:
    - *A. p. prevostii* Lesson, 1832 is distributed in southern Mexico, Guatemala, Belize, and El Salvador.
    - *A. p. gracilirostris* Ridgway, 1910 occurs from El Salvador to Costa Rica.
    - *A. p. hendersoni* Cory, 1887 (includes *pinchoti* according to Peters 1945). This taxon is found on the Caribbean islands of San Andres and Old Providence.
    - *A. p. viridicordatus* Cory, 1913 occurs in northeastern Colombia and northern Venezuela.
    - *A. p. iridescens* Gould, 1861 was previously treated as a subspecies of *A. nigricollis* (Peters 1945), and is found in western Colombia, southwestern Ecuador, and northwestern Peru.
- *Anthracothorax nigricollis* Vieillot, 1817 (Black-throated Mango) occurs from western Panama to northeastern Argentina.
- *Anthracothorax veraguensis* Reichenbach, 1855 (Veraguas Mango) is only found in Panama.
- *Anthracothorax dominicus* (Antillean Mango) includes two subspecies:
    - *A. d. dominicus* Linnaeus, 1766 with its range in Hispaniola and nearby islands of Tortue, Gonave, Vache, and Beata.
    - *A. d. aurulentus* Audebert & Viellot, 1801 occurs in Puerto Rico and nearby islands of Culebra and Vieques, and the Virgin Islands (Saint Thomas, Saint John Anegada).
- *Anthracothorax viridis* Audebert & Viellot, 1801 (Green Mango) is endemic to Puerto Rico.
- *Anthracothorax mango* Linnaeus, 1758 (Jamaican Mango) is endemic to Jamaica.

- *Anthracothorax recurvirostris* Swainson, 1822 (Fiery-tailed Awlbill) was previously included in the monotypic genus *Avocettula* (but see Schuchmann 1999), found in southeastern Venezuela, the Guianas, northeastern Brazil, and eastern Ecuador.

Sexual dimorphism in Anthracothorax *and implications for the results*

Coloration in trochilids is mainly related to behavior and social system. In general, two groups of color traits can be distinguished: those that promote concealment and those enhancing conspicuousness (Schuchmann 1999). The possession of one or the other will be greatly dependent on the social system of the species. Hummingbirds are usually territorial (to protect foraging resources) and polygamous, in which some of them exhibit leks. In these cases, the conspicuous colors of hummingbirds relate to sexual advertisement (Schuchmann 1999) and consequently are subject to sexual selection. Bright and iridescent colors on body areas such as throat, crest, or back play important intraspecific and interspecific roles as visual threat signals for territorial defense, self-advertisement during display, or species-specific recognition cues (Schuchmann 1999). The majority of females, by contrast, exhibit a cryptic coloration that might be related to concealment from predators during nesting or other breeding-related activities that are usually carried out by females alone (Schuchmann 1999). Only females of a few hummingbird species hold temporally and spatially limited territories around localized food resources during the reproductive period.

Most of the *Anthracothorax* species show sexual dimorphism. The dimorphic species show a marked plumage coloration difference in which males show some ventral iridescence and have more colorful bodies than females. Females show non-iridescent clear underparts (white, beige, or gray) with a central black stripe. The exceptions to this rule are *A. mango* and *A. viridis*, which seem color monomorphic. The mean color spectra of all body parts of the eight species are shown in the appendices (Appendices 19a, b, c, d and Appendices 20a, b, c, d).

The color sexual dimorphism and similarity among females of this genus may explain why, in the following results, the main color differences and group discriminations are usually found

within males. Differences in coloration within males can be considered important characters with evolutionary consequences, making the results obtained on the taxonomic analysis of the male color data sets relevant, even if the group differences are not very marked in the analyses of female data sets.

Analysis of **Anthracothorax** *at the species level*

General differences among *Anthracothorax* populations were determined by conducting a discriminant function analysis (DFA) for all species together. This analysis also helps to find controversial groups within the taxon. First, principal component analyses (PCA) were conducted on the data of all specimens of *Anthracothorax* by sex (Appendices 21 and 22). The first three PCs were taken to conduct the DFA. The results show that the first two discriminant functions explain 83.8% of the variation in males (Table 13a), and 73.6% of the variation in females (Table 14a). The graphs (Fig. 19 for males, Fig. 20 for females) indicate that *Anthracothorax* species are very overlapping in coloration, except for *A. viridigula*, *A. dominicus*, and *A. veraguensis* in males, and *A. viridis* and *A. dominicus* in females. These species are separated along both first and second factors in each case.

The effect of the third factor can only be observed in the discrimination tables since the graphs show only the interaction of the first two factors. It is important to examine the discrimination results (Table 15 for males, Table 16 for females) as well as the graphs to extract the following preliminary conclusions: There are only three species showing complete discrimination (100%): *A. viridis*, *A. mango*, and *A. recurvirostris*. Overlap is found mainly between *A. prevostii* and *A. nigricollis*. There is also overlap between these two versus *A. veraguensis* and *A. viridigula*. Contrary to the findings in the graphs, *A. dominicus* shows little overlap with *A. nigricollis* (males) and *A. mango* (females). In general, the discrimination is less for females (89.2% of original grouped cases correctly classified) than for males (94.4% of original grouped cases correctly classified). Thus, accepting potential identification errors, these results might be interpreted as "females showing greater color homogeneity than males."

Table 13a. (above). Eigenvalues table showing cumulative percentages of the variance explained by each function; **b.** (below). SCDFC table for the DFA conducted on males of all the species of the genus *Anthracothorax*.

Eigenvalues

Function	Eigenvalue	% of Variance	Cumulative %	Canonical Correlation
1	12,046[a]	51,9	51,9	,961
2	7,431[a]	32,0	83,8	,939
3	2,112[a]	9,1	92,9	,824
4	,804[a]	3,5	96,4	,668
5	,570[a]	2,5	98,8	,603
6	,154[a]	,7	99,5	,365
7	,116[a]	,5	100,0	,322

a. First 7 canonical discriminant functions were used in the analysis.

Standardized Canonical Discriminant Function Coefficients

	Function						
	1	2	3	4	5	6	7
FAC1_1	-,022	-,056	,198	,049	-,017	,259	-,132
FAC2_1	,195	,032	,113	,376	,017	-,107	-,308
FAC3_1	-,013	,036	,164	,198	,006	,161	,232
FAC1_2	-,093	-,011	-,107	-,084	,099	,153	,256
FAC2_2	-,232	-,223	-,235	-,165	-,122	-,154	,265
FAC3_2	-,023	-,142	-,222	,101	,068	-,156	,159
FAC1_3	,039	,005	,007	,096	,013	-,033	-,037
FAC2_3	-,096	-,170	-,598	,250	,606	,342	,464
FAC3_3	,144	,251	,539	-,185	-,615	-,247	-,247
FAC1_4	,182	,089	,042	,117	-,075	,314	-,100
FAC2_4	,612	,233	,125	,088	-,570	,086	-,873
FAC3_4	,276	,063	,269	,051	-,083	-,035	-,154
FAC1_5	-,026	-,017	,152	,201	,001	,078	-,042
FAC2_5	-,273	-,080	-,275	-,163	,854	,318	,552
FAC3_5	-,152	,019	,087	,015	,336	-,246	-,078
FAC1_6	-,100	-,048	-,060	,029	,112	,101	,040
FAC2_6	,039	-,085	-,200	-,402	-,147	1,079	-,664
FAC3_6	,133	,022	,056	,173	-,115	,193	,016
FAC1_12	,819	-,926	,134	-,327	,335	,036	,022
FAC2_12	,360	,714	,007	-,390	,612	,152	,043
FAC3_12	,732	-,081	,181	,069	,766	,148	-,402
FAC1_14	,477	,530	-,265	,582	-,303	-,495	,183
FAC2_14	-,672	-,034	,000	-,119	,930	-,500	,190
FAC3_14	-1,213	-,397	-,697	-,039	,651	-1,241	1,153
FAC1_17	-,127	,179	,654	-,102	,052	,155	-,505
FAC2_17	,029	,578	,338	,333	,109	-,209	-,486
FAC3_17	-,042	,160	,622	-,276	,117	,020	-,516
FAC1_20	-,066	,045	,315	-,101	,005	-,090	,012
FAC2_20	-,252	,217	-,858	-1,325	-,187	1,843	-,226
FAC3_20	-,030	,028	,177	-,375	,167	,124	-,126
FAC1_26	,139	,032	,064	-,091	-,132	-,641	,305
FAC2_26	,282	,018	,327	-,179	-,621	-1,321	1,040
FAC3_26	,163	-,031	,044	,034	-,193	-,640	,495
FAC1_29	,055	-,097	,145	-,085	,022	,021	,057
FAC2_29	,032	-,114	,267	-,321	-,124	-,288	,833
FAC3_29	,046	-,117	,202	,170	,000	-,093	,455
FAC1_30	,534	-,122	,022	,465	,426	,658	-,371
FAC2_30	,517	-,281	-,147	,668	,702	,242	,033
FAC3_30	,391	-,051	,144	,417	,423	,301	-,128
FAC1_32	,028	,090	,106	,006	,056	-,087	,178
FAC2_32	,044	,041	-,102	-,170	-,165	,006	-,130
FAC3_32	,186	-,046	,215	-,252	,000	-,200	,137
FAC1_33	,064	-,017	-,021	,056	,076	,021	,056
FAC2_33	,112	,061	,200	,053	-,176	,065	-,220
FAC3_33	,079	,020	,094	,109	-,149	-,354	-,158
FAC1_34	-,083	,098	,023	-,134	-,138	-,084	-,161
FAC2_34	,004	,067	,044	,256	,104	,176	,003
FAC3_34	-,260	-,245	,207	,561	-,124	,166	-,038
FAC1_39	,013	,024	,107	-,225	-,323	,388	,414
FAC2_39	-,112	-,091	-,174	-,033	,192	,082	,170
FAC3_39	-,150	-,165	-,466	,404	,926	-,591	-1,406
FAC1_40	-,046	,134	,170	,088	-,177	,142	,076
FAC2_40	,617	,020	,013	-,076	-,935	,452	,339
FAC3_40	-,040	-,069	-,354	-,095	,221	-,172	-,148

Table 14. a (above). Eigenvalues table showing cumulative percentages of the variance explained by each function. **b** (below). SCDFC table for the DFA conducted on females of all the species of the genus *Anthracothorax*.

Eigenvalues

Function	Eigenvalue	% of Variance	Cumulative %	Canonical Correlation
1	8,999[a]	55,1	55,1	,949
2	3,019[a]	18,5	73,6	,867
3	1,681[a]	10,3	83,9	,792
4	1,080[a]	6,6	90,5	,721
5	,651[a]	4,0	94,5	,628
6	,542[a]	3,3	97,8	,593
7	,362[a]	2,2	100,0	,516

a. First 7 canonical discriminant functions were used in the analysis.

Standardized Canonical Discriminant Function Coefficients

	Function						
	1	2	3	4	5	6	7
FAC1_1	,156	-,007	,222	-,115	-,160	,041	-,122
FAC2_1	-,162	,047	,494	,362	-,146	-,359	,484
FAC3_1	,031	,125	,373	-,286	,118	-,279	-,330
FAC1_2	-,223	-,018	-,279	-,018	,112	,063	-,104
FAC2_2	,395	-,210	-,779	,258	,145	-,303	-,175
FAC3_2	-,006	,131	,185	,134	,135	,344	,071
FAC1_3	,178	,080	,029	,171	,213	,185	,000
FAC2_3	-,093	,227	-,017	-,552	-,264	,483	,736
FAC3_3	-,022	,300	,077	-,470	-,041	,302	,487
FAC1_4	,007	-,070	,080	-,053	-,062	-,188	,395
FAC2_4	-,312	-,233	,771	,197	-,114	-,515	1,193
FAC3_4	,060	,030	,246	,112	-,029	-,318	,558
FAC1_5	-,109	-,027	-,058	,094	,070	,486	,033
FAC2_5	,136	-,003	-,674	,248	,605	,186	-,125
FAC3_5	,139	,058	-,059	-,008	-,010	,084	-,107
FAC1_6	-,072	-,126	,229	-,075	-,187	,059	-,509
FAC2_6	-,130	,321	-,457	-,344	-,762	-,580	-,952
FAC3_6	-,156	,020	,125	-,143	-,269	-,085	-,345
FAC1_12	,787	,010	-,071	,272	-,091	,175	,016
FAC2_12	-,411	,132	-,247	-,565	,338	-,166	,491
FAC3_12	,076	,863	,217	,205	,215	,115	,077
FAC1_13	-,475	-,099	,201	,110	,044	,154	,072
FAC2_13	,516	,143	-,535	-,087	-,207	-,070	-,054
FAC3_13	-,020	,040	-,701	-,400	,229	-,311	-,651
FAC1_14	,642	,442	-,022	-,093	,059	-,488	-,337
FAC2_14	-,241	1,128	,199	,954	-1,440	,068	-,419
FAC3_14	,468	,712	,131	,274	-,582	-,585	-,007
FAC1_15	-,146	-,217	,098	,130	-,148	-,267	,153
FAC2_15	,255	-,551	,108	-,357	,158	,363	-,170
FAC3_15	,062	-,547	,119	-,100	-,066	,618	,360
FAC1_17	,096	-,067	-,008	-,146	-,032	,209	-,076
FAC2_17	-,050	,199	,018	-,056	,975	,169	,184
FAC3_17	,119	,049	,077	,000	,502	,804	,160
FAC1_18	-,002	-,015	,088	,104	,091	-,157	-,021
FAC2_18	,142	-,085	-,124	,131	,042	,189	-,061
FAC3_18	-,122	-,200	,046	,345	,268	-,118	-,191
FAC1_20	,074	-,063	,157	-,149	-,199	-,021	,422
FAC2_20	,179	,187	-,270	,170	,143	-,423	,368
FAC3_20	,037	-,209	,005	-,234	,086	-,494	,159
FAC1_21	,002	-,196	,091	,303	,045	,094	-,002
FAC2_21	-,085	,005	,077	,082	-,134	,277	,038
FAC3_21	,277	,032	,149	,155	-,214	,292	-,144
FAC1_26	,182	,069	,007	,062	-,012	-,156	,027
FAC2_26	-,733	,162	,459	-,084	-,121	-,361	-,694
FAC3_26	-,168	,174	,088	,341	-,285	-,096	-,207
FAC1_29	-,091	-,033	,220	-,468	,086	,021	,148
FAC2_29	-,300	,032	,837	-,527	,178	-,301	,752
FAC3_29	,118	-,033	,119	,032	,131	,035	,158
FAC1_30	,041	-,503	-,253	-,159	,398	,516	-,541
FAC2_30	,221	-,828	-,473	,176	,244	1,028	-1,081
FAC3_30	,011	-,370	-,048	-,280	,208	,353	-,048
FAC1_32	,153	-,184	,111	,121	-,006	-,097	,011
FAC2_32	,215	-,347	,013	-,149	-,491	,331	,083
FAC3_32	-,150	,398	-,258	-,003	-,250	-,226	-,001
FAC1_33	,055	-,050	-,234	-,135	,176	-,136	,022
FAC2_33	,048	,134	,300	-,240	,110	-,207	,222
FAC3_33	,050	,058	-,064	,262	,170	,037	,073
FAC1_39	-,066	-,239	,138	-,367	,120	,076	,344
FAC2_39	-,117	,094	,190	,387	-,229	-,195	-,247
FAC3_39	,108	-,090	,294	,584	,263	-,421	-,169

Fig. 19. Results of the DFA conducted on the color data of males of all *Anthracothorax* species.

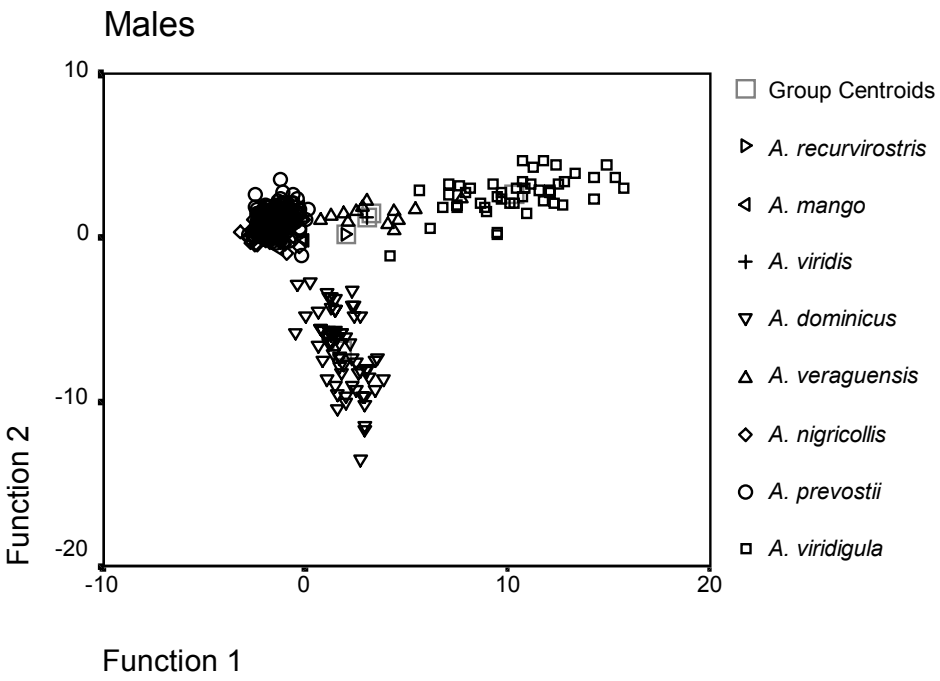


Fig. 20. Results of the DFA conducted on the color data of females of all *Anthracothorax* species.

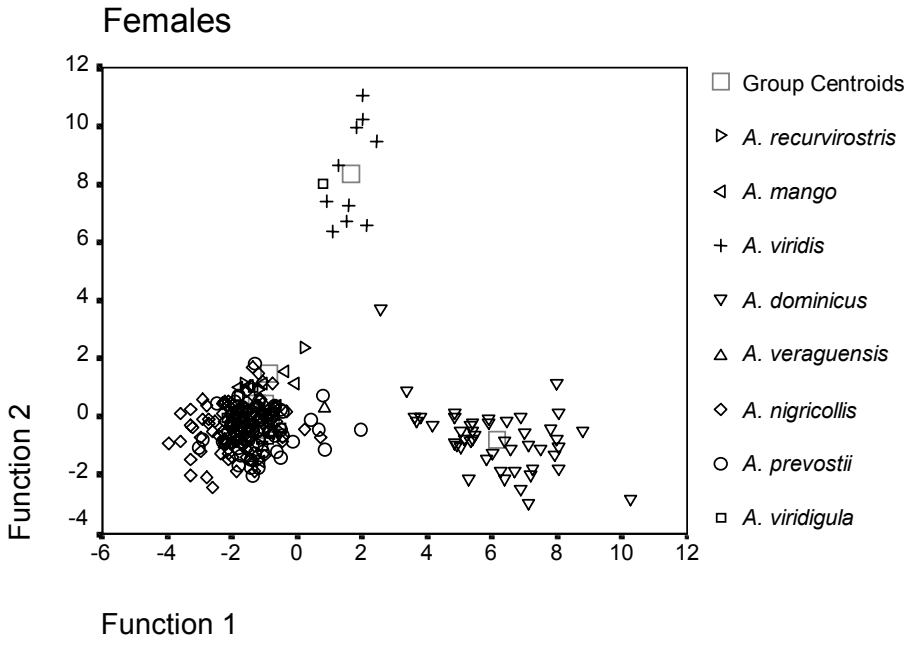


Table 15. Classification results of the DFA conducted on the color data of males of the genus *Anthracothorax*.

SPECIES	**Predicted Group Membership (%)**							
	A. viridigula	***A. prevostii***	***A. nigricollis***	***A. veraguensis***	***A. dominicus***	***A. viridis***	***A. mango***	***A. recurvirostris***
A. viridigula	**95.7**	0	0	**4.3**	0	0	0	0
A. prevostii	0	**86.2**	**12.3**	0	0	0	**1.4**	0
A. nigricollis	0	**1.2**	**98.0**	0	0	0	0	0
A. veraguensis	0	**14.3**	0	**85.7**	0	0	0	0
A. dominicus	0	0	**2.9**	0	**97.1**	0	0	0
A. viridis	0	0	0	0	0	**100.0**	0	0
A. mango	0	0	0	0	0	0	**100.0**	0
A.recurvirostris	0	0	0	0	0	0	0	**100.0**

94.4% of original grouped cases correctly classified

Table 16. Classification results of the DFA conducted on the color data of females of the genus *Anthracothorax*.

SPECIES	**Predicted Group Membership (%)**							
	A. viridigula	***A. prevostii***	***A. nigricollis***	***A. veraguensis***	***A. dominicus***	***A. viridis***	***A. mango***	***A. recurvirostris***
A. viridigula	**76.9**	**7.7**	**7.7**	0	0	**7.7**	0	0
A. prevostii	**8.8**	**82.5**	**8.8**	0	0	0	0	0
A. nigricollis	**5.1**	**6.0**	**88.9**	0	0	0	0	0
A. veraguensis	0	**33.3**	0	**66.7**	0	0	0	0
A. dominicus	0	0	0	0	**97.9**	0	**2.1**	0
A. viridis	0	0	0	0	0	**100.0**	0	0
A. mango	0	0	0	0	0	0	**100.0**	0
A.recurvirostris	0	0	0	0	0	0	0	**100.0**

89.2% of original grouped cases correctly classified

According to the standardized canonical discriminant function coefficients (SCDFC) obtained after the DFA, for males (Table 13b) the body parts making the most contribution to the overall discrimination (first three functions explain 92.9% of the variance) are the ventral areas of the gorget (Fac1_12, Fac2_12, Fac3_12), low throat (Fac1_14, Fac2_14, Fac3_14), and breast (Fac1_17, Fac2_17, Fac3_1). Additionally, the color of the secondary feathers and the tip of the fifth rectrices contribute to this difference (Appendix 23). For females the differences are more dispersed along the body (Table 14b), in which the first three functions explain 83.9 % of the overall coloration variance. Both the ventral (Fac1, Fac2 and Fac3 for codes 12, 13, 14, and 15) and dorsal sections of the body (Fac2 for codes 1, 2, 4, 5) contribute to the variance (Appendix 24).

The analysis of the genus at the species level shows considerable overlap among some of the species. This result, in addition to a revision in the literature (Peters 1945, Schuchmann 1999, Dickinson 2003) indicate potential inadequacies in the current taxonomy of the group, and the need for a more detailed revision of the species. This will be done and discussed in the following sections.

Anthracothorax recurvirostris

The Fiery-tailed Awlbill or Swainson's Hummingbird occurs in southeastern Venezuela (Bolivar State) and the Guianas to north-central Brazil (lower Amazon east to Marañao and Piaui). It is said to also inhabit eastern Ecuador on the Napo River, but no specimen from this area was found in any of the collections visited. It ranges in lowlands from sea level to 500 m.a.s.l. in open savanna-like vegetation near granite outcrops within primary forests, or sometimes at edges of low secondary vegetation near rivers (Schuchmann 1999).

This *Anthracothorax* species has usually been placed within the monospecific genus *Avocettula* (Peters 1945) mainly due to the remarkable bill shape. Schuchmann (1999) has pointed out that other morphological characters, as well as behavior and nest structure, support the positioning of this group within the genus *Anthracothorax*. Furthermore, the results from

the previous section show on the basis of plumage coloration it is not possible to separate the "*recurvirostris*" group from the other *Anthracothorax* species. Figures 19 (males) and 20 (females) show complete overlap of this group with the other species of *Anthracothorax*, which indicates that they belong to the same genus.

Controversies in populations of *Anthracothorax nigricollis* and *Anthracothorax prevostii*

The Black-throated Mango, *Anthracothorax nigricollis* is the most widely distributed species of this genus, being the only one occurring in both Central and South America. It inhabits the lowlands up to 1000 m from eastern Panama and Colombia to Venezuela, Trinidad, and Tobago, to the south reaching Paraguay and Argentina (Schuchmann 1999). Although widely distributed, they are not common in their range. They occur in tropical rainforests, but can also be observed in plantations, gardens, and parks where they prefer flowers found at about 15 m height (Schuchmann 1980a). The Green-breasted Mango *Anthracothorax prevostii* occurs in Central America and also a few Caribbean islands such as Old Providence and San Andres. It inhabits mostly lowlands (900-1200 m) in tall second growth, or borders of gallery forests and mangroves and it can be found in savannas, pastures, parks, and some plantations, such as coffee (shaded) (Schuchmann 1999).

These two species are the most widely distributed of all *Anthracothorax*. They are occasionally regarded as conspecifics and seem to form a superspecies with *A. veraguensis*, and probably also with *A. viridigula* (Schuchmann 1999). *A. nigricollis* and *A. prevostii* replace each other geographically and show some overlap in northern Venezuela. *A. nigricollis* is considered a monotypic species (Schuchmann 1999, Dickinson 2003); however, according to Peters (1945), *A. nigricollis* includes two subspecies: *A. n. nigricollis*, and *A. n. iridescens* (Fig. 21). Schuchmann (1999), includes the subspecies "*iridescens*" in *A. prevostii* (Fig. 22) but states that the systematic position of these populations is still a matter of opinion.

The identification of data collected from museum specimens reflected this controversy, and two groups of "*iridescens*" appear, one as part of *A. nigricollis* and the other as part of *A. prevostii*. In order to elucidate these differences I conducted a plumage color analysis for the specimens of the two species together and made a separate more detailed analysis.

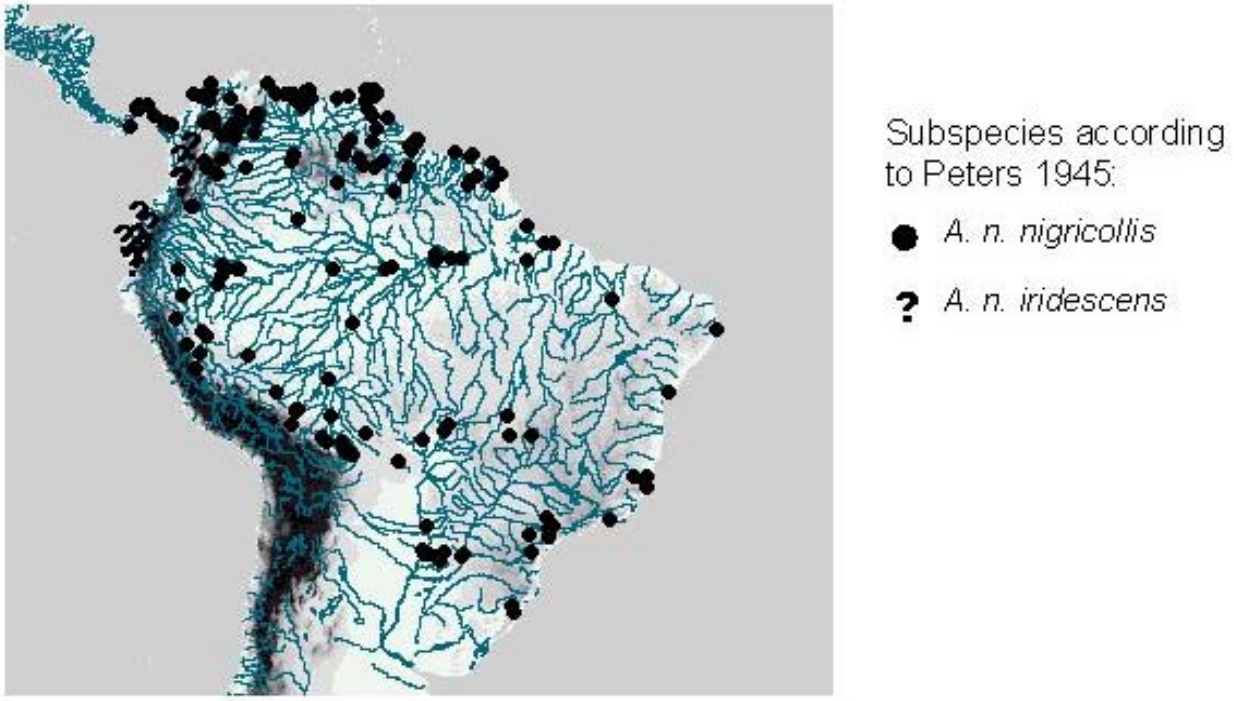
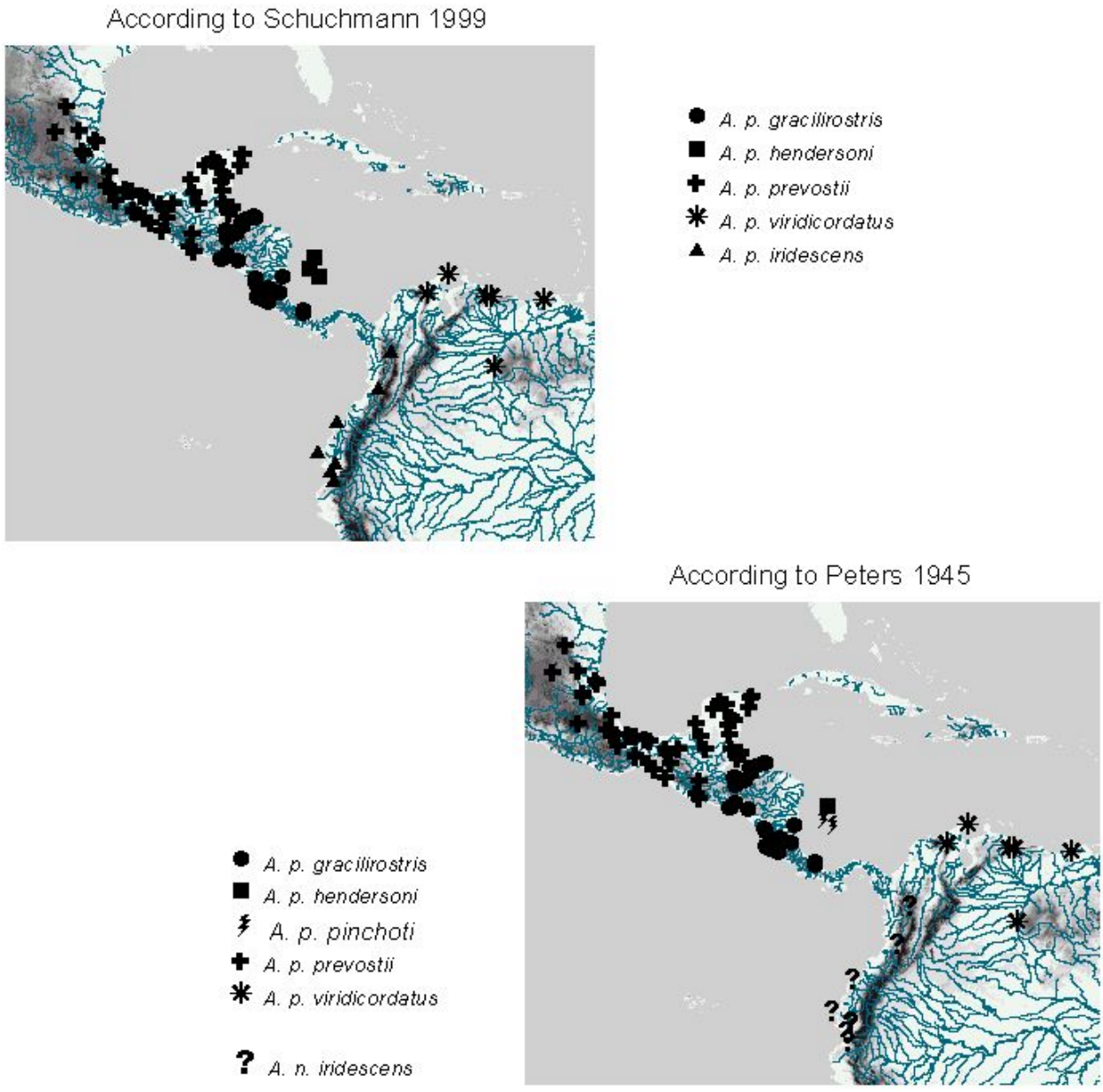


Fig. 21. Subspecies of *Anthracothorax nigricollis* according to Peters (1945) (Schuchmann 1999 considers this species as monotypic).

Fig. 22. Subspecies of *Anthracothorax prevostii* according to Schuchmann (1999) (above), and to Peters (1945) (below) giving special attention to the subspecies "*iridescens*."



Elucidating the difference:

I conducted a plumage color analysis by sex. I performed a PCA for each body part of all specimens of both species together. Then the PC scores were taken to conduct a DFA (Appendix 25 for males and 26 for females). The groups analyzed by the DFA are the species and subspecies considered by both Schuchmann (1999) and Peters (1945), identifying and separating those controversial taxa between the two authors (Fig. 21 and Fig. 22). Additionally, I considered two separate groups of "*iridescens*", one belonging to *A. nigricollis* and the other to *A. prevostii*, as they were labeled in the ornithological collections, to better determine the correct taxonomic position of these populations.

I show the results in Fig. 23 (males) and Fig. 24 (females), where the filled symbols indicate the subspecies of *A. prevostii* and the open symbols *A. nigricollis*, including the two groups of "*iridescens*" whose centroids are closer to the other subspecies of *A. nigricollis*. The first two functions explain 75.5% of the variation in males (Table 17) and 59.1% in females (Table 18).

The distribution of individuals from the two "*iridescens*" populations (open squares and triangles) falls within the distribution of *A. nigricollis* (open symbols) and not of *A. prevostii* (filled symbols), indicating that the populations of *Anthracothorax* occurring west of the Andes in Ecuador and southern Colombia, "*iridescens*", are part of *A. nigricollis*, as stated by Peters (1945). Consequently, all specimens from these populations will be considered *A. nigricollis iridescens* for further analysis.

I conducted a second DFA to determine which variables (parts of the body) are most relevant to differentiate between these two species: *A. nigricollis* and *A. prevostii*. Only one factor for each sex was sufficient to explain the differences and extract the important variables (Tables 19 and 20). According to the SCDFC (Table 19), the variables that explain most of the variation between both species in males are low throat (Fac1_14, Fac2_14) and color of the lateral iridescence of the breast (Fac2_21), undertail coverts (Fac2_26), and r5 (Fac3_39). In females (Table 20), the ventral areas of neck (Fac2_2), shoulder (Fac2_3 and Fac3_3), gorget

(Fac2_12), and low throat (Fac_14) are significant, in addition to the color of the wing coverts (Fac2_29).

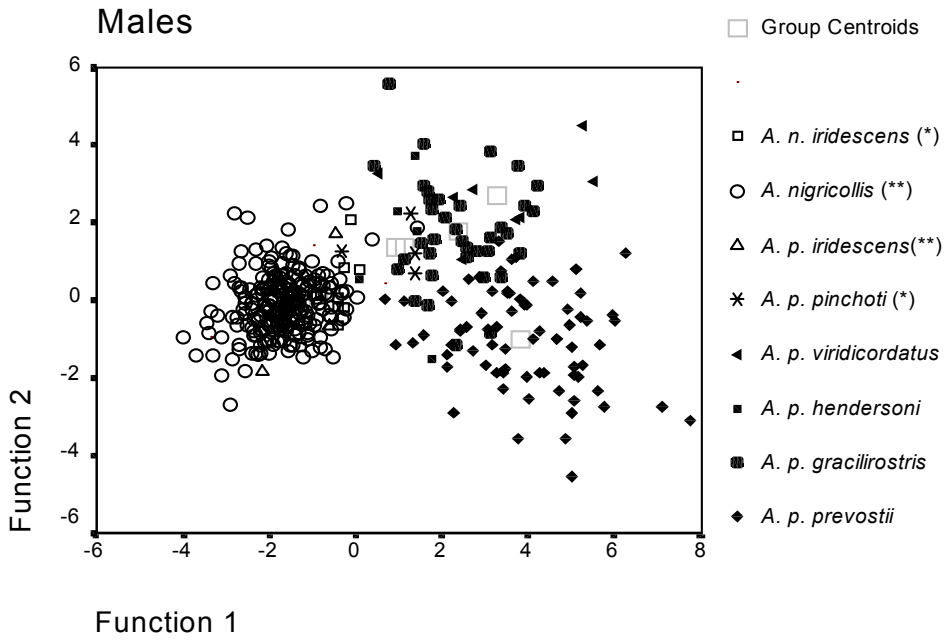


Fig. 23. Results of the DFA conducted on the color data of males of *A. nigricollis* and *A. prevostii* separated by subspecies. (*) *sensu* Peters 1945. (**) *sensu* Schuchmann 1999.

Eigenvalues

Function	Eigenvalue	% of Variance	Cumulative %	Canonical Correlation
1	5,673[a]	66,8	66,8	,922
2	,732[a]	8,6	75,5	,650
3	,642[a]	7,6	83,0	,625
4	,569[a]	6,7	89,7	,602
5	,368[a]	4,3	94,1	,519
6	,307[a]	3,6	97,7	,485
7	,194[a]	2,3	100,0	,403

a. First seven canonical discriminant functions were analysis

Table 17. Eigenvalues and percentages of variance found after the DFA conducted on the color data of males from *A. nigricollis* and *A. prevostii* separated by subspecies.

Fig. 24. Results of the DFA conducted on the color data of females of *A. nigricollis* and *A. prevostii* separated by subspecies. (*) *sensu* Peters 1945. (**) *sensu* Schuchmann 1999.

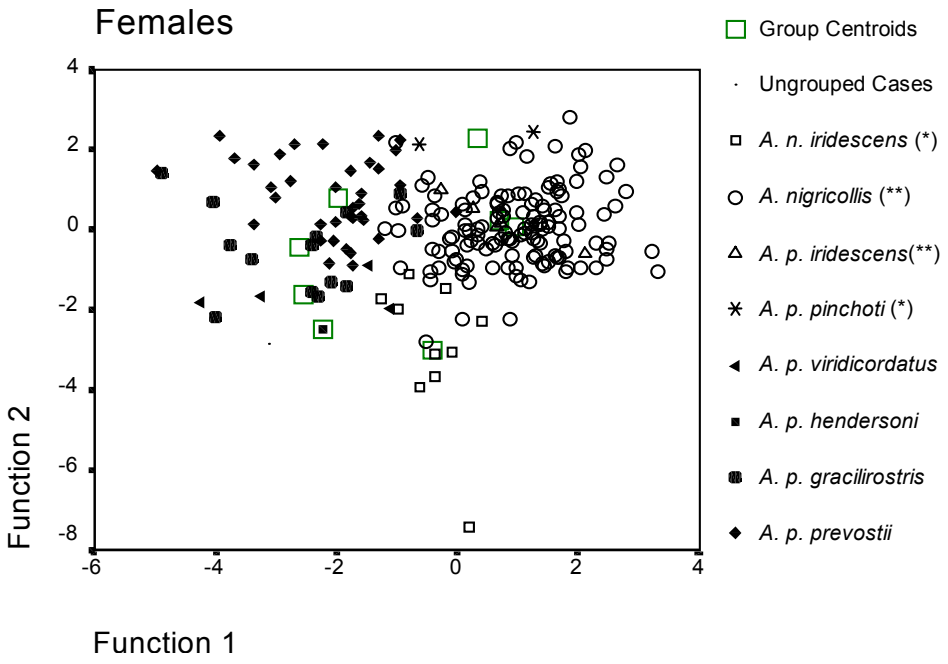


Table 18. Eigenvalues and percentages of variance found after the DFA conducted on the color data of females from *A. nigricollis* and *A. prevostii* separated by subspecies.

Eigenvalues

Function	Eigenvalue	% of Variance	Cumulative %	Canonical Correlation
1	2,009[a]	43,3	43,3	,817
2	,730[a]	15,7	59,1	,649
3	,587[a]	12,7	71,7	,608
4	,422[a]	9,1	80,8	,545
5	,414[a]	8,9	89,8	,541
6	,257[a]	5,5	95,3	,452
7	,217[a]	4,7	100,0	,423

a. First seven canonical discriminant functions were analysis

Table 19. Eigenvalues, percentages of variance and SCDFC table for the DFA conducted on males of *A. nigricollis* and *A. prevostii* to extract the relevant variables that explain differences between groups.

Eigenvalues

Function	Eigenvalue	% of Variance	Cumulative %	Canonical Correlation
1	3,66 [a]	100,	100,	,88

a. First canonical discriminant function was used in the analysis

	Function
	1
FAC1_1	,208
FAC2_1	,082
FAC3_1	,058
FAC1_2	-,114
FAC2_2	,140
FAC3_2	-,150
FAC1_3	,056
FAC2_3	-,257
FAC3_3	,304
FAC1_4	,149
FAC2_4	,183
FAC3_4	,411
FAC1_5	,050
FAC2_5	-,283
FAC3_5	,013
FAC1_6	,019
FAC2_6	-,259
FAC3_6	-,017
FAC1_12	,012
FAC2_12	,198
FAC3_12	,064
FAC1_13	,120
FAC2_13	-,439
FAC3_13	,273
FAC1_14	-,551
FAC2_14	-,971
FAC3_14	-,341
FAC1_15	-,404
FAC2_15	-,003
FAC3_15	,207
FAC1_17	,361
FAC2_17	-,052
FAC3_17	,106
FAC1_18	-,058
FAC2_18	,294
FAC3_18	,114
FAC1_20	,340
FAC2_20	-,237
FAC3_20	,212
FAC1_21	,072
FAC2_21	-,835
FAC3_21	-,148
FAC1_26	,256
FAC2_26	,541
FAC3_26	-,194
FAC1_29	,329
FAC2_29	,474
FAC3_29	,392
FAC1_30	,315
FAC2_30	,152
FAC3_30	,168
FAC1_32	,123
FAC2_32	-,117
FAC3_32	-,135
FAC1_33	,080
FAC2_33	-,006
FAC3_33	,126
FAC1_34	,005
FAC2_34	-,008
FAC3_34	-,134
FAC1_39	,186
FAC2_39	-,325
FAC3_39	-,536
FAC1_40	,069
FAC2_40	,130
FAC3_40	-,349

Table 20. Eigenvalues, percentages of variance and SCDFC table for the DFA conducted on females of *A. nigricollis* and *A. prevostii* to extract the relevant variables that explain differences between groups.

Eigenvalues

Function	Eigenvalue	% of Variance	Cumulative %	Canonical Correlation
1	3,66 [a]	100,	100,	,88

a. First canonical discriminant function was used in the analysis

	Function
	1
FAC1_1	,208
FAC2_1	,082
FAC3_1	,058
FAC1_2	-,114
FAC2_2	,140
FAC3_2	-,150
FAC1_3	,056
FAC2_3	-,257
FAC3_3	,304
FAC1_4	,149
FAC2_4	,183
FAC3_4	,411
FAC1_5	,050
FAC2_5	-,283
FAC3_5	,013
FAC1_6	,019
FAC2_6	-,259
FAC3_6	-,017
FAC1_12	,012
FAC2_12	,198
FAC3_12	,064
FAC1_13	,120
FAC2_13	-,439
FAC3_13	,273
FAC1_14	-,551
FAC2_14	-,971
FAC3_14	-,341
FAC1_15	-,404
FAC2_15	-,003
FAC3_15	,207
FAC1_17	,361
FAC2_17	-,052
FAC3_17	,106
FAC1_18	-,058
FAC2_18	,294
FAC3_18	,114
FAC1_20	,340
FAC2_20	-,237
FAC3_20	,212
FAC1_21	,072
FAC2_21	-,835
FAC3_21	-,148
FAC1_26	,256
FAC2_26	,541
FAC3_26	-,194
FAC1_29	,329
FAC2_29	,474
FAC3_29	,392
FAC1_30	,315
FAC2_30	,152
FAC3_30	,168
FAC1_32	,123
FAC2_32	-,117
FAC3_32	-,135
FAC1_33	,080
FAC2_33	-,006
FAC3_33	,126
FAC1_34	,005
FAC2_34	-,008
FAC3_34	-,134
FAC1_39	,186
FAC2_39	-,325
FAC3_39	-,536
FAC1_40	,069
FAC2_40	,130
FAC3_40	-,349

Anthracothorax nigricollis

In order to perform a more specific taxonomic analysis, I divided the entire *A. nigricollis* group into pools following the criteria explained in the Methodology section (see Fig. 2). A total of 21 pools resulted from this division and they are shown in Figure 25. Plumage color data from specimens previously considered as *A. prevostii* "*iridescens*" were added to the *A. nigricollis* data set. A PCA was conducted and the first three factors (PCs) were extracted (see Appendix 27 for males and Appendix 28 for females). A DFA was performed taking the 21 defined pools.

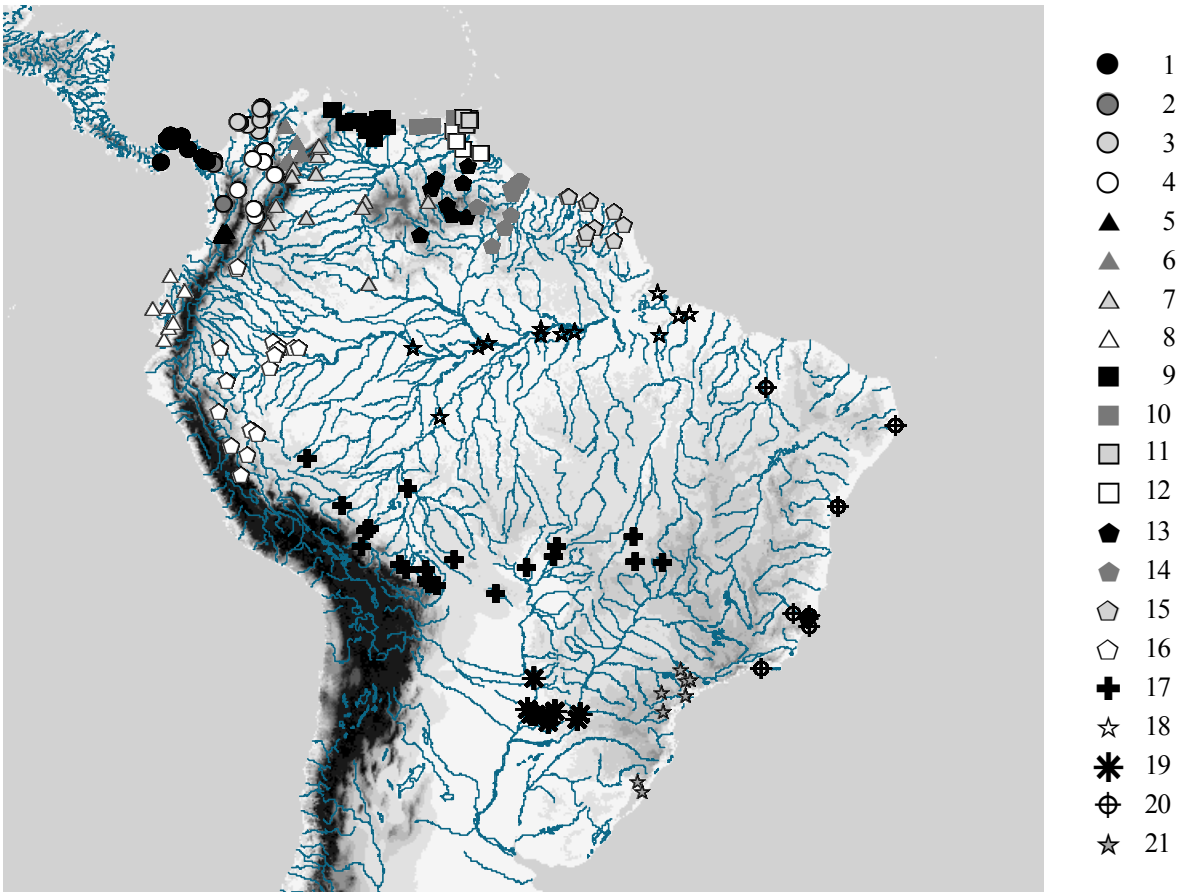


Fig. 25. Pools of *Anthracothorax nigricollis* used to conduct taxonomic analysis on the species. The figure shows 21 numbered pools.

Table 21. Eigenvalues and percentages of variance found after the DFA conducted on the color data of males from the 21 pools of *A. nigricollis.*

Eigenvalues

Function	Eigenvalue	% of Variance	Cumulative %	Canonical Correlation
1	3,669[a]	22,4	22,4	,886
2	2,987[a]	18,3	40,7	,866
3	1,799[a]	11,0	51,7	,802
4	1,324[a]	8,1	59,8	,755
5	,950[a]	5,8	65,6	,698
6	,757[a]	4,6	70,2	,657
7	,705[a]	4,3	74,5	,643
8	,621[a]	3,8	78,3	,619
9	,567[a]	3,5	81,8	,602
10	,492[a]	3,0	84,8	,574
11	,450[a]	2,7	87,6	,557
12	,413[a]	2,5	90,1	,540
13	,300[a]	1,8	91,9	,480
14	,286[a]	1,7	93,7	,472
15	,259[a]	1,6	95,2	,453
16	,225[a]	1,4	96,6	,428
17	,201[a]	1,2	97,8	,409
18	,157[a]	1,0	98,8	,368
19	,126[a]	,8	99,6	,335
20	,070[a]	,4	100,0	,255

a. First 20 canonical discriminant functions were used in the analysis.

Table 22. Eigenvalues and percentages of variance found after the DFA conducted on the color data of females from the 21 pools of *A. nigricollis.*

Eigenvalues

Function	Eigenvalue	% of Variance	Cumulative %	Canonical Correlation
1	5,169[a]	20,6	20,6	,915
2	3,156[a]	12,6	33,2	,871
3	2,625[a]	10,5	43,7	,851
4	2,209[a]	8,8	52,5	,830
5	2,072[a]	8,3	60,8	,821
6	1,624[a]	6,5	67,3	,787
7	1,301[a]	5,2	72,4	,752
8	1,175[a]	4,7	77,1	,735
9	1,040[a]	4,1	81,3	,714
10	,900[a]	3,6	84,9	,688
11	,724[a]	2,9	87,8	,648
12	,689[a]	2,8	90,5	,639
13	,456[a]	1,8	92,3	,560
14	,414[a]	1,7	94,0	,541
15	,372[a]	1,5	95,5	,521
16	,323[a]	1,3	96,8	,494
17	,272[a]	1,1	97,8	,462
18	,204[a]	,8	98,7	,411
19	,189[a]	,8	99,4	,399
20	,147[a]	,6	100,0	,358

a. First 20 canonical discriminant functions were used in the analysis.

The first two discriminant functions explained only 40.7% of the variance in males (Table 21) and 33.2% in females (Table 22). This low percentage could be due to the number of pools represented in the analysis and to the fact that the color differences in this case are not that specifically strong or marked; however, these results show the pools ordering themselves in three geographically separated groups. The graph obtained by using only these first two factors as coordinates makes a good separation of the pool centroids, showing three clear clouds in the case of males (Fig. 26) that represent three main groups: *A. nigricollis iridescens*, *A. nigricollis nigricollis*, and a potential new subspecies that will be preliminarily called *A. nigricollis* "new subspecies." Although each pool is represented by a different symbol, a gradation of grays is used to facilitate the interpretation and differentiation of the three groups. The centroids with numbers are also shown to identify each pool. The filled symbols correspond to *A. nigricollis iridescens*, the open symbols indicate groups of *A. nigricollis nigricollis*, and the gray symbols constitute the potential new subspecies within *A. nigricollis* (all from Venezuela and adjacent areas).

In the analysis of the females (Fig. 27), the pools of *A. n. iridescens* overlap with those of the "new subspecies"; however, they are both apart from *A. n. nigricollis*. This may be due to the similarity among females of this genus already discussed. Nevertheless, the separation of pools of the Venezuelan area from the rest is also clear in females. The results of this analysis support the existence of a differentiated group within *A. nigricollis*, geographically distributed in the area of Venezuela, northernmost tip of Brazil, and eastern Colombia. The potential new subspecies of *A. nigricollis* is represented in Figure 28.

A second DFA was conducted for males and females, taking into account only the three described groups in order to determine the parts of the body that account for most of the color difference among them. The first two functions are enough to explain 100% of the variation in both sexes (Tables 23 and 24). The SCDFC table obtained for males (Table 23) indicates that the colors of the gorget (Fac1_12 and Fac2_12), and of the breast are the most significant. In females the differences are found in dispersed areas of the body, such as undertail coverts

(Fac2_26), shoulders (Fac2_3 and Fac3_3), gorgets (Fac2_12), secondary feathers (Fac1_30 and Fac2_30), and wings coverts (Fac2_29 and Fac_3_29) (Table 24).

Graphs showing plumage color differences on each body part of members of the three final groups are presented in Appendix 29 (males) and Appendix 30 (females). In addition to the color variation there are also differences in some of the morphometric measurements of the body (Table 25 for males, 26 for females). According to ANOVAS and LSD *post hoc* tests (Appendix 31 for males, 32 for females) both sexes of the subspecies *A. n. iridescens* are significantly larger than those of the other two subspecies. This relationship is found in all measurements except wing length, which shows no significant difference among the three groups. With regard to the "new subspecies" the main difference is found in the bill length of both sexes, which is medium compared with the other two subspecies. Rectrix 2 in this group is also significantly smaller than in the others.

Fig. 26. Results of the DFA conducted on the color data of males of *Anthracothorax nigricollis* showing three separate groups: *A. nigricollis nigricollis* (open symbols), *A. n. iridescens* (black symbols), and *A. n*. "new subspecies" (gray symbols).

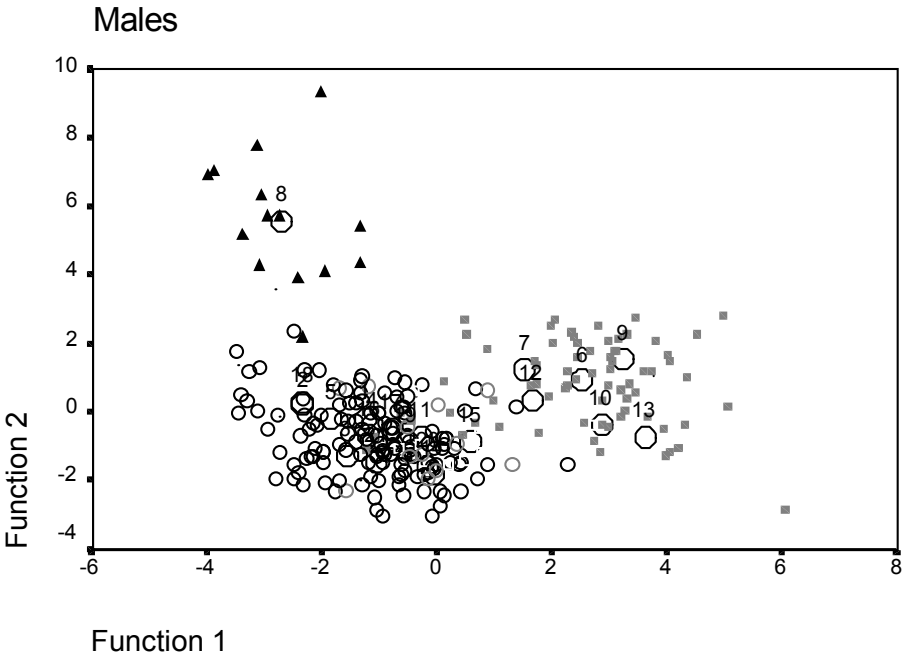


Fig. 27. Results of the DFA conducted on the color data of females of *Anthracothorax nigricollis* showing *A. n*. "new subspecies" (gray symbols) separated from *A. nigricollis nigricollis* (open symbols).

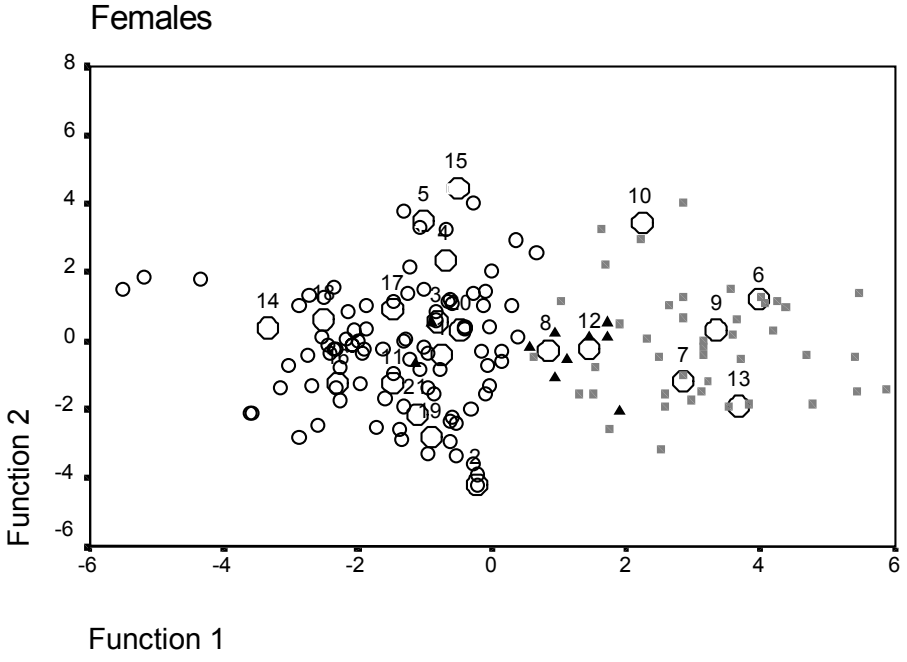


Fig. 28. Proposed subspecies of *Anthracothorax nigricollis* as a result of the analysis: *A. nigricollis nigricollis*, *A. nigricollis iridescens*, and *A. nigricollis "new subspecies*".

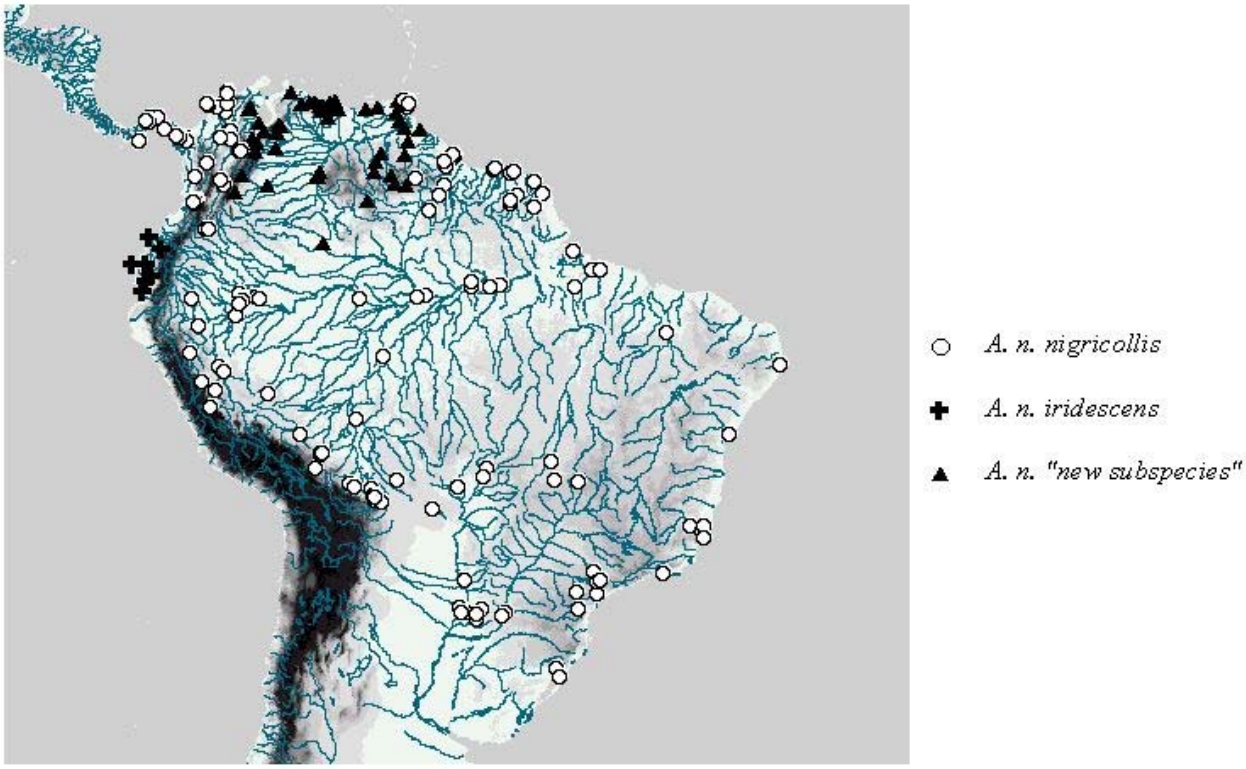


Table 23. Eigenvalues, percentages of variance and SCDFC table for the DFA conducted on males of *A. nigricollis* to extract the relevant variables that explain differences between subspecies.

Eigenvalues

Function	Eigenvalue	% of Variance	Cumulative %	Canonical Correlation
1	2,727[a]	55,7	55,7	,855
2	2,171[a]	44,3	100,0	,827

a. First 2 canonical discriminant functions were used in the analysis.

	Function	
	1	2
FAC1_1	-,060	,046
FAC2_1	-,003	-,072
FAC3_1	-,288	-,122
FAC1_2	-,059	,021
FAC2_2	,202	,172
FAC3_2	-,152	-,066
FAC1_3	-,021	,355
FAC2_3	,161	-,203
FAC3_3	-,297	,585
FAC1_4	-,202	-,166
FAC2_4	-,089	-,486
FAC3_4	-,096	-,220
FAC1_5	,395	-,188
FAC2_5	,745	-,341
FAC3_5	,573	-,113
FAC1_6	-,227	-,002
FAC2_6	-,373	,420
FAC3_6	,144	,022
FAC1_12	1,544	-,508
FAC2_12	1,269	-,495
FAC3_12	,168	,295
FAC1_13	-,107	,464
FAC2_13	-,050	-,096
FAC3_13	,147	,772
FAC1_14	,210	,261
FAC2_14	-,564	,575
FAC3_14	,077	,119
FAC1_15	,491	,409
FAC2_15	-,402	-,618
FAC3_15	-,157	-,228
FAC1_17	-,177	,232
FAC2_17	-,230	1,549
FAC3_17	-,034	-,253
FAC1_18	-,423	-,059
FAC2_18	-,218	-,646
FAC3_18	,053	-,470
FAC1_20	-,081	-1,067
FAC2_20	-,040	-1,644
FAC3_20	-,040	,206
FAC1_21	-,090	-,420
FAC2_21	,659	,579
FAC3_21	,174	,210
FAC1_26	-,181	,126
FAC2_26	-,362	,676
FAC3_26	-,105	,132
FAC1_29	-,240	,214
FAC2_29	,621	,148
FAC3_29	-,101	-,206
FAC1_30	,213	,572
FAC2_30	-,107	,251
FAC3_30	,041	,316
FAC1_32	,113	-,013
FAC2_32	,125	-,283
FAC3_32	-,092	,197
FAC1_33	-,046	,156
FAC2_33	,376	,068
FAC3_33	,070	-,050
FAC1_34	,180	-,020
FAC2_34	,239	-,016
FAC3_34	,166	-,348
FAC1_39	-,150	-,204
FAC2_39	-,010	,367
FAC3_39	,010	,180
FAC1_40	-,104	,183
FAC2_40	,115	-,037
FAC3_40	-,038	-,126

Table 24. Eigenvalues, percentages of variance and SCDFC table for the DFA conducted on females of *A. nigricollis* to extract the relevant variables that explain differences between subspecies.

Eigenvalues

Function	Eigenvalue	% of Variance	Cumulative %	Canonical Correlation
1	3,672[a]	77,9	77,9	,887
2	1,039[a]	22,1	100,0	,714

a. First 2 canonical discriminant functions were used in the analysis.

	Function	
	1	2
FAC1_1	,553	-,059
FAC2_1	-,649	,626
FAC3_1	,177	-,072
FAC1_2	-,390	,148
FAC2_2	-,498	,414
FAC3_2	,461	,176
FAC1_3	-,159	-,278
FAC2_3	,442	1,449
FAC3_3	-,512	-1,493
FAC1_4	-,100	-,284
FAC2_4	-,077	-,236
FAC3_4	,007	-,379
FAC1_5	-,053	,319
FAC2_5	,663	,424
FAC3_5	,215	,491
FAC1_6	-,087	-,265
FAC2_6	-,009	,270
FAC3_6	-,214	,359
FAC1_12	,417	,763
FAC2_12	,710	1,763
FAC3_12	-,213	-,260
FAC1_13	-,016	,163
FAC2_13	-,115	-,243
FAC3_13	-,046	-,425
FAC1_14	,115	,078
FAC2_14	,431	-,259
FAC3_14	,497	-,413
FAC1_15	,507	-,435
FAC2_15	-,588	,209
FAC3_15	,378	,340
FAC1_17	,059	,272
FAC2_17	,258	,313
FAC3_17	,030	,045
FAC1_18	,325	-,001
FAC2_18	-,390	,551
FAC3_18	-,726	,432
FAC1_26	-,301	,001
FAC2_26	-1,798	-,094
FAC3_26	-,002	,102
FAC1_29	,265	-,714
FAC2_29	,343	-1,207
FAC3_29	,048	-1,096
FAC1_30	1,922	-,036
FAC2_30	1,846	-,187
FAC3_30	,457	-,202
FAC1_32	-,012	,314
FAC2_32	-,075	,099
FAC3_32	-,029	,057
FAC1_33	,242	-,046
FAC2_33	,053	-,349
FAC3_33	-,088	,180
FAC1_39	-,055	,298
FAC2_39	-,031	-,147
FAC3_39	-,094	-,117
FAC1_40	,424	-,328
FAC2_40	,220	,353
FAC3_40	-,409	,379

Table 25. Morphometric measurements of males from the three groups of the species *Anthracothorax nigricollis*, indicating statistically significant differences between them.

Taxon (males)		Bill length (mm) **	Wing length (mm)	Rectrix 1 (mm) **	Rectrix 2 (mm) **	Rectrix 5 (mm) **
Anthracothorax	$x=$	**29,31**	**66,42**	**35,70**	**35,96**	**38,41**
nigricollis	$\sigma=$	1.01	1.95	1.11	1.05	1.13
iridescens	$n=$	22	21	22	19	22
Anthracothorax	$x=$	**27,28**	**65,82**	**33,16**	**34,14**	**37,51**
nigricollis	$\sigma=$	1.21	1.84	1.11	1.17	1.56
nigricollis	$n=$	201	206	202	192	200
Anthracothorax	$x=$	**27,69**	**66,14**	**33,13**	**33,88**	**36,69**
nigricollis	$\sigma=$	1.06	1.70	1.15	1.17	1.77
"new subspecies"	$n=$	88	91	88	88	85

*Significant difference (t-test; $p<0.05$) among subspecies for this variable.
**Significant difference (t-test; $p<0.01$) among subspecies for this variable.

Table 26. Morphometric measurements of females from the three groups of the species *Anthracothorax nigricollis*, indicating statistically significant differences between them.

Taxon (females)		Bill length (mm) **	Wing length (mm) **	Rectrix 1 (mm) **	Rectrix 2 (mm) **	Rectrix 5 (mm) **
Anthracothorax	$x=$	**31.22**	**67.11**	**36.32**	**36.64**	**36.86**
nigricollis	$\sigma=$	1.15	1.78	1.66	1.15	1.23
iridescens	$n=$	12	12	12	12	10
Anthracothorax	$x=$	**27.97**	**64.20**	**32.97**	**33.99**	**34.93**
nigricollis	$\sigma=$	1.26	1.77	1.16	1.18	1.36
nigricollis	$n=$	107	108	106	95	101
Anthracothorax	$x=$	**28.93**	**64.60**	**33.12**	**33.54**	**34.65**
nigricollis	$\sigma=$	1.19	1.80	1.05	1.15	1.63
"new subspecies"	$n=$	41	47	45	42	43

*Significant difference (t-test; $p<0.05$) among subspecies for this variable.
**Significant difference (t-test; $p<0.01$) among subspecies for this variable.

Anthracothorax prevostii

This species seems to show greater color variation compared with *A. nigricollis*. If the subspecies "*iridescens*" is considered as belonging to *A. nigricollis*, the only controversy in *A. prevostii* is the validity of subspecies *A. prevostii pinchoti* occurring on San Andrés Island (Fig. 22). After excluding the information on "*iridescens*" from the *A. prevostii* data set, I regrouped the species (defined pools) according to my criteria (see General Methodology). A total of 12 pools were found to conduct further analysis (Fig. 29), the population of *A. prevostii hendersoni* from San Andrés Island being pool number 8 and *A. prevostii pinchoti* (according to Peters 1945) pool number 12.

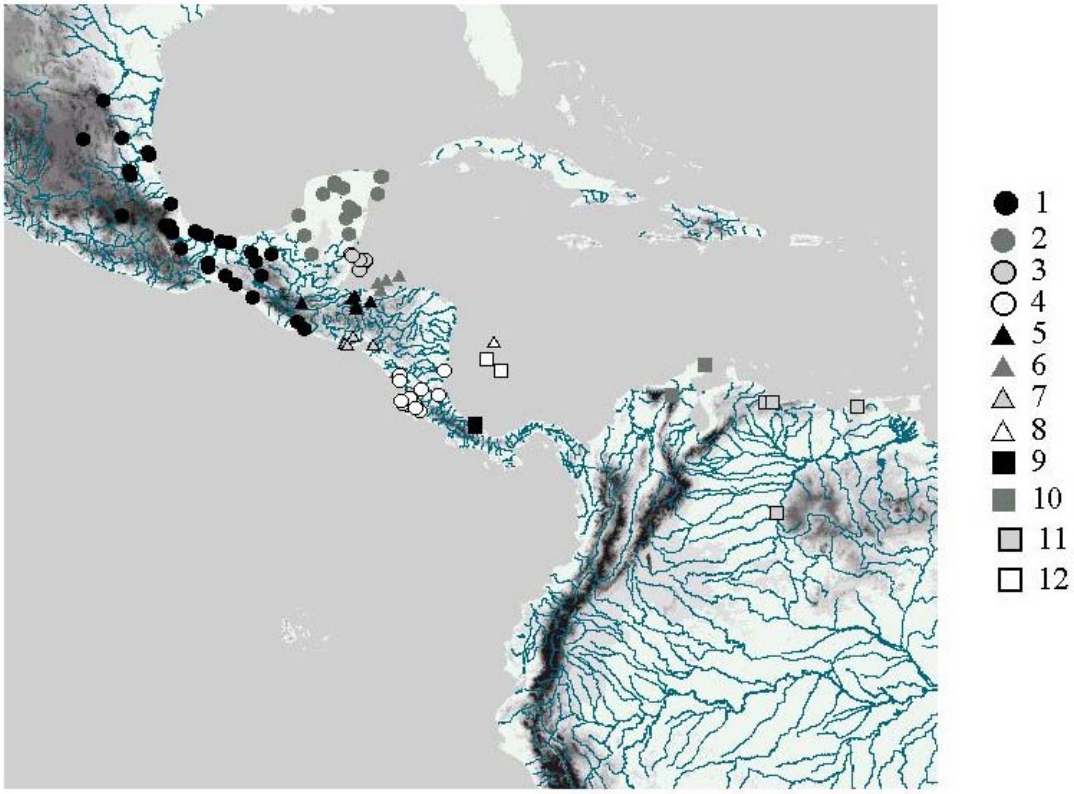


Fig. 29. Pools of *Anthracothorax prevostii* used to conduct taxonomic analysis on the species. The figure shows 12 numbered pools.

I performed a DFA using the first three PCs resulting from the PCA on males (Appendix 33) and females (Appendix 34) as separate data sets. The first two functions explained 43.7 % of the variance in males (Table 27) and 69.2 % in females (Table 28). These percentages were higher than in *A. nigricollis* perhaps due to the lower number of groups analyzed here (only 12). The results given by the DFA (Fig. 30 for males, 31 for females) indicate a substantial difference between *A. prevostii hendersoni* and *A. p. pinchoti,* so that they should not be considered as part of the same group. The DFAs also indicate the potential existence of other groups not previously considered and that appear to be different from the remainder of *A. prevostii*. The population of the Costa Rican Atlantic area (number 9) can be separated from the rest of *A. p. gracilirostris*, and the population from the Yucatán peninsula (number 2) appears to be different from *A. p. prevostii* occurring in the rest of the distribution area. In the first case, only six males and two females were included in the final analysis. In the case of the Yucatán specimens, there were 23 males and 10 females in the final analysis, which allows more confidence in the results. However, there is a group number 7 (from western Central America) that overlaps with the Yucatán group in the case of males. This group includes only two males and three females which makes it difficult to reach any conclusion. For the populations of Atlantic Costa Rica and Yucatán, I consider that the existence of a color difference between these groups has been shown; however, I would rather be conservative until further analyses can be conducted.

Eigenvalues

Function	Eigenvalue	% of Variance	Cumulative %	Canonical Correlation
1	7,523[a]	27,7	27,7	,940
2	4,322[a]	15,9	43,7	,901
3	3,979[a]	14,7	58,4	,894
4	2,549[a]	9,4	67,8	,847
5	2,245[a]	8,3	76,0	,832
6	2,045[a]	7,5	83,6	,820
7	1,615[a]	6,0	89,5	,786
8	1,008[a]	3,7	93,3	,708
9	,697[a]	2,6	95,8	,641
10	,665[a]	2,5	98,3	,632
11	,465[a]	1,7	100,0	,563

a. First 11 canonical discriminant functions were used in the analysis.

Table 27. Eigenvalues and percentages of variance found after the DFA conducted on color data of males from the 12 pools of *A. prevostii.*

Table 28. Eigenvalues and percentages of variance found after the DFA conducted on color data of females from the 12 pools of *A. prevostii.*

Eigenvalues

Function	Eigenvalue	% of Variance	Cumulative %	Canonical Correlation
1	195,928[a]	54,5	54,5	,997
2	52,792[a]	14,7	69,2	,991
3	42,608[a]	11,9	81,0	,988
4	39,092[a]	10,9	91,9	,987
5	9,881[a]	2,7	94,7	,953
6	7,194[a]	2,0	96,7	,937
7	4,953[a]	1,4	98,0	,912
8	3,839[a]	1,1	99,1	,891
9	1,921[a]	,5	99,6	,811
10	1,307[a]	,4	100,0	,753

a. First 10 canonical discriminant functions were used in the analysis.

For the phylogenetic analysis I considered the following seven taxonomic units (TUs) of *A. prevostii*: *A. p. prevostii* (5), *A. p.* "Yucatan" (6), *A. p. gracilirostris* (7), *A. p.* "Atlantic Costa Rica" (8), *A. p. hendersoni* (9), *A. p. pinchoti* (10), *A. p. viridicordatus* (11). I included numbers 6 and 8 to evaluate the results from the phylogenetic analysis and possibly help in arriving at a conclusion about their validity.

Differences in plumage coloration of all body parts on the seven TUs are presented in Appendix 35 (males) and Appendix 36 (females). The main differences in coloration according to the SCDFC (Table 29a and Table 29b) extracted from a second DFA by analyzing the seven TUs are (taking only the first two functions into account) in males the ventral parts of gorget (Fac2_12), central low throat (Fac1_14, Fac2_14, and Fac3_14), lateral low throat (Fac1_15 and Fac2_15), and chest (Fac2_17). In females the differences are mainly found in the dorsal region at the shoulder level (Fac1_3, Fac2_3, and Fac3_3), and also in the gorget (Fac2_12).

Fig. 30. Results of the DFA conducted on color data of males of *Anthracothorax prevostii* showing the separation of *A. prevostii hendersoni* (number 8) but not of *A. p. pinchoti* (number 12).

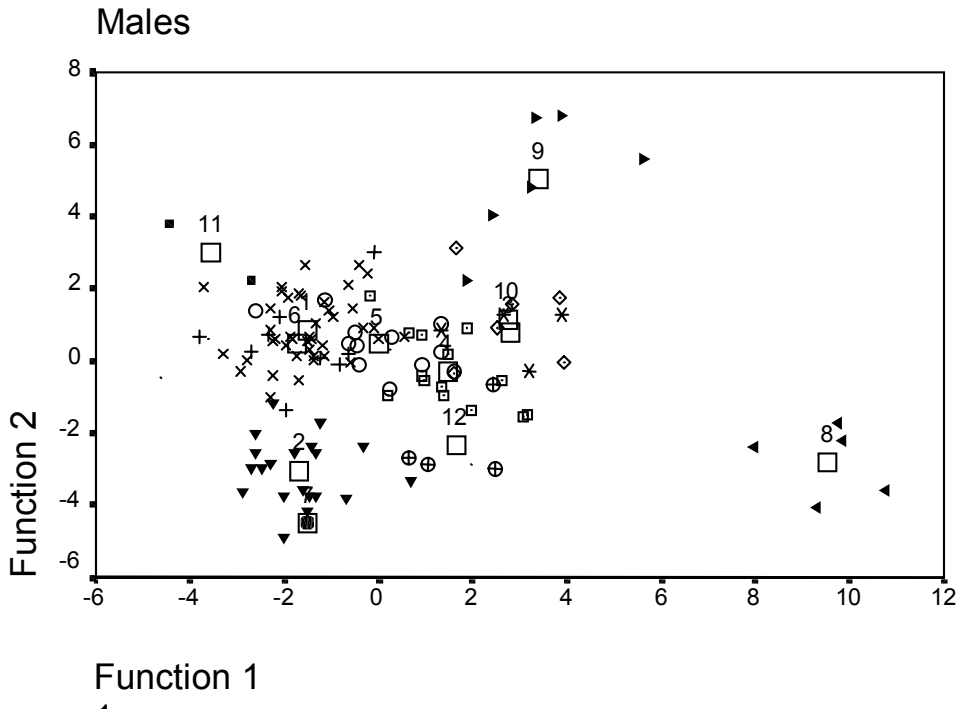


Fig. 31. Results of the DFA conducted on color data of females of *Anthracothorax prevostii.*

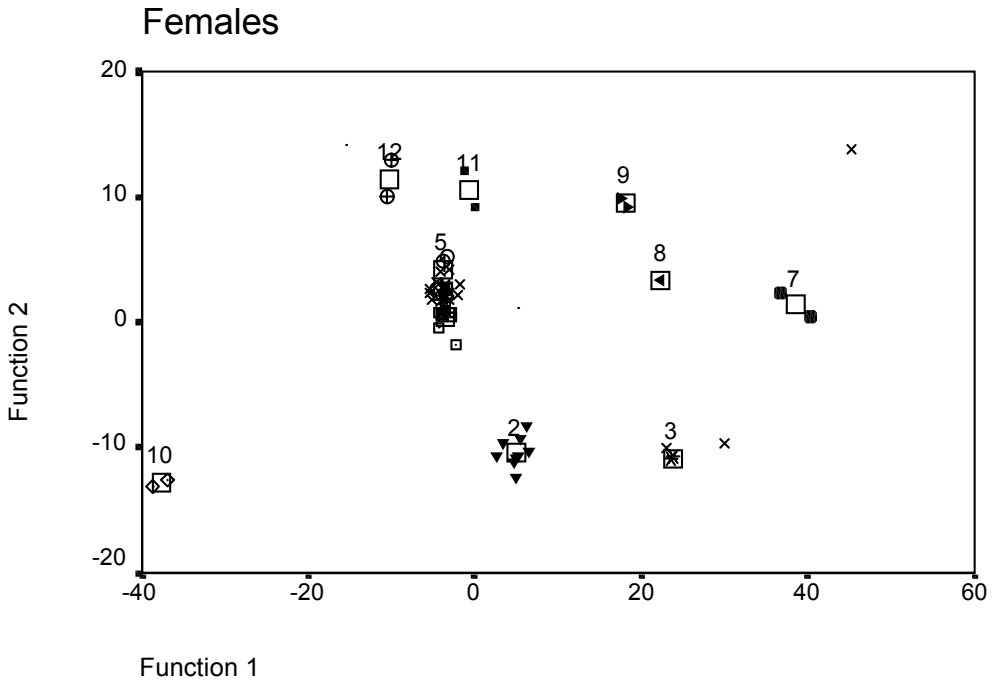


Table 29a. SCDFC table for the second DFA conducted on males of *A. prevostii* to extract the relevant variables that explain differences between groups.

Standardized Canonical Discriminant Function Coefficients

	Function					
	1	2	3	4	5	6
FAC1_1	,022	,067	,023	,085	,652	-,177
FAC2_1	-,339	-,860	-,357	1,275	-,585	-,088
FAC3_1	-,447	-,095	-,504	-,637	-,129	,298
FAC1_2	,084	-,255	-,107	-,524	-,430	,123
FAC2_2	,694	-,159	,508	,637	1,554	,020
FAC3_2	-,866	,183	-,358	-,823	-,680	-,054
FAC1_3	-,420	-,214	-,458	,518	,222	,012
FAC2_3	1,354	-,007	,601	-1,299	,372	,379
FAC3_3	-1,532	,036	,223	,525	-,332	,122
FAC1_4	-,576	,231	-,175	,067	,178	,339
FAC2_4	-2,707	-,209	,131	1,355	,692	-,648
FAC3_4	-1,605	-,703	-,117	,593	,738	-,053
FAC1_5	,471	-,144	-,073	-,202	,112	,104
FAC2_5	1,617	,255	-,145	-,858	,623	,525
FAC3_5	1,152	,100	,044	-,229	,220	,045
FAC1_6	-,782	,101	,108	,018	,575	,023
FAC2_6	-1,057	-,328	-,267	,440	,417	-,089
FAC3_6	,096	,162	-,214	,057	-,292	-,258
FAC1_12	-,289	,670	-,045	,786	-,726	-,215
FAC2_12	-2,818	,461	-3,028	-,534	-1,367	-1,843
FAC3_12	-,712	,654	-,379	,699	-,333	-,300
FAC1_13	-,222	,081	,959	,686	,450	-,023
FAC2_13	,497	,534	-,569	-,275	,083	,072
FAC3_13	-,457	-,015	-,360	-,254	,230	-,154
FAC1_14	2,420	,535	1,200	-,353	-,079	1,037
FAC2_14	6,439	,276	,821	-1,009	,168	2,100
FAC3_14	4,275	,062	1,044	-,468	,035	,899
FAC1_15	1,402	-2,265	,092	-,957	-1,139	-,400
FAC2_15	-,641	1,309	-,396	,540	,475	,620
FAC3_15	1,502	-,643	-,981	-1,078	-,043	-,445
FAC1_17	-,508	-,119	-,198	-,273	,211	,577
FAC2_17	-3,334	-,787	,319	,952	,518	,214
FAC3_17	,053	,622	-,096	,346	,318	-,436
FAC1_18	-,274	,488	-,286	,720	,386	-,043
FAC2_18	1,636	-1,048	-,384	-,869	-1,729	-1,394
FAC3_18	,277	-,429	,117	-,849	-,613	-,739
FAC1_20	1,191	-,477	,110	-,371	-,153	-,348
FAC2_20	1,360	,654	,355	-,143	4,347	,301
FAC3_20	-,716	,260	,171	,440	,161	-,010
FAC1_21	-,064	1,496	-,929	,095	,454	-,068
FAC2_21	,258	-1,273	,881	,031	-,559	,318
FAC3_21	,837	-,544	,234	,001	-,379	,245
FAC1_26	-,160	,668	-,459	,309	,337	,008
FAC2_26	,573	-,433	1,141	-,286	-,920	,005
FAC3_26	-,392	-,283	-,318	-,041	,246	,002
FAC1_29	,129	-,300	,314	,264	,395	,041
FAC2_29	-1,752	-,209	,758	-,051	,096	,402
FAC3_29	-,020	1,023	,120	,192	,146	,175
FAC1_30	,810	-,411	-,305	,765	-,538	-,725
FAC2_30	2,211	,044	-,718	1,608	,195	-,872
FAC3_30	-,157	,477	-,218	-,293	,166	,073
FAC1_32	,241	,417	,340	-,069	-,186	,156
FAC2_32	,513	-,091	-,359	,120	-,277	,382
FAC3_32	-,556	,016	-,378	,062	-,458	-,041
FAC1_33	,496	-,010	-,066	,023	,203	-,074
FAC2_33	,072	-,528	,670	-,013	-,464	-,028
FAC3_33	-,214	,247	,118	-,005	-,432	-,078
FAC1_34	,190	-,210	,493	,749	-,463	,059
FAC2_34	,076	-,187	,048	-,137	,768	-,002
FAC3_34	-1,752	1,119	1,158	1,123	-,873	,151
FAC1_39	-,970	,266	-,256	-,191	,234	-,526
FAC2_39	1,781	-,727	-,121	-,289	-,103	,279
FAC3_39	-,506	-,173	,335	,260	,152	,159
FAC1_40	-,323	,018	,270	-,417	-,189	,134
FAC2_40	-2,727	,933	,441	,078	,806	,999
FAC3_40	,537	,177	-,368	-,196	-,475	,056

Table 29b. SCDFC table for the second DFA conducted on females of *A. prevostii* to extract the relevant variables that explain differences between groups.

Standardized Canonical Discriminant Function Coefficients

	Function					
	1	2	3	4	5	6
FAC1_1	2,713	4,345	,892	-,291	,209	,095
FAC2_1	2,956	-,011	,532	1,489	2,402	2,178
FAC3_1	-6,712	,665	-2,117	-1,388	-1,684	-2,540
FAC1_2	-10,339	-6,150	-1,163	2,211	-1,253	,650
FAC2_2	13,669	-4,573	3,491	4,190	,756	3,368
FAC3_2	5,219	1,127	2,054	,708	,333	1,013
FAC1_3	9,354	6,656	,583	,895	,597	-,388
FAC2_3	-24,143	-13,046	4,738	8,129	1,213	2,881
FAC3_3	-18,390	-8,917	1,378	6,556	-,362	1,036
FAC1_4	2,699	-,675	-,863	1,540	,827	1,144
FAC2_4	15,968	2,734	1,412	-3,215	2,843	-,899
FAC3_4	11,340	,118	6,469	-2,539	1,953	-1,876
FAC1_5	1,319	-,898	2,707	-,633	1,840	1,115
FAC2_5	11,900	4,355	1,203	-1,823	-,146	,997
FAC3_5	,681	-1,350	1,613	-1,455	,242	-,994
FAC1_6	,753	3,408	-,090	,091	,019	-,431
FAC2_6	5,525	6,916	-2,720	1,284	,578	,294
FAC3_6	3,686	-4,465	2,758	,190	,929	,717
FAC1_12	7,651	8,031	-,618	-2,231	-,824	-1,238
FAC2_12	10,094	20,088	-,852	-2,408	1,134	,271
FAC3_12	1,330	3,059	-1,147	,581	-,535	-,278
FAC1_13	6,994	,419	2,391	,111	2,218	,796
FAC2_13	2,727	2,043	1,344	-,175	1,429	-,028
FAC3_13	,317	-2,783	-,331	-3,843	,150	1,413
FAC1_14	2,613	-1,360	,333	-1,595	1,622	1,078
FAC2_14	-4,365	-6,230	-8,870	3,700	2,766	4,792
FAC3_14	,690	-1,818	-3,061	1,928	1,083	1,274
FAC1_15	-6,007	-5,531	,394	1,708	-1,405	-,061
FAC2_15	1,633	3,143	-1,542	,166	-4,306	-3,832
FAC3_15	-5,112	2,758	,047	-,393	-3,817	-3,973
FAC1_17	-4,910	-2,065	,346	-2,568	,539	,093
FAC2_17	-17,407	-4,506	-,700	-1,875	,764	-,869
FAC3_17	-1,411	5,844	-1,172	2,681	1,407	,256
FAC1_18	,087	3,870	,897	1,045	,551	-,502
FAC2_18	-2,557	-5,053	-2,236	-,508	-2,441	-1,743
FAC3_18	-,702	,102	,146	-1,053	,841	,130
FAC1_20	7,186	,371	-1,132	-1,273	,046	,181
FAC2_20	1,588	-1,414	3,002	-4,449	-,404	-,737
FAC3_20	1,924	-5,026	1,676	-2,498	-1,396	-,952
FAC1_21	1,737	1,455	-1,037	-,676	-,634	-,675
FAC3_21	-1,789	,840	-1,924	-,504	-1,315	-,662
FAC1_26	-3,739	3,249	2,812	1,859	,853	,297
FAC1_32	-3,997	4,068	-,411	,312	-,545	-,748

The morphometric measurements taken on the seven groups of *A. prevostii* indicate more variation in males than in females also at this level. According to Table 30, the main differences in males are found in all the measurements except for rectrix 5. In females the morphometric differences are found in bill length and rectrix 1 (Table 31).

Taxon (males)		**Bill length (mm) ****	**Wing length (mm) ***	**Rectrix 1 (mm) ****	**Rectrix 2 (mm) ****	**Rectrix 5 (mm)**
Anthracothorax prevostii prevostii	$x=$ $\sigma=$ $n=$	**30,14** 1.23 58	**65,35** 1.91 60	**34,37** .95 59	**34,59** 1.15 52	**35,98** 1.73 57
Anthracothorax prevostii "Yucatán"	$x=$ $\sigma=$ $n=$	**29,84** 1.11 21	**64,21** 1.39 22	**34,13** 1.19 22	**34,76** 1.10 22	**35,29** 1.40 22
Anthracothorax prevostii gracilirostris	$x=$ $\sigma=$ $n=$	**28,30** 1.04 39	**65,39** 1.85 40	**34,06** 1.13 39	**34,47** 1.04 37	**35,16** 1.45 39
Anthracothorax prevostii "AtlanticCoast"	$x=$ $\sigma=$ $n=$	**28,74** 1.21 5	**66,99** 1.36 6	**34,44** 1.19 6	**35,41** 1.37 6	**35,81** 1.31 6
Anthracothorax prevostii hendersoni	$x=$ $\sigma=$ $n=$	**25,54** .95 6	**65,90** .55 6	**35,24** 1.56 6	**35,53** 1.40 6	**35,44** 1.67 6
Anthracothorax prevostii pinchoti	$x=$ $\sigma=$ $n=$	**26,02** .50 4	**65,96** 1.01 5	**35,66** .78 5	**35,92** 1.28 5	**35,69** 1.76 5
Anthracothorax prevostii viridicordatus	$x=$ $\sigma=$ $n=$	**28,53** .88 7	**65,50** 1.50 9	**33,28** .92 9	**33,84** 1.22 9	**34,40** 1.83 9

*Significant difference (t-test; $p<0.05$) among subspecies for this variable.
**Significant difference (t-test; $p<0.01$) among subspecies for this variable.

Table 30. Morphometric measurements of males of the seven groups of *Anthracothorax prevostii*, indicating statistically significant differences between them.

Table 31. Morphometric measurements of females of the seven groups of *Anthracothorax prevostii*, indicating statistically significant differences between them.

Taxon (females)		Bill length (mm) **	Wing length (mm)	Rectrix 1 (mm) **	Rectrix 2 (mm)	Rectrix 5 (mm)
Anthracothorax prevostii prevostii	$x=$ $\sigma=$ $n=$	**31,55** 1.42 34	**64,56** 2.08 34	**35,20** 1.11 32	**35,07** 1.17 32	**33,96** 1.30 34
Anthracothorax prevostii "Yucatán"	$x=$ $\sigma=$ $n=$	**31,14** 1.16 10	**63,44** 1.20 10	**34,43** .97 10	**34,56** .88 10	**33,83** 1.37 10
Anthracothorax prevostii gracilirostris	$x=$ $\sigma=$ $n=$	**29,36** 1.13 14	**64,58** 1.68 15	**34,40** .92 14	**34,56** 1.25 14	**33,56** 1.34 13
Anthracothorax prevostii "AtlanticCoast"	$x=$ $\sigma=$ $n=$	**29,30** .12 2	**66,39** .77 2	**35,99** .23 2	**35,74** .65 2	**34,11** .16 2
Anthracothorax prevostii hendersoni	$x=$ $\sigma=$ $n=$	**25,38** - 1	**66,57** - 1	**35,64** - 1	**35,57** - 1	**33,17** - 1
Anthracothorax prevostii Pinchoti	$x=$ $\sigma=$ $n=$	**26,72** - 1	**65,04** .03 2	**33,99** .01 2	**34,02** .91 2	**34,80** .02 2
Anthracothorax prevostii viridicordatus	$x=$ $\sigma=$ $n=$	**30,00** 1.28 4	**64,75** 1.98 4	**33,09** .76 4	**33,77** 1.48 4	**32,71** 1.24 3

*Significant difference (t-test; $p<0.05$) among subspecies for this variable.
**Significant difference (t-test; $p<0.01$) among subspecies for this variable.

Anthracothorax viridigula

The Green-throated Mango is distributed in northeastern Venezuela, reaching the island of Trinidad. It also ranges from the Guianas to northern Brazil in the states of Amapá, northern Parà, and northern Maranhao. It forages mainly in treetops between sea level and 500 m along coastal zones, including mangrove, marshy savannas and open swamp-like areas with scattered large trees (Schuchmann 1999).

I separated this species into five pools (Fig. 32) according to the decribed criteria and applied a PCA followed by a DFA using the first three PCs calculated on the data set of the species by sex (Appendices 37 and 38). Although I found good discrimination in males (except for pools 2 and 3), in females the situation is unclear and the discrimination is only partial (see Figs. 33a, b and Tables 32a, b). As explained, the DFA is a good tool to allocate objects to natural groups. Here I created somewhat artificial groups that had a good chance of being discriminated. However, to determine how much difference is important is somewhat subjective, and in this case the scale of the difference might be a problem in reaching any conclusions. Consequently, I regarded *A. viridigula* as a monospecific group for further analyses.

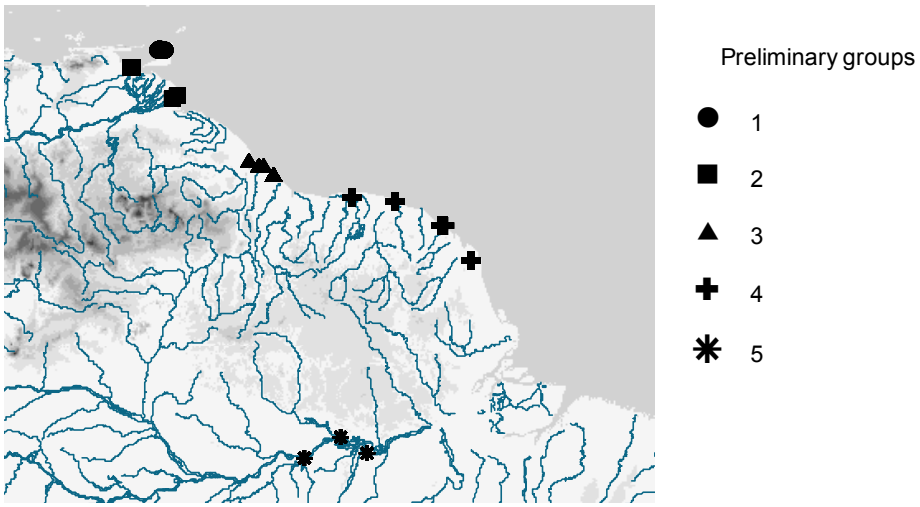


Fig. 32. Pools of *Anthracothorax viridigula* used to conduct the taxonomic analysis of the species. The figure shows 5 numbered pools (preliminary groups).

Fig. 33a. Results of the DFA conducted on color data of males of *Anthracothorax viridigula* showing the five pools.

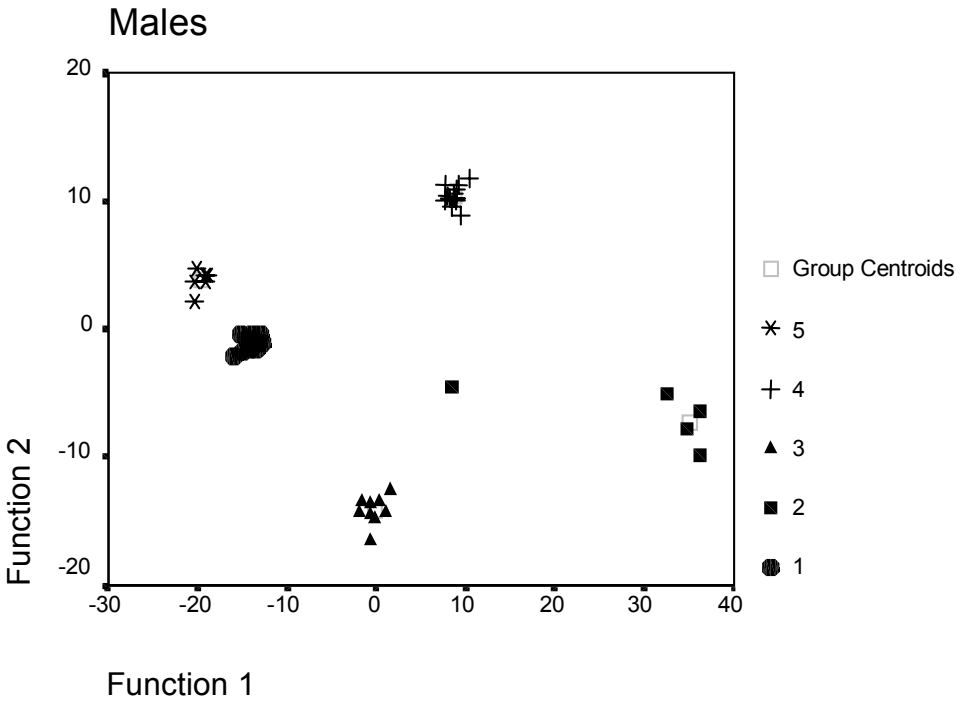


Fig. 33b. Results of the DFA conducted on color data of females of *Anthracothorax viridigula* showing the five pools

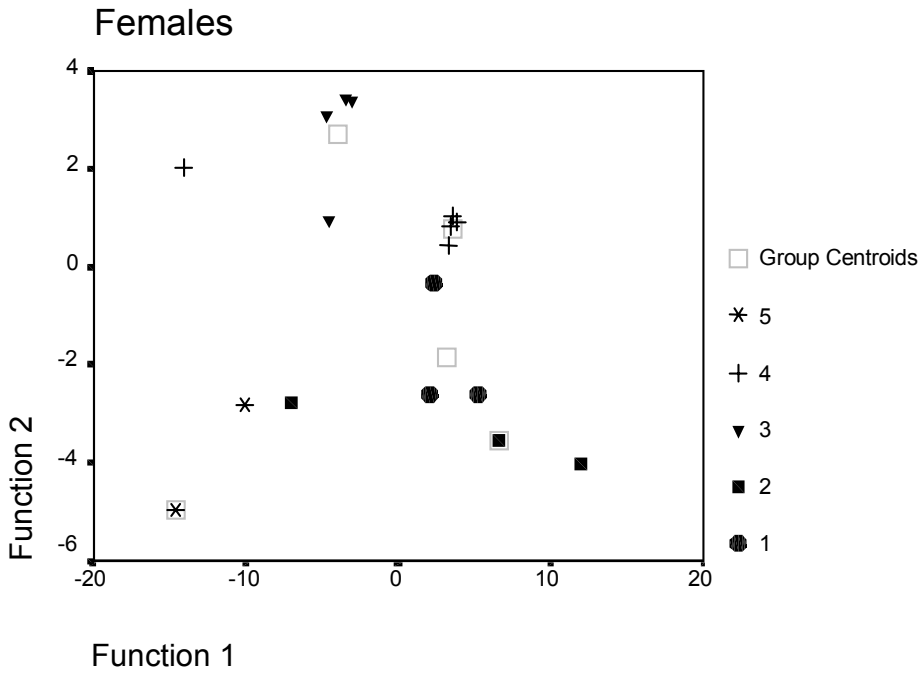


Table 32a. Classification results of the DFA conducted on color data of males of the genus *Anthracothorax viridigula*.

Preliminary Group	**Predicted Group Membership (%)**							
	1	2	3	4	5			
1	**100.0**	0	0	0	0	0	0	0
2	0	**80.0**	**20.0**	0	0	0	0	0
3	0	0	**100.0**	0	0	0	0	0
4	0	0	0	**100.0**	0	0	0	0
5	0	0	0	0	**100.0**	0	0	0

97.7% of original grouped cases correctly classified

Table 32b. Classification results of the DFA conducted on color data of females of the genus *Anthracothorax viridigula*.

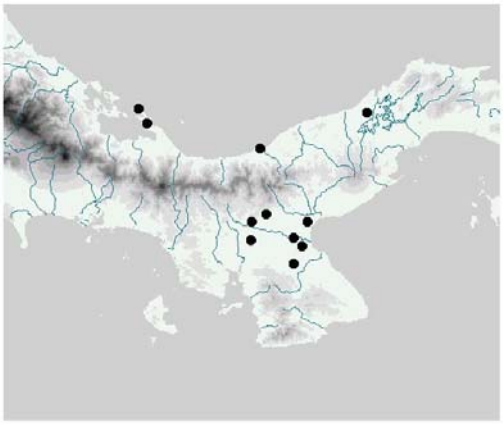
Preliminary Group	**Predicted Group Membership (%)**							
	1	2	3	4	5			
1	**100.0**	0	0	0	0	0	0	0
2	0	**66.7**	**33.3**	0	0	0	0	0
3	0	0	**100.0**	0	0	0	0	0
4	0	0	0	**80.0**	**20.0**	0	0	0
5	0	0	0	0	**100.0**	0	0	0

88.2% of original grouped cases correctly classified

Anthracothorax veraguensis

This species shows a more restricted distribution in the Pacific lowlands from Chiriquí to the Canal Zone in Panama (Fig. 34), and is found in open vegetation of pastures and stream edges with shrubs and scattered trees (Schuchmann 1999).

Fig. 34. Geographical distribution of *Anthracothorax veraguensis* showing the collecting localities.



Anthracothorax veraguensis has often been included within *A. prevostii* and they both occur in Panama. For this reason I conducted a PCA on the coloration data of the 12 pools of *A. prevostii* and the unique pool of *A. veraguensis* together and took the first three PCs (Appendices 39 and 40) to continue with the DFA. In the case of females, as always within this genus, the groups are more dispersed (Fig. 35) and 10 functions were needed to explain the whole variation (Table 33). Although the *A. veraguensis* pool appeared independent, the discrimination of the others is also high, making the findings difficult to interpret. However, in the DFA conducted on the male spectral color data the first two functions explain 55.9% of the variance (Table 34) and the graph obtained from these functions (Fig. 36) indicates that *A. veraguensis* is clearly different from *A. prevostii*. A second DFA was conducted to extract the most important parts of the body regarding this separation. From the SCDFC (Table 35), in males the difference in coloration is mainly found in the ventral area: gorget (Fac1_12 and Fac3_12), low throat (Fac2_14 and Fac3_14), central chest (Fac2_17), lateral chest (Fac2_18), and breast (Fac2_21).

Fig. 35. Results of the DFA conducted on color data of females of *A. veraguensis* and *A. prevostii*.

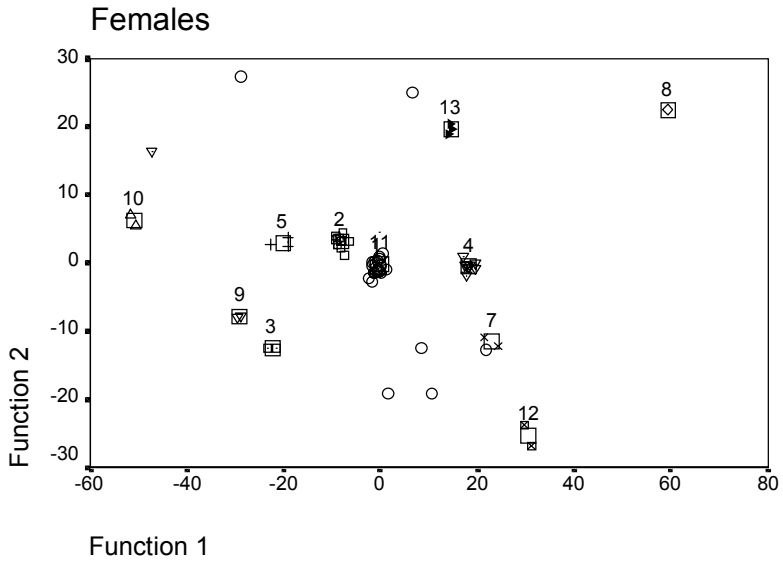


Table 33. Eigenvalues table showing cumulative percentages of the variance explained by each function for the DFA conducted on females of *A. veraguensis* and *A. prevostii*.

Eigenvalues

Function	Eigenvalue	% of Variance	Cumulative %	Canonical Correlation
1	464,720[a]	71,4	71,4	,999
2	92,060[a]	14,1	85,5	,995
3	55,681[a]	8,6	94,1	,991
4	17,912[a]	2,8	96,9	,973
5	7,881[a]	1,2	98,1	,942
6	3,956[a]	,6	98,7	,893
7	3,394[a]	,5	99,2	,879
8	3,137[a]	,5	99,7	,871
9	1,272[a]	,2	99,9	,748
10	,835[a]	,1	100,0	,675

a. First 10 canonical discriminant functions were used in the analysis.

Table 34. Eigenvalues table showing cumulative percentages of the variance explained by each function for the DFA conducted on males of *A. veraguensis* and *A. prevostii*.

Eigenvalues

Function	Eigenvalue	% of Variance	Cumulative %	Canonical Correlation
1	14,445[a]	44,3	44,3	,967
2	3,768[a]	11,6	55,9	,889
3	3,193[a]	9,8	65,7	,873
4	2,665[a]	8,2	73,9	,853
5	1,758[a]	5,4	79,3	,798
6	1,615[a]	5,0	84,2	,786
7	1,466[a]	4,5	88,7	,771
8	1,221[a]	3,7	92,5	,741
9	,918[a]	2,8	95,3	,692
10	,597[a]	1,8	97,1	,611
11	,545[a]	1,7	98,8	,594
12	,392[a]	1,2	100,0	,531

a. First 12 canonical discriminant functions were used in the analysis.

Fig. 36. Results of the DFA conducted on color data of males of *A. veraguensis* and *A. prevostii* showing the clear separation of both species. The graph indicates the separation of pool 13 (*A. veraguensis*) from the other numbered pools (all of *A. prevostii*).

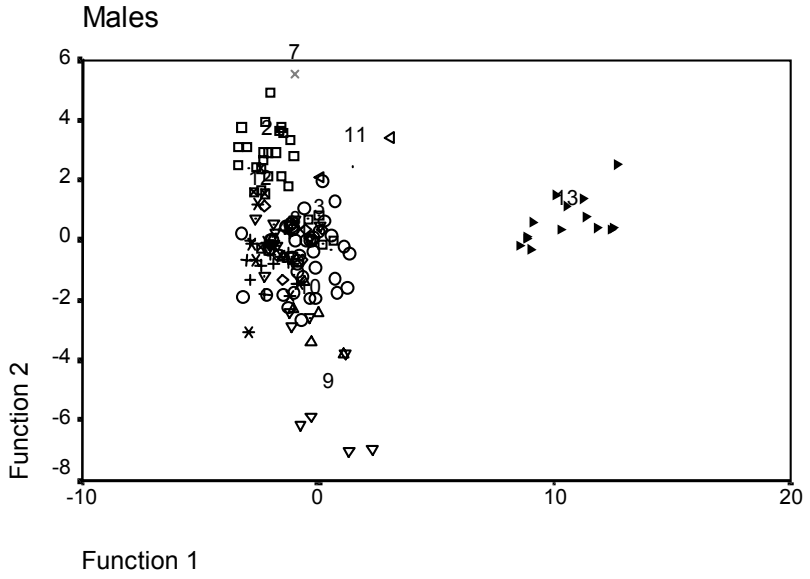


Table 35. Eigenvalues, percentages of variance, and SCDFC table for the second DFA conducted on males of *A. veraguensis* and *A. prevostii*.

Eigenvalues

Function	Eigenvalue	% of Variance	Cumulative %	Canonical Correlation
1	11,34 [a]	100,	100,	,95

a. First canonical discriminant function was used in the analysis

	Function
	1
FAC1_1	,068
FAC2_1	-,308
FAC3_1	,027
FAC1_2	-,220
FAC2_2	,684
FAC3_2	,007
FAC1_3	-,490
FAC2_3	,696
FAC3_3	-1,074
FAC1_4	-,003
FAC2_4	,930
FAC3_4	,625
FAC1_5	-,340
FAC2_5	-,161
FAC3_5	-,216
FAC1_6	-,221
FAC2_6	,118
FAC3_6	,016
FAC1_12	1,539
FAC2_12	,762
FAC3_12	-1,541
FAC1_13	,372
FAC2_13	,075
FAC3_13	-,263
FAC1_14	-,406
FAC2_14	1,474
FAC3_14	-1,124
FAC1_15	-,237
FAC2_15	,017
FAC3_15	-,522
FAC1_17	-,204
FAC2_17	1,346
FAC3_17	,519
FAC1_18	,754
FAC2_18	2,510
FAC3_18	,544
FAC1_20	-,491
FAC2_20	-,087
FAC3_20	,348
FAC1_21	,219
FAC2_21	1,615
FAC3_21	-,342
FAC1_26	,129
FAC2_26	-,513
FAC3_26	,126
FAC1_29	-,233
FAC2_29	-,612
FAC3_29	,140
FAC1_30	,300
FAC2_30	,804
FAC3_30	-,194
FAC1_32	,453
FAC2_32	-,161
FAC3_32	,103
FAC1_33	,077
FAC2_33	-,321
FAC3_33	,064
FAC1_34	-,298
FAC2_34	,227
FAC3_34	-1,047
FAC1_39	-,337
FAC2_39	,816
FAC3_39	-,601
FAC1_40	-,030
FAC2_40	-,345
FAC3_40	,285

Anthracothorax dominicus and *Anthracothorax mango*

The ranges of the Antillean Mango (*Anthracothorax dominicus*) and the Jamaican Mango (*Anthracothorax mango*) are geographically close, the latter being of very limited distribution. For these reasons an analysis of the two species together was conducted. It is important to remember the focus of this study on the use and implications of the methodology.

The Antillean Mango has two recognized subspecies: 1) *A. dominicus dominicus* is regular in open woodlands, especially in the lowlands but also in the mountains of Hispaniola and the offshore islands of Tortue, Gonave, Vache, and Beata. 2) *A. dominicus aurulentus* occurs in lowlands and occasionally high up in man-made clearings of Puerto Rico and its offshore islands of Culebra, Vieques, and in the Virgin Islands (St. Thomas, St. John, and Anegada) (Lack 1973, Schuchmann 1999). The Jamaican Mango, with a distribution limited to the island of Jamaica, is common in forests near see level, especially where it is fairly open and is sparse in open woodland in the hills (Lack 1973, Schuchmann 1999).

I separated the data set into 13 pools on the basis of potential barriers in Hispaniola and those populations inhabiting adjacent islands (Fig.37). This artificial separation of *A. dominicus* into 12 pools was only done to allow the comparison with the *A. mango* pool by the DFA. The species *A. mango* is considered as a unit since it has a limited geographical distribution only on Jamaica.

The results of the DFA using the first three PCs resulting from the PCA made by sex (Appendices 41 and 42) gave, as expected, clear results on the greater difference of *A. mango* from the rest of the analyzed group (Table 36 and Fig. 38 for males, Table 37 and Fig. 39 for females). The two clouds corresponding to the two recognized subspecies of *A. dominicus* are closer to each other than to the *A. mango* cloud (Fig. 38). In the results for females, the clouds formed are, as always for females, smaller and more dispersed than those for males (Fig. 39). However, the *A. mango* group shows a clear differentiation from the *A. dominicus* group.

The SCDFC (Table 38) extracted from the second DFA indicates that in males the differences in coloration are both in dorsal and ventral areas of the birds, mainly in shoulder (Fac1_3 and Fac2_3), back (Fac2_4), rump (Fac2_5), and low throat (Fac1_14 and Fac2_14). Additionally, the coefficients indicate certain color differences in wing coverts (Fac2_29) and secondary feathers (Fac2_30).

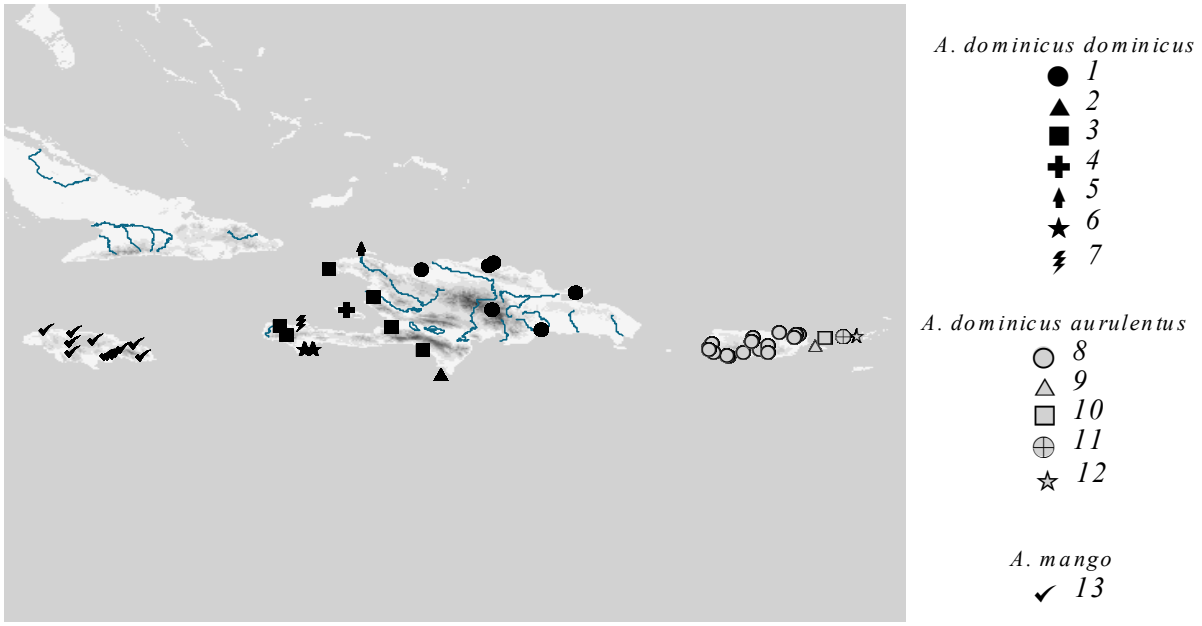


Fig. 37. Pools of *A. dominicus* and *A. mango*. The symbols represent collecting localities of *A. d. dominicus* (filled symbols (1-7)), of *A. d. aurulentus* (gray symbols (8-12)), and of *A. mango* (Jamaican symbols).

Table 36. Eigenvalues table showing cumulative percentages of the variance explained by each function extracted from the DFA conducted on males of *A. dominicus* and *A. mango.*

Eigenvalues

Function	Eigenvalue	% of Variance	Cumulative %	Canonical Correlation
1	53,330[a]	50,1	50,1	,991
2	15,797[a]	14,8	64,9	,970
3	13,607[a]	12,8	77,7	,965
4	10,997[a]	10,3	88,0	,957
5	3,914[a]	3,7	91,7	,892
6	3,436[a]	3,2	94,9	,880
7	1,830[a]	1,7	96,6	,804
8	1,735[a]	1,6	98,2	,796
9	1,069[a]	1,0	99,2	,719
10	,826[a]	,8	100,0	,673

a. First 10 canonical discriminant functions were used in the analysis.

Fig. 38. Results of the DFA conducted on color data of males of *Anthracothorax dominicus* and *Anthracothorax mango* showing the separation of both species.

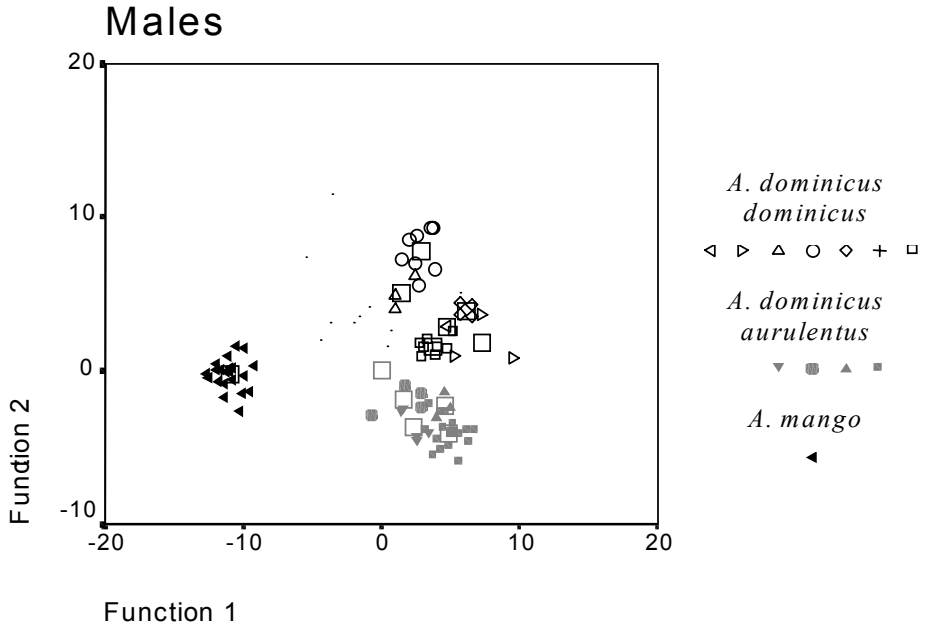


Table 37. Eigenvalues table showing cumulative percentages of the variance explained by each function extracted from the DFA conducted on females of *A. dominicus* and *A. mango.*

Eigenvalues

Function	Eigenvalue	% of Variance	Cumulative %	Canonical Correlation
1	907,510[a]	82,2	82,2	,999
2	102,693[a]	9,3	91,5	,995
3	39,324[a]	3,6	95,1	,988
4	25,902[a]	2,3	97,5	,981
5	11,758[a]	1,1	98,5	,960
6	4,769[a]	,4	99,0	,909
7	3,896[a]	,4	99,3	,892
8	3,370[a]	,3	99,6	,878
9	1,847[a]	,2	99,8	,805
10	1,287[a]	,1	99,9	,750
11	1,141[a]	,1	100,0	,730

a. First 11 canonical discriminant functions were used in the analysis.

Fig. 39. Results of the DFA conducted on color data of females of *Anthracothorax dominicus* and *Anthracothorax mango*.

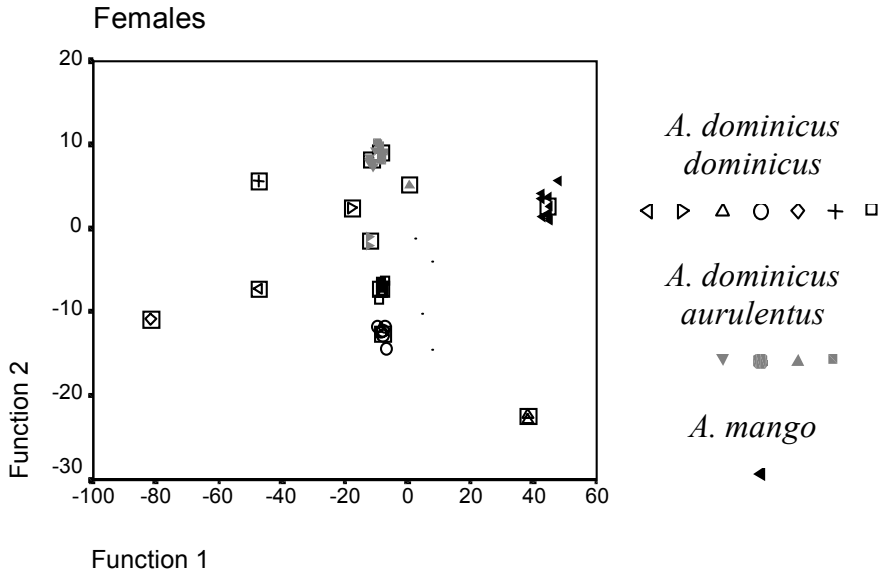


Table 38. Eigenvalues, percentages of variance, and SCDFC table for the second DFA conducted on males of *A. dominicus* and *A. mango* to extract the relevant variables that explain differences between the two species.

Eigenvalues

Function	Eigenvalue	% of Variance	Cumulative %	Canonical Correlation
1	23,462[a]	100,0	100,0	,979

a. First canonical discriminant function was used in the analysis

	Function
	1
FAC1_1	,104
FAC2_1	,322
FAC3_1	,354
FAC1_2	-,363
FAC2_2	,636
FAC3_2	,555
FAC1_3	1,810
FAC2_3	-3,162
FAC3_3	-,487
FAC1_4	-,734
FAC2_4	2,005
FAC3_4	,639
FAC1_5	-,267
FAC2_5	1,514
FAC3_5	-,153
FAC1_6	,378
FAC2_6	-,957
FAC3_6	,372
FAC1_12	,920
FAC2_12	-,779
FAC3_12	-,452
FAC1_13	,088
FAC2_13	-,364
FAC3_13	,777
FAC1_14	1,112
FAC2_14	-3,960
FAC3_14	-,469
FAC1_17	,017
FAC2_17	,083
FAC3_17	,091
FAC1_20	-,259
FAC2_20	,353
FAC3_20	,556
FAC1_26	,802
FAC2_26	-,831
FAC3_26	,312
FAC1_29	-,362
FAC2_29	1,773
FAC3_29	,324
FAC1_30	,308
FAC2_30	1,804
FAC3_30	,873
FAC1_32	,229
FAC2_32	-,077
FAC3_32	,033
FAC1_33	,235
FAC2_33	-,871
FAC3_33	,167
FAC1_34	-1,075
FAC2_34	,638
FAC3_34	,428
FAC1_39	-,880
FAC2_39	,568
FAC3_39	,569
FAC1_40	-,102
FAC2_40	-,901
FAC3_40	,321

Anthracothorax viridis

This Green Mango (*Anthracothorax viridis*) occurs on Puerto Rico island together with the subspecies *A. dominicus aurulentus* and three other hummingbird species (*Chlorostilbon maugaeus*, *Eulampis holosericeus*, and *Orthorhyncus cristatus*). The two species of *Anthracothorax* tend to be segregated by habitat and elevation but overlap in their utilization of eight species of flowers (Kodric *et al*. 1984). *A. dominicus* occurs in drier, more open lowland forests and is replaced, with little overlap, by *A. viridis* in montane forests above 500 m (Kodric *et al*. 1984). The elevational ranges of the two *Anthracothorax* species seem to overlap where they use the same flower species, however, they rarely forage at the same patches. The geographical distribution of the two species reflects the aggressive dominance of the slightly larger *A. viridis* at higher elevations where flower availability is higher, and the advantage of *A. dominicus*, with lower wing disc loading, in foraging for less available resources at lower elevations (Kodric *et al*. 1984).

I conducted, as in the former section, the analysis of the 12 pools of *A. dominicus* together with a unique *A. viridis* pool (Fig. 40). A new PCA was conducted on males and females of *A. dominicus*, but this time together with *A. viridis*. (Appendices 43 and 44).

The results of the DFA for males showed *A. viridis* as a clear cloud in the graph, set apart from the two clouds formed by the two *A. dominicus* subspecies that are here very close together due to the relatively greater separation from the first species (Fig. 41 and Table 39). In addition, these results indicate the separation of population number 13, corresponding to that of Petit Cayemites, small island to the west of Hispaniola. In this case there was only one male and one female in the analysis, so I would not risk any conclusion at this point. For females (Fig. 42 and Table 40), although the situation, as always, is not as clear as for males, pool number 14, *A. viridis*, separates clearly from the rest, *A. dominicus*.

The SCDFC (Table 41) resulting from the second DFA conducted on this data set indicates that the ventral sections of gorget (Fac3_12) and low throat (Fac3_14), in addition to the

uppertail coverts (Fac2_6), wing coverts (Fac2_29 and Fac3_29), secondary feathers (Fac2_30), and the fifth rectrix (Fac2_39), best explains the separation of the two species.

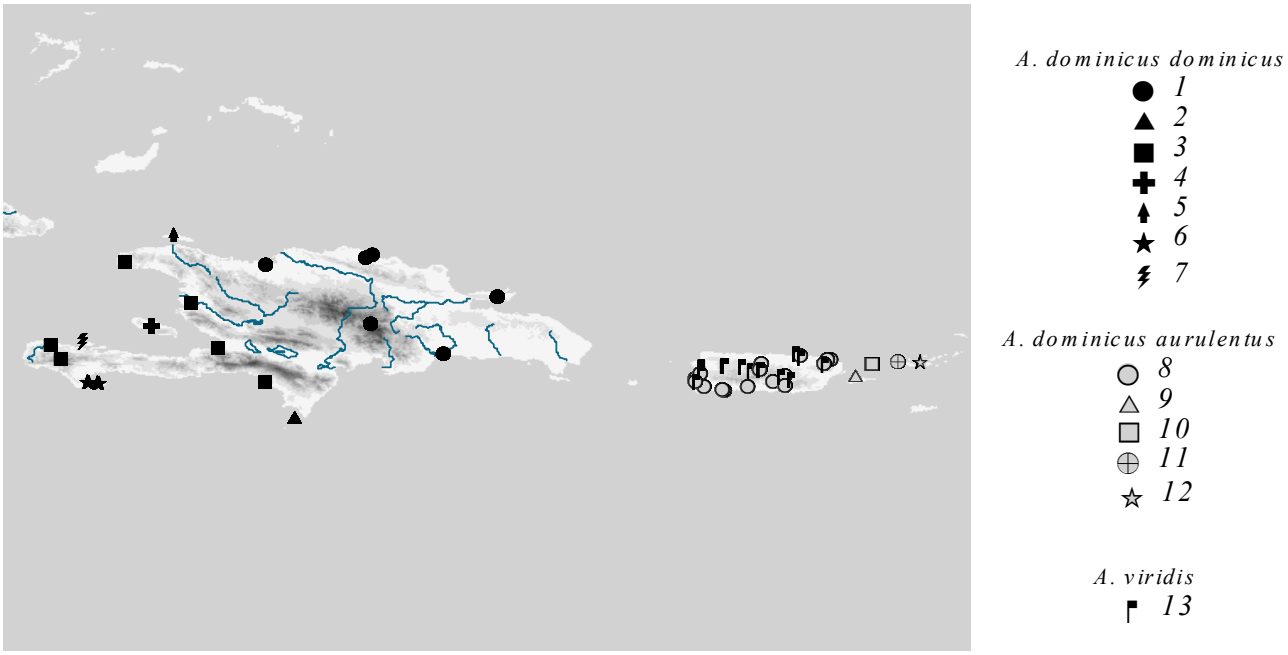


Fig. 40. Pools of *A. dominicus* and *A. viridis*. The symbols represent collecting localities of *A. d. dominicus* (filled symbols (1-7)), of *A. d. aurulentus* (gray symbols (8-12)), and of *A. viridis* (flag symbols).

Fig. 41. Results of the DFA conducted on color data of males of *A. dominicus* and *A. viridis* showing the clear separation of both species.

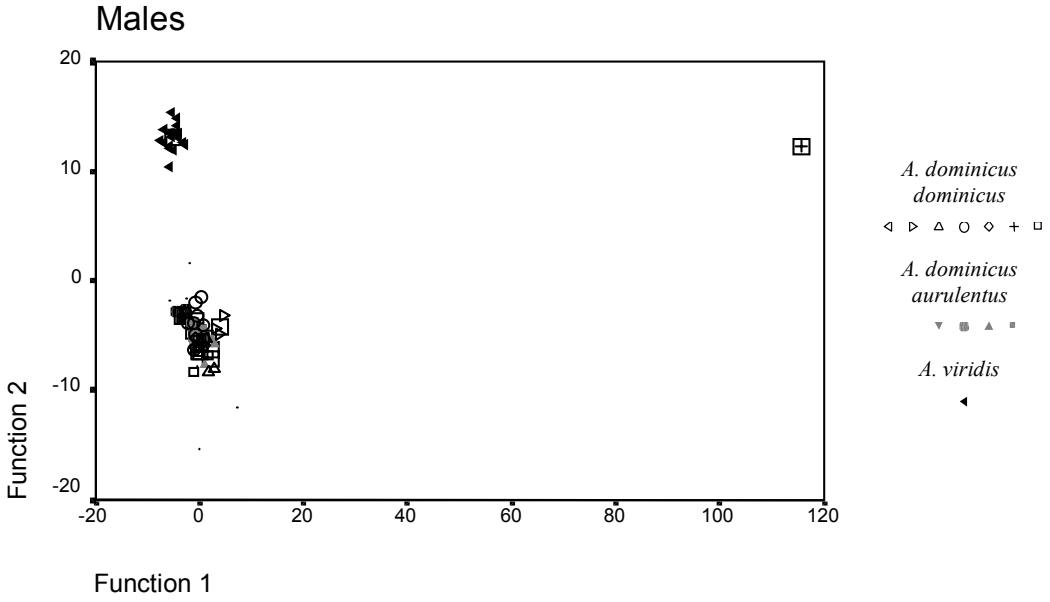


Table 39. Eigenvalues table showing cumulative percentages of the variance explained by each function extracted from the DFA conducted on males of *A. dominicus* and *A. viridis.*

Eigenvalues

Function	Eigenvalue	% of Variance	Cumulative %	Canonical Correlation
1	206,571[a]	66,3	66,3	,998
2	76,994[a]	24,7	91,0	,994
3	8,763[a]	2,8	93,9	,947
4	7,175[a]	2,3	96,2	,937
5	4,448[a]	1,4	97,6	,904
6	2,259[a]	,7	98,3	,833
7	1,940[a]	,6	98,9	,812
8	1,415[a]	,5	99,4	,765
9	,965[a]	,3	99,7	,701
10	,606[a]	,2	99,9	,614
11	,337[a]	,1	100,0	,502

a. First 11 canonical discriminant functions were used in the analysis.

Fig. 42. Results of the DFA conducted on color data of females of *A. dominicus* and *A. viridis*.

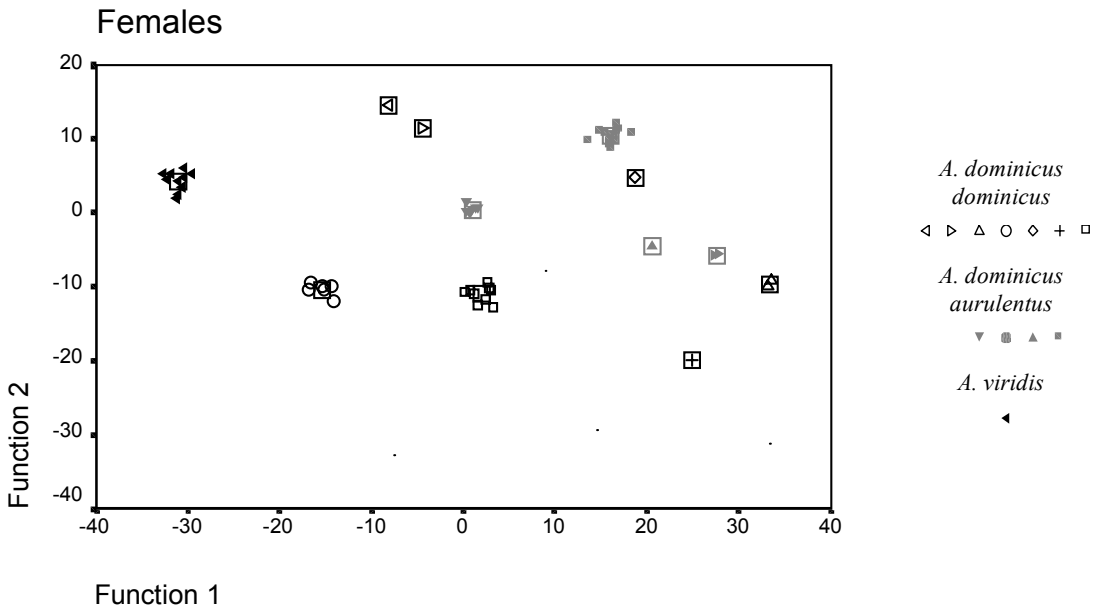


Table 40. Eigenvalues table showing cumulative percentages of the variance explained by each function extracted from the DFA conducted on females of *A. dominicus* and *A. viridis.*

Eigenvalues

Function	Eigenvalue	% of Variance	Cumulative %	Canonical Correlation
1	482,798[a]	68,4	68,4	,999
2	107,453[a]	15,2	83,7	,995
3	42,885[a]	6,1	89,7	,989
4	31,555[a]	4,5	94,2	,985
5	14,172[a]	2,0	96,2	,966
6	10,788[a]	1,5	97,8	,957
7	7,357[a]	1,0	98,8	,938
8	4,485[a]	,6	99,4	,904
9	1,681[a]	,2	99,7	,792
10	1,275[a]	,2	99,9	,749
11	1,030[a]	,1	100,0	,712

a. First 11 canonical discriminant functions were used in the analysis.

Table 41. Eigenvalues, percentages of variance, and SCDFC table for the second DFA conducted on males of *A. dominicus* and *A. viridis* to extract the relevant variables that explain differences between the two species.

Eigenvalues

Function	Eigenvalue	% of Variance	Cumulative %	Canonical Correlation
1	36,19 [a]	100,	100,	,98

a. First canonical discriminant function was used in the analysis

	Function
	1
FAC1_1	,182
FAC2_1	-,171
FAC3_1	-,231
FAC1_2	-,282
FAC2_2	-,978
FAC3_2	-,189
FAC1_3	,160
FAC2_3	,695
FAC3_3	,007
FAC1_4	,006
FAC2_4	,727
FAC3_4	,486
FAC1_5	,114
FAC2_5	,853
FAC3_5	-,476
FAC1_6	,102
FAC2_6	-1,060
FAC3_6	-,238
FAC1_12	-,639
FAC2_12	,584
FAC3_12	,987
FAC1_14	,182
FAC2_14	,231
FAC3_14	-1,138
FAC1_17	,437
FAC2_17	,708
FAC3_17	,229
FAC1_20	,656
FAC2_20	-,007
FAC3_20	,735
FAC1_26	-,010
FAC2_26	,422
FAC3_26	,539
FAC1_29	-,102
FAC2_29	,956
FAC3_29	,895
FAC1_30	-,047
FAC2_30	-,965
FAC3_30	,118
FAC1_32	-,391
FAC2_32	,119
FAC3_32	-,148
FAC1_33	-,273
FAC2_33	,426
FAC3_33	-,152
FAC1_39	-,083
FAC2_39	-1,034
FAC3_39	-,047

***Phylogenetic relationships within* Anthracothorax**

The phylogenetic analysis of *Anthracothorax* was performed (defining the genus *Campylopterus* as outgroup) by using the same arguments advanced in the *Topaza* phylogenetic study. The analysis will be done at two levels:

1) Species level: the taxonomic units (TU) to be considered for the analysis resulting from the taxonomic study:

    - *Anthracothorax viridigula*
    - *Anthracothorax prevostii*
    - *Anthracothorax nigricollis*
    - *Anthracothorax veraguensis*
    - *Anthracothorax dominicus*
    - *Anthracothorax viridis*
    - *Anthracothorax mango*
    - *Anthracothorax recurvirostris*

    - *Campylopterus largipennis* (outgroup)

2) Subspecies level: the TUs are all groups resulting from the taxonomic analysis, including the potential new subspecies:

    - *Anthracothorax viridigula* (Aviridigula)
    - *Anthracothorax nigricollis iridescens* (Aniridescens)
    - *Anthracothorax nigricollis nigricollis* (Annigricollis)
    - *Anthracothorax nigricollis* "Venezuela" (AnVenezuela)
    - *Anthracothorax prevostii prevostii* (Apprevostii)
    - *Anthracothorax prevostii* "Yucatán" (ApYucatan)
    - *Anthracothorax prevostii gracilirostris* (Apgracilirostris)

- *Anthracothorax prevostii* "AtlanticCoast" (ApAtlanticCoast)
- *Anthracothorax prevostii hendersoni* (Aphendersonii)
- *Anthracothorax prevostii pinchoti* (Appinchotii)
- *Anthracothorax prevostii viridicordatus* (Apviridicordatus)
- *Anthracothorax veraguensis* (Averaguensis)
- *Anthracothorax dominicus dominicus* (Addominicus)
- *Anthracothorax dominicus aurulentus (*Adaurulentus)
- *Anthracothorax mango* (Amango)
- *Anthracothorax viridis* (Aviridis)
- *Anthracothorax recurvirostris* (Arecurvirostris)

- *Campylopterus largipennis* (outgroup)
- *Campylopterus cuvierii* (outgroup)

Species level

I conducted the generalized frequency coding (GFC) and then applied PAUP following the same seven steps defined in the *Topaza* section. In summary, I conducted a PCA to the raw spectral color data from each body part by sex, and created new data sets containing the first three PC scores representing the color of each body part (66 variables for males and 66 for females), and the morphometric data (seven variables) of the individuals included in the analysis (Appendices 45 and 46). After the subdivision of the original variables, a total of 10,293 (66*141)+(7*141)) working variables for males and the same for females were used to create matrix A (Appendices 47 and 48) and matrix B (Appendices 49 and 50). The codifying was completed, the data from both sexes combined, and the uninformative characters eliminated to construct the final matrix (Appendix 51) containing nine taxa (one outgroup) and 3984 parsimony informative characters. They are weighted (Appendix 52) and entered in the phylogenetic computer program PAUP.

Fig. 43. Phylogenetic tree resulting from the PAUP analysis of *Anthracothorax* species using *Campylopterus largipennis* as outgroup according to both plumage coloration and morphometric data. Nodes are represented by bold numbers above the lines, and branch lengths are represented by numbers under the lines. The Bootstrap percentages are shown in parentheses at the side of each branch length.

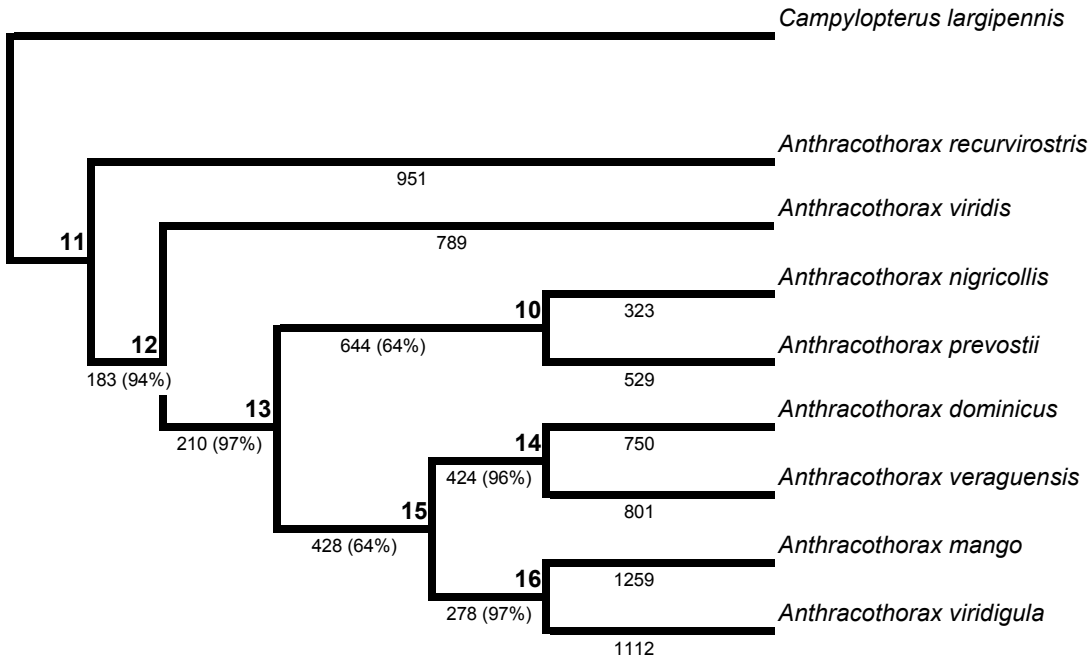


Table 42. Main descriptive parameters of the phylogenetic tree resulting from the PAUP analysis of *Anthracothorax* species using *C. largipennis* as outgroup.

Tree characteristics	Values
Tree length	8444.89
Consistency Index (CI)	0.57
Homoplasy Index (HI)	0.43
Retention Index (RI)	0.31
Rescaled Consistency Index (RC)	0.18

The results of the analysis at this level are shown in the phylogenetic tree of Figure 43 and Table 42, showing significant support according to the Bootstrap percentages. At this point we have to recall the idea of Schuchmann (1999) that *A. nigricollis*, *A. prevostii*, *A. veraguensis* and *A. viridigula* seem to form a superspecies. According to the results of this study the situation appears to be different. The resulting phylogenetic tree indicates that *A. nigricollis* and *A. prevostii* are sister taxa. They seem to be very close to each other, which explains the confusion on the taxonomy of some of their populations. *A. veraguensis* and *A. dominicus* on one side, and *A. viridigula* and *A. mango* on the other are also sister taxa combined in one clade. Thus, *A. veraguensis* appears closer to *A. dominicus* than to *A. prevostii*, which would add interesting facts to our understanding of the history of the genus and consequently ideas about the biogeography of the area.

A. viridis is presented as a very distinct taxon, as is *A. recurvirostris*. It is interesting to point out that the taxonomic analysis was conducted using only the plumage color data. According to the taxonomic results the species *A. recurvirostris* is quite close, forming one group with the other species of the genus *Anthracothorax*. The phylogenetic tree is a result of the combination of plumage color and morphometric information, and after adding the information on morphometrics the difference in morphology between this species and the others of the genus is striking. The results indicate that *A. recurvirostris* might be placed in the genus *Avocettula*, as was previously thought, and separated from *Anthracothorax* (but see next section).

Subspecies level:

I conducted a PAUP analysis following the same sequence as previously. This time I calculated new PCs from the color data of *Anthracothorax* specimens and two species of *Campylopterus* (*C. largipennis* and *C. cuvierii*) for the phylogenetic analysis at the subspecies level (Appendices 53 and 54). I used the same number of working variables for males and females (10,293) as in the analysis at the species level. I create matrix A (Appendices 55 and 56) and matrix B (Appendices 57 and 58) including frequencies at the subspecies level. The

final matrix (Appendix 59) contained 19 TUs (two from outgroups) and 4391 parsimony-informative weighted characters (Appendix 60). They were entered in the PAUP.

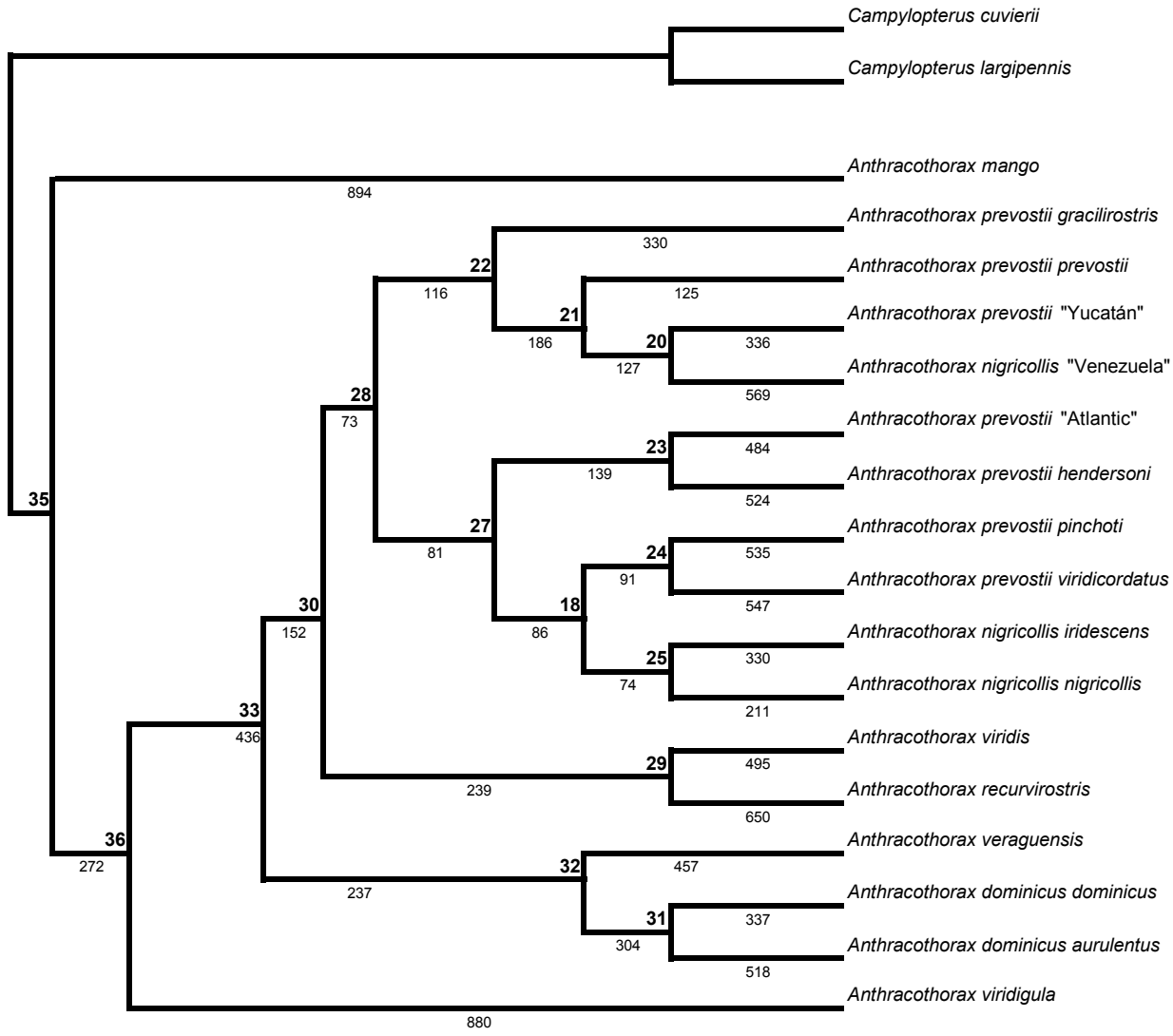


Fig. 44. Phylogenetic tree resulting from the PAUP analysis of *Anthracothorax* subspecies using *C. largipennis* and *C. cuvierii* as outgroups. Nodes are represented by bold numbers above the lines, and branch lengths are represented by numbers under the lines.

The analysis at this level resulted in a more complicated view of the phylogenetic relationships within *Anthracothorax*. The results are shown in the phylogenetic tree, supported by more than 50% on each node according to the Bootstrap analysis (Figure 44 and Table 43). These relationships indicate that *A. mango* and *A. viridigula* represent separate branching in the group. The phylogenetic relationships found here also explain the reason for the controversy between *A. nigricollis* and *A. prevostii*. The group formed by these two species needs a taxonomic rearrangement. All groups of *A. nigricollis* and *A. prevostii* form a unique monophyletic clade with many subbranches.

Table 43. Main descriptive parameters of the phylogenetic tree resulting from the PAUP analysis of *Anthracothorax* subspecies using *C. largipennis* and *C. cuvierii* as outgroups.

Tree characteristics	Values
Tree length	11322.33
Consistency Index (CI)	0.41
Homoplasy Index (HI)	0.60
Retention Index (RI)	0.32
Rescaled Consistency Index (RC)	0.13

A. n. nigricollis seems to be, as expected, closer to *A. n. iridescens*, but they form a clade with some members of *A. prevostii*: *A. p. viridicordatus*, *A. p. pinchoti*, *A. p. hendersoni*, and *A. p.* "Atlantic." *A. p. viridicordatus* is distributed in northern South America (Venezuela area), while *A. p. pinchoti* and *A. p. hendersoni* from the San Andrés and Old Providence islands are very close to the mainland of Panama-Costa Rica in the Atlantic zone (the area of the potential new group *A. p.* "Atlantic"). The other groups of *A. prevostii* (*A. p. gracilirostris*, *A. p. prevostii*, and *A. p.* "Yucatán") from Central America, together with *A. nigricollis* "new subspecies", distributed in the Venezuelan area of South America, form a separate clade.

This analysis presented conflicting views on the case of *A. recurvirostris*, which appears as sister group of *A. viridis* in an inner branch of the group as sister clade of the "*A. nigricollis*-*A. prevostii* complex". However, the phylogenetic relationships that will be discussed in the next chapter, bringing *Topaza* and *Eulampis* to the analysis, will indicate other interesting results that will help to clarify the phylogenetic scenario.

The relationship between the *A. dominicus* subspecies and *A. veraguensis* seems to be clear. They constitute a separate clade that indicates that *A. veraguensis* is farther away from *A. prevostii* than previously thought, the group having a closer relationship with groups from the island. This fact was already noted in the last section, and it will be more extensively discussed in the biogeographical analysis.

These results reinforce the need for a new taxonomy for the group, since the accepted taxonomy may not be appropriate. They also indicate that vicariance is not enough to explain the situation of these taxa, as will also be discussed later. These findings should be complemented in the future by the inclusion of information on coloration of additional body parts that could be important to clear this phylogenetic scenario. A few body parts were already measured but not incorporated in the analysis due to the standardized nature of the methodology to be tested by this research. There are areas in the rectrices and some small iridescent regions of the body in some members that show great variability and may be interesting to further consider.

Geographical variation and review of taxonomy of the genus *Eulampis* BOIE, 1831

Theoretical background

The caribs, genus *Eulampis*, belong to the so-called mango hummingbirds that occur on the Caribbean islands Puerto Rico and Lesser Antilles (Plate 3). Currently, this genus includes two species (Schuchmann 1999): *Eulampis jugularis* Linnaeus, 1766, and *Eulampis holosericeus*, both previously considered as the monotypic genera *Eulampis* and *Sericotes* respectively (Peters 1945). *E. jugularis* constitutes a monotypic species while *E. holosericeus* includes two subspecies: *E. h. holosericeus* Linnaeus, 1758 and *E. h. chlorolaemus* Gould, 1857.

A few studies on the ecology of the carib species have been published (Wolf 1975a, Norton & Hobbs 1988). Additionally, some information is available as part of avifauna studies of the Caribbean islands (Bond 1939, Lack 1973, Feinsinger *et al.* 1982). The breeding habits of *E. jugularis* have also been described (Wolf & Wolf 1971, Wolf 1975b) together with a few studies on its anatomy (Zusi & Bentz 1984), physiology (Hainsworth & Wolf 1970, Wolf & Hainsworth 1971), behavior (Schuchmann 1977) and foraging habits, including territoriality (Wolf 1975a, b; Ingels 1976).

The Purple-throated Carib (*Eulampis jugularis*) is a brightly colored and relatively large hummingbird endemic to the Lesser Antilles (except Grenada). It is found at forest edges and in treetops of secondary and primary forests between 800 and 1200 m altitude (Schuchmann 1980b, 1999). It is found in all the mountainous islands, where it feeds both in and below the canopy, from near the ground to the top of the trees (Lack 1973). The Green-throated Carib (*Eulampis holosericeus*) has its geographical range in both the Greater and Lesser Antilles and inhabits from forest clearings, cultivated areas and open vegetation to mangroves, semi-deciduous and rain forests (Schuchmann 1980b, 1999). The species feeds from near the ground to the tops of the trees (Lack 1973).

The two species of *Eulampis*, sexually monomorphic in color, are among the 20 species of hummingbirds in which both sexes are brightly colored and have identical, or very similar plumage patterns (Wolf 1975a). Although the sexes in both species have the same coloration, they have distinctly different bill shapes (male's straight, female's decurved and longer than male's) (Wolf 1975a, b). *E. holosericeus* is slightly smaller than *E. jugularis* and the difference in bill length and shape between the sexes is less pronounced and less obvious in *E. holosericeus* than in *E. jugularis* (Wolf 1975a).

Bright colors in hummingbirds are probably important as aggressive signals closely associated with territoriality, especially defensive behavior (Wolf 1975a). Both *E. jugularis* and *E. holosericeus* are territorial around certain flower species and also females hold territories during the non-breeding season (although female territoriality may be less common in *E. holosericeus* than in *E. jugularis*) (Wolf 1975a, Ingels 1976, Schuchmann 1977). The evolution of the bright monomorphism in these species was probably a result of selection for female territoriality associated with availability of resources and their occurrence on ecological islands (Wolf 1975a).

***Taxonomic study of the genus* Eulampis**

The current taxonomic situation of the genus *Eulampis* was corroborated by conducting a plumage color analysis of the group. I combined male and female data of the two recognized species because of the color monomorphism of the genus. This can be well seen in the color spectra graphs obtained per species and body part (Appendix 61). Only a few sexual differences in the mean reflectance of some body areas of *E. holosericeus* (both males and females) were observed.

I subdivided and analyzed the *Eulampis* group considering each island as a separate pool (Fig. 45). A total of 30 pools (9 of *E. jugularis* and 21 of *E. holosericeus*) resulted from this separation. It is important to note that the maps indicating geographical distribution of these species were made showing only data from the collecting localities, and only from islands

with a sample of more than one specimen. Moreover, I did not consider for analysis those individuals that were the only sample for a given island. The geographical distribution of the two subspecies of *E. holosericeus* according to the current taxonomy is shown in Fig. 46.

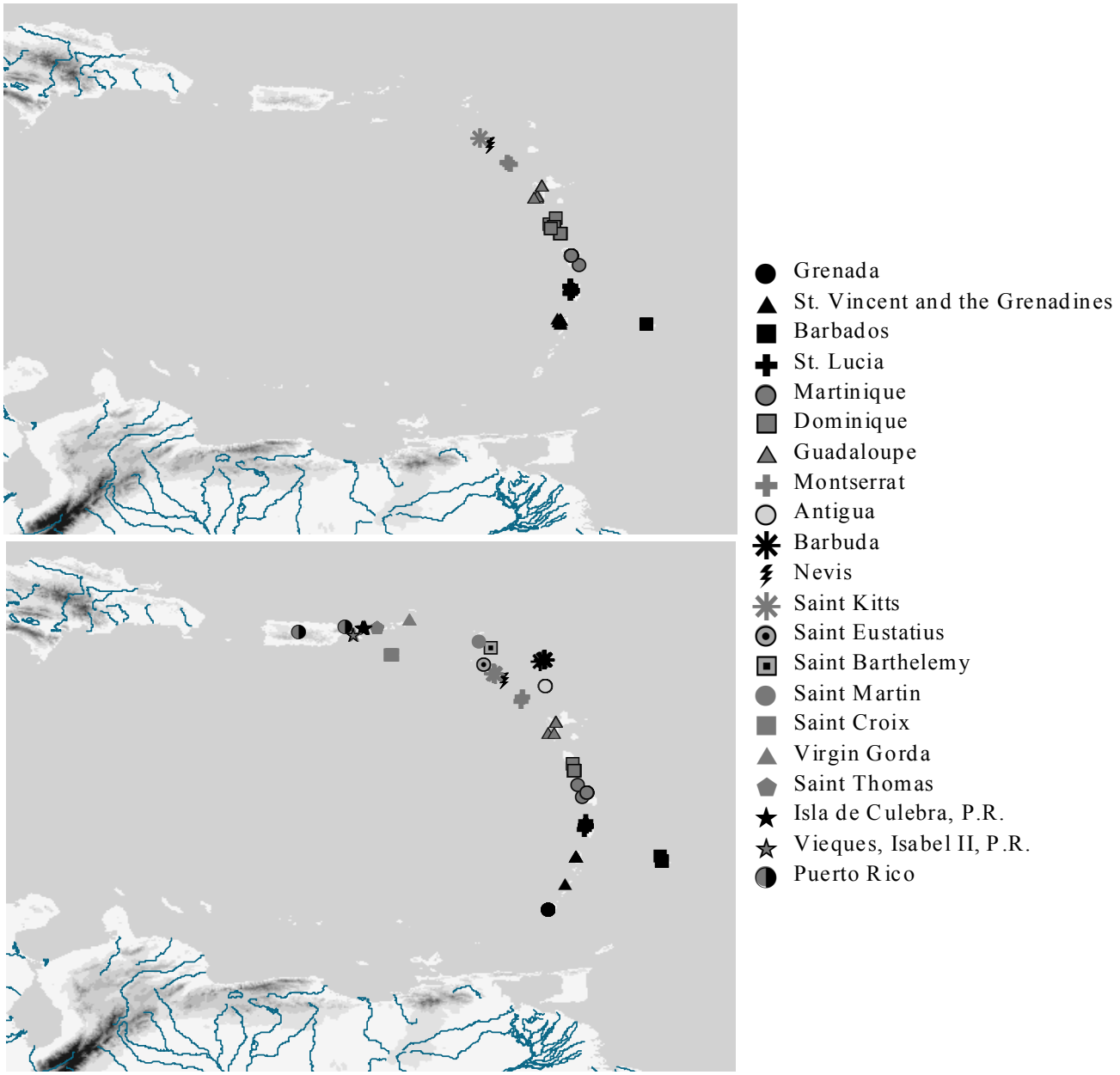
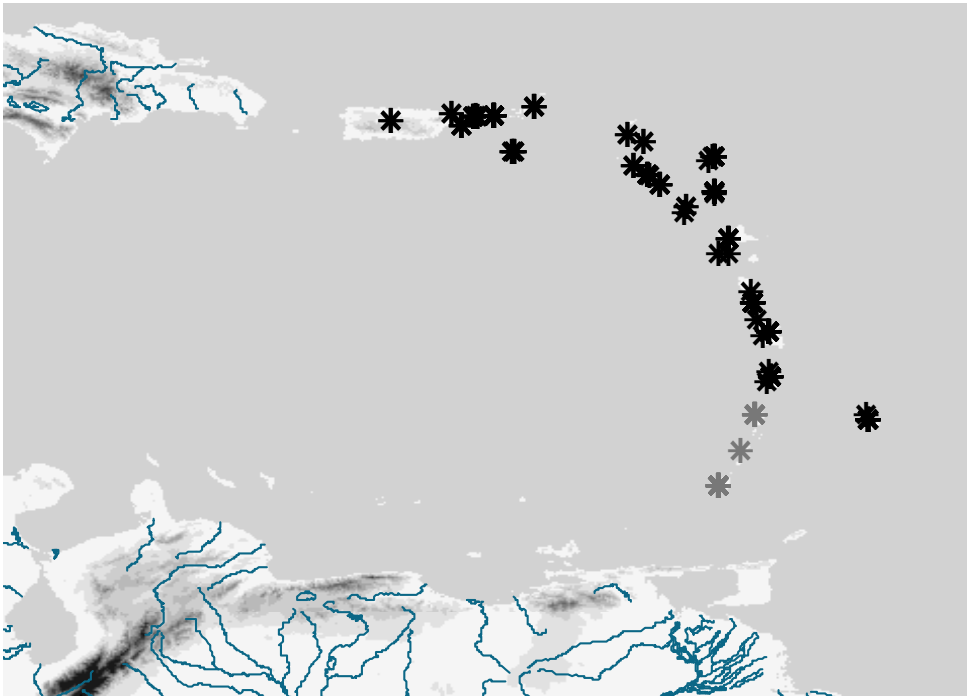


Fig. 45. Geographical distributions of the two species of *Eulampis*: *E. jugularis* (above) and *E. holosericeus* (below).

Fig. 46. Geographical distributions of the two subspecies of *Eulampis holosericeus: E. h. holosericeus*, and *E. h. chlorolaemus*.



I conducted a PCA on the color spectral data for each body part of all specimens of both species together. As already carried out for *Topaza* and *Anthracothorax*, the first three PC scores were taken to conduct a DFA (Appendix 62). The results indicated that the first two discriminant functions explained 78.8% of the variation (Table 44). The graph resulting from the first two functions of the DFA (Fig. 47) shows a clear separation of the two *Eulampis* species (*E. jugularis* and *E. holosericeus*) along the coordinate corresponding to the first function that alone represents 75.1% of the overall variation.

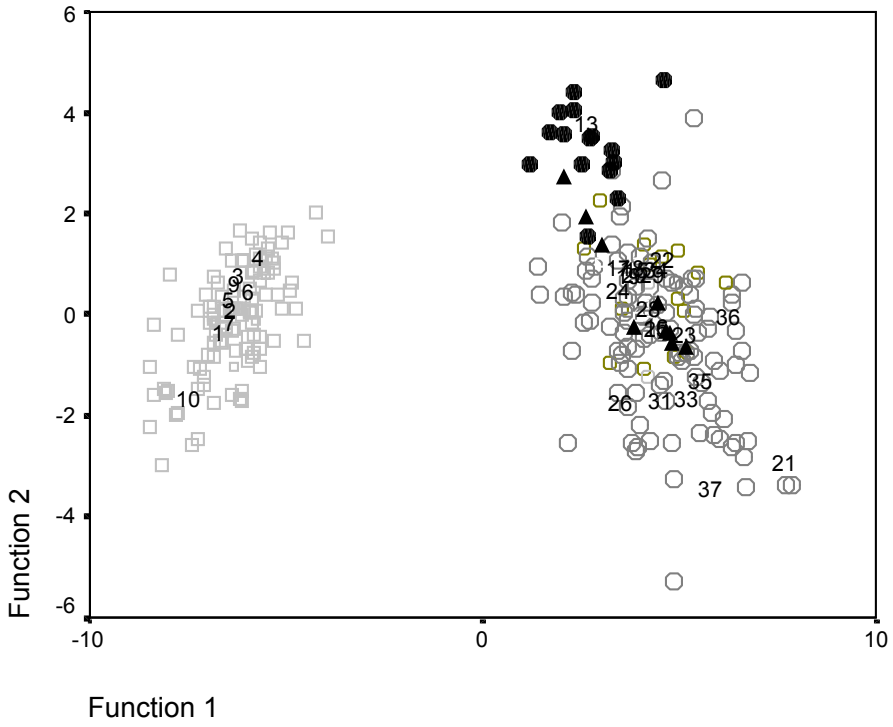
Table 44. Eigenvalues and percentages of variance found after the DFA conducted on color data from the 30 pools of *Eulampis.*

Eigenvalues

Function	Eigenvalue	% of Variance	Cumulative %	Canonical Correlation
1	30,656[a]	75,1	75,1	,984
2	1,521[a]	3,7	78,8	,777
3	1,077[a]	2,6	81,5	,720
4	1,004[a]	2,5	83,9	,708
5	,791[a]	1,9	85,9	,664
6	,750[a]	1,8	87,7	,655
7	,673[a]	1,6	89,3	,634
8	,589[a]	1,4	90,8	,609
9	,501[a]	1,2	92,0	,578
10	,403[a]	1,0	93,0	,536
11	,393[a]	1,0	94,0	,531
12	,359[a]	,9	94,8	,514
13	,282[a]	,7	95,5	,469
14	,254[a]	,6	96,2	,450
15	,222[a]	,5	96,7	,426
16	,209[a]	,5	97,2	,416
17	,195[a]	,5	97,7	,404
18	,175[a]	,4	98,1	,386
19	,139[a]	,3	98,5	,350
20	,107[a]	,3	98,7	,311
21	,102[a]	,3	99,0	,305
22	,089[a]	,2	99,2	,286
23	,086[a]	,2	99,4	,281
24	,061[a]	,1	99,6	,240
25	,053[a]	,1	99,7	,224
26	,049[a]	,1	99,8	,215
27	,036[a]	,1	99,9	,186
28	,033[a]	,1	100,0	,178
29	,013[a]	,0	100,0	,115

a. First 29 canonical discriminant functions were used in the analysis.

Fig. 47. Results of the first DFA conducted on color data of the 30 pools of *Eulampis*. The open squares represent populations of *E. jugularis* (cloud on the left). The open circles represent *E. holosericeus holosericeus*, the black circles *E. holosericeus* from Grenada (*E. h. chlorolaemus*), and the black triangles *E. holosericeus* from Saint Vincent and the Grenadines (presumably also of *E. h. chlorolaemus*).



The first two functions indicated segregation, at a smaller level, of the two subspecies of *E. holosericeus*: *E. h. holosericeus* and *E. h. chlorolaemus*. This last subspecies is only found on the island of Grenada and in the graph is represented by black circles (pool number 13). However, there is a pool represented by black triangles (number 15) that corresponds to those individuals collected on the islands of Saint Vincent and the Grenadines. These islands form an almost linear sequence that includes a large island (Saint Vincent) followed by a group of small ones that reach to Grenada. These small islands constitute a demographic unit with Saint Vincent (Saint Vincent and the Grenadines), and the labels of most of the specimens collected there are only labeled as Saint Vincent, making it difficult to determine exactly from which exact geographic unit they come. Consequently, the specimens occurring in this region are assigned to the same pool for analysis (number 15).

It is interesting that in the graph resulting from the DFA (Fig. 47) this pool (number 15) is placed in the center between the Grenada group (*E. h. chlorolaemus*), and the group formed by the rest of the pools (*E. h. holosericeus*), showing a small overlap. In order to define the situation of the specimens coming from pool 15, I made a second DFA by regrouping individuals as: 1) *E. jugularis*, 2) *E. h. chlorolaemus*, 3) *E. h. holosericeus*, leaving out the data from specimens from Saint Vincent and the Grenadines to be classified by the DFA itself. The first two functions explained 100% of the variation, allowing precise conclusions (Table 45). The results show that, according to overall plumage coloration, 77.8% of these individuals are placed within *E. h. holosericeus*, and 22.2% within *E. h. chlorolaemus* from Grenada (Fig. 48 and Table 46). These results imply a possible clinal zone between the two subspecies. This situation makes it difficult to set the limits of both distributions, if they exist, until more specific location information is gathered on *Eulampis* individuals from this "problematic" area.

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Eigenvalues

Function	Eigenvalue	% of Variance	Cumulative %	Canonical Correlation
1	24,710[a]	96,6	96,6	,980
2	,869[a]	3,4	100,0	,682

a. First 2 canonical discriminant functions were used in the analysis.

Table. 45. Eigenvalues and percentages of variance found after the second DFA conducted on the regrouped data of *Eulampis* in order to determine the membership of *E. holosericeus* pools from Saint Vincent and the Grenadines

Fig. 48. Results of the second DFA conducted on the regrouped data of *Eulampis* in order to determine the membership of the pools of *E. holosericeus* from Saint Vincent and the Grenadines.

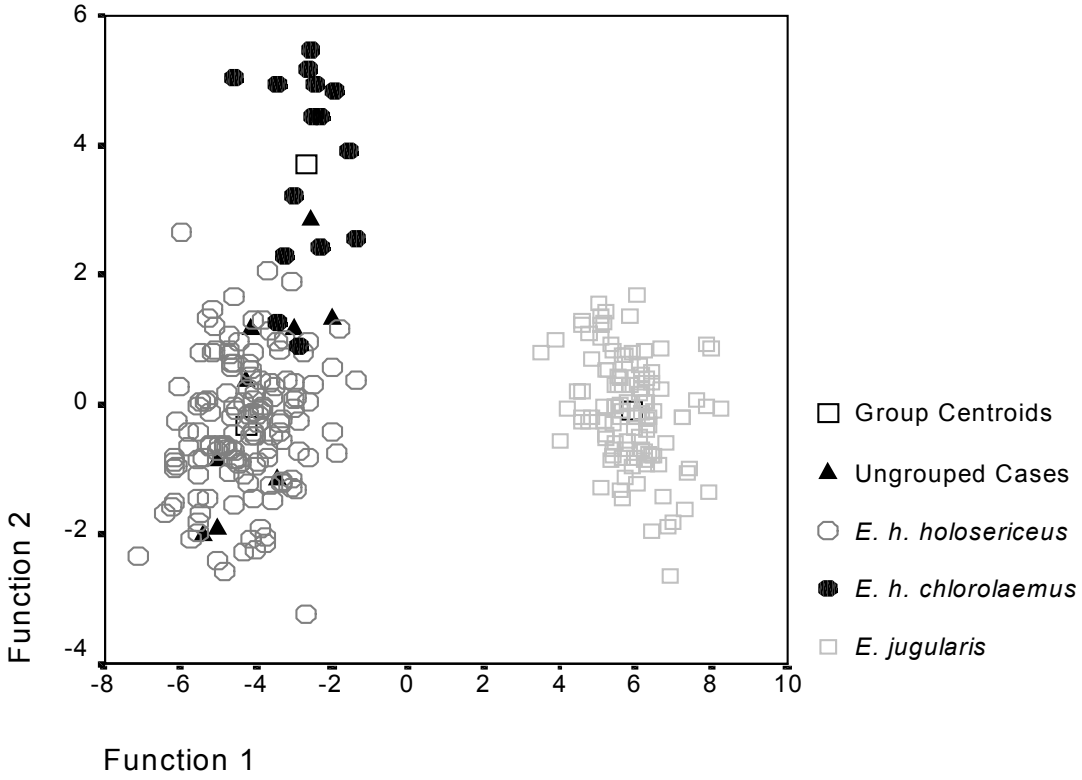


Table. 46. Classification results of the second DFA conducted on the regrouped data of *Eulampis* in order to determine the membership of *E. holosericeus* pools from Saint Vincent and the Grenadines.

Classification Results a

			Predicted Group			
		Final Groups	1,00	2,00	4,00	Total
Original	Count	1,00	108	0	0	108
		2,00	0	13	2	15
		4,00	0	3	135	138
		Ungrouped	0	2	7	9
	%	1,00	100,0	,0	,0	100,0
		2,00	,0	86,7	13,3	100,0
		4,00	,0	2,2	97,8	100,0
		Ungrouped	,0	22,2	77,8	100,0

a. 98,1% of original grouped cases correctly

The standardized canonical discriminant function coefficients (SCDFC, Table 47) for the second DFA also indicated the body parts that made the most contribution to the overall differentiation of the groups. According to the coefficients of function 1, the separation between the two *Eulampis* species is determined mainly by the color of the dorsal areas of shoulder (Fac2_3) and back (Fac2_4), and the ventral areas of gorget (Fac1_12), low throat (Fac1_14), and breast (Fac2_20). These differences can be very easily appreciated by the naked eye: *E. holosericeus* shows a green iridescent gorget with a bluish spot on the low throat, and greenish soft iridescence. *E. jugularis* shows instead an homogeneous reddish iridescent gorget, and basically dark breast. The mean color spectra showing the body part differences between the two species are shown in Appendix 63.

Schuchmann (1999) states that *E. h. chlorolaemus* differs from *E. h. holosericeus* in having a darker green throat and broad deep violet-blue patch on the center of the breast. I also find this distinction in this study. The coefficients of function 2 indicated that differences between the two subspecies of *E. holosericeus* with regard to plumage coloration can be found mainly on ventral areas of the low throat (Fac2_14) and breast (Fac2_20), in addition to the color of rectrix 5 (Fac2_39).

Morphological differences

The two species of *Eulampis* differ in overall size, with *E. jugularis* being larger than *E. holosericeus*, showing significant differences in the five body measurements taken (unfortunately there is not enough information on body mass and total length on the labels) (Table 48). Although monomorphic in color, *E. jugularis* shows a pronounced sexual morphological dimorphism in every character measured (Table 49). These clear differences make it possible to use a DFA to sex specimens marked as "unknown sex" in order to use the data for phylogenetic analysis. By contrast, *E. holosericeus* shows sexual dimorphism only in bill length (Table 49), which is not sufficient difference to sex specimens by means of DFA.

Table. 47. SCDFC of the second DFA conducted on the regrouped data of *Eulampis* in order to determine the body parts that explain most of the variance among subspecies.

	Function	
	1	2
FAC1_1	-,308	-,002
FAC2_1	,185	,008
FAC3_1	-,206	,048
FAC1_2	-,325	-,225
FAC2_2	-,116	-,208
FAC3_2	-,168	-,259
FAC1_3	-,017	-,031
FAC2_3	,705	-,186
FAC3_3	,413	-,092
FAC1_4	-,309	-,313
FAC2_4	,864	,104
FAC3_4	,156	,362
FAC1_5	-,255	,352
FAC2_5	,546	,056
FAC3_5	,300	-,355
FAC1_6	,109	-,040
FAC2_6	,001	,423
FAC3_6	-,197	,086
FAC1_12	,568	-,030
FAC2_12	-,273	-,188
FAC3_12	-,164	,377
FAC1_14	,704	,071
FAC2_14	-,367	-,546
FAC3_14	-,107	,128
FAC1_17	-,248	-,101
FAC2_17	,054	,074
FAC3_17	,120	,429
FAC1_20	-,034	,292
FAC2_20	-,840	-,552
FAC3_20	,181	,052
FAC1_23	-,005	-,048
FAC2_23	-,198	-,060
FAC3_23	-,054	-,173
FAC1_26	,061	-,128
FAC2_26	,001	-,151
FAC3_26	-,010	,072
FAC1_29	,094	,023
FAC2_29	-,073	,087
FAC3_29	-,308	,325
FAC1_32	-,098	,392
FAC2_32	-,260	-,026
FAC3_32	,124	,002
FAC1_39	,149	-,189
FAC2_39	-,320	,629
FAC3_39	,035	,232

Table 48. Morphometric measurements comparing both species of *Eulampis*, indicating statistically significant morphometric differences. **a** (above) males, and **b** (below) females.

** Significant differences (t-test; $p<0.001$) for this variable.

Sex	Taxon		**Bill length (mm)****	**Wing length (mm)****	**Rectrix 1 (mm)****	**Rectrix 2 (mm)****	**Rectrix 5 (mm)****
males	*E. jugularis*	$x=$	**27.93**	**73.86**	**34.62**	**35.47**	**41.39**
		$\sigma=$	1.56	2.67	1.26	1.53	2.44
		$n=$	56	56	55	53	54
	E. holosericeus	$x=$	**26.53**	**59.54**	**33.70**	**33.41**	**31.08**
		$\sigma=$	1.39	1.97	1.04	1.00	1.40
		$n=$	84	86	85	84	79

Sex	Taxon		**Bill length (mm)****	**Wing length (mm)****	**Rectrix 1 (mm)**	**Rectrix 2 (mm)****	**Rectrix 5 (mm)****
females	*E. jugularis*	$x=$	**31.15**	**69.85**	**33.39**	**34.35**	**37.78**
		$\sigma=$	1.78	2.42	1.03	1.41	2.46
		$n=$	37	37	33	34	32
	E. holosericeus	$x=$	**28.67**	**59.01**	**33.65**	**33.62**	**30.72**
		$\sigma=$	1.72	1.90	0.98	0.88	1.36
		$n=$	61	62	59	61	61

Table 49. Morphometric measurements of the genus *Eulampis*, indicating statistically significant sexual differences for each species.
** Significant differences (t-test; $p<0.001$) between sexes for this variable.

Taxon	Sex		Bill length (mm)	Wing length (mm)	Rectrix 1 (mm)	Rectrix 2 (mm)	Rectrix 5 (mm)
Eulampis jugularis	males	$x=$	**27.93****	**73.82****	**34.62****	**35.46****	**41.39****
		$\sigma=$	1.55	2.78	1.26	1.51	2.40
		$n=$	58	58	57	55	56
	females	$x=$	**31.15****	**69.85****	**33.39****	**34.35****	**37.78****
		$\sigma=$	1.78	2.42	1.03	1.41	2.46
		$n=$	37	37	33	34	32
Eulampis holosericeus	males	$x=$	**26.51****	**59.54**	**33.69**	**33.42**	**31.08**
		$\sigma=$	1.38	1.95	1.03	1.00	1.44
		$n=$	86	88	87	86	81
	females	$x=$	**28.61****	**59.05**	**33.68**	**33.63**	**30.75**
		$\sigma=$	1.77	1.91	1.00	.88	1.36
		$n=$	62	63	60	62	62

The Lesser Antilles provide a good latitudinal sequence of islands, which facilitates the search for potential correlations between a geographical reference point and the morphology of the two *Eulampis* species. For males of *E. jugularis*, a significant positive correlation was found between each body measurements taken and latitude (Table 50a). This correlation is in concordance with the ANOVA performed on the same data (Table 51). Bill and wing lengths showed a slight but significant correlation with latitude that did not translate into significant differences between islands. However, the stronger correlation shown by the rectrices translated into significant statistical differences between islands. The LSD *post hoc* test performed after the ANOVA (Table 52), together with the graphs extracted from the morphological measurements by island (Fig. 49a, b, c) showed that the main statistical difference was found for individuals from Saint Vincent Island, which have smaller rectrices relative to the others.

For females of *E. jugularis*, a significant positive correlation was found only for rectrices 2 and 5 (Table 50b), and significant differences between islands were found for bill length and the two rectrices showing a positive correlation (Table 51). Although the situation for bill length is not that clear, the situation for rectrices 2 and 5 in males repeated itself in the case of Saint Vincent females, according to the LSD *post hoc* test conducted (Table 52). The graphs (Fig. 50a, b, c) also showed the same tendency as for males. These results indicate that the population of *E. jugularis* from Saint Vincent might constitute a separate group. However, I would rather be conservative until further studies are conducted for two main reasons: The data set does not include enough samples of males and females from all islands, and there is only one male from Barbados, while the females of this population show no significant differences from those of Saint Vincent.

Peters (1945) and Schuchmann (1999) recognize two subspecies of *Eulampis holosericeus* (*Sericotes holosericeus* in the case of Peters): *E. h. holosericeus* and *E. h. chlorolaemus*. For this species I performed the same analysis as for *E. jugularis*. For both males and females of *E. holosericeus* I found only a slight significant negative correlation of bill and wing length with latitude (Table 53a) that did not translate into statistical differences between islands

(Table 54). Contrary to *E. jugularis*, the distribution of *E. holosericeus* in the Greater Antilles might provide a longitudinal component to the characteristics of the group; however, the results show no certainty in this regard. The results indicate that the two subspecies of *E. holosericeus* vary only in plumage coloration, as already discussed.

The morphological differences between populations of different islands, together with the existence of species like *E. holosericeus* with two distinct subspecies within its range in the Antilles, are difficult to interpret, since hummingbirds frequently travel between the islands (Lack 1973, Norton & Hobbs 1988). Specifically, *E. jugularis* has been recorded on many other islands outside its breeding range, including Barbados, which is 160 km away from its nearest breeding site on Saint Vincent (Lack 1973). This species has also been seen on Antigua, Barbuda, Desiderade, and other islands (Lack 1973, Schuchmann 1999). *E. holosericeus* has been seen flying from one island to the other in the Caribbean, making it difficult to determine the limits of its range. Other trochilids, such as *Florisuga mellivora*, *Amazilia tobaci*, and *Chrysolampis mosquitus*, which breed on Tobago, have also been recorded in the Lesser Antilles, 120 km away from their breeding ranges. *Archilochus colubris* migrates in winter through the Gulf of Mexico (about 850 km). Hurricanes have also created conditions in which some bird species reach islands from the mainland in this area. Additional taxa have been reported as occasional breeders or as vagrant species in the southern United States (Bleiweiss 1998). In addition, although *Anthracothorax viridigula* inhabits the mainland of northeastern South America and Trinidad, it has also been recorded in the Grenadines (Lack 1973).

This indicates that the hummingbird communities established on each island seem not to be determined by movement difficulties or limited dispersal capacities. On the contrary, the organization of hummingbird communities and its morphological consequences have been well studied (Feinsinger *et al*. 1979; Feinsinger & Swarm 1981; Feinsinger *et al*. 1982; Brown & Bowers 1985; Wolf & Gill 1986; Bleiweiss 1990; Hinkelmann 1990; Temeles & Roberts 1993; Cotton 1998a, b, c; Schuchmann 1999; Temeles *et al*. 2000) and seem to be closely

related to ecological limitations, such as partition of resources, which is more accentuated on islands.

An example of specific interest is the situation of the two *Eulampis* species. Both species are resident throughout their respective ranges, although they overlap to a small degree. When they overlap, *E. holosericeus* tends to occur in drier and lower areas of each island than *E. jugularis* creating a clear segregation of habitat ranges (Lack 1973, Wolf 1975a, Schuchmann 1981). In Puerto Rico, where four other species of hummingbirds occur (*A. dominicus*, *A. viridis*, *Chlorostilbon maugaeus*, and *Orthorhyncus cristatus*), and there are no Purple-throated Caribs, the Green-throated Carib is confined to the less dry regions of the extreme northeast (Lack 1973, Kodric *et al*. 1984) without any obvious geographical barrier.

E. holosericeus occurs on every island of the Lesser Antilles, primarily in the lowlands. On Grenada, it occurs up to an altitude of 600 m above sea level, and its presence can be linked with the absence from Grenada of *E. jugularis*, the large hummingbird of the rain forest on the other islands (Lack 1973). On Grenada there is another large hummingbird species, *Glaucis hirsuta*, living in the rain forest, which explains not only why *E. jugularis* is absent from this island (Schuchmann 1980c) but also why *E. holosericeus* is found in the canopy but not inside the forest; however, there have been sightings of *E. jugularis* vagrants in Grenada (Lack 1973). This dispersal has been related to long-term changes in environmental conditions in the Antilles (Norton & Hobbs 1988), the destruction of native forests by man, and natural forces such as hurricanes (Alaska 1976, Thompson 1983, Boucher 1990, Reading 1990, Bellingham *et al.* 1995, Turner *et al.* 2003). The potential for dispersal and habitat segregation in this group will be further discussed below.

Table 50a. Pearson correlation of the morphometric measurements from males of *E. jugularis* in relation to latitude and longitude.
** Sig. (2-tailed) < 0.01, * Sig. (2-tailed) < 0.05

***Eulampis jugularis* (males)**						
		Bill length (mm)	**Wing length (mm)**	**Rectrix 1 (mm)**	**Rectrix 2 (mm)**	**Rectrix 5 (mm)**
Latitude	Pearson Correlation=	.259*	.281*	.497**	.469**	.441**
	n=	74	74	72	70	72
Longitude	Pearson Correlation=	-.124	-.084	-.213	-.210	-.137
	n=	74	74	72	70	72

Table 50b. Pearson correlation of the morphometric measurements from females of *E. jugularis* in relation to latitude and longitude.
** Sig. (2-tailed) < 0.01, * Sig. (2-tailed) < 0.05

***Eulampis jugularis* (females)**						
		Bill length (mm)	**Wing length (mm)**	**Rectrix 1 (mm)**	**Rectrix 2 (mm)**	**Rectrix 5 (mm)**
Latitude	Pearson Correlation=	.187	.076	.222	.418**	.473**
	n=	51	51	47	48	46
Longitude	Pearson Correlation=	-.090	.020	-.116	-.253	-.244
	n=	51	51	47	46	46

Table 51. ANOVAs on the morphometric measurements of *Eulampis jugularis* from different islands: males (above) and females (below).

ANOVA

		Sum of Squares	df	Mean Square	F	Sig.
BILL_LEN	Between Groups	18,187	7	2,598	1,176	,329
	Within Groups	141,434	64	2,210		
	Total	159,621	71			
WING_LEN	Between Groups	72,356	7	10,337	1,800	,103
	Within Groups	367,461	64	5,742		
	Total	439,817	71			
R1	Between Groups	45,554	7	6,508	5,464	,000
	Within Groups	73,849	62	1,191		
	Total	119,402	69			
R5	Between Groups	184,016	7	26,288	5,936	,000
	Within Groups	274,591	62	4,429		
	Total	458,607	69			
R2	Between Groups	57,066	7	8,152	4,942	,000
	Within Groups	98,976	60	1,650		
	Total	156,042	67			

ANOVA

		Sum of Squares	df	Mean Square	F	Sig.
BILL_LEN	Between Groups	60,094	6	10,016	6,125	,000
	Within Groups	67,044	41	1,635		
	Total	127,137	47			
WING_LEN	Between Groups	33,280	6	5,547	,933	,482
	Within Groups	243,643	41	5,943		
	Total	276,923	47			
R1	Between Groups	8,802	6	1,467	1,481	,212
	Within Groups	36,657	37	,991		
	Total	45,459	43			
R5	Between Groups	86,405	6	14,401	3,891	,004
	Within Groups	133,228	36	3,701		
	Total	219,633	42			
R2	Between Groups	34,908	6	5,818	4,809	,001
	Within Groups	47,186	39	1,210		
	Total	82,095	45			

Table 52. *Post hoc* test on the morphometric measurements of *Eulampis jugularis* from different islands (left) males and (right) females.

Island (i)	Island (j)	R1 (Sign.)	R2 (Sign.)	R5 (Sign.)
Saint Vincent	Saint. Lucia	,002	,002	,001
	Martinique	,000	,000	,000
	Dominique	,000	,001	,000
	Guadaloupe	,000	,000	,000
	Montserrat	,000	,000	,000
	Nevis	,001	,000	,013
	Saint Kitts	,107	,242	,392
Saint Lucia	Saint Vincent	,002	,002	,001
	Martinique	,438	,494	,101
	Dominique	,218	,468	,176
	Guadaloupe	,060	,153	,141
	Montserrat	,032	,071	,020
	Nevis	,049	,034	,345
	Saint Kitts	,935	,677	,457
Martinique	Saint Vincent	,000	,000	,000
	Saint. Lucia	,438	,494	,101
	Dominique	,625	,908	,876
	Guadaloupe	,191	,360	,812
	Montserrat	,087	,157	,156
	Nevis	,108	,072	,879
	Saint Kitts	,767	,459	,128
Dominique	Saint Vincent	,000	,001	,000
	Saint. Lucia	,218	,468	,176
	Martinique	,625	,908	,876
	Guadaloupe	,362	,444	,728
	Montserrat	,159	,196	,141
	Nevis	,175	,090	,818
	Saint Kitts	,591	,435	,158
Guadaloupe	Saint Vincent	,000	,000	,000
	Saint. Lucia	,060	,153	,141
	Martinique	,191	,360	,812
	Dominique	,362	,444	,728
	Montserrat	,517	,516	,266
	Nevis	,473	,256	1,000
	Saint Kitts	,295	,222	,123
Montserrat	Saint Vincent	,000	,000	,000
	Saint. Lucia	,032	,071	,020
	Martinique	,087	,157	,156
	Dominique	,159	,196	,141
	Guadaloupe	,517	,516	,266
	Nevis	,889	,606	,388
	Saint Kitts	,152	,113	,027
Nevis	Saint Vincent	,001	,000	,013
	Saint. Lucia	,049	,034	,345
	Martinique	,108	,072	,879
	Dominique	,175	,090	,818
	Guadaloupe	,473	,256	1,000
	Montserrat	,889	,606	,388
	Saint Kitts	,151	,057	,207
Saint Kitts	Saint Vincent	,107	,242	,392
	Saint. Lucia	,935	,677	,457
	Martinique	,767	,459	,128
	Dominique	,591	,435	,158
	Guadaloupe	,295	,222	,123
	Montserrat	,152	,113	,027
	Nevis	,151	,057	,207

Island (i)	Island (j)	Bill length (Sign.)	R2 (Sign.)	R5 (Sign.)
Saint Vincent	Barbados	,261	,271	,077
	Saint. Lucia	,016	,000	,004
	Martinique	,000	,009	,017
	Dominique	,784	,000	,000
	Guadaloupe	,138	,003	,001
	Nevis	,030	,001	,000
Barbados	Saint Vincent	,261	,271	,077
	Saint. Lucia	,446	,058	,541
	Martinique	,009	,339	,857
	Dominique	,354	,028	,250
	Guadaloupe	,982	,200	,269
	Nevis	,532	,097	,201
Saint. Lucia	Saint Vincent	,016	,000	,004
	Barbados	,446	,058	,541
	Martinique	,014	,211	,596
	Dominique	,030	,699	,516
	Guadaloupe	,297	,407	,547
	Nevis	,878	,795	,406
Martinique	Saint Vincent	,000	,009	,017
	Barbados	,009	,339	,857
	Saint. Lucia	,014	,211	,596
	Dominique	,000	,097	,228
	Guadaloupe	,001	,668	,253
	Nevis	,012	,343	,178
Dominique	Saint Vincent	,784	,000	,000
	Barbados	,354	,028	,250
	Saint. Lucia	,030	,699	,516
	Martinique	,000	,097	,228
	Guadaloupe	,223	,217	,975
	Nevis	,052	,524	,810
Guadaloupe	Saint Vincent	,138	,003	,001
	Barbados	,982	,200	,269
	Saint. Lucia	,297	,407	,547
	Martinique	,001	,668	,253
	Dominique	,223	,217	,975
	Nevis	,398	,590	,793
Nevis	Saint Vincent	,030	,001	,000
	Barbados	,532	,097	,201
	Saint. Lucia	,878	,795	,406
	Martinique	,012	,343	,178
	Dominique	,052	,524	,810
	Guadaloupe	,398	,590	,793

Fig 49. Graphs showing the tendency of the significant body measurements according to the ANOVA and LSD *post hoc* tests for males of *E. jugularis*. The arrangement of the islands from left to right in the X coordinate is: Saint Vincent, Barbados, Saint Lucia, Martinique, Dominique, Guadaloupe, Montserrat, Antigua, Nevis, and Saint Kitts.

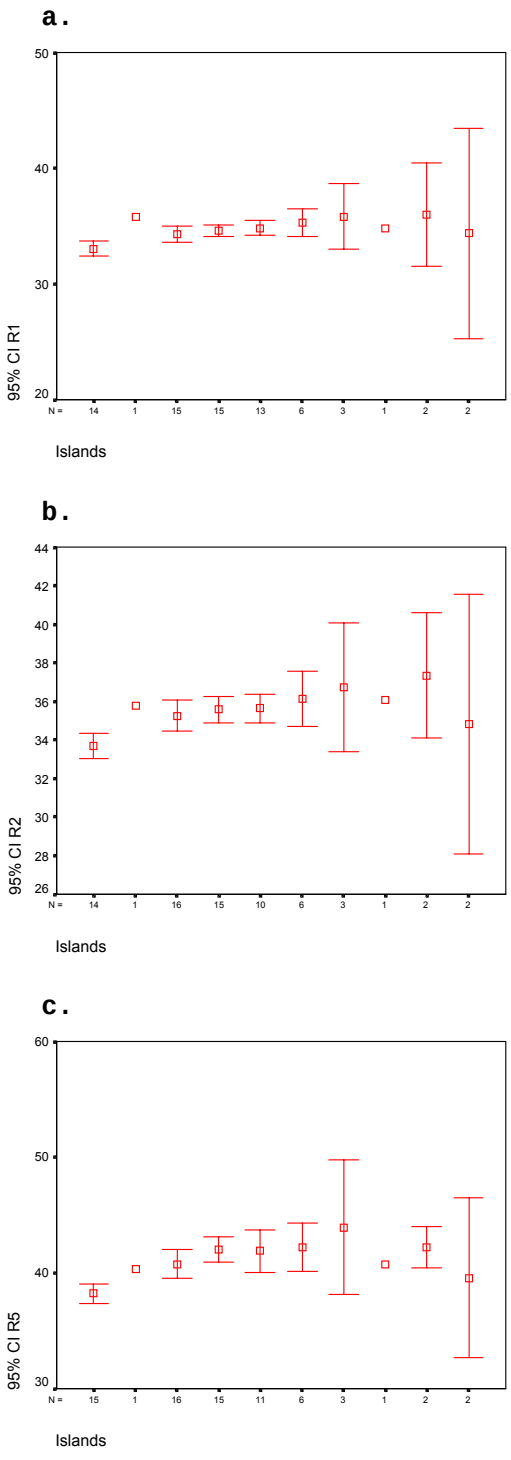
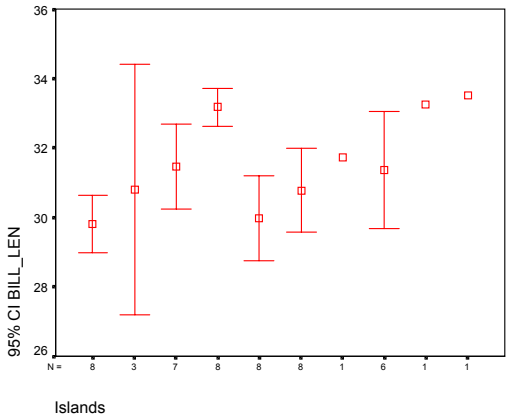
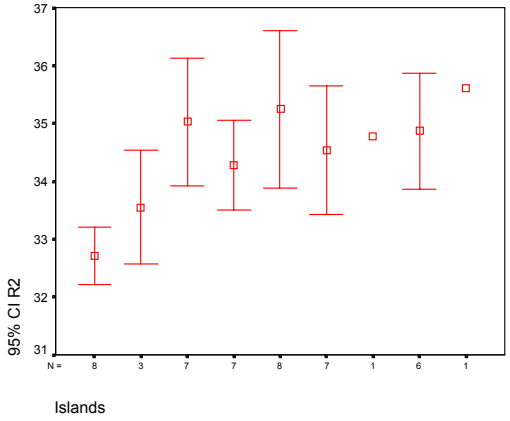


Fig 50. Graphs showing the tendency of the significant body measurements according to the ANOVA and LSD *post hoc* tests for females of *E. jugularis*. The arrangement of the islands from left to right in the X coordinate is: Saint Vincent, Barbados, Saint Lucia, Martinique, Dominique, Guadaloupe, Montserrat, Nevis, Saint Kitts, and Saba.

a.



b.



c.

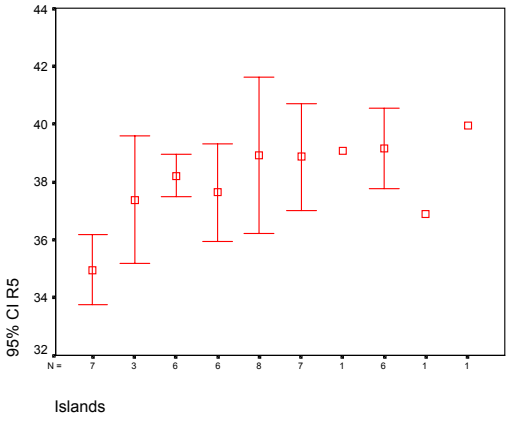


Table 53a. Pearson correlation of the morphometric measurements from males of *E. holosericeus* in relation to latitude and longitude.
** Sig. (2-tailed) < 0.01, * Sig. (2-tailed) < 0.05

***Eulampis holosericeus* (males)**						
		Bill length (mm)	**Wing length (mm)**	**Rectrix 1 (mm)**	**Rectrix 2 (mm)**	**Rectrix 5 (mm)**
Latitude	Pearson Correlation=	-.316**	-.254*	-.144	-.086	-.092
	n=	84	86	85	84	79
Longitude	Pearson Correlation=	.264*	.144	-.144	-.086	-.092
	n=	84	86	85	84	79

Table 53b. Pearson correlation of the morphometric measurements of females of *E. holosericeus* in relation to latitude and longitude
** Sig. (2-tailed) < 0.01, * Sig. (2-tailed) < 0.05

***Eulampis holosericeus* (females)**						
		Bill length (mm)	**Wing length (mm)**	**Rectrix 1 (mm)**	**Rectrix 2 (mm)**	**Rectrix 5 (mm)**
Latitude	Pearson Correlation=	-.325*	-.304*	-.157	-.128	.037
	n=	61	62	59	61	61
Longitude	Pearson Correlation=	.109	.204	.000	-.067	-.138
	n=	61	62	59	61	61

Table 54. ANOVAs on the morphometric measurements of *Eulampis holosericeus* (including individuals of the two species) from different islands: males (above) and females (below).

ANOVA

		Sum of Squares	df	Mean Square	F	Sig.
BILL_LEN	Between Groups	41,867	22	1,903	,979	,501
	Within Groups	118,541	61	1,943		
	Total	160,408	83			
WING_LEN	Between Groups	83,407	22	3,791	,973	,509
	Within Groups	245,509	63	3,897		
	Total	328,916	85			
R1	Between Groups	22,698	22	1,032	,945	,542
	Within Groups	67,707	62	1,092		
	Total	90,405	84			
R2	Between Groups	25,084	22	1,140	1,186	,293
	Within Groups	58,642	61	,961		
	Total	83,726	83			
R5	Between Groups	40,724	22	1,851	,920	,571
	Within Groups	112,676	56	2,012		
	Total	153,400	78			

ANOVA

		Sum of Squares	df	Mean Square	F	Sig.
BILL_LEN	Between Groups	50,094	16	3,131	1,075	,406
	Within Groups	128,164	44	2,913		
	Total	178,258	60			
WING_LEN	Between Groups	70,625	16	4,414	1,319	,228
	Within Groups	150,607	45	3,347		
	Total	221,231	61			
R1	Between Groups	14,007	16	,875	,891	,583
	Within Groups	41,267	42	,983		
	Total	55,274	58			
R2	Between Groups	20,107	16	1,257	2,087	,028
	Within Groups	26,494	44	,602		
	Total	46,601	60			
R5	Between Groups	33,783	16	2,111	1,215	,295
	Within Groups	76,433	44	1,737		
	Total	110,216	60			

Phylogenetic relationships of the three genera *Topaza*, *Anthracothorax*, and *Eulampis*

The genera *Eulampis*, *Anthracothorax*, and *Topaza* are included within the mango group, considered basal within hummingbird phylogeny (Zusi & Bentz 1982, Sibley & Ahlquist 1990, Bleiweiss *et al*. 1997). According to Schuchmann (1980b, c; 1981) the genus *Eulampis* seems to be phylogenetically close to the genus *Anthracothorax* due to similarities in nest form and construction, which he considers an important criterion in hummingbird systematics. This author considers that the origin of *Eulampis* is in northeastern South America and that it is also phylogenetically close to the genus *Topaza* from this region. Although these two genera are different in overall coloration they do show similarities in the iridescence of some plumage areas and in their habits (Schuchmann 1980c). Also, the nest of *Topaza* shows great similarity to those constructed by *Anthracothorax* and *Eulampis*. The following analysis was performed to test if the relationships between these taxa are indeed so close. This analysis should also serve as a conclusive description of the phylogenetic relationships among the three genera studied in this research, using the genus *Campylopterus* as outgroup (*C. cuvierii* and *C. largipennis*) for the reasons outlined earlier.

Descriptive information on *Campylopterus* (outgroup)

At this point, I would like to complement the descriptive information on the groups under study by adding something about the outgroup genus *Campylopterus*. The sabrewings, *Campylopterus* Swainson, 1827, are of wide distribution in Central and South America, ranging from Mexico to Paraguay and southeastern Brazil (Plate 4). According to Schuchmann (1999), they constitute an unusual group of trochilines, with up to three modified outermost primaries. Their feather shafts are thickened to various degrees, mainly in males, possibly contributing to a strengthening of the wing during their fast, swift-like gliding through semi-open vegetation (Schuchmann 1999). According to Peters (1945) and Schuchmann (1999), the genus includes 13 species: *C. cuvierii*, *C. curvipennis*, *C. largipennis*, *C. rufus*, *C. hyperythrus*, *C. hemileucurus*, *C. ensipennis*, *C. falcatus*, *C.*

phainopeplus, *C. villaviscensio*, *C. duidae*, *C. cirrochloris*, and *C. macrourus*. Here I consider only two of these species, *C. cuvierii* and *C. largipennis*, since they have wide geographical distributions and the most "generalized" plumage coloration within the group.

Phylogenetic analysis

The phylogenetic analysis was performed on the following taxonomic units (TUs):

- *Topaza pella*
- *Anthracothorax viridigula*
- *Anthracothorax prevostii*
- *Anthracothorax nigricollis*
- *Anthracothorax veraguensis*
- *Anthracothorax dominicus*
- *Anthracothorax viridis*
- *Anthracothorax mango*
- *Anthracothorax recurvirostris*
- *Eulampis jugularis*
- *Eulampis holosericeus*

- *Campylopterus cuvierii* (outgroup)
- *Campylopterus largipennis* (outgroup)

The phylogenetic analysis was conducted following the same steps as in all previous sections. In *Eulampis* I separated the specimens by sex to join the data to the other species for the analysis. I conducted a PCA on the raw spectral color data from each body part by sex, and I created a new data set for each sex containing the first three PC scores that represented plumage coloration (51 variables for males and 60 for females), plus the morphometric data (five variables per sex) (Appendices 64 and 65). A total of 7,896 ((51*141)+(5*141)) working variables for males and 9,165 ((60*141)+(5*141)) for females resulted from the subdivision of

the original variables, which were then used to create matrix A (Appendices 66 and 67) and matrix B (Appendices 68 and 69) of the GFC. The codification of the matrices was completed, the data from both sexes combined, and the uninformative characters eliminated to construct the final matrix (Appendix 70). This matrix contained 13 taxa (two outgroups) and 3039 parsimony-informative characters that were weighted (Appendix 71) and entered in PAUP.

The analysis resulted in a fully resolved phylogenetic tree (Fig. 51, Table 55), with strong support according to the Bootstrap percentages. The three genera under study form a monophyletic clade, of which the species *Topaza pella* and *Anthracothorax mango* are at the base forming a separate clade. Another monophyletic clade contains the remainder of *Anthracothorax* and *Eulampis*. This clade branches again in two monophyletic clades, one containing both species of *Eulampis* together with *A. viridis*, and the other containing the rest of the current *Anthracothorax* group.

These results not only indicate that, in agreement with Schuchmann (1980b, c; 1981) *Eulampis* and *Anthracothorax* are sister taxa, close to *Topaza*, but that a reconsideration of the taxonomy of the mango group would be in order. Within the current genus *Anthracothorax*, the species *A. mango* and *A. viridis* are the most distinct, not only in general plumage coloration patterns but also in showing sexual color monomorphism. This pattern is also present within the genus *Eulampis*, as already discussed, and the character might be important in placing it together with *A. viridis*.

Topaza, on the contrary, shows color sexual dimorphism. The degree of dimorphism in this species, however, cannot be compared to the very distinct patterns that define the sexes of *Anthracothorax* (except for the two species mentioned). The general plumage color patterns in *Topaza* are the same in both males and females, being only brighter and more defined in males.

Fig. 51. Concluding phylogenetic tree of *Topaza*, *Anthracothorax*, and *Eulampis* using *Campylopterus* as outgroup according to both plumage coloration and morphometric data. Nodes are represented by bold numbers above the lines, and branch lengths are represented by numbers under the lines. The Bootstrap percentages are shown in parentheses at the side of each branch length.

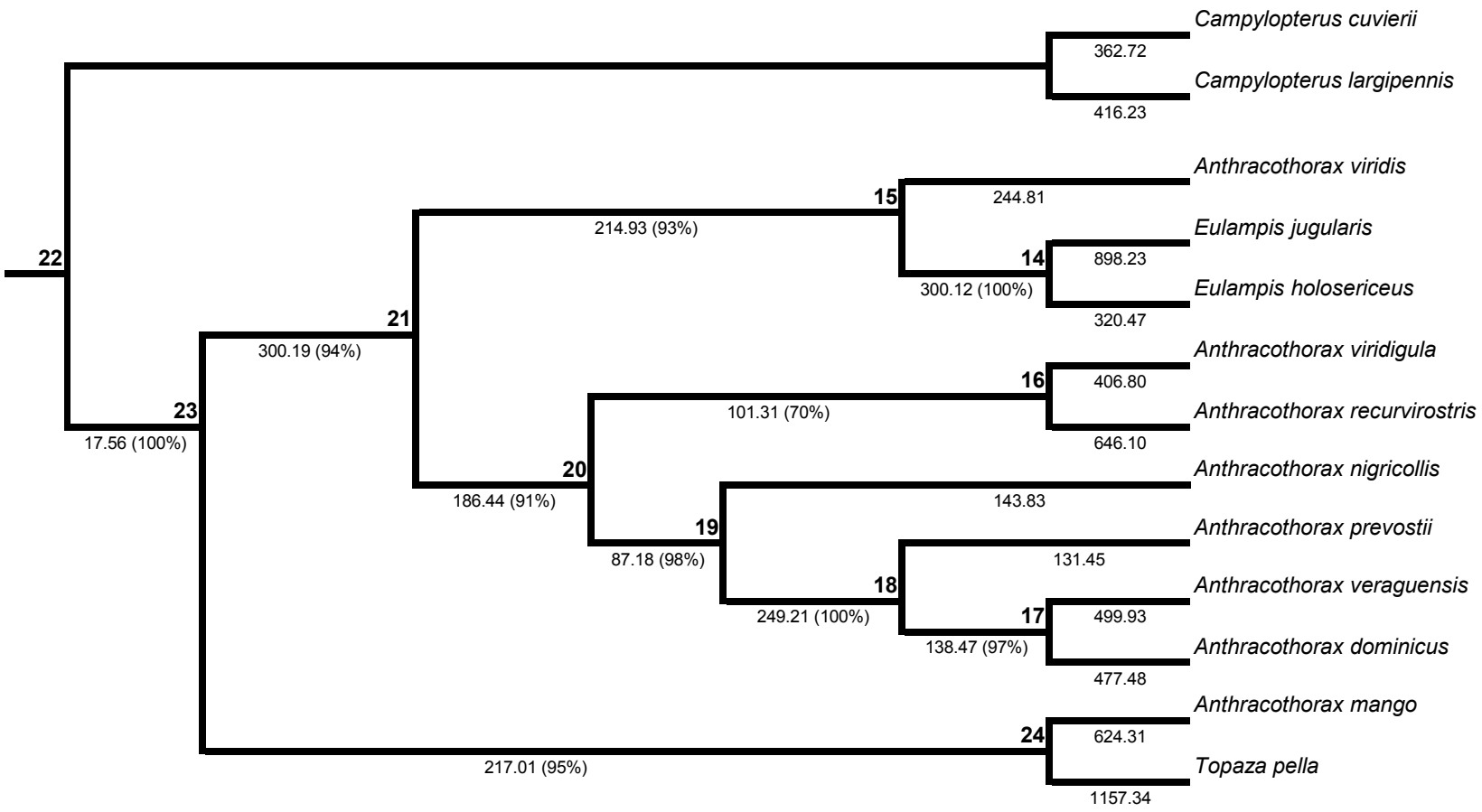


Table 55. Main descriptive parameters of the phylogenetic tree resulting from the PAUP analysis of *Topaza, Anthracothorax,* and *Eulampis* using *Campylopterus* as outgroup.

Tree characteristics	Values
Tree length	7695.35
Consistency Index (CI)	0.50
Homoplasy Index (HI)	0.50
Retention Index (RI)	0.34
Rescaled Consistency Index (RC)	0.17

Within the "real" *Anthracothorax* clade (excluding *A. mango* and *A. viridis*) there are other interesting relationships to discuss. As previously noted, there is a close relationship between *A. veraguensis* (from the Central American mainland) and *A. dominicus* (from the Caribbean islands of Hispaniola and Puerto Rico). These species are also closely related to *A. prevostii* and *A. nigricollis* (from the Central and South American mainland respectively). The species *A. viridigula* and *A. recurvirostris* (both distributed in northeastern South America) appear more isolated at the base of this *Anthracothorax* clade, but according to the results of this section, there is no controversy concerning the status of *A. recurvirostris* as a member of *Anthracothorax*.

The tree shown here presents some inconsistencies regarding the grouping of *Anthracothorax* at the species level carried out in an earlier section. For that section the analysis was conducted only on *Anthracothorax*; however, I think that adding the other groups has resulted in a stronger support for the phylogenetic relationships found between and within clades. For this reason the results of this section will be the basis for discussing the historical biogeographical events in the speciation process of our studied group.

Historical biogeographical events in the speciation process of the study group

Based on the phylogeny and geographical distribution of a group of taxa, it is possible to reconstruct the speciation events and biogeographical history of the area they occupy. A few methods have been proposed as suitable for this purpose (Page 1988, Morrone & Carpenter 1994, Brooks *et al.* 2001). However, many of these are based mainly on the concept of vicariance as the main source of speciation, and are of limited use in the case of my study material, which is known to have great dispersal potential. Additionally, I present results for only three genera of the mango group, two of them with restricted distributions. For these reasons, I limit my discussion to producing a theoretical picture of the historical biogeographical events on speciation. This discussion is based on the history of the region where these taxa are found, published ideas about the origin of hummingbirds, and the phylogenetic results of this research.

The history of hummingbird taxa presents a complex situation of ancestry, colonization, extinction, and recolonization to explain the great diversity of the group and the coexistence of numerous unrelated lineages. According to Bleiweiss *et al*. (1997) and Bleiweiss (1998) hummingbirds have a Paleocene origin, and the most basal extant hummingbird groups, the hermits and mangoes (among non-hermits), come from lowland tropical Miocene ancestors. Although it has been suggested that lowland and highland non-hermits were initially separated by a vicariance event, the phylogeny of the group does not support this idea (Bleiweiss *et al*. 1994, 1997; Bleiweiss 1998). According to Bleiweiss (1998), the hermit/non-hermit split appears to have occurred in the lowlands, followed by separate and independent colonization events by these lowland ancestors not only to the highlands of the Andes, but also to the Caribbean islands and temperate Central and North America. Several to many lineages contributed over time to the development of all hummingbird faunas, except those north of Mexico, where a single clade predominates.

The phylogenetic results of this study corroborate the idea that *Anthracothorax* and *Eulampis* are sister taxa, close to *Topaza*. Moreover, the mango hummingbirds must have also originated in the lowlands of South America and subsequently occupied other regions (see

Schuchmann 1980b, Bleiweiss 1998). Specifically, Schuchmann indicates that the origin of the genus *Eulampis* (currently endemic to the Caribbean Antilles) is in northern South America, where *Topaza* and some species of *Anthracothorax* also occur. Other species of *Anthracothorax* occur also in the Greater Antilles and Central America. To explain the speciation history of the study group, and its present geographical distribution, it is necessary to understand the dynamic history of the South American continent and its connection with Central America and the Caribbean islands.

Miocene climate changes were more gradual than those of the Quaternary, during which glacial-interglacial climate cycles are thought to have driven younger Plio-Pleistocene avian radiations, by repeated range fragmentation and population isolation in regions of stable habitat refugia (Haffer 1969, 1974b, 1977). These changes might have been important in the later stages of the evolution of hummingbirds, mainly in the subspecific variations in South and Central America. However, hummingbird data suggest that Pleistocene-style changes are not necessary to drive rapid cladogenesis (Bleiweiss *et al*. 1997). The Miocene radiation of certain groups appears to have coincided with the creation of new habitats that provided ecological opportunities for evolutionary radiation (Bleiweiss *et al*. 1997). The ability to exploit those habitats was probably an important factor in the radiation of the groups under study, which are known to be generalists compared with other hummingbird groups.

The early Miocene date for the radiation of extant hummingbird taxa effectively rules out a vicariant origin for West Indian hummingbirds because the Antillean island arc and North and South America were separated from each other by large water expanses from late in the Eocene to late in the Pliocene (Bleiweiss 1998). Additionally, it has been said that even if vicariance occurred at that time, its relevance for understanding the origin of the modern Antillean biota is minimal. Over-water dispersal has been strongly advocated as the major and perhaps only method of vertebrate faunal formation in the Caribbean region (Iturralde-Vinent & MacPhee 1999).

It seems that the main sources of speciation in the hummingbird taxa examined here were dispersal (to the Caribbean islands and Central America), and *in situ* speciation via habitat

segregation and utilization of the new habitats available in the region (those found in mainland South America and parts of Central America). These aspects were already discussed, with examples, in the previous section. It is known that although some lineages of hummingbirds are poor over-water colonizers, the mango hummingbirds show a great capacity for over-water dispersal. On numerous occasions, hummingbirds have crossed potential dispersal barriers, from water gaps to strong elevational gradients and latitude (Bleiweiss 1998). However, ecological aspects interacted with geography to filter out some hummingbird lineages from certain geographic regions (Bleiweiss 1998).

The development of the varied hummingbird communities is the result of local conditions, contemporary interactions, the existence of strong territoriality, and the tendency to character displacement. Potential for coevolution also allows a potential for habitat segregation that seems to have been specially important in the early stages of radiation (Bleiweiss 1998). This scenario seems to be important on islands, but also on the mainland where we find that birds such as hermits occupy the forest interior and the non-hermits mainly the canopy and forest edges (chiefly mangoes) (Bleiweiss 1998). In tropical lowlands, in contrast to islands or the Andes, the basic separation between the forest-dwelling hermits and canopy and edge-dwelling non-hermits appears to have evolved *in situ* (Bleiweiss 1998).

Given the relationship of some hummingbird species to "their" flowers, and the resulting high level of territoriality, there is great potential for *in situ* vicariance, which explains why closely related genera, such as *Anthracothorax* and *Topaza*, can cohabit in the same general geographic range in South America. *In situ* vicariance in the lowlands was probably a predominant but not exclusive mechanism for the development of those faunas (Bleiweiss 1998).

In general, the earliest times of trochilid evolution coincided with the substantial tectonic complexity that characterized the northern Andes throughout the Cenozoic (Cracraft & Prum 1988), creating numerous potential physiographical barriers that could produce vicariance of the forest biota (Irving 1975). The topography of the Andes of South America is the result of strong orogenic activities since the Oligocene (Heindl & Schuchmann 1998) and the

mountain-building in the west caused important changes in the positions of main rivers, such as the Amazon and Orinoco. Due to the continued uplift of the Andes, there was a reversal of the drainage pattern from previous western and northwestern directions to an eastern direction (Haffer 1969, 1974b, 1977; Haffer & Prance 2001). Occasional marine incursions from the Pacific Ocean and the Caribbean Sea could also have reached western Amazonia. This area was at various times probably covered with huge lakes, swamps, and rivers (Haffer 1977), and in the middle Miocene the Amazon area was closed off from the Pacific Ocean. During the early Pliocene (5 mya) the emergence of the Panamanian Isthmus completed the Central American land bridge and later led to the great American biotic interchange.

The history of the Caribbean region begins in the Middle Jurassic (Iturralde-Vinent & MacPhee 1999), and in subsequent geological periods until the end of the Miocene the area was characterized by submergence and emergence of islands. The evolution of birds in the area has been related to the idea that, at that time, tectonic upheavals gave birth to many islands in the region where today Central America bridges both American continents. Additionally, some Caribbean islands were never connected to either of the two land masses (Schuchmann 1980b, 2002). According to this author, many birds reached the Antilles (mainly Greater Antilles and the Bahamas) from North America during the Oligocene and Miocene (37-5 mya), when the climate in the south of North America was tropical. Only a few Neotropical bird taxa colonized the northern Caribbean island arc at that time, using the Central American islands as stepping stones during their northward expansion. In contrast, most of the species of the Lesser Antilles have their closest relatives in the South American continent and in Central America through the Greater Antilles (Schuchmann 1981). Some ornithologists place the hummingbirds and tanagers among the first successful South American colonizers of the Antillean islands (Bleiweiss 1998).

According to Schuchmann (2002), hummingbirds reached the Greater Antilles and the Bahamas most likely during two historical colonization events: one early radiation, via stepping stone islands now constituting the Central America land bridge, gave rise to endemic genera (*Trochilus*, *Mellisuga*), whereas a more recent colonization via the Central American land bridge gave rise to endemic species like *Anthracothorax mango*. He believes that this

latter species, like the other *Anthracothorax* species from the Greater Antilles, stems from Central American *Anthracothorax* populations, and that Jamaica and the other Greater Antillean islands were probably colonized via Honduras during the Pleistocene. Based on the results of this study I will argue a different scenario for these taxa. Specifically, *Anthracothorax mango* from Jamaica, being phylogenetically closer to *Topaza*, must have been an early arrival to the island.

Iturralde–Vinent & MacPhee (1999) made a thorough analysis of the development of the Caribbean region from its beginning, when an embryonic Caribbean sea was originated as a consequence of the breakup of Pangaea and separation of Laurasia and Gondwana. According to the authors, the existing land bridge (Panamanian Isthmus) was in fact complete in the Pliocene; however, extensive geological evidence exist to show that, during the Eocene-Oligocene transition, the developing northern Greater Antilles and northwestern South America were connected by a "land span" centered on the emergent Aves Ridge (about 32 mya). The Eocene–Oligocene period was a time of general uplift and the amount and extent of subaerial land in the Caribbean should have been at a maximum (probably more extensive then than at any other time in the Cenozoic, including the late Quaternary). Thereafter, Caribbean neotectonics resulted in the subdivision of existing land areas.

The Aves Ridge was originally contiguous with the Greater Antilles Ridge and could have constituted a single entity (called Gaarlandia) during the Oligocene. Therefore it has been proposed as a potential site for the dispersal of mammals and reptiles within the region (Iturralde-Vinent & MacPhee 1999). However, the possibilities of this area being reached by birds could have lasted many years longer due to their dispersal potential. It could have constituted an important site for the history of hummingbirds in the area, especially for the genera included here, as will be discussed below. Additionally, the islands that today constitute the Lesser Antilles were to the east and not directly connected to this Aves Ridge, and at the time there was no connection through Central America. Jamaica, on the other hand, although geographically a member of the Greater Antilles, has a tectonic history quite different from that of other islands in the group. The Blue Mountain Block, currently part of Jamaica, might have had a connection to the evolving land span (Gaarlandia). Jamaica might

in this way have received immigrants from South America directly via the stepping stones formed from the former Aves Ridge (Iturralde-Vinent & MacPhee 1999).

Hummingbirds diversified from South to North America well before the closure of the Panamanian Isthmus late in the Pliocene. This longer history of interchange is reflected in the complex historical structure of regional faunas (Bleiweiss 1998). The history of the trochilids reaching the Caribbean islands has been dynamic, being subjected to repeated colonization events by different phyletic lines. This dynamism is supported by fossil evidence indicating that extinction has also been frequent in the hummingbird groups of the Caribbean islands. Pleistocene fossils of species belonging to extant genera, namely of mangoes and emeralds, are known from the Grand Bahamas Bank (Olson & Hilgartner 1982).

Unlike the Antillean communities, the number of species in Amazonian hummingbird communities is apparently relatively unpredictable (Cotton 1998b), making the mainland hummingbird communities more complex than those on islands because once on the islands the birds are subjected to different evolutionary pressures. In addition, almost all species of hummingbirds of the Caribbean archipelago show distinctly greater food and habitat versatility than most continental hummingbird species.

Therefore, I speculate the following scenario for the group: I believe, with Schuchmann (2002), that the origin of the mango hummingbirds was in northern South America with an ancestral form of *Topaza*. However, my contention is that *A. mango* must have been an early arrival to the island of Jamaica (contrary to Schuchmann 2002). From the original northwestern South American ancestor, a group may have colonized Jamaica and become established there, with the potential to evolve as a completely different group (*A. mango*) than *Topaza* on the mainland. After this first dispersal burst the sea level changed and many of these stepping stones were probably under water, leaving this group isolated for a long time.

The same ancestor from South America may have given rise to another closely related group, *Eulampis*, but including *A. viridis* as has been argued here. This group dispersed at a later time from the northeast, via the bridge formed by the Lesser Antilles until reaching Puerto

Rico (*A. viridis*). Then another group (*Anthracothorax*) moved down to the remainder of South America and up to Central America, following the Pliocene connection of North and South America, reaching Mexico. This group also effected a recent colonization of the Greater Antilles (*A. dominicus*) from Central America. In Puerto Rico they came into contact with *Anthracothorax* species coming from both the Lesser and the Greater Antilles.

I would also speculate that *A. veraguensis* constitutes a case of reverse dispersal from the islands, again to the Central American mainland. However, at the time of its arrival, *A. prevostii* was already well established, which limited the distribution of *A. veraguensis* to a small area in Central America. The relationship between *A. dominicus* and *A. veraguensis* seems to be clear. *A. veraguensis* is phylogenetically farther away from *A. prevostii* than was previously thought, having a closer relationship with those taxa from island groups, which would explain why this species did not intermix with *A. prevostii* when arriving on the mainland from the islands. In general the current systematic and geographical status of this group results from a complex situation of *in situ* speciation and a history of colonization-recolonization.

Concluding remarks

On the methodology of plumage color comparison

I present here a method of taking integral information on bird plumage coloration to study the geographic variation, taxonomy and phylogeny of different bird groups. This method is based on the comparison of color as an integral variable. Mainly, I want to improve previous efforts in two directions: First, to make the process of color measurement itself more objective and the methods of handling the data statistically comparable; and second, to avoid the subjective method of choosing *a priori* the "important" color characters to be analyzed. In the methodology section, the fact that humans do not perceive their surroundings in the same way that birds do was discussed, making it important to have a suitable way of measuring coloration, independent of the human color perception system.

There have been studies investigating the relationship between two distinct levels of color representation, namely the reflectance spectra of Munsell color samples as measured by a spectrophotometer, and human perceptions of color obtained in psychophysical experiments (see Romney & Indow 2002). They concluded that both color-matching functions provide virtually identical estimations. Consequently, they may be considered as substitutes for each other, which would diminish the relevance of the present study. However, the Munsell reflectance spectra were estimated directly from cone sensitivity curves measured in humans. In terms of our research interests, the effect of light conditions when taking the measurements was not taken into account. The same background was used and the effect of different observers or how tired they might be after several hours of observing colors on museum specimens was not allowed for. Zuk & Decruyenaere (1994) added that scanning all the samples in a single session with a standard light source would minimize day-to-day variation in both observer judgment and environmental conditions. However, this cannot be applied to studies of geographical variation, taxonomy, and related topics, which are based on a large series of skins found in different collections around the world.

The present research assumes that the focus on specific body parts of the specimens under study needs not to be set *a priori.* When researchers concentrate on a specific part of the body of the animal that "they" (the researchers) perceive as the most important, they are including another source of subjectivity in the process. We humans have a different perception than our study subjects, so we cannot say *a priori* which areas of the body should be more important from the evolutionary point of view. A definition, *a posteriori*, of those "interesting" body parts presenting the most variation allows the researcher to guide efforts toward those specific color differences that might need more attention.

The use of principal component analysis (PCA) to compare color spectral data has been proved to be adequate. Other authors, such as Thorpe (2002), have introduced other ways of segmenting the spectra without the use of PCA. However, I think that those segments, as parts of the spectrum, are not necessarily independent of each other. This independence is obtained with the orthogonal PCs from the PCA, which are additionally available on standard statistical software packages. Furthermore, all results from PCA analyses are completely independent of the visual system of the animal perceiving the wavelengths. The PCA approach to analyzing reflectance spectra will remain highly effective even if information on species color perception, or light environments, subsequently becomes available (Cuthill *et al*. 1999).

Interpretation of spectral color data in terms of real morphological differences

In this research, I included the entire range to which birds are sensitive, performing statistical analyses to determine if differences among spectra were significant. It is not necessary to have complete series of specimens in front of our eyes for them to be compared, which allows work in different museums and light conditions. However, the technique presented here makes the research somewhat abstract, since the researcher must wait until the end of the analyses to determine which parts of the body of the taxa under study are more important to separate the groups (or not).

The results obtained here might appear somewhat abstract to taxonomists and other biologists, and might not be quickly translated into easy-to-measure color differences between taxa but

they make more biological and evolutionary sense. In order to make these results useful for taxonomic purposes they need to be translated into observable characters to the human eye. To make this translation, the discriminant function analysis gives us an idea of which PCs, coming from which parts of the body, show the most variation. This information can be used to further analyze specific differences among groups, providing taxonomically diagnosable characters for each taxon under study.

Because of their visual orientation, humans often find it convenient to use color and color pattern in systematic definitions and descriptions, particularly at lower taxonomic levels (Thorpe 2002). However, my approach is that evolutionary trends have to be found within the subjects under study. The color differences that have biological meaning to the study animals need to be found, taking into account the visual systems of the potential receptors of a given color signal. After we are able to do this, then it may be possible to correlate this "real" differences with other characters, or with the perceptions of characters that we as humans are able to "see" (or at least measure) and thus make our research a little easier.

Adapting the methodology for phylogenetic analysis

The discriminant function analysis provides a tool to find similarities and differences in groups of birds according to plumage coloration. Although this method does not allow finding phylogenetic implications, it provides a way to determine the relevant taxonomic units to be included in phylogenetic analyses. Additionally, the generalized frequency coding method provides an adequate method of codifying spectral color and other morphometric continuous data for use in phylogenetic analysis by PAUP.

***Taxonomic conclusions and phylogenetic relationships of the three genera* Topaza, Anthracothorax*, and* Eulampis**

Hummingbirds present particularly difficult phylogenetic relationships because their locomotor and feeding systems are highly modified for hovering flight, perching, and drinking nectar, affecting virtually all aspects of the birds (Zusi & Bentz 1984). Different evolutive pressures affect plumage coloration and morphometric measurements (characters taken during this study). A few structures, such as bill and wing, can be very flexible and homoplastic characters that greatly depend on foraging pressures, while coloration is more related to sexual selection. Homoplastic characters are supposedly misleading for phylogeny reconstruction. However, I believe that in order to better approach the reality, a phylogenetic analysis should be conducted with as many characters as possible, provided that they follow the logical principles on which this analysis is based. Phylogenetic analysis is based on one of the basic principles of evolution, i.e., descent with modification. If the characters chosen match the logical principles of phylogenetic analysis, there is no acceptable reason to exclude them (see Grandcolas *et al.* 2001). Under this argument, I included morphometric data together with the plumage color data to conduct the phylogenetic analyses.

The results of the present study, based on the methodology developed by using discriminant function analysis and generalized frequency coding to conduct phylogenetic analysis with morphological continuous variables, such as plumage color spectra and morphometric data, led to the following conclusions:

1. The species of the mango clade: *Topaza*, *Anthracothorax*, and *Eulampis* seem more closely related to each other than previously considered. In fact, according to these results, the taxonomy of the group should be revised. The most relevant changes suggested by this study would be to consider the species *Anthracothorax mango* as part of the *Topaza* group, and the species *Anthracothorax viridis* as part of the genus *Eulampis*.

2. The potential for hummingbird dispersal (especially of this group) makes the situation more complicated than solely the identification of geographic barriers. I postulate that the mango clade originated in South America where the taxa adapted to the changing conditions and habitats of the region, and from where they dispersed in three basic directions: towards Jamaica using the last vestiges of the Aves Ridge (*A. mango*), towards the lesser Antilles (*Eulampis*), and towards Central America (some of the *Anthracothorax* species).

3. The species *Topaza pella* includes 5 subspecies: *T. pella amaruni*, *T. pella pyra*, *T. pella pamprepta*, *T. pella pella*, and *T. pella microrhyncha*.

4. The species *Anthracothorax recurvirostris* definitively belongs in the genus *Anthracothorax* and not *Avocettula*. The population of *Anthracothorax* occurring in western Ecuador is part of *A. nigricollis* (*A. n. iridescens)* and not of *A. prevostii*. There is a new potential subspecies of *A. nigricollis* found in Venezuela and adjacent areas, and a new potential subspecies of *A. prevostii* found in the Yucatán area of Mexico.

5. The species "*Sericotes" holosericeus* is definitively congeneric with *Eulampis*.

It is important to note that in future studies using this methodology in certain taxa it would be necessary to include other specific body parts. For example there are differences in the malar, post-ocular region, and tarsus of *Topaza* that have been previously used to delimit und define species and subspecies. In the present study, measurements of the color of these areas of the body were not considered.

I consider that the methodology introduced here is only the beginning of a potentially new method of using traditional morphological measurements in a more objective way that allows us to conduct better supported taxonomic, systematic, and phylogenetic studies.

Summary

I have developed a methodology to obtain and compare integral information on bird plumage coloration, using color spectral data to conduct studies on geographic variation, taxonomy and phylogeny of different bird groups. I use principal component analysis and discriminant function analysis to analyze and compare the color spectra of different body parts of the individuals included in the groups. I take this spectral data to perform phylogenetic analyses using PAUP by adapting the generalized frequency coding method as a tool to code the continuous spectral and morphometric data into discrete variables. Using these methods and statistical tools, I have reviewed the taxonomy of three mango hummingbird genera occurring in South and Central America and the Caribbean islands (*Topaza*, *Anthracothorax*, and *Eulampis*). This constitutes an applied example of the methodology that allowed me to make some conclusions and suggestions about the taxonomy and phylogeny of the group.

These species of the mango clade appear to be more closely related to each other than previously considered and the taxonomy of the group should be revised. I suggest several changes, the most relevant being to consider the species *Anthracothorax mango* as part of the genus *Topaza*, and the species *Anthracothorax viridis* as part of the genus *Eulampis*. Some clarifications are also made on controversial populations within the mango hummingbirds. I also suggest the possibility of a new subspecies of *A. nigricollis* found in Venezuela and adjacent areas, and a new subspecies of *A. prevostii* found in the Yucatán area of Mexico. Additionally, I postulate that the mango clade originated in South America, where the taxa adapted to the changing conditions and habitats of the region, and dispersed in three basic directions: towards Jamaica using the last vestiges of the Aves Ridge (*A. mango*), towards the lesser Antilles (*Eulampis*), and towards Central America (some of the *Anthracothorax* species). I consider that the methodology introduced here is only the beginning of a potentially new method of using traditional morphological measurements in a more objective way to conduct better supported taxonomic, systematic, and phylogenetic studies.

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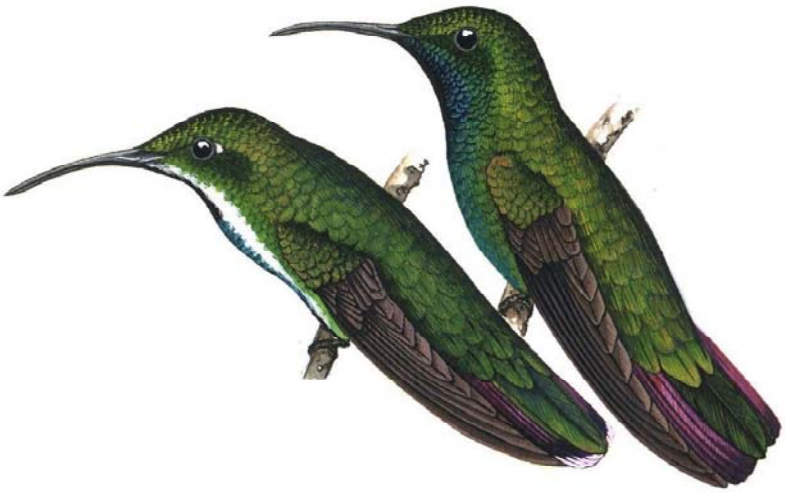
Plate 1. Species of the genus *Topaza* Gray 1840 (above: "*pella* group"; below: "*pyra* group"). (Courtesy of D. Alker).

(left females, right males)

Plate 2. **part I**. Species of the genus *Anthracothorax* Boie 1831. (Courtesy of D. Alker).

A. viridigula (above male, below female)



A. prevostii (left female, right male)

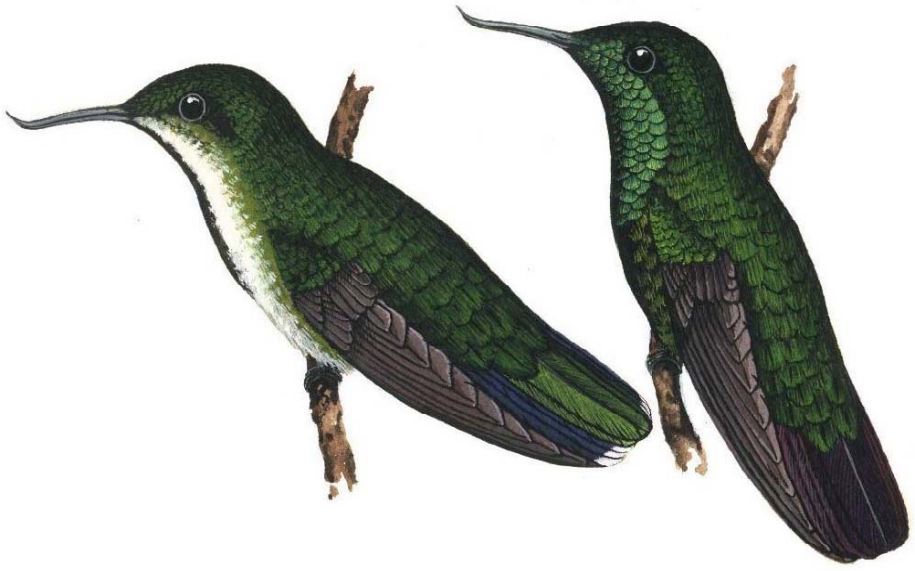
A. nigricollis (above male, below females)

A. dominicus (above male, below female)

Plate 2. part II. Species of the genus *Anthracothorax* Boie 1831. (Courtesy of D. Alker).

A. mango (above male, below female)

A. viridis



A. recurvirostris (left female, right male)

Plate 3. Species of the genus *Eulampis* Boie 1831. (Courtesy of D. Alker).

E. jugularis (above male, below female)

E. holosericeus (above male, below female)

Plate 4. Genus *Campylopterus* Swainson, 1827, represented by one species. (Courtesy of D. Alker).

C. largipennis (above female, below male)

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